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Review

# Sharks, rays and abortion: The prevalence of capture-induced parturition in elasmobranchs

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ABSTRACT

The direct impacts of fishing on chondrichthyans (sharks, rays and chimeras) are well established. Here we review a largely unreported, often misinterpreted and poorly understood indirect impact of fishing on these animals — capture-induced parturition (either premature birth or abortion). Although direct mortality of discarded sharks and rays has been estimated, the prevalence of abortion/premature birth and subsequent generational mortality remains largely unstudied. We synthesize a diffuse body of literature to reveal that a conservative estimate of > 12% of live bearing elasmobranchs (n = 88 species) show capture-induced parturition. For those species with adequate data, we estimate capture-induced parturition events ranging from 2 to 85% of pregnant females (average 24%). To date, capture-induced parturition has only been observed in live-bearing species. We compile data on threat-levels, method of capture, reproductive mode and gestation extent of premature/aborted embryos. We also utilise social media to identify 41 social-media links depicting a capture-induced parturition event which provide supplementary visual evidence for the phenomenon. The mortality of embryos will have implications for elasmobranch populations, and there are limited options to deal with this problem. This review is the first to synthesize available data on capture-induced parturition in sharks and rays, and highlights an important ethical and management issue for fishers and managers deserving of much greater attention.

## 1. Introduction

Sharks, rays and their relatives (chondrichthyans; Table 1) are some of the slowest growing and oldest maturing vertebrate animals (Dulvy et al., 2014). They also exhibit some of the highest levels of maternal investment and longest gestation periods in the animal kingdom (Cortés, 2000; Dulvy et al., 2014). These combined life-history traits make them sensitive to overfishing and many population declines have been observed (e.g. Graham et al., 2001; Stobutzki et al., 2002; Cortés et al., 2007; Oliver et al., 2015). The direct effects of both targeted and incidental capture of chondrichthyans has been the focus of much directed research including numerous reviews (Stevens et al., 2000; Frisk et al., 2005; Worm et al., 2013; Dulvy et al., 2014; Oliver et al., 2015). Although direct fishing mortality is of concern, capture-induced abortion/parturition (Table 1) is a less obvious, but potentially pervasive effect on the reproductive potential of many sharks and rays. We define capture-induced parturition as any birthing event prompted by interaction with fishing gear. A capture-induced parturition event is either a premature birth or an abortion depending on the gestation extent of embryos (Table 1; Fig. 1).

### 1.1. Defining capture-induced parturition

Capture-induced parturition in sharks and rays is by no means a novel phenomenon; there are numerous anecdotal observations in the scientific literature, some of which date to > 200 years ago.

The phenomenon has so far attracted very little interest, other than sporadic references to the inconvenience it causes when measuring fecundity (e.g. Struthsaker, 1969; Ebert, 1984; Snelson et al., 1988). There seems to be a general lack of awareness among recreational fishers of the occurrence of capture-induced parturition in sharks and rays (see Table A.2). There is also a distinct lack of targeted research into the occurrence and cause of capture-induced parturition, making it difficult for managers to incorporate into by-catch management. Our

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**Table 1**
List of terms and definitions as referred to in this review.

| List of definitions | |
|---|---|
| Stress-induced parturition | The premature birthing of offspring stimulated by physiological processes which involve a response to a 'stressor' via complex pathways modulated by hormones. |
| Capture-induced parturition | The birthing of offspring prompted by interaction with fishing gear. The pathways stimulating birth are expected to vary and could be caused by interactions between physical trauma and physiological stress. |
| Premature birth | The parturition of pre-term offspring, which often have reduced fitness due to lack of development and smaller body size. |
| Abortion | The termination of a pregnancy by the expulsion of a foetus or embryo before it can survive outside the uterus. |
| Shark | Shark generally refers to those elasmobranchs with gill slits located laterally and includes all the nine orders of chondrichthyans that are not deemed skates, rays or chimeras: sawsharks (Pristiophoriformes), angel sharks (Squatiniformes), dogfish (Squaliformes), sixgilled sharks (Hexanchiformes), mackerel sharks (Lamniformes), ground sharks (Carcharhiniformes), carpetsharks (Orectolobiformes), bullhead sharks (Heterodontiformes) and bramble sharks (Echinorhiniformes). |
| Ray | Ray generally refers to the three orders of chondrichthyans that are not deemed sharks, skates or chimeras. All rays are live-bearing and have gill slits that are located ventrally: stingrays (Myliobatiformes), electric rays (Torpediniformes) and shovelnose rays/guitarfish (Rhinopristiformes). |
| Skate | Skate refers to all species in the order Rajiformes. All skates are egg-laying and have gill slits that are located ventrally. |
| Chimera | Chimera refers to all species in the order Chimaeriformes, a cartilaginous fish order that together with the elasmobranch orders makes up the chondrichthyan class of fishes. All chimeras are egg-laying and have gill slits that are located laterally. |

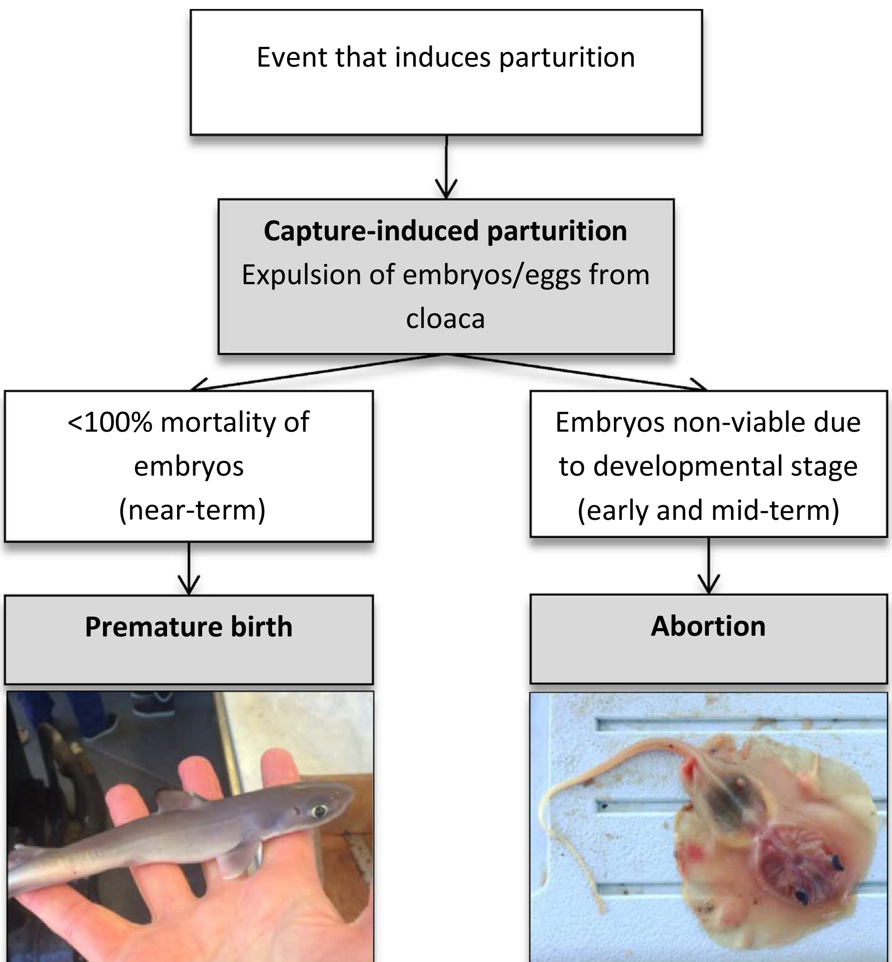


**Fig. 1.** Decision tree showing the terminology relating to capture-induced parturition used in this review. Left image shows a near-term spikey dogfish (*Squalus megalops*) of approximately 24 cm total length. Photographer: L. Fetterplace. Right image shows an early term Atlantic stingray (*Hypanus sabinus*) embryo that is notably pale. The yolk sac is not present but may have ruptured during parturition. Photographer: C. Collatos.

suspicion is that these casual reports, when viewed as a whole, indicate that capture-induced parturition is a common event with potential impacts on the reproductive capabilities of species. This may lead to effects on recruitment in shark and ray populations.

The earliest record of capture-induced parturition we have identified was by Risso (1810):

> "*A female of Squatina, of a considerable size, taken from our net, gave fifteen to twenty pups at the time where, due to lack of water, it was asphixed by the action of the atmosphere on its gills.*"

It is therefore surprising that 200 years later the phenomenon of capture-induced parturition remains unstudied and unquantified in any detail, other than sporadic observations and reports. Although it has been noted that fecundity in elasmobranchs is sometimes difficult to estimate because they abort their young on capture (Struthsaker, 1969), we are yet to develop a clear understanding of the frequency, specific cause, and impact of these "abortions". We know of no studies that have been specifically interested in capture-induced parturition beyond incidentally observing and recording it.

The phenomenon of capture-induced parturition in elasmobranchs

**Fig. 2.** Capture-induced parturition event in the spikey dogfish (*Squalus megalops*) caught via demersal trawl off eastern Tasmania, Australia. The head of the near-term pup can be seen protruding from the cloaca (top). The bottom photograph shows the same pup alongside the mother. Photographer: L. Fetterplace.

has been noted in the literature under a variety of terms, including 'abortion', 'capture-induced abortion', 'spontaneous abortion', 'slip', 'sudden parturition', 'dropping young' and 'premature birth'. Given that nothing is currently known about the survival of embryos after the event, 'abortion' may not correctly describe the process in all cases, given that some near-term offspring may survive. We propose that "capture-induced parturition" is the most suitable blanket term for the process, with capture-induced abortion most appropriate for cases where complete embryo mortality occurs (Fig. 1; Table 1). Importantly, until mortality estimates for these embryos are determined, application of the precautionary principle (Lauck et al., 1998) suggests that all capture-induced parturition events should be viewed as capture-induced abortions (i.e. all pups are assumed to die). We also propose that 'spontaneous abortion' is not an appropriate characterisation given that it ignores the fact that the parturition events are capture-induced, and may not be spontaneous.

