Ecology Letters, (2005) **8**: 1095–1104 doi: 10.1111/j.1461-0248.2005.00807.x

LETTER

Direct and indirect fishery effects on small coastal elasmobranchs in the northern Gulf of Mexico

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Abstract

Globally, bycatch in tropical/subtropical shrimp trawl and longline fisheries is threatening many marine species. Here we examine the joint effects of increased mortality caused by shrimp trawling bycatch, and reduced predation caused by losses of large sharks because of longline fishing. Research surveys in the Gulf of Mexico (1972–2002) demonstrated precipitous declines in shallow water coastal elasmobranchs where shrimping effort was highest (bonnethead 96%, Bancroft's numbfish (lesser electric ray) 98%, smooth butterfly ray > 99%) and consistent increases in deeper water elasmobranchs (Atlantic angel shark, smooth dogfish). These increases are the first empirical support for predation release caused by the loss of large sharks, which have been theorized to structure tropical/subtropical marine ecosystems. Bycatch of elasmobranchs in shrimp trawls is a critical conservation concern which is not solved by present mitigation measures; similar loss of elasmobranchs is expected to be occurring in tropical/subtropical regions worldwide where ever intensive shrimp trawling occurs.

Keywords

Bycatch, community structure, elasmobranchs, fisheries, Gulf of Mexico, predation release, rays, sharks, shrimp trawling, top-down effects.

Ecology Letters (2005) 8: 1095–1104

INTRODUCTION

The relative importance of top-down vs. bottom-up effects on species abundance and community structure has been one of the dominant, long-term areas of uncertainty in marine ecology. Some argue that top-down effects can regulate oceanic as well as coastal food webs (Verity & Smetacek 1996; Pace *et al.* 1999; Bascompte *et al.* 2005), while others argue that environmental stochasticity will counter such effects (Strong 1992; Jennings & Kaiser 1998). Recently, several studies have demonstrated the importance of top-down controls in marine systems on relatively short lived organisms, e.g. shrimp (Worm & Myers 2003) and smaller prey in the open ocean (Ward & Myers 2005) and continental shelves (Daan *et al.* 2005). What has been lacking is an analysis of the importance of top-down effects on larger, long-lived species such as elasmobranchs. Elasmobranchs are typically long lived, late-maturing and have low fecundities. As such, they are inherently less resilient and may be disproportionately affected by fishing mortality as compared with other marine species (Stevens *et al.* 2000) and their response to the removal of top-down effects in unknown. Patterns of community response to top-down effects can be complicated by coincident direct fishery removals (Daan *et al.* 2005). Both these factors may interact to shape species abundance and community structure.

The Gulf of Mexico provides a model system in which we can examine how both the removal of top-down effects and intensive trawling activity affect elasmobranch community structure. The Gulf of Mexico is the site of both an intensive bottom longline fishery and a demersal shrimp trawl fishery in which elasmobranchs are captured. Both are likely affecting elasmobranch community structure. The removal of large, predatory fish is typical of longline fisheries which can lead to both individual species declines and changes in community structure (Baum *et al.* 2003; Ward & Myers 2005). In the Gulf of Mexico, a number large elasmobranchs declined precipitously during the 20th century, presumably because of removals by the pelagic longline fishery (Baum & Myers 2004), and many are listed by the World Conservation Union (IUCN) as being at risk (see Table S1 in Supplementary Material).

Considerable undirected fishing mortality of demersal elasmobranchs occurs via the shrimp trawl fishery in the Gulf of Mexico. Globally, shrimp trawl fisheries generate very high bycatch rates. Historically, the Gulf of Mexico shrimp fishery has been no exception with bycatch rates of more than 10 kg of fish per kg of landed shrimp (Alverson *et al.* 1994) and it has been identified as a source of mortality of the endangered smalltooth sawfish, *Pristis pectinata* (NMFS 2000; Simpfendorfer 2000). Of the 272 000 mt of finfish estimated bycaught by the Gulf of Mexico shrimp trawl fishery in 1993, 2720 mt were sharks (Schmied & Nance 1995). Shrimp trawl bycatch is such a concern in the Gulf of Mexico that legislation was introduced in the 1980s and 1990s that required that most shrimp trawls be outfitted with turtle exclusion devices (TEDs) and fish bycatch reduction devices (BRDs). While these measures were helpful in reducing fish bycatch (Gallaway & Cole 1999), total bycatch likely remains high given the 4–5 million shrimp trawl hours fished in the Gulf annually.

Here we investigate trends in coastal elasmobranch abundance, estimated from research trawl surveys conducted in a subtropical coastal/shelf marine ecosystem (northern Gulf of Mexico) that is subject to the joint effects of intensive bottom longline fisheries and intensive shrimp trawl fisheries. This analysis is facilitated by the use of long-term fishery-independent surveys which are virtually unique in subtropical or tropical continental shelves. Because of this, our findings here can be used to project how elasmobranch communities are affected in similar areas where long-term monitoring is absent and these types of fisheries occur in unison.

