Estimating collateral mortality from towed fishing gear

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Abstract

More than 50% of the world's total marine catch (approximately 81 million tonnes) is harvested using towed fishing gears (i.e. Danish seines, dredges and otter and beam trawls). As for all methods, the total fishing mortality of these gears comprises the reported (landed) and unreported catch and other unaccounted, collateral deaths due to (i) avoiding, (ii) escaping, (iii) dropping out of the gear during fishing, (iv) discarding from the vessel, (v) ghost fishing of lost gear, (vi) habitat destruction or subsequent (vii) predation and (viii) infection from any of the above. The inherent poor selectivity of many towed gears, combined with their broad spatial deployment, means that there is considerable potential for cumulative effects of (i)-(viii) listed above on total fishing mortality, and subsequent wide-scale negative impacts on stocks of important species. In this paper, we develop a strategy for minimizing this unwanted exploitation by reviewing all the primary literature studies that have estimated collateral, unaccounted fishing mortalities and identifying the key causal factors. We located more than 80 relevant published studies (between 1890 and early 2006) that quantified the mortalities of more than 120 species of escaping (26 papers) or discarded (62 papers) bivalves, cephalopods, crustaceans, echinoderms, elasmobranches, reptiles, teleosts and miscellaneous organisms. Seven of these studies also included the estimates of mortalities caused by dropping out of gears, predation and infection [(iii), (vii) and (viii) listed above]. Owing to several key biological (physiology, size and catch volume and composition), environmental (temperature, hypoxia, sea state and availability of light) and technical (gear design, tow duration and speed) factors, catch-and-escape or catch-and-discarding mechanisms were identified to evoke cumulative negative effects on the health of most organisms. We propose that because the mortalities of discards typically are much greater than escapees, the primary focus of efforts to mitigate unaccounted fishing mortalities should concentrate on the rapid, passive, size and species selection of nontarget organisms from the anterior sections of towed gears during fishing. Once maximum selection has been achieved and demonstrated to cause few mortalities, efforts should be made to modify other operational and/or post-capture handling procedures that address the key causal factors listed above.

Keywords by-catch management, dredges, selectivity, survival, trawls, unaccounted fishing mortality

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Introduction

Towed or dragged commercial fishing gears, including Danish seines, dredges and otter and beam trawls are commonly used throughout the world and responsible for more than 50% of the total annual landed catch (approximately 81 million tonnes; Kelleher 2005) in marine fishing areas. Many towed gears are characterized by disproportional catches of unwanted organisms, often comprising a diverse assemblage of non-target individuals, including juveniles of the targeted species (collectively termed by-catch - for reviews see Andrew and Pepperell 1992; Alverson et al. 1994; Kelleher 2005). This is especially the case for shrimp and demersal finfish otter trawls, which contribute more than 27 and 25%, respectively, of the global annual weight of by-catch (approximately 7.3 million tonnes; Kelleher 2005) discarded at sea.

Concerns over the negative impacts on the stocks of key species associated with by-catch from towed gears date back to the first recorded use of beam trawls during the 14th century (Dyson 1977; Jones 1992). But it has only been during the last few

decades that these concerns have been translated into concerted efforts at quantifying by-catches and discard rates for different fisheries and/or examining mitigation methods (Andrew and Pepperell 1992; Alverson et al. 1994; Kennelly 1995; Kelleher 2005). Excluding temporal and spatial closures, the most common way of addressing the issue of by-catch in towed gears has been to improve gear selectivity (Davis 2002; Cook 2003; Valdemarsen and Suuronen 2003). This has generally involved (i) regulating mesh sizes or openings to control size selection for the targeted species and, in more recent years, (ii) physical modifications like by-catch reduction devices (BRDs) in conventional codends designed to improve species selection, via the behavioural and/or mechanical separation of unwanted organisms (Broadhurst 2000; Fig. 1). In some cases, compared to conventional gears, these latter sorts of BRDs have been demonstrated to completely eliminate problematic by-catches (Christian and Harrington 1987), although rates of reduction typically range between 30 and 70% (Broadhurst 2000).

While extensive research has been done to quantify by-catches and improve the species and size selection of towed gears, less attention has been



Figure 1 An example of a rigid by-catch reduction device (Nordmøre grid) attached to a square mesh codend in an eastern Australian shrimp trawl.

directed towards estimating the collateral mortality of organisms after either escaping or being discarded (often termed 'non-vield', 'indirect' or 'unacfishing mortalities; Naidu counted' 1988; McLoughlin et al. 1991; Chopin et al. 1996). More importantly, even fewer attempts have been made to consider this sort of information as part of a coherent strategy to address the issue of by-catch in particular fisheries. An important step towards solving by-catch problems is the identification and prioritization of the main by-catch species of concern (Kennelly and Broadhurst 1996, 2002). This process inherently requires species-specific biological and ecological information, including estimates of the mortality of discards (Milton 2001; Stobutzki et al. 2001). Further, to ultimately validate existing and/or modified gears, the mortality of organisms escaping various selective mechanisms during fishing needs to be quantified. Unless most unwanted individuals survive towed-gear interactions, technical solutions designed to improve selection may not be justified, other than for reducing the visual impact of by-catch and/or sorting times onboard the vessel.

The importance of considering unaccounted fishing mortality in the overall management of by-catch has been well documented (Jean 1963; McLoughlin *et al.* 1991; Alverson and Hughes 1996). Nevertheless, many relevant discussion-type papers continue to either ignore this issue (Hall and Mainprize 2005) or assume that all discarded organisms die (Chopin *et al.* 1996) and that all escapees survive (Pascoe and Revill 2004). In addition, information on the fate of by-catch often is not considered in manipulative studies examining technical modifications to improve the size and species selection of towed gears (Robins-Troeger *et al.* 1995; Rogers *et al.* 1997; Rose and Gauvin 2000; Özbilgin and Tosunoğlu 2003; Tokaç *et al.* 2004), and almost never used to validate or refine designs.

Despite the above, studies quantifying the unaccounted fishing mortality of several species caught by a variety of fishing methods have been summarized in previous reviews (Andrew and Pepperell 1992; Muoneke and Childress 1994; Chopin and Arimoto 1995; Kennelly 1995; Davis 2002; Suuronen 2005); of which at least five directly concern towed gears. In particular, Andrew and Pepperell (1992), Kennelly (1995) and Davis (2002) each reviewed relevant studies quantifying the fate of bycatches after being discarded, as well as some of the factors influencing mortalities. Chopin and Arimoto (1995) summarized papers that estimated the mortality of escapees from different gears. More recently, Suuronen (2005) updated some of the information for otter trawls but with an emphasis towards assessing the mortality of escaping fish.

Although much of the early quantitative data and some of the factors influencing unaccounted mortalities from towed gears were presented in the above reviews, there lacks a comprehensive up-todate definitive synthesis of this field. Our aims here, therefore, were to (i) review all the relevant studies detailing quantitative estimates of unaccounted fishing mortalities for towed gears, and then use this information to (ii) identify the key biological, technical and environmental causal factors involved and (iii) develop a recommended protocol for minimizing problematic mortalities. For the most part, we have limited our review to those papers published in internationally refereed scientific journals, books and relevant symposia. We acknowledge that many other studies have been presented at regional conferences or in other non-refereed and/ or more obscure literature, but these have only been included where they describe new or unique results that were not subsequently published in the primary literature. Further, although there have been numerous studies examining the wider implications of towed gears on marine environments (for reviews see Hutchings 1990; Messieh et al. 1991; Jones 1992) and interactions with predators (Thompson 1992; Broadhurst 1998; Tasker et al. 2000), this review is restricted to only those available quantitative estimates of unaccounted fishing mortality.

Defining unaccounted fishing mortality

Historically, the total mortality (Z) of aquatic stocks has been presented as the sum of the fishing (F) and natural mortalities (N) (Cushing 1968; King 1995). An implicit assumption of early stock assessments was that the fishing mortality component of this Gompertz Equation represented the landed catch (Cushing 1968). However, it has long been recognized that such 'accounted' mortality is simply one component among a range of other, often indirect, unaccounted fishing mortalities (Jean 1963; Medcof and Bourne 1964; McLoughlin et al. 1991; Alverson and Hughes 1996; Chopin et al. 1996; Harley et al. 2000). In 1995, an international study group on unaccounted fishing mortality in fisheries (under the auspices of the 'International Council for the Exploration of the Sea'; ICES 1995) reduced F to 'the sum of all fishing-induced mortalities occurring directly as a result of catch or indirectly as a result of contact with or *avoidance of the fishing gear*', with at least eight components, most recently presented by ICES (2004) as:

$$F = F_{\rm C} + F_{\rm B} + F_{\rm D} + F_{\rm E} + F_{\rm O} + F_{\rm G} + F_{\rm A} + F_{\rm H}$$

where $F_{\rm C}$ is the catch mortality that includes all commercial, recreational and subsistence fishing landings; $F_{\rm B}$, misreported catch mortality which includes catches that are not reported, underestimated or misreported; $F_{\rm D}$, discard mortality that includes organisms discarded after being landed by the fishing operation; $F_{\rm E}$, escape mortality that includes organisms that actively escape from a gear prior to the catch being landed by the fishing operation; F_{Ω} , drop out mortality that includes captured organisms dying and dropping out of the gear prior to the catch being landed on deck; F_{G} , ghost fishing mortality that includes organisms caught in discarded or lost components of fishing gears; F_A , avoidance mortality that is directly or indirectly associated with organisms actively avoiding a fishing gear; and $F_{\rm H}$, habitat degradation mortality that is associated with the degradation of an aquatic environment because of a fishing activity.

In addition, ICES (2004) identified mortalities associated with predation (F_P) and infection (F_I) as subcomponents of F_D – F_H listed above. The stages of a towed gear fishing operation where some of these relevant components and subcomponents of mortality occur are displayed in Fig. 2.

In recent years, studies have provided overwhelming evidence of the potential for cumulative influences of the various components and subcomponents listed above on the total fishing mortality of organisms encountering towed gears, including mortality due to ghost fishing (Laist 1996) and especially habitat destruction (Jones 1992; Schratzberger et al. 2002; Gasper et al. 2003) and predation (Thompson 1992; Broadhurst 1998; Arcos et al. 2001; Ryer 2004; Svane 2005). But with few exceptions, most quantitative estimates of unaccounted fishing mortality are restricted to discarded and escaping organisms. Consequently, these two types of unaccounted fishing mortality and their subcomponents (where they were concurrently examined) form the basis of this review.

Experiments to quantify unaccounted fishing mortality

We located 88 definitive or primary literature studies for towed gears (1890–early 2006), which



Figure 2 Schematic diagram of some of the components and subcomponents of unaccounted fishing mortality for towed gears. F_D , discard mortality; F_E , escape mortality; F_P , predation mortality; F_A , avoidance mortality; F_H , habitat degradation mortality; F_I , infection mortality.

estimated discard (57 papers) or escape (21 papers) mortalities or both (5 papers) for more than 120 species of bivalves, cephalopods, crustaceans, echinoderms, elasmobranches, reptiles and teleosts (Tables 1 and 2). Seven of these studies also included estimates of other sources of unaccounted fishing mortalities, such as those caused by predation, infection and dropping out of fishing gear (Table 2). Most studies have involved shrimp and benthic fish otter trawls and are limited to developed countries, particularly those with fishing interests in the north Atlantic (Table 2). This reflects the regional importance of stocks of boreal and polar fish and crustacean species such as haddock, whiting, Atlantic cod, saithe, sole, American plaice, winter flounder, European plaice, Atlantic halibut, Norway lobster and brown shrimp. By comparison, despite penaeid shrimp-trawl fisheries being responsible for the largest component of discarded by-catch throughout the world (Alverson et al. 1994; Kelleher 2005), and the subject of considerable efforts to improve selection via technical modifications (Broadhurst 2000), comparatively less work (i.e. 14 studies) has been done to quantify their unaccounted fishing mortalities. Furthermore, nearly all this work has been restricted to eastern and northern Australia (Table 2).

Prior to reviewing the available estimates for discard and escape mortalities and their determinant factors, the different experimental methods employed and some of their benefits and/or limitations require consideration. This discussion is separated into (i) field-based studies involving commercial fishing operations, with subsequent monitoring of escapees or discards either at sea or in laboratories, (ii) work performed entirely under simulated conditions in the laboratory and (iii) common considerations for all experiments.

