PERSPECTIVE

Key principles for understanding fish bycatch discard mortality

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Abstract: The mortality of discarded fish bycatch is an important issue in fisheries management and, because it is generally unmeasured, represents a large source of uncertainty in estimates of fishing mortality worldwide. Development of accurate measures of discard mortality requires fundamental knowledge, based on principles of bycatch stressor action, of why discarded fish die. To date, discard mortality studies in the field have focused on capture stressors. Recent laboratory discard experiments have demonstrated the significant role of environmental factors, size- and species-related sensitivity to stressors, and interactions of stressors, which increase mortality. In addition, delayed mortality was an important consideration in experimental design. The discard mortality problem is best addressed through a combination of laboratory investigation of classes of bycatch stressors to develop knowledge of key principles of bycatch stressor action and field experiments under realistic fishing conditions to verify our understanding and make predictions of discard mortality. This article makes the case for a broader ecological perspective on discard mortality that includes a suite of environmental and biological factors that may interact with capture stressors to increase stress and mortality.

Résumé : La mortalité des prises accessoires rejetées à l'eau est une question d'importance dans la gestion des pêches; parce qu'elle est rarement mesurée, elle représente une source considérable d'incertitude dans les estimations de la mortalité due à la pêche à l'échelle mondiale. L'élaboration de mesures précises de la mortalité des prises accessoires nécessite des connaissances fondamentales sur les causes de cette mortalité basées sur les modes d'action des facteurs de stress. À ce jour, les études se sont concentrées sur les stress reliés à la capture. Des études récentes en laboratoire ont souligné le rôle significatif des facteurs de l'environnement, de la sensibilité au stress spécifique à la taille et à l'espèce et des interactions entre les facteurs de stress, qui accroissent tous la mortalité. De plus, la mortalité retardée est un élément important du plan d'expériences. La meilleure façon d'aborder le problème de la mortalité des prises accessoires est par une combinaison d'études de laboratoire des différentes classes de facteurs de stress pour obtenir des connaissances sur les principes fondamentaux de leur mode d'action et par des expériences sur le terrain dans des conditions de pêche réalistes pour vérifier ces connaissances et faire des prédictions sur la moralité. Il faut donc utiliser dans l'étude de la mortalité des prises accessoires une perspective écologique élargie qui considère une série de facteurs environnementaux et biologiques qui peuvent interagir avec les facteurs de stress lors de la capture pour accroître le stress et la mortalité.

[Traduit par la Rédaction]

Introduction

Mortality of fish released after capture (discarded bycatch) because of harvest restrictions (i.e., number, size or sex limits, or incidental catch as nontarget species) is one of the most significant issues affecting marine fisheries management today. Total discarded bycatch has been estimated to be approximately one-quarter of the worldwide fisheries catch, with discard mortality representing a large source of uncertainty in estimates of fishing mortality (Alverson et al. 1994; Pascoe 1997). Discard mortality rates in specific fisheries are rarely known, and general methods for estimating discard mortality rates in a wide range of threatened fisheries are not yet available. Although a few field studies have measured discard mortality by holding fish for short time periods after capture or by using tag and recapture methods, they resulted in qualitative mortality estimates with limited accuracy. Development of accurate quantitative methods to measure discard mortality in the field requires fundamental knowledge of why fish die after being discarded and how to measure this endpoint under a wide range of realistic fishing conditions.

In recent years there have been several workshops and review papers defining the discard problem, outlining specific actions that have been taken, and suggesting possible solutions for the future (Alverson et al. 1994; Pascoe 1997; Hall et al. 2000). Solutions to the discard problem have focused on preventing bycatch from landing on deck by avoiding ar-

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eas containing potential bycatch, modifying fishing gears in ways that reduce bycatch capture, and allowing for bycatch to escape through grids, panels, or increased mesh sizes (e.g., Kennelly and Broadhurst 1995; Broadhurst 2000). Although a great deal of progress has been made in reducing discards through improvements in fishing gear selectivity, there remains the problem of undetected bycatch mortality for fish that escape gear or are discarded after landing on deck. In this paper, we address the question of discard mortality and leave the problem of mortality in fish escaping fishing gear for a future discussion.

Because discard mortality results from the interactions of animals and fishing gear, efforts at resolution of the discard problem should rely on a combination of social, economic, engineering, and biological solutions. Fishing is conducted under social and economic constraints with gear that has traditionally been designed to modify fish behaviour in ways that facilitate capture. For fixed gear (hook and line, pots and traps), fish are attracted to gear by baits, which elicit chemosensory and gustatory responses resulting in capture. For towed gear, the avoidance response of fish is used to herd fish into the cod-ends of nets. Although seines are not towed, they also use avoidance behaviour to herd fish for capture. Gill nets act as passive capture devices, which are generally not detected by fish before capture. Fishing gear has been modified to use fish behaviour for decreasing capture of bycatch species. Relatively little attention has been paid to the role that biology and ecology of fishery resources might play in reduction of mortality in fish that are captured and discarded, especially the interaction of fishing practices with environmental factors (light conditions, temperature, air exposure, anoxia, sea conditions, and pressure changes) and biological factors (fish size and species, behaviour, physiology, and potential mortality).

