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The understudied and underappreciated role of predation in the mortality of fish released from fishing gears

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Abstract

The assumption that animals released from fishing gears survive has frequently been scrutinized by researchers in recent years. Mortality estimates from these research efforts can be incorporated into management models to ensure the sustainability of fisheries and the conservation of threatened species. Post-release mortality estimates are typically made by holding the catch in a tank, pen or cage for short-term monitoring (e.g. 48 h). These estimates may be inaccurate in some cases because they fail to integrate the challenges of the wild environment. Most obvious among these challenges is predator evasion. Stress and injury from a capture experience can temporarily impair physiological capacity and alter behaviour in released animals, a period during which predation risk is likely elevated. In large-scale commercial fisheries, predators have adapted their behaviour to capitalize on impaired fishes being discarded, while in recreational catch-and-release fisheries, exercise and air exposure can similarly impede the capacity for released fish to evade opportunistic predators. Owing to the indirect and often cryptic nature of this source of mortality, very few studies have attempted to document it. A survey of the literature demonstrated that <2% of the papers in the combined realms of bycatch and catch-and-release have directly addressed or considered post-release predation. Future research should combine field telemetry and laboratory studies using both natural and simulated predation encounters and incorporate physiological and behavioural endpoints. Quite simply, predation is an understudied and underappreciated contributor to the mortality of animals released from fishing gears.

Keywords Bycatch, discards, fish behaviour, fish impairment, unobserved mortality

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Introduction

In recent years, the literature on the fate of fishes and other animals released from fishing gears has grown rapidly (e.g. Davis 2002, 2010; Broadhurst *et al.* 2006; Coggins *et al.* 2007; Donaldson *et al.* 2008). Releasing of fish and other animals, including target species, occurs in both commercial and recreational sectors due to management regulations requiring release based on harvest regulations (e.g. focused on animal size, season, quantity, species; Johnson and Martinez 1995; Hall *et al.* 2000; Ryer 2002), and because of lack of economic value or market (Hall 1996), or due to conservation ethic (Arlinghaus *et al.* 2007; Cooke and Schramm 2007). No matter the reason, releasing animals from fishing gears alive is associated with an assumption of survival and that no reduction in fitness will result (Broadhurst *et al.* 2005; Cooke and Schramm 2007; Pollock and Pine 2007; Hall *et al.* 2009). However, this premise has come under scrutiny (e.g. Chopin and Arimoto 1995; Davis 2002; Coggins *et al.* 2007) and is of concern in some fisheries to managers and conservation scientists given the high number of fishes and other animals released. An estimated 7.3 million tonnes of fish biomass is discarded at sea from commercial fisheries each year (Kelleher 2005), and bycatch and discard rates are simply unknown for many fisheries (e.g. in freshwater and small-scale fisheries; Raby *et al.* 2011). In recreational fisheries, release rates vary widely among species (Cooke and Suski 2005), gear types and angler types, but are sometimes quite high (Muoneke and Childress 1994; Bartholomew and Bohnsack 2005; Arlinghaus *et al.* 2007). For example, release rates for specialized fisheries such as bonefish (Policansky 2002) and muskellunge (Kerr 2007) often exceed 95%. Global estimates of recreational fishing release rates suggest that as many as 30 billion fish, representing approximately 60% of captured fish, are released annually with an estimated mass of over 10 million tonnes (Cooke and Cowx 2004). Evidently, research on the fate of animals released from fishing gears represents a useful step towards ensuring sustainable fisheries and the development of effective management and conservation plans.

By far, the most commonly employed means of studying post-release mortality (PRM) is the use of artificial enclosures (tanks and pens; Cooke and Schramm 2007). Research studies evaluating mortality that include long-term monitoring and sublethal endpoints of fish released into the wild are far fewer, despite the fact that their findings are more robust (Cooke and Schramm 2007; Donaldson *et al.* 2008). A standout limitation of using artificial holding environments is that it is not possible to account for 'indirect' sources of mortality, such as predation. Indeed, post-release predation (PRP) has not often been seriously considered as a source of mortality for the diversity of animal taxa that are captured and released, and as such has rarely been studied, despite being first introduced in the literature more than 30 years ago (see Jolley and Irby 1979). Perhaps the reason for this apparent lack of attention is the inherent difficulty in studying it: PRP is cryptic and may occur hours to days after release (Coggins *et al.* 2007). Although predation is a natural occurrence and an important mediator of community interactions in aquatic ecosystems (Kerfoot and Sih 1987), animals released in an impaired condition are at an elevated risk of predation until they recover from capture-caused exhaustion. Despite the fact that predators are a potentially important source of mortality for released animals, to date there have been few studies that have considered PRP, and even fewer that directly addressed the issue. Moreover, reviews of bycatch, discards and catch-and-release (C&R) recreational fisheries have often lacked substantial discussion of PRP and/or failed to highlight the lack of available data (Hall 1996; Davis 2002; Cramer 2004).