Field-based studies

More than 80% of all quantitative estimates of escape and discard mortalities have been made in the field (Table 2). The methods have varied

Group	Family	Latin name	Common name
Bivalves	Mactridae	Spisula solida Spisula solidissima Chlamys islandica	Surf clam Atlantic surf clam
	i connoae	Pecten fumatus Pecten maximus Placopecten magellanicus Zygochlamys patagonica	Southern scallop King scallop Deep-sea scallop Patagonian scallop
Cephalopods	Loliginidae Sepiidae Sepiolidae	Loligo sp. Sepia sp. Sepiola atlantica	Squid Cuttlefish Altantic bobtail
Crustaceans	Crangonidae Galatheidae Lithodidae Majidae	Crangon crangon Munida rugosa Paralithodes camtschaticus Chionoecetes bairdi Leotomithrax qaimardii	Brown shrimp Rugose squat lobster Red king crab Tanner crab Spider Crab
	Nephropidae Paguridae Penaeidae Portunidae	Nephrops norvegicus Homarus americanus Pagurus bernhardus Metapenaeus macleayi Liocarcinus depurator	Norway lobster American lobster Common hermit crab School prawn Harbour crab
Echinoderms	Asteriidae Ophiolepidae	Asterias rubens Ophiura ophiura	Common starfish Brittle star
Elasmobranchs	Rajidae Scyliorhinidae	Bathyraja spp. Scyliorhinus canicula	Skates Small-spotted cat shark
Reptiles	Cheloniidae	Caretta caretta Chelonia mydas Eretmochelys imbricata Lepidochelys kempi Lepidochelys olivacea Natator depressa	Loggerhead turtle Green turtle Hawksbill turtle Kemp's Ridley turtle Olive Ridley turtle Flatback turtle
Teleosts	Agonidae Clupeidae Cottidae Cyprinidae Cyprinidae Gadidae	Agonus cataphractus Clupea harengus membras Myoxocephalus scorpius Rutilus rutilus Abramis brama Gadus morhua Melanogrammus aeglefinus Merlangius merlangus Pollachius virens Theragra chalcogramma	Hooknose Baltic herring Shorthorn sculpin Roach Carp bream Atlantic cod Haddock Whiting Saithe Walleye pollock
	Hexagrammidae Mullidae Osmeridae Percidae Pleuronectidae	Ophiodon elongatus Mullus barbatus Osmerus eperlanus Stizostedion lucioperca Glyptocephalus cynoglossus Hippoglossus hippoglossus Hippoglossus stenolepis Limanda limanda Microstomus kitt Platichthys flesus Pleuronectes platessa Pseudopleuronectes americanus Correcopus albula	Lingcod Red mullet European smelt Zander Witch flounder Atlantic halibut American plaice Pacific halibut Dab Lemon sole Flounder European plaice Winter flounder
	Saimonidae	Coregonus aibula Coregonus spp.	Vendace Whitefish

Table 1 The groups, family, Latin and common names of species referred to in the text.

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Table 1 Continued.

Group	Family	Latin name	Common name
		Salmo trutta trutta	Brown trout
		Salmo salar	Atlantic salmon
	Sciaenidae	Micropogonias undulates	Atlantic croaker
	Scorpaeniformes	Anoplopoma fimbria	Sablefish
	Sillaginidae	Sillago ciliata	Sand whiting
	Soleidae	Solea solea	Common sole
	Sparidae	Acanthopagrus australis	Yellowfin bream
		Pagrus auratus	Snapper
		Stenotomus chrysops	Scup
	Triglidae	Eutrigla gurnardus	Grey gurnard
	Zoarcidae	Zoarces viviparus	Eel pout
Miscellaneous	Buccinidae	Buccinum undatum	Common whelk
	Pyuridae	Pyura stolonifera	Cunjevoi
	Laridae	Larus marinus	Black-backed gull
		Larus fuscus	Lesser black-backed gul
		Larus argentatus	Herring gull
		Rissa tridactyla	Kittiwake
		Sterna hirundo	Little tern
	Myxinidae	Myxine glutinosa	Hagfish
	Styelidae	Cnemidocarpa etheridgii	Sea cucumber

according to the component of mortality being assessed. However, these usually range from qualitative assessments of discard status immediately after being landed onboard (Vinogradov 1960; Henwood and Stunz 1987; Stobutzki *et al.* 2002) to short-term, field-based monitoring of escapees (Main and Sangster 1988; Suuronen *et al.* 1996a,b; Ingülfsson *et al.* 2006a,b) and discards (Wassenberg and Hill 1989; Stevens 1990), or the transfer of discards to shore-based aquaria (Smith and Howell 1987; Mensink *et al.* 2000; Bergmann and Moore 2001a,b). These experiments encompass a range of complexities that have remained fairly consistent for estimating the mortality of discards but have evolved considerably for escapees.

In most discard-mortality studies, organisms have been caught, retrieved to a vessel, handled according to conventional practices and then monitored in tanks at the surface or in sea cages at appropriate depths. In some cases, observers (scientists or fishers) have recorded data on the immediate mortalities of discards, usually ancillary to other research performed during commercial fishing (Henwood and Stunz 1987; Poiner *et al.* 1990). More often, chartered or research vessels have been fitted with purpose-built, onboard aquaria comprising tanks continuously supplied with seawater and aeration (Neilson *et al.* 1989; Wassenberg and Hill 1989; Stevens 1990; Ross and Hokenson 1997; Lancaster and Frid 2002).

A universal problem with holding discards in tanks at the surface is that important parameters, like temperature, availability of light, pressure and stocking densities often are not similar to those at the discarded organisms' normal habitats. In addition, in some cases, discards have been housed in single flow-through systems, possibly violating assumptions of independence among replicates (van Beek et al. 1990; Kaiser and Spencer 1995). As one example of the potential for such effects, van Beek et al. (1990) placed discarded flatfish from North Sea beam and otter trawlers in small plastic tanks that were stacked vertically in a frame onboard a vessel and either (i) supplied with continuous seawater that flowed down through each of the tanks or (ii) immersed in a larger container full of water. By not separating replicates among independent tanks, this type of design increases the potential for confounding effects because of the cumulative transferral of waste, antagonistic encounters between individuals and crossinfection by pathogens (Neilson et al. 1989).

Some researchers have attempted to guard against psuedoreplication by holding discards in separate replicate cages returned to appropriate depths (Oddsson *et al.* 1994; Bergmann and Moore

Table 2 Chronology of fishing gears.	internationally refereed an	d/or definitive studies g	uantifying the mortality of unwa	nted organisms after being discarded or escaping fi	om commercial towed
Location	Towed gear	Species examined	Mortality and time	Comments	Reference
Scotland	Fish beam trawl ¹	European plaice Dab Lemon sole Atlantic cod Whiting Grey gurnard	^{FD} 2% immediate ^{FD} 41% immediate ^{FD} 57% immediate ^{FD} 100% immediate ^{FD} 100% immediate	FD was recorded for all fish at time of landing. Author suggests that tow duration influences FD.	Fulton (1890)
Baltic Sea	Fish trawl ¹	Baltic herring Whitefish Zander Roach Carp bream Atlantic cod	^{FE} up to 100% immediate ^{FE} up to 50% immediate ^{FE} up to 50% immediate ^{FE} approaching 0% immediate ^{FE} approaching 0% immediate ^{FE} 0% immediate	Definitive study that aimed to estimate FE using a codend cover. But catches were immediately retrieved at the surface and so estimates may not be entirely accurate. FE was positively correlated with scale loss.	Vinogradov (1960)
Eastern Canada	Fish trawl ¹	Atlantic cod American plaice	^{ED} 0-100% over 1 h ^{ED} 22-100% over up to 2 h	Definitive study. For both species, FD was negatively and positively correlated with fish size and air temperature, respectively. Study concluded that most discarded fish die.	Jean (1963)
	Scallop dredge ¹	Deep-sea scallop	^{FD} 11-42% immediate	FD was attributed to air exposure and mechanical	Medcof and Bourne
	Fish trawl ¹	Haddock	^{FD} 7–78% over 12 h	Stress was measured as blood lactic acid and shown to be positively correlated with discard mortality. No differences in stress or FD between sexes.	Beamish (1966)
		American plaice	^{FD} 95–100% over up to 50 min	FD was negatively and positively correlated with size and air exposure (5-45 min), respectively.	Powles (1969)
Denmark	Fish trawl and Danish seine ¹	Haddock	^{FD} 12–65% over up to 12 days	Discarded fish were transferred to seabed cages by SCUBA divers. FD was partially attributed to decompression.	Hislop and Hemmings (1971)
Irish Sea	Crustacean trawl ¹	Norway lobster	^{FD} 12–56% over 1 h	FD was positively correlated with air exposure and physical damage but showed no effect due to sex or size.	Symonds and Simpson (1971)
United Kingdom	Scallop dredge ¹	King scallop	FE. FO. FP. FI<10% annual ^{FD} 0−76% over 30 days	Estimate includes natural mortality and was based on a mark-recapture experiment.	Gruffydd (1972)

Location	Towed gear	Species examined	Mortality and time	Comments	Reference
Eastern Canada	Scallop dredge ¹	Deep-sea scallop	^{FE, Fo, FF} 13–17% over up to 1 h	A submersible was used to observe the condition of escaped scallops up to 1 h after towing a dredge.	Caddy (1973)
Germany	Shrimp trawl ¹	European plaice Sole Dab	^{FD} 30–88% over 7 days ^{FD} 41–67% over 7 days ^{FD} 42–99% over 7 days	FD was positively correlated with tow duration, handling time and size of fish for all species. Fish exposed to the sun incurred high mortality.	Kelle (1976)
Eastern USA	Clam dredge ¹	Atlantic surf clam	FE, FO, FP1-92% immediate	Combined F.O., FE and FP were estimated using divers. Mortalities were generally greater for larror clams.	Meyer <i>et al.</i> (1981)
	Shrimp trawl ¹	Loggerhead turtle Kemp's Ridley turtle	^{FD} 21–38% immediate ^{FD} 22–38% immediate	Used scientific observers. Some positive correlation between turtle FD and tow duration.	Henwood and Stunz (1987)
	Fish trawi ¹	Green turtle American lobster	- 22-33% immediate FD1-21% over 14 days	FD of lobsters was positively correlated with their physical condition and the sea temperature during fishing.	Smith and Howell (1987)
Scotland	Fish-trawl codend (diamond and square mesh) ¹	Haddock	^{FE} 0−100% over up to 52 days	Definitive study that used divers to collect and transfer escapees to anchored cages. FE was worst for diamond-shaped mesh, but the results were not conclusive. Independent of size, most fish lost scales during escape.	Main and Sangster (1988)
Eastern Canada	Scallop dredge ¹	Icelandic scallop	FE, FO, FP, FI17-31% annual	Annual, unaccounted fishing mortality was estimated for scallops using total and	Naidu (1988)
	Fish traw ¹	Atlantic halibut	^{FD} 11–93% predicted	FD was positively correlated with handling time beyond 2 days onboard the vessel and catch weight in the codend and negatively correlated with fish size. There was little association between apparent physical damage and FD.	Neilson <i>et al.</i> (1989)
Eastern Australia	Shrimp trawl ¹	Crustaceans Teleosts	$^{\rm FD}$ ~15% over 8 h $^{\rm FD}$ ~80% over 8 h	FD after 30 min air exposure greatly varied among seven species (three crustaceans and four teleosts) examined.	Wassenberg and Hill (1989)

Table 2 Continued.