This perspective is not meant to be an exhaustive discussion of the general fish discard problem, but rather to highlight key principles that underlie stress and mortality in discarded fish bycatch. These principles are also of general ecological interest and include the following: (*i*) increased mortality caused by interactions of stressors; (*ii*) the importance of environmental factors; (*iii*) species- and size-specific differences in sensitivity to stress; and (*iv*) delayed mortality after discarding. Although field studies could be made of the seemingly unlimited interactions among specific fishing gear types, environmental conditions, and fish species, we are more likely to uncover patterns and generalities for discard mortality with systematic laboratory experiments than by making random combinations of conditions in field experiments. It would be prudent and more efficient to understand principles controlling discard mortality and then to correlate innovative behavioural and physiological measures of stress and mortality with potential discard mortality in the laboratory. These assays of mortality could then be used in situ under all types of fishing conditions to predict discard mortality and evaluate new fishing methods designed to reduce or eliminate discards (Schreck 1990; Davis et al. 2001).

Capture and gear effects

All major fishing gear types involve some degree of injury to fish by internal and external wounding, crushing, scale loss, and hydrostatic effects, with the severity of injury dependant on gear type. Contact among fish in gear ranges from little in hook and line and gill-netting to moderate in traps and abundant in trawling and purse-seining with brailing. Fish interactions with gear vary widely, e.g., wounding from hooking, scraping in trawls, seines, brailing nets, and traps, and gilling in gill nets. Gear deployed in surface waters does not include effects associated with depth, including differences in pressure, temperature, and light conditions. Susceptibility to injury varies with species and stressor type, although comparisons are difficult because experiments with controlled, comparable stressor conditions are rare (Olla et al. 1997). Differences in injury type among gear types is an important consideration in discard mortality, but beyond the scope of this paper.

Characteristics of fish may control discard mortality. Fish with organs (gas bladders, eyes) that inflate after capture because of pressure changes become trapped near the surface after discarding and generally experience complete mortality. They would not be considered candidates for reduction of discard mortality rates except through the use of gear avoidance and escape measures before landing on deck or when captured in shallow depths. For fish that do not have a gas bladder, or have a gas bladder or other organs that do not inflate after capture, mortality after release may be variable and sometimes quite low (Alverson et al. 1994). These fish are excellent candidates for a variety of measures that could reduce discard mortality. Mortality associated with scale loss may be greater in clupeids than in gadids (Suuronen et al. 1996*a*, 1996*b*). In round fish, mortality caused by increased temperature was greater in sablefish (*Anoplopoma fimbria*) than in lingcod (*Ophodion elongatus*) (Davis et al. 2001; Davis and Olla 2002). Flatfish (e.g., Pacific halibut (*Hippoglossus stenolepis*)) may be more sensitive than round fish (walleye pollock (*Theragra chalcogramma*), sablefish, and lingcod) to suffocation in nets by pressure on the operculum (M.W. Davis, unpublished data).

Interacting factors

The increase of stress in fish caused by interactions of stressors is probably a common occurrence (Wedemeyer et al. 1990; Barton and Iwama 1991). Stress and mortality in discarded fish from towed- or fixed-gear fisheries often results from several classes of interacting stressors (Fig. 1). These classes include capture stressors (net entrainment, mesh passage, crushing and wounding, sustained swimming until exhaustion, changes in pressure), fishing conditions (towing time, light conditions, water and air temperatures, anoxia, sea conditions, time on deck, handling procedures), and biological attributes (behaviour, size, and species) (Chopin and Arimoto 1995; Murphy et al. 1995; Richards et al. 1995).

The variety of potential stressors in fishing and the lack of controlled experimental conditions in situ makes it difficult to conduct studies that systematically examine the strength of interactions among stressors. In the field studies cited above, delayed mortality was estimated in captured fish that either were held in net pens, cages, or tanks or were tagged and recaptured to estimate survival. These methods have only been applied in a limited number of fisheries because of the inherent logistical difficulties in holding fish in the

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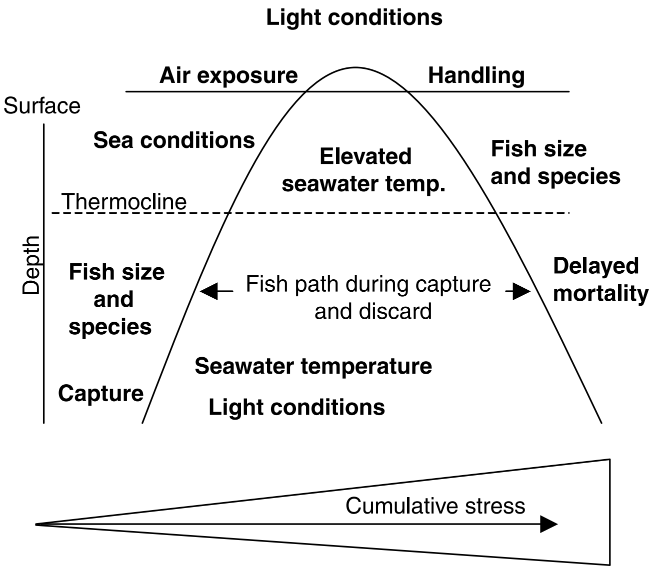
Fig. 1. Conceptual diagram of interacting factors in discard mortality for fish caught with deepwater gear (trawl, trap, hook and line). Fish caught with surface fishing gear (seine, hook and line, gill net) would not be subjected to the temperature and pressure changes associated with depth. The curved line indicates fish path at depth and the surface during capture and discard. Selected key factors are indicated in bold letters. Increasing stress level is indicated at the bottom of the diagram as interaction of factors increases initial capture stress.



field and using tagging studies to estimate bycatch mortality. The most extensive tag and recapture studies of discard mortality have been made on Pacific halibut, with the results being used in management to predict discard mortality rates based on halibut wounding observed in various fisheries (Kaimmer and Trumble 1998; Trumble et al. 2000). Although tag and recapture studies may be an accurate way to assess discard mortality, the results from these studies suffer from being obtained under a limited range of fishing, environmental, and biological (e.g., mixtures of sizes and species of animals) conditions and their interactions. Confidence in generalizing a discard mortality index to a wide range of fishing conditions is lacking until the effects of factor variation and interaction on mortality are understood. Holding fish in cages after capture to assess discard mortality also suffers from lack of generality in a range of fishing, environmental, and biological conditions.