The primary objective of this article is to draw attention to PRP as an understudied issue in fisheries science. We broadly use the term 'post-release' to include both animals landed and released and animals that encounter and subsequently escape fishing gear (e.g. Chopin and Arimoto 1995; Ryer 2004). Although it is an important and related topic, we do not include depredation, wherein predators remove or kill fish hooked on longlines or rod and reel, or entangled in gill nets prior to landing (e.g. Zollett and Read 2006; Sigler *et al.* 2008; O'Toole *et al.* 2010). It is not our objective to provide an overlong accounting of all current knowledge on PRP, particularly given that as an area of research, PRP is in its infancy so such analyses would be premature. As such, the paper is divided into four brief sections: (i) results of a literature survey, (ii) highlights of relevant findings and concepts, (iii) identification of research opportunities and (iv) synthesis and conclusions. We acknowledge and recommend the excellent review by Ryer (2004) on behavioural impairment of fish escaping trawls that focused on synthesizing three laboratory studies. Cooke and Cowx (2006) suggested there are similarities between commercial and recreational fishing sectors that provide opportunities for knowledge crossover and for addressing common issues, such as the fate of released animals. Therefore, our approach is global, inclusive of both recreational and commercial fisheries in marine and freshwater environments. Given that this is a fish-oriented journal and acknowledging that the expertise of the authors is in the realm of fishes, the review naturally tends to focus on fishes from a conceptual standpoint, without wholly excluding other taxa (e.g. the shellfish literature). It is our hope that this paper will draw attention to the potential magnitude and consequences of PRP on released animals, leading to additional research that could inform effective management and conservation of aquatic biota.

Literature survey

We conducted a literature survey that focused on research papers that contained a study objective related to PRP, made obvious through description of study objectives and/or study design. However, we also attempted to locate PRM papers whose text included the word 'predation', 'predators' or 'killed' (e.g. to locate phrases like 'individual X was killed by a shark after release'). Web of Science (ISI) and Google Scholar were used for this search. An initial search was conducted between 1 November 2009 and 18 February 2010, which was subsequently revised and updated between 1 May 2012 and 19 July 2012. Additional papers were located by using cited reference searches and through manual examination of reference lists.

We found 25 papers that in some form sought to study PRP (listed in Table 1). This represents a small proportion of the studies that have been conducted on PRM. For context, Donaldson *et al.* (2008) surveyed the recreational C&R literature and identified a total of 242 papers related to C&R mortality. The commercial bycatch/discards literature is even larger, with >1000 papers from the marine environment and approximately 40 in freshwater (although many bycatch papers do not focus on PRM; Raby *et al.* 2011). During our search for studies focusing on PRP, we also identified 56 papers on PRM that gave some mention to predation as a potential contributor to mortality, albeit without any incorporation of predation into study objectives. Locating papers that merely mention PRP was not a focus of our search; therefore, we assume that the number of such papers substantially exceeds 56. In general, it is evident that many (or most) fisheries scientists who study PRM are aware of capture-mediated predation as a potential confounder of mortality estimates derived using traditional research methods. Nevertheless, studies focusing on PRP represent <2% of the combined realms of C&R and the bycatch/discard literature, and we hope that this review will stimulate further interest in the topic.

There are related papers and areas of study that commonly appeared in our searches that were not included in our list of PRP papers (Table 1). For example, in some studies on PRM, there was incidental documentation of predation without *a priori* objectives made obvious in the introduction or methods of those papers (e.g. Thorstad *et al.* 2004; Overton *et al.* 2008). Likewise, papers focusing on basic biology that incidentally documented predation events were not included – such as in the satellite tagging of large marine pelagics (e.g. Block *et al.* 1992; Kerstetter *et al.* 2004). There has also been substantial research on the behavioural ecology of predator-prey interactions in fishes (reviewed by Mesa *et al.* 1994; Godin 1997), and considerable knowledge has been developed

Table 1 List of peer-reviewed papers located using a literature survey that contained study objectives related to post-release mortality for animals released from fishing gears ($N = 25$), either made obvious in the introduction or the methods of those papers. Papers that incidentally documented post-release predation (PRP) without *a priori* study objectives were not included in this list.

N	References	Released species	Fishing sector	Study approach	PRP observed?	Predator type
1	Jolley and Irby (1979)	Atlantic sailfish (*Istiophorus albicans,* Istiophoridae)	Marine recreational, rod and reel	Caught and released fish manually tracked in the open ocean using acoustic telemetry	Yes	Shark
2	Brown and Caputi (1983)	Western rock lobster (*Panulirus cygnus*, Palinuridae)	Marine commercial, trap net	Laboratory and field observations of behaviour and predation rates following air exposure	Yes	Octopus
3	Vermeer (1987)	Spiny lobster (*Panulirus argus*, Palinuridae)	Marine commercial, trap net	Laboratory-based assessment of physiological disturbance, escape response and antipredator defence after air exposure	No	Not specified
4	Evans *et al.* (1994)	34 fish species and 23 invertebrate taxa	Marine commercial, trawl	Trial releases of live discards from a commercial vessel with direct observation of immediate predation by birds	Yes	Seabirds
5	Gitschlag and Renaud (1994)	Red snapper (*Lutjanus campechanus,* Lutjanidae)	Marine recreational, rod and reel	Used divers to follow released fish and monitor PRP in the field	No	N/A
6	Olla *et al.* (1997)	Walleye pollock (*Theragra chalcogramma,* Gadidae)	Marine commercial, trawl	Used simulated trawling in the laboratory, subjected discards to presence of predators and monitored predation rates relative to control fish	Yes	Sablefish (*Anoplopoma fimbra*, Anoplopomatidae)
7	Ross and Hokenson (1997)	American plaice (*Hippoglossus platessoides*, Pleuronectidae), winter flounder (*Pseudopleuronectes americanus,* Pleuronectidae), witch flounder (*Glyptocephalus cynoglossus,* Pleuronectidae), pollock (*Pollachius virens*, Gadidae)	Marine commercial, trawl	Fish captured in the field in an operational fishery, and immediate PRP at the surface observed after a 1- to 2-h holding period	Yes	Great black-backed gulls (*Larus mariuns*, Laridae)

Table 1 (Continued).