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Berghahn (1990)	Hill and Wassenberg (1990)	Poiner <i>et al.</i> (1990)	Stevens (1990)	van Beek <i>et al.</i> (1990)	McLoughlin <i>et al.</i> (1991)	Berghahn <i>et al.</i> (1992)	DeAlteris and Reifsteck (1993)	Soldal <i>et al.</i> (1993)	Wassenberg and Hill (1993)
FD varied according to total catch and handling methods.	Trawls were limited to 1 h and catches exposed to air for 30 min before discarding. Study concluded that most discards died, and many were	Used scientific observers to collect data. FD was positively correlated with tow duration (15–180 min).	FD depended on injuries, but could be reduced by minimizing air exposure and trawling when crabs are not moulting.	FD for both species caught by beam trawl was positively correlated with tow duration and water temperature. FE of sole was positively correlated with tow duration.	Study used a model to estimate combined indirect fishing mortality.	FD varied according to species, but in many cases was positively correlated with tow duration, catch volume and duration of processing. FD of European plaice was negatively correlated with size.	All fish were fatigued and allowed to escape through towed, simulated codends. Few control fish died.	Used cages to collect escapees. Laboratory and field studies showed similar results. Few control fish died.	Most invertebrates (10 species) survived. Most fish (four species) died in the first 3 days and a maximum of 4 days observation was recommended for future studies.
^{FD} 0–35% over 5 days ^{FD} 100% immediate ^{FD} 0% over 5 days ^{FD} 0–13% over 5 days ^{FD} 0–17% over 5 days	^{FD} 20–77% over 12 h ^{FD} 88–100% over 12 h ^{FD} 97–99% over 12 h	^{FD} 5–7% immediate	^{FD} 79% over 2 days ^{FD} 78% over 2 days	^{FD} 63-96% over up to 3.5 days ^{FE} 27-95% over up to 3.5 days ^{FD} 52-100% over up to 3.5 days	FD, FE, FO, FI, FP78–88% over up to 9 months	$^{\rm FD}$ O-100% over up to 5 days $^{\rm FD}$ O-29% over up to 5 days $^{\rm FD}$ O-67% over up to 5 days $^{\rm FD}$ O-66% over up to 5 days $^{\rm FD}$ 65-100% over up to 5 days $^{\rm FD}$ O-29% over up to 5 days $^{\rm FD}$ 3-17% over up to 5 days $^{\rm FD}$ O-17% over up to 5 days $^{\rm FD}$ O-17% over up to 5 days	^{FE} 0–50% over 10 days ^{FE} 0–15% over 10 days ^{FE} 0% over 10 days	^{FE} <3% over 14 days ^{FE} <6% over up to 28 days ^{FE} 10−20% over up to 28 days	^{FD} 0% over 7 days FD0% over 7 days FD0–54% over 7 days FD0% over 7 days FD4% over 7 days FD16–92% over 7 days
Dab European smelt Shorthorn sculpin Hooknose Eel pout	Crustaceans Cephalopods Teleosts	Turtles	Red king crab Tanner crab	Sole European plaice	Southern scallop	European plaice Sole Dab Flounder Whiting Shorthorn sculpin Hooknose Eel pout	Scup Winter flounder Atlantic cod	Saithe Atlantic cod Haddock	Coelenterates Tunicates Crustaceans Molluscs Echinoderms Teleosts
Shrimp trawl ¹	Shrimp trawl ¹		Fish trawl ¹	Fish trawl and beam trawl ¹	Scallop dredge ¹	Shrimp beam trawl ¹	Fish-trawl codend (diamond and square mesh) ²	Fish-trawl codend (diamond mesh) and sorting grid ^{1,2}	Shrimp trawl ¹
Germany	Northern Australia		Bering Sea, USA	North Sea	Australia	North Sea	Eastern USA	Northern Norway	Eastern Australia

Location	Towed gear	Species examined	Mortality and time	Comments	Reference
United Kingdom	Crustacean trawl ¹	Norway lobster Mixed teleosts (nine species) Hagfish	^{FD} 15–79% over up to 4 h ^{FD} 100% over 15 min ^{FD} 0% over 15 min	Injuries to Norway lobster were positively correlated with tow duration. More females than males were injured.	Evans <i>et al.</i> (1994)
Northwestern USA	Fish trawl ¹	Pacific halibut	^{FD} 18–45% over 7 days	FD was significantly greater for longer hauls. No tractable relationship between stress indicators and FD.	Oddsson <i>et al.</i> (1994)
Eastern Finland	Fish trawl ¹	Brown trout	^{FD} 15% over 7 days	FD potentially was related to physical damage. Important variables positively correlated with stress (blood lactate) were catch volume and water temperature during fishing.	Turunen <i>et al.</i> (1994)
North Wales, UK	Fish beam trawl ¹	Polychaetes Crustaceans Molluscs Echinoderms Pisces	^{FD} 9-10% over up to 5 days ^{FD} 0-45% over up to 6 days FE0-26% over up to 2.5 days FD0-13% over up to 6 days FD0-13% over up to 6 days FD0-62% over up to 6 days FD0-62% over up to 6 days FD0-65% over up to 6 days	Catches from a beam-trawl codend and cover were landed onboard a vessel and used to estimate FD and FE for >25 spp. Abrasion during capture was listed as a contributing factor towards the mortality of fish.	Kaiser and Spencer (1995)
Northeastern Australia	Shrimp trawl ¹	Turtles	^{FD} 1-18% immediate (total estimated at 1-7%)	FD was calculated using logbooks and was positively correlated with tow duration (10–240 min).	Robins (1995)
Finland	Fish-trawl codend (square mesh) ¹	Vendace	^{FE} 16–64% (mean) over 3–15 days	Used cages to collect codend escapees. Evidence of temporal effects on FE. <13% of control fish died.	Suuronen <i>et al.</i> (1995)
Northwestern USA	Fish trawl ¹	Pacific halibut	^{FD} 42–87% over up to 3 days ^{FD} 38–90% immediate	Some evidence of a positive correlation between sorting time and FD. FD showed some evidence of a positive relation ship with catch size.	Trumble <i>et al.</i> (1995) Williams and Wilderbuer (1995)
Northern Australia	Shrimp trawl ¹	Flatback turtle Loggerhead turtle Olive Ridley turtle Green turtle Hawksbill turtle	^{FD} 8–14% immediate ^{ED} 19–33% immediate ^{ED} 8–19% immediate ^{ED} 9–14% immediate ^{ED} 17–33% immediate	Used logbooks to record the FD of turtles by trawlers over 2 years. Some evidence of a positive correlation between FD and tow duration.	Poiner and Harris (1996)
Scotland UK	Fish-trawl codend (diamond mesh) ¹	Haddock Whiting	^{FE} 11–52% over 60 days ^{FE} 14–48% over 60 days	Used cages to collect codend escapees. All control fish survived. FE was negatively correlated with size.	Sangster <i>et al.</i> (1996)

Table 2 Continued.

Baltic Sea	Fish-trawl codend (exit windows) ¹	Atlantic cod	^{FE} <1% over 10−14 days	Used cages to collect escapees. Scale loss was evident on some escapees, but was not correlated with size.	Suuronen <i>et al.</i> (1996a)
Baltic Sea, Finland	Fish-trawl codend (diamond mesh) and sorting grid ¹	Baltic herring	^{FE} 77–100% over 14 days	Used cages to collect codend escapees. All escaping fish lost many scales. Up to 55% of control fish also died. Most damage to fish occurred in the anterior section of the trawl.	Suuronen <i>et al.</i> (1996b)
	Fish-trawl codend (diamond mesh) ¹		FE62-91% predicted over 14 days	Used cages to collect codend escapees. <13% of control fish died. FE was negatively correlated with size.	Suuronen <i>et al.</i> (1996c)
Eastern Australia	Shrimp-trawl codend (square mesh) ²	Sand whiting	^{FE} 3% over 30 days	Fish were fatigued and forced through square mesh. Escapees lost <4% of scales. No control fish died.	Broadhurst <i>et al.</i> (1997)
Northwestern USA	Fish-trawl codend (diamond mesh) ²	Walleye pollock Sablefish	^{FE,FD} 100% over 14 days ^{FE,FD} 0–25% over 14–30 days	Light intensity and tow velocity and duration demonstrated to affect the ability of both species to avoid contact with meshes, and their subsequent physical damage and stress. The ability of escaping walleye pollock to evade predation was quantified.	Olla <i>et al.</i> (1997)
Northeastern USA	Shrimp trawi ¹	American plaice Winter flounder Witch flounder Saithe	$^{\text{FD}}$ -60% over up to 3.5 h $^{\text{FP}}$ 35% of live discards $^{\text{FD}}$ -9% over up to 2.5 h $^{\text{FD}}$ -64% over up to 2. h $^{\text{FD}}$ -64% over up to 2 h $^{\text{FD}}$ -64% over up to 2 h $^{\text{FD}}$ -7-64% over up to 2 h $^{\text{FD}}$ -11-52% over up to 2 h $^{\text{FD}}$ -63% of live discards	FD was negatively and positively correlated with size and air temperature, respectively for American plaice and witch flounder. FP was estimated by observing the rate of consumption of live discards by sea birds.	Ross and Hokenson (1997)
Northern Norway	Shrimp-trawl codend (sorting grid) ¹	Atlantic cod Haddock Whiting	^{FE} 0% over up to 12 days ^{FE} 0% over up to 12 days ^{FE} 0% over up to 12 days	All species incurred minimal physical damage. Other gadoid species sustained high mortalities, but the results were unreliable.	Soldal and Engås (1997)
Northwestern USA	Fish-trawl codend (diamond mesh) ²	Sablefish	^{FD} 0–100% over up to 60 days	FD and stress (cortisol) increased after exposure to seawater above 15 °C for 30 min followed by 15 min exposure to air.	Olla <i>et al.</i> (1998)
Southern Australia	Scallop dredge ¹	Spider crab Cunjevoi Sea cucumber	^{FD} 22–54% immediate ^{FD} >7% over 6 weeks ^{FD} >3% over 6 weeks	FD of crabs was based on severe damage. Most of the tunicates were removed from the study area by storms and believed to have subsequently died.	Currie and Parry (1999)

Location	Towed gear	Species examined	Mortality and time	Comments	Reference
Eastern Australia	Shrimp-trawl BRD (separator panel) ²	Yellowfin bream	^{FE} 2% over 30 days	Fish were fatigued to exhaustion and then passed through the guiding panel of a Nordmøre-grid. Total scale loss was <2%.	Broadhurst <i>et al.</i> (1999)
Eastern USA	Fish trawl ²	Scup	^{FE} 0% over 10 days	Scup demonstrated a physiological response (blood lactate) to simulated catch and escape, but recovered within 6 h.	DeAlteris and Valley (1999)
Portugal	Clam dredge ¹	Surf clam	^{FD} 0–54% over up to 3 h	FD was positively correlated with air exposure (0-240 min).	Gasper and Monteiro (1999)
Eastern Finland	Fish trawl ¹	Zander Brown trout Atlantic salmon	^{FD} 1–47% over 7 days ^{FD} 1–14% over 7 days ^{FD} 5–100% over 7 days	Some evidence of gear- and species-specific mortalities. No detectable effect of tow duration or water temperature during fishing.	Jurvelius <i>et al.</i> (2000)
the Netherlands	Beam trawl ¹	Common whelk	^{FD} <60% over 6 weeks	FD remained elevated over two weeks. FD was not correlated with physical damage. Most controls survived.	Mensink <i>et al.</i> (2000)
Gulf of Mexico	Shrimp trawl ¹	Total bycatch (up to 33 species) Atlantic croker	^{FD} 66-87% over up to 1 day ^{FD} 38-71% over up to 1 day	FD was positively correlated with tow duration and catch separation time, but showed no effect due to a short period of immersion in hypersaline water during onboard sorting.	Colura and Bumguardner (2001)
Western Scotland	Crustacean trawi ^{1,2}	Harbour crab Rugose squat Iobster Common hermit	^{FD} 28-49% over 21 days ^{FD} 16-32% over 21 days ^{FD} 6-13% over up 1.5 h	Delayed FD of decapods was influenced by several biological, technical and environmental factors. Study recommended monitoring periods of 10–14 days.	Bergmann and Moore (2001a)
		Common starfish Brittle star	^{FD} 0-96% over up to 29 days ^{FD} 91-100% over up to 29 days	Both echinoderms suffered damage and infection that could have increased FI and FP. Minimizing	Bergmann and Moore (2001b)
	Crustacean trawl ¹	Harbour crab Rugose squat Iobster	^{FD} 0% over up to 1 day ^{FD} 0% over up to 1 h	all exposule reduced FD. Crabs were physiologically impacted by trawling and emersion, that could have increased susceptibility to FI and FP.	Bergmann <i>et al.</i> (2001b)
Northwestern USA	Fish trawl ²	Pacific halibut	^{FD} 0–78% over 60 days	FD occurred after exposure to increased water temperatures, followed by air. Delayed FD for up to 30 days.	Davis and Olla (2001)

Table 2 Continued.

