

## Review

# Looking beyond the mortality of bycatch: sublethal effects of incidental capture on marine animals



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## ABSTRACT

There is a widely recognized need to understand and reduce the incidental effects of marine fishing on non-target animals. Previous research on marine bycatch has largely focused on simply quantifying mortality. However, much less is known about the organism-level sublethal effects, including the potential for behavioural alterations, physiological and energetic costs, and associated reductions in feeding, growth, or reproduction (i.e., fitness) which can occur undetected following escape or release from fishing gear. We reviewed the literature and found 133 marine bycatch papers that included sublethal endpoints such as physiological disturbance, behavioural impairment, injury, reflex impairment, and effects on reproduction, feeding, and growth for animals that survived a fisheries interaction. Of the 133 identified articles, 22 documented sublethal effects of capture using metrics directly related to fitness, life history, or population-level processes. Sublethal effects were classified as either short-term (e.g., acute stress response), which could lead to long-term or delayed sublethal outcomes (e.g., growth, reproduction), which are directly fitness-relevant and could have had population-level effects. We recommend further investigation into the effects of injury on fitness, and the effects of capture stress on reproduction. It is completely unknown whether sublethal effects can have significant consequences at the population- or ecosystem-level. To date, the potential for discards to suffer from sublethal fitness effects has been almost entirely ignored, and added knowledge on the topic could benefit both conservation and management.

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## 1. Introduction

The catch of non-target animals (bycatch) in small-scale and industrial commercial fisheries has been widely recognized as a leading threat to the conservation of Earth's biodiversity (Gray, 1997; Kappel, 2005; Davies et al., 2009). Particularly over the last two decades, this issue has come to the forefront both in fisheries management (Crowder and Murawski, 1998; Gilman, 2011) and in conservation science (Lewison et al., 2004a; Soykan et al., 2008). From a conservation perspective, a number of globally important issues have been identified whereby populations of key species (often charismatic megafauna) have been affected by fishing activity targeting other species (e.g., Hall, 1998; Tuck et al., 2001; Lewison et al., 2004b). In many marine commercial fisheries, the landed non-target catch is returned to the sea (referred to as discards) because of economic (e.g., lack of market, inefficient economic return), regulatory (e.g., harvest regulations, endangered species legislation), or other (e.g., social pressure, conservation ethic) reasons, often with the hope that some or all of the released animals will recover from the capture stress and survive. Global estimates of marine bycatch and discards have varied considerably (Alverson et al., 1994; Kelleher, 2005), but could be as high as 40% of total catch (38.5 million tonnes of biomass annually; Davies et al., 2009). Global discard rates may be declining, likely owing to technological innovation (e.g., Broadhurst, 2000), and a shift to using previously-discarded species (Kelleher, 2005). However, if a real downward trend in discarding rates does exist, it may be largely attributable to declining overall catches (Zeller and Pauly, 2005). Fisheries bycatch can thus be considered a significant component of the overall issue of overexploitation, which is the primary driver of declining abundance and diversity of life in the oceans (Gray, 1997; Gilman, 2011).

Given the global scope of the problem, considerable resources have been devoted to examining various aspects of bycatch, resulting in over 1000 research papers published in peer-reviewed journals over the last few decades (Soykan et al., 2008; Raby et al., 2011). The majority of research in the realm of bycatch and discards has been conducted from a high level of biological organization, focusing on the quantity of bycatch and discards and then attempting to consider those values relative to overall population size as well as natural mortality. For example, there have been a number of important reports on bycatch rates, both on a broad scale (Alverson et al., 1994; Kelleher, 2005; Harrington et al., 2005; Davies et al., 2009) and in specific contexts (Romanov, 2002; Rogan and Mackey, 2007). Resulting species declines have been documented, highlighting the need for management intervention (Hall, 1998; Tuck et al., 2001; Lewison et al., 2004b; Wallace et al., 2008).

Important as that research is, additional studies aimed at lower levels of biological organization (e.g., organismal) have the potential to add to bycatch management (e.g., Farrell et al., 2001a; Davis, 2010). The organism-level endpoint that is easiest to incorporate into management is whether an animal is dead or alive following a fisheries interaction. Conveniently, mortality (especially immediate mortality at time of landing or haul back) is also relatively easy to observe – at least to the extent that it has regularly been measured in a variety of contexts (e.g., using biotelemetry or net pen holding – see Donaldson et al., 2008; Yergey et al., 2012). While much of the bycatch literature has focused on bycatch rates or immediate mortality, numerous studies have also evaluated the survival of animals (primarily fish) being released from fishing vessels (i.e., post-release or delayed mortality; Kaimmer and Trumble, 1998; Davis, 2002; Parker et al., 2003; Broadhurst et al., 2006; Carruthers et al., 2009; Campana et al., 2009; Benoit et al., 2012). It is now well known that bycatch is often dead when

it is discarded or that discards can die after release (Hill and Wasenberger, 2000; Davis, 2002). In cases where it is not possible to avoid bycatch there has been a growing effort to understand the fate of organisms that escape fishing gears or are landed and released alive (Davis, 2002; Ryer et al., 2004; Moyes et al., 2006; Stoner, 2012a, 2012b). In some instances, that research has generated solutions to mortality (e.g., Farrell et al., 2001a, 2001b; Broadhurst et al., 2008, 2009).