N	References	Released species	Fishing sector	Study approach	PRP observed?	Predator type
8	Broadhurst (1998)	Whiting (*Sillago* spp., Sillaginidae)	Marine commercial, trawl	Video monitoring used to document rates of dolphin predation on small fish escaping a trawl codend	Yes	Bottlenose dolphin (*Tursiops truncatus*, Delphinidae)
9	Ramsay and Kaiser (1998)	Whelks (*Buccinum undatum*, Buccinidae)	Marine commercial, scallop dredge	Laboratory-based evaluation of righting response and predator evasion behaviour following simulated encounter with scallop dredge	No	Starfish (*Asterias rubens*, Asteriidae)
10	Milliken *et al.* (1999)	Atlantic cod (*Gadus morhua*, Gadidae)	Marine commercial, longline	Visual observation in field setting of at-surface predation on released fish conducted alongside cage holding study	Yes	Seabirds
11	Pepperell and Davis (1999)	Black marlin (*Makaira indica*, Istiophoridae)	Marine recreational, rod and reel	Acoustic telemetry used to monitor post-release behaviour for up to 27 h	Yes	Shark
12	Jenkins and Brand (2001)	Great scallop (*Pecten maximus*, Pectinidae)	Marine commercial, scallop dredge	In the laboratory, dredge capture simulated and its effects on predator-relevant escape response tested	No	Starfish (*A. rubens*, Asteriidae), crab (*Cancer pagarus*, Cancridae)
13	Ryer (2002)	Walleye pollock	Marine commercial, trawl	Used simulated trawling in the laboratory, subjected escapees to predators and monitored predation rates relative to control fish	Yes	Lingcod (*Ophiodon elongatus*, Hexagrammidae)
14	Ryer (2004)	Atlantic cod, walleye pollock, sablefish	Marine commercial, trawl	Review and synthesis of three laboratory investigations on impairment of and predation upon trawl codend escapees	No	N/A
15	Cooke and Philipp (2004)	Bonefish (*Albula vulpes*, Albulidae)	Marine recreational, rod and reel	Visual observation and acoustic transmitter tags used to monitor post-release movement of angled fish	Yes	Lemon sharks (*Negaprion brevirostris*, Carcharhinidae)
16	Ryer *et al.* (2004)	Sablefish	Marine commercial, trawl	Laboratory experiments with simulated trawling and subsequent monitoring of behavioural impairment and mortality rates in the presence of predators	Yes	Lingcod
17	Davis and Parker (2004)	Sablefish	Marine commercial, non-specific	Fish exposed to air in laboratory experiment and tested for behavioural impairment related to predation risk	No	N/A

Table 1 (Continued).

N	References	Released species	Fishing sector	Study approach	PRP observed?	Predator type
18	Parsons and Eggleston (2005)	Spiny lobster	Marine recreational, divers with hand-nets	Tethering experiments in the field used to compare predation rates between control animals and those subjected to capture stress and injury	Yes	Sharks
19	Parsons and Eggleston (2006)	Spiny lobster	Marine recreational, divers with hand-nets	Field and laboratory experiments used to examine behaviour and PRP following capture-release disturbance	Yes	Triggerfish (*Balistes capriscus*, Balistidae)
20	Danylchuk *et al.* (2007a)	Bonefish	Marine recreational, rod and reel	Fish angled and released in the field and visually tracked for approximately 1 h to monitor predation rates relative to control fish	Yes	Lemon sharks, great barracuda (*Sphyraena barracuda*, Sphyraenidae)
21	Danylchuk *et al.* (2007b)	Bonefish	Marine recreational, rod and reel	Fish angled or beach seined in the field, released with gastric-implanted acoustic transmitter and tracked for 3 weeks after release	Yes	Lemon sharks
22	Baker and Schindler (2009)	Sockeye salmon (*Oncorhynchus nerka*, Salmonidae)	Marine commercial, gill net	Bear predation rates on fish migrating through shallow streams with and without old gill net injuries	Yes	Brown bear (*Ursus arctos*, Ursidae)
23	Campbell *et al.* (2010a)	Red snapper	Marine recreational, rod and reel	In a laboratory setting, developed indicators of delayed mortality and PRP risk for predictive use in the field	No	N/A
24	Campbell *et al.* (2010b)	Red snapper	Marine recreational, rod and reel	Field study involving comparison of impairment levels with immediate release mortality and observation of predation at surface	Yes	Bottlenose dolphin, barracuda
25	Dallas *et al.* (2010)	Bonefish	Marine recreational, rod and reel	In a laboratory setting, examined chemical excretions of fish following simulated capture and studied behavioural response of a predator to those chemical cues	No	Lemon sharks

