Respiratory mode and gear type are important determinants of elasmobranch immediate and post-release mortality

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Abstract

Estimated declines in shark and ray populations worldwide have raised major, widespread concern about the impacts of global fisheries on elasmobranchs. The mechanisms causing elasmobranch mortality during fisheries' capture are not fully understood, but we must gain greater clarity on this topic for fisheries managers to develop effective conservation plans to mitigate further population declines. To evaluate how two important factors, respiratory mode and fishing gear type, impact elasmobranch survival, we compiled publicly available data sources on the immediate mortality percentages of 83 species and post-release mortality percentages of 40 species. Using Bayesian models, we found that sharks and rays captured in longlines had significantly lower immediate mortality than those caught in trawls or gillnets. Our models also predicted the mean total discard mortality (combined immediate and post-release mortality) percentages of obligate ram-ventilating elasmobranchs caught in longline, gillnet and trawl gear types to be 49.8, 79.0 and 84.2%, respectively. In contrast, total discard mortality percentages of stationary-respiring species were significantly lower (longline capture mean = 7.2%, gillnet capture mean = 25.3%, trawl capture mean = 41.9%). Our global meta-analysis provides the first quantified demonstration of how mortality is affected by these two factors across a broad range of species. Our results and approach can be applied to data-deficient elasmobranchs and fisheries to identify species that are likely to experience high rates of mortality due to respiratory mode and/or fishing methods used, so that appropriate mitigation measures can be prioritized and investigated.

Keywords Fishing mortality, gillnet, longline, ray, shark, trawl

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Introduction

Anthropogenic impacts on elasmobranch populations have raised concerns that species population declines, species extinctions and ecosystem change are likely or imminent under the current levels of global fishing pressure (FAO 1999; Stevens *et al.* 2000; CITES 2006; Dulvy *et al.* 2014). Many elasmobranch species are inherently vulnerable to overexploitation because of their K-selected life-history strategies, which increase their susceptibility to fishing pressures (Holden 1974; Hoenig and Gruber 1990), and concerns have risen because many vulnerable elasmobranch species are commercially (Gilman *et al.* 2008) and ecologically important (Stevens *et al.* 2000; Bascompte *et al.* 2005; Heithaus *et al.* 2008). Although the economic and ecological ramifications of localized elasmobranch population declines remain largely unknown, the International Union for the Conservation of Nature (IUCN) currently lists 73 species of shark and 107 species of ray as threatened with extinction (IUCN, 2013) and recent estimates predict that at least 24% of chondrichthyans (sharks, rays and chimaeras) are threatened with extinction (Dulvy *et al.* 2014).

Most global elasmobranch catch is landed in longline, gillnet and trawl fisheries, divided approximately equally between ray and shark catch (Walker 1998). Despite sensitivities to fishing pressure, reported global shark landings from 1950 to 2010 have increased from 121 000 to 383 000 tonnes and reported ray landings increased similarly (Worm *et al.* 2013). In 2006, shark products (e.g. meat, fins, skin, cartilage and liver) derived from reported landings were worth an estimated US$800 million and are considered a lucrative component of many commercial fishing industries (Musick and Musick 2011). However, the majority of sharks discarded (Clarke *et al.* 2006) or illegally captured (Agnew *et al.* 2009) are not reported in fisheries statistics and remain unaccounted for in many stock assessments (Bonfil 1994; Lack and Sant 2008). As a result, estimates derived from the sales of shark fins indicate that the global shark catch may be up to four times greater than the reported landings of sharks (Clarke *et al.* 2006). The biological characteristics of elasmobranchs, the intensive fishing pressure that they are subjected to and the high demand for elasmobranch products have resulted in many species being harvested at unsustainable rates (Clarke *et al.* 2006; Worm *et al.* 2013). Consequently, although the magnitude of population declines of elasmobranchs has been contentious (Baum and Myers 2004; Burgess *et al.* 2005), it is broadly recognized that fisheries have negatively impacted many elasmobranch species (Stevens *et al.* 2000; Field *et al.* 2009).

In response to several countries adopting laws prohibiting the finning or controlling retention of sharks (e.g. minimum size restrictions, maximum size restrictions, catch quotas and full bans on shark retention), discard rates have increased globally (Gilman *et al.* 2008; Lack and Sant 2009; Biery and Pauly 2012). Although the implementation of fisheries and trade regulations is a major success for elasmobranch conservation, regulating finning or retention of sharks will only prove effective if elasmobranch by-catch (discarded catch) is reduced or elasmobranchs survive both immediate capture and subsequent release when by-catch cannot be reduced. If sharks and rays are returned to the water in a state where they are either dead or will die from damage caused by capture and the number of these animals caught does not decrease, elasmobranch populations may continue to be negatively impacted despite regulatory measures.

Mortality of captured elasmobranchs can occur prior to retention or discarding by fishers, which we describe here as an *immediate mortality* percentage (Fig. 1). However, mortality can also occur after release, from the severe physical and/

or physiological trauma caused by fisheries capture (Davis 2002; Skomal 2007), which we describe as *post-release mortality* (Fig. 1). We define a combination of both the immediate mortality percentage and the post-release mortality percentage as the *total discard mortality* percentage (Fig. 1). The total discard mortality percentage thus represents the total mortality percentages of a species during and following fisheries capture.

Although fisheries capture may alter the immune function, growth rates, susceptibility to predation and reproductive processes of sharks and rays (Cooke *et al.* 2002; Van Rijn and Reina 2010; Skomal and Mandelman 2012; Gilman *et al.* 2013), many studies have attributed immediate and post-release mortality of elasmobranchs to metabolic, respiratory and/or intracellular acidoses (Cliff and Thurman 1984; Manire *et al.* 2001; Moyes *et al.* 2006; Frick *et al.* 2010a,b). Mortality may occur when these physiological disruptions manifest by decreasing blood pH and/or increasing blood potassium concentrations (Cliff and Thurman 1984). Metabolic, respiratory and intracellular acidoses can be exacerbated by impaired respiration, so respiratory mode may be an important factor affecting elasmobranch survival during a capture event (Manire *et al.* 2001; Morgan and Burgess 2007; Frick *et al.* 2009; Braccini *et al.* 2012). Despite the potential importance of respiratory mode, the magnitude of its impact on immediate, post-release and total discard mortality percentages has not yet been quantified in elasmobranchs.

