

Causes and methods to estimate cryptic sources of fishing mortality^a

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Cryptic, not readily detectable, components of fishing mortality are not routinely accounted for in fisheries management because of a lack of adequate data, and for some components, a lack of accurate estimation methods. Cryptic fishing mortalities can cause adverse ecological effects, are a source of wastage, reduce the sustainability of fishery resources and, when unaccounted for, can cause errors in stock assessments and population models. Sources of cryptic fishing mortality are (1) pre-catch losses, where catch dies from the fishing operation but is not brought onboard when the gear is retrieved, (2) ghost-fishing mortality by fishing gear that was abandoned, lost or discarded, (3) post-release mortality of catch that is retrieved and then released alive but later dies as a result of stress and injury sustained from the fishing interaction, (4) collateral mortalities indirectly caused by various ecological effects of fishing and (5) losses due to synergistic effects of multiple interacting sources of stress and injury from fishing operations, or from cumulative stress and injury caused by repeated sub-lethal interactions with fishing operations. To fill a gap in international guidance on best practices, causes and methods for estimating each component of cryptic fishing mortality are described, and considerations for their effective application are identified. Research priorities to fill gaps in understanding the causes and estimating cryptic mortality are highlighted.

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IMPORTANCE OF CRYPTIC FISHING MORTALITIES

Achieving sustainable marine fisheries requires effective management of the main sources of fishing mortality, including retained and discarded target and incidental catch, and cryptic losses (Fig. 1 and Table I) (FAO, 1995, 2003, 2011; Hall *et al.*, 2000). Cryptic sources of fishing mortality are largely unobservable during

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fishing operations, as they are not manifested or readily detectable (Coggins *et al.*, 2007; Pollock & Pine, 2007). Several components of fishing mortality, especially components of cryptic fishing losses, however, are not routinely accounted for in fisheries management owing to a lack of adequate data, and for some components, a lack of accurate estimation methods (ICES, 1995, 2005; Chopin *et al.*, 1996; Hall, 1996; Gilman *et al.*, 2013). Figure 1 provides a graphical model of possible outcomes of encounters with fishing operations, including the five components of cryptic fishing mortality: (1) pre-catch losses, (2) ghost-fishing mortality, (3) post-release losses, (4) collateral sources of mortality and (5) mortalities from synergistic and cumulative effects of fishery interactions. The relative proportions of all components vary by fishing gear and method, by fishery, and spatially, temporally and by vessel within a fishery (Kelleher, 2005; Gilman *et al.*, 2007a). Here, these five components are collectively referred to as cryptic fishing mortality, which share the characteristic of being largely undetectable and not being possible to directly observe in the course of fishing operations, but instead must be indirectly estimated (Table I).

Errors can result when stock assessments and population models do not account for cryptic mortalities in marine capture fisheries, potentially compromising the efficacy of fisheries conservation and management measures (Crowder & Murawski, 1998; Davis & Ryer, 2003; ICES, 2005; Coggins *et al.*, 2007; Pollock & Pine, 2007). Cryptic fishing mortality that is unaccounted for in estimates of total fishing mortality can therefore compromise both the sustainability of stocks of principal market species as well as of species that are relatively vulnerable to population declines due to their k-selected life-history characteristics and susceptibility to mortality in fishing operations, and more broadly, can also contribute to exceeding multispecies, ecosystem-level threshold reference points, adversely affecting ecosystem structure and processes (Pikitch *et al.*, 2004; ICES, 2005). Cryptic mortalities are also a source of wastage and reduce the sustainable production of fishery resources and economic opportunities for the marine capture sector (Crowder & Murawski, 1998; Goñi, 1998; ICES, 2005).

In 2011, the Committee on Fisheries of the Food and Agriculture Organization of the United Nations endorsed *International Guidelines on Bycatch Management and Reduction of Discards*. The guidelines included recommendations for member States to identify, quantify and reduce impacts of mortality from pre-catch losses and ghost fishing by identifying this as an objective in fisheries management plans, improving scientific information on the magnitude and causes of these mortality sources and developing technology for assessment and mitigation (FAO, 2011).

In order to contribute towards implementing these guidelines and provide the basis for supplemental guidance, this paper identifies causes and best practice methods for estimating levels and rates of the components of cryptic fishing mortality, considerations for their application and gaps in knowledge. Previous studies have reviewed a sub-set of components of cryptic mortality (ICES, 1995; Neilson *et al.*, 2012) or have been gear or taxa-specific (Gilman *et al.*, 2003, 2007b; Broadhurst *et al.*, 2006) but have not provided comprehensive assessments nor guidance on applying methods to estimate the full suite of components of cryptic losses. Non-lethal fishery interactions where the individuals are released unharmed and are expected to survive, observable mortality sources such as retained catch and dead discards, fishing losses that are unaccounted for owing to unreported and misreported, discarded and

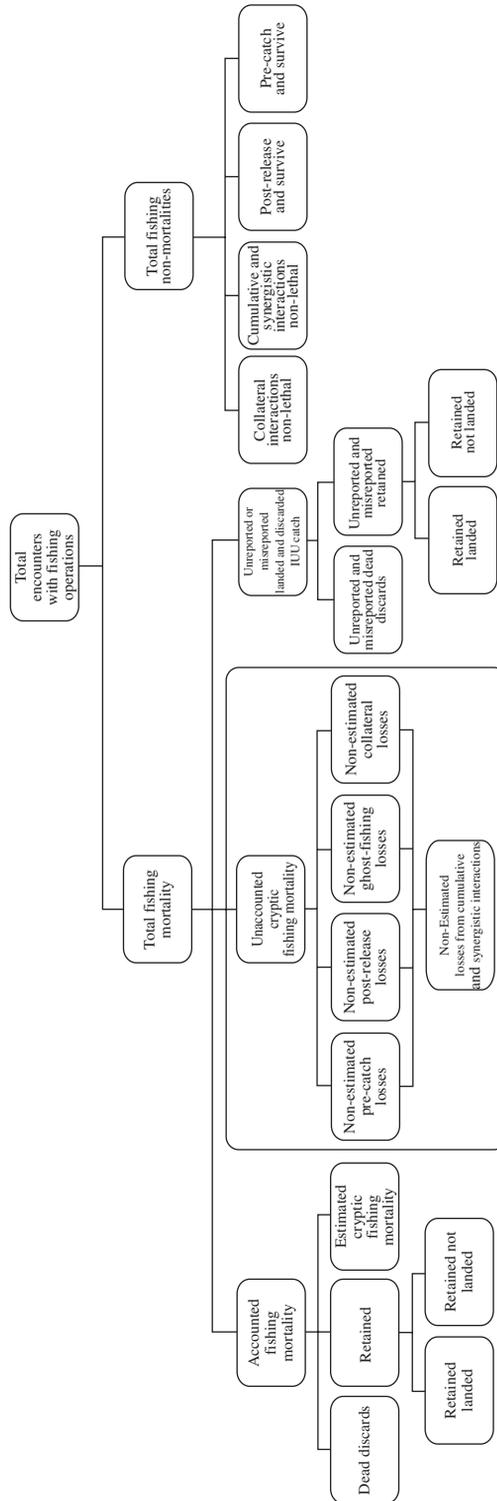


FIG. 1. Graphical summary of the components comprising total encounters with fishing operations, including the components of total fishing mortality, which includes the five components of cryptic removals (encircled) (adapted from Chopin *et al.*, 1996; ICES, 2005; FAO, 2011). IUU, illegal, unreported and unregulated.

TABLE I. Definitions of the components and sub-components (indented) of total fishing mortality and of non-lethal encounters with fishing operations, as presented in Fig. 1 (adapted from Chopin *et al.*, 1996; ICES, 2005; FAO, 2011)

Component	Definition
Total encounters with fishing operations	All of the ways an organism can interact with a fishing vessel and its gear, encompassing both interactions that result in mortality and survival
<i>Interactions that result in mortality</i>	
Total fishing mortality	All direct and indirect removals resulting from fishing operations
Accounted fishing mortality	All catch that dies from the interaction that is observed or otherwise estimated, recorded, reported and accounted for
Dead discards (sometimes referred to as by-catch)	Observed, recorded, reported and accounted for catch that is discarded dead, meaning that the catch is brought onboard and subsequently returned to the sea dead
Retained	Observed, recorded, reported and accounted for catch that is retained
Retained landed	Observed, recorded, reported and accounted for catch that is retained and landed, or retained, trans-shipped and landed
Retained not landed	Observed, recorded, reported and accounted for catch that is retained but not landed, including catch consumed by the crew, used for bait or rejected at port
Estimated cryptic fishing mortality	Cryptic fishing mortality that is estimated, reported and accounted for. Cryptic sources of fishing mortality are those that are largely not detectable, and comprise five categories: pre-catch losses, post-release mortalities, ghost-fishing mortalities and mortalities resulting from collateral, cumulative and synergistic effects of fishing operations
Unaccounted cryptic fishing mortality	Cryptic fishing mortality that is not estimated or accounted for
Non-estimated pre-catch losses	Non-estimated or accounted catch that dies from the fishing operation but is not brought onboard. Includes catch that dies and falls from the gear before retrieval, catch that is discarded dead or is released alive prior to being retrieved onboard (slipped catches) and dies from the interaction, catch that dies in the gear but is completely removed from the gear by predators prior to gear retrieval, and mortalities from collisions with fishing gear and vessels
Non-estimated post-release losses	Non-estimated or accounted catch that is retrieved and then released alive but dies later as a result of stress or injury sustained during the fishery interaction

TABLE I. Continued

Component	Definition
Non-estimated ghost-fishing losses	Non-estimated or accounted mortalities in lost, abandoned and discarded fishing gear
Non-estimated collateral losses	Non-estimated or accounted mortalities indirectly caused by ecological effects of fishing: <i>e.g.</i> an organism stressed or injured from a fishery interaction, including from encountering and avoiding the fishing gear and vessel, or escapees and live-released catch that are displaced from suitable habitat for shelter and foraging, die as an indirect result of the fishing operation. Predation of escapees, live-released catch and live organisms from the gear facilitated by the fishing operation are additional examples. Loss and degradation of habitat from fishing can also result in collateral mortalities. Or, <i>e.g.</i> collateral mortalities can result from anoxic areas of the seabed caused by discarded offal, spent bait and dead catch at sea
Non-estimated losses from cumulative and synergistic interactions	Non-estimated or accounted mortalities caused by synergistic and cumulative effects of individual sub-lethal stressors from fishing operations: <i>e.g.</i> an organism may be caught and released injured, and due to fishing operations having degraded habitat, lack protected and foraging habitat where they can recover from the injury, increasing the probability of mortality due to these cumulative and synergistic effects of multiple fishery effects. Or, cumulative stress and injury from repeated fishery interactions can eventually cause or contribute to an organism's mortality
Unreported or misreported landed and discarded IUU catch	Retained and discarded dead catch that is either not reported or is misreported
Unreported and misreported dead discards	Catch that is brought onboard and subsequently returned to the sea dead and is not reported or is misreported
Unreported and misreported retained Retained landed	Retained catch that is not reported or is misreported
Retained not landed	Catch that is retained and landed or trans-shipped at sea and subsequently landed, and is not reported or is misreported
	Catch that is retained but not landed, including catch consumed by the crew, used for bait or rejected at port, that is not reported or is misreported
<i>Interactions that do not result in mortality</i>	
Total fishing non-mortalities	Organisms that encounter the fishing operation and survive

TABLE I. Continued

Component	Definition
Collateral interactions non-lethal	Indirect effects of fishing operations that do not result in mortality. This includes, for example, organisms that encounter and avoid the gear and vessel and survive, and organisms that are affected by but do not die from areas with localized hypoxia caused by fishery discards
Cumulative and synergistic interactions non-lethal	Synergistic and cumulative stressors from fishing operations that do not result in mortality: <i>e.g.</i> an organism may be repeatedly captured and released alive and survive. Or, an organism may be captured and released alive, and in addition be temporarily displaced from suitable habitat for shelter and foraging, resulting in sub-lethal stress and injury
Post-release and survive	Catch that is caught and brought on deck, released alive and survives
Pre-catch and survive	Catch that interacts with the fishing operation but is not brought onboard and survives. Includes organisms that escape from the gear before being brought onboard and survive, catch that is released alive prior to being retrieved onboard (slipped catches) and survive and organisms that collide with fishing gear and vessels and survive

IUU, illegal, unreported and unregulated.

retained (illegal, unreported and unregulated, IUU) catches (Fig. 1) and methods for mitigating cryptic sources of fishing mortality are excluded from this paper, as they are covered elsewhere (Agnew *et al.*, 2009; Gilman, 2011).

PRE-CATCH LOSSES

CAUSES OF PRE-CATCH LOSSES

Pre-catch losses occur when organisms are caught, or collide with the vessel or gear, and die but are not brought onboard when the gear is retrieved (Chopin & Arimoto, 1995; Broadhurst *et al.*, 2006). For example, catch may die and fall from the gear before retrieval, or crew may intentionally release a portion of or the entire catch prior to landing onboard, referred to as slipped catch (Lockwood *et al.*, 1983; Misund & Beltestad, 1995; Gilman *et al.*, 2003, 2007*b*; Watkins *et al.*, 2008; Huse & Vold, 2010). Pre-catch losses may also occur when organisms escape from the gear alive but die later. Examples include small and juvenile finfishes escaping through a trawl codend and later dying due to stress and injury experienced during the interaction, and demersal dredging resulting in pre-catch mortality of scallops from shell damage and subsequent disease (Caddy, 1973; McLoughlin *et al.*, 1991; Chopin



FIG. 2. While partial removal of catch by predators is easily observed, such as this shark-depredated bigeye tuna *Thunnus obesus*, complete removals via depredation is an example of pre-catch fishing mortality (courtesy U.S. National Marine Fisheries Service Hawaii Pelagic Longline Observer Program).

& Arimoto, 1995; Borucinska *et al.*, 2002; Davis & Ryer, 2003; Suuronen, 2005; Broadhurst *et al.*, 2006). Depredation, the partial or complete removal of catch from the gear by predators, is documented to occur for several gear types. For instance, sharks and cetaceans depredate catch from pelagic longlines, and crabs, octopus and other predators depredate catch from traps and set nets. This constitutes pre-catch loss when an organism dies as a direct result of the fishing operation but is not present upon gear hauling because a predator completely removes it from the gear (Fig. 2) (Klimker, 1994; Kaiser *et al.*, 1996; Visser, 2000; Kauppinen *et al.*, 2005; Matsuoka *et al.*, 2005; Ramos-Cardelle & Mejuto, 2008; Gilman *et al.*, 2008).

Cumulative and interacting synergistic effects of multiple factors that an organism encounters during the pre-catch process may cause more mortalities than the sum of mortalities resulting from the individual factors (Fig. 3). For example, while moderate damage to finfish skin alone is unlikely to induce mortality, when combined with exhaustive swimming in a trawl along with extreme temperature changes, this may cause fish mortality, for instance, through metabolic acidosis or osmoregulatory failure. Some stressors that contribute to determining the probability of pre-catch mortality occur during the process of interacting with the gear, such as, in trawls, from being crushed and wounded against the trawl netting, colliding with other organisms, having to endure sustained swimming until exhaustion, lack of oxygen in a net with a high density of catch and incurring injuries when escaping through a mesh or by-catch reduction device (BRD) (Suuronen *et al.*, 1996*a, b*; Davis, 2002; Huse & Vold, 2010). Collisions with caught organisms having hard parts or sharp external structures cause more severe injuries relative to interactions with smooth-bodied fishes. Very high catch densities amplify the effects of these stressors. Other stressors are related to environmental factors that the organism encounters after escaping from the gear, such as water temperature, light conditions, currents, pressure and sea state.