		Sablefish	^{FD} 0-100% over 60 days	FD (33, 83 and 100%) was positively correlated with air temperature (12, 14 and 16 °C, respectively). Stress was not a useful predictor of mortality.	Davis <i>et al.</i> (2001)
Portugal	Clam dredge ¹	Bivalves Gastropods Echinoderms Crustaceans	^{FD} D100% immediate ^{FD} 0% immediate ^{FD} 082% immediate ^{FD} 0-100% immediate	Tow duration (5, 10 and 15 min) had no effect on the physical damage to bycatches.	Gasper <i>et al.</i> (2001)
United Kingdom	Beam trawl, scallop dredge and otter trawl ¹	Common starfish	^{FD} 4–11% over up to 28 days	The main physical damage to starfish was arm loss, which was positively correlated with catch size. FD occurred for up to 21 days.	Ramsay <i>et al.</i> (2001)
Northern Australia	Shrimp and fish trawls ¹	Sea snakes	^{FD} 328% immediate ^{FD} ∼30% over up to 4 days	Most dead snakes (>17 species) were either drowned or crushed in the codend. FD was positively correlated with tow duration (<30 to >300 min).	Wassenberg <i>et al.</i> (2001)
Eastern Australia	Shrimp-trawl codend (square mesh) ²	School prawn	FE11% over 30 days	Shrimp were repeatedly forced to escape through meshes up to 10 times. Individuals incurred minimal physical damage and stress (measured as L-lactate).	Broadhurst <i>et al.</i> (2002a)
Portugal	Shrimp beam trawl ¹	Teleosts Crustaceans	^{FD} 0–75% over 30 min ^{FD} 0–42% over 30 min	FD of crustaceans (four species) and teleosts (seven species) was generally greater in spring/ summer than autumn/winter.	Cabral <i>et al.</i> (2002)
Northwestern USA	Fish trawl ²	Lingcod	^{FD} 0–100% over 60 days	FD increased with exposure to seawater above 16 °C for 30 min and air for 15 min and was negatively correlated with size.	Davis and Olla (2002)
Irish Sea, UK	Shrimp beam trawl ¹	Brown shrimp	^{FD} <9% over 24 h ^{FP} <5% over <45 min	FP was calculated by quantitying the rate of consumption of live shrimp by sea birds.	Lancaster and Frid (2002)
Ireland	Scallop dredge ^{1,2}	King scallop	^{FD} 0% over up to 1 week	Effects of dredging and discarding on the stress (measured as adenylic energetic charge) of scallops was examined. Discarded scallops probably sustained at least some FP.	Maguire <i>et al.</i> (2002)
Northern Australia	Shrimp trawl ¹	Elasmobranchs	^{FD} 10–82% (total of 56%) immediate	FD was negatively correlated with size. Males had a greater probability of dying.	Stobutzki <i>et al.</i> (2002)
Southern Portugal	Crustacean trawl ¹	Norway lobster	^{FD} 40–88% over 5–9 days (total estimate of 65%)	FD depended on season and tow duration.	Castro <i>et al.</i> (2003)

Location	Towed gear	Species examined	Mortality and time	Comments	Reference
Western Portugal	Shrimp beam trawl ¹	Brown shrimp	^{FD} 0—96% over 30 min	FD was positively correlated with tow duration and the temperature in the sorting tray.	Gamito and Cabral (2003)
Northwestern USA	Fish trawi ¹	Lingcod	^{FD} 094% over 21 days	The effects of tow duration, fish size and air exposure on FD and physiological responses were evaluated. Air exposure had a dominant effect on FD.	Parker <i>et al.</i> (2003)
Argentina	Scallop trawl ¹	Patagonian scallop	^{FD} 0-14% over 5-12.5 days	No correlation between FD of scallops and air exposure (30-240 min).	Bremec <i>et al.</i> (2004)
Northwestern USA	Fish trawl ²	Sablefish	^{FD} 0–67% over 7 days	Study involved exposing fish to different air temperatures for different periods. FD was negatively correlated with fish size.	Davis and Parker (2004)
Sweden	Crustacean trawl ²	Norway lobster	^{FD} 25–42% over 5 days	The effects of simulated descent through a low salinity layer were examined and concluded to increase FD.	Harris and Ulmestrand (2004)
Finland	Fish trawl ²	Brown trout	^{FD} 0% over 24 h	Immersion in onboard tanks containing freezing water caused unconsciousness for up to 10 min, which could increase FP.	Hyvärinen <i>et al.</i> (2004)
Falkland Islands, UK	Squid trawl ¹	Skates	^{FD} 29–100% (total of 41%) over up to 3 h	Most (total of 32%) FD occurred immediately.	Laptikhovsky (2004)
Aegean Sea, Turkey	Fish-trawl codend (diamond mesh) ¹	Red mullet	^{FE} 5–9% over 6 days	Most FE occurred in the first 24 h and was negatively correlated with size. Dead fish lost up to 50% of their scales.	Metin <i>et al.</i> (2004)
Northwestern USA	Fish trawl (diamond mesh) ²	Sablefish	^{FD} >40-80% over 35 days	Study demonstrated behavioural impairment for 3– 24 h after discarding, as well as skin injuries and delayed mortality.	Davis (2005)
Eastern Australia	Shrimp trawl ¹	School prawn	^{FD} 35% over 3 days	Shrimp were trawled, landed and subjected to various handling procedures. Stress (t-lactate) remained elevated over 3 days.	Macbeth <i>et al.</i> (in press)
United Kingdom	Fish beam trawl ¹	Small-spotted cat shark	^{FD} 0–8% over up to 2.5 days	Low FD of dogfish was attributed to its robustness.	Revill <i>et al.</i> (2005)

Eastern Australia	Shrimp trawl ¹	Snapper	^{FD} 35-100% over 8 h	FD was positively correlated with air exposure. Few fish survived >10 min exposure after a 30-min haul.	Sumpton and Jackson (2005)
Baltic Sea, Finland	Fish-trawl codends (diamond and square mesh) ¹	Atlantic cod	FE2-18% over up to 14 days	Used cages to collect escapees (3 experiments) and involved controls. FE was positively correlated with water temperature and showed some response to codend catch.	Suuronen <i>et al.</i> (2005)
Barents Sea, Norway	Fish-trawl codends (BRD and diamond mesh) ¹	Atlantic cod Saithe Haddock	^{FE} 0% over 7 days ^{FE} 0% over 7 days c ^{FE} 2–50% over 7 day	Used cages to collect escapees. Haddock FE was negatively correlated with size. Mortality was not correlated with selection mechanism.	Ingülfsson <i>et al.</i> (2006a)
Barents Sea, Norway		Atlantic cod Saithe Haddock	FE-6% over 6 days FE-3% over 6 days FE1-79% over 6 days	Used cages to collect escapees. Haddock FE was negatively correlated with size. There were no differences in mortality after escape from meshes or a BRD or at different fishing intensities.	Ingülfsson <i>et al.</i> (2006b)
Unless stated otherwise tra	wil refers to otter trawl and mo	ortality rates include the ful	I range of observations (to the neares	tt 1%).	

Unless stated otherwise, traw refers to otter trawl and mortality rates include the full range of observations (to the nearest 1%). BRD, bycatch reduction device; FD, fishing mortality directly associated with catching and discarding; FE, fishing mortality directly associated with catching and escape; FP, fishing mortality due to predation after escape or discarding; FI, fishing mortality because of infection after escape or discarding; FI, fishing mortality because of infection after escape or discarding; FO, fishing mortality due to predation after escape or discarding; FI, fishing mortality because of infection after escape or discarding; FO, fishing mortality due to dropping out of the gear. ¹Field experiment involving commercial fishing. ²Laboratory experiment involving simulated fishing.

2001a,b; Ramsey *et al.* 2001; Castro *et al.* 2003). Castro *et al.* (2003) achieved this by placing Norway lobsters discarded from crustacean trawlers off southern Portugal into multiple iron-framed cages, each comprising a matrix of separate compartments. The cages were secured to the seabed at sites within the distribution range of the lobsters and at the same depths and temperatures. Alternatively, other researchers have briefly held discards in simple onboard tanks before transferring them to more complicated shore-based aquaria that were sometimes configured in attempts to represent their normal environment (Berghahn *et al.* 1992; Bergmann and Moore 2001a,b; Maguire *et al.* 2002; Parker *et al.* 2003).

Early work to estimate the mortality of escapees involved similar experimental designs as those for discards, in that escapees were collected in finemeshed bags or covers surrounding the codend, brought to the surface with the trawl and then monitored in onboard tanks as described above (Vinogradov 1960; van Beek *et al.* 1990; Kaiser and Spencer 1995). This methodology was simple and inexpensive, but the severe departure from normal catch-and-escape mechanisms underwater meant that it had minimal utility in terms of estimating the actual escape mortalities.

Based on pioneering work by Hislop (1969) and Hislop and Hemmings (1971) to tag haddock, Main and Sangster (1988) developed another early and more novel method for estimating the mortality of gadoids escaping from the codends of fish trawls off Scotland. A cluster of large replicate cages were secured on the seabed near the trawl ground. Using a towed underwater vehicle at depths between 25 and 40 m, SCUBA divers followed the trawl and manually collected escaping fish (mostly haddock) in black polyethylene bags. The escapees were then quickly transported at the same depth to the sea cages. Other treatments (including fish retained in the codend) and controls (caught by hook and line) were similarly transferred underwater and placed in the cages. In all, more than 200 escapees were collected from a variety of different codend configurations and fed and monitored for mortalities over up to almost 8 weeks (Table 2).

Although innovative, Main and Sangster's (1988) study was quite labour intensive. Most other early field-based experiments used hooped codend covers rigged to posterior cages, usually made from some sort of rigid frame covered in netting (Fig. 3). At the required location, the cages were separated from the trawl using remote- or diver-operated release systems (Soldal et al. 1993; Suuronen et al. 1995, 1996a,b, 2005; Soldal and Engås 1997; Metin et al. 2004). However, all the early cover and cage configurations were limited to short tow durations at shallow depths and small catches. typically not representative of commercial conditions (Soldal et al. 1993; Sangster et al. 1996; Suuronen et al. 1996a,b). Further, this methodology raised concerns over the potential for interactions between the cover/cage configurations and escapees (Suuronen 2005). As evidence of these effects, Soldal et al. (1993) and Suuronen et al. (1996b) observed that small gadoids and Baltic herring, respectively, were impinged against cover/ cage configurations within minutes of escaping



Figure 3 Diagram of a trawl and early cover/cage configuration used to retain codend escapees.

from codends and concluded that this probably contributed towards stress and physical damage. Covers can also affect water flow in the codend (Madsen *et al.* 2001), potentially altering escape mechanisms and the subsequent damage to escapees.

Lehtonen et al. (1998) developed a codend cover/ cage configuration that addresses many of the problems with earlier methods for collecting escapees from towed gears (Fig. 4). Their system consists of a normal codend cover attached to a rectangular collection cage with two horizontally orientated gates at the anterior and posterior ends that can be closed with timers (Fig. 4). The entire configuration is secured to the extension section of a trawl and deployed with both gates open so that codend escapees initially are not retained in the cage (Fig. 4a,b). At the required predetermined time, the posterior and then anterior gates can be automatically and sequentially closed to retain a sample of escapees in the cage (Fig. 4c,d). The sealed cage is then automatically released from the cover (Fig. 4e) and sinks to the seabed before a float rises to the surface to mark its position. This methodology and subsequent refinements were successfully used to estimate the mortality of several species escaping from trawls (Suuronen et al. 2005; Ingülfsson et al. 2006b).

Although mostly limited to scallop- and clamdredge fisheries, other methods to quantify unaccounted fishing mortality (and especially that associated with escape, drop out, infection and predation) have involved mark-recapture studies (Gruffydd 1972; Naidu 1988) and/or direct observations by scuba divers (Caddy 1973; Meyer et al. 1981; McLoughlin et al. 1991; Currie and Parry 1999). For example, Gruffydd (1972) seeded tagged king scallops across a commercial scallop ground off the Isle of Man, UK and then used the returns from commercial fishers to estimate the annual 'natural mortality' that included components of unaccounted fishing mortalities (because of escape, drop out, infection and predation). Naidu (1988) also tagged Iceland scallops to determine their rate of haulinduced disarticulation and adjusted mortality estimates accordingly. In other studies off northeastern America, Caddy (1973) and Meyer et al. (1981) employed scuba divers to directly observe the damage and unaccounted fishing mortality (caused by escape, drop out and predation) of deep-sea scallops and Atlantic surf clams, respectively, after dredging. While such methods have not been extensively applied to other towed gears (Richards *et al.* 1995), mark–recapture studies have been used to estimate the mortality of fish released from capture by hook and line (Trumble *et al.* 2000) and could have some utility in future work with trawls, provided there is sufficient effort and cooperation among fishers to guarantee an adequate rate of tag returns.

Laboratory studies

Nearly all laboratory-based studies quantifying unaccounted fishing mortality have been done during the past 10 years, and most since 2000 (Table 2). The recent increase in this type of work may partially reflect advancements in marine husbandry and the availability of appropriate facilities. It is equally likely that more information about the factors influencing unaccounted fishing mortalities. provided by the numerous field-based studies, has also had an impact. Because it is almost impossible to simulate the entire catch-and-escape or catchand-discarding processes for a particular species in a laboratory, such studies are limited to examine hypotheses formulated using a priori, field-based information about the likely influence of specific mechanisms on damage and mortality (Broadhurst et al. 1997; Olla et al. 1997, 1998; Bergmann and Moore 2001a,b; Davis and Olla 2002).