The physical trauma and physiological disruption caused by capture can vary with the fishing gear type used and the sensitivity of the captured species to the various stressors associated with these different gear types (Davis 2002; Rufilson 2007; Frick *et al.* 2010a; Jones *et al.* 2010). For example, elasmobranchs caught in trawls typically experience longer periods of aerial exposure when handled on the vessel than those caught in longline or gillnet fisheries, because of the differing methods by which catch is processed on deck. Similarly, the capacity of hooked animals to move within some limited radius will be determined by the specifics of the gear set-up (e.g. gangion length) of different longline configurations. Thus, we argue that a better understanding of the interactions between elasmobranch survival and fishing gear type, in combination with the resilience or vulnerability of different respiratory modes, will be an important advance in the development of strategies to maximize the potential for both immediate and post-release survival.

Obtaining immediate, post-release and total discard mortality percentages are important for fisheries management (Carruthers *et al.* 2009) and a key input to the assessment we propose. Ultimately, combined immediate mortality and post-release mortality percentages provide more accurate estimates of fishing mortality than using immediate mortality percentages alone when undertaking stock assessments (Kitchell *et al.* 2004; Simpfendorfer *et al.* 2005) or ecological risk assessments for the effects of fishing (Hobday *et al.* 2011). Although post-release and total discard mortality studies should be used in support of stock assessments to ensure accurate results, these studies are logistically challenging, expensive and limited to a handful of elasmobranch species (Kitchell *et al.* 2004; Musyl *et al.* 2011).

Nevertheless, in the absence of total discard mortality data, immediate mortality percentages can identify elasmobranch species which are vulnerable to fisheries capture. For example, a particular species may have a high immediate mortality percentage (e.g. longline-caught great

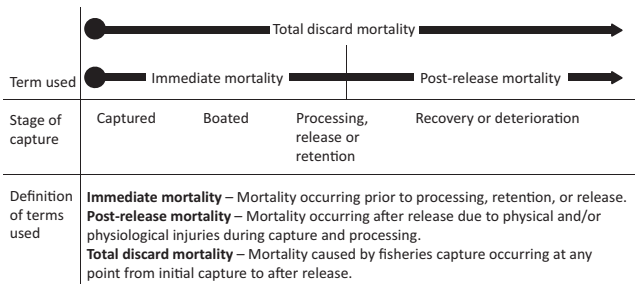

Figure 1 Mortality terms used throughout the study. Each is defined by the stage of the capture event when mortality is recorded.

hammerhead sharks (*Sphyrna mokarran,* Sphyrnidae) – 96% immediate mortality, Morgan *et al.* 2009) and is consistently captured dead. In this situation, a high immediate mortality percentage identifies the need for investigation into strategies which reduce the number of individuals caught.

Here, we present a review and comprehensive meta-analysis of elasmobranch immediate and post-release mortality percentages. We evaluate how respiratory mode and fishing gear type affect immediate survival percentages in a wide range of elasmobranch species. Additionally, we examine current literature on post-release mortality in sharks and rays, quantitatively assess how respiratory mode and gear type impact total discard mortality percentages and explore probable mortality trends in data-deficient elasmobranch groups. We briefly explore the implications and relevance of our study for bony teleost species and recommend future research to explore how respiratory mode impacts mortality during capture in bony fish species. Because the analysis incorporates data from a diverse array of species and locations, results can be applied globally and provide the first immediate and post-release mortality estimates for elasmobranch groups of a given respiratory mode and capture method.

Methods

Literature search

Structured literature searches were performed to create the data set used in the immediate mortality and post-release mortality meta-analyses. These searches were conducted using Web of Science, Google Scholar and Scopus from April to July of 2013 and in June 2014. The Boolean (AND/OR) search terms used in all searches consisted of combinations of the following: at-vessel, post-capture, post-release, hooking mortality, immediate, delayed, mortality, survival, trawl, longline, gillnet, elasmobranch, shark and ray. Using various combinations of these search terms, the results were examined for data pertaining to immediate mortality, post-release mortality or total discard mortality percentages. The vast majority of literature searched (approximately 90%) did not report immediate mortality, post-release mortality or total discard mortality percentages, and these sources were excluded from this study. Despite some studies (approximately 5% of the sources which reported mortality percentages) reporting the immediate mortality and total discard mortality percentages of elasmobranchs caught in recreational catch and release angling (Heberer *et al.* 2010; Lynch *et al.* 2010) and purse seine fisheries (Filmalter *et al.* 2012), these gear types were excluded from the current analysis because information on these fisheries is scarce compared to longline, trawl and gillnet fisheries.

We included data sources from a wide variety of global fisheries, although we only included literature sources that were available in English in either original or translated form. We used nine data sources which were not peer-reviewed (eight government reports or data sets and one report published by the World Wildlife Fund) to increase the total number of species and geographic locations examined. These sources were found by performing a Google search using the aforementioned key terms. Additionally, one data source (the United States Pelagic Fisher Logbook data) which did not appear in our literature search was included in the analysis at the suggestion of a reviewer.

Three data sources used in the analysis were compiled from annual reports by the United States National Marine Fisheries Service (NMFS). The first includes observer data publicly available from the Shark Gillnet Observer Program from 1998 to 2009. Sources compiled from this data source include Carlson and Lee (1999, 2000), Carlson (2000), Carlson and Baremore (2001, 2002a,b, 2003), Carlson *et al.* (2004a), Baremore *et al.* (2007), Carlson and Bethea (2007), Passerotti and Carlson (2009) and Passerotti *et al.* (2010). For the remainder of this analysis, we refer to this collective data source as Southeast Gillnet Observer Program (SGOP). Another gillnet data source was compiled from publicly available NMFS sources on the California/Oregon drift gillnet fishery from 1990 to 2011 (CODGF 2013). A third data source, the Pelagic Fisher Logbook Dataset (hereafter referred to as PFLD 2014), encompassed multiple gear types. Only sets that used a single gear type were included in the analysis when this data set was incorporated. Additionally, only sets from 1992 to 2008 were included in the PFLD data source, as prior to these dates, the life status of sharks at the time of discarding was not recorded and data after 2008 were not publicly available.