Several factors have a significant effect on the probability of pre-catch mortality. Size can be a significant factor, where, for instance, smaller size classes of finfishes have been observed to have higher vulnerability to pre-catch mortality (Suuronen

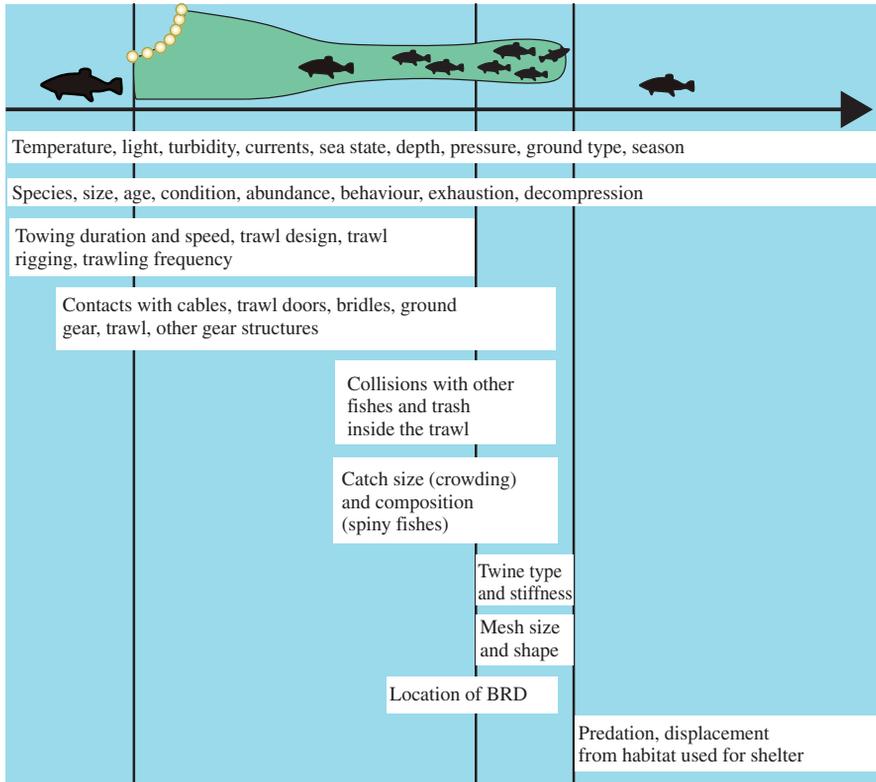


FIG. 3. The cumulative stress and injury of numerous factors may have a significant effect on the probability of pre-catch mortality of fishes that escape trawl gear. Text boxes describing single stressors are positioned horizontally to correspond to one or more of four temporal phases of an organism's interaction with the trawl-fishing operation, from before encountering the gear (up to the first vertical line), in the gear (between the first and second vertical lines), escaping (between the second and third vertical lines), to after the organism escapes (following the third vertical line) (adapted from Suuronen, 2005). BRD, by-catch reduction device.

et al., 1996a, b; Ingólfsson *et al.*, 2007; Tenningen *et al.*, 2012). Variability in pre-catch losses among species has also been documented, for instance, between species of fishes escaping through sorting grids in trawls and purse seines (Misund & Beltesstad, 2000; Ingólfsson *et al.*, 2007), and as a result of cetaceans selectively depredating on some species caught on longlines (Visser, 2000). There can also be significant variation in pre-catch mortality by season, time of day of fishery interactions, variability in fishing methods (such as gear soak and haul duration) and gear design (such as the location and design of BRD in trawl nets) (Suuronen *et al.*, 1995; Diaz & Serafy, 2005; Breen *et al.*, 2007; Suuronen & Erickson, 2010; Gilman *et al.*, 2012).

EXAMPLES OF METHODS TO ESTIMATE FINFISH PRE-CATCH ESCAPEE LOSSES FROM TRAWL CODENDS

Most experiments to study pre-catch losses have focused on mortality of fishes escaping trawl codends, documenting relatively high pre-catch survival for almost

all finfish species investigated (Broadhurst *et al.*, 2006). Measuring the mortality of fishes escaping from towed gear under commercial fishing conditions, however, is subject to high variability and imprecise estimation methods (Main & Sangster, 1990; Breen *et al.*, 2002, 2007; Suuronen, 2005). Estimates have been affected by the methods employed to collect, transport and monitor escapees. Full-scale experiments are expensive and technically challenging to conduct. As a result, data are available only for a limited number of species and fisheries.

For most trawl-escape mortality studies, fishes escaping through trawl codend meshes or through a BRD installed in the trawl have been caught inside a smaller mesh cover placed over the codend or BRD. Typically, a removable netting cage is attached to the cover and escapees retained in the cage are subsequently held for observation on the seabed or in the water column. For example, Suuronen *et al.* (1996a) used this method and found that the mortality of Baltic herring *Clupea harengus* L. 1758 escaping from trawl codends was 30–80%. The causes of these mortalities were probably skin injuries and exhaustion from being inside the narrowing part of the net and inside the codend, factors that are unaffected by the codend mesh size. *Clupea harengus* that escaped through an open codend suffered the same rate of mortality as fish that passed through codend meshes. Significant differences in mortalities were observed between small (<12 cm) and large (12–17 cm) *C. harengus* mortality rates were on an average 72% for small and 30% for large fish.

Qualitative analyses from *in situ* observations of the trawl capture process have been used to infer causes of trawl pre-catch losses. Analyses of underwater observations showed that *C. harengus* swimming in the rear part of the trawl often strike the netting, collide with each other and lose a large number of scales before they escape through the codend meshes (Suuronen & Millar, 1992). Underwater observations also suggested that *C. harengus* more easily escape through a rigid sorting grid than through diamond or square-shaped meshes (Suuronen *et al.*, 1996b). A subsequent survival study, using the cover method and large holding cages, assessed whether *C. harengus* mortality after escaping through a rigid sorting grid with 12 mm bar spacing placed in front of the codend was different from that of *C. harengus* after escaping through a 36 mm diamond-shaped mesh codend (Suuronen *et al.*, 1996b). Survival of larger *C. harengus* that escaped through the grid was 2–18% higher than that of codend escapees. The survival rate of small escapees, however, was not improved by the sorting grid. Consistent with the findings by Suuronen *et al.* (1996a), *C. harengus* escapee mortality was inferred to be largely due to exhaustion and physical contact with the trawl net during the capture process in the net before fish reached the codend, which causes scale loss and subsequent infection.

The traditional, covered codend methods used in many previous experiments may have been detrimental to escapees, *e.g.* by causing additional damage and stress as a result of excessive towing of organisms inside collection covers and cages (Suuronen *et al.*, 1996a, b; Breen *et al.*, 2002). Vast improvements recently made in the coverage methods (Erickson *et al.*, 1997; Lehtonen *et al.*, 1998; Breen *et al.*, 2007), however, have permitted the collection of fishes escaping from the codend during any chosen interval of a tow, enabling an assessment of survival under realistic commercial settings in terms of the duration of the tow and catch quantities, and reducing the risk of injury and stress during the collection of escapees (Fig. 4)

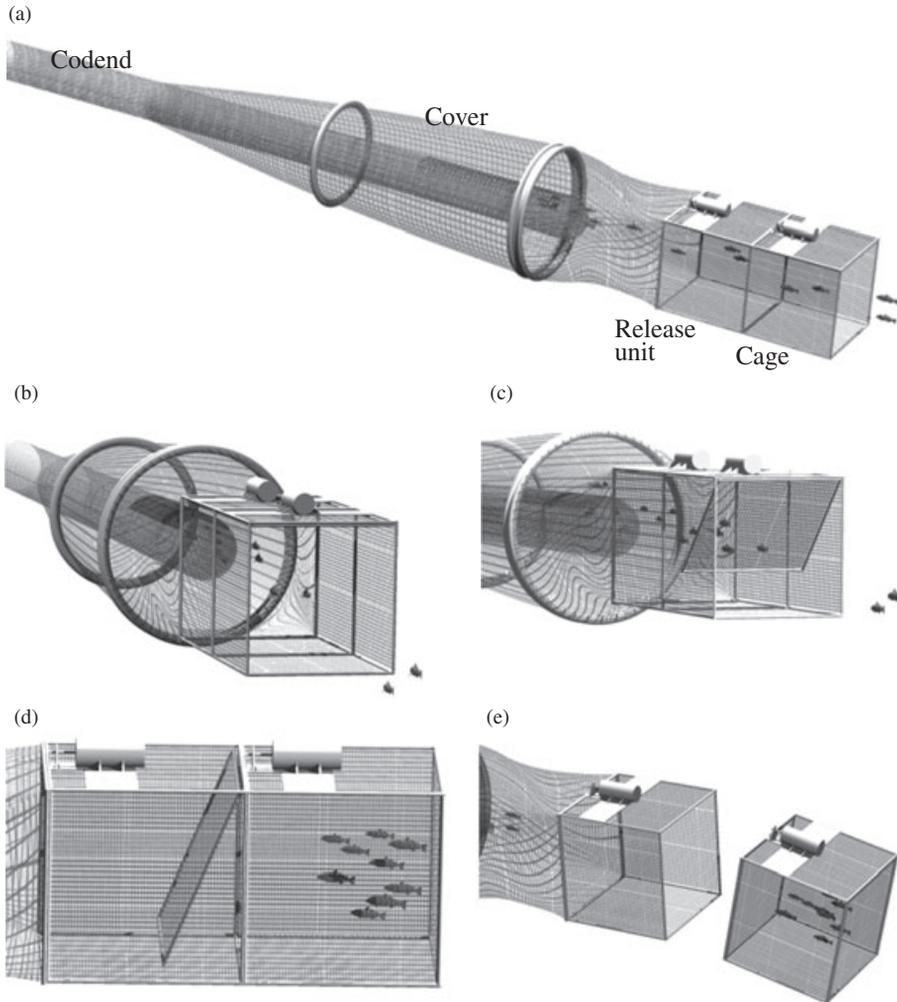


FIG. 4. Technology to sample trawl codend escapees: (a, b) when gates are open, escapees can swim freely into the open sea. (c) Collection starts when the rear gate is closed. (d) Escapees are collected. (e) After front gate is closed, the cage is separated from the release unit and dropped to the seabed, and a float rises to the surface indicating cage position (adapted from Lehtonen *et al.*, 1998; Broadhurst *et al.*, 2006).

(Pikitch *et al.*, 2002; Suuronen *et al.*, 2005; Ingólfsson *et al.*, 2007). Using these new technologies, survival can be assessed for short and long tows, and for small and large catch volumes. Sampling periods can be kept sufficiently short to avoid cover-induced injury, but long enough to provide an adequate number of escapees, with realistic tow durations and codend catch volumes.

For instance, full-scale field experiments using an improved cover-cage method, as described by Lehtonen *et al.* (1998) (Fig. 4), were conducted to estimate the mortality of Atlantic cod *Gadus morhua* L. 1758 after escaping through trawl codend meshes under commercial conditions (Suuronen *et al.*, 2005). Three codend types were tested in 30 h tows. Escapees were collected during the last 20 min of each haul. Fish were

allowed to pass through the codend cover and escape until an adequate commercial catch had accumulated in the codend. Escapees were collected by remotely closing the rear door of a cage that was attached to the codend cover. Then, the front door of the cage was remotely closed and the cage was released from the trawl and sank to the seabed. Escapees were retained in cages on the seabed and observed over 9.5 days. The mortality of fish was low (<3%) in normal water temperatures (<10° C) for all the three codend types. Higher mortalities (up to 75%) were observed when cages were held in temperatures >15° C. The majority of mortalities occurred during the first day after the tow. Apparently, these fish experienced strong thermal stress when they were towed through the thermal stratification layer to a shallow site. No clear differences in skin injuries or mortality between the three codend types nor between the different size groups were observed, but escape mortality was somewhat higher with larger codend catches. The results support the conclusion that there is low mortality of *G. morhua* escaping through trawl codends in normal (<10° C) seawater temperatures, and that the water temperature at the cage site can be an important factor in causing mortality (Soldal *et al.*, 1993; Suuronen *et al.*, 1996c, 2005; Ingólfsson *et al.*, 2007).

In subsequent survival experiments conducted with Alaska pollock *Theragra chalcogramma* (Pallas 1814) escaping from a square-mesh panel installed in the codend, the use of underwater video cameras enabled monitoring and managing specimen collection in real time (Erickson *et al.*, 1997). This technique made it possible to collect a statistically adequate sample size of escapees per cage while nearly eliminating unsuccessful, low-catch tows.

Fishes often escape near the surface while the trawl is being hauled onboard (Madsen *et al.*, 2008). Very little is known about the mortality of these fishes. Preliminary experiments showed that a much smaller proportion of haddock *Melanogrammus aeglefinus* (L. 1758) escaping at the surface survived compared with those escaping at depth (Breen *et al.*, 2007). The higher mortality rate of surface escapees was most likely owing to decompression injuries, higher temperatures and suffocation.

To date, most laboratory studies of pre-catch losses have assessed injuries to fishes passing through netting meshes or other BRD, and exhaustion caused by forced swimming inside towed gear. Laboratory studies enable assessment of the significance of single factors in causing injury, stress and mortality, and allow a systematic determination of the general behavioural, biological and physiological characteristics of stress response up to mortality in different species, which is rarely possible in at-sea experiments (Olla *et al.*, 1997; Davis, 2002). Laboratory experiments help identify key stressors and understand cumulative effects of pre-catch factors incurred during the capture and escape processes. Laboratory experiments have also been used to calibrate measures of fish condition and vitality, such as wounding and behavioural impairment, that serve as indicators of the probability of post-release mortality (Davis, 2005). It is difficult, if not impossible, however, to simulate all potential capture stressors in the laboratory. Furthermore, organisms held in captivity experience sensory-deprived environments, potentially causing behavioural and stress responses that differ from those under commercial fishing conditions, thus introducing uncertainty in results. Nevertheless, laboratory experiments are cost-effective methods to investigate stress responses and

injuries, and for corroborating or predicting results of field investigations (Broadhurst *et al.*, 2006).

EXAMPLES OF METHODS TO ESTIMATE SEABIRD PRE-CATCH LOSSES IN LONGLINE AND TRAWL FISHERIES

For seabird species with limited diving capacity, because capture primarily occurs at the sea surface as gear enters the water, estimates of pre-catch losses can be made by observers from the deck. A small number of studies have estimated levels of seabird pre-catch losses by comparing estimates of seabird catch levels during gear setting to the number retrieved during gear hauling (Brothers, 1991; Gilman *et al.*, 2003, 2007b; Watkins *et al.*, 2008; Brothers *et al.*, 2010). Studies of pelagic longline fisheries found that about one third of birds caught during setting were no longer present upon hauling, while a study in a trawl fishery found that >90% of seabirds observed to be entangled and submerged on trawl cables during setting were no longer on the gear upon hauling (Brothers, 1991; Gilman *et al.*, 2003, 2007b; Watkins *et al.*, 2008; Brothers *et al.*, 2010).

In the pelagic longline studies, observations of each baited hook during setting were maintained for a minimum of 30 s, at which time the terminal tackle was *c.* 150 m astern of the vessel. Studies were conducted in areas where the seabird assemblage typically did not include species with deep-diving abilities. If observations had been made in regions where seabird assemblages scavenging from fishing vessels included deep-diving seabirds, seabird capture events would have occurred too far astern to be accurately observed (Gilman *et al.*, 2003, 2007b; Brothers *et al.*, 2010).