surrounding predator evasion by hatchery-reared fishes being released into the wild for stocking purposes (e.g. Olla and Davis 1989; Kellison *et al.* 2003; Masuda and Ziemann 2003). Some studies have examined predator aggregations around discarding commercial vessels – those papers generally focused on the biology and feeding ecology of the predators in relation to fishing activity (e.g. Kaiser and Spencer 1994; Ramsay *et al.* 1997; Hill and Wassenberg 2000; Veale *et al.* 2000; Link and Almeida 2002; Furness *et al.* 2007). For example, some researchers have inferred PRP of discards based on gut contents of predators surveyed in the area of an active fishery for which some discarding data exist (e.g. Kaiser and Ramsay 1997; Olaso *et al.* 1998). Those papers, while important in illustrating how fisheries discards change ecosystem structure, are unable to identify whether discards are already dead when consumed – a key consideration given that this paper is inherently about *unobserved* mortality. Thus, we confined this review to papers focusing on observations of the discarded prey species itself, being released alive with an assumption of survival (e.g. documenting predation rates, identifying factors relating to behavioural impairment). Nevertheless, research on shifts in predator gut contents in relation to fishing activity (Kaiser and Spencer 1994; Link and Almeida 2002) has provided evidence of the occurrence of PRP on live discards, leading to other studies directly examining PRP, notably of shellfish damaged by fishing gear (e.g. Ramsay and Kaiser 1998; Jenkins and Brand 2001).

Of the 25 relevant studies found (Table 1), 18 focused on fishes, six focused on shellfish, while one study monitored PRP on a range of fish and invertebrate taxa (Evans *et al.* 1994). No papers were located that addressed PRP of mammalian, avian or reptilian taxa – presumably because it is a less common issue in those taxa than in small fish and shellfish. As such, the remainder of this paper is focused primarily on fishes although we acknowledge that PRP could be a problematic issue for non-fish taxa in some contexts. There was a notable concentration of the research in four distinct 'themes', usually associated with a specific region, group of species, fishery type and/or research team. The first 'theme' involved four laboratory studies conducted at the Hatfield Marine Science Centre (Newport, OR, USA) that focused primarily on sablefish (*Anoplopoma fimbria*, Anoplopomatidae) and walleye pollock (*Theragra chalcogramma*, Gadidae) subjected to simulated capture (Olla *et al.* 1997; Ryer 2002; Davis and Parker 2004; Ryer *et al.* 2004). The second 'theme' involved a series of field and laboratory experiments in The Bahamas that have examined PRP on bonefish (*Albula vulpes*, Albulidae) angled in a sports fishery (Cooke and Philipp 2004; Danylchuk *et al.* 2007a,b; Dallas *et al.* 2010). The third 'theme' focused on red snapper (*Lutjanus campechanus*, Lutjanidae) captured in a Gulf of Mexico sport fishery (Gitschlag and Renaud 1994; Campbell *et al.* 2010a,b), and this research is ongoing (K. Drumhiller, personal communication). Finally, there have been a series of papers on behavioural impairment and PRP risk in lobster in Australian and Floridian fisheries, namely western rock lobster (*Panulirus cygnus*, Palinuridae; Brown and Caputi 1983) and spiny lobster (*Panulirus argus*, Palinuridae; Vermeer 1987; Parsons and Eggleston 2005; Parsons and Eggleston 2006).

Ten of the 25 papers listed in Table 1 describe laboratory studies, two were combined laboratory/field studies (Brown and Caputi 1983; Parsons and Eggleston 2006), and the remainder (13) were field studies. The one study that took place in freshwater (Baker and Schindler 2009) involved only a minor component on PRP and used sockeye salmon (*Oncorhynchus nerka*, Salmonidae) that had incurred gill net injuries in the marine environment *en route* to spawning areas in freshwater. Thus, all 25 studies were from a marine fisheries context: 15 involving commercial gears (nine trawl, two scallop dredge, two lobster trap, one gill net and one mixed) and 10 from recreational fisheries (eight rod and reel and two sport diving).

Post-release predation is thought to occur partly as a result of physiological and behavioural impairment in fish being released that renders them incapable of evading predators. Ten of the studies we found used metrics for assessing behavioural impairment (Olla *et al.* 1997; Jenkins and Brand 2001; Ryer 2002, 2004; Cooke and Philipp 2004; Davis and Parker 2004; Ryer *et al.* 2004; Danylchuk *et al.* 2007a; Campbell *et al.* 2010a,b). For example, Olla *et al.* (1997) monitored swimming capacity and feeding behaviour subsequent to simulated capture in (in addition to measuring plasma physiology and predation rates). Danylchuk *et al.* (2007a) demonstrated that bonefish angled and released with negative orientation were significantly more likely to be killed by a lemon shark (*Negaprion brevirostris*, Carcharhinidae) within minutes of release than those able to maintain positive equilibrium. Physiological metrics have been used in four laboratory studies: Olla *et al.* (1997) and Campbell *et al.* (2010a) measured plasma cortisol to monitor the relative effects of their fishing simulations, and Dallas *et al.* (2010) measured excretions of cortisol, lactate, urea and ammonia by exhausted bonefish and the accompanying behavioural response of a predator exposed to those olfactory cues. Hemolymph pH, lactic acid and ammonia were monitored in spiny lobsters exposed to air in a further laboratory study by Vermeer (1987) – measurements that accompanied metrics of antipredator defence and escape behaviour.

