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Contribution to the Supplement: '*Effects of Fishing on Benthic Fauna, Habitat and Ecosystem Function*'

Review

The impacts of deep-sea fisheries on benthic communities: a review

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Deep-sea fisheries operate globally throughout the world's oceans, chiefly targeting stocks on the upper and mid-continental slope and offshore seamounts. Major commercial fisheries occur, or have occurred, for species such as orange roughy, oreos, cardinalfish, grenadiers and alfonsino. Few deep fisheries have, however, been sustainable, with most deep-sea stocks having undergone rapid and substantial declines. Fishing in the deep sea not only harvests target species but can also cause unintended environmental harm, mostly from operating heavy bottom trawls and, to a lesser extent, bottom longlines. Bottom trawling over hard seabed (common on seamounts) routinely removes most of the benthic fauna, resulting in declines in faunal biodiversity, cover and abundance. Functionally, these impacts translate into loss of biogenic habitat from potentially large areas. Recent studies on longline fisheries show that their impact is much less than from trawl gear, but can still be significant. Benthic taxa, especially the dominant mega-faunal components of deep-sea systems such as corals and sponges, can be highly vulnerable to fishing impacts. Some taxa have natural resilience due to their size, shape, and structure, and some can survive in natural refuges inaccessible to trawls. However, many deep-sea invertebrates are exceptionally long-lived and grow extremely slowly: these biological attributes mean that the recovery capacity of the benthos is highly limited and prolonged, predicted to take decades to centuries after fishing has ceased. The low tolerance and protracted recovery of many deep-sea benthic communities has implications for managing environmental performance of deep-sea fisheries, including that (i) expectations for recovery and restoration of impacted areas may be unrealistic in acceptable time frames, (ii) the high vulnerability of deep-sea fauna makes spatial management—that includes strong and consistent conservation closures—an important priority, and (iii) biodiversity conservation should be balanced with options for open areas that support sustainable fisheries.

Keywords: deep sea, fisheries, fisheries management, fishing impacts, recovery, sensitivity.

Introduction

Fishing operations that contact the seabed can have unwanted, and often severe, environmental effects. Impacts most commonly documented include the scraping and ploughing of the seabed, resuspension of sediments smothering the fauna, killing of non-target benthic animals, and the dumping of processing wastes (Jones, 1992; Dayton *et al.*, 1995; Jennings and Kaiser, 1998; Hall, 1999; Clark and Koslow, 2007). There is also growing evidence that environmental changes attributable to fisheries practices can have negative impacts on habitat quality, biodiversity, and the structural and functional integrity of ecological assemblages (Hutchings, 1990; Auster *et al.*, 1996; Collie *et al.*, 1997; Auster and Langton, 1999; Koslow *et al.*, 2001). The majority of studies reporting on fishing impacts come from coastal areas or the continental shelf (Collie *et al.*, 2000; Kaiser *et al.*, 2002; Kaiser *et al.* 2006), compared with more limited work in the deep ocean.

Conventionally, the deep sea is regarded to be >200 m depth and beyond the shelf break (Thistle, 2003). In this zone, a number of finfish species characterized by low productivity and high vulnerability are the target of commercial fishing (FAO, 2009), including species that can be abundant on offshore seamounts and ridge systems, such as alfonsino (*Beryx splendens*), orange roughy (*Hoplostethus atlanticus*), pelagic armourhead (*Pseudopentaceros wheeleri*), macrourid rattails (roundnose grenadier *Coryphaenoides rupestris*), and oreos (several species of the family Oreosomatidae) (Koslow *et al.*, 2000; Clark *et al.*, 2007).

Deep-sea fisheries have become economically important in recent decades. As many shelf stocks became overexploited, the search for commercial fisheries moved into deeper offshore waters (Koslow *et al.*, 2000; Clark *et al.*, 2007; Pitcher *et al.*, 2010). Expansion of fishing into upper (200–700 m) and mid (700–1500 m) continental slope environments extended harvests to new target species and it broadened the depth range over which previously fished species are caught (Morato *et al.*, 2006; Watson and Morato, 2013). Many of these fisheries were not sustainable (Clark, 2009; Pitcher *et al.*, 2010; Norse *et al.*, 2012). They were also recognized as causing substantial ecological impacts in several areas of operation, and probably globally (Koslow *et al.*, 2001; Hall-Spencer *et al.*, 2002; Waller *et al.*, 2007; Althaus *et al.*, 2009; Clark and Rowden, 2009). Halpern *et al.* (2007) identified ‘demersal, destructive fishing’ (e.g. demersal trawl) as the most consistently high-scoring threat to oceanic deep-sea ecosystems.