METHODS

Data for this study was obtained from the dedicated autumn shrimp/groundfish research trawl survey carried out by the Southeast Area Monitoring and Assessment Program (SEAMAP). Before 1985, the survey was conducted solely by the National Marine Fisheries Service (NMFS). Since 1985, it has been conducted cooperatively with NMFS, state, and university SEAMAP participants, with gear configuration and vessel operation characteristics being maintained between participants. We examined trends in elasmobranch abundance from the area with the longest continuous temporal coverage (1972–2002), i.e. the northern Gulf of Mexico shelf waters (between 10 and 110 m depth) near Alabama, Mississippi and Louisiana (NMFS statistical zones 11, 13–16; Fig. S1). Temporal consistency with respect to depth distribution and spatial coverage of survey data was verified prior to analysis. It must be noted that a species captured in this survey, the lesser electric ray, *Narcine brasiliensis*, von Olfers 1831, has been historically misidentified. In fact, the electric ray which occurs in this area is Bancroft's numbfish, *N. bancroftii*, Griffith 1834 (de Carvalho 1999; Carpenter 2002). Thus, we refer to any identification in the SEAMAP survey of the lesser electric ray as Brancroft's numbfish.

Trends in species abundance were analysed using generalized linear models with a negative binomial error structure and a log link. All analyses were conducted using SAS v9.1 (SAS Institute Inc., Cary, NC, USA). Only species which occurred in three or more years of the survey were included in the analysis. The probability of catching C_i individuals of a given species in survey tow i was assumed to follow a negative binomial distribution with the mean μ_i,

$$p(C_i; k; \mu_i) = \frac{\Gamma\left(C_i + \frac{1}{k}\right)}{\Gamma(C_i + 1)\Gamma\left(\frac{1}{k}\right)} \frac{(k\mu_i)^k}{(1 + k\mu_i)^{C_i + \left(\frac{1}{k}\right)}}, \quad \text{for } C_i = 0, 1, 2, \ldots, \tag{1}$$

where Γ is the gamma function and k is the negative binomial dispersion parameter. The expected mean catch of a given species is then,

$$\log(\mu_i) = \beta_y y_i + \beta_d d_i + \beta_z z_{i,j} + \beta_t t_{i,j} + \log(A_i), \tag{2}$$

where y_i is the year in which survey tow i occurred, d_i is the depth of the tow and A_i is the area of bottom swept by the trawl, treated as an offset term. The term $z_{i,j}$ is an indicator variable for the statistical zone in which the tow occurred such that $z_{i,j} = 1$ if tow i was in the jth statistical zone or $z_{i,j} = 0$ otherwise. Likewise, $t_{i,j}$ is an indicator variable for the time of day such that $t_{i,j} = 1$ if tow i was in the jth time of day period (day or night), otherwise $t_{i,j} = 0$. The full model was reduced by sequentially removing $z_{i,j}$ and $t_{i,j}$ if they were not significant in order of the least significant first. For many species, the number of observed positive catches was low (Table 1). This often led to the failure of the maximum likelihood estimation of the negative binomial dispersion parameter, k. In these cases, k was acquired from the same species from an alternate data set. The alternate data set used was the portion of the SEAMAP database encompassing the coastal region of the southeast US from 1989 to 2002. If the equivalent species was not present in the southeast US data set, a value for k was taken from a taxonomically closely related species from the northern Gulf of Mexico data set (this study). We were concerned about how assumptions about the value of k may affect results. Thus, we conducted a sensitivity analysis by varying k for each species such that $k = 1, 5, 10,\ldots,100$. We found in all but one case, the significance of trends in abundance were not affected by values of k. In general, increasing k led to a larger variance in estimates of temporal abundance trends, and in the case of Atlantic stingray, a significant positive trend was evident when k was less than 30.

An index of susceptibility to shrimp trawling effort for each species was calculated from historic effort data for the Gulf of Mexico (Ocean Studies Board 2002). Shrimp trawling effort data was available for the two time periods 1991–1993 and 1998–1999 in the form of average shrimp trawl fishing days for each statistical zone and from depths of 0 m to *c.* 100 m and greater. Effort data was aggregated across time periods by averaging effort within each statistical

Table 1 Occurrence patterns of elasmobranchs captured in the northern Gulf of Mexico shrimp trawl survey and demersal longline fishery. Occurrence in the demersal longline fishery is expressed as the percentage of the total shark catch comprised by each species*