Monitoring of predation on released fish in the field was accomplished by visual observation in a number of studies, with such observations generally limited to the short term (<1 h; Gitschlag and Renaud 1994; Cooke and Philipp 2004; Danylchuk *et al.* 2007a) or exclusively to immediate predation by seabirds at the surface (Evans *et al.* 1994; Ross and Hokenson 1997). A few studies attempted to identify PRP events using biotelemetry, sometimes through fortuitous direct observation during manual tracking of released animals (Jolley and Irby 1979; Cooke and Philipp 2004; Danylchuk *et al.* 2007a) and sometimes through inferences drawn from the tracking data (Pepperell and Davis 1999). Gitschlag and Renaud (1994) used divers to follow discarded animals as they descended back to the sea floor from the fishing vessel, but did not observe a single predation event – highlighting the notion that predator abundance could be a key variable to consider in predation studies. PRP has also been instigated in a laboratory environment following capture simulation where discards were released alongside control fish into tanks containing predators (Brown and Caputi 1983; Olla *et al.* 1997; Ryer 2002, 2004; Ryer *et al.* 2004). As with most fields of study, laboratory simulations have obvious limitations. However, so long as absolute rates of predation are kept in context, these studies have been helpful in understanding mechanisms and factors associated with PRP mortality (e.g. Olla *et al.* 1997; Ryer 2002).

Key findings and relevant concepts

Stress and injury

When predators are the proximate cause of mortality for fishes released from fishing gears, the ultimate cause of the predation event is anthropogenic imposition of stress and injury. A fish's encounter with fishing gear always includes both physical injury (Trumble *et al.* 2000; Baker and Schindler 2009) and physiological stress (Wood *et al.* 1983); indeed, it is not possible to capture a fish, at least on a hook, without causing both (Cooke and Sneddon 2007). Examples of common physical injuries are hooking wounds, loss of protective mucous, scale loss, skin loss or loss of appendages (e.g. fins, opercula), all of which can lead to fungal infections (Davis 2002; Baker and Schindler 2009). Severe injuries have the potential to increase predation risk if they alter the morphology of the fish significantly enough to detract from swimming performance (Brouwer *et al.* 2006), hinder defensive capabilities (Parsons and Eggleston 2005), or if they increase the conspicuousness of the animal (Mesa *et al.* 1994). Similarly, significant blood loss or exposure of subsurface tissues could cause short-term performance impairment and attract the attention of predators through chemosensory cues (Parsons and Eggleston 2005). From the shellfish literature, it is known that the extent of damage to shellfish following gear encounters positively influences their attraction of predators and scavengers (Jenkins *et al.* 2004). In addition to injury, fisheries capture usually involves exhaustive anaerobic exercise (caused by struggling in a net or on a line) and air exposure (during landing, de-hooking or sorting). During recovery from these physiological disturbances, the scope for activity in fish is often severely reduced (Jain and Farrell 2003). The result can often be fish released with loss of equilibrium (i.e. no swimming ability), a state of obvious vulnerability to predation (Danylchuk *et al.* 2007a). Aside from swimming performance, the stress of exhaustion could sufficiently impair fish that they fail to engage in predator avoidance behaviour, including shoaling, the use of refugia or other decision-making processes associated with minimizing predation risk (Mesa *et al.* 1994; Ryer 2004). In a novel experiment, Dallas *et al.* (2010) found evidence that as a consequence of capture-related exhaustion stress, bonefish provide olfactory cues for lemon sharks that an opportunistic feeding opportunity is nearby. Over the long term, the immune-suppressing effect of a capture-induced stress response could interact with physical injury, leading to infection and disease (Lupes *et al.* 2006) that could impair predator evasion behaviour while disease is being overcome (or it could directly lead to mortality in the absence of predators).

Predator behaviour

Predators have adapted their behaviour to capitalize on animals weakened (or killed) by capture. Scavengers have been observed following trawls until discarding occurs and often congregate during the haul of nets (Hill and Wassenberg 2000; Ryer 2002; Broadhurst *et al.* 2009). Following commercial fishing vessels provides scavengers and predators ample opportunity to prey on both escaped and discarded animals (Ryer 2002). As a result, many predators have learned to associate commercial boats with food availability (Stevens *et al.* 2000). Apex predators can congregate around schools of fish, choosing fish that escape netting (Broadhurst 1998), that lose the ability to shoal or that fall behind as a result of capture (Ryer 2002). Injured and stressed animals emit chemical cues that attract predators (Jenkins *et al.* 2004; Dallas *et al.* 2010). This is especially true following trawls where a large percentage of animals are injured (Ryer 2002). Bottlenose dolphins (*Tursiops truncatus*, Delphinidae) have been particularly successful at taking advantage of fishing activities, and have been observed actively pushing at the cod-end netting of prawn trawls in order to free struggling undersized fish that then make easy targets (Broadhurst 1998). Dolphins are quite selective during this process, choosing fish and squid over crustaceans (Broadhurst 1998). In a laboratory experiment, octopus predators exclusively chose to attack lobsters that had been exposed to air, ignoring those lobsters that had not been exposed and despite multiple hours of recovery for the prey before predator exposure (Brown and Caputi 1983). Predation can also affect the fitness of animals that provide parental care in that predation of their offspring occurs during temporary removal of the parent by a recreational angler, a phenomenon that has been well studied among the black bass, *Micropterus* spp. (e.g. Kieffer *et al.* 1995; Suski *et al.* 2003; Steinhart *et al.* 2004; Hanson *et al.* 2007).