To recognise a capture-induced parturition, premature pups (see Figs. 48 and 54 in Babel, 1966 for example photographs of the different gestation stages of *Urolophus halleri*) are visibly protruding from the cloaca or present on deck (Fig. 2; Table A.1). It is important to differentiate capture-induced embryos from captured young-of-the-year given that many fishing methods may mix embryos with small juveniles. For *U. halleri*, with a three-month gestation period, the yolk sac is almost fully absorbed approximately two weeks before birth (Babel, 1966), which offers a simple method to determine gestation extent. This time frame for yolk sac absorption may differ for species with longer gestation periods. An important consideration is that chondrichthyan embryos tend to acquire most species characteristics by the middle of the gestation period (Babel, 1966, Fig. 48), which could lead to them being mistakenly reported as full-term (Pratt and Casey, 1990) especially if there is no known size-at-birth for the species. Upon dissection, a distended uterus with broken uterine compartments can also indicate that a capture-induced parturition has occurred (Pratt and Casey, 1990), however, this method cannot exclude the possibility of a recent natural birth.

Stress appears to be a key contributing factor that induces parturition/abortion given that such births have been reported to occur following various methods of fishing, stranding (Williams et al., 2010) and possibly an unsuccessful predation event (Marshall and Bennett, 2010). Parturition has also been observed after administration of anaesthetic (Ferreira, 2013; Silbernagel and Yochem, 2016), injection of quinine (Rall and Zubrod, 1962), during an inter-uterine endoscopy (Carrier et al., 2003) and during a sonogram (Mollet et al., 2002). It remains unclear, however, whether it was these specific procedures or the stress on the animal that induced these parturitions. In fishery capture-induced parturition, common stress-inducing stimuli include physical trauma (e.g. harpoons, netting injuries) or asphyxiation (e.g. caught in mesh net, left on deck). The physical trauma and physiological stress caused by capture is likely to vary with fishing method and the sensitivity of the species involved (Dapp et al., 2015). The nature and magnitude of stress responses are species-specific, and linked to physiology as well as the form and intensity of the stressor (Skomal and Mandelman, 2012). We know that fishing can cause major stress to sharks and their relatives, however the species-specific thresholds that induce parturition remain undetermined.

Stress-induced parturition events do not appear to be isolated to capture. The fact that they can occur in nature means that the phenomenon may have adaptive significance. The earliest record of abortion in sharks and rays appears in the fossilised embryos of a Devonian chondrichthyan (*Delphyodontos dacriformes*), with a yolk sac still attached but lacking an adult nearby, dated 318 m.y.a. (Lund, 1980). There is further evidence of abortion occurring in the now extinct *Harpagofututor volsellorhinus* ~318 m.y.a. (Grogan and Lund, 2011). Stress-inducing stimuli that exist in nature may include stranding, predation attempts, toxic dinoflagellate blooms, thermal shock and hypoxia.

### 1.2. Sensitivity of chondrichthyans to fishing

Sharks, rays and their relatives share a number of life-history traits which make them particularly sensitive to overfishing. Bycatch, or incidental capture is a major concern for many of the approximately 1145 species of elasmobranchs (sharks, rays and skates) and 49 species of holocephalans (chimeras), which together comprise the chondrichthyes class of fishes (Oliver et al., 2015; Naylor and Davies, 2017). For species caught as bycatch that are commonly discarded, the impact of fishing is often assumed to be low if post-capture mortality is low (Oliver et al., 2015). This may not always be the case, with capture-induced parturition representing a potential source of generational mortality for discarded species. The low fecundity and low natural mortality of many sharks and rays leads to a close relationship between the number of pups produced and the size of the breeding population (Stevens et al., 2000). Due to a combination of slow growth rates and late maturation, overfished shark populations can take decades to recover (Stevens et al., 2000).

Even for well managed fisheries with monitored by-catch levels, we lack a definitive list of which species give birth on capture, and the frequency at which it occurs. In fisheries where the majority of shark, ray and chimera species are discarded (e.g. Henry and Lyle, 2003; Braccini et al., 2012) the process of capture-induced parturition has the potential to lead to mortality of recruits, even if the mature female survives the capture event. Although the individual survival of many discarded species may be high (Braccini et al., 2012), pregnant females that give birth during or after capture will lose some, if not all, of their pups for that reproductive cycle. With some elasmobranch species having gestation periods of 2 years or more (e.g. *Squalus acanthias*, Ford, 1921), an abortion event represents a major loss of maternal investment. Pregnant females of some species are known to aggregate seasonally in shallow, warm waters (e.g. *Triakis semifasciata*, Nosal et al., 2013), making them especially vulnerable to fisheries capture.

Capture-induced parturition is only expected to be problematic and potentially unmanaged when pregnant females are discarded alive rather than landed. Recording of species-specific ray and skate discards is notoriously poor on a global scale (Stevens et al., 2000). Shark discards, however, have undergone some assessment, with Worm et al. (2013) estimating a global discard amount totalling 1,135,000 t of sharks for

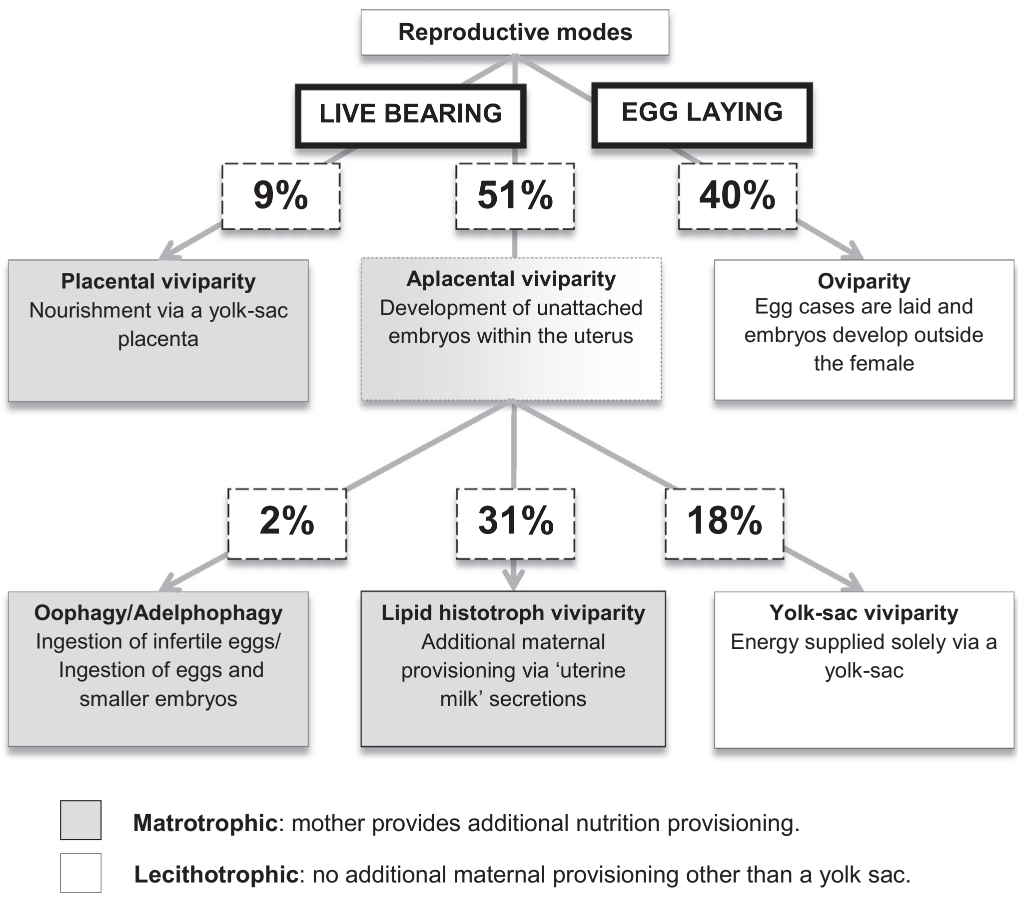


**Fig. 3.** Patterns of reproduction in chondrichthyan species with subdivisions by reproductive modes and maternal input. Percentages in each reproductive category are taken from Dulvy and Reynolds (1997).

the year 2000. Further, Worm et al. (2013) estimate that 80% of these discarded sharks were finned and subsequently died, while the remaining 227,000 t were released alive. Of these live discards, many that were pregnant had the potential to lose pups. If current and proposed management strategies for shark finning are implemented, such as banning finning at sea, the number of sharks discarded alive would likely increase, and so too would the potential for capture-induced parturition to impact these species. Recreational fishing also causes capture-induced parturition, and has the potential to affect shark and ray populations given the often high levels of catch and release for these species. For example, an estimated 81% of the 1,252,728 sharks and rays caught over a 12 month period by Australian recreational fishers were discarded (Henry and Lyle, 2003).

### 1.3. Reproductive modes and maternal provisioning in chondrichthyans

The different reproductive modes in chondrichthyans may influence the potential and impact of capture-induced parturitions. Sharks and their relatives can be subdivided into two main reproductive groups; live-bearing (viviparous ~700 species) and egg-laying (oviparous ~500) (Fig. 3). Although all sharks develop inside an egg case, the eggs of live-bearing species 'hatch' inside the uterus while egg-laying species hatch externally. An important distinction is that all live-bearers fall within Elasmobranchii. Elasmobranchs have also been categorised into two further modes of reproduction based on maternal provisioning. These two means of nutrient delivery are matrotrophy, where embryonic development is supported by additional maternal input of nutrients; and, lecithotrophy, where development is sustained wholly by a yolk-sac (Wourms, 1981) (Fig. 3).