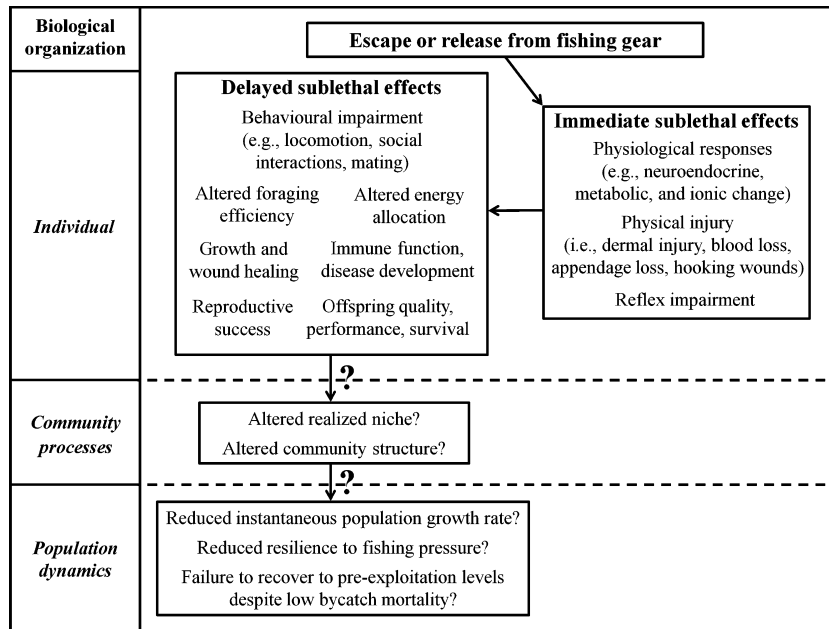
Although mortality is the most significant possible impact on fitness, sublethal effects such as stress and injury experienced by captured (or escaped) animals could alter their behaviour, growth, or reproduction, reducing their performance relative to conspecifics. Despite the now-extensive literature on the fate of discards, exceptionally few studies have used sublethal endpoints. Added information on the potential sublethal consequences of capture and release could provide a more holistic understanding of fisheries bycatch as a conservation problem. Fisheries managers are normally concerned with biological parameters beyond mortality. Indeed, changes in growth and reproduction have obvious and direct effects on population dynamics and life-tables. Yet, our understanding of sublethal effects in discards is sparse and in most cases, non-existent. Nevertheless, there has been considerable work describing injury (Kaimmer and Trumble, 1998), vitality and reflex impairment (Davis, 2010; Benoit et al., 2013), and physiological disturbances (Chopin et al., 1996; Farrell et al., 2001a; Marçalo et al., 2006; Renshaw et al., 2012) following capture. Though these “at-release” sublethal metrics have frequently been described, they have seldom been linked to fitness outcomes other than survival.

The primary objective of this review is to synthesize research that looks beyond bycatch mortality and provides information about sublethal outcomes. Special attention was given to sublethal fitness outcomes, here defined as a measure of lifetime reproductive success, as it is through changes in fitness that sublethal effects can have a population-level influence. The second and final objective was to identify gaps and recommend future directions of research. The general layout of the paper is as follows: (i) a summary of results of a literature survey, (ii) a concise review of existing knowledge and case studies, (iii) commentary on research opportunities and approaches, and (iv) summary and conclusions.

## 2. Literature survey

For the purpose of this review, sublethal effects were defined as any non-lethal physical, physiological, or behavioural consequence that resulted from capture and release or escape from fishing gear. We classified sublethal effects as either short-term (e.g., injury or acute stress response) or delayed (e.g., growth, reproduction; Fig. 1). For simplicity, the focus of this study was marine commercial fisheries. We certainly recognize that bycatch occurs in freshwater fisheries (see Raby et al., 2011), but there are very few papers that examine sublethal outcomes (e.g., Colotelo et al., 2012). In recreational fisheries, the failure to demonstrably link capture stress with sublethal fitness measures has been a persistent challenge to translating research into management action (Cooke et al., 2013). Although we explicitly exclude freshwater and recreational fishing from this review, the principles and research trends described below are generally transferrable to those sectors, as has been advocated by Cooke and Cowx (2006).

To gather all research papers relevant to the sublethal effects of capture, we conducted a literature search ending 30/04/13 using a two-step process. The first step used a variety of search term combinations (fish\*, discard\*, capture\*, stress, capture stress, injury, impair\*, escap\*, gear, encounter, bycatch, bird, mammal, turtle, invertebrate, response, physiology, sublethal) in ISI Web of Science and Google Scholar to generate a comprehensive list of >600 studies



**Fig. 1.** Conceptual diagram outlining the immediate and long-term effects of escape or release from commercial fishing gear and how it relates to each level of biological organization. Question marks (?) denote areas for which no primary literature exists, and present future avenues of research.

on the effects of capture and release on all taxa. That list was then manually searched for papers that included sublethal endpoints, including physiological measurements, behavioural impairment, injury, reflex impairment, and effects on reproduction, feeding, and growth for individuals that survived the fisheries interaction. Although many of the published research papers focused on quantifying discard mortality, several included qualitative injury or condition scores in addition to assessing mortality by holding fish in pens or cages. That is, they attempted to make associations between injury, the vigour of the animals (both sublethal assessments), and short-term mortality; often with mortality being the entire focus of the discussion. Such papers whose discussions focused entirely on a mortality endpoint were not always excluded from this review but we did not search exhaustively to identify all of them. The second step of the process focused on finding any remaining papers that used sublethal metrics as stand-alone study endpoints with direct fitness relevance. We attempted to exhaust the literature by examining reference lists and by searching “cited by” lists of already-located papers of high relevance in Web of Science Cited Reference Search and Google Scholar.

Our search yielded 133 peer-reviewed articles that reported or discussed sublethal measurements in the context of marine bycatch. Our initial breakdown of those papers was as follows: 30 included sublethal measures (usually injury or reflex impairment) only as accompaniment to mortality data, with little to no consideration of these measures as stand-alone endpoints or discussion of any potential fitness cost other than mortality. We are confident that there are more such papers but did not focus on finding them. The remaining papers had considerable focus on sublethal measures as endpoints such that they were included in the discussion, usually with some acknowledgment that fitness outcomes other than mortality could occur. Twenty-seven studies were conducted in a laboratory setting, without necessarily *excluding* mortality as a metric. Similarly, 55 papers included some focus on sublethal non-fitness measures in a field context. Eleven of the 133 papers in our search were review papers that included some mention or discussion of sublethal effects. We were able to locate a total of 22 articles that documented sublethal effects of capture using metrics directly related to fitness, life history, or population-level processes (e.g., [Wade et al., 2007](#)).