In these studies, observations of birds caught during setting were categorized into three degrees of certainty: (1) highest certainty that the bird was caught, where either a bird was observed to have struggled persistently with outstretched, flapping wings, making repeated attempts to fly off with the line, and was either finally lost to view astern as it maintained the same position of attachment to a hook, or was observed to have been dragged underwater as the gear sank, (2) less certainty of the capture event and (3) lowest certainty. Observations are categorized as lower certainty when, for instance, a bird was seen caught and rough sea conditions or high bird abundance made it difficult for the researcher to keep track of the caught bird long enough to verify the catch with high confidence (Gilman *et al.*, 2003, 2007b; Brothers *et al.*, 2010).

Seabird mortality in trawl fisheries occurs through collisions with trawl warps and other cables, entanglement on cables and capture in the trawl net (Watkins *et al.*, 2008). Watkins *et al.* (2008) used onboard observers to record incidences of seabird captures in the trawl net, seabird collisions with trawl warps, seabirds being dragged underwater entangled on warps and the number of birds hauled aboard. A bird was assumed to have drowned during setting from entanglement with the warp when observed to have been dragged underwater and not resurface within *c.* 30 s. Similar to the longline studies, if, owing to a high density of birds in the area, the observer was unable to determine with certainty whether the bird resurfaced or not, then the observer recorded this as a lower certainty capture event. For part of the study, a video camera was employed to monitor the area astern over the warps and was reviewed after the trip to confirm the observer real-time documentation of interactions. Using the video footage, however, did not significantly improve visual observations. There

were no pre-catch losses from seabird interactions in the trawl net; all 10 seabirds observed caught in the trawl net during setting were present upon gear hauling. But, there was a relatively high rate of pre-catch mortality due to entanglement and submergence on trawl warps; of the 30 high-certainty entanglements on trawl warps, only two were still present upon gear hauling (Watkins *et al.*, 2008). In addition, there were observations of seabirds entangled on a warp being dragged along the sea surface and escaping before being dragged underwater, and observations of aerial collisions with the cable that did not result in entanglement (Watkins *et al.*, 2008), for which the degree of injury and post-interaction mortality rate were not estimated.

An unknown proportion of birds observed being captured during setting but not present upon hauling may have escaped the gear unobserved by the researchers. The remainder is inferred to have been removed from the gear due to depredation or mechanical action during the gear soak and haul (Gilman *et al.*, 2003, 2007*b*). It is possible that observed captures of seabirds during setting may overestimate actual captures because some seabirds may free themselves. There are also seabirds caught during setting that go undetected by the observer, such as when large numbers of seabirds are following a vessel, obstructing the view of the observer (Gilman *et al.*, 2003).

EXAMPLES OF METHODS TO ESTIMATE PELAGIC FISH PRE-CATCH LOSSES FROM SLIPPING IN PURSE SEINE FISHERIES

Slipping, commonly practised in many purse-seine fisheries, primarily occurs when there are undesired species, sizes or qualities of fishes caught, when there is insufficient space in the vessel hold to accommodate the entire catch, and when the vessel needs to meet quota limitations (Stratoudakis & Marcalo, 2002). Very little is known about the quantities of slipped fishes and about the proportion that dies owing to the slipping process, while even less is known about the causes of mortality from slipping. Shoaling pelagic species, such as Atlantic mackerel *Scomber scombrus* L. 1758 and *C. harengus*, probably do have high mortality rates as a result of slipping due to their high sensitivity to crowding and physical contact with gear (Lockwood *et al.*, 1983; Misund & Beltestad, 1995; Huse & Vold, 2010).

Huse & Vold (2010) employed an improved field method to study *S. scombrus* mortality due to crowding and subsequent slipping from a purse seine. Fish were allowed to swim from a purse seine through a transfer channel into two identical floating net pens. One pen used as a control was left floating in the sea without further treatment. The second pen was used to simulate crowding and slipping. The volume of the pen was gradually decreased by raising the bottom of the pen using a crane until the fish began to show signs of panic. This volume was maintained for 10–15 min. The volume was then returned to normal and the pen was left to drift freely in the open sea for 3–6 days. The experiment was repeated five times. Crowding was found to have a major effect on survival rates; pre-catch mortality was significantly higher among the crowded fish (80–100% mortality) than the control treatment fish (0.1–46% mortality) (Huse & Vold, 2010).

Tenningen *et al.* (2012) studied the effects of crowding in purse seines on the stress response and post-slipping survival of *C. harengus* through large-scale field experiments employing the methodology developed by Huse & Vold (2010). Three

replicated trials were conducted. Each trial employed one control and two treatment circular net pens. The purse seine was set around a *C. harengus* school and the net was hauled approximately halfway in. The fish were then transferred through a netting channel into the net pen while the hauling of the net still continued. The channel was closed once 3–9 t of *C. harengus* had been transferred into the pen. Three pens were filled with the catch from a single haul. One pen was used as a control and left to drift freely after the transfer of fish. The other two pens were used for the crowding treatment. Crowding was simulated by lifting the bottom of the pen with a crane, leading the fish to one side of the pen. The fish density was increased until it corresponded to the densities during a late phase of purse seining. The full crowding density was maintained for 10 min. The pen was then returned full volume, and the pens were left to drift freely and monitored for 4–5 days. There was a 28% mortality rate at a crowding density of 221 kg m⁻³, which increased with increasing density. Crowding densities <150 kg m⁻³ did not result in a higher mortality rate than observed for the control treatment of 0.9–2.0%. Smaller fish were more vulnerable to the effects of crowding. Blood analyses showed a considerable increase in cortisol, lactate and blood ions in the crowded fish. Lactate levels returned to control levels a few days after crowding, whereas cortisol and blood ion levels continued to increase during a 4–5 day monitoring period. Furthermore, plasma glucose was substantially reduced at the end of the trial, an indication that the *C. harengus* were incapable of restoring homeostasis and were approaching exhaustion.

GHOST FISHING

CAUSES OF GHOST-FISHING MORTALITY IN LOST, ABANDONED AND DISCARDED FISHING GEAR

Ghost fishing occurs when lost, abandoned and discarded fishing gear continues to catch and kill organisms (Fowler, 1987; Matsuoka *et al.*, 2005). There are intentional and unintentional causes for gear to become derelict. For example, fishers may lose gear as a result of breakage or malfunction of tracking systems, abandon gear when operating illegally and a risk of detection occurs, lose or abandon gear because of inclement weather and discard unwanted gear at sea when deemed more practical or economical to disposal onshore. In addition, fishers may lose gear when it is damaged by passing vessels or active gear (*e.g.* passive gear is inadvertently, or intentionally, towed away or marker buoy moorings are cut), or when it is snagged on submerged features (Pawson, 2003; UNEP & FAO, 2009; FAO, 2010a).

Various factors affect the ability, efficiency and duration of derelict gear to result in ghost fishing. Organisms caught in derelict nets, traps and other gear types can attract scavengers, which subsequently are caught, causing long-term ghost fishing owing to this self-baiting (Kaiser *et al.*, 1996; Matsuoka *et al.*, 2005; FAO, 2010a). Other important explanatory factors include the condition of the gear upon being lost, abandoned or discarded, including whether it was set for fishing, and environmental conditions such as currents, depth and the type of the substratum (Erzini *et al.*, 1997; Pawson, 2003; Matsuoka *et al.*, 2005; UNEP & FAO, 2009; FAO, 2010a).

For example, studies have observed that when gillnets and entangling nets are deployed on a flat substratum, their ghost fishing catching efficiency and longevity decline rapidly over the initial few days of release, and decline to within *c.* 5% of initial catching efficiency within weeks to months. The gear quickly loses its profile, and meshes become obstructed owing to the accumulation of debris and particulate matter, and because biofouling increases the net's visibility (Kaiser *et al.*, 1996; Erzini *et al.*, 1997; Pawson, 2003; Matsuoka *et al.*, 2005). In some studies, physical damage to derelict gear occurred from interactions with other commercial fishing gear (Erzini *et al.*, 1997). In these cases, when a net becomes derelict on a flat substratum, the gear causes ghost-fishing mortality of demersal fishes over the first few days of release, and then, once most of the net area has collapsed, the gear mainly kills scavenging crustaceans until the net structure is no longer intact (Kaiser *et al.*, 1996; Pawson, 2003).

When derelict nets become entangled on three-dimensional objects, and environmental conditions, such as currents and weather, and interactions with other fishing gear do not damage the gear, gillnets and entangling nets can maintain high ghost-fishing catch rates for >2 years (Kaiser *et al.*, 1996; Pawson, 2003; Matsuoka *et al.*, 2005; Nakashima & Matsuoka, 2005).

Gear type is another factor determining the efficiency and duration of ghost fishing. Ghost fishing is thought to be particularly problematic for passive (static) fishing gear after setting (*e.g.* pelagic and demersal longlines, gillnets, trammel nets, pots and other trap gear), while the catching process of active gear (*e.g.* purse seines and trawls) typically ceases when the gear collapses upon detachment from the vessel (Matsuoka *et al.*, 2005; FAO, 2005; SEAFO, 2009). Gillnets, entangling nets and traps have relatively high ghost-fishing potential, and almost all research on ghost fishing has been conducted on these gear types (Pawson, 2003; Matsuoka *et al.*, 2005; UNEP & FAO, 2009). For example, observations of derelict traps in shallow waters found that some maintain catching efficiency for >3 years, while deep-water traps and other static gear that are subject to relatively less physical stress and biofouling, probably continue fishing for longer periods (Humborstad *et al.*, 2003; Matsuoka *et al.*, 2005). Some studies have estimated ghost-fishing removals of target demersal fish species in trammel and gillnet fisheries to be <1.5% of total catches (Sancho *et al.*, 2003; Santos *et al.*, 2003*a, b*). For some fisheries and species, however, ghost-fishing mortality levels can be considerable. For instance, octopus ghost-fishing mortality in a southern Japanese coastal fish trap fishery was estimated to be at least equal to, and as much as double, that of annual octopus landings in the fishery (Matsuoka *et al.*, 2005).

There has been some progress in documenting the frequency of loss and the duration of the catching efficiency of passive gears, primarily trammel nets, gillnets and traps. There remains, however, a large gap in the knowledge of removals due to other gear types, especially active gears, where effective methods to estimate the frequency of gear loss, and the duration and efficiency that such gears continue to fish have yet to be developed. Ghost fishing has also been observed in active gears, including seines, and there are observations of marine mammal entanglement in trawl-net fragments (Jones, 1995; Donohue *et al.*, 2001; Matsuoka *et al.*, 2005). Ghost fishing also occurs in derelict fish aggregating devices (FAD) *via* entanglement in their appendages (webbing and other materials that hang vertically from floating objects) and in webbing wrapped around FAD floating materials (Gilman, 2011).

In large purse seines, such as used by tuna purse seiners, the loss of a full net is a very rare event. Sections of the net, however, may be ripped off when the net entangles in the purse cable or in another section of the net. This type of event is also infrequent. Ghost-fishing mortalities also occur from discarded offal (processed fishes) and bait containing hooks (Weimerskirch & Jouventin, 1987).

In addition to ghost fishing, derelict fishing gear can cause collateral mortalities. Mass concentrations of marine debris, of which <10% is fishing gear, tend to occur in ocean convergence zones for extended periods of time (Derraik, 2002; UNEP & FAO, 2009; FAO, 2010a). An estimated 70% of marine debris sinks to the seabed where its accumulation could smother benthic communities, and adversely affect benthic fauna and the substratum when dragged by currents and wind, or during retrieval (FAO, 2010a). Derelict gear and other marine debris transport invasive alien species (Derraik, 2002; UNEP & FAO, 2009; FAO, 2010a). The accumulation in marine food webs of synthetic compounds derived from marine debris is an additional potential source of collateral mortalities (Derraik, 2002; Moore, 2008).

EXAMPLES OF METHODS TO ESTIMATE GHOST-FISHING MORTALITY IN DEMERSAL GILLNETS AND TRAMMEL NETS

Several studies have estimated mortality rates from ghost fishing per unit of time in derelict gillnets and trammel nets, or in experimental nets deployed to simulate derelict gear (Kaiser *et al.*, 1996; Erzini *et al.*, 1997; Pawson, 2003; Matsuoka *et al.*, 2005; Nakashima & Matsuoka, 2005). In most studies, experimental nets were deployed at conventional fishing grounds, where one end of each net was cut loose to simulate a derelict net. Ghost-fishing mortalities have been estimated either by monitoring the number and fate of organisms that became captured, or by placing captive organisms in the gear and monitoring their fate during the study period, with monitoring conducted *in situ* directly by divers using still photography and video surveys, or by retrieving a sub-set of the nets at various time intervals (Kaiser *et al.*, 1996; Erzini *et al.*, 1997; Pawson, 2003; Matsuoka *et al.*, 2005; Nakashima & Matsuoka, 2005). No study has attempted to estimate levels of predation of organisms caught in derelict nets (Erzini *et al.*, 1997).

Matsuoka *et al.* (2005) developed a model of ghost-fishing removals per unit of time by extrapolating from experimentally derived estimates of ghost fishing. Model inputs included estimates of average species-specific mortality rates per derelict gear per unit of time, the area of the fishing grounds, the estimated amount of derelict gear in the fishing ground, determined, for example, using surveys of fishermen and side-scan sonar, and the proportion of total derelict gear in the area that continues to maintain some catching efficiency (Matsuoka *et al.*, 2005).

POST-RELEASE FISHING MORTALITY

CAUSES OF POST-RELEASE MORTALITY

Post-release fishing mortality occurs when catch is retrieved and then released alive but stressed and injured to a degree that causes it to die later. Post-release mortality may occur owing to fatal wounds or increased probability of fatal diseases resulting

from injuries incurred through the fishery interaction (Borucinska *et al.*, 2002; Ryer *et al.*, 2004; Davis, 2005; ICES, 2005; Gilman *et al.*, 2006, 2008; Swimmer *et al.*, 2006; Snoddy & Williard, 2010; Gilman, 2011). In particular, many multi-species bottom trawl fisheries have relatively high discard levels (Kelleher, 2005) where post-release mortality represents a large source of uncertainty for estimates of total fishing mortality (Suuronen, 2005). Unlike pre-catch escapees, studies on the survival of finfishes released alive from trawlers have generally documented high post-release mortality rates, although the types and severity of injuries are highly specific to fishing gear, operational modes, environmental conditions, species and size, and handling and release practices (Hill & Wassenberg, 1990; Kaiser & Spencer, 1995; Pikitch *et al.*, 1996; Erickson *et al.*, 1997; Davis, 2002; Lancaster & Frid, 2002; Bremec *et al.*, 2004; Broadhurst *et al.*, 2006; Parker *et al.*, 2006; Benoît *et al.*, 2010, 2012).

Higher probability of post-release survival is often associated with shorter air-exposure times and lower air temperature (above freezing) on deck (Suuronen, 2005). Effects of air temperature on deck may be compounded by direct sunlight (Pikitch *et al.*, 1996). Extreme thermoclines with high surface-water temperatures may strongly and adversely affect the survival of released fishes (Erickson *et al.*, 1997). Duration of the gear soak in passive gear or the tow in active gear, gear soak and tow depth, catch size and composition in towed nets and temperature of seawater are other factors that may significantly affect the probability of post-release mortality (Benoît *et al.*, 2010; Suuronen & Erickson, 2010; Gilman *et al.*, 2012).