To improve the general understanding of capture-induced parturition/abortion in chondrichthyan species, we present the first systematic review of the prevalence of the phenomenon in the reproductive literature on sharks and rays. To understand how prevalent capture-induced parturition is across chondrichthyan species, we have compiled a list of species that are known (or are inferred) to have experienced parturition once they have been captured (Adams, 2017). To help direct future research and conservation efforts, we assess whether some species groups have been reported to experience capture-induced parturition more or less frequently than expected by chance. From a subset of the papers identified in our literature search, we estimate the rate of capture-induced parturition for a number of elasmobranch species caught using a range of fishing methods. This rate represents an estimate of the percentage of pregnant females of a species that give birth on capture. This rate also provides the first assessment of the potential impact of capture-induced parturition on commonly discarded species. Additionally, we investigate whether reproductive mode affects the occurrence of capture-induced parturition. To assess whether the occurrence of abortion may correlate with increased extinction risk we test whether capture-induced parturition may correlate with higher IUCN threat levels. We briefly explore different fishing methods and how stress and subsequent pup mortality during capture may be reduced. The analysis incorporates data from a wide range of species and locations and therefore provides a worldwide synthesis of capture-induced parturition in chondrichthyans. We also use reports from social media to further assess parturition across sharks and rays in relation to recreational and commercial fishing. Videos which depict suspected induced parturition events provide anecdotal and supplementary evidence to scientists, and provide a novel source to document capture-induced parturition which is independent of the scientific literature and represents 'real world' occurrences of these events. Furthermore, we supplement this dataset with our own images documenting capture-induced parturition events during our own scientific investigations and compile a list of other such videos found on social media. Finally, we highlight areas for further research and provide recommendations for researchers and fishers to reduce the chance of causing stress and inducing parturition.

## 2. Methods

### 2.1. Literature search

In order to compile a list of species that exhibit capture-induced parturition/abortion we used structured literature searches. These searches were conducted using Google Scholar, Scopus and Web of Science. The Boolean (AND/OR) search terms used in Google Scholar consisted of:

Chondrichthyes AND abort and elasmobranch AND abort

These search terms were not applicable in Scopus and Web of Science as these two databases can only locate search terms in titles and abstracts, unlike Google Scholar, which searches whole texts. Given the lack of targeted literature it was rare for 'abortion' to be mentioned in either the title or abstract. We deemed an alternative search strategy was therefore necessary for Scopus and Web of Science.

The modified Boolean (AND/OR) search terms used in subsequent Web of Science and Scopus searches consisted of the following:

Stingray* OR ray OR shark OR skate OR wedgefish OR guitarfish OR batoid* OR elasmobranch* OR chondrichthy* AND reproduc* OR fecundity

After nuisance terms were removed via term filters and duplicates were accounted for, these searches identified 314 texts in Google Scholar, 168 texts in Web of Science, and 168 texts in Scopus. The results of these searches were examined for any references to the abortion of embryos. Any relevant references cited in these papers that were not identified in the database searches were also included. All relevant references were examined for the species, capture method, gestation stage of the embryos, and reproductive mode.

Species were categorised into those in which capture-induced parturition was directly observed ($n = 139$ instances) or those in which we inferred capture-induced parturition ($n = 92$ instances). These observed and inferred capture-induced parturitions included multiple reports of individual species. Observations of capture-induced parturition were categorised by the presence of eggs or embryos either in nets, on the deck of fishing vessels or seen being expelled from pregnant females. Inferences of capture-induced parturition were usually based on comments from the author, noting empty and distended uteri after capture, or reference to abortion in related species.

The threat level of each species known to experience capture-induced parturition was determined using the search function in the IUCN Redlist of Threatened Species (IUCN, 2016). If species were not listed on the IUCN Redlist they were assigned a separate category of Not Evaluated. The IUCN Redlist currently lists 1095 species, however Naylor and Davies (2017) lists 1194 species. This review relies on the Chondrichthyan Tree of Life (Naylor and Davies, 2017) for species classification and numbers of shark and ray species.

### 2.2. Calculating estimates of the frequency of capture-induced parturition

To estimate the rate of capture-induced parturition, one of two methods was used depending on the data available. Twenty six studies included adequate information to estimate capture-induced parturition rates. Each estimate provides a rate of parturition for a single species within a study for the reported fishing method. The criteria for the inclusion of a study required reporting of data that satisfied both the numerator and denominator of either of the following two equations:

1) The number of females reported to abort compared to the total number of gravid females in the study:

$$\frac{\textit{Number of females that showed induced parturition}}{\textit{Total number of gravid females (pregnant} + \textit{'induced')}}$$

Fourteen observations of a single gravid female showing capture-induced parturition were excluded (see Adams, 2017) as these estimates would inflate the abortion frequency (i.e. 100%).

2) The proportion of embryos resulting from capture-induced parturition (usually on deck) was compared to the total number of embryos reported in the study (in uteri embryos were determined via dissection):

$$\frac{\textit{Number of embryos from induced parturition (on deck)}}{\textit{Total number of embryos (in uteri} + \textit{on deck)}}$$

If either the numerator or denominator of either formula could not be satisfied then the study could not be included in the estimate of the capture-induced parturition frequency. All four categories were not reported for any study, presumably because once embryos are on deck it is impossible to identify which female they came from. This means the number of females that showed induced parturition cannot be known once embryos are on deck or free in the net. Both methods described would underestimate the true capture-induced parturition rate due to unobserved capture-induced parturition events leading to a loss of embryos before landing or after release. Eggs resulting from capture-induced parturition were not included in our estimates.

### 2.3. Categorising capture-induced parturition events by reproductive mode, embryo's developmental stage and method of capture

To determine if reproductive mode may influence the occurrence of capture-induced parturition, reports were classified into the following categories (Fig. 3):

1) placental viviparous
2) oviparous
3) aplacental viviparous (yolk-sac)
4) aplacental viviparous (histotroph)
5) aplacental viviparous (oophagy/adelphophagy)

Reproductive mode was determined from the literature using either the original literature search reference, the IUCN threat assessment (IUCN, 2016), or from Compagno (1990). To gain an understanding of the range of gestation extents of embryos, the developmental stage was noted as described in the paper in which capture-induced parturition was reported. Importantly, although eggs were aborted, these came from live-birthing (viviparous) species and were presumed to be very early stage or unfertilized.

The fishing method/s used in each study were classified into 12 categories based on the studies in which capture-induced parturition was observed. These 12 categories were artisanal fishing, gill-nets, harpoon, hook-and-line, longlines, net (unspecified), seine-net, gunshot, tangle net, trawling, multiple and unspecified. Some studies reported outcomes from multiple fishing methods; therefore, the method being used when capture-induced parturition was observed was unable to be determined.

### 2.4. Compiling anecdotal observations of capture-induced parturition

In order to supplement parturition events documented in the literature, videos of capture-induced parturition events where compiled via Youtube, Instagram and Facebook. We used variations of the search terms "ray birth" and "shark birth" and also the related video algorithms provided by these networks. Only videos with live females actively aborting were included. The number of views, location and suspected species were also recorded. Confident species identification was not possible in many cases due to the quality of the video, the lack of adequate viewing angles and limited geographical information.

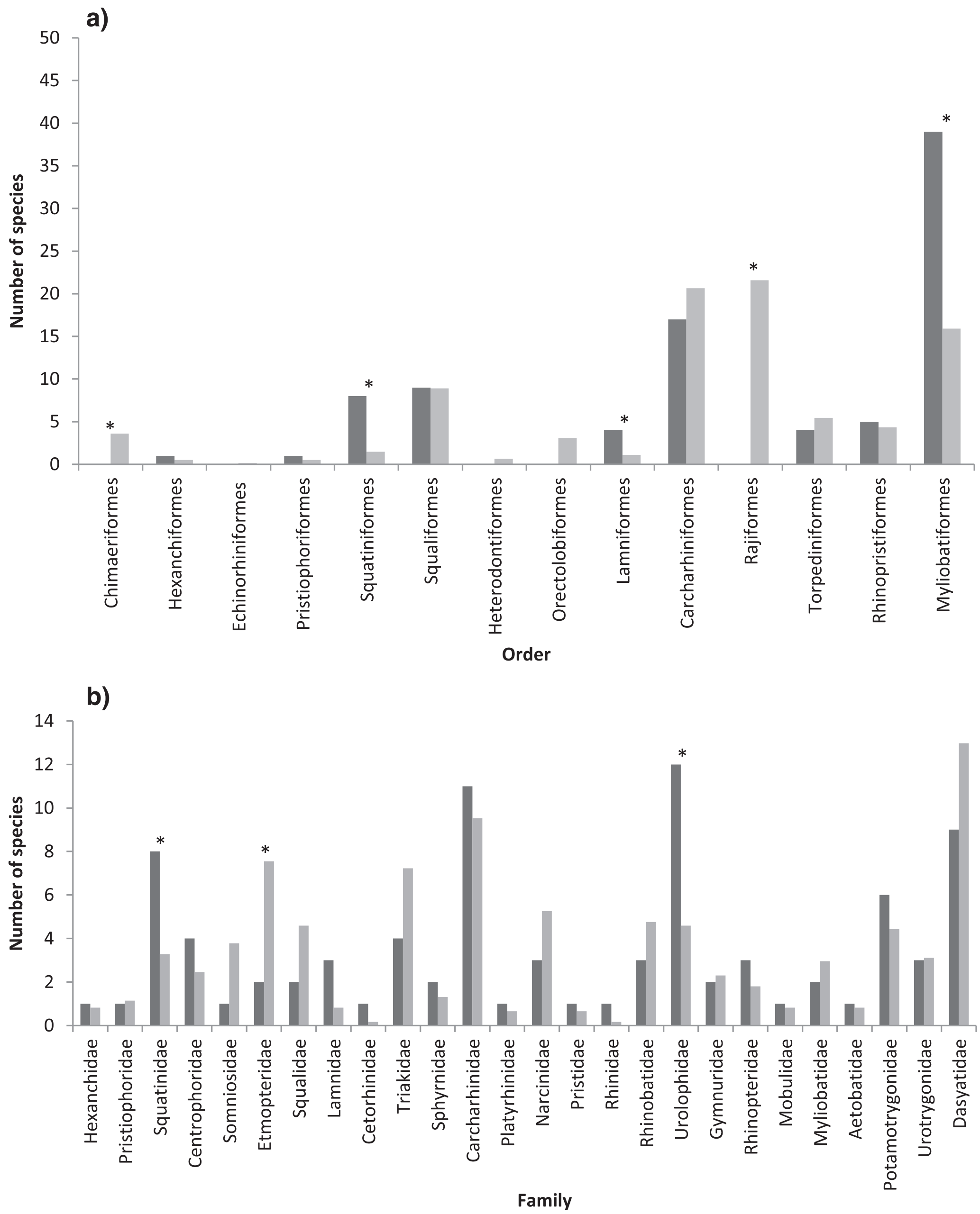


**Fig. 4.** a) Order level classification of chondrichthyans comparing the number of species observed to experience (black bars) and expected to experience capture- induced parturition if it occurs independent of order classification (grey bars). Expected frequencies are calculated using the number of species in each order (from Naylor and Davies, 2017) compared to the total number of chondrichthyans (n = 1194). Significant differences ($\alpha < 0.05$) are denoted by *.
b) Family level classification of elasmobranchs for the 26 families which contain species observed to experience capture-induced parturition. The number of species observed (black bars) is compared to the number of species expected (grey bars) if capture-induced parturition were independent of species classification. Expected frequencies are calculated using the number of species in each family (from Naylor and Davies, 2017) compared to the total number of species in families exhibiting capture-induced parturition (n = 536). Significant differences ($\alpha < 0.05$) are denoted by *.