	Species		Shrimp trawl survey		
Common name	Latin name	Last observed	Years occurred (*n* captured)	Demersal longline fishery	*k*
Dusky shark	*Carcharhinus obscurus*	1973	1 (1)	0.2	n.a.
Smalltail shark	*Carcharhinus porosus*	1973	1 (1)	0.0	n.a.
Scalloped hammerhead	*Sphyrna lewini*	1977	4 (4)	1.6	19.1†
Manta	*Manta birostris*	1979	1 (1)	0.0	n.a.
Smooth butterfly ray	*Gymnura micrura*	1979	3 (8)	0.0	5.0†
Great hammerhead	*Sphyrna mokarran*	1979	4 (4)	1.2	19.1‡
Spotted eagle ray	*Aetobatus narinari*	1980	3 (4)	0.0	17.9†
Bull shark	*Carcharhinus leucas*	1984	2 (2)	5.0	n.a.
Speckled skate	*Leucoraja lentiginosa*	1985	1 (1)	0.0	n.a.
Roughtail stingray	*Dasyatis centroura*	1985	4 (4)	0.0	12.1†
Nurse shark	*Ginglymostoma cirratum*	1992	1 (1)	7.3	n.a.
Atlantic guitarfish	*Rhinobatos lentiginosus*	1994	4 (4)	0.0	15.2†
Silky shark	*Carcharhinus falciformis*	1997	5 (12)	1.1	49.6§
Florida smooth-hound	*Mustelus norrisi*	1997	10 (26)	0.0	32.3
Lesser devil ray	*Mobula hypostoma*	1998	1 (1)	0.0	n.a.
Bullnose eagle ray	*Myliobatis freminvillii*	1999	4 (4)	0.0	8.5†
Atlantic stingray	*Dasyatis Sabina*	2000	16 (39)	0.0	89.2
Southern eagle ray	*Myliobatis goodie*	2001	1 (1)	0.0	n.a.
Blacktip shark	*Carcharhinus limbatus*	2001	9 (18)	19.9	49.6
Blacknose shark	*Carcharhinus acronotus*	2001	12 (12)	18.4	25.0
Cownose ray	*Rhinoptera bonasus*	2001	18 (44)	0.0	147.7
Bancroft's numbfish	*Narcine bancroftii*	2001	19 (78)	0.0	33.5
Bluntnose stingray	*Dasyatis say*	2001	23 (61)	0.0	5.0†
Southern stingray	*Dasyatis americana*	2001	24 (90)	0.0	13.3†
Spreadfin skate	*Dipturus olseni*	2002	8 (12)	0.0	20.7¶
Atlantic angel shark	*Squatina dumeril*	2002	15 (29)	0.0	1.3
Smooth dogfish	*Mustelus canis*	2002	22 (60)	0.0	8.4†
Clearnose skate	*Raja eglanteria*	2002	25 (62)	0.0	28.4
Bonnethead	*Sphyrna tiburo*	2002	28 (210)	0.1	20.7
Roundel skate	*Raja texana*	2002	30 (233)	0.0	20.7
Atlantic sharpnose shark	*Rhizoprionodon terraenovae*	2002	31 (911)	10.2	8.8

The term *k* is the negative binomial dispersion parameter used in the generalized linear models.

**Data source*: Burgess & Morgan (2003), only species which occurred in the trawl survey were included from the demersal longline observer data.

†Same species from southeast US data set.

‡Scalloped hammerhead from southeast US data set.

§Blacktip shark from northern Gulf of Mexico data set.

¶Roundel skate from northern Gulf of Mexico data set.

zone/depth contour combination. To generate the susceptibility index, we first estimated relative effect of each depth, statistical zone combination (z') on mean catch of each species using generalized linear models with a negative binomial error structure (eqn 1) and a log link,

$$\log(\mu_i) = \beta_y y_i + \beta_{z'} z'_{i,j} + \beta_t t_{i,j} + \log(A_i), \qquad (3)$$

where $z'_{i,j}$ is an indicator variable for the depth, statistical zone such that $z'_{i,j} = 1$ if tow i was in the jth depth, statistical zone combination or $z'_{i,j} = 0$ otherwise.

Estimates of $\beta_{z'}$ were then used to prorate shrimp trawling effort in each depth, statistical zone combination to generate an index of susceptibility to shrimp trawling (I) for each species,

$$I = \sum_{z'} \left[\frac{\exp(\beta_{z'})}{\sum_{z'} \exp(\beta_{z'})} E_{z'} \right], \qquad (4)$$

where $E_{z'}$ is the mean annual shrimp trawling effort (24 h shrimping days) in each depth, statistical zone combination.

It is possible that coastal hypoxic episodes which occur annually in this area of the Gulf of Mexico (Rabalais *et al.* 2002) could have affected temporal trends in abundance. To investigate this, we repeated the generalized linear models (eqns 1 and 2) for those areas east of the Mississippi (statistical zone 11) where hypoxic episodes are not a concern. Model variables and dispersion parameters used were those equivalent to those applied to a given species for the entire northern Gulf of Mexico (Table 1). We also investigated whether trends in elasmobranch abundance changed subsequent to the requirements of having TEDs and BRDs on shrimp trawls. Since 1992, TEDs have been required on virtually all shrimp trawls in the Gulf of Mexico, while BRDs have been required since 1998. We examined the differences between abundance trends for the time periods 1992–2002 and 1972–1991 using a piecewise linear model,

$$\log(\mu_i) = \beta_y y_i + \beta_y^* y_i^* + \beta_d d_i + \beta_z z_i + \beta_t t_i + \log(A_i), \quad (5)$$

where $y_i^* = 0$ if $y_i < 1992$ and $y_i^* = y_i - 1992$ otherwise and β_y^* is the difference in the instantaneous rate of change in abundance before and after 1992. Only those species which occurred for three or more years in each time period were included in the analysis. Mean differences between trends of the two time periods (μ_y) were estimated using a restricted maximum likelihood, random effect meta-analysis (Normand 1999) for both species targeted by shark fisheries and those not targeted by shark fisheries.