In most cases, laboratory experiments have involved well-replicated treatments monitored under appropriate conditions (Olla et al. 1997, 1998; Harris and Ulmestrand 2004). The specific treatments examined have usually reflected the relevant information available for a particular species. For example, Broadhurst et al. (1997) hypothesized that most physical damage to sand whiting escaping through BRDs comprising square mesh in eastern Australian shrimp trawls occurred during their contact with the meshes and depended on their level of fatigue. Replicate circular tanks were used to hold individuals that were either non-fatigued or fatigued (using a portable pump to create flow in the tanks and to induce swimming) and forced to pass through panels of square mesh rotated around the tanks. Control fish were similarly non-fatigued and fatigued but not forced through meshes. Olla et al. (1997) used a comparable system of circular tanks and net assemblies to simulate the key mechanisms involved in the capture of sablefish and walleve pollock in trawl codends. This methodology subse-





Figure 4 Schematic representation of Lehtonen *et al.*'s (1998) (a) cover, release unit and cage configuration attached to a trawl codend, (b) both cage gates open during fishing, (c) the posterior gate closed, followed by the (d) anterior gate and then (e) the cage separated from the release unit.

quently was used in a further five published studies to isolate the influences of a range of key factors on the physiology and mortality of these species as well as Pacific halibut and lingcod (Olla *et al.* 1998; Davis and Olla 2001, 2002; Davis *et al.* 2001; Davis 2005).

Unfortunately, however, the inherent limitations of laboratory experiments have meant that they are unlikely to provide definitive estimates of the absolute mortality of discards and escapees. Nevertheless, because they facilitate replication in space and time, are amenable for using appropriate controls, relatively inexpensive and can be used to investigate the response of organisms to specific stressors, their application has been important – especially for validating or supporting concurrent field trials (Soldal *et al.* 1993).

Common considerations for all experiments

Irrespective of whether experiments have been done in the field or laboratory, their utility in terms of estimating unaccounted fishing mortality depends on several criteria. These include (i) the use of appropriate controls, (ii) sufficient duration of monitoring, (iii) representation of actual catchand-escape or catch-and-discarding mechanisms, and (iv) adequate assessment and correlation of concomitant physical and physiological effects.

Controlling treatment effects is an inherent prerequisite to the attribution of causality in experimental designs (Underwood 1997). Ideally, where organisms are temporally or spatially monitored and then released, various control groups (typically comprising organisms collected from passive gears -Main and Sangster 1988; Suuronen et al. 1996b; Mensink et al. 2000) are required to isolate any confounding influences associated with the handling and confinement practices. Any mortalities of control organisms can then be used to adjust the estimates of treatment effects. The potential for mortalities to controls are real, with most studies recording experimentally induced deaths (Suuronen et al. 1995, 1996b: Mensink et al. 2000: Bergmann and Moore 2001a,b). Despite the clear need for adequate controls as part of valid hypothesis testing, severe logistical constraints associated with their collection and housing have meant that these have not been used in most experiments examining the mortality of discards (Jean 1963; Beamish 1966; Symonds and Simpson 1971; Gruffydd 1972; Neilson et al. 1989; Wassenberg and Hill 1989; Berghahn et al. 1992; Turunen et al. 1994; Kaiser and Spencer 1995: Trumble et al. 1995: Ross and Hokenson 1997; Gasper and Monteiro 1999; Jurvelius et al. 2000; Cabral et al. 2002; Castro et al. 2003; Gamito and Cabral 2003; Parker et al. 2003; Hyvärinen et al. 2004; Revill et al. 2005) and several studies concerned with escapees (Vinogradov 1960; van Beek *et al.* 1990; Kaiser and Spencer 1995).

The complete absence of controls in the above studies has probably resulted in considerable biases in estimates of mortality. Further, where confounding influences had cumulative effects on mortality, these were probably exponentially exacerbated over the duration of monitoring. Wassenberg and Hill (1993) recognized the potential for such effects in the absence of controls and designed an experiment to establish an appropriate duration for monitoring the mortality of subtropical fish and invertebrates. Based on a general plateau in deaths at 3 days, they suggested that 4 days monitoring was adequate for most discards. However, in subsequent work, Wassenberg et al. (2001) acknowledged that species-specific variabilities in susceptibility to various trauma associated with catch-and-discarding mechanisms mean that some individuals can suffer considerable protracted mortality. Other recent, longer term studies that have used controls support these results, with Ramsey et al. (2001) noting an extended mortality of more than 3 weeks for common starfish discarded by UK otter trawlers, while Bergmann and Moore (2001a) observed that the discard mortality of several decapods did not stabilize until 10 days after trawling. The potential for delayed deaths clearly illustrates the benefits of using adequate controls to differentiate between treatment and experimental effects.

While a lack of appropriate controls increases the probability of over-estimating mortality, other factors, such as confining escapees and discards to cages, may have the opposite effect. Unlike in captivity, escapees or discards in the wild could experience a protracted recovery from stress and/or behavioural impairment (Ryer 2002, 2004; Ryer *et al.* 2004) that might (i) reduce their ability to feed or more likely (ii) increase their susceptibility to predation or infection. These sorts of effects are very difficult to control and increase the potential for considerable biases in most estimates of mortality.

As well as quantifying mortality, numerous studies have attempted to determine the influences of catch-and-escape or catch-and-discarding mechanisms on the physiological and physical status of organisms. In some cases, this sort of information has been used as a potential index of mortality (Farmer *et al.* 1998; Rose 1999; Pranovi *et al.* 2001). For fish, physiological response indicators have commonly included concentrations of blood cortisol, lactate, glucose, chloride, sodium, potassium and haematocrit (Beamish 1966: Oddsson et al. 1994: Turunen et al. 1994: Olla et al. 1997. 1998; DeAlteris and Valley 1999; Davis et al. 2001; Parker et al. 2003), while physical damage has encompassed scale loss, bruising and wounds (Main and Sangster 1988; Kaiser and Spencer 1995; Suuronen et al. 1996a.b.c; Broadhurst et al. 1997. 1999: Soldal and Engås 1997). Similar sorts of variables have been collected for invertebrates including L-lactate, ammonia, D-glucose, adenvlic energetic charge, skeletal or shell damage, arm or limb loss and body mass changes (Meyer et al. 1981; Bergmann et al. 2001a,b; Ramsay et al. 2001; Broadhurst et al. 2002a; Maguire et al. 2002; Harris and Ulmestrand 2004; Macbeth et al. in press).

Detailed discussion of the merits of the various physical and physiological response indicators is beyond the scope of this review, although it is apparent that their benefit in terms of providing a tractable relationship with mortality has varied considerably. For example, Beamish (1966) demonstrated a positive correlation between peak concentrations of blood lactic acid in haddock (as a measure of fatigue) and their discard mortality. Conversely, Oddsson et al. (1994) and Davis et al. (2001) failed to demonstrate any conclusive relationships between several stress indicators and the discard mortalities of Pacific halibut and sablefish, respectively. Similarly, while many researchers have shown that minimal physical damage can indicate few mortalities (Broadhurst et al. 1997, 1999), others have demonstrated the opposite (Neilson et al. 1989; Mensink et al. 2000). Such contradictions highlight the need for caution in seeking to extrapolate the estimates of physical and physiological condition as indices of mortality (Farmer et al. 1998). Rather, the utility of these data seems to be in helping to identify the severity of particular stressors that might have negative cumulative effects.

The logistical difficulties associated with all experiments quantifying the fate of escaping and discarding organisms from towed gears undoubtedly mean that there are considerable inaccuracies in most estimates of unaccounted fishing mortalities. While this precludes accurate extrapolation of these data to overall assessments of the effects on stocks of particular species, the relevant work done so far nevertheless has identified many of the key causal effects. This is important because understanding the factors influencing mortalities is a prerequisite to coherent attempts at mitigation.

It is clear that unaccounted fishing mortalities are influenced by, but not limited to, the fishing operation and location as well as the species involved and their mechanisms of escape or discard (Davis 2002; Suuronen 2005). In many cases, the estimated mortalities rarely have been attributed to a single cause and often have occurred as a consequence of cumulative sublethal disruptions evoked by combinations of various factors. In the following three sections, we firstly identify and examine the influence of these different factors separately for escape and discard mortalities, and then consider some of the cumulative effects and influences on other subcomponents of unaccounted fishing mortality. Although many of the factors influencing the mortalities of escapees also contribute towards those for discards, the actual mechanisms frequently differ. Therefore, escapes and discards are considered separately.

Mortality of organisms that escape during fishing

Compared to discards, there have been considerably fewer quantitative estimates of the mortality of escapees (Fig. 5; Table 2), which probably reflects the relatively greater complexity and cost of experiments to examine the fate of escaping organisms, as well as differences in the visual impact and awareness of this as an issue. Unlike discards, the fate of escapees is rarely witnessed and therefore considerably less likely to evoke public concerns over sustainability. But understanding this latter



Figure 5 Graphical representation of the cumulative number of papers published in the primary literature between 1985 and 2005, which have quantified escape and discard mortalities.

component of total fishing mortality is nevertheless very important, primarily because (i) low escape mortalities are required to justify universally applied input controls to towed gears, such as legislated mesh sizes and configurations and BRDs and (ii) many of the deleterious factors influencing the escape mortality of a particular species contribute towards other components of its unaccounted fishing mortality.

Estimated escape mortalities range between 0 (Main and Sangster 1988; DeAlteris and Reifsteck 1993; Kaiser and Spencer 1995; Soldal and Engås 1997; Ingülfsson *et al.* 2006a) and 100% (Main and Sangster 1988; Kaiser and Spencer 1995; Suuronen *et al.* 1996b) but more commonly are less than approximately 20% (DeAlteris and Reifsteck 1993; Soldal *et al.* 1993; Suuronen *et al.* 1996a, 2005; Broadhurst *et al.* 1997, 1999, 2002a; Soldal and Engås 1997; Metin *et al.* 2004). In reviewing the relevant studies in Table 2, we identified several biological, environmental and technical factors that were demonstrated to, or could, contribute towards escape mortality.

Biological factors

Ouantitative estimates of escape mortality have been made for more than 20 species of teleosts, molluscs and crustaceans (Table 2). Where particular organisms were examined under comparable conditions, there were clear intra- and inter-specific differences in mortalities, indicating some influence of the type of species for determining its fate (DeAlteris and Reifsteck 1993; Soldal et al. 1993; Kaiser and Spencer 1995; Olla et al. 1997). Gadoid fish, and especially haddock, whiting, and Atlantic cod have received the most attention (Table 2). Of these species, haddock have suffered the highest mortality rates (Main and Sangster 1988; Ingülfsson et al. 2006a,b), although in most cases fewer than 20% of all gadoids have died after escaping through codends containing either diamond- and square-shaped meshes or BRDs. Other warmer water fish, like sand whiting, yellowfin bream and red mullet, have incurred considerably lower escape mortalities (typically <10%; Broadhurst *et al.* 1999; Metin et al. 2004). Molluscs and crustaceans have not been examined in detail, although many have also been characterized by low rates of deaths (Gruffydd 1972; Caddy 1973; Kaiser and Spencer 1995; Broadhurst et al. 2002a). One exception was Atlantic bobtail (squid), 100% of which died after passing through the codend of a beam trawl (Kaiser and Spencer 1995). However, the methodology used to estimate this latter escape mortality (i.e. a covered codend retrieved at the surface) probably added considerably to the observed stress and injury. Like some cephalopods, and in contrast to most other fish, Baltic herring have consistently incurred mortalities between 60 and 100% after escaping from otter trawls (Vinogradov 1960; Suuronen *et al.* 1996b,c; Table 2).

Such species-specific variability reflects the robustness and ability of different species to withstand the physical stressors and fatigue associated with catch-and-escape mechanisms. Unlike cephalopods, many other invertebrates have durable shells or exoskeletons that are less likely to be damaged during contact and escape from towed gears (Rose 1999; Bergmann et al. 2001a,b; Broadhurst et al. 2002a). While crustaceans can lose limbs (Broadhurst et al. 2002a; Bottari et al. 2003), this often occurs distal to the plane of autotomy, resulting in few mortalities (Simonson and Hochberg 1986, but see Kennelly et al. 1990). Likewise, the ability of teleosts to withstand skin injury varies according to the durability of their scales; the removal of which often is the most prevalent visible injury associated with escape (Main and Sangster 1988; Kaiser and Spencer 1995; Suuronen et al. 1996a). Many fish damage their skin during capture, and especially when they are in the codend where numerous organisms are exhausted and crowded together (Suuronen et al. 1996a,b). For species with deciduous scales, like Baltic herring, contact with codend meshes and other components of the catch during escape often results in considerable scale loss. Although severe skin injury (>20% loss of scales) may not directly account for all short-term deaths, this inevitably can expose individuals to secondary infections from bacteria and fungi, contributing towards longer term mortalities (Mellergaard and Bagge 1998; Jones 1993).