In contrast, the role of a wide range of stressors and their interactions, which can increase stress, may be studied in the laboratory. However, it is difficult to simulate all bycatch stressors in the laboratory (e.g., catch size and composition, crushing and wounding, large changes in pressure). Although laboratory studies of discarding can be criticized for lack of realism, they allow for a systematic determination of general behavioural, biological, and physiological principles of stress response up to mortality in different species that is not possible in the field. Interactions of capture stressors (towing in a net and hooking), temperature, and air in the laboratory have been examined in walleye pollock, sablefish, Pacific halibut, and lingcod using changes in behaviour, blood physiology, and mortality as measures of stress (Davis et al. 2001; Davis and Olla 2001, 2002). In these studies, stress measured as deficits in feeding, orientation, and predator evasion and mortality increased with increased stressor intensity. Initially, capture caused stress, which was greater after towing in a net than after hooking, and then additional environmental stressors (temperature and air) increased stress reactions.

Physiological measures of stress in sablefish (plasma cortisol, lactate, glucose, potassium, sodium) increased in response to interactions of laboratory bycatch stressors (Spencer 2000; Davis et al. 2001). For example, exposure of sablefish to a gradient of bycatch stressors (increased temperature, hooking and increased temperature, and towing and increased temperature) resulted in increased plasma cortisol and lactate corresponding to the intensity of stressors. However, these plasma variables did not predict mortality, with no difference in maximum concentrations between fish that died and fish that were less stressed and survived (Fig. 2; all regression slopes not different from zero). An earlier study on the cause of death in stressed fish reached similar conclusions about predicting mortality with plasma stress variables and suggested that other physiological variables should be investigated (Wood et al. 1983). This key problem remains unsolved and physiological methods for predicting mortality are lacking.

Light conditions

Efforts to lessen or eliminate discards in trawl fisheries have centered on gear modifications that cause undersized fish or unwanted species to pass through net mesh or escape panels and not be retained in the cod-end. The success of these modifications in reducing discards often requires that fish be able to detect the gear and be volitionally guided out of the net while the targeted fish are retained (Kim and Wardle 1998). Because vision plays a dominant role in the response of at least some species to trawls, light quantity would be a limiting factor for net mesh detection (Blaxter and Parrish 1965; Glass and Wardle 1989; Walsh and Hickey 1993). Light quantity adequate for visual mesh detection is often not present, as fishing operations are commonly conducted at depths or at night. Therefore, developing effective gear modifications to reduce discards requires a clear understanding of how fish react to gear under conditions when vision is limited or not operative. Observations and measurement of fish behaviour under conditions of low light and darkness have been carried out in the laboratory with infrared illumination and video cameras sensitive to infrared light (Batty 1983; Olla and Davis 1990; Ryer and Olla 1998). Infrared technology has rarely been applied in field situations, but it has been shown to be a useful tool for measurement of animal behaviour in trawls (Matsuoka et al. 1997; Olla et al. 2000). Other possible methods currently under development for visualizing fish in trawls and traps include acoustic and laser technologies.

Observations of walleye pollock towed in a net under light and dark conditions demonstrated the value of laboratory studies for discovering key biological principles that apply to the discard problem (Olla et al. 1997). Fish in light conditions could see the net and were able to swim for up to 3 h with no resulting mortality, whereas fish in dark conditions were not able to see and respond to the net and became pinned against net meshes, ultimately resulting in mortality

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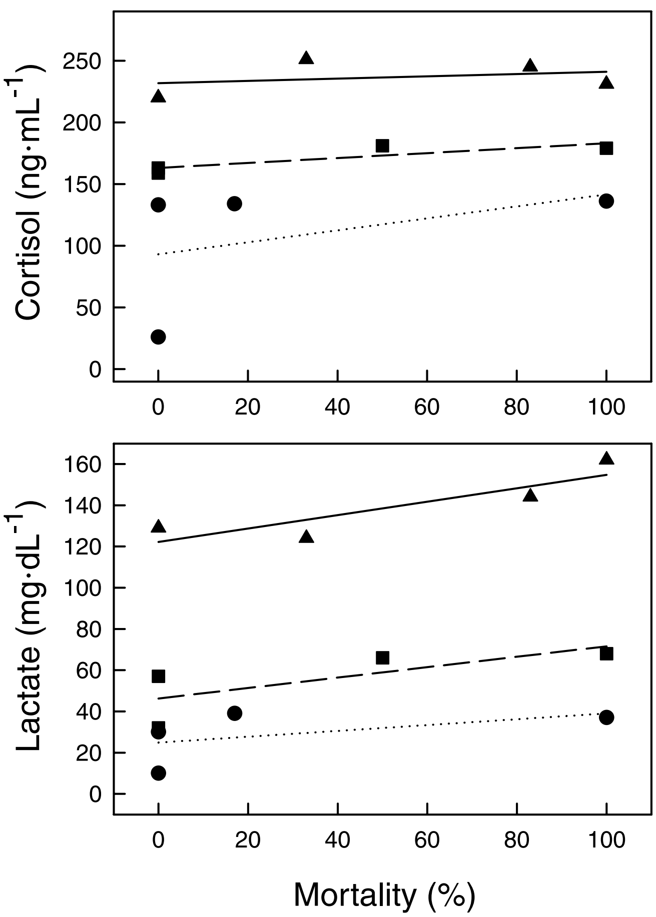
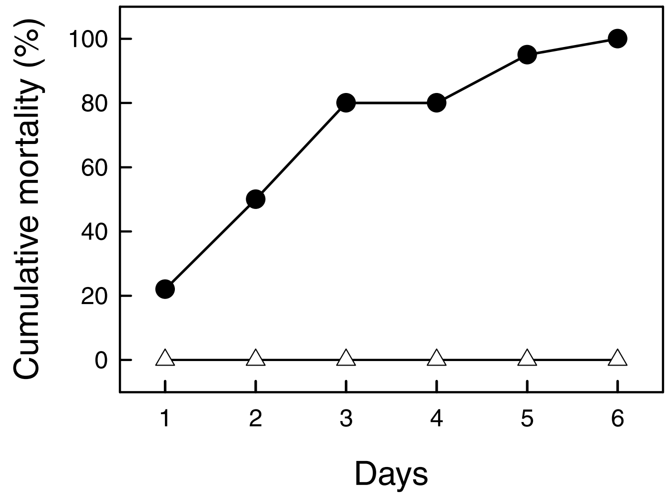
Fig. 2. Plasma physiology remains constant as mortality increases in sablefish, *Anoplopoma fimbria*. Plasma physiology (cortisol (ng·mL^{-1}) and lactate (mg·dL^{-1})) and mortality (%) for fish that were exposed to 4, 12, 14, or 16°C seawater for 30 min and air for 15 min (temperature, ●); hooking for 24 h followed by 4, 12, 14, or 16°C seawater for 30 min and air for 15 min (hooking, ■); and towing in a net for 4 h followed by 4, 12, 14, or 16°C seawater for 30 min and air for 15 min (towing, ▲). Data points are means for results at each experimental temperature treatment. Slopes of all regression lines are not different from zero. Experiments and data were described by Davis et al. (2001).