Many factors that affect the survival prospects of live releases are similar to those affecting escapees. Released organisms, however, experience additional stress and injury from being handled and released, which can be significant causes of post-release mortality. Additional stressors faced by live releases that influence survival probability include the method employed to lift them onto the vessel deck (*e.g.* brailer, pump, dipnet and gaff), air exposure, on-deck handling practices, duration out of the water, physical conditions onboard such as air temperature, the release method (*e.g.* thrown from the vessel and then sinking or swimming back to their habitat) and the tackle remaining attached to the organisms after release (Davis, 2002; Broadhurst *et al.*, 2006; Ryder *et al.*, 2006; Benoît *et al.*, 2010, 2012; IATTC & OFCF, 2011; Neilson *et al.*, 2012).

The probability of post-release mortality has been shown to vary between species, and by size and sex within a species (Broadhurst *et al.*, 2006; Ryder *et al.*, 2006), and these explanatory factors are probably of relevance to the other components of cryptic mortality. For instance, the size and species of pelagic sharks have been observed to have a significant effect on the probability of post-release mortality (Diaz & Serafy, 2005; Hight *et al.*, 2007; Mandelman *et al.*, 2008). Smaller fishes are generally weaker and more sensitive to capture and handling stress (Broadhurst *et al.*, 2006). Fish species with gas bladders and other organs that cause positive buoyancy are vulnerable to barotrauma, and as a result, are more likely to suffer internal injuries, be trapped near the surface after release, and have higher rates of post-release mortality from predation and thermal shock relative to species lacking gas bladders (Davis, 2002; Benoît *et al.*, 2013).

Probability of post-release mortality between and within taxonomic groups is also related to fragility and physical characteristics. For instance, invertebrates with

durable shells or exoskeletons are less likely to be fatally damaged from gear contact and handling, than fishes (Hill & Wassenberg, 1990; Lancaster & Frid, 2002; Bremec *et al.*, 2004). For example, leatherback sea turtles *Dermochelys coriacea* may be more delicate and of higher risk of injury from fishery interactions than hard-shelled turtles (Ryder *et al.*, 2006). Other reasons for differential probability of cryptic mortality between species and higher taxonomic groupings include differences in propensity for scale loss and skin damage, and differences in sensitivity to changes in temperature, both in the water during haul-back and air temperature on the deck (Suuronen & Erickson, 2010). Furthermore, species that rely on agility and speed to catch prey or avoid predation may have a higher probability of post-release mortality as a result of scale loss and superficial injuries relative to species not relying on speed and mobility, *e.g.* those that rely upon camouflage to forage and avoid predators.

EXAMPLES OF METHODS TO ESTIMATE SEA-TURTLE POST-RELEASE MORTALITY IN PELAGIC LONGLINE FISHERIES

Several methods have been employed to estimate post-release mortality rates of sea turtles following capture in pelagic longline fisheries (Swimmer & Gilman, 2012). A common method involves observing captured turtles that were subsequently placed into captivity (Aguilar *et al.*, 1995; Casale *et al.*, 2008). Inclusion of control animals in survival experiments provides a basis for separating fishery-induced mortality from mortality caused by stressors associated with being held in captivity and other possible contributing sources, including natural mortality (Suuronen, 2005; Neilson *et al.*, 2012). As with laboratory experiments to estimate pre-catch mortality rates, stressors from captivity may artificially reduce survival probability, while the elimination of predation risk, provision of food and other aspects of captivity can artificially increase survival probability relative to that in the wild, confounding observations of mortality rates. To be able to account for these potentially significant factors, information is required on the condition of individual turtles upon capture, including the manner of capture and injuries incurred, and information on methods employed to manage turtles while in captivity.

Post-release mortality rates have also been estimated from satellite data collected from tags attached to sea turtles caught and released from pelagic longline gear (Swimmer *et al.*, 2002, 2006; Chaloupka *et al.*, 2004; Parker *et al.*, 2005; Ryder *et al.*, 2006; Godley *et al.*, 2008). The two main types of tags used are platform terminal transmitters (PTTs) and pop-up satellite archival tags (PSATs). Both devices can provide data on geo-spatial location (PTTs use GPS or Doppler shift and PSATs use changes in ambient light intensity), temperature and depth (pressure), *via* transmission to the Argos satellite system (Musyl *et al.*, 2011a). PSATs are programmed to release from the turtle and float to the sea surface and commence data transmission under three conditions pre-set by the researcher: (1) on a specified date, (2) if they remain below the sea surface at a constant depth for a designated time period and (3) if they reach a threshold depth (Musyl *et al.*, 2011a). PTTs transmit a satellite signal at a programmed rate when they are at the sea surface, and continue to transmit until the device fails (*e.g.* battery or antenna failure), or if the device remains submerged (Godley *et al.*, 2008).

Dated transmissions from a telemetry device can be used to infer turtle survival based on the observations of: (1) signal transmission for a threshold duration (months), and until PTT cessation of signal transmission or PSAT pop-up, (2) normal diving patterns, (3) normal distance travelled and (4) normal velocity. Most studies have inferred a tagged turtle to have died as a result of the fishery interaction based on observations of: (1) post-release behaviour indicative of injury and lack of vigour (*e.g.* remaining at a constant depth for several days, a short distance travelled or slow movements) prior to cessation of PTT signal transmission or PSAT pop-up and (2) the turtle sank beyond the species' depth capacity, causing the PSAT to engage the pop-up mechanism (PSATs but not PTTs are able to document this event) (Godley *et al.*, 2008).

Unless a PTT is recovered, it is not possible to determine the cause of termination of signals. Causes of a PTT to stop transmitting include: a turtle dies as a result of injuries incurred from the fishery interaction and sinks, a turtle dies owing to other anthropogenic causes (*e.g.* subsequent fisheries capture and marine debris entanglement) and sinks, natural mortality factors (*e.g.* predation) and failure of the tag (*e.g.* battery failure, biofouling, antenna damage and attachment failure such as from fishing gear entanglement causing the tag to be shed from the turtle's carapace and sink) (Swimmer *et al.*, 2002, 2006; Chaloupka *et al.*, 2004; Ryder *et al.*, 2006; Hays *et al.*, 2007; Musyl *et al.*, 2011a). Given multiple causes of PTTs to terminate issuing signals, there is uncertainty in differentiating a mortality event from other causes of cessation of PTT data transmission. Similarly, PSAT failure to transmit data may be due to either turtle mortality or tag failure (Chaloupka *et al.*, 2004; Musyl *et al.*, 2011a).

The duration of satellite tagging studies has implications for correctly interpreting observations. Short studies fail to observe post-release mortalities occurring beyond the study period. Sea turtles may require >9 months to expel an ingested hook and recover from forced submergence and other stressors incurred from longline capture (Aguilar *et al.*, 1995; Ryder *et al.*, 2006). Thus, studies <9 months duration might fail to observe mortalities caused or influenced by injuries sustained during the fishery interaction. To differentiate between natural and fishing mortality, relatively long studies require control treatments, such as attaching tags to turtles that had been free-swimming upon capture (Chaloupka *et al.*, 2004; Ryder *et al.*, 2006).

Capture–mark–recapture and capture–mark–dead recovery studies have low potential to estimate sea-turtle post-release mortality caused by gear interactions. This is because there would be very low recapture rates of longline-released turtles due to both the short time period (months) required for post-release studies and the low probability of recapture on the high seas (Godley *et al.*, 2003). Sample sizes would be too small to provide such studies with sufficient statistical power. Conventional tagging has been effectively employed to estimate finfish post-release mortality rates when extremely large sample sizes and high recapture rates were achieved (Trumble *et al.*, 2000). Typically low rates of tag recapture, and confounding by tag shedding and low reporting of recaptured tags, however, generally preclude estimating post-release mortality rates using conventional tagging methods (Neilson *et al.*, 2012).

Information on stranded moribund and dead sea turtles, including information from necropsies of dead turtles, have been used to estimate the relative risk of different mortality sources for stranded turtles (Chaloupka *et al.*, 2008), and do

not enable estimating fishery post-release mortality rates. Also, strandings do not provide information on mortality sources that occur far from land, such as occurring in high-seas fisheries, or in areas where currents carry dead organisms away from land.

On the basis of the assumption that injuries and stress incurred during capture are the most significant factors determining mortality rates, it has been hypothesized that, for some pelagic species, mortality rates observed upon gear retrieval and post-release mortality rates are correlated and of similar values (*i.e.* if $x\%$ of a species are alive upon gear retrieval, then $c \cdot x\%$ of live releases will survive the interaction) (Moyes *et al.*, 2006; Campana *et al.*, 2009; Musyl *et al.*, 2011*b*). While this has been observed for blue sharks *Prionace glauca* (L. 1758) in a small number of studies (Moyes *et al.*, 2006; Campana *et al.*, 2009; Musyl *et al.*, 2011*b*), this hypothesis is yet to be assessed more broadly, including for other taxonomic groups. A meta-analysis of pooled datasets from multiple studies may prove instructive.

Prediction of the probability of post-release mortality of turtles can be done by assessing one or more key variables that are thought to increase the probability of death. The type and severity of injuries have been used to predict sea turtle post-release survival by, for example, the U.S. National Marine Fisheries Service (NMFS), which considers whether turtles were comatose upon retrieval and resuscitated prior to release as one factor of a model for predicting survival (Ryder *et al.*, 2006). The location of hooking has also been used as an indicator of severity of injury and concomitant probability of sea turtle post-release survival (Chaloupka *et al.*, 2004; Ryder *et al.*, 2006; Gilman *et al.*, 2006, 2007*b*; IATTC & OFCF, 2011; Parga, 2012). For instance, the NMFS uses a graded key to determine the severity of injury. This assumes declining seriousness of injury and hence lower probability of mortality in the following order: (1) turtles deep-hooked in the oesophagus at or below the level of the heart, (2) turtles deep-hooked in the cervical oesophagus (above the level of the heart), glottis, jaw joint, soft palate, tongue or other jaw and mouth tissue parts, (3) those hooked in the upper or lower jaw of the mouth but without penetrating other jaw and mouth tissue parts, (4) turtles light-hooked in the body and (5) those captured *via* entanglement only and not hooked (Ryder *et al.*, 2006).

The manner of turtle capture also provides an indication of stress and injury. Hook design (*i.e.* circle *v.* j-shaped and degree of offset of the point of the hook from the plane in which the shaft is situated) and its width at the narrowest point have been shown to affect hooking location, and hence severity of injury, and thus have significant effects on post-release survival (Gilman *et al.*, 2006, 2007*a*; FAO, 2010*b*; Gilman, 2011; Musyl *et al.*, 2011*b*). Gear soak time, which determines how long a caught turtle would be on the gear before being hauled to the vessel, and depth of terminal tackle when soaking and mass of the gear, which determines how much energy a turtle would need to expend to reach the surface to breathe during the gear soak, are additional factors that can affect post-release survival (Musyl *et al.*, 2011*b*; Gilman *et al.*, 2012).

Biochemical indicators of mortality and morbidity, which include assessing plasma constituents for the degree of blood loss, muscle and other tissue damage, and physical stress, have been used for sea turtles caught in U.S. Atlantic Ocean gillnet fisheries (Snoddy *et al.*, 2009; Snoddy & Williard, 2010), and are being tested with turtles caught in a Mediterranean Sea longline fishery (Swimmer & Gilman, 2012).

Reflex action mortality predictors (RAMP), which measure the degree of impairment of reflexes following gear interaction (Davis, 2005, 2007; Davis & Ottmar, 2006), and bio-electrical impedance analysis, which estimates physiological variables, including health as indicated by water distribution within fishes, by measuring resistance and reactance of tissue to applied electrical current (Cox & Heintz, 2009; Cox *et al.*, 2011), have been used to provide an indication of severity of injury and stress incurred during fishery interactions and to predict post-release mortality of finfishes, and are addressed in the following section. These latter two methods may also be suitable for estimating post-release mortality rates of sea turtles.

Whether gear remains attached upon release is another factor significantly affecting the probability of sea-turtle post-release mortality (Ryder *et al.*, 2006; Parga, 2012). Removal of hooks from lightly hooked turtles and removal of fishing line are hypothesized to improve the probability of sea-turtle survivability. Leaving hooks in place that are in the oesophagus at or below the level of the heart is hypothesized to result in less injury than would result from their removal (Ryder *et al.*, 2006; Parga, 2012). Trailing line that exceeds half the length of the turtle's carapace length is hypothesized to cause higher post-release mortality probability relative to a shorter line, while turtles that are released entangled in line have a relatively lower probability of survival than if not entangled but with line trailing (Ryder *et al.*, 2006). The ingestion of line, the length of line swallowed relative to the turtle size, and whether the line was attached to a hook are additional factors hypothesized to have significant effects on the probability of sea-turtle post-release survival (Bjorndal *et al.*, 1994; Oros *et al.*, 2004; Casale *et al.*, 2008).

The species of released sea turtles can have a significant effect on the probability of post-release mortality. Leatherback sea turtles are hypothesized to have lower rates of post-release survival compared to hard-shelled turtles because of their more delicate external and internal hard and soft tissue structures, which makes them more susceptible to injury from interactions with pelagic longline gear (Ryder *et al.*, 2006). Furthermore, leatherbacks are hypothesized to be relatively less resilient to the stresses incurred during fishery interactions. For instance, leatherbacks require a longer time than hard-shelled turtles to recover from acidosis and to resume normal dive behaviour (Ryder *et al.*, 2006). While probably important, the effect of the size and sex of released turtles on post-release survival probability has not been explored.

EXAMPLES OF METHODS TO ESTIMATE FINFISH POST-RELEASE MORTALITY IN TRAWL FISHERIES

Methods to estimate post-release mortality rates of fishes that are released alive from trawlers generally produce results with high uncertainty because there is high variability in mortality rates and a broad suite of confounding factors (Suuronen, 2005; Broadhurst *et al.*, 2006). In most of the post-release mortality studies, organisms were caught, retrieved, handled and then monitored while being held either in tanks placed at the sea surface, on-board fishing vessels or in cages at depths consistent with the species' natural vertical distribution (Broadhurst *et al.*, 2006). Holding released organisms in tanks at the sea surface is problematic for estimating post-release survival rates because temperature, pressure, light, food, risk of predation, stocking densities and other variables with a significant effect on survival probability deviate from conditions of the organism's natural habitats. Holding large

migratory species of fishes in captivity is typically not feasible (Neilson *et al.*, 2012). Instead, more accurate estimates of post-release mortality rates in trawl fisheries can be achieved through tagging prior to release. Advanced electronic tags, including those described for use on sea turtles, are now available to estimate post-release survival across species and sizes.

As with sea turtles, finfish post-release mortality may also be accurately predicted by observing fish condition and vitality. For example, condition indices have been developed for Pacific halibut *Hippoglossus stenolepis* Schmidt 1904 based on wounding, and for sharks based on revival time following release (Trumble *et al.*, 2000; Hueter *et al.*, 2006). Reflex impairment (Davis & Ottmar, 2006) is a quantitative measure of fish condition that is correlated with stress and may be rapidly evaluated in experiments. Reflex impairment has been used as a predictor for mortality in sablefish *Anoplopoma fimbria* (Pallas 1814) that were towed in a net and exposed to air and increased temperature (Davis, 2005). Davis & Ottmar (2006) further tested the efficacy of reflex impairment in predicting mortality of flatfishes and roundfishes that had been towed in a net at the laboratory. Reflex impairment in *T. chalcogramma*, *A. fimbria*, northern rock sole *Lepidopsetta polyxystra* Orr & Matarese 2000 and *H. stenolepis* was significantly related to mortality in a biphasic relationship described by sigmoid curves. Davis & Ottmar (2006) noted that measuring sub-lethal and lethal effects of seemingly unlimited combinations of fishing-related stressors using RAMP would greatly enhance models in order to estimate escapee and post-release mortality rates. Measurements of reflex impairment may become powerful tools for the assessment of survival likelihood in the field and be used to compare mortalities among various fishing practices and fisheries. The obvious advantage of using fish vitality indicators onboard is that it is done under the actual range of commercial fishing conditions (Benoît *et al.*, 2010). General use of fish condition and vitality (*e.g.* wounding and plasma constituents) to predict delayed mortality can be limited because these measures could show inconsistent responses to different types of fishing stressors (Davis, 2002). In addition, categorizations of wounding are typically subjective, introducing bias in mortality estimates.