In addition to the actual species, the size of organisms is also an important biological factor affecting the mortality of escapees – at least for fish, with several studies demonstrating negative correlations between length and skin injury or mortality (Soldal *et al.* 1993; Sangster *et al.* 1996; Suuronen *et al.* 1996b,c; Metin *et al.* 2004; Ingülfsson *et al.* 2006a,b). Such relationships might be expected, as a fish's swimming ability is a positive function of its length (Bainbridge 1958; Beamish 1978). Hence, smaller individuals are less able to avoid tactile

stressors (e.g. abrasion from netting panels and other catch) in a towed gear. Further, small fish have less endurance in which to make sustained escape attempts and could remain in a trawl longer than their larger conspecifics – thereby suffering greater damage and stress. Such effects are likely to be exacerbated at greater towing speeds.

Severe capture-induced exhaustion considerably increases the potential for escape mortalities. Irrespective of the species, most organisms are confined and exercised during capture which, in some cases, could directly cause death, or alternatively form the basis of other sublethal stress (Beamish 1966). Any effects of exhaustion are likely to be species specific. as Turunen et al. (1996) and Suuronen et al. (1995) attributed some influence on the mortality of escaping vendace, but Soldal et al. (1993) noted that haddock and Atlantic cod survived severe muscular fatigue with no apparent ill effects. Further, Broadhurst et al. (1997) demonstrated that although exhausted sand whiting lost significantly more scales than the non-fatigued individuals after simulated escape through square meshes, mortalities remained below 3%.

Other biological factors influencing escape mortality are the size of catches and their composition. It is reasonable to assume that large volumes of catch in the codend would increase contact and abrasion between organisms. But in one of the few studies where catch size was analysed, Suuronen et al. (2005) failed to detect any significant effect on escape mortality. Nevertheless, other researchers have suggested that the proportion of abrasive objects, such as spiny fish, crustaceans and debris in codends, could increase physical damage (Main and Sangster 1988; Berghahn et al. 1992; Pranovi et al. 2001; Bottari et al. 2003). The effects of catch size and composition require more attention, particularly as methodological constraints have meant that the majority of studies have been performed with small catches not typically representative of commercial conditions (Suuronen 2005).

Environmental factors

Water temperature affects the physiological and behavioural responses of most aquatic organisms (Penn 1976; He and Wardle 1988), and notwithstanding species-specific variabilities to tolerances, should have at least some measurable impact on escape mortality. Nevertheless, very little work has been done to test hypotheses about the effects of

water temperature. Most observations are ancillary to research directed at quantifying other factors. In one of the few relevant studies. Suuronen et al. (2005) observed that fewer than 3% of Atlantic cod died after escaping at water temperatures lower than 10 °C but that mortalities increased to 75% when fish were released into cages at shallower, warmer water (>15 °C). Although these mortalities were an artefact of the experimental design, the potential exists for individuals to be caught in deep, cold water and then exposed to warmer temperatures as a gear is towed to shallow areas or retrieved. This could increase escape mortalities, especially for smaller individuals, as their core body temperature would increase at a greater rate in proportion to their size.

The availability of light (and/or diurnal effects) is also an important environmental factor potentially influencing escape mortalities. The effects of light on crustaceans in towed gears are not consistent (Clarke and Pascoe 1985; Pascoe 1990) but commonly influence the response of many fish (Wardle 1989; Olla et al. 1997, 2000), and conceivably could affect their mortality. Olla et al. (2000) observed that when the light levels fell below that necessary to visually detect a trawl, walleve pollock swam less and did not orient in a uniform direction. This sort of behaviour could greatly increase injury in escapees as a result of collisions. In support of these effects, Suuronen et al. (1995) noted that significantly more juvenile vendace died after escaping from a pelagic trawl codend at night than during the day. Similarly, during laboratory experiments on walleye pollock and sablefish, Olla et al. (1997) noted that a reduction in light intensity affected the ability of both species to avoid contact with meshes and their subsequent physical damage and stress.

A remaining environmental factor that could influence escape mortalities recognized by Suuronen (2005), but has received little attention, is the effects of sea state. Fishing vessels roll and pitch in response to waves and wind, which can affect codend geometry and therefore the overall selectivity (O'Neill *et al.* 2003). Variations in gear selectivity could either increase the rates of escape for some organisms, especially during gear retrieval (Engaas *et al.* 1999), or alternatively, the probability of being caught in meshes and injured. Any concomitant changes in water flow within the gear as a result of sea state might also make it difficult for fish to orient towards BRDs and/or

infection and predation mortalities) up to seven

times the rate of natural mortality. In another

increase their rate of collisions and therefore affect their escape mortality.

Technical factors

The ability of an organism to escape from inside a towed gear largely depends on its transverse morphology in relation to available openings, and so the size and shape of meshes might be expected to influence physical damage and mortality. However, the effects of mesh size are inconsistent, with some studies indicating the potential for some correlation with mortality across similar sizes of fish, while others have clearly demonstrated no relationship (Main and Sangster 1988; Suuronen et al. 1996b). The influence of mesh configuration or shape also remains unclear. Main and Sangster (1988) observed that proportionally more haddock died after escaping through square- than diamond-shaped meshes in the North Sea, but DeAlteris and Reifsteck (1993) did not detect similar effects for scup, winter flounder and Atlantic cod off Northeastern United States.

For some species, escape from BRDs could cause less damage and mortality than escape through meshes (Suuronen *et al.* 1996b). BRDs are usually designed to facilitate the rapid mechanical or behavioural separation of unwanted catches, and because they are located anterior to the codend (Fig. 1), should minimize contact between escapees and other catch. However, as for mesh size and configuration, the effects of BRDs on the injury and mortality of escapees are poorly understood and require further assessment (Ingülfsson *et al.* 2006a,b).

Another technical factor that could influence the mortality of escapees involves the frequency of collisions with various sections of the gear prior to escape. The extent to which this occurs is probably influenced by biological factors like species and their sizes, as well as other technical factors such as towing speed. Irrespective of these interacting variables, however, it is apparent that most individuals impact with various gear components which causes substantial variation in the type of injuries (Naidu 1988, McLoughlin et al. 1991; Walsh and Hickey 1993; Rose 1999). For example, McLoughlin et al. (1991) observed that dredges used to catch southern scallops in Bass Strait damaged considerably more individuals than were caught, contributing towards an unaccounted fishing mortality (including escape, drop out,

example, Rose (1999) estimated that up to 10% of red king crabs contacting and passing under the footropes of bottom trawls damaged their carapace, abdomen or legs, which in turn could have caused some deaths. Because most experiments have quantified escape mortality at the codend, the potential for mortalities as a result of collisions and escape through other parts of the gear have largely been ignored.

Mortality of discarded by-catch

The mortality of discards has received substantial attention, especially during the past 5 years (Fig. 5; Table 2). The almost exponential increase in the number of these studies reflects global concerns directed at the issue of by-catch during the end of the last century and recognition of the need for quantitative data to elucidate the wider implications of discarding on marine environments (Andrew and Pepperell 1992; Alverson et al. 1994; Hall 1996). As for organisms escaping during fishing from towed gears, discard mortalities have been estimated to range between 0 (Jean 1963; Wassenberg and Hill 1993; Kaiser and Spencer 1995; Cabral et al. 2002; Revill et al. 2005) and 100% (Fulton 1890; Jean 1963; Berghahn 1990; Hill and Wassenberg 1990; Jurvelius et al. 2000; Lapitkhovsky 2004), although unlike escape mortality, the estimated proportions of discarded individuals dying often greatly exceeds those which survive (Table 2).

Many of the biological, environmental and technical factors affecting discard mortality include components of those already described above for escapees. However, discarded organisms are also subjected to considerable additional cumulative stress associated with being brought to the surface, exposed to air, thrown from the vessel and then sinking or swimming back to their habitats. As with escapees, various interacting factors contribute towards mortalities (Davis 2002). The main factors important for a general understanding of the stress, injury and mortality of discarded by-catch are detailed below.

Biological factors

Estimates of discard mortality have been made for at least 50 species of teleosts, 25 reptiles, 20 crusta-

ceans and 20 elasmobranchs, echinoderms, cephalopods and bivalves (Table 2). While there are considerable inter- and intra-specific variabilities in these estimates, and although few species have been examined in replicate studies or under similar conditions, some generalizations concerning specific vulnerabilities can be made.

Many crustaceans, bivalves and especially airbreathing reptiles, such as marine turtles and snakes, have consistently incurred lower discard mortalities than teleosts and cephalopods (Table 2). For example, Henwood and Stunz (1987), Poiner et al. (1990), Robins (1995) and Poiner and Harris (1996) observed that, irrespective of the contributing influences of other factors on mortalities, fewer than 38% of all marine turtles died after being discarded from shrimp trawlers, and for many individuals, mortalities were nearly always less than 10%. Similarly, commercially important crustaceans, including Norway lobster, American lobster, brown shrimp and school prawns as well as bivalves such as deep-sea and Patagonian scallops, typically have incurred less than 50% discard mortalities (Medcof and Bourne 1964: Symonds and Simpson 1971; Smith and Howell 1987; Lancaster and Frid 2002; Bremec et al. 2004; Macbeth et al. in press; Table 2). In contrast, Hill and Wassenberg (1990) observed that all cuttlefish and squid were dead within 1 h of being discarded from shrimp trawlers. A few benthic teleosts, like hooknose, eelpout and winter flounder appear quite resilient (e.g. discard mortalities < 20%), but most of those listed in Table 2 have been characterized by high, frequently variable mortalities (Jean 1963; Berghahn et al. 1992; Ross and Hokenson 1997).

The observed inter- and intra-specific differences in discard mortality can be at least partly attributed to the various physiological and physical characteristics that determine the overall fragility of organisms. Species with robust skin, shells or exoskeletons and/or air-breathing abilities (including turtles, sea snakes and some crustaceans -Nakamura 1994; Samet et al. 1996) might be expected to tolerate a range of potential stressors associated with being caught in a towed gear and then discarded. An important consideration for crustaceans, however, is their stage of moult, as Stevens (1990) identified that the mortality of discarded trawl-caught red king and tanner crabs in the Bering Sea was negatively correlated with their shell durability. Unlike reptiles and robust invertebrates, many fish lose scales and often sustain considerable skin damage during capture, retention in the codend and discard. As for escapees, such effects are exacerbated in smaller fish, contributing towards a typical negative correlation between size and discard mortality for many species, including American (Jean 1963; Powles 1969) and European plaice (Kelle 1976; Berghahn *et al.* 1992), Atlantic cod (Jean 1963), dab (Kelle 1976; Ross and Hokenson 1997), sablefish (Davis and Parker 2004) and Atlantic (Neilson *et al.* 1989) and Pacific halibut (Davis and Olla 2002).

Owing to inherent biological differences between sexes, gender might also have an influence on discard mortality, although the few relevant studies have not demonstrated clear trends. Beamish (1966) and Symonds and Simpson (1971) did not detect any effect of sex on the discard mortality of haddock and Norway lobster, respectively, although Evans et al. (1994) did observe proportionally greater injuries to female Norway lobsters discarded by crustacean trawlers off the United Kingdom (but with no clear cause). Conversely, Stobutski et al. (2002) noted that female sharks and rays (total of 79 species) caught by northern Australian shrimp trawlers had a lower probability of immediate mortality than males prior to discarding. The authors suggested that this result might have been a function of the relatively smaller sizes of males rather than gender per se, which according to the discussion above, could have increased their susceptibility to various stressors during the catching process.

A potentially important biological factor influencing the mortality of discarded fish is the presence or absence of a closed swim bladder. The effects of depressurization have not been examined in detail for fish discarded from towed gears (but see Hislop and Hemmings 1971), although this may at least partially account for the proportionally lower mortalities often observed for discarded elasmobranchs (Laptikhovsky 2004) and some benthic teleosts that lack closed swim bladders (Ross and Hokenson 1997). Related studies for hook-and-line fisheries indicate that in the worst case scenario, species with well-developed gas chambers that inflate because of pressure changes will have protruded internal organs, emboli and subsequently die before, or soon after, discarding (Burns and Restrepo 2002). Venting affected fish onboard the vessel could reduce these mortalities (McGlennon and Partington 1997), but this will have no effect on emboli. Hislop and Hemmings (1971) observed that haddock

brought to the surface by Danish seines and trawls from depths of between 25 and 50 m and then returned to the seabed by divers suffered minimal obvious physical impairment, although some individuals may have ruptured their swim bladders. Any gas remaining in the abdominal cavity of these fish could have contributed towards delayed mortalities (up to 65% over 6 days). The potential for such effects warrants further consideration of these factors for discards from towed gears used in depths greater than about 30 m.