RESULTS

A total of 31 elasmobranch species occurred in the survey (Table 1). Eight species occurred only rarely in the survey (< 3 years) and 10 species did not occur after 1985 (Table 1). Four of these 10 species were large coastal sharks for which directed demersal longline fisheries exist. Trends in abundance were estimated for the 23 species which occurred for 3 or more years of the survey. Of these 23 species, 16 exhibited negative trends in abundance (Fig. 1), nine of which were significant (Fig. 2). A number of these species declined to under 5% of their 1972 survey abundance: bonnethead, *Sphyrna tiburo* Linnaeus 1758, 4% (95% CI: 2–8%); Bancroft's numbfish, 2% (95% CI: 0.5–5%); scalloped hammerhead, *S. lewini* Griffith & Smith 1834, < 1% (95% CI: 5.2×10^{-4}–23%); smooth butterfly ray, *Gymnura micrura* Bloch & Schneider 1801, < 1% (95% CI: 9.9×10^{-10}–1.5×10^{-6}%). Positive abundance trends were found in the seven remaining species (Fig. 1), three of which were significant (Fig. 2). Of the nine species which exhibited declines in the survey, six were associated with shallow waters while six showed no significant relationship with depth (Fig. 3). Conversely, all three species which increased in the survey were associated with deeper waters. In no case did we find a significant, positive trend in abundance associated with a significant, negative association with depth, or vice versa. We examined this relationship between trend in abundance and depth for all species with a weighted regression between instantaneous rates of change in abundance per year (β_y) and instantaneous rates of change in abundance per meter of depth (β_d). We found this relationship to be significantly positive (slope = 0.254, $F = 10.72$, $P = 0.004$). It should be noted that estimation error in the independent variable (β_d) will cause this regression to be biased towards zero, i.e. the significance level will be conservative.

In the northern Gulf of Mexico, the majority of shrimp trawling effort is found near shore at depths less than 20 m (McDaniel *et al.* 2000). This was reflected in the index of

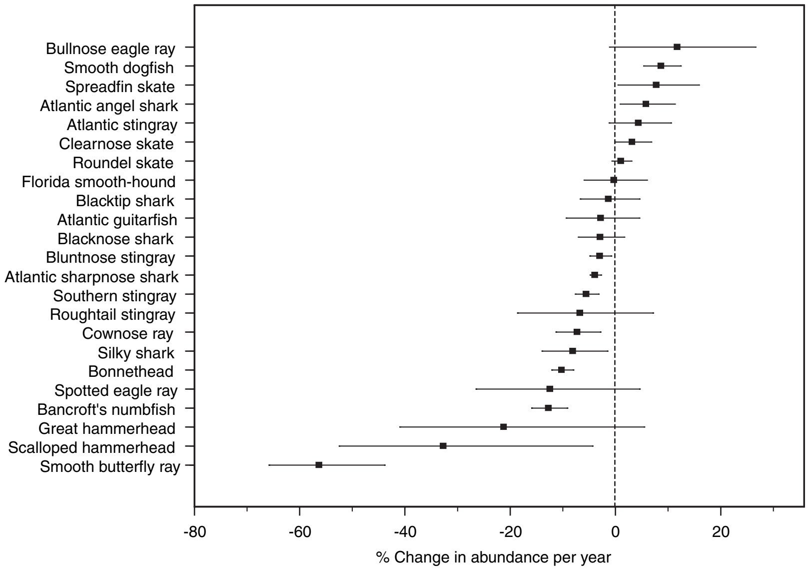

Figure 1 Rates of change in abundance with time for 23 elasmobranch species from the northern Gulf of Mexico. Estimates are in the linear scale back transformed from the log scale generalized linear model estimates. Error bars are 95% confidence intervals of the mean.