Predator abundance

The number and type of predators in the area of release from fishing gear can affect the likelihood of PRP occurring, in addition to whether refuge is available nearby. Cooke and Philipp (2004) examined the effect of predator density on PRP of bonefish. They released angled fish into high- and low-density environments and determined that almost 40% of the bonefish released in high predator density areas succumbed to predation, despite the fact that they had been more carefully handled than bonefish in low predator areas, while in the low predator density area, all released bonefish survived. Danylchuk *et al.* (2007a) examined whether refuge from predators played an important role in PRP. They released bonefish at varying distances to adjacent mangroves where bonefish could seek shelter, but found that distance from shelter did not play a significant role in predation and that some fish (20%) swam away from the mangrove into deep water. It was suggested that bonefish may avoid mangroves due to the fact that they are often nursing grounds for their predators, lemon sharks (Danylchuk *et al.* 2007b). Researchers believe that bonefish can alter their behaviour in the presence of predators and potentially threatening habitat. Specifically, bonefish can alter their swimming speed, exhibit shoaling tendencies and avoid typical predator habitat (Cooke and Philipp 2004; Humston *et al.* 2005; Danylchuk *et al.* 2007b). This demonstrates that the location of release may affect how bonefish avoid predation. Therefore, where an angler chooses to release fish will ultimately play a role in susceptibility to predation (Danylchuk *et al.* 2007b). In general, the abundance of predators at a release site has not been quantified or considered in studies of PRM, and could be a major cause of context-specific variation in mortality rates.

Fish size

An important consideration in predator-prey ecology is size, both of predators and of prey, which may have relevance in the context of PRP. In our literature search, we exclusively found studies from the marine environment and did not find a single research example of PRP in a freshwater fishery. At a broad scale, the diversity and size of predators tends to be higher in the marine environment than in freshwater, evidenced by the longer food chains in the marine environment, particularly when marine mammals are factored in (Vander Zanden and Fetzer 2007). With increasing predator body size, the range of prey sizes eaten expands (Scharf *et al.* 2000) and, with very few exceptions, predators tend to be larger than their prey (Layman *et al.* 2005). The contrast in predator sizes between marine and freshwater systems may be especially true when comparing freshwater ecosystem types where most freshwater fisheries research capacity exists – in North America, Australia and Europe – and may explain the focus on marine issues in the PRP literature. For example, freshwater recreational fisheries in many cases are releasing fishes that are themselves top predators, inherently limiting their risk of predation (e.g. northern pike, *Esox lucius*, Esocidae). Gape limitation means that each predator is limited as to the size of prey it is physically capable of ingesting. In a natural context, the escape response of prey is associated with body size, with smaller fish being more susceptible to predation because of decreased visual acuity and swimming performance (Scharf *et al.* 2000). A general assumption one might then make is that smaller fish and shellfish will tend to be more vulnerable to PRP. Certainly that would be the case when considering the example of predation by dolphins (Broadhurst 1998). Dolphins are among the most intelligent aquatic animals and have learned to capitalize on fish escaping and being discarded from commercial fisheries, but because of gape limitation mostly focus on taking small-bodied fishes (Broadhurst 1998). In making decisions about which prey to target, predators must consider the relative costs of pursuit, capture, ingestion and digestion (collectively known as handling time; Godin 1997; Woodward and Warren 2007). If a potential prey item has been recently discarded from a commercial fishery and is impaired through either injury or exhaustion, the pursuit and capture components of handling time decrease considerably, making predation attempts more likely. Larger prey have higher ingestion and digestion costs (Scharf *et al.* 2000; Woodward and Warren 2007), but with a decreased cost of pursuit and capture, even smaller predators may attempt to prey upon discards larger than what they would normally prefer to target. An assumption that a fish may be too large to be opportunistically targeted by local predators may therefore be invalid in some cases.

Capture techniques

Whether predators play a role in the mortality of fishes being released depends on the condition of the individuals being released, which itself is partly dependent on variables under control of the fisher. Gear type, capture depth, duration of entanglement, duration of air exposure and handling techniques all can affect the severity of physiological and behavioural effects (e.g. Ross and Hokenson 1997; Davis 2002; Davis and Parker 2004). Although these capture variables have been considered in the study of PRM, they have usually not been studied in isolation from one another or compared for their relative importance. In general, the extent of physiological exhaustion, via overloading of anaerobic pathways, is likely most often the determining factor in whether a fish will be able to evade predators upon release. In particular, air exposure is probably a common precursor to PRP for fishes because it exacerbates physiological disturbance already caused by exhaustive exercise – a status characterized by exhaustion of tissue energy stores, metabolic acidosis and hypoxemia (Ferguson and Tufts 1992). In recreational fisheries, air exposure occurs during de-hooking and photography, while in commercial operations air exposure can be particularly extensive during on-deck sorting of catch. When a fish is removed from the water, its gill lamellae collapse and gas exchange is prevented. The result is an accumulation of anaerobic metabolites in body tissues that must be cleared following release before the full exercise capacity of the fish is restored, a period during which it may be vulnerable (e.g. Davie and Kopf 2006; Gingerich *et al.* 2007; Arlinghaus *et al.* 2009). These effects can be apparent with only a few minutes of air exposure (Danylchuk *et al.* 2007a). This is important, especially for commercial fisheries where sorting can take up to an hour (Ross and Hokenson 1997; Davis and Parker 2004). Cooke and Philipp (2004) and Danylchuk *et al.* (2007a) showed that bonefish with longer handling times and greater air exposure were more susceptible to shark predation as a result of an inability to maintain equilibrium upon release. Air exposure has also been associated with impaired escape responses, antipredator behaviour and increased PRP in undersized lobsters captured and released by commercial trap net and recreational sport diver fisheries (Brown and Caputi 1983; Vermeer 1987; Parsons and Eggleston 2005). Hypoxia can also occur while fish are still in water but where severe in-net crowding and high ventilation rates cause localized depletion of dissolved oxygen (G.D. Raby, unpublished data).