However, are the effects of fishing in the deep sea any different from in shallower waters? In this review, we summarize the state of knowledge of fisheries impacts on benthic fauna and communities in the deep sea, bringing together published studies and grey literature reports, as well as drawing inferences from appropriate shallow-water studies. We focus primarily on hard-substrate invertebrate communities, although also consider soft sediment in less detail. The review has three main sections which move logically through a summary and review of fishing impacts, to an assessment of the sensitivity of deep-sea fauna to fishing, then an examination of their recovery potential. We conclude by considering the implications of benthic impacts for deep-sea fisheries management.

Deep-sea fish and fisheries

There is no universally accepted or applicable definition of what constitutes a “deep-sea” species for commercial fisheries, but generally include species being fished mainly deeper than 200–500 m (Clark, 2001; FAO, 2005). Species lists of deep-sea fisheries typically include species with lower productivity (based on characteristics such as slower growth rates, higher longevity, and lower fecundity) than shallow shelf species, and those which often occur on offshore topographic features such as ridges and seamounts (FAO, 2004; Sissenwine and Mace, 2007; Clark, 2009; European Parliament, 2014). It is not our intention here to give a detailed list of deep-sea fish and fisheries (e.g. Sissenwine and Mace, 2007; European Parliament, 2014) but it is useful to illustrate the types of fisheries (Table 1) that are associated with the environmental impacts reviewed in this paper. The total catch of these significant fisheries for deep-sea species amounted to 475 000 t in 2012 (FAO FishStat data). Based on reported catches, deep-sea fisheries are therefore very small on a global scale (representing $<1\%$ of marine fish catches), but in some areas (e.g. Azores with 5000 t of scabbardfish in 2012: New Zealand with 128 000 t of blue grenadier, 3200 t of alfonsino, 6200 t of orange roughy, 11 800 t oreos in 2012) they are locally a very important component of the national catch.

A key consideration when estimating the ecological impacts of deep-sea fisheries is the geographic extent over which they operate (i.e. the likely area of impact). There are, however, few published accounts to make these estimates. Benn *et al.* (2010) estimated that in 2005 $\sim$30 000 km^2 at depths $>$200 m in the Hatton Bank and Rockall areas of the Northeast Atlantic Ocean were trawled with bottom gear. Within the New Zealand EEZ, the total trawled area deeper than 200 m amounts to 180 000 km^2 (Black *et al.*, 2013) out of a fishable area of 1.4 million km^2-hence deep-sea fishery impacts can be widespread. In addition, deep-sea fishing can be concentrated on particular habitat types, especially oceanic ridges and seamounts. For example, in New Zealand the seabed trawled between 800 and 1200 m accounts for 12% of the total swept-area deeper than 200 m (Black *et al.*, 2013) but 80% of known seamount features in this depth range have been fished; in some years, these seamount fisheries comprise up to 50% of total orange roughy trawling effort and catch (Clark and O’Driscoll, 2003; O’Driscoll and Clark, 2005).

Deep-sea fisheries use several types of gear that can damage seabed habitats and their fauna: bottom otter trawls, bottom longlines, deep midwater trawls, sink/anchor gillnets, pots and traps, and tanglenets (Clark and Koslow, 2007). None is exclusive to deep-sea fisheries, and hence the general types of impacts would be expected, *a priori*, to be similar to shelf fisheries. The most common techniques used in many deep-sea fisheries are bottom trawling and bottom longlines. The main difference to shallow-water trawl rigs is the size and weight of the groundgear: trawl doors can weigh up to 2000 kg, and nets designed for fishing on rough seabed at mid-ocean ridges or seamounts are frequently fitted with many bobbins or rock-hopper discs of 60 cm diameter or greater, weighing several tonnes.

Hence, although the amount of deep-sea fishing is much less than on the shelf, effects are, nevertheless, likely to be appreciable due to larger and heavier trawl gears used, and the very high intensity of fishing in localized areas on certain features, such as seamounts and ridges, where deep-sea fish aggregate (Clark *et al.*, 2007).