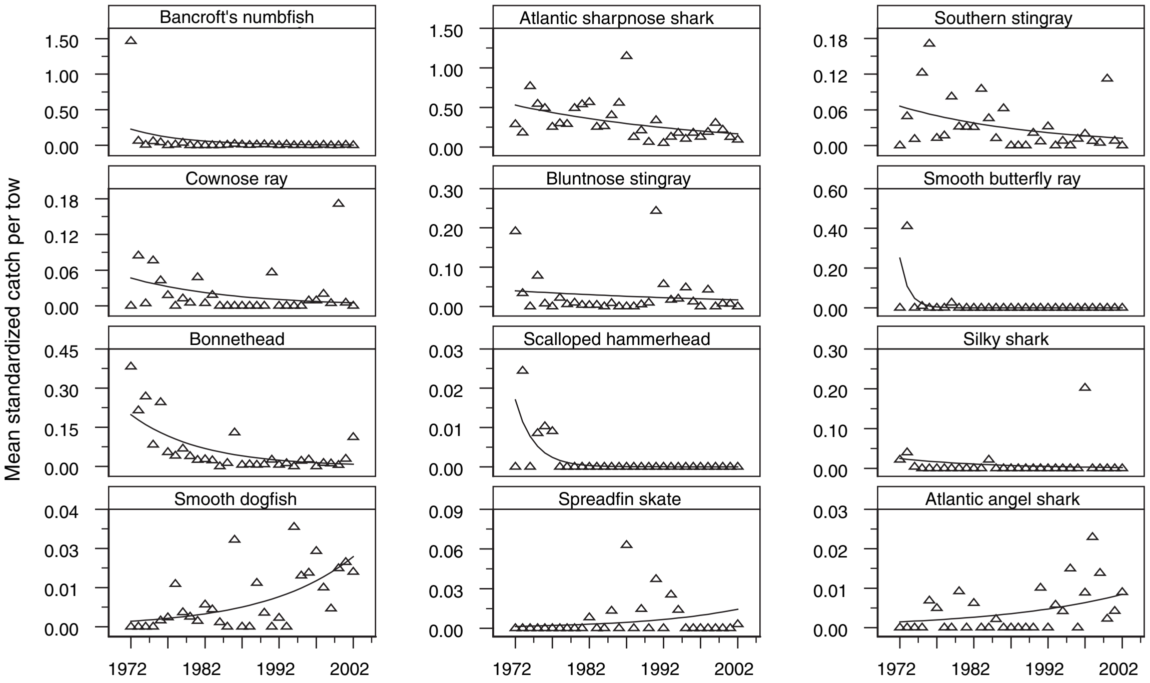

Figure 2 Trends in mean standardized catch per tow for 12 elasmobranchs from the northern Gulf of Mexico (only those that are statistically significant are plotted here). Panels are sorted by association with depth such that Bancroft's numbfish is associated with the shallowest waters and Atlantic angel shark is associated with the deepest waters. The overlaid solid lines are the results from the generalized linear models (eqns 1 and 2) treating year as a continuous variable, while triangles are individual year estimates obtained treating year as a class variable.

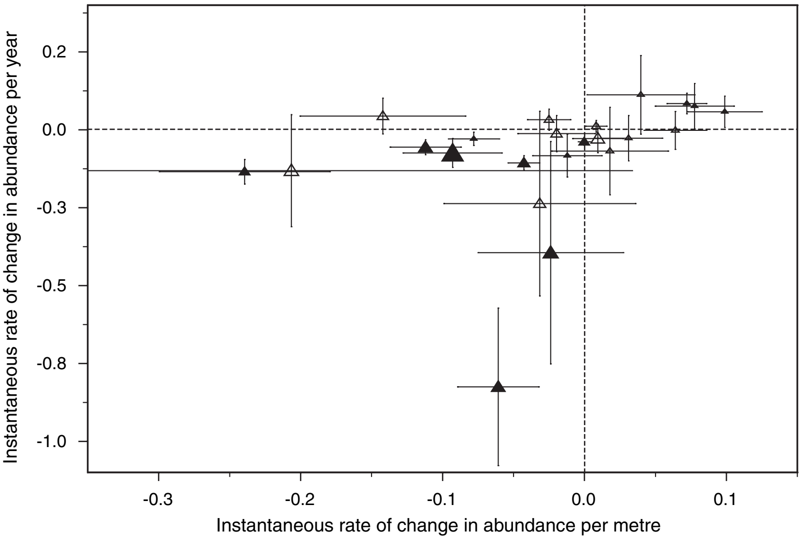

Figure 3 Rates of change in abundance with time vs. rates of change in abundance with depth for 23 elasmobranchs from the northern Gulf of Mexico. Error bars are 95% confidence intervals of the mean. Size of triangles is proportional to the index of annual shrimp trawling effort applied to a given species. Solid triangles represent species with significant temporal trends in abundance.

shrimp trawling effort applied to each species. In general, those species exhibiting negative associations with depth were more susceptible to shrimp trawling effort, and vice versa (Fig. 3). Likewise, those species in decline appeared to be more susceptible to shrimp trawling effort than those species which increased. The patterns of temporal trends in abundance did not appear to be affected by the Gulf of Mexico hypoxic zone. Rates of decline or increase were similar between the entire northern Gulf of Mexico and only those areas east of the Mississippi where the hypoxic episodes are not a concern (Fig. 4). Abundance trends were not significantly more positive after 1992 than before 1992

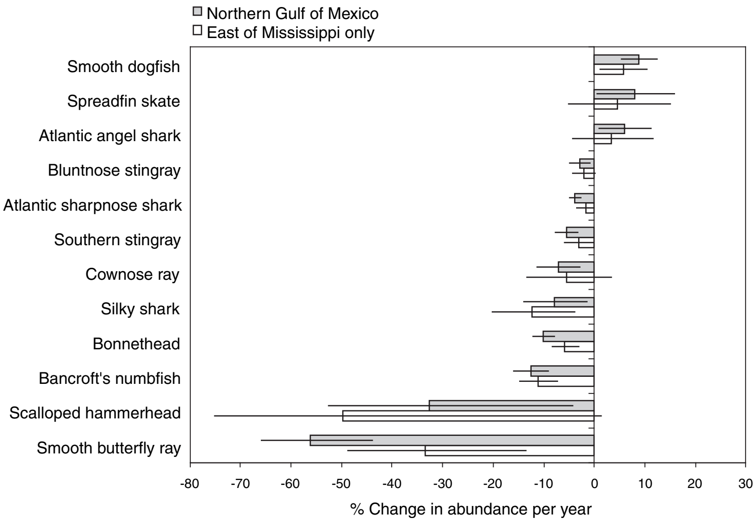

Figure 4 Rates of change in abundance with time in the northern Gulf of Mexico vs. only those areas east of the mouth of the Mississippi. Estimates are in the linear scale back transformed from the log scale generalized linear model estimates. Error bars are 95% confidence intervals of the mean.

for species not targeted by shark fisheries ($\mu_y = -0.061$, SE = 0.066, $P = 0.377$) (Fig. S2). As a whole, results were also not significant for species targeted by shark fisheries ($\mu_y = 0.179$, SE = 0.114, $P = 0.213$), although individually, two of the four species examined showed more positive trends after 1992 (blacknose shark, *Carcharhinus acronotus* Poey 1860: $\mu_y = 0.281$, SE = 0.126, $P = 0.026$; bonnethead: $\mu_y = 0.451$, SE = 0.064, $P < 0.001$) (Fig. S2).