Standardizing capture terms

There are a number of terms used to report elasmobranch by-catch mortality and survival percentages that occur due to fishing, with several terms used interchangeably. For example, the following terms are all used to convey percentages of dead elasmobranchs when they are brought onboard the vessel: at-vessel mortality (Morgan and Burgess 2007), hooking mortality (Coelho *et al.* 2012), immediate mortality (Mandelman *et al.* 2013), initial mortality (Rufilson 2007), within-net survival (Stobutzki *et al.* 2002) and immediate post-capture trawl mortality (Mandelman and Farrington 2007). The terms we used ('immediate mortality' and 'post-release mortality'; Fig. 1) are standard in elasmobranch mortality studies. The term 'total discard mortality' was used instead of 'total fishing mortality' because some forms of cryptic fishing mortality (e.g. individuals that escape fishing gear prior to capture and die due to physical or physiological injuries) were not included in this calculation, because individuals retained are not accounted for, and to avoid confusion with terms commonly used in stock assessments [e.g. fishing mortality rate (F) and total mortality rate (Z)]. We adopted these terms because they can be applied to any form of fisheries capture, irrespective of gear type and use of a vessel. Use of these terms in future studies reporting mortality percentages in elasmobranchs would improve clarity for readers comparing multiple gear types and fishing methods.

Immediate Mortality

Data were gathered from 37 sources, including 28 peer-reviewed journal articles, eight government reports or data sets, and one report published by the World Wildlife Fund. Although a wide range of geographic areas were represented in the analysis, most sources used in the analysis came from the United States, Australia or the United Kingdom (Table 1). In accordance with previously published reviews (Cooke and Suski 2004; Serafy *et al.* 2009), if a researcher recorded immediate mortality percentages of multiple species in a single study, results were not grouped and species-specific results were considered an independent study.

For each study, we recorded the species, presence of large spiracles in that species, number of animals examined, gear type and immediate mortality percentage. Spiracle size of each species was determined using taxonomic literature (Compagno 1988, 1998, 1999) and is presented in Table S1. To ensure accurate mortality estimates, if the sample size for a species within a data source was <15 animals, that specific species–data source combination was excluded from the immediate mortality analysis. One species, the whiskery shark (*Furgaleus macki*, Triakidae), was removed from all quantitative analyses because Compagno (1988) reported that spiracle size in the family Triakidae, which the whiskery shark belongs to, ranged from 'small to moderately large' and we were unable to find any reports in the literature or obtain conclusive advice on the respiratory mode of this species from experts in the field. Despite exclusion from the quantitative analysis, we reported the observed immediate mortality, post-release mortality and total discard mortality percentages of the whiskery shark in Tables S2 and S3.

The presence of large spiracles was used as a defining characteristic of respiratory mode within this study. We assumed that all species with large

Table 1 Geographic locations of studies used in the immediate mortality percentage analysis.

Location	Number of studies examined
Southeast North America	8 (Manire *et al.* 2001; Beerkircher *et al.* 2002; Hueter *et al.* 2006; Morgan and Burgess 2007; Morgan *et al.* 2009; Thorpe and Frierson 2009; Scott-Denton *et al.* 2011; SGOP)
Australia	6 (Stobutzki *et al.* 2002; Walker *et al.* 2005; Kranz 2007; Frick *et al.* 2010a,b; Braccini *et al.* 2012)
United Kingdoms	5 (Kaiser and Spencer 1995; Revill *et al.* 2005; Rogan and Mackey 2007; Ellis *et al.* 2008; Bendall *et al.* 2012)
Northeast North America	4 (Mandelman and Farrington 2007; Rufilson 2007; Campana *et al.* 2009; Mandelman *et al.* 2013)
Central Pacific Ocean	3 (Moyes *et al.* 2006; Musyl *et al.* 2011; Bromhead *et al.* 2012)
Western North America	3 (Hight *et al.* 2007; CODGF 2013; Lyons *et al.* 2013)
Atlantic Ocean	2 (Coelho *et al.* 2012; PFLD 2014)
South Africa	2 (Fennessy 1994; Petersen *et al.* 2008)
New Zealand	2 (Francis *et al.* 2001; Griggs and Baird 2013)
Brazil	1 (Afonso and Hazin 2014)
Southeast Madagascar	1 (Coelho *et al.* 2011)

spiracles are capable of respiring while stationary and that species which lacked large spiracles could not do so. These assumptions were made because enlarged spiracles have been identified as key respiratory structures for species which respire while stationary (Hughes 1960; Grigg 1970) and spiracles of a reduced size have been shown to have little to no ability to aid respiration (Grigg 1970). Some exceptions were noted because a few species that had reduced or absent spiracles could still perform buccal pumping or ventilation through the first gill slit while stationary. Examples of such species are presented in Table S1 and include the bull shark (*Carcharhinus leucas,* Carcharhinidae), nurse shark (*Ginglymostoma cirratum,* Ginglymostomatidae), Port Jackson shark (*Heterodontus portusjacksoni,* Heterodontidae), lemon shark (*Negaprion brevirostris,* Carcharhinidae) and rusty carpetshark (*Parascyllium ferrugineum,* Parascylliidae) (Grigg 1970; Manire *et al.* 2001; Morgan *et al.* 2009; Brooks *et al.* 2011; Goto *et al.* 2013). Although we performed extensive literature searches, contacted experts in the field for advice on specific species and used the best available knowledge to confirm the respiratory mode of each species within this study, we acknowledge that the respiration mode of some species could not be verified. Throughout the rest of this study, we collectively refer to buccal pumping exception species and species with large spiracles as being capable of stationary respiration. We refer to species which are not capable of stationary respiration as obligate ram ventilators. Obligate ram ventilators must continuously move forward to respire because they possess reduced brachiostegal systems which are incapable of forcing water over their gills once movement stops (Roberts 1975; Carlson *et al.* 2004b).

If several sources reported immediate mortality percentages of the same species captured in a particular gear type, the immediate mortality percentage for that species–gear-type combination was calculated and reported as the arithmetic mean of the sources. These values were used in all subsequent statistical analyses pertaining to immediate mortality.

Some studies (SGOP; CODGF 2013; PFLD 2014) did not report immediate mortality percentages explicitly, but recorded whether a species was retained, discarded dead, discarded alive or discarded without recording the life status of the animal. In those studies, immediate mortality percentage had to be estimated because it was unknown whether animals were retrieved from fishing gear alive before they were retained or discarded. To include all available sources, these studies were used in the analysis if they met the following criteria, which allowed us to make accurate estimations of immediate mortality percentages:

1. The total number of animals within a species with an unknown immediate mortality, due to either retention or an unrecorded life status, was ≤5% of the total number reported.
2. Total individual counts for the species examined exceeded 15 animals, consistent with other data sources used in quantitative analyses throughout the review.

Immediate mortality for species in these data sets was calculated as a range of minimum and maximum immediate mortality percentage.