For example, in beach seine fisheries in the lower Fraser River, coho salmon (*Oncorhynchus kisutch*, Salmonidae) become progressively more impaired and likely to lose equilibrium with greater sorting time before release from crowded seines (Raby *et al.* 2012). Complete physiological recovery from exercise and air exposure can take minutes, hours or days and can even result in direct mortality in the absence of predators (Wood *et al.* 1983; Ferguson and Tufts 1992; Davis 2002). Until recovery is complete, released fish and shellfish are likely impaired in their ability to evade predators, and the duration of such a recovery is significantly affected by factors under control of the fisher.

Barotrauma

The depth from which fishes are captured can influence their susceptibility to PRP if barotrauma results. Barotrauma occurs when fish encounter gear at depth (typically >20 m) and are rapidly brought to surface, most commonly characterized by a distended swim bladder (Davie and Kopf 2006; Gravel and Cooke 2008). Crucially, a distended swim bladder can prevent fish from returning to depth, where shelter from predators is afforded. Fish with distended or ruptured swim bladders floating at the surface after capture are extremely vulnerable to predation from aquatic and avian predators (Ross and Hokenson 1997; Jarvis and Lowe 2008; Nguyen *et al.* 2009). Gitschlag and Renaud (1994) concluded that post-release survival of red snapper (*L. campechanus*, Lutjanidae) was inversely related to the depth from which the fish was captured. Although they found that red snapper often floated at the surface after release and considered predation in their study design, they did not document it, perhaps a result of low predator abundance. A lack of predation was surprising, given a lack of a startle response by red snapper approached by divers, a proxy test for behavioural impairment relevant to predation risk (Gitschlag and Renaud 1994). Also in the red snapper, Campbell *et al.* (2010a,b) developed a condition index that incorporated indicators of behavioural impairment with barotrauma injury. They demonstrated that a condition index that incorporates appropriate barotrauma metrics can successfully predict immediate PRP at the water's surface. In research involving commercial trawl fisheries, scavenging on discarded, floating fish has frequently been observed – barotrauma may be a substantial contributor to PRP in these fisheries (e.g. Hill and Wassenberg 2000; Stevens *et al.* 2000).

Water temperature

Little is known about the influence of water temperature on the risk of PRP for released fishes. Water temperature is commonly correlated with (predator-independent) PRM and, as the most important abiotic variable affecting fishes, it surely has some role in PRP (Davis 2002; Hall *et al.* 2009; Gale *et al.* 2013). Few studies have considered the effects of temperature on either predator or prey during PRP events. Danylchuk *et al.* (2007b) showed that angled and released bonefish spent significantly more time resting after release at higher water temperatures. Post-release 'resting' behaviour is exhibited by fish attempting to repay the oxygen debt that is incurred by heavy use of anaerobic metabolism during capture. A paradox of temperature and capture-release mortality is that physiological recovery is actually accelerated at higher temperatures (Wilkie *et al.* 1997) while PRM becomes more likely (Gale *et al.* 2013). Until physiological recovery is complete, released fish lack their full scope for activity. Thus, even for a fish that would ultimately survive at low temperatures in the absence of predation risk, there may be a longer period of vulnerability to predation while recovery takes place.

Research challenges and opportunities

There has been so little research on this challenging issue that there is little understanding of: (i) the magnitude of the problem in different fisheries, (ii) the factors affecting rates of PRP and (iii) what solutions are available where they might be needed. The summary of findings and key concepts presented above therefore remains mostly conceptual. High PRP rates could be affecting fisheries productivity, especially if large numbers of small or undersized fish are being preyed upon that otherwise would survive. An improved understanding of the magnitude of, and solutions to, this potentially serious problem could improve the efficacy of fisheries management. The important first step is the identification of systems where PRP is frequent and a significant contributor to PRM. It was notable that we did not find any papers on non-fish taxa. Presumably, there are some instances where sharks or other large predators prey on weakened seabirds or marine mammals released from commercial fisheries, and this would surely be a concern, particularly for threatened species. Clearly though, not all fisheries operate in an environment where predation contributes to PRM. In addition, the nature of some commercial fisheries may be such that discarded animals are rarely alive; research in such cases can (and does tend to) focus on bycatch reduction rather than reducing PRM. Nevertheless, many commercial and recreational fisheries release (or facilitate the escape of) animals with an un-validated assumption of survival that is challenged partly by predation risk for the released fish. Some of the authors of this paper are avid anglers and have witnessed PRP events in a range of systems and where it was well known by fishing guides and charter operators, but to our knowledge has not been addressed by researchers (e.g. Auckland Harbour NZ, undersized grey snapper predation by birds; coastal waters of BC, Pacific salmon predation by seals; coastal waters of the Gulf of Mexico, red drum and sea trout predation by dolphins and seabirds, and of Atlantic tarpon by sharks). A probable reason for a lack of published research on the topic is the inherent difficulty of directly observing predation in wild aquatic systems.