### *2.5. Statistical analyses*

To identify species groups with higher than expected observations of parturition, and thus those species/taxa that might be particularly vulnerable, we calculated the number of species expected in each group if we assume capture-induced parturition is equally likely to be reported across all species groups. In order to generate an expected value for a given category (e.g. order, family, IUCN category, reproductive mode) it was assumed that all taxa had an equal probability of being drawn. If a subset of shark or ray species were drawn randomly from all chondrichthyans (in our case a subset of 88), the total number of species in each category can be used to predict the number expected in the smaller subset. For example, the Order Myliobatiformes contains 217 of the 1194 extant chondrichthyan species i.e. 18% (Naylor and Davies, 2017). Using this ratio we expect 16 from a random draw of 88 chondrichthyans will be Myliobatiformes i.e. our expected value. These expected values were compared to the observed number of species showing capture-induced parturition in each category by using exact tests of goodness-of-fit with a Monte Carlo approach (ntrial = 1e + 7, atOnce = 1e + 6). For calculating expected frequencies, we assumed that all species were equally likely to experience capture-induced parturition due to fishing. This requires the assumption that all species within taxa were equally exposed to fishing. Those species groups identified by such analyses provide a clear starting point for targeted research; however the cause of such patterns is open to interpretation and could be the result of innate vulnerability or sampling bias. All chondrichthyan species (species = 1194) were used to calculate the expected distribution of capture-induced parturition based on the number of species in each order (from the Chondrichthyan Tree of Life). For the family analysis, only families with at least one species showing capture-induced parturition were used (species = 535). To determine whether those species which show capture-induced parturition experience the same threat levels as other elasmobranchs, we also used an exact test of goodness-of-fit using a Monte Carlo approach (ntrial = 1e + 7, atOnce = 1e + 6) with the expected distribution calculated from the IUCN red list (species = 851 see Table A.5). Finally, we used an exact test to determine whether capture-induced parturition was more or less frequent in each of the four live-bearing modes of reproduction.

Those categories driving any differences indicated by the exact tests were determined using post hoc tests. Analyses were performed in R 2.14.2 (R Core Team, 2016) using the EMT package (Menzel, 2013) multinomial.test() function for Goodness-of-Fit Test for Discrete Multivariate data using methods from Mangiafico (2016). Post hoc tests were conducted using the binom.test() function using methods specified by Mangiafico (2015). Chi square goodness-of-fit tests were not used due to the number of expected values below 5.

## 3. Results and discussion

### 3.1. The prevalence of capture-induced parturition in the scientific literature

Our literature search collected 139 reports of 88 species from 26 families directly observed to exhibit capture-induced parturition (see Adams, 2017 for the full species list). Capture-induced parturition was only observed in live-birthing (viviparous) species and, to date, does not appear to have been reported in the scientific literature for egg-laying (oviparous) species. We note that 12% (n = 88 species) of live-bearing elasmobranch species have been observed to show capture-induced parturition. If the additional species which have been inferred in the literature to exhibit capture-induced parturition are confirmed, the prevalence of capture-induced parturition could increase to 18% (n = 127 species) of live-bearing elasmobranchs.

Capture-induced parturition was reported more frequently than expected in the Orders: Myliobatiformes (stingrays; observed: 39/88 expected: 16/88, $p < 0.001$), Lamniformes (mackerel sharks; observed: 4/88 expected: 1/88, $p = 0.018$) and Squatiniformes (angel sharks; observed: 8/88 expected: 1/88, $p < 0.001$) (Fig. 4a). Capture-induced parturition was reported less frequently than expected for the Orders: Rajiformes (skates; observed: 0/88 expected: 22/88, $p < 0.001$) and Chimaeriformes (chimeras; observed: 0/88 expected: 4/88, $p = 0.035$) presumably because all species in these orders are egg-laying.

Family level analysis showed capture-induced parturition to be reported more frequently than expected in the Families: Urolophidae (stingarees; observed: 12/88 expected: 5/88, $p = 0.004$), and Squatinidae (angel sharks; observed: 8/88 expected: 3/88, $p = 0.011$) (Fig. 4b). Importantly, angel sharks are the second most threatened family of chondrichthyans after sawfishes (Dulvy et al., 2014). Interestingly, in the Family Etmopteridae (lantern sharks) capture-induced parturition was reported less frequent than expected (observed: 1/88 expected: 6/88, $p = 0.024$). We can only speculate that this may be due to the majority species in this deep-water family being poorly-known and rarely encountered (Kyne et al., 2007).

Whether these groups experience capture-induced parturition more commonly due to shared traits or whether the induced parturition occurrence is an artefact of sampling bias requires further analysis. The IUCN (2016) red list shows only 11% of Urolophidae and 25% of Squatinidae are Data Deficient compared to 51.8% of all skates and rays (Dulvy et al., 2014). This may indicate that these two families are relatively well studied and the high number of observed species experiencing capture-induced parturition is an artefact of sampling effort for these two families. It is indeed possible that these two families have received greater attention regarding capture-induced parturition. This is indicated by the fact that Osaer et al. (2015) give references to all 8 species of Squatinidae known to experience capture-induced parturition. For Urolophidae, 9 of the 12 reports of capture-induced parturition come from papers where White or Trinnie are either a lead or a co-author. This may indicate that these two species groups have experienced a form of bias whereby one observation has led to an apparent increase in capture-induced parturition being reported. Alternatively, Squatinidae (angel sharks) are known to exhibit cloacal gestation whereby embryos complete their development within a uterine-cloacal chamber, which is open to the exterior via the cloacal vent (Sunyem and Vooren, 1997). This form of gestation may contribute to the apparent increased occurrence of capture-induced parturition in this family (Sunyem and Vooren, 1997) and deserves further research.

Given that parturition was not isolated to capture (see Williams et al., 2010; Marshall and Bennett, 2010) we suggest that stress-induced parturition may have adaptive significance. We propose two hypotheses for the occurrence of this phenomenon in chondrichthyans:

1) The self-sacrifice hypothesis; whereby a pregnant female is stranded by wave action or a retreating tide and gives birth to increase the chances of survival of her pups and ensure continuation of her genes. Induced parturition due to stranding has only been documented in the literature for *Hexanchus griseus* (Williams et al., 2010).

2) The predation/self-preservation hypothesis; a pregnant female when stressed gives birth to facilitate her escape and potentially the survival of the remainder of her litter. For example, stress-induced parturition due to a predation attempt has been inferred for *Manta alfredi* (Marshall and Bennett, 2010). As a terrestrial comparison, female kangaroos have the tendency to drop their pouch-young if they are stressed by a predator (Ealey, 1963), or during capture and handling (NHMRC, 2014). Low (1978) theorises that a female who deliberately abandons her offspring is more likely to escape predation due to the loss of encumbrance and the diversion created by the abandoned young.

### 3.2. The frequency of capture-induced parturition events

The average capture-induced parturition frequency across 26 studies, covering 24 species, was 24% (Table 2). This indicates that where data are available, ~2 in 10 gravid females across a subset of species showed capture-induced parturition. The rate of parturition is, however, quite variable amoung species (Table 2); it ranged from 2% of embryos being induced in *Carcharhinus brevipinna* (Capapé et al., 2003) and *Galeocerdo cuvier* (Jaquemet et al., 2013) to 85% of females releasing embryos on capture for *Pteroplatytrygon violacea* (Mollet, 2002). Given this variability, the induced parturition rate is likely to be highly species specific; however there are currently insufficient data to support reliable conclusions given the variation in fishing methods used across these studies.

An important consideration in estimating the frequency of capture-induced parturition is the time of year when captured. For example, we have observed two species experiencing capture-induced parturition in the same trawl; one species released near-term pups (premature birth) and the other species released mid-term embryos (abortion) (authors', pers. obs.). This is indicative of the importance of reproductive seasonality determining the potential impact of a capture-induced parturition based on the extent of gestation. Future estimates of the frequency of capture-induced parturition should attempt to factor in the reproductive periodicity of different species to provide a temporal estimate that may inform managers when considering temporal closures.

### 3.3. Correlates of capture-induced parturition

#### 3.3.1. IUCN threat levels

The occurrence of capture-induced parturition does not appear to correlate with a heightened threat of extinction in elasmobranch species. There are, however, considerably fewer species reported than expected in the Data Deficient (DD) (observed: 17/88 expected: 33/88, $p < 0.001$) category (Fig. 5). This is concerning since the majority of chondrichthyans are currently DD (n = 475; IUCN, 2016). This means that they have not been studied in great detail, and extrapolation points to a potentially large proportion of the ~700 live-bearing species exhibiting capture-induced parturition in response to fishing. During the assessment of these species, we would encourage publication of observations of any species which show capture-induced parturition, and that an estimation of the frequency be included if possible. Capture-induced parturition was observed more frequently (20/88) than