Ecological effects of deep-sea fishing

Ecological impacts on seabed communities attributable to fishing in the deep sea are—in general terms—of the same type as documented in shallow systems (Gage *et al.*, 2005; Clark and Koslow, 2007). Ploughing and scraping of the seabed and resuspension of sediment are likely to occur also in deep-sea habitats (and see other papers in this volume). In the following sections, we summarize some of the key impacts of demersal fishing in the deep sea on the physical environment and benthic fauna. General lessons from shelf work are sometimes included, but whenever possible we focus on results from deep-sea studies.

Changes to the seabed environment

Few deep-sea studies have explicitly examined direct changes to substrate and topography of the seabed caused by fishing gear. Clark and Koslow (2007) summarized general impacts, which they noted depend on the gear type, its weight and rigging, as well as the nature of the substrate and the frequency of disturbance. In shelf habitats heavy trawl doors and sleds gouge, scrape and plough the seabed and homogenize unconsolidated sediments (Handley *et al.*, 2014; Palanques *et al.*, 2014). In the deep sea, trawling can alter the physical properties of surface sediments, either by thorough mixing of soft sediments, or by causing the erosion of upper layers, exposing denser, older sediments in the trawl path (Martin *et al.*, 2014). Trawls can also uproot semi-buried glacial drop stones or boulders (Gage *et al.*, 2005; Hall-Spencer *et al.*, 2007). Line gears

Table 1. Selected species that are the target of significant deep-sea fisheries, in decreasing order of their 2012 reported catch (from FAO FishStats), their main commercial depth range, geographic distribution, and principal commercial gear types.

Common name	Scientific name	Total catch 2012 (t)	Depth (m)	Geographic area (ocean basin)	Gear type
Patagonian and blue grenadier	*Macruronus novaezelandaie, M. magellanicus*	307 401	300–800	South Pacific	Bottom trawl, midwater trawl
Redfish	*Sebastes* spp.	56 255	400–800	North Atlantic, North Pacific	Bottom and midwater trawl, longline
Sablefish	*Anaplopoma fimbria*	21 017	500–1000	North Pacific	Bottom trawl, line, pot
Scabbard fish (silver and black)	*Aphanopus carbo*	18 951	600–800	North Atlantic	Bottom, and midwater trawl, longline
Moras (ribaldos)	*Mora moro*	16 951	500–1000	North Atlantic, South Pacific	Bottom, and midwater trawl
Oreos	*Pseudocyttus maculatus, Allocyttus niger*	11 850	600–1200	Southwest Pacific, South Indian	Bottom trawl
Blue ling	*Molva dypterygia*	7994	250–500	North Atlantic	Bottom trawl
Orange roughy	*Hoplostethus atlanticus*	6731	600–1200	North Atlantic, South Atlantic, South Pacific, Indian	Bottom trawl
Alfonsino	*Beryx splendens, B. decadactylus*	6369	300–600	North Atlantic, South Atlantic, North Pacific, South Pacific, Indian	Bottom, and midwater trawl, some longline, gillnet
Red shrimps	*Aristeus* spp.	6267	400–800	Mediterranean, Central Atlantic	Bottom trawl
Roundnose grenadier	*Coryphaenoides rupestris*	4945	800–1000	North Atlantic	Bottom, and midwater trawl
Toothfish	*Dissostichus eleginoides, D. antarcticus*	4217	500–1500	Southern Ocean	Longline, bottom trawl
Rough-head grenadier	*Macrourus berglax*	3099	300–500	North Atlantic	Bottom and midwater trawl
Bluenose warehous	*Hyperoglyphe antarctica*	1378	300–700	South Pacific	Bottom, and midwater trawl
Smootheads	*Alepocephalus bairdii*	930	500–1200	North Atlantic	Bottom trawl
Cardinalfish	*Epigonus telescopus*	658	500–800	North Atlantic, South Atlantic, South Pacific, Indian	Bottom (and midwater trawl)
Armourheads	*Pseudopentaceros wheeleri, P. richardsoni*	193	250–700	North Pacific, South Pacific, South Atlantic, Indian	Bottom and midwater trawl
Deepwater crab	*Geryon* spp.	153	500–800	North Atlantic	Trap, pot
Total		475 359			