Minimum immediate mortality percentage was calculated as:

$$M_{\min} = 100 \times \left(\frac{d}{r+d+a+u}\right),$$

Maximum immediate mortality percentage was calculated as:

$$M_{\max} = 100 \times \left(\frac{r+d+u}{r+d+a+u}\right),$$

Variables r, d, a, and u symbolize the number of animals reported as retained, discarded dead, discarded alive or discarded with unrecorded life status, respectively. Differences in minimum and maximum immediate mortality percentage within a specific data source were small, and the largest difference noted was in the blue shark (*Prionace glauca,* Carcharhinidae), which ranged from a 75 to 81% immediate mortality percentage following gillnet capture in PFLD 2014. In all subsequent statistical analyses, the arithmetic mean of the minimum immediate mortality percentage and maximum immediate mortality percentage was used to provide an estimate of mortality percentages.

Post-release mortality, total discard mortality

For our study, we only considered total discard mortality percentages of discarded elasmobranchs because animals that were consistently retained by fishers would have much lower percentages of

survival (0%), unrelated to the biology of the species, environmental conditions or gear-specific attributes. Several studies reported the post-release mortality and/or total discard mortality percentages of a species with sample sizes <15. Despite the small sample sizes used, we included these species within the tables in the supporting information section due to the lack of data available on elasmobranch post-release mortality and total discard mortality percentages. However, consistent with the immediate mortality analysis criteria above, species which had a sample size of <15 were excluded from the quantitative portion of the post-release mortality analysis.

We were unable to test for the effects of an interaction effect between respiratory mode and fishing gear type on post-release mortality percentages because our literature searches yielded post-release mortality percentages for only five species captured in longline fisheries with sample sizes larger than 15. Additionally, we were unable to find publicly available post-release mortality percentages of obligate ram-ventilating species caught in trawl fisheries. Due to these limitations, the quantitative post-release mortality analysis was restricted to measuring the effect of respiratory mode and gear type.

Statistical analysis

The effects of gear type, respiratory mode and an interaction on immediate mortality percentages were tested in a Bayesian framework by performing a factorial analysis of variance. During model selection, we tested Gaussian, Poisson, zero-inflated Poisson and negative binomial distributions to determine the most appropriate model given the data. The data were most suited to a Gaussian distribution and the final model used took the form:

$$\mathrm{IM} = \mathrm{FS} + \mathrm{RM} + \mathrm{FS} \times \mathrm{RM},$$

where IM was the immediate mortality percentage, FS was the fishing method examined (gillnet, longline, and trawl), and RM was the respiratory mode examined (obligate ram ventilator, stationary respiring).

We used an uninformative prior distribution (mean = 1×10^{-6}) and a Monte chain Carlo Markov (MCMC) estimation (iterations = 5×10^{6}, burn-in length = 6×10^{3}, thinning rate = 100) in each model. Differences in group means and 95% credibility intervals were used to determine groups that were statistically different in all immediate mortality analyses.

To model mean differences in immediate mortality following capture in each gear type, we used the following equations:

$$D = ((\mathrm{F1R1} + \mathrm{F1R2})/2) - ((\mathrm{F2R1} + \mathrm{F2R2})/2),$$

$$D = ((\mathrm{F2R1} + \mathrm{F2R2})/2) - ((\mathrm{F3R1} + \mathrm{F3R2})/2),$$

$$D = ((\mathrm{F1R1} + \mathrm{F1R2})/2) - ((\mathrm{F3R1} + \mathrm{F3R2})/2),$$

To model mean differences in immediate mortality following capture for each respiratory mode, we used the following equation:

$$D = ((\mathrm{F1R1} + \mathrm{F2R1} + \mathrm{F3R1})/3) - ((\mathrm{F1R2} + \mathrm{F2R2} + \mathrm{F3R2})/3),$$

where F1R1, F1R2, F2R1, F2R2, F3R1 and F3R2 are the means of gear-type and respiratory mode groupings. R1 and R2 correspond to respiratory modes (obligate ram ventilator vs. stationary respiring), and F1, F2 and F3 correspond to the gear types compared. D is the mean difference between gear types or respiratory modes examined.

In the post-release mortality analysis, a non-parametric Kruskal–Wallis test was used to determine differences (significant if $P < 0.05$) between obligate ram-ventilating and stationary-respiring elasmobranchs captured in gillnets. Due to small sample sizes, differences in post-release mortality percentages of obligate ram-ventilating and stationary-respiring species caught in longlines were not tested. Instead, post-release mortality percentages of longline-caught groups are reported as an arithmetic mean of the species examined. Our literature searches yielded no studies that examined post-release mortality percentages of obligate ram-ventilating sharks or rays caught in trawls, so we determined post-release and total discard mortality percentages for this group under three different scenarios. The first scenario assumed that respiratory mode did not affect post-release mortality and we used the mean post-release mortality percentage of stationary-respiring species to model the post-release mortality percentage of obligate ram-ventilating species. In the second scenario, we calculated the magnitude of difference in immediate mortality percentages between trawl-caught stationary-respiring and trawl-caught obligate

ram-ventilating species. It was then assumed that changes in immediate mortality percentages caused by respiratory mode would be similar to changes in post-release mortality percentages caused by respiratory mode in trawl-caught species (eq. S1). The final scenario assumed that the impact of respiratory mode on post-release mortality percentages of trawl-caught species was similar to the impact of respiratory mode on post-release mortality percentages of gillnet-caught elasmobranchs (eq. S2).

Total delayed mortality percentage was calculated via the following equation:

$$\mathrm{TDM} = \left[1 - \left(1 - \frac{\mathrm{IM}}{100}\right) \times \left(1 - \frac{\mathrm{PRM}}{100}\right)\right] \times 100,$$

where IM, PRM and TDM are the immediate, post-release and total discard mortality percentages of the species or group examined.

All statistical analyses were conducted using the 'R Project for Statistical Computing' version 2.14.2 (R Development Core Team, 2013) and 'Just Another Gibbs Sampler' version 3.4.0 (http://mcmc-jags.sourceforge.net/). To portray biologically meaningful results, all results are reported as mean ± standard error unless otherwise specified.

Results and discussion

Immediate mortality studies

Immediate mortality percentages were collated for 111 species gear-type combinations and are collectively reported in the Supporting Information section (Table S2). A total of 83 different species were examined in the study because immediate mortality percentages for some captured species were available for multiple gear types. There was an unequal number of species examined in each gear type (longline – 40 species; gillnet – 41 species; trawl – 30 species, Table S2) because more data sources were available for longline and gillnet than trawl gear types. Additionally, immediate mortality percentages of elasmobranchs captured in trawl fisheries were rarely reported, perhaps due to the rapidity with which fishermen process retained catch and discard bycatch (Jones *et al.* 2010).