**Table 2**
The frequency of capture-induced parturition calculated for 26 species from a variety of fishing methods.

| Common name | Species | Capture-induced event | Total number of gravid females or embryos | Frequency (%) | Fishing method | Author/s |
|---|---|---|---|---|---|---|
| Pelagic stingray | *Pteroplatytrygon violacea* | 41 capture-induced parturitions | 48 gravid females | 85 | Longlines | Mollet, 2002 |
| Ornate angel shark | *Squatina tergocellata* | 32 capture-induced embryos | 50 total embryos | 64 | Trawling | Bridge et al., 1998 |
| Common stingray | *Dasyatis pastinaca* | 27 capture-induced parturitions | 45 gravid females | 60 | Multiple | Saadaoui et al., 2015 |
| Thorny stingray | *Dasyatis centroura* | 3 capture-induced parturitions | 5 gravid females | 60 | Trawling | Struthsaker, 1969 |
| Scaly whipray | *Brevitrygon imbricata* | 1 capture-induced parturition | 2 gravid females | 50 | Longlines | Henderson and Reeve, 2011 |
| Pelagic stingray | *Pteroplatytrygon violacea* | 2 capture-induced parturitions | 5 gravid females | 40 | Hook-and-line | Siqueira and Sant'Anna, 2007 |
| Banded stingaree | *Urolophus cruciatus* | 51 capture-induced embryos | 145 total embryos | 35 | Multiple | Trinnie, 2013 |
| Venezuela round stingray | *Urotrygon venezuelae* | 10 capture-induced parturitions | 35 gravid females | 29 | Seine-net | Acevedo et al., 2015 |
| Roger's round ray | *Urotrygon rogersi* | 113 capture-induced embryos | 582 total embryos | 19 | Trawling | Mejía-Falla et al., 2012 |
| Spotted stingaree | *Urolophus paucimaculatus* | 106 capture-induced embryos | 553 total embryos | 19 | Multiple | Trinnie, 2013 |
| Blue shark | *Prionace glauca* | 6 capture-induced parturitions | 37 gravid females | 16 | Longlines | Tavares et al., 2012 |
| Finetooth shark | *Carcharhinus isodon* | 2 capture-induced parturitions | 13 gravid females | 15 | Multiple | Castro, 1993 |
| Blacktip shark | *Carcharhinus limbatus* | 6 capture-induced embryos | 40 total embryos | 15 | Gill-net | Capapé et al., 2004 |
| Dusky smooth-hound | *Mustelus canis* | 2 capture-induced parturitions | 15 gravid females | 13 | Longlines | Zagaglia et al., 2011 |
| Blue shark | *Prionace glauca* | 2 capture-induced parturitions | 15 gravid females | 13 | Longlines | Hazin et al., 1994 |
| Sawback angelshark | *Squatina aculeata* | 1 capture-induced parturitions | 8 gravid females | 13 | Multiple | Capapé et al., 2005 |
| Sandyback stingaree | *Urolophus bucculentus* | 15 capture-induced embryos | 128 total embryos | 12 | Multiple | Trinnie et al., 2012 |
| Birdbeak dogfish | *Deania calcea* | 2 capture-induced parturitions | 18 gravid females | 11 | Multiple | Irvine et al., 2012 |
| Bluespotted stingray | *Neotrygon kuhlii* | 1 capture-induced embryo | 10 total embryos | 10 | Multiple | Pierce, 2009 |
| Brown guitarfish | *Rhinobatos schlegelii* | 1 capture-induced parturition | 10 gravid females | 10 | Multiple | Schluessel et al., 2015 |
| Eastern shovelnose stingaree | *Trygonoptera imitata* | 9 capture-induced embryos | 115 total embryos | 8 | Multiple | Trinnie et al., 2009 |
| Greenback stingaree | *Urolophus viridis* | 6 capture-induced embryos | 83 total embryos | 7 | Multiple | Trinnie et al., 2015 |
| Round stingray | *Urobatis halleri* | 1 capture-induced parturition | 22 gravid females | 5 | Seine-net | Jirik and Lowe, 2012 |
| Sandbar shark | *Carcharhinus plumbeus* | 2 capture-induced embryos | 46 total embryos | 4 | Gill-net | Cliff et al., 1988 |
| Tiger shark | *Galeocerdo cuvier* | 1 capture-induced embryo | 43 total embryos | 2 | Unspecified | Jaquemet et al., 2013 |
| Spinner shark | *Carcharhinus brevipinna* | 2 capture-induced embryos | 88 total embryos | 2 | Multiple | Capapé et al., 2003 |

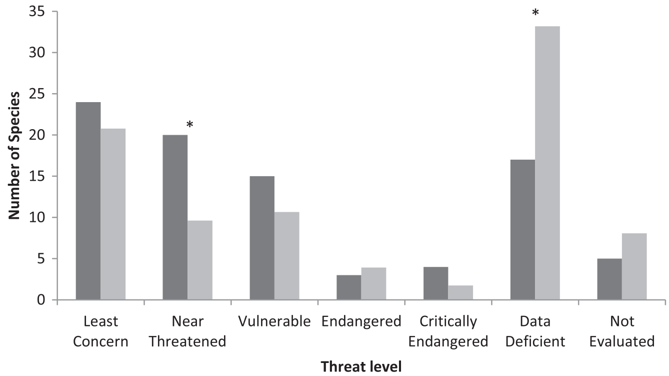


**Fig. 5.** The number of chondrichthyan species in each IUCN category for elasmobranchs that experience capture-induced parturition (black bars, n = 88 species) compared to the distribution expected calculated from all 851 elasmobranchs that are not classified as either skates or chimeras (grey bars). See Appendix A Table A.5 for the number of species in each IUCN category. Significant differences are denoted by *.

expected (10/88) for species in the Near Threatened category ($p = 0.002$, Fig. 5). Although induced parturition does not appear to correlate with higher threat levels, there are 7 species known to exhibit capture-induced parturition that are either Critically Endangered or Endangered (Table 3).

### 3.3.2. *Fishing methods*

The most common capture method associated with inducing parturition was trawling, followed by longlines and gill-nets (Table 4). This difference may be due to a preference for the capture method used in the research, rather than induced parturition rate being influenced directly by fishing method. Another explanation for the greater rate of capture-induced parturition in trawl nets may be that parturition may be less likely observed when using methods such as gill nets or longlines since the loss of pups can occur at any time during the fishing process and neonates are not retained by these fishing techniques. Interestingly, it appears that more parturition events have been observed for rays than sharks (Table 4), and this is likely to be indicative of biases in catch composition for fishing methods. Globally, pelagic longline fisheries have the largest total annual shark bycatch, and deep-sea and coastal trawl fisheries have the largest total annual ray bycatch (Oliver et al., 2015). Two estimates for the frequency of capture-induced parturition caused by the same method (longlines) for *Prionace glauca* showed a discrepancy of just 3% (Table 2). On the other hand, estimates for both longlines and hook-and-line for *Pteroplatytrygon violacea* showed a discrepancy of 45% (Table 2). This provides some measure of the level of consistency of estimates within and across fishing methods and points to fishing method having some influence on the rate of capture-induced parturition. Further study is warranted to determine the extent to which fishing methods may influence the occurrence and rate of capture-induced parturition.

Capture-induced parturition may occur at any time during the fishing process but is most often observed as animals are brought onto deck. Observation of capture-induced parturition prior to animals being brought on deck may be possible using gear mounted cameras. In addition, capture-induced parturition may be inferred from empty and distended uteri on capture, but would likely be an overestimate as some females may have recently given birth naturally. Parturition would be likely to be easiest to observe using capture techniques where the animal is hauled on deck relatively quickly and/or retained within a net. The mechanism causing parturition could be driven by interactions between a number of factors including oxygen deprivation, physical pressure due to the weight of other fish, lack of a support medium due to being removed from the water and stress caused by restraint or physical injury.

**Table 4**
The percentage of capture-induced parturitions observed with each fishing method differentiated into sharks and rays (n = 139 observations from 88 species).

| Fishing method | Rays (%) | Sharks (%) | Total (%) |
|---|---|---|---|
| Artisanal fishing | 0.7 | 0 | 0.7 |
| Harpoon | 0.7 | 0 | 0.7 |
| Net (unspecified) | 0 | 0.7 | 0.7 |
| Gunshot | 0 | 0.7 | 0.7 |
| Tangle net | 0.7 | 0 | 0.7 |
| Hook-and-line | 1.4 | 2.2 | 3.6 |
| Seine-net | 3.6 | 0 | 3.6 |
| Gill-nets | 3.6 | 8.7 | 11.6 |
| Longlines | 5.1 | 7.2 | 12.3 |
| Trawling | 12.3 | 4.3 | 16.7 |
| Unknown or unspecified | 8 | 11.6 | 19.6 |
| Multiple | 18.1 | 10.1 | 28.3 |
| Total | 54.2 | 45.5 | 99.7 |

### 3.3.3. *Reproductive mode*

A major finding of this review is that the occurrence of capture-induced parturition is currently limited to live-bearing species, and there is no evidence that egg layers (skates, chimeras and some shark species) experience this condition. Within live-bearers, reproductive mode does not appear to influence the occurrence of capture-induced parturition. The proportion of species with capture-induced parturition was no different to that which would be expected if the 88 species were drawn randomly from all live-bearing species ($p = 0.640$) (Fig. 6).

The consequence of capture-induced parturition for different reproductive modes is likely to differ for both the mother and the offspring. In terms of maternal input, matrotrophic viviparity through histotrophic uterine milk enables the female to gestate multiple, large offspring due to additional nutrient input (Grogan and Lund, 2011). They are likely to grow faster and have a greater birth-size than those supported through lecithotrophy because they are not limited to yolk sac nutrition (Grogan and Lund, 2011). This means that for matrotrophic species an abortion event is costlier to the female due to higher levels of maternal nutrient investment. On the other hand, matrotrophic offspring may be more likely to survive a capture-induced parturition at later stages of gestation due to their larger size.

Although observations of capture-induced parturition are currently

**Table 3**
Species listed as endangered or critically endangered on the IUCN red-list that are known to exhibit capture-induced parturition.

| Common name | Species | IUCN category | Author/s |
|---|---|---|---|
| Largetooth sawfish | *Pristis pristis* | Critically endangered | Marden, 1944 |
| Sawback angel shark | *Squatina aculeata* | Critically endangered | Capapé et al., 2005 |
| Angel shark | *Squatina squatina* | Critically endangered | Risso, 1810 |
| Caribbean electric ray | *Narcine bancroftii* | Critically endangered[a] | Carvalho et al., 2007 |
| Scalloped hammerhead shark | *Sphyrna lewini* | Endangered | Clarke, 1971 |
| Argentine angel shark | *Squatina argentina* | Endangered | Cousseau, 1973 |
| Coastal stingaree | *Urolophus orarius* | Endangered | Baker et al., 2008 |

[a] May no longer warrant this level of extinction risk; see Carlson et al. (2017).