(Fig. 3). This study led to the prediction that walleye pollock captured in the field under dark conditions would not be able to orient within a trawl. Results of a field study with walleye pollock confirmed that vision played a major role in fish interactions with trawls (Olla et al. 2000). There were clear differences in fish orientation and swimming behaviour when light quantity fell below that necessary for vision-mediated swimming in a trawl. In darkness, captured fish swam less, passed along the trawl faster, and did not orient to the long axis of the trawl. This loss of orientation and swimming ability may result in less ability to escape through trawl mesh and more injury and mortality. The concordance of results between laboratory and field studies demonstrated the compatibility of these two approaches in bycatch studies.

Clearly, when escape relies on vision with active movement through openings or mesh, design of trawls to enhance bycatch escape must consider reactions under dark conditions in the field. The visual stimulus of towed fishing gear has been modeled using data from laboratory and field measurements, with predictions made on the strength of visual stimuli in trawls under various light conditions (Kim and Wardle 1998). Assessing the efficacy of trawl modifications designed to reduce discards would in part be dependant on light quantity measurements made in the gear during field trials. Differences in trawl catching efficiency between day and night have been attributed to visibility of the trawl (Casey and Meyers 1998). Differences in contrast in nets may also be important for herding fish in a trawl and increasing escape through net mesh (Glass et al. 1993). Few studies provide information about light quantity in fishing gears, making it difficult to compare results or to assign causes to observed variations in catching efficiency and reduction in bycatch.

Fig. 3. Walleye pollock, *Theragra chalcogramma*, had higher cumulative mortality (%) after towing 3 h in a net in darkness (●) than in light (△). Experiments and data were described by Olla et al. (1997).



Temperature

The additional stress and mortality resulting from the interaction of capture and exposure to increased temperature may be a widespread condition in fisheries conducted during warmer seasons of the year or in tropical areas where fish are caught in cooler deep water. Under these conditions, when fish are captured at depth by towed or fixed gear, they may be exposed to warmer water temperatures during retrieval (Olla et al. 1998). Fish may also be exposed to warmer air temperatures, regardless of capture depth. Exposure to warmer temperature results in increased body core temperature, with smaller fish warming at a more rapid rate (Spigarelli et al. 1977; Davis et al. 2001). The effects of exposure to increased temperature are well known for freshwater and marine fishes, where physiological stress and deficits in behaviour have been commonly observed (Brett 1970; Fry 1971; Schreck et al. 1997). Capture in the field under conditions of increased temperature has been observed to increase physiological stress and mortality in freshwater (e.g., Plumb et al. 1988; Schisler and Bergersen 1996) and marine fish (Barton and Iwama 1991; Muoneke and Childress 1994; Ross and Hokenson 1997).

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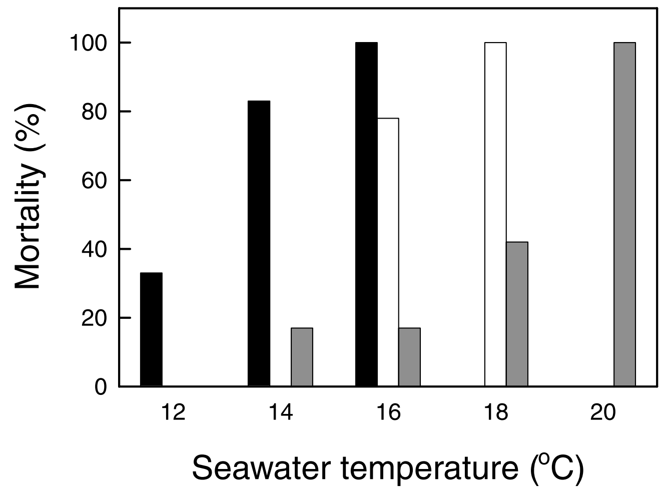
Exposure of sablefish held at 5°C to a range of seawater temperatures between 12 and 16°C in the laboratory resulted in loss of feeding and increased physiological stress and mortality (Davis et al. 2001). Mortality occurred after towing in a net at 5°C and exposure to 12°C or hooking at 5°C and exposure to 14°C. Exposure to 16°C resulted in complete mortality for fish that had no capture stress or had been hooked or towed (Davis et al. 2001). Similarly, towing in a net at 5°C for Pacific halibut and 8°C for lingcod caused stress, which was increased by subsequent exposure to 16°C (Davis and Olla 2001, 2002). In these three marine species, mortality rates increased with increasing seawater temperature for fish that were towed and then exposed to increased temperature, with 100% mortality reached at 16°C in sablefish, 18°C in Pacific halibut, and 20°C in lingcod (Fig. 4). These results demonstrate species-specific differences in mortality, with sablefish being most sensitive to increased temperature, followed by Pacific halibut and lingcod.