The ratio of elasmobranch species capable of stationary respiration to obligate ram-ventilating species examined also varied based on gear type (longline – 63% obligate ram ventilators, gillnet – 44% obligate ram ventilators, trawl – 23% obligate ram ventilators, Table S2). Attributes inherent to specific gear types are the cause of this bias. All bottom-dwelling rays and many bottom-dwelling sharks examined have large functional spiracles (Table S1) and were commonly caught in benthic fisheries. Although three of the included longline studies came from benthic longline sets, the majority of studies examined described pelagic longline sets (83%). Benthic gillnet sets comprised the majority of the examined gillnet data sources (64%), and benthic trawls comprised all of the examined trawl data sources (100%).

Immediate mortality percentages varied greatly and were species specific. The highest documented immediate mortality percentage was noted in the salmon shark (*Lamna ditropis,* Lamnidae), which had a 100% immediate mortality when captured in gillnet fisheries (Table S2). Thirteen species were recorded as having a 0% immediate mortality percentage in at least one gear type (Table S2). Across all gear types and species, the mean immediate mortality percentage was 31.9 ± 2.8%. Across all gear types, rays had a mean immediate mortality percentage of 18.4 ± 3.9% and sharks had a mean immediate mortality percentage of 37.9 ± 3.4%.

Respiratory mode

Obligate ram-ventilating species had significantly higher immediate mortality percentages compared to species capable of stationary respiration (mean = 41.3% higher, 95% credibility intervals = 33.0–49.7% higher). The five exception species that lacked large spiracles but could respire, while stationary by buccal pumping or drawing in water through the first gill slit (Grigg 1970) had comparable mortality percentages to stationary-respiring elasmobranchs which possess large spiracles (Fig. 2).

Previous studies have suggested that species capable of stationary respiration are more likely to survive fisheries' capture than obligate ram ventilators (Manire *et al.* 2001; Morgan and Burgess 2007; Braccini *et al.* 2012). However, ours is the first study to examine this concept quantitatively on a broad range of species across multiple gear types. The three gear types examined severely restrict movement of captured elasmobranchs

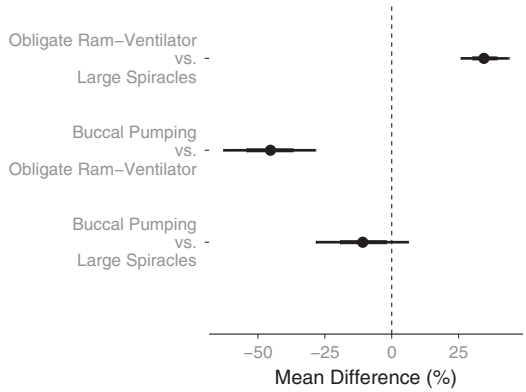

Figure 2 Comparisons of the effects of respiratory morphology on elasmobranch immediate mortality. 'Buccal pumping' represents species which can respire while stationary without large spiracles (Table S1). 'Large spiracles' represents species which have large spiracles and can respire while stationary. 'Obligate ram ventilator' represents species which cannot respire while stationary. Accordingly, 'Buccal pumping vs. large spiracles' compares differences in immediate mortality between species that can respire while stationary without large spiracles and stationary-respiring species which have large spiracles. Circles represent the mean differences between each group. Thick bars represent the 68% credibility intervals, and thin bars represent the 95% credibility intervals. Group differences are designated as statistically significant when 95% credibility intervals do not overlap zero.

(Morgan and Burgess 2007), thus, the respiratory ability of obligate ram ventilators is impaired or ceases during a capture event because the animal cannot effectively pass water over its gills. The active lifestyle of obligate ram ventilators is linked to higher rates of metabolism and oxygen consumption than other types of elasmobranch (Carlson *et al.* 2004b). Compounding this, fisheries capture causes an escape response in elasmobranchs characterized by increased rates of muscle activity and oxygen consumption (Skomal and Mandelman 2012). Consequently, after respiration is impaired and oxygen demand increases, obligate ram-ventilating elasmobranchs caught in fishing gear suffer from relatively rapid asphyxiation. For an extensive review on the physiological response of sharks and rays to stress and anaerobic glycolysis, see Skomal and Mandelman (2012).

Gear type

In all gear types, species which were capable of stationary respiration had lower immediate mortality percentages than species which were not (Fig. 3). Sharks and rays captured by longlines had significantly lower immediate mortality percentages compared to elasmobranchs captured in trawl (mean = 22.7% lower immediate mortality percentage, 95% credibility interval = 12.0–33.6% lower, Fig. 4) or gillnet (mean = 19.0% lower immediate mortality percentage, 95% credibility interval = 9.8–28.0% lower, Fig. 4) gear types. Anecdotal reports in the literature have similarly described higher immediate mortality percentages for elasmobranchs captured in trawl (Coelho and Erzini 2008) and gillnet (Jones *et al.* 2010) gear types than longline gear types.

We found a statistically significant interaction effect between gear type and respiratory mode on immediate mortality percentages, as respiratory mode plays a larger role in determining immediate mortality percentages during gillnet capture than longline capture (Fig. 3). Stationary-respiring species have similar immediate mortality percentages in longline and gillnet capture, but obligate ram-ventilating species caught in gillnets have significantly higher immediate mortality percentages than those caught on longlines (Fig. 3). This

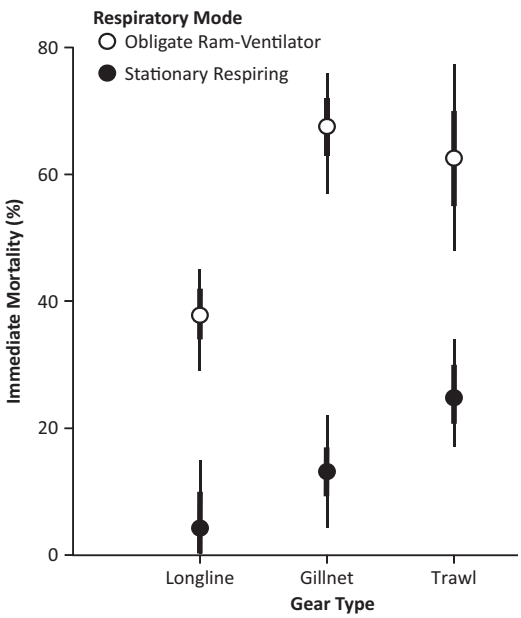

Figure 3 Immediate mortality percentage comparisons of elasmobranchs capable of stationary respiration with obligate ram-ventilating species in longline, gillnet and trawl fisheries. Circles represent the mean of each group. Thick bars represent the 68% credibility intervals, and thin bars represent the 95% credibility intervals.