alter the seabed to a lesser extent due to their much narrower footprint; lines can, however, drag on the seabed stirring up sediments (Ewing and Kilpatrick, 2014). Trawl gear mobilizes sediments creating plumes of particles in their wake (O'Neill *et al.*, 2013) which are typically 2–4 m high (Palanques *et al.*, 2001; Durrieu de Madron *et al.*, 2005), and 120–150 m in width depending on the size of trawl gear (Bradshaw *et al.*, 2012). In low-current deep-sea environments, these can disperse very slowly over large distances (Bluhm, 2001; Rolinski *et al.*, 2001), and potentially affect areas well beyond, and deeper than the area of the fishery (Black and Parry, 1999; Martin *et al.*, 2014). O'Neill and Summerbell (2011) estimated that a typical Scottish demersal trawl would suspend up to 3 kg m^{-2} of sediment between the trawl doors, and trawling-induced sediment gravity flows can remove large volumes of sediment from the shelf (Puig *et al.*, 2012).

Compared with inshore fisheries, it is likely that deep-sea trawling and lining have very similar effects on the seabed. The main difference would be the heavier groundgear often used in deep-sea fisheries on rough-bottom habitat such as seamounts, which can increase the depth of gouging in areas of soft sediment. The physical effects can also remain longer than in shallow shelf waters. Whereas trawl door gouges and tracks can often disappear from shallower sandy substrate after just a few months (Lokkeborg and Fossa, 2011) or 1–2 years in mud substrate (Ball *et al.*, 2000), in the deep sea the physical scars can remain much longer. Clear marks from orange roughy trawling on soft-sediment areas were visible 5 years after fishing ceased on several seamount features off New Zealand (Clark *et al.*, 2010a).

Impacts on epifauna

Direct interactions of fishing gear with epibenthic animals that results in physical damage can be classified into three basic types (Ewing and Kilpatrick, 2014): (i) blunt impacts—the motion of a broad object through the benthos (e.g. groundrope, trawl doors, mesh, codend, or chafe mat); (ii) line shear—the motion of a narrow object across or through the benthos (e.g. trawl sweeps and lower bridles, longlines when dragging across the seabed); (iii) hooking—direct interaction of hooks with the benthos (e.g. snagging animals). Blunt interactions generally result in the dislodgement or crushing of individuals, particularly larger, erect forms that are anchored to the seabed such as corals, sponges, and crinoids (Koslow *et al.*, 2001; Hall-Spencer *et al.*, 2002; Denisenko, 2007; Althaus *et al.*, 2009; Clark and Rowden, 2009; Rooper *et al.*, 2011; Munoz *et al.*, 2012). These organisms can also be sheared off, hooked, or tangled in longlines (Orejas *et al.*, 2009; Munoz *et al.*, 2011; Bo *et al.*, 2014; Sampaio *et al.*, 2012).

Table 2 illustrates the types of observed impacts caused by demersal fishing practices on deep-sea fauna, and provides some detail of specific studies in the deep sea where changes attributed to fishing have been quantified. Most involve comparisons of fished and unfished areas, although direct observations on damage to fauna or removal of individuals in visible trawl tracks have been reported by Hall-Spencer *et al.* (2002) and Williams *et al.* (2009); Fossa *et al.* (2002) extrapolated such observations into an estimate of spatial damage of the total *Lophelia* reef in their Norwegian study area (Table 2).

Table 2. Selected examples of deep-sea studies illustrating the extent of some of the ecological changes from trawling.