Low water temperature may alter fishing processes. Swimming speed and endurance in saithe (*Pollachius virens*), cod (*Gadus morhua*), and American plaice (*Hippoglossoides platessoides*) were reduced by low temperature (Beamish 1966; He and Wardle 1988; Winger et al. 1999). Reduced swimming speed and endurance would influence the herding of fish by sweeps, the ability of fish to maintain position in the trawl mouth, and the active escape of fish from trawls, which requires swimming through mesh or bycatch reduction devices (He 1993). Deficits in swimming performance and orientation in a trawl associated with low temperature could cause fish to be injured more frequently and may result in increased mortality. Freezing temperature on deck may also contribute to discard mortality but has not been investigated.

Fig. 4. Mortality (%) in sablefish (*Anoplopoma fimbria*; solid bar), Pacific halibut (*Hippoglossus stenolepis*; open bar), and lingcod (*Ophodion elongatus*; shaded bar) after exposure to 4 h towing in a net followed by increased seawater temperature (°C) for 30 min and air for 15 min. Experiments and data were described by Davis et al. (2001) and Davis and Olla (2001, 2002).



Anoxia

Lack of oxygen in towed fishing gear packed with fish, in purse seine sets, or in piles of fish and slime or mucus on deck could lead to conditions of anoxia and fish death. This subject has not been researched and deserves attention in fisheries where close packing of fish exists. The interactions of anoxia with other stressors would probably be significant also. Experiments with anoxia and discard mortality are probably best done in the field, as simulation of realistic conditions of fish packing and slime in the laboratory would be difficult.

Sea conditions

Few studies of discards have accounted for possible effects of sea state and current regimens in discard mortality. In the presence of strong currents or as sea conditions become rougher during the passage of storms, several changes leading to increased fish injury and mortality would be expected for both towed- and fixed-gear fishing. Direct interaction with trawl and longline gear resulted in scale loss, crushing, and hook damage for Atlantic halibut (*Hippoglossus hippoglossus*; Neilson et al. 1989). Similar wounding was observed in Atlantic cod caught by trawl (Suuronen et al. 1996*b*). Trawl selectivity increased and then decreased as sea state increased, with fewer haddock (*Melanogrammus aeglefinus*) retained as selectivity increased (Kynoch et al. 1999). Trawl surging associated with increased sea state altered current speeds in a shrimp trawl and led to increased trawl interaction and escapement in red snapper (*Lutjanus campechanus*) during haul-back, as changes in trawl orientation and surging caused red snapper to nose into the trawl while maintaining horizontal orientation (Engaas et al. 1999). Hauling and landing of trawls and handling time on deck would be expected to take longer in rougher seas (Maeda and Minami 1976). Increased sea motion and surging during drying and landing of trawl or pot gear would probably increase pressure on fish, although this has not been measured. Increased strain and resulting injury in hooked fish would probably occur with increased sea motion and bottom currents as gear is soaked and retrieved.

Air exposure

Exposure to air is an integral part of fish capture and increases any stress and mortality that may result from capture. Exposure times are a function of handling times on deck and can range from a few minutes when catches are small to greater than 60 min when catches are large. At least for species without gas bladder or other organ inflation, any changes in fishing practices that reduce handling time and exposure to air (e.g., reduced towing times, catch sorting times, and times to release from hooks, traps, or gill nets) would reduce discard stress and mortality, assuming that lethal stressors had not already been encountered. Exposure to air during fishing occurs over a wide range of temperatures. The differential effects of air exposure and increased temperature have generally not been separated and should be investigated in the laboratory by performing air exposures over a range of temperatures.

Relative resistance to air exposure after trawl capture was noted in winter flounder (*Pleuronectes americanus*), which did not show measurable mortality until after 45 min on

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deck (Ross and Hokenson 1997). In contrast, other discard species were more sensitive to air, with mortality occurring after 15 min in air for Pacific halibut, witch flounder (*Glyptocephalus cynoglossus*), American plaice, and saithe (Fig. 5; Hoag 1975; Richards et al. 1995; Ross and Hokenson 1997).

Lingcod were relatively resistant to air exposure at 20°C in the laboratory but had an abrupt threshold of response. No mortality was observed after 45 min of air exposure and 100% mortality occurred after 60 min in air (Davis and Olla 2002). When fish were towed in a net for 4 h and then exposed to air at 20°C, there was no mortality after 30 min of exposure and 100% mortality after 45 min (Fig. 5). In a related field study, when lingcod were captured by trawl with towing times ranging from 1 to 4 h (at 8°C) and held on deck in the air (at 13°C) for up to 60 min, mortality was not related to towing time but increased to 100% between 45 and 60 min in air, depending on total amount of catch (Steve Parker, Oregon Department of Fish and Wildlife, Newport, Oreg., personal communication).