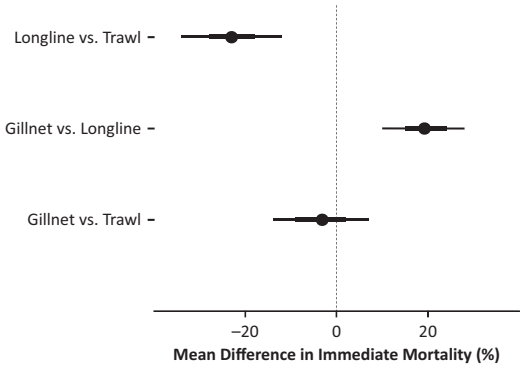

Figure 4 Comparisons of the effects of fishing gear type on elasmobranch immediate mortality. Circles represent the mean differences between each group. Thick bars represent the 68% credibility intervals, and thin bars represent the 95% credibility intervals of group differences. Group differences are designated as statistically significant when 95% credibility intervals do not overlap zero.

observation may be caused by differences in the degree of movement restriction elasmobranchs that are subjected to across gear types.

Shark and ray movements are restricted in all three gear types because elasmobranchs caught in longlines must stay within close proximity to the mainline, those caught in gillnets are tightly confined by the net, and those caught in trawls may be compacted in the codend by the weight of the catch. However, degree of movement restriction varies in each gear type. Elasmobranchs captured on longline gear types have been observed maintaining swimming or resting while captured (Frick *et al.* 2010a), which can lead to physiological convalescence while hooked on fishing gear (Brooks *et al.* 2012). In contrast, elasmobranchs captured in gillnet gear types perform frequent bouts of struggling (Frick *et al.* 2010a) and are unable to swim forward. Movement restriction in trawls can vary, but compaction against other catch in the net is likely to cause some degree of movement impairment. Due to these conditions, obligate ram-ventilating species captured in gillnets and trawls may suffer from asphyxiation more rapidly than those caught in longlines.

Although asphyxiation caused by movement restriction may account for the diminished immediate survival percentages of elasmobranchs captured in trawl gear types compared to longline gear types, increased mortality during trawl capture may also be the result of increased occurrences of physical injuries. Physical injuries are more prevalent during trawl operations (Neilson *et al.* 1989; Davis 2002; Coelho and Erzini 2008; Jones *et al.* 2010) than longline operations and occur in a variety of ways. Catch weight inside the codend can crush captured elasmobranchs during hauls and when the codend is lifted from the water (Fennessy 1994; Enever *et al.* 2009). The typically large catches of trawl operations require long processing times, increasing aerial exposure time and the likelihood of elasmobranchs being crushed under other unsorted catch (Revill *et al.* 2005). Further, tight compression against the spines, teeth or scales of other catch in the codend or on deck can cause lacerations, scraping and haemorrhaging (Kaiser and Spencer 1995; Davis 2002).

Although the primary reason for increased immediate mortality percentages of elasmobranchs captured in gillnet gear types compared to longline gear types is the increased likelihood of asphyxiation (Fig. 3), gillnet capture is also more likely to cause physical injury to elasmobranchs than longline capture (Jones *et al.* 2010). Tight entanglement and confinement around the gill or head region associated with gillnet capture can result in fin damage, abrasions of the skin and mesh-shaped wounds around the head or body (Manire *et al.* 2001; Rufilson 2007; Bendall *et al.* 2012). Additionally, sharks and rays left in fishing gear for extended periods of time become susceptible to predation by isopods, teleosts or other elasmobranchs (Gilman *et al.* 2008; Jones *et al.* 2010; Bendall *et al.* 2012). Due to the movement-restricted nature of gillnet capture, risk of predation by isopods may be heightened compared to longline capture. The physical injuries sustained by predatory isopod infestation, initially in the gills and cloaca, can lead to death in elasmobranchs (Jones *et al.* 2010; Bendall *et al.* 2012).

We were unable to measure physical injury occurrences quantitatively because these data are often unreported in elasmobranch immediate mortality studies. Despite our conjecture that the primary drivers of differences in immediate mortality percentages across gear types are physical injury and susceptibility to asphyxiation, we acknowledge that mortality induced by capture involves complex interactions with a multitude of factors (e.g. sea surface temperature, capture duration, handling practices, degree of entrapment in fishing gear, capture depth, gangion length and location of entrap-

ment in fishing gear; Davis 2002; Endicott and Agnew 2004; Campana *et al.* 2009; Thorpe and Frierson 2009; Morgan and Carlson 2010; Braccini *et al.* 2012). Many of these factors were not measured in the present study because a large portion of the studies examined did not report gear-specific or environmental attributes and incorporation of these factors was not possible (see Supporting information for additional details). In general, immediate mortality ranges within species–gear-type combinations were small, but some data points (15 of 111) varied by over 30% in the range of immediate mortality percentages reported across studies. These ranges indicate that gear-specific or environmental factors not measured in the present study may impact mortality during capture. When these 15 variable species–gear-type combinations were removed from the analysis, results were similar to the full analysis (Table S4).

Despite the potential impact of unmeasured factors, the majority of the variance within our data set (76.5%) was explained by our model (Fig. 5) and we can adequately explain a large amount of the variation in immediate mortality percentages among elasmobranch species–gear-type combinations. Respiratory mode explained the largest percentage of the finite population variance (44.8%), while gear type and an interaction between respiratory mode and gear type accounted for 19.5 and 12.3% of the variance, respectively. Therefore, we are confident that respiratory mode is the most influential factor we examined for determining the immediate mortality percentages of elasmobranchs.

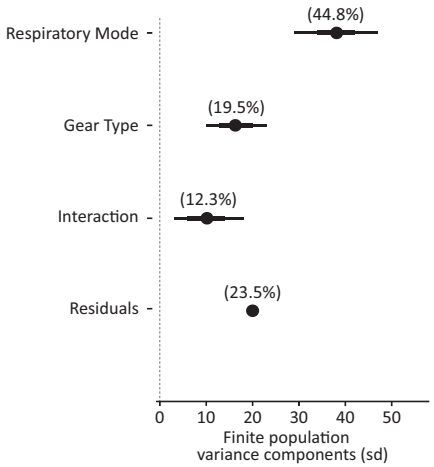

Figure 5 Finite population variability explained by respiratory mode, gear type and an interaction effect during the immediate mortality analysis. Residuals demonstrate the variability which is unexplained in the data set by the factors we provided. Circles represent the mean of each group. Thick bars represent the 68% credibility intervals, and thin bars represent the 95% credibility intervals.