Many of the studies conducted to date have been laboratory based, meaning that, in general, there has not been quantification of PRP rates in a true fishery setting. Those studies that have quantified PRP rates in the field have generally been limited to short-term post-release monitoring – often <10 s (Evans *et al.* 1994; Campbell *et al.* 2010b). Laboratory studies are most useful for identifying causal factors and should continue to be exploited as such, but should be paired with rigorous field studies in all cases (e.g. Brown and Caputi 1983; Parsons and Eggleston 2006). Researchers should consult excellent reviews by Mesa *et al.* (1994) and Ryer (2004) for primers on the behavioural theory surrounding PRP in fishes. Where predation is identified to be a problem, solutions-based research could begin in the laboratory before field tests. For example, it is possible that modified sorting techniques (Broadhurst *et al.* 2009) or using tools that facilitate physiological recovery pre-release (Farrell *et al.* 2001) could improve the vigour of released fish and thus their ability to evade predators. Facilitated recovery has yet to be evaluated in the context of PRP, and this is likely the context where it would be most useful – the provision of a 'safe' short-term recovery environment before exposure to predation risk. Papers on laboratory studies should better report how their designs are grounded in field realism. For example: Is the model predator species selected the most common consumer of the discarded species in such scenarios? What are predator densities in the field where fish are released? What are impairment levels for released fishes in the operational fishery? In designing laboratory studies, scientists should attempt to answer such questions with simple field investigations. Predator abundance in the field could be estimated using high definition underwater videography or the use of divers, while impairment levels of fish released from an operational fishery can be readily measured by an observer using simple techniques already developed in the laboratory (e.g. Davis 2007; Campbell *et al.* 2010a).

Field-based research on PRP, in particular, is in its infancy. In addition to a lack of understanding of how variation in predator abundance affects PRP rates, there has simply been very little rigorous study of PRP rates in the field. Novel biotelemetry technologies that provide information additional to position would be most useful for identifying incidences of predation in the wild (e.g. accelerometers; for reviews on biotelemetry, see Cooke *et al.* 2004; Donaldson *et al.* 2008). Even with the most advanced technologies currently available, challenges exist for field research. Biotelemetry tools remain somewhat limited to larger animals, and there is a need to develop tag application techniques that are rapid and non-invasive – particularly for the more sensitive smaller fish that are likely most affected by PRP. Even where biotelemetry is available, telemetry-based position alone does not provide a straightforward identification of predation events (Yergey *et al.* 2012). In developing field methods, it may be necessary to additionally tag predators, to understand the 'baseline' behaviour and movement of the prey species being released and to accompany manual telemetry tracking with diver observations and high definition videography. As a halfway point between laboratory and field studies, mesocosm field experiments (i.e. large enclosures) could be a possible starting point for bringing new techniques into the field. In general, creative solutions will be required from both biologists and engineers in order to advance an understanding of PRP.

Synthesis and conclusions

Our review has shown that there is a paucity of research on PRP as a contributor to mortality in fish released from fishing gears. Given that animals experience injury and physiological disturbance during capture and release, it is not surprising that they could exhibit altered behaviour that may make them vulnerable to predation. Non-inclusion of PRP as a consideration in unobserved mortality estimates is a concern that has been alluded to in previous papers (Ryer 2004; Alós 2009) because it could lead to gross underestimates of fishing-induced mortality (Coggins *et al.* 2007). Our supposition is that PRP has not been identified or studied in a number of fisheries where it plays a substantial role in unobserved mortality. A lack of research in this area is not surprising, as it is easy to imagine why quantifying predation in the wild is a challenging task. The important first step is for fishers, managers and researchers to identify systems where predation is likely to be a substantial contributor to unobserved fishing mortality. Most study of capture-and-release mortality involves quantifying the effects of factors such as temperature, capture depth or fight time. Predator type and abundance could be considered new 'phantom' factors that are dynamic and would be challenging to incorporate into research. A conservative approach would be to assume a constant level of predation threat for a given fishery and focus on examining the capacity of released fish to evade predators and the accompanying rates of predator-induced mortality. PRP is a unique contributor to mortality because it is probably most often characterized by a short period (minutes or hours) of risk, which could simply be overcome by using pre-release techniques that reduce the impairment of fish being released (Farrell *et al.* 2001; Broadhurst *et al.* 2009).

An improved understanding of PRP could not only improve fisheries management and conservation but also a basic understanding of predator-prey interactions (Godin 1997). Fish physiologists and particularly behavioural ecologists should embrace PRP as an opportunity to use their expertise for an applied fisheries issue. We hope that this review will encourage researchers to combine new technologies and techniques with their creativity to advance our understanding of the role of predation in the mortality of fish released from fishing gears: an understudied source of unobserved fishing mortality.

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