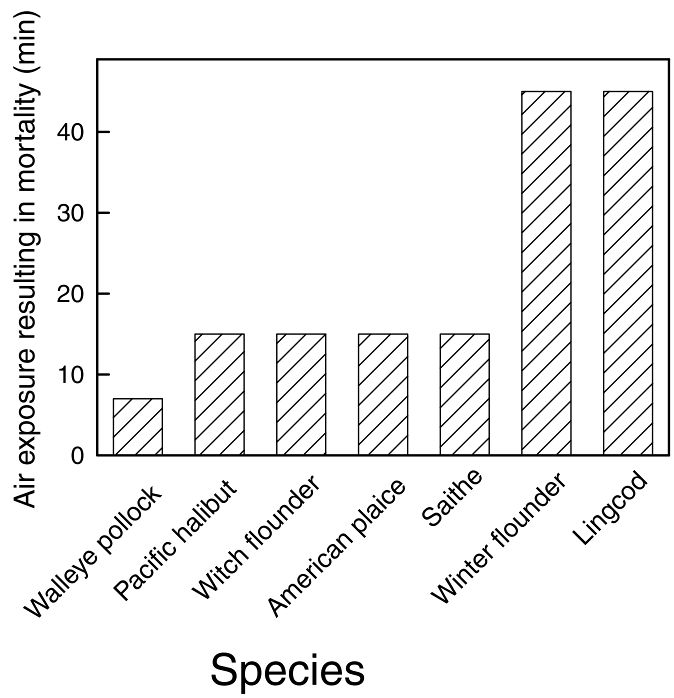
Fish size

Size-specific mortality of discards, with smaller fish showing greater mortality, is an important principle to consider in models of recruitment and yield (Neilson et al. 1989; Sangster et al. 1996; Milliken et al. 1999). Fisheries management strategies often rely on minimum-size rules for harvest, with the assumption that release of undersized fish may contribute to future recruitment and yield (Halliday and Pinhorn 2002). Target species may also be subjected to the process of "highgrading" in which smaller fish are discarded for economic reasons and larger fish are landed. Highgrading would not be recommended when smaller fish have higher mortality rates, as this would disproportionally increase discard mortality. Mortality rates of relevant size classes of fish are needed to validate the assumptions of management rules for undersized discards (Wilson and Burns 1996; Bettoli and Osborne 1998).

Smaller fish can be more sensitive to bycatch stressors and show greater discard mortality. This size effect has been observed in several species that were captured and passed through trawl gear into a net pen for observation of delayed mortality, including haddock, whiting (*Merlangius merlangus*), vendace (*Coregonus albula*), and Atlantic herring (*Clupea harengus*) (Suuronen et al. 1995, 1996*c*; Sangster et al. 1996). Increased sensitivity in smaller fish was generally attributed to fatigue from swimming as they passed down the net and greater injury from abrasion as they passed along and through the net mesh. Other studies with trawl-caught Atlantic halibut and Pacific halibut that were held in tanks after capture also found that injury and mortality was greater in smaller fish (Neilson et al. 1989; Richards et al. 1995). Size effects were also evident in longline discards, with mortality in Atlantic halibut and Atlantic cod being greater for smaller fish that were held in sea cages after capture (Neilson et al. 1989; Milliken et al. 1999).

In laboratory studies with lingcod, smaller fish reached 100% mortality after shorter exposures to air and towing and air exposure (Fig. 6; Davis and Olla 2002). Smaller lingcod reached 100% mortality also at lower temperatures when exposed to increased temperature after towing in a net, and

Fig. 5. Time of exposure to air (min) resulting in observed mortality in walleye pollock (*Theragra chalcogramma*; 14–21 cm length), Pacific halibut (*Hippoglossus stenolepis*; 60–100 cm), witch flounder (*Glyptocephalus cynoglossus*; 13–22 cm), American plaice (*Hippoglossoides platessoides*; 11–29 cm), saithe (*Pollachius virens*; 14–16 cm), winter flounder (*Pleuronectes americanus*; 9–28 cm), and lingcod (*Ophodion elongatus*; 41–67 cm). Data taken from Olla et al. (1997), Hoag (1975), Richards et al. (1995), Trumble et al. (1995), Ross and Hokenson (1997), and Davis and Olla (2002).



similar size effects were suggested in sablefish and Pacific halibut as body core temperature warmed faster in smaller fish (Davis et al. 2001; Davis and Olla 2001, 2002). Size differences in fish sensitivity to increased temperature should be widespread, based on the observed inverse relationship between the rate of body core temperature increase and fish size (Spigarelli et al. 1977).

Discard mortality of fish packed in nets may be a function of size. If catch includes a wide range of fish sizes, injury and crushing in the net, brailer, trap, or other equipment may be different than if similar-sized fish are caught together. Also the characteristics of the other species in the net may have an effect. If mixtures of individuals with hard parts (e.g., spines, shells, carapaces) and more fragile species are caught, the level of injury and mortality may be greater than when only soft-bodied individuals are present. These effects have not been investigated systematically in the field and would be difficult to study in the laboratory.