Post-release mortality studies

Due to the challenging nature of research on post-release mortality (Kitchell *et al.* 2004; Musyl *et al.* 2011), few studies have examined post-release mortality percentages of elasmobranchs. We were unable to analyse the relationship between immediate mortality percentages and post-release mortality percentages due to the paucity of post-release mortality data currently available. Data pertaining to the post-release mortality percentages of longline-captured species were scarce and limited to five species (two obligate ram-ventilating, three stationary-respiring) with sample sizes >15. Given these data restrictions, we explored how respiratory mode impacts the post-release mortality percentages of gillnet-captured elasmobranchs, modelled and estimated the post-release mortality percentages of data-deficient groups (obligate ram-ventilating trawl-captured, obligate ram-ventilating longline-captured and stationary-respiring longline-captured species), and calculated the mean total discard mortality percentages for each fishing gear type and respiratory mode combination.

Within the 18 data sources used in the post-release mortality analysis, 40 different species were represented. Of the 40 species, 28 had sample sizes larger than 15 and were used in the quantitative post-release mortality analysis. Unlike studies focusing on immediate mortality percentages, most post-release mortality studies (50%) focused on trawl gear types. Comparatively, few examined longline (33%) or gillnet gear types (28%). Arithmetic mean immediate mortality percentages of the species examined in the post-release mortality analysis were lower ($19.5 \pm 4.0\%$) than the species examined in the immediate mortality analysis ($31.9 \pm 2.8\%$). We attribute this difference to a greater proportion of species capable of stationary respiration observed in the post-release mortality analysis 76% (24 of 33 data points) compared to the immediate mortality analysis 55% (61 of 111 data points). Overall, the arithmetic mean post-release mortality percentage for elasmobranchs across all gear types within our data set was 20.0 ± 2.9 (SE) %.

Stationary-respiring species caught in gillnets had significantly lower post-release mortality percentages than obligate ram-ventilating species (Kruskal–Wallis test, $P < .01$, Table 2). The mean post-release mortality percentages of captured elasmobranchs ranged between 2.7% (longline-caught stationary-respiring species, Table 2) and 58.0% (trawl-caught obligate ram-ventilating species modelled under scenario 3, Table 2). Given the mean immediate and post-release mortality percentages of each group, mean total discard mortality percentages were calculated for each gear-type respiratory mode combination. Total discard mortality percentages ranged from low risk (7.2% longline-caught stationary-respiring species, 25.3% gillnet-caught stationary-respiring species, Table 2), to medium risk (41.9% trawl-caught stationary-respiring species, 49.8% longline-caught obligate ram-ventilating species, Table 2), to high risk (79.0% gillnet-caught obligate ram-ventilating species, 70.8–84.2% trawl-caught obligate ram-ventilating species, Table 2).

Increased occurrence of post-release mortality in obligate ram ventilator compared to stationary-respiring species demonstrates a reduced ability to recover from fisheries capture. Fisheries-captured elasmobranchs are often released alive but in an unmoving state due to severe physiological disruption (Laptikhovsky 2004; Hight *et al.* 2007; Enever *et al.* 2009). Stationary-respiring species are able to recover from this state by remaining motionless and resuming normal breathing activity (Laptikhovsky 2004; Enever *et al.* 2009; Frick *et al.* 2010a), in a recovery process that can take up to six hours (Laptikhovsky 2004). However, it is unlikely that obligate ram ventilators would have the same capacity to physiologically recover from an unmoving state as stationary-respiring species and therefore, their post-release mortality is higher.

For some groups, post-release mortality percentage estimations were performed with small sample sizes (longline-caught groups) or with no available data (trawl-caught obligate ram ventilators). Consequentially, an interaction effect was not included in the models used to estimate post-release mortality percentages. Despite this limitation, it was necessary to generate gear-specific percentages because gear type is likely to exhibit a strong influence on post-release mortality percentages. Mean total discard mortality percentages experienced by trawl-captured obligate ram-ventilating by-catch predicted by various scenarios are high (70.8–84.2%, Table 2), and we think this trend reflects the sensitivity of these species to capture. Of the three scenarios presented, scenario 1 (i.e. respiratory mode does not affect post-release mortality in trawl-caught sharks and rays) seems highly unlikely, as this scenario would contradict our findings for other gear types. Modelling of scenarios 2 and 3 predicted similar post-release mortality percentages (54.4 and 58.0%, respectively) and is more likely to indicate actual post-release mortality percentages of trawl-caught obligate ram-ventilating elasmobranchs. Because all scenarios predict that obligate ram-ventilating trawl by-catch is highly susceptible to mortality caused by capture, research directed at quantifying the post-release mortality percentages for this data-deficient group is urgently needed. Additionally, we recommend future research on the post-release mortality of longline-caught elasmobranchs to verify group means calculated with a small sample size in our analysis.

Like immediate mortality, post-release and total discard mortality percentages are not solely influenced by respiratory mode or gear type. There are

Table 2 Mean immediate mortality (IM), post-release mortality (PM) and total discard mortality (TDM) percentages calculated during both analyses. SR represents stationary-respiring species and ORV represents obligate ram-ventilating species.

Gear type	Respiratory mode	IM (%)	PM (%)	TDM (%)
Gillnet	Obligate ram-ventilating	67.3	35.9	79.0
Longline	Obligate ram-ventilating	37.6	19.5[1]	49.8
Trawl – Scenario 1	Obligate ram-ventilating	62.5	22.1[2]	70.8
Trawl – Scenario 2	Obligate ram-ventilating	62.5	54.4[2]	82.9
Trawl – Scenario 3	Obligate ram-ventilating	62.5	58.0[2]	84.2
Gillnet	Stationary respiring	13.4	13.7	25.3
Longline	Stationary respiring	4.6	2.7[1]	7.2
Trawl	Stationary respiring	25.4	22.1	41.9

[1]Estimates derived with small sample sizes (<5 species); [2]estimates derived with no existing data available under three different scenarios.

a myriad of other factors and complex interactions that determine whether a species is likely to survive fisheries capture. In addition to gear type and respiratory mode, future studies should concentrate on factors such as sea surface temperature, soak time, handling practices, gear-specific attributes (e.g. hook sizes, gangion length, and hook types in longlines, codend weight in trawls), species-specific attributes (e.g. dermal thickness, body shape, body size, behaviour on fishing gear, metabolic rates) and duration of aerial exposure, which may influence post-release and total discard mortality percentages (Rodríguez-Cabello *et al.* 2001; Campana *et al.* 2009; Frick *et al.* 2010a; Braccini *et al.* 2012; Mandelman *et al.* 2013). Another consideration to take into account when assessing factors contributing to post-release mortality is the type of study conducted (e.g. satellite tagging, tag and recapture, estimation and captive studies). Ideally, post-release mortality studies should reflect real world values of captured animals irrespective of the method used, but it is unknown how estimations made using differing methods could influence results. Although the magnitude of how these factors affect post-release and total discard mortality is presently unknown, our study shows that respiratory mode and gear type can substantially impact the immediate, post-release and total discard mortality percentages of a species.