As for escapees, the catch volume and its composition represent biological factors that can negatively impact the fate of discards (Kelle 1976; Neilson et al. 1989; Berghahn et al. 1992; Turunen et al. 1994; Pranovi et al. 2001; Ramsey et al. 2001). Many of the deleterious influences of catch volume and composition in the codend during fishing, like compression and abrasion, will have cumulative effects on the physical and physiological status of discards. Neilson et al. (1989) surmised that, although small quantities of by-catch in the codends of fish trawls used to target Atlantic halibut might have reduced the abrasion of juvenile conspecifics by meshes, larger catches resulted in greater mortalities (owing to crushing and suffocation). Perhaps equally importantly, the amount of catch landed onboard the vessel directly influences the time required to sort by-catches and their subsequent air exposure (discussed below) (Berghahn et al. 1992). Turunen et al. (1994) identified these ancillary effects of catch volume to be the most important variables causing stress and mortality in brown trout landed from fish trawls used in Finnish lakes. Such effects also extend to invertebrates, with Ramsey et al. (2001) noting a positive correlation between catch volume and arm loss and mortality of common starfish discarded from beam trawls. dredges and otter trawls off the United Kingdom.

Environmental factors

For many discarded organisms, the key deleterious environmental factors are exposure to air and temperatures of water and air, all of which can have either main or interacting effects on mortality (Jean 1963; Medcof and Bourne 1964; Kelle 1976; Smith and Howell 1987; Stevens 1990; Turunen *et al.* 1994; Bergmann and Moore 2001b). Exposure to air and subsequent hypoxia in many species is unavoidable when the catch is brought onto the deck and can occur over a few minutes or several hours across a range of temperatures. There are considerable species-specific variabilities in the rates of tolerance to these factors. Bivalves (scallops -Bremec et al. 2004 and clams - Gasper and Monteiro 1999) and air-breathing reptiles are least affected, while some crustaceans and most fish have demonstrated positive correlations between discard mortality and (i) their duration of exposure or hypoxia (Symonds and Simpson 1971; Stevens 1990; Berghahn et al. 1992) and/or (ii) the temperature of the air (Jean 1963; Kelle 1976; Cabral et al. 2002). The effects of air exposure and temperature often interact and can be extreme (Davis 2002). In one of the earliest primary literature studies done to estimate discard mortality. Jean (1963) observed that incrementally more Atlantic cod died (between 40 and 90%) when exposed to warmer air temperatures across various exposure durations (5–45 min), prior to discarding. While crustaceans typically are more tolerant of extended exposure to air, Gamito and Cabral (2003) showed similar effects of temperature for beamtrawled brown shrimp exposed to air for up to 10 min, with mortality rates of 0-96% associated with surface temperatures in sorting trays between 10 and 50 °C, respectively. Notwithstanding these trends, it is also apparent that extremely low air temperatures on deck (i.e. <0 °C) may contribute towards mortality, particularly if such temperatures are lower than those at a species' normal habitat (Stevens 1990; van Tamelen 2005).

Like the effects of exposure to air and temperature, and despite considerable species-specific differences in sensitivity (Jurvelius et al. 2000), there has often been a positive correlation between water temperature and mortality (Smith and Howell 1987; Turunen et al. 1994). This relationship was clearly demonstrated by Olla et al. (1998). Davis and Olla (2001) and Davis et al. (2001) in a series of laboratory experiments designed to simulate the capture of sablefish and Pacific halibut in a trawl, their retrieval through warmer water (e.g. a thermocline), exposure to air and subsequent discarding. Compared to fish that were fatigued at a constant water temperature (5–6 $^{\circ}$ C), exposed to air (for 15 min) and then discarded, individuals that were transferred to warmer water (12-20 °C) prior to exposure suffered significantly greater stress and mortality (e.g. up to 100% for sablefish exposed to 20 °C).

The effects of water temperature are not only limited to catch-and-retrieval processes but also include the use of onboard holding tanks to sort catches (commonly termed 'hoppers'; Heales et al. 2003). Differences in temperature between an organism's normal habitat and a holding tank can increase mortality rates or invoke potentially detrimental physiological responses. For example, Hyvärinen et al. (2004) showed that brown trout fatigued to exhaustion by swimming in water at 13–14 °C (to simulate herding in a trawl) and then placed in an iced holding tank $(0.2^{\circ}C - \text{to simulate a})$ cold-water hopper on a vessel) were rendered unconscious for up to 10 min. There was no apparent long-term physical or physiological damage, although the authors hypothesized that discarded comatose fish could be vulnerable to predation. Because the same sorts of treatment can have an anaesthetic effect on crustaceans (Broadhurst et al. 2002a), similar susceptibilities could occur across a range of species.

Technical factors

As for organisms that escape during fishing, technical factors associated with the deployment and retrieval of towed gears, including towing speed, depth and duration can also negatively affect the fate of discards. The influences of towing speed on discards are similar to those for escapees, and mainly relate to the ability of free-swimming organisms to avoid contact with various components of the gear and other species or debris in the codend. Depth-related effects often are confounded by interactions with the other biological and/or environmental factors discussed above, like the presence of gas-filled organs in fish (Burns and Restrepo 2002) and/or variations in temperature as a result of thermoclines (Davis and Olla 2001). The effects of tow duration on discard mortality are more evident (but see Jurvelius et al. 2000; Parker et al. 2003), typically manifesting as a clear positive relationship for a range of discarded teleosts (Kelle 1976; Berghahn et al. 1992), crustaceans (Castro et al. 2003; Gamito and Cabral 2003) and reptiles (Henwood and Stunz 1987; Wassenberg et al. 2001).

The deployment of towed gears can vary from less than 5 min (Gasper *et al.* 2001) to more than 10 h (Castro *et al.* 2003). The extent to which this contributes towards discard mortality mainly varies according to the type of gear, volume of the catch and when a particular species is caught. In general, poorly selective gears, like penaeid-shrimp trawls

that are towed for several hours and often retain large assemblages of non-target species, are much more likely to demonstrate significant effects of tow duration on discard mortality than comparatively smaller scale dredges which often are towed for shorter periods (i.e. <30 min - McLoughlin et al. 1991; Maguire et al. 2002). In support of this, Gasper et al. (2001) failed to detect any effects of the tow duration (5, 10 and 20 min) of Portuguese clam dredges on the damage caused to 36 species of by-catch (mostly bivalves). Conversely, using data collected from shrimp trawlers in the Gulf of Mexico, Colura and Bumguardner (2001) identified that tow duration (mean \pm SD of 1.5 \pm 0.62 h) explained 48% of the variation in the mortality (66-87%) of discarded by-catch (mostly teleosts). Such effects have been exacerbated for reptiles (Poiner et al. 1990; Poiner and Harris 1996; Wassenberg et al. 2001), with Henwood and Stunz (1987) and Robins (1995) demonstrating that 98 and 75% of the variation in the immediate mortality of discarded sea turtles off the eastern United States and northeastern Australia, respectively, was due to tow duration.

Interactive, cumulative effects and other unaccounted fishing mortalities

As stated earlier, the damage and mortality of escaping and discarded organisms from towed gears is rarely attributed to a single cause but more often to a combination of the numerous, interacting biological, environmental and technical factors discussed above. The stressors evoked during catch and escape or discarding can have a cumulative and exponentially negative effect on the health of an organism, broadly illustrated by the general trend of greater percentages of dead discards than escapees (Table 2). Few attempts have been made to compartmentalize the mortality of a particular species according to the many different stages in the catchand-escape or catch-and-discarding processes and, in doing so, isolate the cumulative effects of different stressors. But by considering studies that have independently quantified escape and discard mortalities for the same species, it is possible to at least estimate some of these interacting effects.

In one example, during a controlled laboratory experiment in Australia, Broadhurst *et al.* (2002a) showed that 11% of unwanted juvenile school prawns died over 2 weeks (Table 2) after simulated, repeated (up to 10 times) catch and escape from

shrimp trawls. During subsequent field experiments carried out as part of normal commercial operations onboard an estuarine shrimp trawler. Macbeth et al. (in press) partitioned the total short-term discard mortality (35% over 3 days) of unwanted juvenile school prawns into 16 and 19% - attributable to (i) being trawled (1 h tow duration) and retrieved at the surface and then (ii) sorted, graded in air for up to 15 min and discarded, respectively. Although the above experiments were carried out across divergent temporal and spatial scales, and using different methodologies, they nevertheless support the potential for a cumulative increase in the unaccounted fishing mortality of school prawns because of the above treatments. That is, less than 11% when individuals contact codend meshes during fishing to 19% when they are retrieved and landed on board and then 35% after being discarded. Similar sorts of differences have also been observed for other species where concurrent estimates of escape and discard mortality are available (saithe - Soldal et al. 1993; Ross and Hokenson 1997).

The cumulative influences of various factors on escapees and discards potentially extend well beyond the short term and probably contribute to ongoing mortalities caused by infection or predation. Owing to logistical constraints, few quantitative estimates are available for these subcomponents of discard and escape mortality. Most of the relevant studies are limited to scallop-dredge fisheries (Gruffydd 1972; Caddy 1973; Naidu 1988; McLoughlan et al. 1991) and have estimated the total unaccounted fishing mortality, without separation into components and subcomponents. Two more recent studies attempted to actually quantify one of these types of mortalities by observing sea birds preying on live discards. Ross and Hokenson (1997) noted that black-backed and herring gulls consumed between 6 and 63% of live saithe, winter and witch flounder and American plaice discarded from shrimp trawls off the northeastern United States. For most of these fish, there was a positive correlation between their predation mortality and exposure to air during sorting, presumably because those fish exposed for relatively longer periods were in poorer condition and less able to quickly return to depth and evade predation at the surface. Similarly, Lancaster and Frid (2002) observed that up to 5% of all live brown shrimp discarded by beam trawlers in the Irish Sea were eaten by the same species of birds as discussed above, in addition to the lesser blackbacked gulls, kittiwakes and little terns. Further,

because other researchers have observed that pelagic and benthic predators also consume escapees (Broadhurst 1998) as well as live and dead discards (Wassenberg and Hill 1989; Hill and Wassenberg 2000; Castro *et al.* 2005; Svane 2005), the potential exists for these sorts of mortalities to contribute towards the overall fishing mortality for a particular species. Clearly, such mortalities require future assessment and actual quantification.

Minimizing unaccounted fishing mortalities

The absence of quantitative data describing many of the key components and subcomponents of unaccounted fishing mortality, and the potential for considerable biases in the existing estimates of escape and discard mortalities discussed above, precludes the formulation of comprehensive fishing mortality models for most species. This makes it difficult to assess the actual rates of exploitation and therefore the impacts on stocks by towed-gear fisheries. While such information ultimately will be required for effective management, in the interim it would nevertheless seem highly appropriate to minimize unaccounted fishing mortalities wherever possible.

As for the general management of by-catch (Andrew and Pepperell 1992), four strategies for achieving the above objective are to (i) encourage fishers to retain previously discarded organisms (thereby converting a component of fishing mortality from 'unaccounted' to 'accounted' - Peterkin 1982), (ii) restrict fishing to locations and times known to have relatively small abundances and distributions of non-target organisms (Caddy 1982), (iii) prohibit fishing in some areas altogether or (iv) modify the gears used and their methods of operation. The first three options could be effectively applied in some cases, although they are associated with either high ecological [(i) listed above] or economical [(ii) and (iii) listed above] costs that might effectively limit their potential throughout the majority of fisheries. The fourth approach is more pragmatic and less likely to economically impact the fishing operation.

Considerable work has been done to investigate the utility of various modifications to towed gears as a means for improving species and size selection and, therefore, reducing unwanted by-catch. However, in most cases the extent to which such changes actually mitigate relevant components of unaccounted fishing mortality remains unknown. Nevertheless, the information provided in the primary literature and discussed in the preceding sections support a simple protocol by which this might be achieved.

First, because it is apparent that for the majority of species, the mortalities of discards are considerably greater than escapees, the primary focus of modifications to gears should always be to facilitate the rapid selection of unwanted organisms during fishing. Obviously, any selection mechanisms need to be designed and demonstrated to have minimal negative effects on escapees. Second, once maximum species and size selection has been achieved. there should be ancillary efforts to modify operational and/or post-capture handling procedures to address those key biological, technical and environmental factors known to influence components of other unaccounted fishing mortalities. The specific details involved in these two stages are expanded in more detail below.