DISCUSSION

Coastal elasmobranch community structure has undergone significant change since the early 1970s in the northern Gulf of Mexico. Abundance patterns of small coastal elasmobranchs associated with shallow water have been dominated by patterns decline, from a 60% decline in bluntnose stingray, *Dasyatis say* Lesueur 1817, to over a 99% decline in smooth butterfly ray. Conversely, a number of deeper water, continental shelf elasmobranchs have increased from 6 (Atlantic angel shark, *Squatina dumeril* Lesueur 1818), to over 13 times (smooth dogfish, *Mustelus canis* Mitchill 1815) their 1972 abundance. These observed changes in species abundance appear to be independent of areas typically subject to hypoxic events. Our hypothesis to explain these patterns is twofold.

We have shown that those species in decline are associated with more shallow waters, where shrimp trawling effort is most intense (McDaniel *et al.* 2000). While direct evidence of elasmobranch bycatch in this fishery is sparse, it is likely small coastal shark bycatch in the Gulf of Mexico shrimp trawl fishery exceeds their landings in other commercial and recreational fisheries (Cortés 2002b). As well, other shrimp trawl fisheries are known to capture substantial numbers of sharks, skates and rays (Martinez & Nance 1993; Stobutzki *et al.* 2002; Cedrola *et al.* 2005). There is little reason to believe this fishery would be any different given the shrimp trawl used in this survey catches elasmobranchs in the same area industrial shrimp trawling takes places. Historically, fish bycatch in this fishery is known to have been high (Alverson *et al.* 1994) and has it been implicated as one of the primary reasons for the decline of smalltooth sawfish (NMFS 2000; Simpfendorfer 2000). While a suitable time series of elasmobranch bycatch in this fishery was not available, our results and supporting evidence suggest that the declines we observed are because of bycatch in the shrimp trawl fishery, from which deeper waters provide a refuge.

The second aspect of our hypothesis relates to predation release because of the reduction of top-down effects. Others have shown a number of large coastal sharks have declined precipitously in the Gulf of Mexico, i.e. dusky shark *C. obscurus* (Baum & Myers 2004), tiger shark *Galeocerdo cuvier*, white shark *Carcharodon carcharias*, hammerheads *S.* sp. and members of the *Carcharhinus* genus (Baum *et al.* 2003). For example, Baum & Myers (2004) found the dusky shark to have declined by 79% between the 1950s and 1990s while we found it has been absent from the northern Gulf of Mexico shrimp survey since 1973. As well, in the most recent large coastal shark assessment by NMFS, the large coastal shark complex as a whole was found to be over fished and overfishing was continuing in both the Gulf of Mexico and US Atlantic coasts (Cortés *et al.* 2002). The demise of large coastal sharks in the Gulf of Mexico is also reflected in their conservation status. Three are listed as 'species of concern' by NMFS (dusky shark, sand tiger, *C. taurus* Rafinesque 1810, and the night shark, *C. signatus* Poey 1868), and further, a number of large coastal sharks which occur in the Gulf of Mexico are classified as being at risk by the IUCN (Table S1).

A key component of the diet of large sharks is smaller elasmobranchs (Clark & von Schmidt 1965) and the likely only important predators of sharks are other sharks

(Springer 1967). In a review of previous studies, Cortés (1999) found a number of large coastal sharks, native to the Gulf of Mexico, contain a considerable percentage of Chondrichthyan species in their diet (great hammerhead *S. mokarran* 41.7%, bignose shark *C. altimus* 36.7%, white shark 35.7%, bull shark *C. leucas* 35.4%, dusky shark 12.0% and tiger shark 8.0%). In a general sense, the majority of coastal sharks reportedly eat sharks, skates and rays (Compagno 1984). While data on specific prey species is lacking, the species which we found that have increased, are reported in the diet of dusky sharks and great hammerheads (Compagno 1984), two species which have not occurred in these surveys since the 1970s (Table 1). Given that large coastal sharks are such important predators on other elasmobranchs, their lowered abundance would thus result in less predation on these smaller species. Due to the presence of high bycatch by shrimp trawls in shallow water, only deeper water elasmobranchs reflected this reduction in predation through increases in abundance.