We did not determine whether respiratory mode and gear type can impact the immediate and post-release mortality of bony fish, but our results suggest that this subject is worthy of investigation. Although we recognize there are many physiological and biological differences between bony teleosts and elasmobranchs, several species in the families Scrombridae, Istiophoridae and Xiphidae rely on ram ventilation to respire effectively (Wegner *et al.* 2013). Obligate ram-ventilating bony fish captured on longlines exhibit comparable immediate mortality percentages [yellowfin tuna (*Thunnus albacares,* Thunnini) – 55.3%; blue marlin (*Makaira nigricans,* Istiophoridae) – 42–51.4%; white marlin (*Tetrapterus albidus,* Istiophoridae) – 52.5–56.1%; Indo-Pacific sailfish (*Istiophorus platypterus*, Istiophoridae) – 53.9–68.2%; longbill spearfish (*Tetrapturus pfleugeri,* Istiophoridae) – 66.4%; swordfish (*Xiphias gladius,*Xiphidae) – 82.3%] to the elasmobranchs examined in the present study (Cramer 1998; Jackson and Farber 1998). In contrast, Scott-Denton *et al.* (2011) report that stationary-respiring bony fish captured on longlines have low mortality percentages prior to retention or release (mean = 18.8 ± 3.3%, n = 40 species). Like elasmobranchs, obligate ram-ventilating bony fish may be more susceptible to fishery-induced mortality than stationary-respiring bony fish, and although this was beyond the scope of the our study, we think it needs investigation.

Management implications, future direction and concluding remarks

Currently, 46.8% (n = 487) of chondrichthyans are classified by the IUCN as data deficient and fisheries capture (both as target catch and incidental bycatch) is thought to be the main threatening process to shark, ray and chimaera populations worldwide (Dulvy *et al.* 2014). Using spiracle size as a proxy for respiratory mode (Table S1), our results highlight the vulnerability of 13 data-deficient obligate ram-ventilating elasmobranch species (Table S5) to fisheries capture. Some of these species, such as the scoophead (*Sphyrna media*, Sphyrnidae) and bignose (*Carcharhinus altimus*, Carcharhinidae) shark, are caught by fisheries throughout their range as by-catch or target catch, are likely to have high total discard mortality percentages and deserve urgent attention. We also show that data-deficient stationary-respiring species captured as by-catch are also likely to be impacted by fisheries capture, because these species groups will have mean total discard mortality percentages as high as 41.9% (Table 2) depending on the capture method used.

Our results can be readily applied to species which have not yet had post-release or total discard mortality percentages quantified. For example, the scalloped hammerhead (*Sphyrna lewini,* Sphyrnidae) is classified as endangered by the IUCN and is listed in appendix II of CITES, and some populations have been listed as endangered by the United States Endangered Species Act. Immediate mortality percentages of the species have been documented in seven studies (57% longline, 89% gillnet, 80% trawl; Table S1). In the absence of quantified post-release mortality percentages for the species, we can assume that many of the scalloped hammerheads released alive will die, because the average post-release mortality percentage for an obligate ram ventilator in each gear type is high (Table 2). Given its known high immediate mortality and probable high post-release mortality percentage, research directed at

minimizing scalloped hammerhead interactions with fishing gear is urgently required. This example is one of many elasmobranchs lacking a quantified post-release mortality percentage, so our results can be broadly applied by fisheries managers, shark biologists and conservation biologists to prioritize species of particular management and conservation concern.

Mortality estimates derived from fishing and natural mortality are necessary to perform population assessments on elasmobranchs (Simpfendorfer *et al.* 2005). Future research directed at understanding how species-specific and fishery-specific factors affect elasmobranch immediate mortality and post-release mortality will allow more accurate fishing mortality estimates. We concluded that two such factors, gear type used and respiratory mode, can affect elasmobranch mortality percentages, and we provide the first quantified estimates of the mean immediate, post-release and total discard mortality for specific respiratory mode gear-type groupings.

Additional post-release mortality and total discard mortality studies should be conducted to provide more accurate fishing mortality estimates, because immediate mortality surveys do not account for elasmobranchs which die from physical or physiological damage after release (Gilman *et al.* 2013). Although additional post-release mortality data are necessary for many groups and species, these future efforts should concentrate on how capture affects the post-release and total discard mortality of poorly understood groups, such as longline-caught elasmobranchs and trawl-caught obligate ram-ventilating elasmobranchs. Post-release mortality studies which focus on a vast array of species and gear types will allow a greater understanding of the causes of fishery-induced mortality. By better understanding the mechanisms affecting elasmobranch survival percentages in response to fisheries capture and by obtaining more accurate estimations of mortality caused by fishing pressures, it will be possible to develop more sustainable fisheries and make well-informed elasmobranch conservation decisions.

Many countries have enacted management plans which focus on returning captured elasmobranchs to the water if incidentally captured. From a management perspective, this is a highly effective strategy for species with low immediate mortality and low post-release mortality percentages. However, for elasmobranchs with high percentages of immediate survival and post-release mortality, a large portion of the catch may be captured dead or moribund. We estimate that the mean total discard mortality percentage of obligate ram-ventilating elasmobranchs is high in each gear type (Table 2) and these species are particularly prone to death when captured as by-catch. Shifting gear type or fishing location to minimize encounter rates with elasmobranch by-catch susceptible to fisheries-induced mortality may prove to be a more effective management strategy than one focused on returning these species to the water.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Classifications used to determine respiratory morphology for individual species.

Table S2. Immediate mortality percentages reported by species and fishing gear type used.

Table S3. Published results of post-release and total discard mortality studies on elasmobranchs.

Table S4. Comparisons between the results of the full model used and a reduced model with variable data points removed.

Table S5. Elasmobranch species classified as data-deficient by the IUCN that are likely to be obligate ram-ventilators.