COLLATERAL FISHING MORTALITY

Collateral sources of fishing mortality are those that are indirectly caused by various ecological effects of fishing (ICES, 2005). The indirect link between these outcomes of fishing activities and mortalities has prevented the development of methods that provide accurate estimates of collateral mortality levels and rates (ICES, 2005). Examples in this category are diverse, complex and relatively difficult to quantify, in part, because there is great uncertainty in inferring what factors were significant in causing the mortalities (Jones, 1992). A description of the wide range of causes and methods for estimating these types of mortalities is facilitated through a few examples. (1) Fishing mortality of one albatross of a breeding pair typically results in chick mortality by starvation, and the remaining albatross will take several years before mating again, further reducing reproductive output (Tasker & Becker, 1992). (2) Tunas, and possibly other pelagic apex predators bring baitfishes to the surface; consequently, reducing the abundance of tunas by fishing in turn reduces the availability of prey to seabirds (Au & Pitman, 1986; Ballance *et al.*, 1997), contributing to increased vulnerability to starvation and other stressors that could

lead to mortality. (3) Purse seines set on dolphin pods have been hypothesized to cause miscarriages and separation and loss of calves but experiments designed to test this hypothesis have failed to find supporting evidence (Archer *et al.*, 2004; Edwards, 2006). (4) Drifting FADs, which aggregate biomass from a surrounding area, may alter the survival probability of organisms that associate with the floating object by altering their spatial distributions over hundreds of kilometres, transporting them to areas outside their normal distribution, modifying their diet composition and changing their behaviour, such as horizontal movements, vertical habitat use and diel vertical migration cycles (Marsac *et al.*, 2000; Hallier & Gaertner, 2008; Dagorn *et al.*, 2010). In some regions, FADs also have the potential to trap organisms in areas of low productivity (Marsac *et al.*, 2000; Hallier & Gaertner, 2008). (5) Disease in organisms injured or killed by fishing operations can spread and kill other organisms. For instance, in one study, the observed loss of almost an entire stock of scallops within 9 months of the start of the fishery was hypothesized to have resulted from a bacterial infection resulting from decomposing scallops killed by the fishery (Caddy, 1973; McLoughlin *et al.*, 1991). (6) Collateral mortality can result from the stress or injuries an organism incurs from avoiding fishing gear (ICES, 2005; Broadhurst *et al.*, 2006).

Increased predation of organisms injured or disturbed by fishing gear can also occur, referred to as facilitated predation (Kaiser & Spencer, 1994; Goñi, 1998; ICES, 2005). For example, live escapees and organisms released alive can be displaced from suitable habitat for shelter and may experience predation near the sea surface and in the water column, increasing the risk of predation as they sink or swim back to their preferred habitat (Fig. 5) (Broadhurst *et al.*, 2006). Furthermore organisms that escape before capture or are released injured or with impaired behaviour (*e.g.* swim slower, allowing predators to approach more closely; reduced responsiveness to various other stimuli) due to the fishery interaction can have an increased probability of predation (Borucinska *et al.*, 2002; Ryer, 2002; Ryer *et al.*, 2004; Davis, 2005; Davis & Ottmar, 2006). For example, captive juvenile *T. chalcogramma* subjected to stress, simulating passage through a trawl (prolonged swimming in the trawl mouth, followed by crowding in the codend and then escape through the mesh) exhibited slower reflexes in response to predator attack, where mortality from predation was significantly higher than that of control fish (Ryer *et al.*, 2004). Collateral mortalities due to facilitated predation can also result because predators are attracted to areas disturbed by fishing gear (Caddy, 1973; Ryer, 2002). For instance, fishery operations' disruption of schooling behaviour may attract predators, resulting in substantial mortalities from this facilitated predation (Ryer, 2002). Depredated catch, discussed previously under the pre-catch component, constitutes a collateral loss *via* facilitated predation when the cause of mortality is indirectly caused by the fishing operation when a predator kills and completely removes a live organism from the gear.

In many fishing operations, the school is not completely captured, either because the size is too large for the gear or because the fishing manoeuvre has failed to capture the whole school. This is another source of collateral fishing mortality: by reducing optimal species-specific and habitat-specific school sizes, fisheries reduce the fitness of the remaining individuals, including by increasing predation risk, and also by reducing efficiency in mating, foraging and energy expenditure (Breder, 1959; Pavlov & Kasumyan, 2000; Pitcher, 2001; White & Warner, 2007; Larsson, 2012).

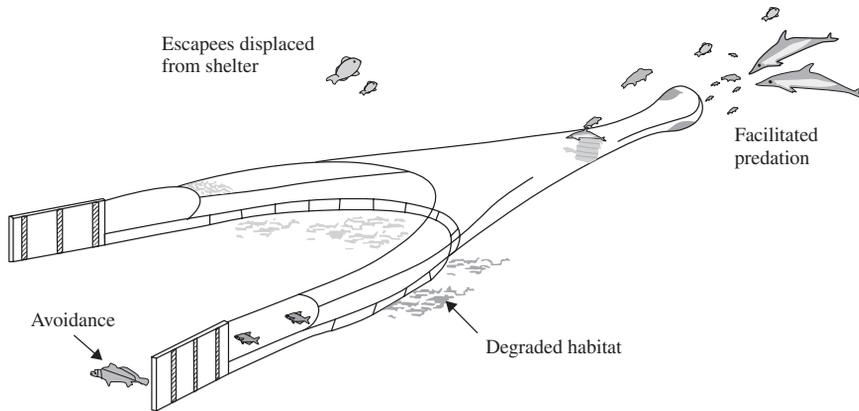


FIG. 5. Examples of collateral sources of fishing mortality from trawl fishing (adapted from Broadhurst *et al.*, 2006).

The increased predation risk to the remaining fraction of the original school that escaped could be mitigated if the group quickly finds and merges with another school, but the dynamics of school encounters is complex (Crofts *et al.*, 2003). Owing to facilitated predation, and the frequent aggregation of predators near fishing operations, the vulnerability of the school fraction to predation is further exacerbated. The effects of this collateral mortality source could be substantial for both target and incidentally caught species. For species with complex social structure such as dolphins, the group social structure could be disrupted if fishing results in the mortality of a dominant individual or pair, impairing the survival of remaining individuals owing to the loss of knowledge and skills of the leader, and through potential additional losses resulting from conflicts that may arise to replace the dominant individual or pair (Hall, 1998; Pryor & Norris, 1998).

Discards present an additional source of collateral fishing mortality. Large quantities of organic matter from the disposal at sea of offal, spent bait and dead by-catch can change foraging behaviour, diet, competition amongst coastal and marine species and community composition (Wassenberg & Hill, 1987; Evans *et al.*, 1994; Hall, 1996; Yamamura, 1997; Goñi, 1998; Furness *et al.*, 2007; Franco *et al.*, 2008; Gilman *et al.*, 2013). Discards can alter food webs and distributions of biomass within an ecosystem (*e.g.* transferring the biomass of discarded demersal species to surface scavengers, and transferring the biomass of discarded pelagic species to benthic scavengers), increase levels of organic material in nutrient-poor benthic ecosystems and, in fisheries where discards are spatially concentrated, and especially in areas of low current flow, may cause localized hypoxia or even anoxia of the seabed, which, if prolonged, can cause substantial mortalities, alter benthic community composition and ecosystem processes and structure (Wassenberg & Hill, 1987; Evans *et al.*, 1994; Yamamura, 1997; Goñi, 1998; Hall *et al.*, 2000; Gray *et al.*, 2002; FAO, 2003; Franco *et al.*, 2008; Levin *et al.*, 2009; Haselmair *et al.*, 2010). This is potentially problematic not just for fisheries discharges occurring in coastal areas, but also for discharges occurring in very deep regions of the ocean, where large proportions of discharges may settle through the water column without being consumed. This could alter the benthic community and transfer and lock-up biomass in bottom currents for

centuries before recycling to the euphotic zone of the pelagic ecosystem (Stockton & DeLaca, 1982; Smith, 1985; Hall *et al.*, 2000).

Fisheries cause the loss and degradation of habitat through increased suspended sediment loads, which causes increased turbidity, reduced light levels and smothering of the benthos, altered substratum from direct gear contact, hypoxia and anoxia from discards and alteration to the benthic community. This results in indirect collateral mortalities by causing increased predation and competition for shelter habitat by the species that had used the fishery-degraded habitat (Goñi, 1998; ICES, 2005; Broadhurst *et al.*, 2006; Kaiser *et al.*, 2006; White & Warner, 2007). Habitat alteration can increase predation from both acute and chronic loss of habitat used for shelter (Goñi, 1998; Moksnes *et al.*, 1998; ICES, 2005; Broadhurst *et al.*, 2006). Many fisheries cause significant increases in water turbidity, which is another way in which predation may be affected by fishing, resulting in mortalities for different species. In some studies, increased water turbidity reduced the response to predators and increased predation rates for some species (Ferrari *et al.*, 2010), but other studies found that increased turbidity had a variable effect on the predation rate of benthic species (Macia *et al.*, 2003). Trawl gear can also vertically mix sediment horizons, redistributing organic-rich surface layers into subsurface layers, redistributing organic matter from the aerobic food chain on the sediment surface to a subsurface anaerobic system (Jones, 1992). Trawl gear can likewise create anaerobic and highly turbid conditions at the sediment surface, unsuitable for the survival of benthic larvae (Jones, 1992).

Several studies have documented changes in benthic community structure and functions due to habitat impacts from fishing gear, which may be irreversible or have very long recovery times (decades or longer) for foundation species to reach maturity and reestablish structural complexities of ecosystems (Bradstock & Gordon, 1983; de Groot, 1984; Jones, 1992; Sainsbury *et al.*, 1992; Kaiser *et al.*, 2006). For example, Sabellaria reefs in the German Wadden Sea and bryozoan beds of Tasman Bay, New Zealand, were removed by demersal trawls and have not recolonized owing to alterations to the substratum (Bradstock & Gordon, 1983; de Groot, 1984). Also, for example, changes in species composition and relative abundance of the North West Shelf, Australia, were linked to habitat degradation from demersal trawling (Sainsbury *et al.*, 1992). As is the case with most sources of collateral mortalities, however, methods are yet to be developed that provide accurate estimates of mortality levels and rates resulting indirectly from fisheries habitat alteration (Jones, 1992; ICES, 2005).

CUMULATIVE AND SYNERGISTIC EFFECTS OF FISHERY INTERACTIONS

Injuries and stress sustained by organisms interacting with fishing operations can be caused by multiple factors, where the cumulative and interacting or synergistic effects of these factors during both individual and repeated sub-lethal interactions result in mortality (Davis, 2002; Broadhurst *et al.*, 2006; Suuronen & Erickson, 2010). Cumulative sub-lethal stressors from fishing, including when an organism repeatedly avoids capture or is repeatedly caught and released alive, may eventually lead to mortality. For example, sea turtles and sharks caught in longline fisheries have been observed to have multiple imbedded hooks, and longline terminal tackle is commonly observed to be bitten off, probably by sharks (Aguilar *et al.*, 1995; Gilman *et al.*,

2008; Ward *et al.*, 2008), suggesting that organisms survive repeated interactions. But, the cumulative injury and stress might eventually cause or contribute to mortality. For example, territorial organisms and those with restricted ranges that routinely overlap with a type of fishing gear may repeatedly escape from the gear, learn to modify their behaviour to avoid the gear or may experience multiple captures and releases. Trawl vessels will commonly make repeated tows at certain grounds, where the probability of recurrent capture and escapement of juvenile fishes may be considerable (Jorgensen *et al.*, 2005; Ingólfsson *et al.*, 2007).

Interactions among individual stressors from fishing operations can also result in cryptic mortality (Davis, 2002; Broadhurst *et al.*, 2006). For example, an organism may be caught and released injured, be displaced from suitable habitat and, because fishing operations have degraded habitat, the organism may lack shelter from predators and foraging habitat where it can recover from the injury, increasing the probability of mortality due to these synergistic effects of multiple stressors from fishing operations. Mortality may ultimately be the result of predation, lack of prey, disease, secondary infections or a combination of these and other stressors. Some of the interacting stressors may result from chronic effects of fishing, such as anoxia from discards, and habitat degradation and loss from bottom fishing. Others may result from acute events, such as from pre-catch escapement and collateral displacement from habitat used for shelter.

As identified for other components of cryptic fishing mortalities, there are probably disparities in vulnerability to cumulative and synergistic effects of fishing operations by species, size, sex and other explanatory factors. For instance, *G. morhua* was found to be robust to cumulative effects of repeated captures relative to other demersal fishes, including *M. aeglefinus* (Ingólfsson *et al.*, 2007).

Mortalities from cumulative and synergistic effects of fishing operations are considered together, as a single component, as there is overlap in the two processes. Mortalities resulting from cumulative stress and injury occur through a temporal series of fishery interactions. Removals due to synergistic effects can occur from the simultaneous interaction of effects of fishing (*e.g.* escape stressed and injured and habitat for shelter has been degraded from fishing operations), from stress and injury due to fishery interactions that occur in sequence, as with cumulative effects or from a combination of simultaneous and sequential stressors (*e.g.* escape stressed and injured, followed by capture and release further stressed and injured, plus being displaced from suitable habitat for shelter).

There are two examples of methods employed to estimate mortality rates and levels from cumulative effects of repeated escapement. Caddy & Seijo (2011) estimated the potential mortalities of locally fished subpopulations from the cumulative effects of repeated escapement from trawl tows by calculating a simple multiplier effect, and concluded that high proportions of juveniles may be subject to mortality from repeated interactions when trawling occurs in nursery areas. Jorgensen *et al.* (2005) and Ingólfsson *et al.* (2007) used electronic tagging and released young *G. morhua* in a fishing ground where these fish were caught intensively with bottom trawls but did not observe any marked additional mortality as a result of repeated escapement. It is worth noting, however, that *G. morhua* is a species that has proved to have a relatively low probability of pre-catch mortality (Breen *et al.*, 2007). As with collateral mortalities, the complex and indirect nexus between synergistic and cumulative

effects of fishing and mortalities has prevented, to date, the development of methods that provide accurate estimates of levels of removals from these sources.

DISCUSSION

Cryptic mortalities typically result from multiple factors, from cumulative and interacting effects of stress and injury sustained during various ways that an organism interacts with fishing operations (Fig. 1). There is a large suite of potentially significant explanatory factors of an individual organism's probability of cryptic fishing mortality. For instance, there are differences between species' behaviour in avoiding and interacting with fishing operations, including response to capture. There are also disparities between species, and by size and sex within species, in the severity of injury and stress, and concomitant probability of mortality, across the components of cryptic fishing mortality and across the individual explanatory factors that are significant for each component (Davis, 2002; Broadhurst *et al.*, 2006).