Fishing affects populations both directly through removals, and indirectly through modification of ecosystem trophic structure and habitat (Jennings & Kaiser 1998). Beyond the population level, the effects of fishing on marine communities are not well known. Recently, evidence has been mounting that removal of predators from marine ecosystems has lead to both competitive (Fogarty & Murawski 1998) and predatory releases (Myers & Worm 2003). For example, Ward & Myers (2005) found that in the tropical Pacific Ocean, large predators underwent considerable declines coincident with the introduction of industrial fishing. Conversely, several smaller species increased in abundance over the same time period. There is considerable debate as to whether large sharks are keystone predators and whether they exert significant top-down effects (Stevens *et al.* 2000; Kitchell *et al.* 2002). For the most part, previous studies have mostly depended on simulation studies, and as such, empirical evidence has been lacking. Elasmobranchs make up a considerable portion of the diet of large coastal sharks (Cortés 1999). It would then be expected the top-down effects they exert to be strong and detectable on smaller elasmobranchs while the effects on a larger suite of species may not be evident. The joint effects of coincident longline and shrimp trawl fisheries on elasmobranch community structure is likely strong given that large coastal sharks are thought to have a low rebound potential (Smith *et al.* 1998) and thus will be strongly affected by fishery removals. At the same time, the rebound potential of small coastal sharks is believed to be relatively high, which would allow them to quickly increase when mortality is decreased. We believe this study provides an empirical demonstration that top-down effects exerted by large coastal sharks on small coastal elasmobranchs are important. These effects appear to be particularly strong given that two of the species we found to be increasing are slow to mature relative to other small, subtropical elasmobranchs, i.e. female smooth dogfish mature at 4–5 years (Conrath *et al.* 2002) while a females of a species from the *Squatina* genus, with a length of maturity similar to Atlantic angel shark, the Pacific angel shark, *S. californica* Ayres 1859, mature at 8–13 years (Cailliet *et al.* 1992).

A central tenet in natural resource management is that larger, slower-growing species will be disproportionately affected by harvesting (Jennings *et al.* 1999; Roberts & Hawkins 1999; Dulvy & Reynolds 2002; Dulvy *et al.* 2003). We found this generalization did not hold in the presence of both indirect fishery effects (predatory release from reduction of large coastal sharks) and direct fishery effects (removals by shrimp trawling). We found that female size at maturity had little relationship to instantaneous rates of decline in abundance (Fig. 5a), especially after accounting for those species directly affected by longline fisheries. For example, one of the larger maturing, small coastal sharks, Atlantic angel shark, increased in abundance by six times over the time series. It was typically found in deep water where shrimp trawling effort is very low (Fig. 5b). Conversely, one of the smallest coastal species, the Bancroft's numbfish, declined by 98% over the time series and was found in shallow waters where intensive trawling occurs. It has previously been suggested that in fishes, differential vulnerability to fishing activity can compromise the expected body size – extinction risk relationship (del Monte-Luma & Lluch-Belda 2003), which our results tend to confirm. We further suggest that this relationship can be compromised by indirect fishery effects. This indicates that in the presence of both indirect and direct fishery effects, size at maturity may be a misleading proxy of extinction risk. Recently, others have also been critical of the notion that body size is positively related in vulnerability in elasmobranchs (Cortés 2002a).

A number of species, we examined here appear to be headed towards eradication from the northern Gulf of Mexico coastal ecosystem. It is difficult to refer to extinction since these surveys likely only provide an image of portions of larger populations. Nonetheless it is difficult to deny the massive declines we show for many small coastal species. Further, it is disturbing that many large, predatory species such as the dusky shark, scalloped hammerhead and the great hammerhead were absent for the last 23 years or more of the survey. Many of these declines may be underestimated since they are measured relative to a 1972 baseline when in fact shrimp trawling began in the Gulf of Mexico between 1912 and 1915, after which landings rapidly increased (Anderson 1949). While the introduction of TEDs and BRDs on shrimp trawls may be effective in reducing bycatch of some fishes (Gallaway & Cole 1999; Steele *et al.* 2002), we found no evidence their introduction has affected