Among the 22 articles we found that documented sublethal life history and fitness effects, seven used invertebrate study species. Those seven invertebrate studies focused on crab or lobster species that suffered limb or appendage loss or other injuries when released from commercial trap fisheries because of size or sex ([Davis, 1980](#); [Carls and O'Clair, 1995](#); [Zhou and Shirley, 1995](#); [Brouwer et al., 2006](#); [Melville-Smith and de Lestange, 2007](#); [Darnell et al., 2010](#)). There are other papers exploring the effects of limb loss in crustaceans, although not in the context of fisheries capture (reviewed by [Juanes and Smith, 1995](#)). One laboratory-based study examined the trans-generational effects of trawl avoidance stress in Atlantic cod (*Gadus morhua*), testing the hypothesis that the stress of fisheries interactions can affect offspring quality ([Morgan et al., 1999](#)). Two field studies examined sublethal life history and fitness effects in fish released into the wild, gathering post-release measurements on growth and reproduction in Pacific halibut (*Hippoglossus stenolepis*) and sockeye salmon (*Oncorhynchus nerka*; [Kaimmer and Trumble, 1998](#), and [Baker and Schindler, 2009](#), respectively).

The majority of the 22 fitness-relevant sublethal effects papers we found were focused on marine mammals. In particular, a series of technical reports were published by NOAA in 2002 as a result of a research program referred to as the Chase Encirclement Stress Studies (CHESS), which focused on exploring a multitude of sublethal effects in dolphins chased and encircled by tuna purse seine fisheries in the eastern tropical Pacific (e.g., [Edwards, 2002a, 2002b](#)), and follow-up studies ([Edwards, 2006, 2007](#); [Noren and Edwards, 2006](#)).

### 3. Relevant findings and concepts

#### 3.1. Immediate sublethal effects

The immediate sublethal effects of fisheries capture (i.e., measurable upon capture, prior to release) have been relatively well documented, to the extent that such studies made up the large majority of the papers in our literature survey (111 of 133 papers). Immediate effects can be generalized into two components: physiological disturbance and injury. Collectively, assessments of injury and physiological disturbance are important tools in bycatch

research and have been mainly used thus far to explain mortality patterns or to compare animal welfare outcomes among capture and handling techniques. For the sake of brevity, we provide only a brief description of physiological disturbance and injury that occurs in bycatch. Further information can be found in the key references highlighted in Table 1.

### 3.1.1. Physiological disturbance

The physiological disturbance caused by capture can be separated into the endocrine response to stress and metabolic disturbance – the latter is associated with anaerobic exercise and hypoxia or anoxia. The extent of physiological disturbance can be

influenced by several factors, but broadly include the fishing gear type, duration of exposure to handling, environmental factors like temperature, and biological variables like age class, size, reproductive status, health status, species, population and sex (see Table 1). For example, Frick et al. (2010a, 2010b, 2012) found that gummy sharks (*Mustelus antarcticus*) were highly susceptible to physiological disturbances by both trawl, gill net and longline capture, while Port Jackson sharks (*Heterodontus portusjacksoni*) did not experience significant physiological changes under the same experimental treatments. The different morphologies of each species may result in disparate physiological outcomes after a fisheries interaction (Frick et al., 2009). Port Jackson sharks, for example, are less

**Table 1**  
A description of the immediate and measurable sublethal effects of capture on marine animals, including physiological disturbance and injury.

Immediate sublethal effect	Taxa	Factors influencing the degree of effect	Description	References
Physiological disturbance	Invertebrates	Gear type, capture duration, emersion time, temperature	Stress response (e.g., increase in crustacean hyperglycaemic hormone, glucose, potassium, sodium and ammonia levels), metabolic disturbance (e.g., hypercapnia, acidosis, decreased glycogen concentrations, and adenylated energy charge), oxidative stress	Vermeer (1987), Bergmann et al. (2001), Gioni et al. (2005), Harris and Andrews (2005a, 2005b), Haupt et al. (2006), Ridgway et al. (2006), Romero et al. (2007), Albalat et al. (2009), Lund et al. (2009) and Lorenzon et al. (2013)
	Fish	Nature of capture experience (e.g., gear type, capture duration, emersion time), environmental factors (e.g., temperature), biological variables (e.g., age class, size, reproductive status, life history, scope of activity, metabolic rate, health status, ontogeny, thermal physiology, anaerobic capacity), differences in behaviour	Stress response (e.g., increase in blood cortisol, and lactate concentrations, decrease in blood glucose), metabolic disturbance (e.g., respiratory acidosis, increased lactate, CO <sub>2</sub> , creatine kinase, Hsp 70 aspartate aminotransferase and lactate dehydrogenase concentrations in the blood and/or muscle tissue)	Olla et al. (1997), Tsunoda et al. (1999), Davis and Olla (2001), Manire et al. (2001), Davis (2005), Haukenes and Buck (2006), Milston et al. (2006), Marçalo et al. (2006, 2010), Moyes et al. (2006), Skomal et al. (2007), Frick et al. (2009, 2010a, 2010b), Mandelman and Skomal (2009), Brooks et al. (2012), Hoffmayer et al. (2012), Hyatt et al. (2012), Mandelman et al. (2012), Marshall et al. (2012) and Tenningen et al. (2012)
	Reptiles	Nature of capture experience (e.g., gear type, capture duration, immersion time), environmental factors (e.g., temperature), biological variables (e.g., age class, size, reproductive status, life history, scope of activity, metabolic rate, health status, anaerobic capacity)	Stress response (e.g., increase in blood cortisol, and lactate concentrations, decrease in blood glucose), metabolic disturbance (e.g., increased lactate, CO <sub>2</sub> , creatine phosphokinase, phosphate and lactate dehydrogenase concentrations in the blood and muscle tissue, respiratory acidosis)	Stabenau et al. (1991), Gregory et al. (1996), Davis and Olla (2001), Jessop et al. (2002, 2004), Harms et al. (2003), Davis (2005), Hight et al. (2007) and Snoddy et al. (2009)
Injury	Invertebrates	Capture type, handling and sorting methods, number of animals, characteristics of species caught (e.g., morphology, fragility and size of the individual)	Loss and damage of appendages, cracked or crushed carapace, punctures, torn or lost opercula, damaged chelae, spines, rostrum	Juanes and Smith (1995), Kaiser and Spencer (1995), Zhou and Shirley (1995), Mensink et al. (2000), Bergmann et al. (2001), Ramsay et al. (2001), Warrenchuk and Shirley (2002), Milligan et al. (2009), Stoner (2012a) and Lorenzon et al. (2013)
	Fish	Capture type, handling and sorting methods, number of animals, depth of capture, characteristics of species caught (e.g., morphology, and size of the individual)	Punctured vital organs, dermal injuries (e.g., skin and scale damage, loss of mucus), barotrauma injuries (e.g., exophthalmia, ruptured swim bladders), bruising on ventral surface	Lockwood et al. (1983), Kaiser and Spencer (1995), Broadhurst et al. (1997, 1999), Ryer (2004), Miller et al. (2005), Davis and Ottmar (2006), Nichol and Chilton (2006), Gilman et al. (2008), Campana et al. (2009), Diamond and Campbell (2009), Humborstad et al. (2009), Neat et al. (2009), Baker and Schindler (2009), Marçalo et al. (2010) and Olsen et al. (2012)
	Reptiles	Gear type, capture duration, immersion time	Cuts and gashes (particularly around the mouth), infection, entanglement with fishing gear	Parker et al. (2001), Yeung (2001), Chaloupka et al. (2004), Epperly et al. (2004), Lewison et al. (2004b), Watson et al. (2005) and Gilman et al. (2006a)
	Mammals	Capture type, length of entanglement	Entanglement with fishing gear, cuts and gashes, hemorrhaging, infection	Fowler (1987), Fowler et al. (1989), Kraus (1990), Angliss and DeMaster (1998), Knowlton and Kraus (2001), Johnson et al. (2005), Gilman et al. (2006b), Forney and Kobayashi (2007), Kot et al. (2009), Moore et al. (2009), Cassoff et al. (2011) and Moore and van der Hoop (2012)