Gear-related factors that can have a significant effect on the probability of cryptic mortality include gear designs that affect mechanisms for escape, gear components that affect the depth and weight of static gear and concomitant ability and energy required for captured air-breathing organisms to reach the surface during the gear soak, and characteristics of gear remaining attached to released catch and escapees. Fishing operations-related factors include the temporal and spatial distribution of fishing effort, duration of each component of the fishing operation, catch composition (*e.g.* incompatible species can cause injuries when caught in towed gear) and fishing methods (*e.g.* offal discard practices may influence the risk of mortality from predation of escapees, live released organisms and organisms avoiding and disturbed by the fishing operation). Environmental conditions onboard and at the fishing grounds, and factors related to crew behaviour of handling and release practices, are additional potentially significant explanatory factors of cryptic mortality (Broadhurst *et al.*, 2006; Ryder *et al.*, 2006).

An understanding of the relative importance of factors in causing cryptic sources of fishing mortality is necessary to both estimate levels and rates of removals and mitigate the sources. As a result of the complexity of causes of cryptic removals from various aspects of fishing operations, few studies that have estimated cryptic fishing mortality have been able to account for the full suite of ways by which an organism can interact with and be stressed and injured by fishing operations (Suuronen, 2005; Broadhurst *et al.*, 2006). This creates uncertainty in estimates of the probability of mortality. This is especially relevant to collateral, cumulative and synergistic sources of mortalities, due to the indirect and relatively highly complex nexus between the stressors and removals for these components.

There has been relatively good progress in developing methods to estimate pre-catch and post-release mortality. These include various experimental methods as well as using explanatory variables to predict the probability of pre-catch and post-release mortality. Of the components of cryptic mortality, in the future, it is most likely that methods and technology could be developed to enable direct observation of pre-catch and post-release removals.

Results of many post-release survival studies suggest that mortality rates are significantly lower when organisms escape *v.* when they are caught, landed on

deck and released (Broadhurst *et al.*, 2006). For some species that will be released alive, significant reductions in post-release mortality rates cannot be easily achieved through improved on-deck handling and release procedures. Efforts should therefore be directed at minimizing fishery interactions with these species, and maximizing their escape when interactions do occur.

While there has been good progress in the development of methods to estimate ghost-fishing mortality in passive gear, primarily in trammel nets, gillnets and traps, there is a large gap in knowledge of methods to estimate removals from other gear types, especially active gears. While the catching process of active gears is understood to typically cease immediately upon gear detachment from the vessel, there is a gap in empirical evidence of ghost-fishing rates in these gear types (Matsuoka *et al.*, 2005; UNEP & FAO, 2009; FAO, 2010a). There is also limited understanding of cryptic removals due to predation of organisms caught in derelict passive or active gear.

The complexity and indirect link between collateral, cumulative and synergistic effects of fishing activities and mortalities have generally prevented the development of methods that provide accurate estimates of mortality levels and rates (ICES, 2005). Understanding of the probability of mortality from repeated interactions is limited to a small number of studies of a narrow range of species and gear types (Ingólfsson *et al.*, 2007; Caddy & Seijo, 2011). There remains limited understanding of collateral mortality rates or broader community-level changes caused by fishing. For example, there is limited knowledge of the relative importance of collateral removals resulting from artificial drifting floating objects, including FADs and masses of derelict gear and other marine debris, or from enduring or permanent shifts in benthic community structure and functions resulting from fishery direct physical contact and discards (Hall *et al.*, 2000; Kaiser *et al.*, 2006; Dagorn *et al.*, 2010; FAO, 2010a). The infinite possibilities of synergistic effects of stressors from different aspects of fishing operations include few scenarios that support accurate estimates of resulting mortality. Studies of predation probability following simulated escapement of catch and live releases (Ryer *et al.*, 2004) is one example of a method to estimate collateral losses, but it may not be feasible to estimate mortality probability resulting from more complex scenarios.

There are some general principles requiring consideration for studies designed to estimate cryptic fishing mortality rates. Sampling bias can confound findings; *e.g.* survival studies need to clearly identify the methods employed to select individual organisms for inclusion in the study, whether they were randomly selected or otherwise if they were chosen or excluded for particular reasons (Swimmer & Gilman, 2012). Controlling for treatment effects is likewise critical; however, a large number of studies estimating cryptic fishing mortality did not include controls owing to logistical constraints related to the study methods (Broadhurst *et al.*, 2006; Swimmer & Gilman, 2012). Relatively long studies require control treatments to differentiate natural from fishing mortality (Chaloupka *et al.*, 2004; Ryder *et al.*, 2006). Also, inclusion of control animals in survival experiments provides a basis for separating fishery-induced mortality from mortality caused by stressors that reduce survival probability as well as factors that increase survivability from being held in captivity, and from other possible confounding factors, including natural mortality (Broadhurst *et al.*, 2006). The duration of studies of cryptic fishing mortality requires consideration, in part, to ensure that sufficient sample sizes are obtained, that the studies

effectively simulate actual commercial fishing conditions and to ensure that observations are correctly interpreted. For example, ghost fishing can continue in the order of years under certain conditions, and post-release mortalities can occur in the order of months following release (Matsuoka *et al.*, 2005; Ryder *et al.*, 2006). Related, insufficient sample sizes can limit findings from survival and other studies designed to estimate cryptic losses. Meta-analyses pool data from multiple studies, and due to the larger pooled sample size plus the number of pooled studies, provide estimates with increased power and precision over estimates from individual studies (Musyl *et al.*, 2011*b*).

Knowledge of the relative importance of individual anthropogenic mortality sources of a stock or population is needed for effective management. While total mortality (Z), which includes all sources of mortality, including cryptic sources of fishing mortality, can be estimated from an age distribution or other methods, natural mortality estimation offers many challenges (Gulland, 1965; Vetter, 1988; Pascual & Iribarne, 1993; Hewitt & Hoenig, 2005), preventing the separation of natural from anthropogenic mortality. Estimates of Z and natural mortality do not enable discrimination among individual mortality sources, including total fishing mortality, cryptic fishing mortality and non-fishing related anthropogenic mortality sources.

Currently, there are sparse examples of capture fisheries where components of cryptic mortality are routinely estimated and reported. Although this is currently a rare practice, the catch model presented here includes this as one component (estimated cryptic fishing mortality; Fig. 1). For instance, the Northeast Fisheries Observer Program requires observers of the New England trawl *C. harengus* fishery to report tows where partial or full slippage events occurred. These data are used by management authorities to provide a first-order estimate of the level of slipped pre-catch, but without a protocol for estimating a pre-catch mortality rate (New England Fishery Management Council, 2011). The observer data collection protocols of the Commission for the Conservation of Antarctic Living Marine Resources include recording information on the disposition of live released or dead discarded catch of specified species in some managed fisheries. For instance, for skates and rays released in trawl fisheries, data collection protocols call for observers to record whether the individual was released alive with life-threatening injuries, alive with injuries serious enough to possibly reduce survival post-release, alive in good condition or with minor injury deemed not to be life threatening, or discarded dead (CCAMLR, 2012*a, b*). Finally, the data collection protocols for the regional observer programme of the Inter-American Tropical Tuna Commission call for the collection of information on the disposition of released turtles and dolphins from pelagic longline and purse seine fisheries. Options for observers to record the disposition of live released turtles caught in longline fisheries are unharmed, minor injuries, grave injuries, hook still present and location of hooking, and dead (IATTC, 2001, 2012).

The guidance presented here on causes and best practices to estimate components of cryptic fishing mortality may contribute towards making it a routine practice to estimate, report and account for these removals in scientific advice to management authorities, and to develop effective mitigation methods.

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References

- Agnew, D., Pearce, J., Pramod, G., Peatman, T., Watson, R., Beddington, J. & Pitcher, T. (2009). Estimating the worldwide extent of illegal fishing. *PLoS One* **4**, e4570. doi: 10.1371/journal.pone.0004570
- Aguiar, R., Mas, J. & Pastor, X. (1995). Impact of Spanish swordfish longline fisheries on the loggerhead sea turtle *Caretta caretta* population in the western Mediterranean. Proceedings of the 12th Annual Workshop on Sea Turtle Biology and Conservation (Richardson, J. & Richardson, T.), 1–6. *NOAA Technical Memorandum NMFS-SEFSC-361*.
- Archer, F., Gerrodette, T., Chivers, S. & Jackson, A. (2004). Annual estimates of the unobserved incidental kill of pantropical spotted dolphin (*Stenella attenuate attenuate*) calves in the tuna purse-seine fishery of the eastern tropical Pacific. *Fishery Bulletin* **102**, 233–244.
- Au, D. & Pitman, R. (1986). Seabird interactions with tuna and dolphins in the eastern tropical Pacific. *Condor* **88**, 304–317.
- Ballance, L. T., Pitman, R. L. & Reilly, S. B. (1997). Seabird community structure along a productivity gradient: importance of competition and energetic constraint. *Ecology* **78**, 502–518.
- Benoît, H., Hurlbut, T. & Chassé, J. (2010). Assessing the factors influencing discard mortality of demersal fishes in four fisheries using a semi-quantitative indicator of survival potential. *Fisheries Research* **106**, 436–447.
- Benoît, H., Hurlbut, T., Chassé, J. & Jonsen, I. (2012). Estimating fishery-scale rates of discard mortality using conditional reasoning. *Fisheries Research* **125–126**, 318–330.
- Benoît, H., Plante, S., Kroiz, M. & Hurlbut, T. (2013). A comparative analysis of marine fish species susceptibilities to discard mortality: effects of environmental factors, individual traits, and phylogeny. *ICES Journal of Marine Science* **70**, 99–113.
- Bjorndal, K., Bolten, A. & Lagueux, C. (1994). Ingestion of marine debris by juvenile sea turtles in coastal Florida habitats. *Marine Pollution Bulletin* **28**, 154–158.
- Borucinska, J., Kohler, N., Natanson, L. & Skomal, G. (2002). Pathology associated with retained fishing hooks in blue sharks, *Prionace glauca* (L.), with implications for their conservation. *Journal of Fish Diseases* **25**, 515–521.
- Bradstock, M. & Gordon, D. (1983). Coral-like bryozoan growths in Tasman Bay, and their protection to conserve commercial fish stocks. *New Zealand Journal of Marine and Freshwater Research* **17**, 159–163.
- Breder, C. (1959). Studies on social groupings in fishes. *Bulletin of the American Museum of Natural History* **117**, 393–482.
- Bremec, C., Lasta, M. & Hernandez, D. (2004). Survival of Patagonian scallop (*Zygochlamys patagonica*, King and Broderip, 1832) after the size selection process on commercial fishing vessels. *Fisheries Research* **66**, 49–52.
- Broadhurst, M., Suuronen, P. & Hulme, A. (2006). Estimating collateral mortality from towed fishing gear. *Fish and Fisheries* **7**, 180–218.
- Brothers, N. (1991). Albatross mortality and associated bait loss in the Japanese longline fishery in the Southern Ocean. *Biological Conservation* **55**, 255–268.
- Brothers, N., Duckworth, A., Safina, C. & Gilman, E. (2010). Seabird bycatch from pelagic longline fisheries is grossly underestimated when using only haul data. *PLoS One* **5**, e12491. doi:10.1371/journal.pone.0012491.
- Caddy, J. (1973). Underwater observations of tracks of dredges and trawls and some effects of dredging on a scallop ground. *Journal of the Fisheries Research Board of Canada* **30**, 173–180.
- Caddy, J. & Seijo, J. (2011). Destructive fishing practices by bottom gears: a broad review of research and practice. *Ciencia Pesquera* **19**, 5–58.

- Campana, S., Joyce, W. & Manning, M. (2009). Bycatch and discard mortality in commercially caught blue sharks *Prionace glauca* assessed using archival satellite pop-up tags. *Marine Ecology Progress Series* **387**, 241–253.
- Casale, P., Freggi, D. & Rocco, M. (2008). Mortality induced by drifting longline hooks and branchlines in loggerhead sea turtles, estimated through observation in captivity. *Aquatic Conservation: Marine and Freshwater Ecosystems* **18**, 945–954.
- CCAMLR (2012a). *CCAMLR Scientific Observer Cruise Report. Version 2012*. North Hobart: Commission on the Conservation of Antarctic Marine Living Resources.
- CCAMLR (2012b). *Scientific Observer Logbook Trawl Fishing. Version 2012*. North Hobart: Commission on the Conservation of Antarctic Marine Living Resources.
- Chaloupka, M., Parker, D. & Balazs, G. (2004). Modelling post-release mortality of loggerhead sea turtles exposed to the Hawaii-based pelagic longline fishery. *Marine Ecology Progress Series* **280**, 285–293.
- Chaloupka, M., Work, T., Balazs, G., Murakawa, S. & Morris, R. (2008). Cause-specific temporal and spatial trends in green sea turtle strandings in the Hawaiian Archipelago (1982–2003). *Marine Biology* **154**, 887–898.
- Chopin, F. & Arimoto, T. (1995). The condition of fish escaping from fishing gears—a review. *Fisheries Research* **21**, 315–327.
- Chopin, F., Inoue, Y. & Arimoto, A. (1996). Development of a catch mortality model. *Fisheries Research* **25**, 377–382.
- Coggins, L., Catalano, M., Allen, M., Pine, W. & Walters, C. (2007). Effects of cryptic mortality on fishery sustainability and performance. *Fish and Fisheries* **8**, 1–15.
- Cox, M. & Heintz, R. (2009). Electrical phase angle as a new method to measure fish condition. *Fishery Bulletin* **107**, 477–487.
- Cox, M., Heintz, R. & Hartman, K. (2011). Measurements of resistance and reactance in fish with the use of bioelectrical impedance analysis: sources of error. *Fishery Bulletin* **109**, 35–47.
- Crofts, D., Krause, J., Couzin, I. & Pitcher, T. (2003). When fish shoals meet: outcomes for evolution and fisheries. *Fish and Fisheries* **4**, 138–146.
- Crowder, L. & Murawski, S. (1998). Fisheries bycatch: implications for management. *Fisheries* **23**, 8–17.
- Dagorn, L., Holland, K. & Filmler, J. (2010). Are drifting FADs essential for testing the ecological trap hypothesis? *Fisheries Research* **106**, 60–63.
- Davis, M. (2002). Key principles for understanding fish bycatch discard mortality. *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 1834–1843.
- Davis, M. (2005). Behaviour impairment in captured and released sablefish: ecological consequences and possible substitute measures for delayed discard mortality. *Journal of Fish Biology* **66**, 254–265.
- Davis, M. (2007). Simulated fishing experiments for predicting delayed mortality rates using reflex impairment in restrained fish. *ICES Journal of Marine Science* **64**, 1535–1542.
- Davis, M. & Otmar, M. (2006). Wounding and reflex impairment may be predictors for mortality in discarded or escaped fish. *Fisheries Research* **82**, 1–6.
- Davis, M. & Ryer, C. (2003). Understanding fish bycatch discard and escapee mortality. *AFSC Quarterly Report* **2003** (January–March), 1–9.
- Derraik, J. (2002). The pollution of the marine environment by plastic debris: a review. *Marine Pollution Bulletin* **44**, 842–852.
- Diaz, G. & Serafy, J. (2005). Longline-caught blue shark (*Prionace glauca*): factors affecting the numbers available for live release. *Fishery Bulletin* **103**, 720–724.
- Donohue, M., Boland, R., Sramek, C. & Antonelis, G. (2001). Derelict fishing gear in the northwestern Hawaiian Islands: diving surveys and debris removal in 1999 confirm threat to coral reef ecosystem. *Marine Pollution Bulletin* **42**, 1301–1312.
- Edwards, E. (2006). Duration of unassisted swimming activity for spotted dolphin (*Stenella attenuate*) calves: implications for mother–calf separation during tuna purse-seine sets. *Fishery Bulletin* **104**, 125–135.
- Erzini, K., Monteiro, C., Ribeiro, J., Santos, M., Gaspar, M., Monteiro, P. & Borges, T. (1997). An experimental study of gill net and trammel net ‘ghost fishing’ off the Alarve (southern Portugal). *Marine Ecology Progress Series* **158**, 257–265.