Impact result	Habitat	Key result	Depth (m)	Main taxa measured	Fishery type	Definition of metrics	Reference
Removal of habitat-formers	*Lophelia* reefs, West Norway	Widespread trawling damage to cold-water coral reefs; extensive damage observed with ROV on *Lophelia* reefs	840–1300	*Desmophyllum cristagalli, Enallopsammia rostrata, Lophelia pertusa, Madrepora oculata* and *Solenosmilia variabilis*	Trawl	Unquantified ROV observation	Hall-Spencer *et al.* (2002)
	Bryozoa thicket Tasmania upper slope	Removal of bryozoan thickets	150–400	Bryozoa based community	Trawl	Unquantified observation of trawl tracks in video	Williams *et al.* (2009)
	Continental margin, northern Europe	Damage to sessile epibenthos (especially cold-water coral reefs); substantial habitat alteration and change in function caused by loss of vulnerable, mainly sessile epibenthos	840–1300	Sessile epibenthos	Trawl	Review	Gage *et al.* (2005)
	Hatton Bank and Hatton Drift	Coral bycatch high from unfished rocky outcrops; large sponge bycatch from eastern flank. Smaller bycatch from heavily fished areas	600–1600	Fish bycatch	Multispecies bottom trawl	Presence of taxon over all tows	Munoz *et al.* (2012)
Decline in diversity	Seamounts, Tasmania	Higher diversity in unfished areas Heavily fished, average species 9 Lightly fished, average species 20	660–1700	Epifauna	Deep trawl	Number of species per sled tow	Koslow *et al.* (2001)
	Upper continental slope, West Africa	Epifaunal diversity and richness decreased with increasing trawl intensity. Average number of species decreased 60% from areas trawled $<0.5/\text{year}$ to $2.5/\text{year}$	350–450	Epifauna and infauna	Trawl	Fine-mesh otter trawl sample	Atkinson *et al.* (2011)
	Continental slope, Bay of Plenty New Zealand	Low richness and diversity in locations with high fishing activity (especially scampi trawling)	200–600	Invertebrate catch - decapods, echinoderms, anemones - from research trawl	Fish and scampi trawl fisheries	Counts per standardized research trawl (0.14 km^2)	Cryer *et al.* (2002)
	Juan Fernandez Ridge, SE Pacific Ocean	Decline in diversity over 8-year period of fishery	550–1000	Invertebrate bycatch from fishery trawls	Trawl	Rarefaction index, Fisher's α, Simpsons' index	Niklitschek *et al.* (2010)
	Barents sea	Shannon diversity index 2.1 in heavily fished, 2.9 in lightly fished areas		General invertebrate trawl bycatch fauna	Trawl		Denisenko (2007) (cited in Lyubin *et al.* (2011))
Change in abundance and biomass	Seamounts, Tasmania	Biomass on fished seamounts 15% of that on unfished (average sled catch 1 vs. 7 kg)	660–1700	Epifauna	Deep trawl	Average catch per sled tow	Koslow *et al.* (2001)
	Slope, Gulf of Alaska	Trawled, areas: average density per 100 m^2 of finger sponges 84, vase sponges 3, *Actinauge verelli* 4 Untrawled, areas: average density of finger sponges 121 vase sponges 4, *Actinauge verelli* 9	206–274	Finger sponges and actinarians	Rockfish trawl	Density (counts multiplied by transect length and width) along a video transect—submersible	Freese *et al.* (1999)
	Slope, *Lophelia* reefs off Norway	Lopphavet reef: Trawled colony height *Paragorgia* 17 cm, *Lophelia* 20 cm Untrawled colony height *Paragorgia* 55 cm, *Lophelia* 30 cm Korallen reef: Trawled colony height *Paragorgia* 34 cm, *Lophelia* 20 cm Untrawled colony height *Paragorgia* 52cm, *Lophelia* 29 cm	200–300	*Lophelia* reef, *Paragorgia* corals		Colony height above seabed (hence proxy for biomass)	Buhl-Mortensen *et al.* (2013)