likely to be gilled in gill nets because of their broad heads, and therefore are released with lower levels of physiological disturbance than other species (e.g., Australian swellshark *Cephaloscyllium laticeps*; Frick et al., 2009).

Similar to the stress response, the degree of the metabolic imbalance can vary substantially, but exhaustive exercise appears to be driven by differences in behaviour, metabolic rate and anaerobic capacity (Table 1). Metabolic stress is also driven by hypoxia, which can be influenced by the gear type and immersion time (Table 1). In turtles, prolonged hypoxia and exercise can result in lactate levels as high as 50.6 mmol/L and can take 4–15 h to clear, during which time turtles rest and recover at the surface, exposing them to potential injury (or death) from boat collisions and marine predators (Snoddy et al., 2009). The ability to cope with additional stressors and a suppressed immune system function likely increases the risk of further harm, prolonging recovery time and subsequently increasing energetic demands. The variability inherent in neuroendocrine and metabolic stress responses makes it difficult to predict the severity and duration of a physiological response.

### 3.1.2. Injury

Some degree of injury is caused by virtually all methods of fisheries capture, and the type, extent, and consequences of injuries vary widely depending on the gear used and the species encountered. Incidentally caught marine animals can become injured due to pressure changes during hauling (i.e., barotrauma), and contact with other organisms, debris, or fishing gear during capture and/or escape (Davis and Ottmar, 2006; Sartor et al., 2006). Once on deck, further damage can occur during the handling and sorting processes and compression from the contents of the net (Kaiser and Spencer, 1995; Zhou and Shirley, 1995). Injury patterns are species-specific and are strongly associated with the morphology, fragility and size of the individual (Pranovi et al., 2001; Sartor et al., 2006; Benoit et al., 2013; Table 1). Physical damage to fishes and crustaceans is commonly due to abrasion with conspecifics and the gear itself due to crowding during hauling (e.g., purse seining; see Table 1). Marine mammal, elasmobranch, and sea turtle injuries are often caused by capture in nets or entanglement with fishing gear (Table 1). Few seabirds are able to escape from pelagic longline fishing gear (Melvin and Parrish, 2001; Stehn et al., 2001) and as a result, there are few reports of incidentally caught, injured seabirds being released alive.

Unlike physiological disturbance, injuries are often macroscopic, permanent, and can result in chronic issues that ultimately affect fitness (Bergmann et al., 2001). Although this has been widely recognized as a conservation concern, there have been few published attempts at quantifying how injuries sustained during fisheries interactions affect individual fitness (e.g., locomotion, reproduction, foraging), let alone how those fitness effects would affect population dynamics or community processes (Juanes and Smith, 1995; Bergmann et al., 2001; Fig. 1).

## 3.2. Delayed sublethal effects

### 3.2.1. Locomotory and behavioural impairment

Marine animals that escape or are discarded from fisheries can be behaviourally impaired due to a spectrum of sublethal stressors (Chopin and Arimoto, 1995; Ryer, 2004). As such, discards may be unable to engage in normal swimming, feeding, and mating behaviours, imposing potential fitness costs. From a management perspective, this should be of concern as discarded individuals that survive (or are assumed to survive) can ideally contribute to future recruitment and yield (Halliday and Pinhorn, 2002).