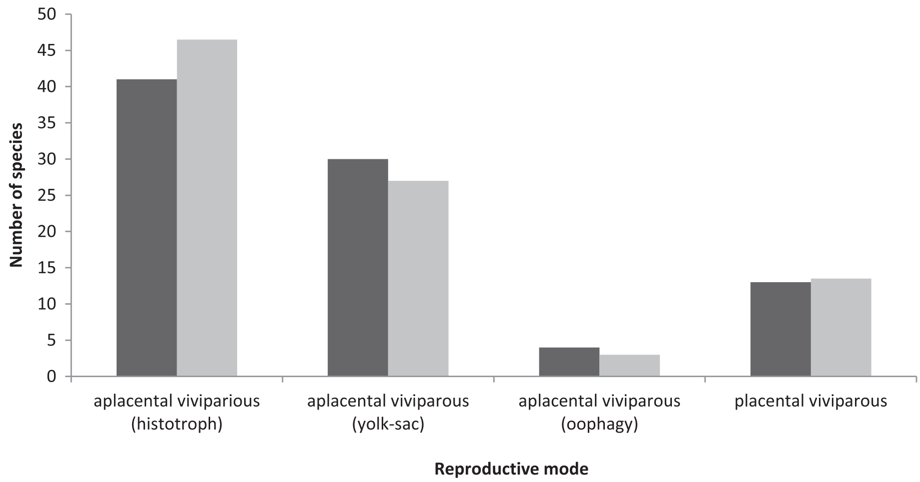


**Fig. 6.** The observed number of live-bearing species known to exhibit capture-induced parturition (black bars, n = 88 species) based on maternal provisioning compared to the number expected in each category calculated from the frequency of different reproductive modes of all live-bearing elasmobranchs (grey bars, estimated from Dulvy and Reynolds, 1997).

limited to live bearing species, the possibility of such a response in egg-laying species remains. Three of the species "inferred" to show capture-induced parturition are egg-laying (see Adams, 2017). Port Jackson sharks (*Heterodontus portusjacksoni*) have also been observed to lay their eggs when handled (authors' pers. obs.). It is debatable whether laying in response to capture could be considered abortion in egg laying species, as the eggs are self- sustaining (Musick and Ellis, 2005). The majority of egg layers are sequential bearers with one egg deposited at a time from each oviduct (Musick and Ellis, 2005), and tens to hundreds of eggs may be deposited over a season (Musick and Ellis, 2005). Also, eggs are laid frequently, with some species such as *Raja clavata* laying every 24 h (Holden, 1975). Therefore, if an egg is released due to capture, it is likely that the egg would have been laid naturally in the near future anyway. One potential issue with releasing eggs on capture is that species such as catsharks (Fa. Scyliorhinidae) secure their egg cases to algae or rock (Smith and Griffiths, 1997). Such eggs may be expected to have a high mortality rate if released on deck and returned loose to the water. Additionally, in oviparous species with 'multiple oviparity', embryos in the egg cases begin to develop inside the mother's body. Usually an egg case is laid when the embryo in it grows to a certain length (Nakaya, 1975). In these species capture-induced laying could result in a reduction of the period inside the mothers' body and therefore an increased rate of mortality.

### 3.3.4. Gestation stage

The gestation extent of capture-induced embryos ranged from early-stage eggs to fully-formed near-term pups. Eggs were aborted by ten live-bearing species in total with the remaining species giving birth to early, mid and near-term embryos (Adams, 2017). No early or mid-term embryos were reported to be birthed by placental viviparous species, possibly because their placental connection may physically reduce the chance of capture-induced parturition. This placental connection, however, only forms part way through gestation; for example, embryos of the smooth dogfish (*Mustelus canis*) develop a yolk-sac placenta about three months into their 10 to 11 month gestation period (Price and Daiber, 1967). Before the placental connection forms, the free-floating embryo could still be capture-induced. At this stage, very little is known about embryo survival, however Charvet-Almeida et al. (2005) observed that the embryos of freshwater stingrays (*Potamotrygon* spp.) hardly ever survived after capture-induced parturition regardless of their developmental stage. Whether this can be considered a rule for this group of species, and for live-bearing elasmobranchs in general, remains undetermined. At least ten live birthing species are also known to have aborted eggs upon capture. Due to their early developmental stage, these would have had no chance of survival. Future studies could assess the post-capture survival of females and capture-induced pups to determine the chance of survival for near-term embryos. The swimming speed of neonates and their feeding ability could also be affected by a premature parturition event and any influence on long-term survivorship and fitness of embryos should be investigated. A lack of standardised terminology was noted when reporting the gestation extent of capture-induced embryos. Future studies should report the presence and size of yolk-sacks and whether embryos appear early, mid or near-term.

### 3.4. Social media as a source of useful information and misinformation

In total, 40 videos and one image series were identified on social media sites showing capture-induced parturition in sharks and rays (Table A.1; Table A.2; Table A.3; Table A.4). In many cases, these videos provide visual documentation that confirm the observations of capture-induced parturition in the literature. Species identification was not possible in many cases as the geographic location was not known and the quality of the footage poor. The majority (61%) of the species in the videos were caught by recreational fishers using hook-and-line, with the remainder caught by researchers using longlines (3%) or strike nets (3%) or with unknown fishing methods (33%). In terms of taxonomy, 12% of the videos show sharks and 88% batoids which may represent a bias in capture not mirrored in the observations identified in the scientific literature. We presume that the uploaders of these videos were unaware of the true nature of the event. This is supported by the optimistic titles of many of these videos: "Man catches stingray while it's giving birth..unhooked and realaesed [sic]…!" (> 1.7 million views); "Caught On Camera: fisherman helps stingray give birth" (> 19 million views and with the hashtag "happybirthray") (Table A.2). The fishers are often seen to intervene and remove the offspring, seemingly thinking they are assisting the animal. Such representation feeds into the narrative that these births are a spontaneous occurrence rather than an event which is caused by capture.

Shark species identifiable in the videos include a lemon shark (*Negaprion brevirostris*) and a longfin mako (*Isurus paucus*) which may have been dead at the time of the video, but in the literature has been observed giving birth after capture (Gilmore, 1983). The video of the lemon shark provides evidence that this species gives birth in response to stress. Notably the individual in the video was tagged with an internal acoustic transmitter prior to release. Nine readily identifiable ray species exhibit capture-induced parturition on camera (Table A.1). These include four additional species not observed in the literature: the critically endangered smalltooth sawfish (*Pristis pectinata*), the endangered giant freshwater stingray (*Urogymnus polylepis*), the lesser guitarfish (*Rhinobatos annulatus*) and the white-spotted whipray (*Maculabatis gerrardi*). Videos confirming capture-induced parturition in ray species already observed in the literature include the white-spotted eagle ray (*Aetobatus narinari*), the estuary stingray (*Hemitrygon* *fluviorum*), the bat ray (*Myliobatis californica*), the Atlantic stingray (*Hypanus sabinus*) and the bluntnose stingray (*Hypanus say*). Interestingly, photos from Lüderitz Marine Research show a likely abortion event caused by stranding in the lesser guitarfish (*R. annulatus*). If those four additional ray species (*P. pectinata, U. polylepis, R. annulatus* and *M. gerrardi*) and one additional shark species (*N. brevirostris*) found via social media are included in our estimate of capture-induced parturition, it brings the total species count to 93 and the endangered species count to 9.

### 3.5. Reducing the likelihood of capture-induced parturition

Until we understand the specific mechanisms that induce parturition on capture, general techniques to reduce stress should be encouraged for scientists and fishers. Cooke and Suski (2005) identify certain handling techniques which can significantly reduce stress and post-release mortality in fish. These general techniques which can be adopted to reduce the impact of fishing are (1) minimising angling duration, (2) minimising air exposure, (3) avoiding angling during extremes in water temperature, (4) use of barbless hooks and artificial lures/flies, and (5) avoiding angling fish during reproductive periods (Cooke and Suski, 2005). For researchers conducting studies on sharks and rays listed above (and more broadly) we would recommend conducting procedures without removing the animal from the water, especially for larger shark and ray species. For endangered species, it would seem logical to avoid sampling in periods or areas where females are pregnant, or use selective fishing techniques so pregnant females can be avoided. We need research to quantitatively assess optimal approaches to reduce capture-induced parturition. Further, a better understanding of the mechanisms of parturition should provide clear guidance on mitigating capture-induced parturition; however, measures outlined above appear to be logical first steps.

## 4. Management strategies, recommendations and concluding remarks

The above synthesis demonstrates the prevalence of capture-induced parturition by live-bearing elasmobranchs in response to various methods of capture. Although capture-induced parturition does not appear to correlate with higher threat levels, it represents a potentially threatening process that is rarely considered within population or fisheries models and threat assessments. This is especially telling as species with high rates of post-release survival are currently considered to be largely unaffected, despite potentially losing considerable reproductive potential for that cycle (the whole reproductive output for up to two years for some species). It is possible that the condition may affect recruitment for a substantial proportion of live-bearing sharks and rays. Clearly, immediate research is required to determine the magnitude of effect on these populations, with focus on threatened species (Table 3).

The data used in this review provides the first list of species known to exhibit capture-induced parturition (Adams, 2017) including a number of elasmobranchs that are highly threatened (Table 3). We recommend that future sampling techniques for such species should be carefully considered, given the likelihood of many common sampling methods causing capture-induced parturition. There is the potential for a large number of currently data deficient species to also exhibit capture-induced parturition, which is concerning given their lack of threat assessment.

Considering it is the stress associated with capture (irrespective of whether the animal is released after capture) that is the source of the problem, the only means of mitigation are likely to be seasonal and/or spatial closures designed to protect species while they are pregnant (especially for those species that are endangered). Internationally, there is a growing body of evidence supporting hypotheses that marine reserves help conserve some shark populations (Meekan and Cappo, 2004; Garla et al., 2006; Heupel et al., 2009; Bond et al., 2012; White et al., 2017). Acting in an analogous fashion to spatial closures, seasonal closures protecting nursery areas or aggregation sites offer a temporary spatial refuge for affected species during critical reproductive periods. An example is the protection of the school shark (*Galeorhinus galeus*) through seasonal closures in certain locations off southern Australia during the pupping season (Bensley et al., 2010). Simpfendorfer (1999) and Prince (2005) suggest that targeting protection of breeding size adults is an important management strategy for chondrichthyan fisheries, rather than juveniles and sub-adults that are conventional targets of fisheries management. This strategy would allow pregnant females to give birth to full-term pups and would contribute to healthy levels of recruitment.