Delayed mortality

Delayed discard mortality may be common and can occur over an extended period of time after capture and release. Design of discard studies in the field or laboratory should consider delayed mortality, which may be underestimated if holding periods are not long enough. Long holding periods

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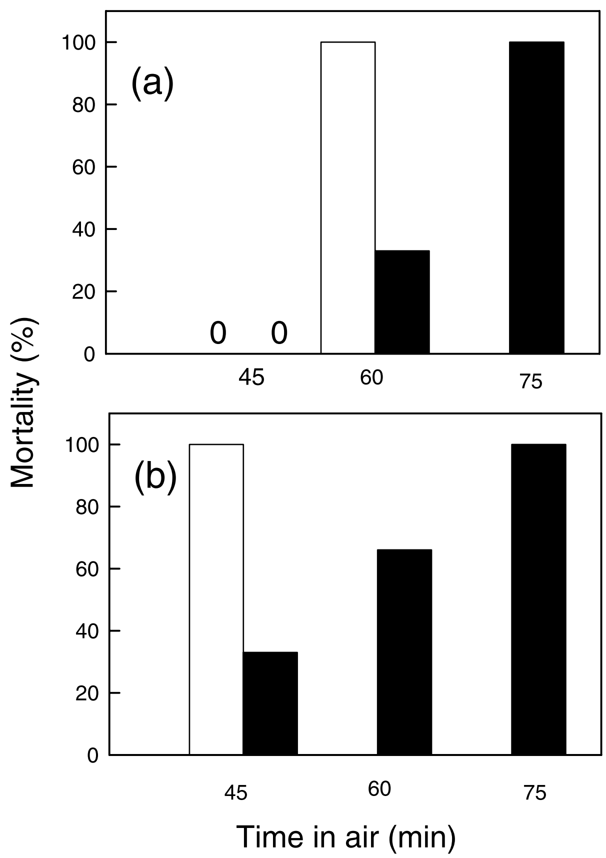
Fig. 6. Small lingcod (*Ophodion elongatus*) reached 100% mortality at lower levels of stressor intensity. Fish (open bar, small, 41–51 cm total length; solid bar, large, 52–67 cm total length) were exposed to (*a*) air for 45, 60, and 75 min and (*b*) 4 h towing in a net followed by air for 45, 60, and 75 min. Zero mortality was noted after 45 min in air for both sizes. Experiments were not performed for small fish after they had reached 100% mortality (75 min in air; 60 and 75 min tow and air). Experiments and data were described by Davis and Olla (2002).



require excellent environmental conditions, use of valid controls, and careful monitoring of fish health as overestimation of delayed discard mortality can occur when there are outbreaks of disease or parasites associated with crowding of injured fish (Neilson et al. 1989; Broadhurst et al. 1999). Although time of holding fish in the field in cages or tanks was generally limited, delayed discard mortality has been observed to vary among species. Mortality was observed up to 6 days after capture in mackerel (*Scomber scombrus*; Lockwood et al. 1983), 2 days in Atlantic halibut (Neilson et al. 1989), 4 days in plaice (*Pleuronectes platessa*), 3.5 days in sole (*Solea solea*; Van Beek et al. 1990), 14 days in Atlantic herring (Suuronen et al. 1996*a*, 1996*c*), and 10 days in Pacific halibut (Kaimmer and Trumble 1998). In laboratory studies with fish held for 60 days after stress induction, delayed mortality was observed up to 30 days in Pacific halibut, 14 days in walleye pollock, 3 days in sablefish, and 1 day in lingcod (Fig. 7; Olla et al. 1997; Davis and Olla 2001, 2002). Differences in time of delayed mortality in Pacific halibut between field and laboratory were probably caused by limited holding time in the field studies.

Delayed mortality resulting from capture has been measured in situ with tag and recapture studies in which all resulting mortality was assumed to result from capture stress. The most extensive studies developed a condition index for delayed mortality in Pacific halibut caught by trawl and hook and line, with fish being recaptured up to several years after tagging (Richards et al. 1995; Kaimmer and Trumble 1998; Trumble et al. 2000). The fish condition index, based on shipboard visual observations of wounding, has been widely used to estimate Pacific halibut discard mortality rates for management. Individual scores for Pacific halibut mortality using the condition index were limited to four quantitative levels of injury and percent mortality, including minor (3.5%), moderate (36.3%), severe (66.2%), and fleas and (or) bleeding (100%). Because this mortality index is based on visible injury, it may not be accurate under all fishing conditions. For example, when fish are exposed to increased temperature, light, air, or interactions of these factors with other capture stressors, visible injury may not accompany mortality. Behaviour may be a more sensitive measure of fish condition and potential mortality, and a behavioural index of discard mortality may be more accurate under a wide range of fishing conditions. Measurements of delayed mortality in sharks caught in gill nets have been made using a system of five levels of condition scoring based on behavioural observations of orientation and swimming ability (Manire et al. 2001). Behavioural assays of discard mortality should be studied in greater detail.

Delayed mortality of discards and fish that escape fishing gear may represent a significant source of unobserved mortality. The prevalence of delayed discard mortality indicates the presence of sublethal effects of bycatch stressors that may eventually result in indirect mortality from predation, physiological stress, or disease. Discarded or escaped fish in an initial “catatonic state” in which they do not respond to stimuli may sink rapidly, and this rapid sinking may result in death from predation or physiological effects of increased pressure. Disruption of schooling and attraction of predators by visual, olfactory, and mechanical cues from injured fish, as well as from fishing vessels and gear, may significantly increase discard and escapee mortality. Other environmental factors, including light, temperature, and sea state, are also expected to control rates of predation on discards. Design of field experiments to quantify delayed mortality will be difficult. When fish were kept in sea cages after capture, predation was not present. Tag and recapture methods may include predation but cannot discriminate among causes for mortality.