Some research has focused on linking stress-induced behavioural impairment to delayed (unobserved) mortality. Several

studies on fishes (Olla et al., 1997; Morgan et al., 1999; Davis and Parker, 2004; Ryer, 2004) and invertebrates (Vermeer, 1987; Haupt et al., 2006) have shown that severe physiological exhaustion is likely the cause for impaired swimming performance and predator evasion behaviour. Recovery from behavioural impairment in finfish is likely dependent on the intensity and duration of the capture stressor and may contribute to the variability in reported recovery times (i.e., 90 min – Olla et al., 1992; days or weeks – Olla et al., 1995, 1997; Morgan et al., 1999; Ryer et al., 2004; Ryer, 2004; Davis, 2005). We found no published field studies that investigated stress-induced behavioural consequences of commercial capture, other than in making links to predation (a lethal outcome; see Gitschlag and Renaud, 1994; Ross and Hokenson, 1997 for examples).

Although injuries to discards have been frequently characterized, few papers have linked injury to behaviours directly associated with fitness. Olsen et al. (2012) used experimentally-controlled de-scaling in herring (*Clupea harengus*) to mimic injury observed in purse seine fisheries to understand the effects of this common injury on physiological state, behavioural competence and survivorship. Following de-scaling, herring increased their swimming speed but were unable to maintain cohesive shoals; a behaviour that increases vulnerability to predation. Interestingly, this finding indicates that even when locomotory performance is maintained, aspects of behaviour can be affected. De-scaling the fish also resulted in a loss of osmoregulatory ability and chronically elevated cortisol (Olsen et al., 2012). Other recent studies have shown that Pacific cod (*Gadus macrocephalus*; Nichol and Chilton, 2006) and Atlantic cod (Neat et al., 2009) become inactive and are susceptible to predation after incurring barotrauma injuries during hauling. Through the use of data-storage tags, these studies were able to associate differences in hydrostatic pressure (i.e., depth) and temperature to changes in swimming behaviour, exhaustion and position in the water column that are likely attributable to the rupture and deflation of the swim bladder. It is unknown whether barotrauma injuries affect important processes like foraging, migration, or reproductive behaviour. However, in one example, juvenile walleye pollock (*Theragra chalcogramma*) and juvenile and adult sablefish (*Anoplopoma fimbria*) were towed in a trawl and air exposed, which resulted in depressed feeding rates for up to 6 days post-release (Olla et al., 1997).

Injuries and entanglement from commercial fishing gear can impede the feeding mechanics and locomotion required for optimal foraging in marine mammals, where the most common attachment site for fishing gear is the mouth (Cassoff et al., 2011). These injuries can impede an animal's foraging ability significantly enough to result in long-term starvation in bottlenose dolphins (Andersen et al., 2008) and baleen whales (Cassoff et al., 2011). A number of marine mammal species carrying fishing gear expend more energy due to increased drag, ultimately leading to severe weight loss (*Zalophus californianus* Feldkamp, 1985; *Callorhinus ursinus* Fowler, 1987; *Eubalaena glacialis* Moore et al., 2012; Moore and van der Hoop, 2012). In fact, Feldkamp (1985) showed that entangled California sea lions expend approximately four times more energy than non-entangled individuals, mainly due to increased drag. Behavioural adaptations to entanglement and injury have been observed in an injured minke whale (*Balaenoptera acutorostrata*) with a prominent laceration around the head and ventral pouch in the Gulf of St. Lawrence, Canada (Kot et al., 2009). Although the whale was not carrying gear, it distended its ventral pouch considerably less than uninjured individuals observed in the same region. The injured whale exhibited an elevated foraging frequency using a new lunge-feeding aerial manoeuvre, possibly as an attempt to overcome the limitations of its injured ventral pouch (Kot et al., 2009). A behavioural adaptation such as this would likely have long-term energetic consequences, potentially affecting

the reproductive success of the individual. Although that case study was focused on the behaviour of one individual, it provided insight into what individual-level outcomes are possible following fisheries interactions.

Papers that contain evidence of fitness-related behavioural impairment in crustaceans have focused on commercial species that are discarded because of size- and sex-restrictions. Similar to the literature on fishes, most invertebrate studies have concentrated on predator avoidance. For example, bouts of air exposure on a commercial vessel were found to reduce the speed and type of escape responses (i.e., walk vs. tail-flip) in western rock lobster (*Panulirus cygnus*; [Brown and Caputi, 1983](#)), spiny lobster (*Panulirus argus*; [Vermeer, 1987](#)) and South African Cape lobster (*Homarus capensis*; [Haupt et al., 2006](#)). Increasing air exposure for crustaceans can decrease activity, often to the point of immobility ([Brown and Caputi, 1983](#); [Haupt et al., 2006](#)). Following air exposure in the laboratory, study subjects were released into tanks with predators (finfish and octopus; [Brown and Caputi, 1983](#); [Haupt et al., 2006](#)), and their sinking, defense and escape behaviours were monitored. Exposed Cape lobsters sank slowly upon release, without exhibiting the tail-flip response observed in controls ([Haupt et al., 2006](#)). As the duration of air exposure increased, lobsters sank in a disoriented manner, reaching the bottom of the tank on their dorsal surfaces or sides ([Haupt et al., 2006](#)). Evidently, air exposure disrupts basic reflexes and could potentially affect behaviours other than predator avoidance – at least in the short term ([Vermeer, 1987](#)).

To our knowledge, only a single paper discusses the behaviour of sea turtles after release from a commercial fishery ([Swimmer et al., 2006](#)). In that study, olive ridley turtles (*Lepidochelys olivacea*) were fitted with pop-up satellite archival tags (PSATs) to monitor diving behaviour and post-release habitat use (geographic location and depth) after their interaction with pelagic longline gear in the Gulf of Papagayo, Costa Rica. The study found no behavioural deficits suffered by olive ridley turtles: controls and longline-caught turtles displayed similar vertical and horizontal movement patterns. [Swimmer et al. \(2006\)](#) suggest that it is reasonable to assume that all turtles were then able to engage in normal breeding behaviours given the absence of behavioural impairment.