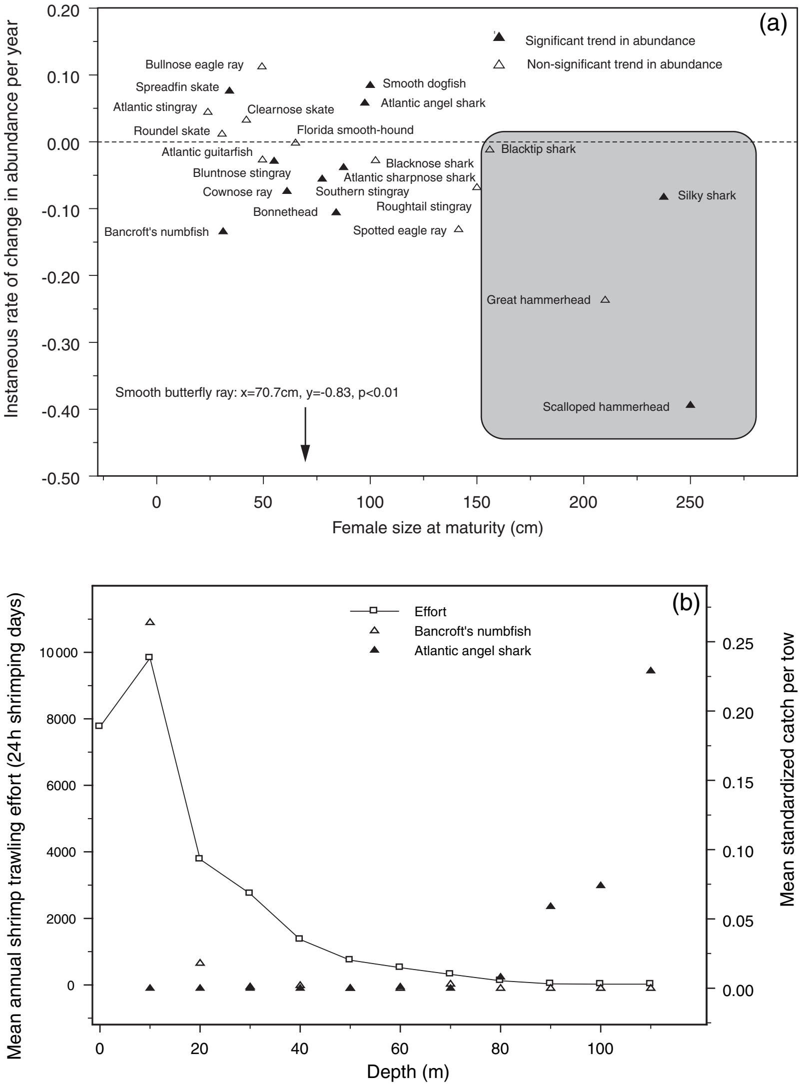

Figure 5 (a) Instantaneous rate of change in abundance per year vs. female size at maturity for 23 elasmobranchs from the northern Gulf of Mexico. Shaded box indicates species which are captured in demersal longline fisheries. (b) Mean annual shrimp trawling effort and mean standardized catch per tow of two elasombranchs vs. depth within the northern Gulf of Mexico.

abundance trends of coastal elasmobranchs in the northern Gulf of Mexico. The more positive abundance trends after 1992 we found for some targeted species cannot solely be attributed to mitigative gear modifications since these species became subject to management measures in 1993 when NMFS implemented their Atlantic sharks fishery management plan. This being the case, if there is to be hope for the future recovery of small coastal elasmobranchs in this region, other management actions, beyond the use of TEDs and BRDs, will be needed.

Patterns of decline in small coastal sharks were also found by Cortés (2002b) across a larger portion of the Gulf of Mexico continental shelf for Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, bonnethead and a small coastal shark aggregate using much of the same data we used. As well as citing support for our results, it is important to consider alternate mechanisms of decline beyond bycatch in the shrimp trawl fishery. It is not likely the declines we found are due to a shift of species' distributions to deeper waters as they do not occur in significant numbers at depths beyond the SEAMAP survey (Powell *et al.* 2003). Nor are patterns of decline likely due to mortality or displacement due to hypoxic episodes (Fig. 4). Further, with the exception of Atlantic sharpnose shark, the small coastal elasmobranchs we found in decline are not subject to significant mortality from Gulf of Mexico demersal longline fisheries (Table 1). In the Gulf of Mexico recreational fisheries, landings of small coastal sharks are small relative to their bycatch in shrimp trawls (Cortés 2002b). While there are substantial catches of skates and rays in recreational fisheries, they are almost exclusively released alive after capture (personal communication, NMFS, Fisheries Statistics and Economics Division, Marine Recreational Fisheries Statistics Survey). The lack of a probable alternate mechanism of decline in small coastal elasmobranchs supports our assertion that shrimp trawl bycatch is the causative factor of decline.

Coincident intensive demersal longline fisheries and shrimp trawl fisheries are common in subtropical and tropical regions worldwide. It is likely the patterns of community change and near extinctions we found in northern Gulf of Mexico coastal elasmobranchs are indicative of change occurring in other subtropical and tropical regions. The magnitudes of change may be even greater in other areas where fisheries are not as tightly regulated as they are in the US. What effects such changes in elasmobranch community structure are having on larger ecosystems is unclear. However, theory and empirical evidence suggests the removal of top-down effects can lead to trophic cascades wherein inverse patterns in abundance are seen across one or more trophic levels (Estes *et al.* 1998; Pace *et al.* 1999). The removal of large predators would lead to an increase in mid-level consumers (as we found here) and a subsequent decrease in low-level consumers. Recently, it has been suggested that overfishing of sharks, and the associated trophic cascades, have been implicated as the cause of decline in Caribbean herbivorous fishes and the subsequent degradation of coral reefs (Bascompte *et al.* 2005). Resolving such patterns will be difficult in the presence of intensive industrial fishing activity, such as shrimp trawling, which removes large numbers of individuals from more than one trophic level. That aside, large coastal sharks appear to exhibit strong top-down effects and their removal has lead to changes in community structure in the northern Gulf of Mexico. The declines in large coastal sharks alone should give force to the priority of their conservation. However, because their declines have lead to changes in other trophic levels, they should receive special attention beyond the simple definition of conservation (Soulé *et al.* 2005).

ACKNOWLEDGEMENTS

This study is a component of the Pew Global Shark Assessment, supported by a grant from the Pew Institute for Ocean Science, and the Future of Marine Animal Population project of the Sloan Census of Marine Life. Additional funding was provided by NSERC. We thank Mark McDuff of the NMFS Mississippi Laboratories for access to the data, and the members of the 'trawl survey team' for their dedication to high quality data collection. We would also like to thank Julia Baum for her insight and constructive comments, and Luis Lucifora for species information.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article from http://www.Blackwell-Synergy.com:

Table S1 IUCN listed elasmobranch species in the Gulf of Mexico.

Figure S1 Map of study area.

Figure S2 Difference between abundance trends before and after 1992.

Editor, Hugh Possingham
Manuscript received 9 May 2005
First decision made 17 June 2005
Manuscript accepted 29 June 2005