Deficits in orientation, swimming ability, phototaxis, feeding, schooling, social interactions, and predator evasion have been observed in walleye pollock, sablefish, and Pacific halibut towed in a laboratory net (Olla et al. 1997; Davis and Olla 2001; Ryer 2002) or exposed to air at various temperatures (M.W. Davis, unpublished data). These behavioural deficits ultimately resulted in increased predation on fish in the laboratory that had been stressed by net towing. Although laboratory experiments are not necessarily comparable to field conditions, it is intuitively obvious that capture-impaired fish have a reduced ability to avoid predation.

Delayed mortality of discards may be reduced by allowing partial or complete recovery from capture stress before release. Although recovery tanks are difficult to use in the lim-

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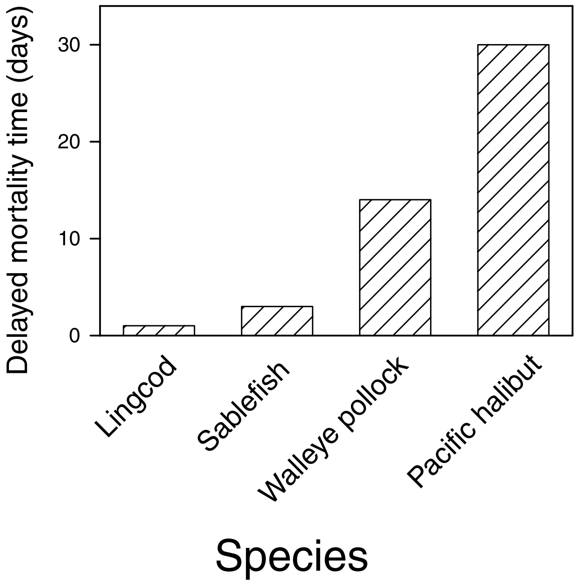
Fig. 7. Time of delayed mortality (days) in bycatch-stressed lingcod (*Ophodion elongatus*), sablefish (*Anoplopoma fimbria*), walleye pollock (*Theragra chalcogramma*), and Pacific halibut (*Hippoglossus stenolepis*) held in laboratory tanks for 60 days. Experiments and data were described by Davis and Olla (2001, 2002), Davis et al. (2001), and Olla et al. (1997).



ited space on a fishing boat in rough seas, recovery may be possible under some circumstances. A study on coho salmon (*Oncorhynchus kisutch*) caught by gill net showed that holding fish on board for a recovery period of 1–2 h may significantly reduce delayed mortality (Farrell et al. 2001).

Synthesis

Studies of discard mortality in the field have generally not addressed the importance of environmental factors and interactions of stressors in determining potential mortality rates. The focus of field studies has been to aid development of fishing gear modifications that may reduce discard mortality, e.g., mesh size, exclusion panels, grates, unhooking practices, species-selective baits, subsurface introduction of baited lines to avoid birds. In some studies, these modifications have included consideration of the behavioural interactions of fish and gear, whereas others, such as changes in trawl mesh size, have often assumed that mesh is a size-specific passive sorting device. Changes in fishing practices have been suggested to avoid areas of potential discards through the use of spatial and temporal refuges. The seemingly overwhelming economic, social, and political constraints of fisheries management seem to have precluded consideration of altering fishing practices in ways that included the effects of environmental factors.

Laboratory studies of bycatch processes have shown that environmental factors can play significant roles in discard mortality, and these results have been corroborated by a limited number of field studies. In cases where environmental factors interact with gear effects to increase mortality, changes in fishing practices could be made to reduce discard stress and mortality. Adjustments in fishing practices such as reduced trawling times or soak times for fixed gear could reduce catch (but not necessarily decrease catch per unit effort) and decrease handling times on deck. Fishing effort could be adjusted into cooler seasons of the year, or deck conditions could be moderated with shade and misted seawater. Reduced time in adverse, but nonlethal, conditions of light, temperature, air, and anoxia would certainly decrease discard stress and mortality. It is no longer sufficient to conduct discard studies in the field under a single set of conditions and expect that the results will contribute to fundamental understanding of the discard problem, either for that specific fishery or in general. The full range of fishing conditions for a gear type must be recognized and studies must include the bounds of these conditions. These study boundaries include variation in fishing practices, as well as light versus dark conditions, temperature range, time in air, anoxia, and sea state. The size-related sensitivity of discards to stressors and species differences in stress resistance are also clearly important in the management of discards.

It remains to be understood why fish die following capture and the relationship between mortality and stress physiology. Commonly measured stress factors (plasma cortisol, lactate, glucose, potassium, sodium) cannot be used to predict mortality. Because stress causes a shift from anabolic to catabolic processes, measurement of factors that control growth, such as IGF-I (insulin-like growth factor) and growth hormone, could be valuable for assessing discard fitness and mortality. Stress also could affect fitness by inhibiting the fish's immune system, either directly through the endocrine system or via energy shunting, as with growth.

How do we accomplish the goal of predicting in situ discard mortality? The combination of laboratory and field experiments is crucial to success. Laboratory experiments will be used to define the capabilities of fish to respond to classes of bycatch stressors and their interactions, with stress responses measured as changes in behaviour, physiology, growth, and immune function, as well as mortality. Then relationships can be defined between physiological variables and stress responses, including behaviour and mortality. Knowledge of these relationships would allow for prediction of direct and indirect (predation, disease) discard mortality using simple behavioural or physiological assays. In the field, discard mortality could then be predicted by sampling fish behaviour and plasma and tissue from a wide variety of fishing operations and conditions. At the same time, discard mortality predicted from in situ tagging and recapture experiments could be compared with the behavioural and physiological results as a confirmation of the prediction technique. Clearly, prediction of discard mortality in a wide range of fisheries requires fundamental knowledge of why discarded fish die and the relationships between mortality, bycatch stressors, and fish stress physiology and behaviour.

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