	Barents sea	Reduction in biomass of 11 of 13 epibenthic species: average bycatch of 3 kg/trawl compared with 30–60 kg/trawl in lightly fished areas	300–400	*Geodia* and *Thenea* sponges, sipunculid worms and polychaetes, barnacles, bivalves, urchins, sea cucumbers and seastars	Trawl		Denisenko (2007) (cited in Lyubin *et al.* (2011))
	Seamounts of South Tasman Rise	Decline in biomass over 3-year period of fishery	800–1000	Invertebrate bycatch from fishery trawls	Deep trawl	Bycatch ratio	Anderson and Clark (2003)
	Juan Fernandez Ridge, SE Pacific Ocean	Decline in abundance over 8-year period of fishery	550–1000	Invertebrate bycatch from fishery trawls	Deep trawl	quotient between total number of individuals collected per tow and tow duration	Niklitscheck *et al.* (2010)
Reduction in distribution	New Zealand seamounts	Stony coral cover on trawled seamounts, average in images 0.04–0.03% Stony coral cover on untrawled seamounts, average in images 12–25%	748–1004	*Solenosmilia* and *Madrepora* coral reefs	Deep trawl	Averaged per cent cover per image	Clark and Rowden (2009)
	New Zealand seamounts	Community difference higher frequency of Solenosmilia, a crab, gastropod and ophiuroids on unfished seamounts	750–1250	*Solenosmilia* and *Madrepora* coral reefs	Deep trawl	Averaged per cent cover per image	Clark and Rowden (2009)
	Tasmanian seamounts	Stony coral cover on trawled seamounts, average in images 0% Stony coral cover on untrawled seamounts, average in images 50%	1100–1350	*Solenosmilia* reef	Deep trawl	Averaged per cent cover per image	Althaus *et al.* (2009)
	Lophelia reefs, Norway	4 reefs, damaged areas up to 450 km^2, ranging from 5 to 50% of total reef area	200–400	*Lophelia pertusa*	Trawl fishery—pre-fishing clearing	Estimate based on ROV observations and fishing footprint	Fossa *et al.* (2002)
Change in community structure	Continental slope, Bay of Plenty New Zealand	11–40% of variation in multivariate pattern in community structure attributed to fishing	200–600	Invertebrate catch—decapods, echinoderms, anemones—from research trawl	Fish and scampi trawl	Counts per standardized research trawl (0.14 km^2)	Cryer *et al.* (2002)
	Graveyard Seamounts, Chatham Rise, New Zealand	Difference in community structure between fished and unfished seamounts	748–1200	Invertebrates (mainly epifauna)	Epibenthic sled	Counts	Clark and Rowden (2009)
	Tasmanian seamounts, Australia	Difference in community structure between fished and unfished seamounts	1099–1353	Epifauna	Towed camera	Counts	Althaus *et al.* (2009)
	Seamounts off Australia and New Zealand (see above)	Differences in community structure between seamounts with different fishing history, and between years since fishing ceased	720–1651	Epifauna	Towed camera	Counts	Williams *et al.* (2010)
	Continental slope, West Africa	Marked differences in infaunal and epifaunal assemblages between heavy and light trawled sites	350–450	Epifauna and infauna	Trawl	Fine-mesh otter trawl sample	Atkinson *et al.* (2011)

The design of studies on seamounts and slope environments off Australia and New Zealand (Koslow *et al.*, 2001; Cryer *et al.*, 2002; Althaus *et al.*, 2009; Clark and Rowden, 2009) is the 'compare-and contrast' type, examining biological differences between areas that are known to have different fishing histories. Similarly, Atkinson *et al.* (2011) described differences in epifaunal abundance and diversity off West Africa with different levels of trawl intensity, and Munoz *et al.* (2012) also observed differences in bycatch levels between areas of high and low fishing effort in the North Atlantic. Denisenko (2007) reported results of surveys in the Barents Sea where there was a widespread reduction in biomass and distribution of 11 of 13 epibenthic species exposed to the demersal trawl fishery. Other bycatch studies have shown, in association with trawling on seamounts, a decline in benthic invertebrate abundance, biomass, or richness over a period of a fishery (Anderson and Clark, 2003; Niklitschek *et al.*, 2010). Most of these studies have indicated strong differences in the biodiversity of benthic fauna, especially coral-associated communities (Table 2). Arguably, attributing observed spatial contrasts in faunal metrics exclusively to fishing impacts is impossible without replicated experiments that are repeated in different geographic areas. However, fishing histories in the above studies are reasonably well known, environmental differences have been accounted for in the analyses and/or design, and observed biological variables are known to be sensitive to trawling impacts (e.g. coral cover). This makes attribution of ecological data to fishing very strong. Additional evidence that fishing operations are the chief cause of observed differences in benthic fauna comes from the fine-scale spatial distribution of fishing effort: remnant populations of corals can persist in areas that are too rough to trawl. An example of this is on "Morgue Seamount" on the Chatham Rise, where dense scleractinian corals occur down a spur that from commercial records and talking with skippers has not been fished (Clark *et al.*, 2010a) (Figure 1).

The trawl gear varies between the fisheries covered in Table 2. Some studies document changes caused by relatively specific gear, such as "deep trawl" which usually refers to orange roughy trawls that have doors weighing 1000–1500 kg, a small net (~25 m wingtip spread) with cut-away lower wings, but heavy bobbin or rock-hopper groundgear that can weigh between 2 and 4 t (Clark and Koslow, 2007). The more mixed trawl fisheries in the North Atlantic and upper continental slope off Australia and South Africa ("trawl" in Table 2) may use similar trawl doors, but typically lighter groundgear than the rough bottom orange roughy trawls. The range of gear types, and intensity of commercial fishing is often not well documented, and hence care is needed when drawing generalizations from the compilation in Table 2.