- Evans, S., Hunter, J., Eliza, L. & Wahju, R. (1994). Composition and fate of the catch and bycatch in the Farne Deep (North Sea) *Nephrops* fishery. *ICES Journal of Marine Science* **51**, 155–168.
- FAO (1995). *Code of Conduct for Responsible Fisheries*. Rome: Food and Agriculture Organization of the United Nations. Available at <http://www.fao.org/docrep/005/v9878e/v9878e00.HTM>
- FAO (2010a). *The State of World Fisheries and Aquaculture 2010*. Rome: Food and Agriculture Organization of the United Nations. Available at <http://www.fao.org/docrep/013/i1820e/i1820e00.htm>
- FAO (2010b). *Guidelines to Reduce Sea Turtle Mortality in Fishing Operations*. Rome: Food and Agriculture Organization of the United Nations. Available at <http://www.fao.org/docrep/012/i0725e/i0725e00.htm>
- FAO (2011). *International Guidelines on Bycatch Management and Reduction of Discards*. Rome: Food and Agriculture Organization of the United Nations. Available at <http://www.fao.org/docrep/015/ba0022t/ba0022t00.pdf>
- Ferrari, M., Lysak, K. & Chivers, D. (2010). Turbidity as an ecological constraint on learned predator recognition and generalization in a prey fish. *Animal Behaviour* **79**, 515–519.
- Fowler, C. (1987). Marine debris on northern fur seals: a case study. *Marine Pollution Bulletin* **18**, 326–335.
- Franco, M., Steyaert, M., Cabral, H., Tenreiro, R., Chambel, L., Vincx, M., Costa, M. & Vznaverbeke, J. (2008). Impacts of discards of beam trawl fishing on the nematode community from the Tagus estuary (Portugal). *Marine Pollution Bulletin* **56**, 1728–1736.
- Furness, R., Edwards, A. & Oro, D. (2007). Influence of management practices and of scavenging seabirds on availability of fisheries discards to benthic scavengers. *Marine Ecology Progress Series* **350**, 235–244.
- Gilman, E. (2011). Bycatch governance and best practice mitigation technology in global tuna fisheries. *Marine Policy* **35**, 590–609.
- Gilman, E., Boggs, C. & Brothers, N. (2003). Performance assessment of an underwater setting chute to mitigate seabird bycatch in the Hawaii pelagic longline tuna fishery. *Ocean and Coastal Management* **46**, 985–1010.
- Gilman, E., Zollett, E., Beverly, S., Nakano, H., Shiode, D., Davis, K., Dalzell, P. & Kinan, I. (2006). Reducing sea turtle bycatch in pelagic longline gear. *Fish and Fisheries* **7**, 2–23.
- Gilman, E., Kobayashi, D., Swenarton, T., Brothers, N., Dalzell, P. & Kinan, I. (2007a). Reducing sea turtle interactions in the Hawaii-based longline swordfish fishery. *Biological Conservation* **139**, 19–28.
- Gilman, E., Brothers, N. & Kobayashi, D. (2007b). Comparison of the efficacy of three seabird bycatch avoidance methods in Hawaii pelagic longline fisheries. *Fisheries Science* **73**, 208–210.
- Gilman, E., Clarke, S., Brothers, N., Alfaro-Shigueto, J., Mandelman, J., Mangel, J., Peterson, S., Piovano, S., Thomson, N., Dalzell, P., Donoso, M., Goren, M. & Werner, T. (2008). Shark interactions in pelagic longline fisheries. *Marine Policy* **32**, 1–18.
- Gilman, E., Chaloupka, M., Read, A., Dalzell, P., Holetschek, J. & Curtice, C. (2012). Hawaii longline tuna fishery temporal trends in standardized catch rates and length distributions and effects on pelagic and seamount ecosystems. *Aquatic Conservation: Marine and Freshwater Ecosystems* **22**, 446–488. doi: 10.1002/aqc.2237
- Gilman, E., Passfield, K. & Nakamura, K. (2013). Performance of regional fisheries management organizations: ecosystem-based governance of bycatch and discards. *Fish and Fisheries* (in press). doi: 10.1111/faf.12021
- Godley, B., Lima, E., Åkesson, S. & Broderick, A. (2003). Movement patterns of green turtles in Brazilian coastal waters described by satellite tracking and flipper tagging. *Marine Ecology Progress Series* **253**, 279–288.
- Godley, B., Blumenthal, J., Broderick, A., Coyne, M., Godfrey, M., Hawkes, L. & Witt, M. (2008). Satellite tracking of sea turtles: where have we been and where do we go next? *Endangered Species Research* **4**, 3–22.
- Goñi, R. (1998). Ecosystem effects of marine fisheries: an overview. *Ocean and Coastal Management* **40**, 37–64.

- Gray, J., Wu, R. & Or, Y. (2002). Effects of hypoxia and organic enrichment on the coastal marine environment. *Marine Ecology Progress Series* **238**, 249–279.
- de Groot, S. (1984). The impact of bottom trawling on benthic fauna of the North Sea. *Ocean Management* **9**, 177–190.
- Hall, M. (1996). On bycatches. *Reviews in Fish Biology and Fisheries* **6**, 319–352.
- Hall, M. (1998). An ecological view of the tuna-dolphin problem. *Reviews in Fish Biology and Fisheries* **8**, 1–34.
- Hall, M., Alverson, D. & Metuzals, K. (2000). By-catch: problems and solutions. *Marine Pollution Bulletin* **41**, 204–219.
- Hallier, J. & Gaertner, D. (2008). Drifting fish aggregation devices could act as an ecological trap for tropical tuna species. *Marine Ecology Progress Series* **353**, 255–264.
- Haselmair, A., Stachowitsch, M., Zuschin, M. & Riedel, B. (2010). Behaviour and mortality of benthic crustaceans in response to experimentally induced hypoxia and anoxia *in situ*. *Marine Ecology Progress Series* **414**, 195–208.
- Hays, G., Bradshaw, C., James, M., Lovell, P. & Sims, D. (2007). Why do Argos satellite tags deployed on marine animals stop transmitting? *Journal of Experimental Marine Biology and Ecology* **349**, 52–60.
- Hewitt, D. & Hoenig, J. (2005). Comparison of two approaches for estimating natural mortality based on longevity. *Fishery Bulletin* **103**, 433–437.
- Hight, B., Holts, D., Graham, J., Kennedy, B., Taylor, V., Sepulveda, C., Bernal, D., Ramon, D., Rasmussen, R. & Lai, N. (2007). Plasma catecholamine levels as indicators of the postrelease survivorship of juvenile pelagic sharks caught on experimental drift longlines in the Southern California Bight. *Marine and Freshwater Resources* **58**, 145–151.
- Hill, B. & Wassenberg, T. (1990). Fate of discards from prawn trawlers in Torres Strait. *Australian Journal of Marine and Freshwater Research* **41**, 53–74.
- Hueter, R., Manire, C., Tyminski, J., Hoenig, M. & Hepworth, D. (2006). Assessing mortality of released or discarded fish using a logistic model of relative survival derived from tagging data. *Transactions of the American Fisheries Society* **135**, 500–508.
- Humborstad, O., Løkkeborg, S., Hareide, N. & Furevik, D. (2003). Catches of Greenland halibut (*Reinhardtius hippoglossoides*) in deepwater ghost-fishing gillnets on the Norwegian continental slope. *Fisheries Research* **64**, 163–170.
- Huse, I. & Vold, A. (2010). Mortality of mackerel (*Scomber scombrus* L.) after pursing and slipping from a purse seine. *Fisheries Research* **106**, 54–59.
- IATTC (2001) Purse seine observer program forms. IATTC STR 01/2001. La Jolla, CA: Inter-American Tropical tuna Commission.
- Ingólfsson, Ó., Soldal, A., Huse, I. & Breen, M. (2007). Escape mortality of cod, saithe and haddock in a Barents Sea trawl fishery. *ICES Journal of Marine Science* **64**, 1836–1844.
- Jones, J. (1992). Environmental impact of trawling on the seabed: a review. *New Zealand Journal of Marine and Freshwater Research* **26**, 59–67.
- Jones, M. (1995). Fishing debris in the Australian marine environment. *Marine Pollution Bulletin* **30**, 25–33.
- Jorgensen, T., Ovredal, J. & Huse, I. (2005). A new pass-through PIT tag detection system for marine use. In *Proceedings of the Fifth Conference on Fish Telemetry held in Europe, Ustica, Italy 2003* (Spedicato, M., Lembo, G. & Marmulla, G., eds), pp. 261–268. Rome: COISPA Teconologia and FAO.
- Kaiser, M. & Spencer, B. (1994). Fish scavenging behavior in recently trawled areas. *Marine Ecology Progress Series* **112**, 41–49.
- Kaiser, M. & Spencer, B. (1995). Survival of bycatch from a beam trawl. *Marine Ecology Progress Series* **126**, 31–38.
- Kaiser, M., Bullimore, B., Newman, P., Lock, K. & Gilbert, S. (1996). Catches in ‘ghost fishing’ set nets. *Marine Ecology Progress Series* **145**, 11–16.
- Kaiser, M., Clarke, K., Hinz, H., Austen, M., Somerfield, P. & Karakassis, I. (2006). Global analysis of response and recovery of benthic biota to fishing. *Marine Ecology Progress Series* **311**, 1–14.
- Kauppinen, T., Siira, A. & Suuronen, P. (2005). Temporal and regional patterns in seal-induced catch and gear damage in the coastal trap-net fishery in the northern Baltic Sea: effect of netting material on damages. *Fisheries Research* **73**, 99–109.

- Kelleher, K. (2005) Discarding in the world's marine fisheries: an update. *FAO Fisheries Technical Paper No. 470*. Available at <http://www.fao.org/docrep/008/y5936e/y5936e00.htm>
- Klimker, A. (1994). Tanner crab survival in closed pots. *Alaska Fishery Research Bulletin* **1**, 179–183.
- Lancaster, J. & Frid, C. (2002). The fate of discarded juvenile brown shrimps (*Crangon crangon*) in the Solway Firth UK fishery. *Fisheries Research* **58**, 95–107.
- Larsson, M. (2012). Why do fish school? *Current Zoology* **58**, 116–128.
- Lehtonen, E., Tschernij, V. & Suuronen, P. (1998). An improved method for studying survival of fish that escape trawl-cod-end meshes. *Fisheries Research* **38**, 303–306.
- Levin, L., Ekau, W., Gooday, A. & Jorissen, F. (2009). Effects of natural and human-induced hypoxia on coastal benthos. *Biogeoscience Discussions* **6**, 3563–3654.
- Lockwood, S., Pawson, M. & Eaton, D. (1983). The effect of crowding on mackerel (*Scomber scombrus* L.) – physical condition and mortality. *Fisheries Research* **2**, 129–147.
- Macia, A., Abrantes, K. & Paula, J. (2003). Thorn fish *Terapon jarbua* (Forskål) predation on juvenile white shrimp *Penaeus indicus* H. Milne Edwards and brown shrimp *Metapenaeus monoceros* (Fabricius): the effect of turbidity, prey density, substrate type and pneumatophore density. *Journal of Experimental Marine Biology and Ecology* **291**, 29–56.
- Madsen, N., Skeide, R., Breen, M., Krag, L. A., Huse, I. & Soldal, A. (2008). Selectivity in a trawl codend during haul-back – an overlooked phenomenon. *Fisheries Research* **91**, 168–174.
- Main, J. & Sangster, G. (1990). An assessment of the scale damage to and survival rates of young fish escaping from the cod-end of a demersal trawl. *Scottish Fisheries Research Report* **46**.
- Mandelman, J., Cooper, P., Werner, T. & Lagueux, K. (2008). Shark bycatch and depredation in the U.S. Atlantic pelagic longline fishery. *Reviews in Fish Biology and Fisheries* **18**, 427–442.
- Marsac, F., Fonteneau, A. & Ménard, F. (2000). Drifting FADs used in tuna fisheries: an ecological trap?. In *Pêche Thonière et Dispositifs de Concentration de Poisons* (Le Gall, J. Y., Cayré, P. & Taquet, M., eds), pp. 537–552. Montpellier: IRD, Laboratoire HEA.
- Matsuoka, T., Nakashima, T. & Nagasawa, N. (2005). A review of ghost fishing: scientific approaches to evaluation and solutions. *Fisheries Science* **71**, 691–702.
- McLoughlin, R., Young, P. & Parslow, J. (1991). The Australian scallop dredge: estimates of catching efficiency and associated indirect fishing mortality. *Fisheries Research* **11**, 1–24.
- Misund, O. & Beltestad, A. (1995). Survival of herring after simulated net bursts and conventional storage in net pens. *Fisheries Research* **22**, 293–297.
- Misund, O. & Beltestad, A. (2000). Survival of mackerel and saithe that escape through sorting grids in purse seines. *Fisheries Research* **48**, 31–41.
- Moksnes, P., Pihl, L. & van Montfrans, J. (1998). Predation on postlarvae and juveniles of the shore crab *Carcinus maenas*: importance of shelter, size and cannibalism. *Marine Ecology Progress Series* **166**, 211–225.
- Moore, C. (2008). Synthetic polymers in the marine environment: a rapidly increasing, long-term threat. *Environmental Research* **108**, 131–139.
- Moyes, C., Fragoso, N., Brill, R. & Musyl, M. (2006). Predicting postrelease survival in large pelagic fish. *Transactions of the American Fisheries Society* **135**, 1389–1397.
- Musyl, M., Domeier, M., Nasby-Lucas, N., Brill, R., McNaughton, L., Swimmer, J., Lutcavage, M., Wilson, S., Galuardi, B. & Liddle, J. (2011a). Performance of pop-up satellite archival tags. *Marine Ecology Progress Series* **433**, 1–28.
- Musyl, M., Brill, R., Curran, D., Fragoso, N., McNaughton, L., Nielsen, A., Kikkawa, B. & Moyes, C. (2011b). Postrelease survival, vertical and horizontal movements, and thermal habitats of five species of pelagic sharks in the central Pacific Ocean. *Fishery Bulletin* **109**, 341–361.
- Nakashima, T. & Matsuoka, T. (2005). Ghost fishing mortality and fish aggregation by lost bottom-gillnet tangled around fish aggregation device. *Nippon Suisan Gakkaishi* **71**, 178–187.