### 3.2.2. Growth and reproduction

Although the physiological stress response is considered to be adaptive, enabling an animal to resist a stressor ([Wingfield et al., 1998](#); [Sapolsky et al., 2000](#)), it can have effects on feeding, swimming behaviour, immune function, and the ability to cope with subsequent stressors ([Cooke et al., 2002](#); [Skomal, 2007](#)). Importantly, a stress response can ultimately affect future fitness ([Pankhurst and Van Der Kraak, 1997](#)) by diverting energy from important investments (e.g., growth, reproduction) to those triggered by the endocrine response (e.g., respiration, cardiac output, gluconeogenesis). Corticosterones such as cortisol directly inhibit androgen synthesis, thus both chronic and acute stressors can influence reproduction (see review by [Schreck, 2010](#)). Given that stressed individuals are more likely to invest minimally into reproduction (see [Wingfield and Sapolsky, 2003](#)), the life stage of by-catch could influence the degree of its stress response and whether reproduction is affected.

Nearly all of the research papers we found that examined effects of capture on growth and reproduction focused on non-legal sized and female crustaceans discarded from trap fisheries. Long-term monitoring of individuals is viable for crustaceans because they often have small home ranges and so can be tagged and recaptured ([Davis, 1980](#)), or held in field enclosures and monitored ([Brouwer et al., 2006](#)). In echinoderms and crustaceans, injuries can reduce foraging efficiency, alter mating success and behav-

iours, increase susceptibility to intra- and inter-specific attacks and decrease reproductive development ([Juanes and Smith, 1995](#); [Bergmann et al., 2001](#); [Warrenchuk and Shirley, 2002](#); [Brouwer et al., 2006](#)). Capture and release commonly results in physical damage, including appendage loss, which can decrease the growth rate and moult increment and alter the timing of ecdysis ([Kuris and Mager, 1975](#); [Davis, 1980](#); [Juanes and Smith, 1995](#); [Brouwer et al., 2006](#)). In fact, [Kuris and Mager \(1975\)](#) found that the degree of moult increment reduction was directly linked to the degree of injury. Not surprisingly, decapod crustaceans with damaged chelae have significantly impaired feeding and foraging efficiency ([Juanes and Smith, 1995](#)). Lobsters affected by loss or damage to appendages may be forced to select smaller prey, resulting in a lower energy intake or perhaps a change in diet altogether ([Juanes and Smith, 1995](#)).

Capture in pot fisheries can also affect reproduction in crustaceans. Oviparous crustaceans carry their eggs externally, meaning that direct physical damage to eggs can easily occur during the course of capture and release ([Darnell et al., 2010](#)). Exposure to rapid temperature changes during sorting can also decrease reproductive output ([Carls and O'Clair, 1995](#)). [Carls and O'Clair \(1995\)](#) found that in sublegal-sized tanner crabs (*Chionoecetes bairdi*) discarded from a commercial pot fishery, egg survival, zoeal production, zoeal viability, viability of extruded clutch and larval swimming ability and viability were not affected by air exposure. However, egg extrusion and timing of larval release were marginally affected. Their findings suggested that exposure to cold air during a commercial pot fishery does not result in changes in reproductive output. [Melville-Smith and de Lestange \(2007\)](#) examined the reproductive output of the western rock lobster in a similar commercial pot fishery with a focus on the effects of appendage loss. They observed a 3–9% decrease in the total number of eggs in captured females which was attributable to appendage loss. When female lobsters lost seven or more appendages, reproduction would cease, while a loss of five appendages would decrease the chance of having more than one clutch of eggs to 15% or less. [Darnell et al. \(2010\)](#) found that capture and release from a similar commercial pot fishery had minimal effects on egg viability in oviparous Atlantic blue crabs (*Callinectes sapidus*). In their study, egg mass was lower in pot captured crabs compared to control crabs. Additionally, the percentage of embryos exhibiting normal development decreased with successive clutch number, depending on the injuries incurred ([Darnell et al., 2010](#)). However, the oviparous crabs were removed immediately rather than held dry after capture, which is the practice of large-scale commercial potters.

Recent research on a sockeye salmon (*O. nerka*) commercial gillnet fishery in Alaska (USA) revealed that injuries caused by gillnet entanglement can have profound effects on spawning success ([Baker and Schindler, 2009](#)) and subsequently affect population dynamics ([Baker et al., 2011](#)). While numerous sockeye salmon are caught using gillnets in the marine environment on their approach to natal spawning sites, others escape through the mesh with substantial internal and external injuries (e.g., scale loss, dermal abrasion and stress), leaving them susceptible to fungal and bacterial infection. Using mark-recapture on pre-spawning adult salmon, [Baker and Schindler \(2009\)](#) found that fish with gillnet-related injuries (and accompanying fungal infections) were unable to maintain residence in their natal stream, whereby >50% of injured, returning adults failed to reproduce. In the same fishery, injuries sustained from gillnets exert distinct selective pressures when compared to harvest selection, as gillnet-injured fish that escaped fishing gear are considerably smaller than harvested fish ([Baker et al., 2011](#)). Moreover, [Baker et al. \(2011\)](#) reason that the selective pressure of delayed mortality affects age and size classes differently, and has the potential to modify the population structure of exploited stocks.

Laboratory experiments have shown that while avoiding trawl gear, Atlantic cod become physiologically stressed, perform an altered courtship sequence and produce eggs and larvae of poor quality (Morgan et al., 1999). Although the individuals that were subjected to capture and confinement stress were still able to spawn successfully, the study found that stressed adults produced abnormal larvae that would most likely produce inferior offspring. The idea that parental stress can reduce offspring quality and impair performance of the next generation is not completely novel in biology (Schreck et al., 2001; Schreck, 2010), but it is in the context of fisheries interactions. Similarly, there has been considerable research on the intergenerational effects of stress on offspring in the context of aquaculture, where adults face chronic confinement and other stressors which can compromise the quality of their offspring (see review by Schreck et al., 2001). It is not known whether these types of effects could be common in a fisheries interaction scenario. Intergenerational effects of stress would perhaps be more likely to manifest where an individual experiences multiple captures, or where capture occurs during the reproductive period, whereby high circulating stress hormones are transferred onto developing gametes.