Experimental studies of fishing impacts in the deep sea are rare, but Freese *et al.* (1999) found in the Gulf of Alaska density differences of 30% for finger sponges and similar reductions in anemone populations between experimental trawl tracks and adjacent un-trawled areas. Off Norway, marked changes in the height of *Paragorgia* and *Lophelia pertusa* colonies have been attributed to trawling, whereby coral colonies were on average about half as high in fished areas relative to intact colonies (Buhl-Mortensen *et al.*, 2013).

Static gears, such as longlines and traps are considered to have lower impacts than mobile gear types (Pham *et al.*, 2014). However, in certain conditions, for example during retrieval, static gear may move laterally across the seabed, resulting in impacts to the habitat and biota (Sampaio *et al.*, 2012; Ewing and Kilpatrick, 2014). Longline impacts on sessile fauna such as sponges and corals have been observed (Fossa *et al.*, 2002; Mortensen *et al.*, 2008), where the animals have been broken by longline weights or by the mainline cutting through them while moving laterally during fishing or hauling (Welsford and Kilpatrick, 2008).

The amount of trawling effort required to cause a certain level of impact has not been well researched in the deep sea. However,

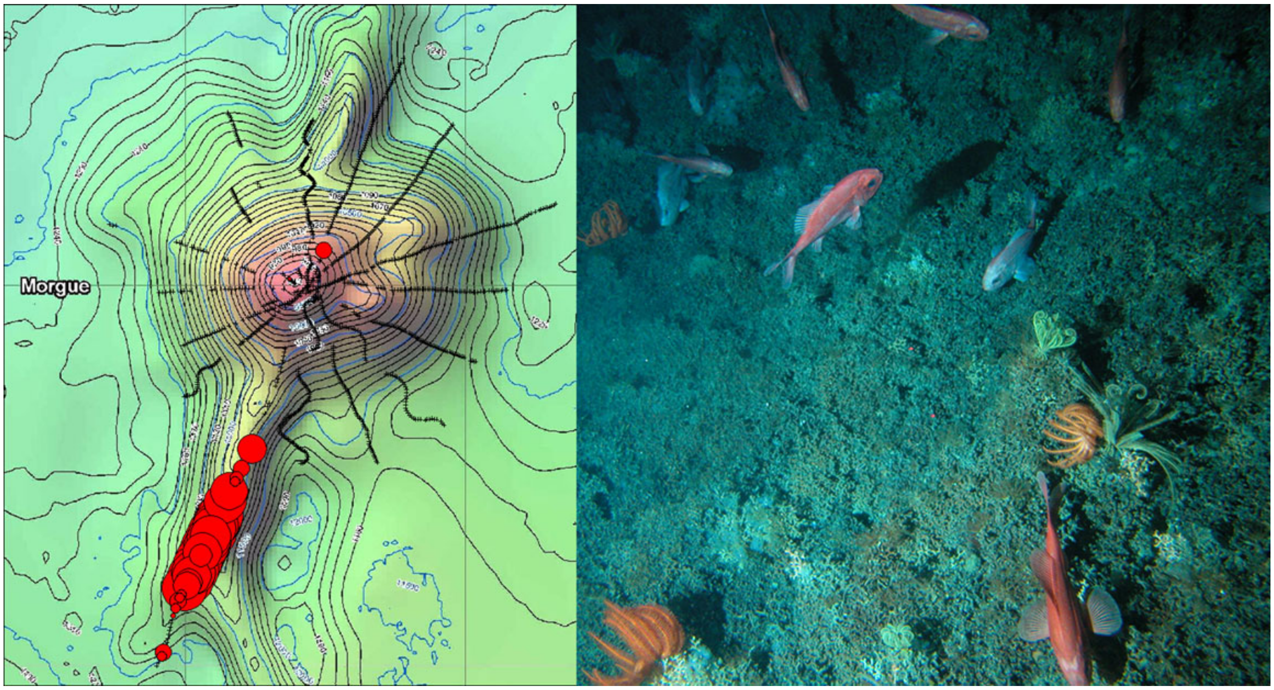

Figure 1. "Morgue" seamount off New Zealand, showing (left panel) the distribution and percentage cover of erect stony coral matrix in seabed photographs, where the crosses are still image positions, and the circles are proportional to percentage areal cover in the image (maximum circle size = 100%). The area of high-density corresponds to a ridge where the seabed is too rough for bottom trawling. The right panel shows a section of the seabed with the erect stony coral matrix on the untrawled ridge (image courtesy of NIWA). This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

Table 3. Summary of selected studies documenting damage to sponge and coral taxa from trawling experiments.