Marine reserves have been predicted to influence surrounding biodiversity due to the 'spill over' of adults and juveniles across borders (Botsford et al., 2003; Gell and Roberts, 2003) thereby replenishing fished areas outside the Marine Reserve (Roberts et al., 2001). Similarly, for species that show capture-induced parturition, permanent marine reserves may represent an important source of juveniles. To be effective, marine reserves need to be designed around the critical life stages of multiple species, and work by protecting the habitats on which these stages depend (Bonfil, 1999). Nursery area protection is important for shark and ray management as these nearshore areas are often intensely used by humans. Further research is needed to develop management strategies that encompass older individuals residing outside nurseries (Kinney and Simpfendorfer, 2009), especially those large females that are susceptible to capture-induced parturition due to fishing.

The posting and sharing of videos by both members of the public and scientific organisations which unconsciously depict capture-induced parturition events, highlights a lack of knowledge regarding this response to stress. There may be some benefit in a broader communication strategy which highlights the risk that the capture of pregnant elasmobranchs can cause premature birth or abortion. It would also be useful to assess if certain post-capture handling techniques can reduce capture-stress and associated parturition for elasmobranchs. In addition, it would be useful to quantify actual mortality of embryos following capture-induced parturition, to better quantify the magnitude of this problem. With better understanding of the physical and physiological mechanisms which induce parturition, it may be possible to develop techniques to reduce stress-induced parturition rates on vulnerable species, and thereby reduce the impact of catch and release angling, or fishing methods where adult elasmobranchs are discarded. At any rate, it is clear that resource managers need to consider the indirect threats to elasmobranchs posed by fishing.

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## Appendix A

Table A.1
Species and link to video or images depicting a capture-induced parturition event (and one stranding: #21).

| # | Species | Link |
|---|---|---|
| 1 | *Aetobatus narinari* | https://www.youtube.com/watch?v=tvT1uLylGN4 |
| 2 | *Hemitrygon fluviorum* | https://www.youtube.com/watch?v=ysHCpH1kEfk |
| 3 | *Hexanchus griseus* | https://www.youtube.com/watch?v=b70GnqY2iQc |
| 4 | *Hypanus sabinus* | https://www.instagram.com/p/BIlX0JyDOAr/?taken-by=scottyjrfishing |
| 5 | *Hypanus sabinus* | https://www.youtube.com/watch?v=LzzCNfh6KoM |
| 6 | *Hypanus sabinus* | https://www.youtube.com/watch?v=4HWNPXiWEh8 |
| 7 | *Hypanus sabinus* | https://www.instagram.com/p/sWNK6Bt1PG/?taken-by=daft_hound |
| 8 | *Hypanus sabinus* | https://www.youtube.com/watch?v=cvGqJ0_mtSo |
| 9 | *Hypanus sabinus* | https://www.youtube.com/watch?v=9ENscXNcxoc |
| 10 | *Hypanus say* | https://www.youtube.com/watch?v=ztximLvx2PQ |
| 11 | *Hypanus say* | https://www.youtube.com/watch?v=qRYiIEs4iVQ |
| 12 | *Hypanus say* | https://www.youtube.com/watch?v=WHUKwqJlmpg |
| 13 | *Hypanus say* | https://www.youtube.com/watch?v=5sv83S_wVRQ |
| 14 | *Isurus paucus* | https://www.youtube.com/watch?v=v6VbtMzMCoY |
| 15 | *Maculabatis gerrardi* | https://www.youtube.com/watch?v=qIt7Gtd3I0M |
| 16 | *Myliobatis californicus* | https://www.youtube.com/watch?v=p06TCTgSnWI |
| 17 | *Myliobatis californicus* | https://www.instagram.com/p/3FWcRvnwU0/?tagged=stingraybabies |
| 18 | *Negaprion brevirostris* | https://www.facebook.com/biminisharklab/videos/937696579676405/ |
| 19 | *Pristis pectinata* | https://www.youtube.com/watch?v=gt-sE14dYXs |
| 20 | *Urogymnus polylepis* | https://www.youtube.com/watch?v=6YKVYJE1HY8 |
| 21 | *Rhinobatos annulatus* | https://www.facebook.com/LuderitzMarineResearch/photos/a.970032346378288.1073741862.696370223744503/970033839711472/?type=3&theater |
| 22 | Unknown | https://www.youtube.com/watch?v=7ZTrHPrCjvs |
| 23 | Unknown | https://www.youtube.com/watch?v=ZDjXS0vnr0g |
| 24 | Unknown | https://www.youtube.com/watch?v=nvF7wjzdIiY |
| 25 | Unknown | https://www.youtube.com/watch?v=BjezRCPVVy4 |
| 26 | Unknown | https://www.youtube.com/watch?v=e1qePnYaFK8 |
| 27 | Unknown | https://www.youtube.com/watch?v=7sCV7DkEtdE |
| 28 | Unknown | https://www.youtube.com/watch?v=NJpeYTf2-O8 |
| 29 | Unknown | https://www.youtube.com/watch?v=MSJzNAz1hbk |
| 30 | Unknown | https://www.youtube.com/watch?v=D1vUNOazblQ |
| 31 | Unknown | https://www.youtube.com/watch?v=PyI5JTCXoVI |
| 32 | Unknown | https://www.youtube.com/watch?v=yVETK5bhpN0 |
| 33 | Unknown | https://www.youtube.com/watch?v=a0bTeKxMBM0 |
| 34 | Unknown | https://www.youtube.com/watch?v=xJVHsn2CC6c |
| 35 | Unknown | https://www.youtube.com/watch?v=8Onq2v7nhBg |
| 36 | Unknown | https://www.youtube.com/watch?v=8qYMtqnQrGU |
| 37 | Unknown | https://www.youtube.com/watch?v=JntF6juiaW4 |
| 38 | Unknown | https://www.youtube.com/watch?v=s7tpluNwUdA |
| 39 | Unknown | https://www.youtube.com/watch?v=0cBfTbvlYxk |
| 40 | Unknown | https://www.youtube.com/watch?v=SXkzlyo77Ho |
| 41 | Unknown | https://www.youtube.com/watch?v=r5Z1GD3FSNU |
| | Re-upload of previous video | Re-upload of previous video |
| 42 | *Hypanus sabinus* | http://imgur.com/gallery/M9EMyUe |
| 43 | Unknown | https://www.youtube.com/watch?v=X5Ke352_F_8 |
| 44 | Unknown | https://www.youtube.com/watch?v=I7M5w_gkC1E |

Table A.2
Species classification, fishing method used and number of embryos resulting from capture induced parturition (and one stranding: #21). The title of the video/images is also given.

| # | Order | Family | Method | Number of embryos seen in video (or reported by uploader) | Title |
|---|---|---|---|---|---|
| 1 | Myliobatiformes | Aetobatidae | Unknown | 4 | Animals 2016 - Fisherman Helps Stingray Give Birth - Stingray Giving Birth #2 |
| 2 | Myliobatiformes | Dasyatidae | Unknown | 10 (12) | RARE FOOTAGE: Stingray Giving Birth Boy Delivers 12 Stingrays! HD |
| 3 | Hexanchiformes | Hexanchidae | Hook and line | 15 | Shark give birth in Florida |
| 4 | Myliobatiformes | Dasyatidae | Unknown | 3 | Well.. @huntfishwrestle@kole_reeves7 and I birthed some baby rays today (the mom and babies were released safely) |
| 5 | Myliobatiformes | Dasyatidae | Hook and line | 3 | Stingray gives birth to live young - Florida Fishing |
| 6 | Myliobatiformes | Dasyatidae | Hook and line | 2 | Caught On Camera: Fisherman Helps Stingray Give Birth |
| 7 | Myliobatiformes | Dasyatidae | Unknown | 3 | #stingray #stingraybirth#yup |
| 8 | Myliobatiformes | Dasyatidae | Hook and line | 4 | Stingray gives live birth! |
| 9 | Myliobatiformes | Dasyatidae | Hook and line | 3 | Stingray Gives Birth On Land After Being Caught By Fishman |
| 10 | Myliobatiformes | Dasyatidae | Hook and line | 2 | Sting Ray Birth on Fishing Line |
| 11 | Myliobatiformes | Dasyatidae | Hook and line | 2 | Man catches stingray while it's giving birth..unhooked and realesed...! |
| 12 | Myliobatiformes | Dasyatidae | Hook and line | 3 | Stingray Gives Birth On Beach Emerald Isle North Carolina July 2014 |
| 13 | Myliobatiformes | Dasyatidae | Hook and line | 3 | Fishermen Caught Stingray and it Gives Birth |
| 14 | Lamniformes | Lamnidae | Unknown | 10 | DEAD shark giving birth |
| 15 | Myliobatiformes | Dasyatidae | Hook and line | 2 | Sting ray giving birth..motherhood so special. |
| 16 | Myliobatiformes | Myliobatidae | Hook and line | 1 | Manta Ray Birth |
| 17 | Myliobatiformes | Myliobatidae | Hook and line | 2 (10) | Helped stingray give live birth to 10 stingray babies. Yes we rescued them and released them back into the ocean. @ rit_chac |
| 18 | Carcharhiniformes | Carcharhinidae | Strike net | 1 | none |
| 19 | Rhinopristiformes | Pristidae | Longline | 5 | Andros Expedition Report: Sawfish Birth |
| 20 | Myliobatiformes | Dasyatidae | Hook and line | 2 (3) | Jeremy Wade Catches A Giant Pregnant Stingray - River Monsters |
| 21 | Rhinopristiformes | Rhinobatidae | Stranding | 6 (8) | Birth of baby sandsharks (lesser guitarfish Rhinobatos annulatus). |
| 22 | | | Unknown | 16 and two eggs | Shark gives birth on beach |
| 23 | | | Unknown | 5 | Sting Ray giving birth full footage |
| 24 | | | Unknown | 3 | Stingray gives birth on boat (warning: lots of foul language in the commentary) |
| 25 | | | Hook and line | 1 | Stingray giving birth to baby |
| 26 | | | Hook and line | 3 | Stingray giving birth1 |
| 27 | | | Hook and line | 3 | The fisherman caught a giant stingray fish give birth |
| 28 | | | Hook and line | 1 (2) | Sting Ray giving birth in Hilton Head SC |
| 29 | | | Hook and line | 5 | Sting Ray gives birth |
| 30 | | | Unknown | 3 | Incredible Stingray giving birth |
| 31 | | | Unknown | 3 | Stingray giving birth. |
| 32 | | | Hook and line | 3 | Stingrays having babies |
| 33 | | | Unknown | 4 | Baby stingrays born on the beach shore |

| | | | | | |
|---|---|---|---|---|---|
| 34 | | | Hook and line | 3 | Caught On Camera Fisherman Helps Stingray Give Birth |
| 35 | | | Hook and line | 2 | Pregnant stingray gives birth in front of me! |
| 36 | | | Hook and line | 4 | Team George - Stingray gives birth to 4 babies |
| 37 | | | Hook and line | 2 | Stingray gives birth on fishing boat |
| 38 | | | Hook and line | 4 | Animals 2016 - Stingray Giving Birth |
| 39 | | | Unknown | 3 | Stingray giving birth |
| 40 | | | Unknown | 14 | Stingray giving birth inside the boat |
| 41 | | | Hook and line | 1 | Shark Gives Birth After Being Caught |
| | Re-upload of previous video | | | | |
| 42 | Myliobatiformes | Dasyatidae | Unknown | 3 | Stingray giving birth to triplets |
| 43 | | | Hook and line | 2 | Look at this stingray having babies |
| 44 | | | Hook and line | 4 | Teen boys deliver stingray mama's 4 babies |