We found one example from the literature of sublethal fitness impacts on mammals caused by fishing gear interactions. Dolphin populations declined dramatically in the 1960s and 1970s due to high bycatch mortality in purse seine fisheries targeting tuna. Despite reducing mortality rates by 99% to sustainably low levels (Hall et al., 2000), some of the dolphin populations have not recovered to pre-fishery levels. Mortality was primarily reduced by facilitating the live release of dolphins encircled by the seines, rather than by reducing bycatch rates *per se*. Thus, high numbers of dolphins continue to experience the stress of capture without direct mortality, and this stress could be preventing population recovery (Gilman, 2011). For example, separation of mothers and their young calves is a regular occurrence (Edwards, 2007). During the “backdown” procedure where the tuna boats reverse rapidly to sink the cork line and facilitate dolphin escape from the pursed net, calves outside of the net have been observed pushing at the netting to try to rejoin their parents. Once dolphins escape seines, they often exhibit some of their highest swimming speeds as they leave the area of the boat, at which point calves can become orphaned if they are in the vicinity of the net (Archer et al., 2004), resulting in the immediate or delayed mortality of calves due to increased energy expenditure and a lack of nutrition (Edwards, 2002b, 2006; Southern et al., 2002; Noeren and Edwards, 2006; Wade et al., 2007). Purse seine sets on dolphins (see Hall, 1998) can even cause miscarriage in pregnant females; such is the extent of the acute stress of capture (Gilman, 2011). Moreover, the stress incurred by adult female dolphins in tuna purse seine fisheries has the potential to disrupt the lactation period of calf-bearing females (Curry, 1999). Such a disruption may be negatively impacting the growth of calves and in turn contributing to a decline in population productivity. Using aerial photography over a 16 year period, Cramer et al. (2008) were able to quantify the reproductive output of two dolphin subspecies (eastern spinner *Stenella longirostris orientalis* and northeastern pantropical spotted *Stenella attenuata attenuata*). The study revealed that there has been an increase in calf mortality and a decrease in the birth rate of delphinid calves. Collectively, this evidence suggests a negative relationship between purse-seine fishing activity and the reproductive output of two dolphin subspecies. Cramer et al. (2008) propose that the sublethal stress of fisheries capture is the proximate cause for the failure of dolphin populations to recover despite virtually eliminating bycatch mortality.

### 3.2.3. Immune function

There are only a few studies which directly indicate that capture can affect immune response (Lupes et al., 2006; Pribyl et al.,

2012). Evidence from outside the bycatch literature shows that stress impairs immune function (e.g., Pickering and Pottinger, 1985; Mommensen et al., 1999; Van Rijn and Reina, 2010). There are also studies which suggest an indirect effect of capture on immune response. Total haemocyte counts (THC) and phenyloxidase (PO) decrease as emersion time for lobsters is increased (Ridgway et al., 2006; Bernasconi and Uglow, 2008). This can leave lobsters more susceptible to subsequent infection whose resolution would necessarily draw from other parts of the energetic budget of the animal (Ridgway et al., 2006). Research on dolphin interactions with purse seine fisheries has focused on sublethal effects like the continuous acute stress (CAS) response (Myrick and Perkins, 1995; St. Aubin, 2002), hyperthermic stress (Pabst et al., 2002), and disease and muscle damage (Cowan and Curry, 2002; St. Aubin et al., 2013). Although Romano et al. (2002) failed to detect a change in the immune function of repeatedly chased and captured dolphins, the authors suggest that the observed changes in lymphocyte percentages over the short study period may reveal an increased susceptibility to disease weeks after the initial chase through the gradual weakening of immune defenses.

## 4. Synthesis and future research directions

Our survey of the literature revealed that there has been little research focused on sublethal fitness endpoints in bycatch and discards. Most of the sublethal measurements in the bycatch literature (111 of 133 studies) have been acute metrics; physiological disturbance and injury at the time of capture – and mostly in teleosts and elasmobranchs. The obvious gap that emerges is the lack of research linking at-release measurements with latent sublethal fitness outcomes such as foraging, energetics, growth, reproduction and offspring quality. The dearth of knowledge in this area is likely based on two realities: (1) a justifiable focus on simply quantifying and reducing bycatch mortality, and (2) the difficulty of long-term monitoring of fitness outcomes in wild animals. Of the reviewed studies, several indicated that physiological disturbance, injury or behavioural impairments may have had long-term implications for growth and reproductive fitness. Further study of sublethal effects could clarify previously unaccounted-for population level consequences of fisheries and better conservation practices to mitigate the impacts of fisheries. In the context of improving the welfare of bycatch (Diggles et al., 2011), and with imperiled animals where legal instruments often include verbiage about not harming, harassing or stressing animals, sublethal endpoints may become increasingly common, necessary and relevant. Indeed, addressing sublethal aspects of bycatch may also be relevant for the certification of marine seafood as “sustainable” (Ponte, 2012).

Although there has been some notable research on crustaceans and mammals, most taxa remain almost wholly unrepresented, particularly fishes, turtles and birds. Research focus is most warranted in scenarios where bycatch and discarding rates are high, where threatened species are affected, or where bycatch mortality has been reduced but populations have not recovered (e.g., some Pacific dolphin species, see Cramer et al., 2008). The highly variable nature of the physiological stress response makes it difficult to predict if a tertiary stress response will occur, that is – long term reductions in fitness (a sublethal effect). Linking stress responses with fitness has been a rare feat in the broader realm of ecological physiology. Research has also demonstrated that a fisheries interaction acutely changes behaviour, but long-term fitness is difficult to predict using behaviour alone. Injury may be the most important consideration where sublethal outcomes such as reduced growth and fitness are concerned, simply because injuries are often irreversible and energetically costly to overcome. Evidence from the literature seems to support this idea, although it may depend

on taxa. For example, in fishes and crustaceans, injury may be particularly important (Brouwer et al., 2006; Baker and Schindler, 2009), whereas in higher-level vertebrates the more complex perception and reaction to a stressor may mean that stress alone can have consequences (e.g., miscarriage mother–calf separation in dolphins escaping from purse seines, Edwards, 2007; Cramer et al., 2008). To date, few studies have successfully linked the severity of injury to reproductive success (except see Melville-Smith and de Lestange, 2007; Darnell et al., 2010; Baker and Schindler, 2009).