- Neilson, J., Busawon, S., Andrushchenko, I., Campana, S., Carruthers, E., Harris, L. & Stokesbury, M. (2012) A review of approaches to assess survival of released catch from Canadian large pelagic longline fisheries. *Canadian Science Advisory Secretariat Research Document* **2011/091**.
- Olla, B., Davis, M. & Schreck, C. (1997). Effects of simulated trawling on sablefish and walleye pollock: the role of light intensity, net velocity and towing duration. *Journal of Fish Biology* **50**, 1181–1194.
- Oros, J., Calabuig, P. & Deniz, S. (2004). Digestive pathology of sea turtles stranded in the Canary islands between 1993 and 2001. *Veterinary Record* **155**, 169–174.
- Parga, M. (2012). Hooks and sea turtles: a veterinarian's perspective. *Bulletin of Marine Science* **88**, 731–741.
- Parker, D., Balazs, G., Murakawa, S. & Polovina, J. (2005). Post-hooking survival of loggerhead sea turtles taken by pelagic longline fishing in the North Pacific. Proceedings of the Twenty-first Annual Symposium on Sea Turtle Biology and Conservation (Coyne, M. & Clark, R.), 50–52. *NOAA Technical Memorandum NMFS-SEFSC-528*.
- Parker, S., McElderry, H., Rankin, P. & Hannah, R. (2006). Buoyancy regulation and barotraumas in two species of nearshore rockfish. *Transactions of the American Fisheries Society* **135**, 1213–1223.
- Pascual, M. & Iribarne, O. (1993). How good are empirical predictions of natural mortality? *Fisheries Research* **16**, 17–24.
- Pavlov, D. & Kasumyan, A. (2000). Patterns and mechanisms of schooling behavior in fish: a review. *Journal of Ichthyology* **40**, S163–S231.
- Pawson, M. (2003). The catching capacity of lost static fishing gears: introduction. *Fisheries Research* **64**, 101–105.
- Pikitch, E., Santora, C., Babcock, E., Bakun, A., Bonfil, R., Conover, D., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E., Link, J., Livingston, P., Mangel, M., McAllister, M., Pope, J. & Sainsbury, J. (2004). Ecosystem-based fishery management. *Science* **305**, 346–347.
- Pitcher, T. (2001). Fish schooling: Implications for pattern in the oceans and impacts on human fisheries. In *Encyclopedia of Ocean Sciences* (Steele, J., Turekian, K. & Thorpe, S., eds), pp. 975–987. London: Academic Press.
- Pollock, K. & Pine, W. (2007). The design and analysis of field studies to estimate catch-and-release mortality. *Fisheries Management and Ecology* **14**, 1–8.
- Pryor, K. & Norris, K. (1998). *Dolphin Societies*. Berkeley, CA: University of California Press.
- Ramos-Cartelle, A. & Mejuto, J. (2008). Interaction of the false killer whale (*Pseudorca crassidens*) and depredation on the swordfish catches of the Spanish surface longline fleet in the Atlantic, Indian and Pacific Oceans. *Collective Volume of Scientific Papers, ICCAT* **62**, 1721–1738.
- Ryder, C., Conant, T. & Schroeder, B. (2006) Report of the Workshop on Marine Turtle Longline Post-Interaction Mortality, Bethesda, Maryland, USA, 15-16 January, 2004. *NOAA Technical Memorandum NMFS-OPR-29*.
- Ryer, C. (2002). Trawl stress and escapee vulnerability to predation in juvenile walleye Pollock: is there an unobserved bycatch of behaviourally impaired escapees? *Marine Ecology Progress Series* **232**, 269–279.
- Ryer, C., Ottmar, M. & Sturm, E. (2004). Behavioural impairment after escape from trawl cod-ends may not be limited to fragile fish species. *Fisheries Research* **66**, 261–269.
- Sainsbury, K., Campbell, R. & Whitelaw, A. (1992). Effects of trawling on the marine habitat on the North West Shelf of Australia and implications for sustainable fisheries management. In *Sustainable Fisheries through Sustaining Fish Habitat, Australian Society for Fish Biology Workshop* (Hancock, D., ed), pp. 137–145. Canberra: Australian Government Publishing Service.
- Sancho, G., Puente, E., Bilbao, A., Gomez, E. & Arregi, L. (2003). Catch rates of monkfish (*Lophius* spp.) by lost tangle nets in the Cantabrian Sea (northern Spain). *Fisheries Research* **64**, 129–140.
- Santos, M., Saldanha, H., Gaspar, M. & Monteiro, C. (2003a). Causes and rates of net loss off the Algarve (southern Portugal). *Fisheries Research* **64**, 115–118.

- Santos, M., Saldanha, H., Gaspar, M. & Monteiro, C. (2003b). Hake (*Merluccius merluccius*, L. 1758) ghost fishing by gill nets off the Algarve (southern Portugal). *Fisheries Research* **64**, 119–128.
- SEAFO (2009). *Report of the SEAFO Scientific Committee. 2009*. Windhoek: South East Atlantic Fisheries Organisation.
- Smith, C. (1985). Food for the deep sea: utilization, dispersal, and the flux of nekton falls at the Santa Catalina Basin floor. *Deep Sea Research* **32**, 417–442.
- Snoddy, J. & Williard, A. (2010). Movements and post-release mortality of juvenile sea turtles released from gillnets in the Lower Cape Fear River, North Carolina, USA. *Endangered Species Research* **12**, 235–247.
- Snoddy, J., Landon, M., Blanvillain, G. & Southwood, A. (2009). Blood biochemistry of sea turtles captured in gillnets in the lower Cape Fear River, North Carolina, USA. *Journal of Wildlife Management* **73**, 1394–1401.
- Soldal, A., Isaksen, B. & Engås, A. (1993). Survival of gadoids that escape from demersal trawl. *ICES Marine Science Symposia* **196**, 122–127.
- Stockton, W. & DeLaca, T. (1982). Food falls in the deep sea: occurrence, quality and significance. *Deep Sea Research* **29**, 157–169.
- Stratoudakis, Y. & Marcalo, A. (2002). Short communication. Sardine slipping during purse-seining off northern Portugal. *ICES Journal of Marine Science* **59**, 1256–1262.
- Suuronen, P. (2005). Mortality of fish escaping trawl gears. *FAO Fisheries Technical Paper* **478**. Available at <http://www.fao.org/docrep/008/y6981e/y6981e00.htm>
- Suuronen, P. & Erickson, D. (2010). Mortality of animals that escape fishing gears or are discarded after capture: approaches to reduce mortality. In *Behavior of Marine Fishes. Capture Processes and Conservation Challenges* (He, P., ed) pp. 265–294. Oxford, UK: Blackwell Publishing.
- Suuronen, P. & Millar, R. (1992). Size-selectivity of diamond and square mesh cod-ends in pelagic herring trawls: only small herring will notice the difference. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 2109–2117.
- Suuronen, P., Turunen, T., Kiviniemi, M. & Karjalainen, J. (1995). Survival of vendace (*Coregonus albula* L.) escaping from a trawl cod end. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 2527–2533.
- Suuronen, P., Erickson, D. & Orrensalo, A. (1996a). Mortality of herring escaping from pelagic trawl cod-ends. *Fisheries Research* **25**, 305–321.
- Suuronen, P., Perez-Comas, J., Lehtonen, E. & Tschernij, V. (1996b). Size-related mortality of herring (*Clupea harengus* L.) escaping through a rigid sorting grid and trawl cod-end meshes. *ICES Journal of Marine Science* **53**, 691–700.
- Suuronen, P., Lehtonen, E., Tschernij, V. & Larsson, P. (1996c). Skin injury and mortality of Baltic cod escaping from two cod-ends equipped with exit windows. *Archive of Fishery and Marine Research* **44**, 165–178.
- Suuronen, P., Lehtonen, E. & Jounela, P. (2005). Escape mortality of trawl-caught Baltic cod (*Gadus morhua*) – the effect of water temperature, fish size and cod-end catch. *Fisheries Research* **71**, 151–163.
- Swimmer, Y. & Gilman, E. (Eds). (2012) *Report of the Sea Turtle Longline Fishery Post-Release Mortality Workshop, November 15-16, 2011*. NOAA Technical Memorandum NMFS-PIFSC-34.
- Swimmer, Y., Brill, R. & Musyl, M. (2002). Use of pop-up satellite archival tags to quantify mortality of marine turtles incidentally captured in longline fishing gear. *Marine Turtle Newsletter* **97**, 3–7.
- Swimmer, Y., Araz, R., McCracken, M., McNaughton, L., Ballester, J., Musyl, M., Bigelow, K. & Brill, R. (2006). Diving behavior and delayed mortality of olive ridley sea turtles *Lepidochelys olivacea* after their release from longline fishing gear. *Marine Ecology Progress Series* **323**, 253–261.
- Tasker, M. & Becker, P. (1992). Influences of human activities on seabird populations in the North Sea. *Netherlands Journal of Aquatic Ecology* **26**, 59–73.
- Tenningen, M., Vold, A. & Olsen, R. (2012). The response of herring to high crowding densities in purse seines: survival and stress reaction. *ICES Journal of Marine Science* **69**, 1523–1531.

- Trumble, R., Kaimmer, M. & Williams, G. (2000). Estimation of discard mortality rates for Pacific halibut bycatch in groundfish longline fisheries. *North American Journal of Fisheries Management* **20**, 931–939.
- UNEP & FAO (2009). *Abandoned, Lost or Otherwise Discarded Fishing Gear* (Macfadyen, G., Huntington, T. & Cappell, R., eds) UNEP Regional Seas Reports and Studies **185**. *FAO Fisheries and Aquaculture Technical Paper No. 523*. Available at http://www.unep.org/regionalseas/marinelitter/publications/docs/Marine_Litter_Abandoned_Lost_Fishing_Gear.pdf
- Vetter, E. (1988). Estimation of natural mortality in fish stocks: a review. *Fishery Bulletin* **86**, 25–43.
- Visser, I. (2000). Killer whale (*Orcinus orca*) interactions with longline fisheries in New Zealand waters. *Aquatic Mammals* **26**, 241–252.
- Ward, P., Lawrence, E., Darbyshire, R. & Hindmarsh, S. (2008). Large-scale experiment shows that nylon leaders reduce shark bycatch and benefit pelagic longline fishers. *Fisheries Research* **90**, 100–108.
- Wassenberg, T. & Hill, B. (1987). Feeding by the sand crab *Portunus pelagicus* on material discarded from prawn trawlers in Moreton Bay, Australia. *Marine Biology* **95**, 387–393.
- Watkins, B., Petersen, S. & Ryan, P. (2008). Interactions between seabirds and deep-water hake trawl gear: an assessment of impacts in South African waters. *Animal Conservation* **11**, 247–254.
- Weimerskirch, H. & Jouventin, P. (1987). Population dynamics of the wandering albatross *Diomedea exulans* of the Crozet Islands: causes and consequences of the population decline. *Oikos* **49**, 315–322.
- White, J. & Warner, R. (2007). Safety in numbers and the spatial scaling of density-dependent mortality in a coral reef fish. *Ecology* **88**, 3044–3054.
- Yamamura, O. (1997). Scavenging on discarded saury by demersal fishes off Sendai Bay, northern Japan. *Journal of Fish Biology* **50**, 919–925.

Electronic References

- Breen, M., Sangster, G., O'Neill, B., Kynoch, R., Jones, E. & Soldal, A. (2002). Evidence of sampling induced biases in mortality estimates from experiments investigating mortality in fish escaping from towed fishing gears. *ICES CM 2002/IV*, 25. Copenhagen: International Council for the Exploration of the Sea. Available at http://brage.bibsys.no/imr/bitstream/URN:NBN:no-bibsys_brage_34427/1/CM_2002_V_25.PDF/ (accessed 5 April 2013).
- Breen, M., Huse, I., Ingolfsson, O., Madsen, N. & Soldal, A. (2007). *An Assessment of Mortality in Fish Escaping from Trawl Codends and its Use in Fisheries Management. Final Report*. Project SURVIVAL: Q5RS-2002-01603. Brussels: European Commission. Available at http://ec.europa.eu/research/agriculture/projects/qlrt_2001_01603_en.htm/ (accessed 5 April 2013).
- Erickson, D., Pikitch, E., Methot, R., Babcock, E., Builder, T., Wallace, J., Crone, P., Brodziak, J. & Conser, R. (1997). Survival of trawl caught and discarded sablefish (*Anoplopoma fimbria*) off the U.S. West Coast. *ICES CM 1997/FF:06*. Copenhagen: International Council for the Exploration of the Sea. Available at <http://info.ices.dk/products/cmdocsindex.asp/> (accessed 5 April 2013).
- FAO (2003). The ecosystem approach to fisheries. *FAO Technical Guidelines for Responsible Fisheries* **4** (Suppl. 2). Available at <ftp://ftp.fao.org/docrep/fao/005/y4470e/y4470e00.pdf>
- FAO (2005). *World Inventory of Fisheries. Ghost Fishing. Issues Fact Sheets*. Rome: Food and Agriculture Organization of the United Nations. Available at <http://www.fao.org/fishery/topic/14798/en/> (accessed 5 April 2013).
- Gulland, J. (1965). Estimation of mortality rates. *Annex to Arctic Fisheries Working Group Report 3. Gadoid Fish Committee*. Copenhagen: International Council for the Exploration of the Seas. Available from the ICES Secretariat at www.ices.dk/explore-us/who-we-are/Pages/Secretariat.aspx

- IATTC (2012). *Longline Observer Program Field Manual. Last update: February 13, 2012.* La Jolla, CA: Inter-American Tropical tuna Commission. Available at <http://www.iattc.org/Downloads/Forms/LonglineNormal-forms-and-manual.pdf/> (accessed 15 November 2012).
- IATTC & OFCF (2011). *Learning How to Release Sea Turtles (Aprendiendo a Liberar Tortugas Marinas)*. La Jolla, CA, and Tokyo: Inter-American Tropical tuna Commission and Overseas Fishery Cooperation Foundation of Japan. Available at <http://www.iattc.org/Downloads/IATTC-OFcf-release-Sea-turtles.mp4/>
- ICES (1995). Report from the Study Group on unaccounted mortality in fisheries. *ICES CM 1995/B:1*. Copenhagen: International Council for the Exploration of the Sea. Available at http://brage.bibsys.no/imr/bitstream/URN:NBN:no-bibsys_brage_32752/1/CM_1995_B_01.pdf/
- ICES (2005) Joint Report of the Study Group on Unaccounted Fishing Mortality (SGUFM) and the Workshop on Unaccounted Fishing Mortality (WKUFM). *ICES CM 2005/B:08* Copenhagen: International Council for the Exploration of the Sea. Available at http://brage.bibsys.no/imr/bitstream/URN:NBN:no-bibsys_brage_3568/1/B08.pdf/ (accessed 5 April 2013).
- New England Fishery Management Council (2011) *Final Herring Plan Development Team (PDT) Report*. Newburyport, MA: New England Fishery Management Council. Available at http://www.nefmc.org/herring/council_mtg_docs/Sept%202011/4_PDT_Summaries.pdf/ (accessed 5 April 2013).
- Pikitch, E., Erickson, D., Suuronen, P., Lehtonen, E., Rose, C. & Bublitz, C. (2002) Selectivity and mortality of walleye pollock escaping from the cod-end and intermediate (extension) section of a pelagic trawl. *ICES CM 2002/V:15*. Copenhagen: International Council for the Exploration of the Sea. Available at waves-vagues.dfo-mpo.gc.ca
- Pikitch, E., Erickson, D., Oddson, G., Wallace, J. & Babcock, E. (1996) Mortality of trawl caught and discarded Pacific halibut (*Hippoglossus stenolepis*). *ICES CM 1996/B:16*. Copenhagen: International Council for the Exploration of the Sea. Available at <https://docs.google.com/viewer?a=v&pid=sites&srcid=ZGVmYXVsdGRvbWFpbXxwdWJsaWNhdGlvbnNlcmljZ2lsbWFufGd4OjI0MDJlOTU5ZDk5ODFjYWQ/> (accessed 7 April 2013).