Table A.3
The upload date and location of videos/images depicting capture-induced parturition (and one stranding: #21). Also given are the social media metrics for each video.

| # | Date uploaded | Location | Views | Shares | Likes | Dislikes | Comments |
|---|---|---|---|---|---|---|---|
| 1 | 9/08/2016 | Unknown | 58,615 | | 75 | 23 | 8 |
| 2 | 1/12/2015 | Australia | 10,947,946 | | 96,404 | 6057 | 14,531 |
| 3 | 22/01/2016 | Florida | 4906 | | 12 | 6 | 5 |
| 4 | 1/08/2016 | North Carolina | 372,906 | | 5381 | | 1376 |
| 5 | 6/07/2015 | Florida | 2894 | | 8 | 0 | 2 |
| 6 | 22/07/2014 | America | 21,152,763 | | 56,194 | 2708 | 4443 |
| 7 | 31/08/2014 | America | unknown | | 23 | | 29 |
| 8 | 16/08/2014 | Gulf coast in Biloxi Mississippi | 624,673 | | 1256 | 279 | 209 |
| 9 | 23/08/2011 | Unknown | 2,083,896 | | 3166 | 11,664 | 6134 |
| 10 | 3/08/2014 | Hilton Head Island in South Carolina | 331 | | 3 | 0 | 0 |
| 11 | 25/06/2014 | St. Augustine Florida | 1,850,704 | | 4321 | 654 | 815 |
| 12 | 29/10/2014 | Emerald Isle, North Carolina | 3434 | | 14 | 3 | 5 |
| 13 | 9/08/2015 | Palms Beach in Charleston South Carolina | 13,378 | | 23 | 11 | 3 |
| 14 | 29/11/2015 | Unknown | 29,988 | | 38 | 32 | 24 |
| 15 | 7/06/2014 | Unknown | 62 | | 0 | 0 | 0 |
| 16 | 21/07/2010 | California | 79,603 | | 52 | 440 | 158 |
| 17 | 24/05/2015 | America | Unknown | | 43 | | 4 |
| 18 | 18/04/2016 | Bimini, Bahamas | 4471 | 29 | 125 | | 0 |
| 19 | 29/12/2016 | Andros, Bahamas | 6411 | | 17 | 0 | 5 |
| 20 | 18/08/2015 | Thailand | 216,877 | | 739 | 12 | 59 |
| 21 | 4/04/2016 | First Lagoon, Luderitz, Namibia | Unknown | 8192 | 5900 | | 364 |
| 22 | 24/01/2016 | unknown | 639,762 | | 1984 | 822 | 1088 |
| 23 | 9/09/2009 | Nansemond River, Suffolk, VA | 15,510 | | 6 | 36 | 28 |
| 24 | 10/10/2014 | Unknown | 148,450 | | 321 | 154 | 76 |
| 25 | 26/05/2009 | Unknown | 10,672 | | 6 | 12 | 12 |
| 26 | 23/07/2009 | Unknown | 2508 | | 3 | 1 | 2 |
| 27 | 30/12/2013 | Unknown | 11,647 | | 19 | 15 | 8 |
| 28 | 13/08/2009 | Hilton Head Island in South Carolina | 41,662 | | 23 | 6 | 9 |
| 29 | 7/07/2014 | Unknown | 247 | | 2 | 0 | 1 |
| 30 | 28/07/2014 | Unknown | 1491 | | 10 | 4 | 1 |
| 31 | 9/07/2015 | Unknown | 223 | | 1 | 0 | 0 |
| 32 | 20/07/2013 | Unknown | 8372 | | 13 | 5 | 4 |
| 33 | 10/07/2016 | Unknown | 671 | | 5 | 0 | 1 |
| 34 | 13/10/2016 | Unknown | 14,844 | | 31 | 2 | 2 |
| 35 | 23/07/2012 | Unknown | 3222 | | 7 | 10 | 4 |
| 36 | 12/07/2013 | UAE | 2898 | | 8 | 1 | 2 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 37 | 29/07/2011 | Unknown | 34,782 | 53 | 52 | 19 |
| 38 | 12/07/2016 | Unknown | 153,088 | 282 | 52 | 85 |
| 39 | 16/06/2008 | Unknown | 904,741 | 931 | 159 | 140 |
| 40 | 26/12/2015 | Unknown | 2,433,953 | 8005 | 1668 | 2684 |
| 41 | 15/09/2013 | Unknown | 4471 | 5 | 17 | 11 |
| | Re-upload of previous video | | | | | |
| 42 | 16/08/2016 | North Carolina | 1491 490 | 4349 | 91 | 346 |
| 43 | 23/08/2013 | Unknown | 4426 | 13 | 4 | 2 |
| 44 | 25/06/2013 | Unknown | 8467 | | 38 | 4 |

Table A.4
The uploader, website and taxonomy (i.e. shark or ray) of the animals depicted in videos/image series showing capture-induced parturition (and one stranding: #21).

| Number | Uploader | Website | Shark or ray |
|---|---|---|---|
| 1 | FUN | Facebook | Ray |
| 2 | Miller Wilson | Facebook | Ray |
| 3 | Manny A | Youtube | Shark |
| 4 | scottyjrfishing | Youtube | Ray |
| 5 | JOSE LIKES FISHING | Youtube | Ray |
| 6 | Barcroft TV | Youtube | Ray |
| 7 | daft_hound | Youtube | Ray |
| 8 | Rhonda Robbins | Youtube | Ray |
| 9 | LetyouTellit | Youtube | Ray |
| 10 | JWBrandon1 | Youtube | Ray |
| 11 | rai martinez | Instagram | Ray |
| 12 | Wyatt Marks | Instagram | Ray |
| 13 | Ryan Copeland | Instagram | Ray |
| 14 | funny videos | Youtube | Shark |
| 15 | jamal koly | Youtube | Ray |
| 16 | ummidontnoe | Youtube | Ray |
| 17 | kahchao | Youtube | Ray |
| 18 | Bimini Biological Field Station - Sharklab | Youtube | Shark |
| 19 | Field School | Youtube | Ray |
| 20 | River Monsters | Youtube | Ray |
| 21 | Lüderitz Marine Research | Youtube | Ray |
| 22 | Bruce Leeroy Maurice | Youtube | Shark |
| 23 | M1keyDank | Youtube | Ray |
| 24 | TheBillSwerski | Youtube | Ray |
| 25 | hrmcdowell | Youtube | Ray |
| 26 | stingray129 | Youtube | Ray |
| 27 | bestvines2014 | Youtube | Ray |
| 28 | Bob Schatz | Youtube | Ray |
| 29 | Brooke Barraclough | Youtube | Ray |
| 30 | Rebeca Garcia | Youtube | Ray |
| 31 | James Anderson | Youtube | Ray |
| 32 | Rene Herrera | Youtube | Ray |
| 33 | Roberton04 | Youtube | Ray |
| 34 | Hafidz Nugroho | Youtube | Ray |
| 35 | HD Gaming | Youtube | Ray |
| 36 | Vinod George Rebeiro | Youtube | Ray |
| 37 | John Moriarty | Youtube | Ray |
| 38 | FUN | Youtube | Ray |
| 39 | pengfli2008 | Youtube | Ray |
| 40 | Javier Capello | Youtube | Ray |
| 41 | fireman7753 | Youtube | Shark |
| | Re-upload of previous video | Re-upload of previous video | Re-upload of previous video |
| 42 | itsfoine | Imgur | Ray |
| 43 | funny2me | Youtube | Ray |
| 44 | Donna Lucarelli | Youtube | Ray |

Table A.5
The total number of species and number observed to exhibit capture-induced parturition in each IUCN category from the following 12 orders of elasmobranch; Hexanchiformes, Echinorhiniformes, Pristiophoriformes, Squatiniformes, Squaliformes, Heterodontiformes, Orectolobiformes, Lamniformes, Carcharhiniformes, Torpediniformes, Rhinopristiformes and Myliobatiformes. The 343 species in the Chimaeriformes and Rajiformes orders were not included due to the results of the order level analysis (Fig. 4a) and to provide a more accurate estimate of expected IUCN frequencies. Seventy-eight species are Not Evaluated and the remaining 773 species from the IUCN red list can be found at the following link: http://www.iucnredlist.org/search/link/593e31a2-4b3dc58d.

| IUCN category | Number of species (% of total) | Number of species observed to exhibit capture-induced parturition |
|---|---|---|
| Least Concern | 201 (23.6) | 24 |
| Near Threatened | 93 (10.9) | 20 |
| Vulnerable | 103 (12.1) | 15 |
| Endangered | 38 (4.5) | 3 |
| Critically Endangered | 17 (2.0) | 4 |
| Data Deficient | 321 (37.7) | 17 |
| Not Evaluated | 78 (9.2) | 5 |
| Total | 851 | 88 |

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