Modifications to gears to improve selection

Most of the modifications to improve species and size selection in towed gears have been done with otter trawls targeting crustaceans and fish (Broadhurst 2000). Variability among the characteristics of different fisheries means that many modifications are available, including simple changes to rigging (Brewer et al. 1996), netting materials (Broadhurst et al. 2000), overall gear design (King et al. 2004) and most commonly, BRDs, which are classified under two categories according to the methods used to facilitate selection. The first category comprises designs that mechanically exclude organisms that are either larger (Isaksen et al. 1992; Christian and Harrington 1987) or smaller (Larsen and Isaksen 1993; Graham et al. 2004) than the targeted species. Usually, these sorts of BRDs comprise a rigid, inclined grid that physically separates individuals simply based on the differences in their size. The second category of modifications have strategically positioned openings that are designed to exploit differences in species' behaviours and physiologies and often are used to exclude fish similar in size or smaller than the target species (Broadhurst et al. 1996; van Marlen 2003).

The effectiveness of the above sorts of technical modifications for improving selection and reducing unaccounted fishing mortality depends on the relative influence of the various interacting factors discussed in earlier sections. As a general rule, however, because much of the damage and mortality of escapees and discards appears to occur in the codend, selective mechanisms should facilitate escape anterior to this region of the gear. For many species, it may be sufficient to install BRDs in the extension section (anterior to the codend), although if performance is not compromised, modifications located further forward in the belly or square (Milliken and DeAlteris 2004) might cause fewer mortalities. This is especially the case for fragile species like Baltic herring, most of which die after escaping from the posterior sections of trawls (Suuronen *et al.* 1996b,c).

While there are few available data, intuitively mechanical sorting would be expected to cause greater injuries than the behavioural-type escape and so, where possible, this latter type of selection should be promoted. Two of the key factors influencing the escape of fish through behavioural-type mechanisms are availability of light and water flow (Glass and Wardle 1995; Broadhurst et al. 2002b). Because vision plays an important role in the response and orientation of fish to trawls, in many cases behavioural-type BRDs need to evoke adequate stimuli so that individuals can detect escape exits (Olla et al. 1997, 2000). Failure to do so may result in a greater rate of collisions within the gear and subsequent deaths (Suuronen et al. 1995). The effects of water flow are equally important, and can be manipulated via panels to guide individuals towards escape openings (Engaas et al. 1999; Broadhurst et al. 2002b). These configurations require careful assessment since it is also possible when designing such modifications to inadvertently create areas of turbulence that could increase collisions between organisms and/or netting panels.

Apart from BRDs, other general technical modifications that exploit behavioural differences between species might also be used to further reduce the components of unaccounted fishing mortality. Specifically, many crustaceans and flatfish remain in the lower sections of towed gears (Watson 1976; Milliken and DeAlteris 2004), while schooling, semi-pelagic species tend to rise and orientate higher in the water column (High and Lusz 1966). Horizontal-separator panels extending throughout the entire gear (Engås *et al.* 1998) can partition these groups into different codends, which might then be configured with species-specific, behavioural-type BRDs or other appropriate selection mechanisms.

Compartmentalizing catches into smaller, separated codends would also reduce relative catch volume, contact between species and therefore the damage to fragile escapees and discards. For shrimp trawls, similar effects can be achieved simply by substituting large, single-rigged trawls with much smaller, multirigged configurations (with the same overall combined headline length). An added benefit of these smaller, multirigged trawls is concomitant reductions in headline height, which, according to the differences in behaviour discussed above, should allow more fish to escape over the trawl headline. Other alterations to the anterior sections of other towed gears warrant attention, particularly since this area can have an important influence on species selection (High et al. 1969; Rose 1999; Broadhurst et al. 2000). This was clearly demonstrated by Brewer et al. (1996) and King et al. (2004) who showed that simply raising the footrope and modifying the headline in fish trawls, respectively, were effective in reducing the by-catches of a range of different species by up to 90%.

As well as modifying the components of existing towed gears to improve selection and reduce mortalities, it might be feasible to consider completely different fishing methods to catch the target species. Many of the species targeted by trawls can be caught by a variety of more selective gears such as longlines, gillnets, jigs and traps (Hovgård and Riget 1992; Halliday 2002; Gray et al. in press). Owing to their passive catching mechanisms, these alternative fishing methods often have lower escape and discard mortalities (Williams and Wilderbuer 1995). For example, Neilson et al. (1989) observed that, on average, 50% fewer undersized Atlantic halibut died after being discarded from capture by longlines, compared to otter trawls off eastern Canada.

Other modifications that could reduce components of unaccounted fishing mortality by towed gears, but have received little attention, include physical, acoustic and electronic deterrents to mitigate the consumption of live escapees by dolphins, sharks and other large marine predators (Lien 1995; Broadhurst 1998; Barlow and Cameron 2003). Such devices could be secured to codends, BRDs or other areas of towed gears where most of the selection occurs. Although there are few quantitative data available (Ross and Hokenson 1997; Lancaster and Frid 2002), the evidence of widescale interactions between marine predators and towed gears (Broadhurst 1998; Wienecke and Robertson 2002) means that even simple deterrents for such predators could equate to significant reductions in unaccounted mortality.

Changes to operational and/or post-capture handling techniques

Irrespective of the type and extent of technical modifications to towed gears discussed above, these are unlikely to result in selection for only the targeted species and their sizes. At least some unwanted organisms will remain in the gear during fishing and eventually be landed and discarded onboard the vessel. But, through changes to operational and/or post-capture handling techniques, it may be possible to further mitigate unaccounted fishing mortalities by (i) increasing the escape of live, unwanted organisms during fishing and/or (ii) reducing the mortality of discards.

Apart from restricting the spatial and temporal deployment of towed gears, the simplest operational changes that might improve species and size selection [and therefore address (i) listed above] involve regulating the towing duration and speed. Catch volume or weight is a positive function of tow duration and, in addition to potentially contributing towards escape and discard mortalities, increases in catch volume have also been demonstrated to inversely affect size selection in diamond-mesh codends because of the concomitant effects of drag on lateral mesh openings (Suuronen et al. 1991; Erickson et al. 1996; Madsen et al. 1999). That is, it may be possible to improve selection and allow more organisms to escape simply by deploying towed gears for shorter periods. One limiting factor for fish trawls is the temporal threshold required to effectively herd and fatigue the target species and their sizes in the codend. Differences in behaviour mean that such effects do not extend to trawls targeting crustaceans, and it may even be more economical for these gears to be towed over shorter durations since Wassenberg et al. (1998) observed significantly lower standardized catches from northern Australian shrimp trawls that were fished for 165 vs. 30 min. One of the hypothesized causes of the lower relative catches during longer tows was the additional drag created by greater catch volumes and subsequent reductions in swept area.

Because the swimming speed and endurance of a fish depends on its body length (Bainbridge 1958; Beamish 1978), towing speed can influence the sizes and quantities of fish retained by towed gears. For shrimp trawls, and possibly some dredges, it

may be possible to promote the anterior avoidance of a gear or the escape of unwanted fish simply by towing at lower speeds. Some authors have also suggested ancillary positive effects on the size selection of codends associated with lower speeds (Dahm *et al.* 2002), although these have not been adequately demonstrated.

One clear effect of reducing towing speed occurs when gears are retrieved. During scuba observations of shrimp trawls in the Gulf of Mexico, Watson (1989) observed that a relatively slower water velocity during the period when towing was stopped and the gear was retrieved to the vessel (termed haulback delay) caused fish in the codend to aggregate, increase their swimming speed and randomly charge meshes. This type of behavioural response can increase the escape of fish through strategically positioned BRDs (Broadhurst *et al.* 1996) and is easily promoted in most towed gears, simply by maximizing delays in haulback.

While the simple operational changes discussed above could improve selection and the fate of unwanted organisms by allowing them to escape during fishing, the greatest potential for these types of procedures is to reduce the mortality of discards. The starting point for achieving this outcome is to identify the key biological, environmental and technical factors that are most likely to affect the main species of concern, and the extent to which these can be practically addressed. It is important to consider that in some cases, a single dominant factor could preclude any attempts at mitigation. This might involve the inherent species-specific vulnerabilities discussed in earlier sections, or alternatively, some limiting technical or environmental factor, like depth or temperature. As an example, owing to the physiological effects of depressurization, some affected species caught in very deep water may not survive discarding, irrespective of any other operational or handling procedures. In such cases, priority should be given to reduce the mortality rates of escapees during fishing. Conversely, the mortality of organisms discarded from towed gears used in shallow estuarine habitats might easily be mitigated via simple changes to one or more of several key factors. As with technological modifications to gears to improve species and size selection during fishing, setting the limits of what might be achievable in terms of reducing discard mortality could save considerable time and effort in the development of appropriate operational or post-capture handling strategies.

Assuming there exists the potential for at least some reduction in the discard mortality of a particular species, three of the simplest changes to operational and onboard handling procedures include shorter tows (discussed above), reduced air exposure and regulated temperature. Limiting tow duration should be fairly straightforward for most gears and, according to the reviewed literature, potentially would benefit a range of different species. The second and third factors listed above might be achieved concurrently by sorting catches in covered, onboard containers or hoppers containing water aerated at appropriate temperatures. Commercial hoppers are available (see Heales et al. 2003 for a description), although most have been designed to facilitate catch separation, rather than discard conservation. Nevertheless, it should be a simple process to configure or design such systems so that they minimize the immediate and short-term mortality of unwanted catches. Sorting catches in onboard water containers like hoppers could benefit some species and especially those with demonstrated resilience to the physical damage and stress incurred during capture but less tolerance to extended air exposure and fluctuating temperatures (e.g. brown shrimp - Gamito and Cabral 200 and school prawns - Macbeth et al. in press).

Simple onboard handling procedures such as those described above will probably improve shortterm survival, but concurrent modifications are also required to ensure that discards return to their habitats and are not injured or consumed by marine and avian predators. As for escapees during fishing mentioned above, predation by sharks and dolphins might be limited by attaching commercially available acoustic and electronic deterrents to the hull of a vessel. Predation by birds could be addressed by adopting methods developed for longline fisheries. Løkkeborg (1998) described different techniques for mitigating bait loss to sea birds during the deployment of longlines and, in particular, visual stimuli created by streamers attached to lines set and towed behind the vessel. Although not directly applicable, other successful methods of reducing avian predation involve deploying longlines through underwater funnels (Løkkeborg 1998; O'Toole and Molloy 2000; Ryan and Watkins 2002). Similar systems could be designed and fitted to hoppers or other onboard water containers as a means for releasing discards underwater.

Irrespective of the actual changes to operational and/or onboard handling techniques, like all mod-

ifications to gears, these need to be practical, easily regulated and demonstrated to clearly mitigate unwanted fishing mortalities. It should be possible to reduce some component of discard mortality, although as stated earlier, because of the cumulative stress on an organism during catch-anddiscarding processes, wherever possible, the escape of unwanted organisms should be promoted during fishing.

Conclusions

Strategies aimed at improving the size and species selectivity of fishing gears often have been separated from the ultimate objective of reducing collateral or unwanted fishing mortality. However, it is clear that unless the majority of organisms survive interactions with towed gears, mandated selection mechanisms will have few conservation benefits. Inherent differences among the effects of different catch-and-escape or catch-and-discard processes mean that there is huge variability in the rates of unaccounted fishing mortality and, therefore, the actual impacts of commercial fishing on stocks. To effectively manage the exploitation of fisheries resources, there needs to be a paradigm shift away from simply regulating selectivity and reducing by-catch, towards the more basal aims of actually minimizing the associated unaccounted fishing mortalities. These concepts are closely related and often confused, but it is important to recognize that achieving the former does not necessarily lead to the latter.

There are likely to be many technical modifications to towed gears and changes to operational and/ or handling procedures that can be developed and implemented to mitigate unwanted fishing mortalities - several of which have been suggested in this review. The specific mechanisms adopted should address the key biological (physiology, size and catch volume and composition), environmental (temperature, hypoxia, sea state and available light) and technical (gear design and tow duration and speed) factors identified here and in other studies (Davis 2002; Suuronen 2005) that contribute towards the mortality of a particular species. Because these factors vary among species as well as the types of towed gears and their areas of operation, it is unlikely that a single strategy will be suitable for all situations.

It is clear, however, that despite considerable species-specific variabilities, in the great majority of cases, the numbers of individuals surviving the short-term effects of escape from towed gears are much greater than the numbers dying. The same cannot be said for organisms discarded after being landed onboard a vessel. Consequently, efforts at mitigating the fishing mortality of by-catch initially should be directed at promoting the avoidance or immediate escape of unwanted organisms during fishing. Once the survival of escapees has been maximized, it would then be appropriate to examine ways of reducing the mortality of discards.

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