In general, advancing our understanding of sublethal fitness outcomes will require creativity and methodological solutions tailored to specific issues and systems. However, the following four general study designs could be used to assess whether delayed sublethal fitness effects occur in bycatch. (1) Use of biotelemetry (Cooke et al., 2004) to determine if an individual migrates to a spawning area. This type of study requires previous knowledge of areas where reproduction occurs and assumes that individuals that make it to those areas breed successfully. This could be carried out in real or simulated fisheries, or existing data sets could be used in cases where tagged animals have been captured and released. (2) Quantification of reproductive success of individuals at spawning/breeding grounds, by comparing individuals with and without macroscopic fishing injuries (e.g., Baker and Schindler, 2009). This study type would measure reproductive success directly, although it would not include individuals that could not reproduce that season due to other sublethal effects (e.g., failed to complete migration, determined using a study design described by '1' above). (3) Measurement of genetic material of adult bycatch released alive, and of control animals sampled immediately after or during reproduction, followed by sampling of resulting offspring in populations with known nursery habitat. This approach would enable direct assessment of individual genetic contribution to the next generation. Such an ambitious study would require a small adult population, such as with some sea turtle populations, as well as previous knowledge of nursery habitat, along with long-term data collection. (4) Holding studies where relevant species are habituated and subjected to simulated capture, followed by long-term analyses of behaviour (e.g., Olla et al., 1997), growth rates (e.g., Brouwer et al., 2006), and reproductive metrics (e.g., Carls and O'Clair, 1995). Once sublethal effects are quantified on an experimental basis, scaling up those effects to predict population-level consequences is a challenge that would likely require an approach unique to specific systems, in addition to continued field validation. Ongoing collection of observer data would be required for such applications whereby the condition and number of individuals being released are combined to adjust recruitment models using condition scores (e.g., severity of injury) that are linked back to fitness outcomes for individuals based on experimental work (analogous to the RAMP approach for predicting mortality; Davis, 2010).

## 5. Conservation, management, and social considerations

Some conservation and species recovery plans could benefit from an improved understanding of the sublethal effects of bycatch, although to date sublethal effects are largely unknown. Recent changes to IUCN include a stress classification scheme (Version 1 – June 2012), which includes mortality but also 'indirect species effects' such as injury or reduced reproductive success. Few, if any, of these criteria have been applied to red-listed species whose assessments identify bycatch as a major threat. Green turtles (*Chelonia mydas*) are classified as endangered by IUCN, and incidental fisheries mortality is identified as a problem. However, while female, nest, and egg numbers are quantified annually, no connections to bycatch or related injuries currently exist (IUCN,

2013). Antipodean Albatross (*Diomedea antipodensis*) are listed as vulnerable in IUCN legislation, partly because of the bycatch mortality in longline fisheries (mostly females; Birdlife International, 2012). Harrison's Dogfish (*Centrophorus harrissoni*), an IUCN red-listed elasmobranch, is noted as suffering from high bycatch in upper slope trawl and longline fisheries (Graham, 2013) but sublethal measurements such as injury are not mentioned for either species. While the development of the IUCN stress classification scheme (Version 1) provides some encouragement that sublethal effects are beginning to be considered by conservation practitioners, this scheme has largely not been implemented. For almost all conservation plans for threatened species, sublethal effects currently represent a 'known unknown'. Before the sublethal effects of bycatch can be addressed by conservation practitioners, more resources need to be directed towards understanding whether this is a significant issue across multiple systems.

Of late, risk assessments have been used to assess the risk of post-capture mortality. Included in most of these assessments are sublethal metrics (e.g., animal condition assessments, including injury), which can be recorded by on-deck observers (Vaughn et al., 2008; Braccini et al., 2012; Gallagher et al., 2012). Animal condition assessments can be developed so as to be consistent and objective across observers, using a presence-absence approach to quantifying reflex impairment or injury (see Davis, 2010; Campbell et al., 2010). Although such metrics are normally used to predict post-capture mortality, sublethal on-deck impairment and injury have been shown to negatively influence fitness in some contexts. Thus, a precautionary approach would involve assuming animals released in poorer condition (i.e., more lethargic and injured) are more likely to experience negative outcomes – inclusive of mortality and sublethal loss of fitness. Management could use economic incentives to encourage fishers to develop ways to improve the condition of bycatch that is discarded (Hall et al., 2000). Effective techniques for improving animal condition that are developed by fishers could eventually be taught to all those involved in the fishery using education programs.

## 6. Summary and conclusions

Although mortality is the simplest fitness endpoint for an animal released from fishing gear, this review demonstrates that sublethal effects should also be considered and can be important in some contexts. Capture and release can result in altered courtship, failure to spawn (e.g., semelparous salmon dying prior to spawning), reduced reproductive output (e.g., egg re-absorption), damage to offspring (e.g., damage to eggs in overigerous crabs, miscarriage in pregnant dolphins), and reduced future reproductive output (e.g., decreased future clutch size in stressed and injured crabs). Many of these possible fitness consequences, and others such as delayed maturity or reduced offspring performance, have yet to be thoroughly investigated. Due to the highly variable inter- and intra-specific nature of the physiological stress response and the difficulty of studying behaviour in marine organisms, it may seem convenient to focus on injury alone. However, we caution against that. A variety of endpoints are needed to refine bycatch management strategies (e.g., informing which on-board handling strategies reduce stress) to maintain the welfare status of bycatch (Diggles et al., 2011) and to ensure that interactions with endangered wildlife are done in a manner consistent with legislation and conservation plans.

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