Location	Depth	Gear	Effort	Taxon	Damage	Reference
Georgia, SE USA	20 m	Fish trawl (16 m footrope, 15–30 cm rubber discs)	1 trawl	Barrel sponges	32%	Van Dolah *et al.* (1987)
Alaska	200–300 m	Fish trawl (rock-hopper, 40–60 cm discs)	8 × 1 trawl	Sponges	67%	Freese *et al.* (1999)
				Gorgonians	55%	
NW Australia	50–200 m	Fish trawl (15 cm rubber discs)	7 × 1 trawl	Sponges	90%	Sainsbury *et al.* (1997)
NE Australia	20–35 m	Prawn trawl (22 m groundrope, ground chain)	6 × 13 trawls	Sponges	78%	Burridge *et al.* (2003)
				Gorgonians	86%	

several studies using fish and prawn trawls have occurred at shelf depths that indicate what impacts might be expected with similar taxa in deeper waters. Table 3 summarizes the results of appropriate studies that describe the incidence of damage to the numbers or density of some coral and sponge taxa that are similar in form and size to various deep-sea species. Results differ, but in general suggest that a single trawl may not necessarily damage everything in its path, but repeated trawling can reduce populations to low levels. The experimental trawling on the Great Barrier Reef (Pitcher *et al.*, 2000; Burridge *et al.*, 2003) showed that 10–20% of gorgonian corals and large sponges were removed during each trawl pass. This work used a prawn trawl which swept a width of ~18 m, and a ground chain was used for close bottom contact. This gear may be more efficient than a deep-sea trawl, as the latter will have heavier groundgear and potentially less-continuous contact with the seabed (and perhaps less direct contact than the other gears used in Table 3 where the groundrope discs range from 15 to 60 cm diameter). Nevertheless, studies on small seamounts at depths of 700–1000 m off New Zealand suggest that as few as 10 "deep-sea" trawls can eliminate corals from 15 to 20% cover to no visible cover (Clark *et al.*, 2010a). The extra weight of such trawl gear over that often used at shelf depths means that the impacts of crushing and gouging can be more severe in deep-sea fisheries.

Indirect impacts on epifauna can arise from the sediment plumes caused by the trawlnet or longline contact with the seabed. Small amounts of sediment settling on the bottom, of the order of only several mm, can smother small cold-water corals such as *Lophelia*, and prevent expansion or recovery of the colony (Rogers, 1999). Impacts on coral feeding and metabolic function are uncertain, although stony corals can actively shed sediment, both in shallow-water species (Riegl, 1995) and on the slope. Larsson and Purser (2011) observed that *Lophelia pertusa* in an aquarium setting was able to survive repeated light smothering by sediment, but polyps died when wholly covered by particles. Hence some taxa can potentially cope with a degree of sediment increase caused by trawling. However, deep-sea sponge respiration has been reported as largely shutting down when subjected to heavy sedimentation loads (Tjensvoll *et al.*, 2013). A number of oil and gas related studies have examined the effects of drilling muds on benthic fauna, but most have focused on aspects of ecotoxicity with chemical contaminants contained in the discharges, which confounds the effects of sedimentation.

Impacts on infauna

Direct effects of fishing disturbance on infauna are relatively well studied in shallow waters (Jennings and Kaiser, 1998; Collie *et al.*, 2000; Kaiser *et al.*, 2000, 2002). On the shelf Sanchez *et al.* (2000) found no short-term impact on muddy bottoms; and similarly O'Neill *et al.* (2013) describe no change in infauna after a single passage of a scallop dredge, despite the animals being swept up in the sediment plume. However, Handley *et al.* (2014) reported that soft-sediment shelf habitats impacted by fishing over longer terms were devoid of large bodied species, as they are more likely to be crushed or removed. Given the more stable nature of deep-sea environments, there would be an expectation that more species could be affected by disturbance, with declines in abundance and species richness (Grassle and Sanders, 1973). Several studies at abyssal plain depths have noted reductions in small infauna (e.g. nematodes, polychaetes) and larger mobile burrowing forms (e.g. urchins, asteroids) following experimental disturbance that ploughed the seabed (Ahnert and Schriever, 2001; Miljutin *et al.*, 2011). More relevant to fishing depths, Leduc and Pilditch (2013) conducted a small-scale experimental disturbance in the laboratory with sediment cores from 345 m depth, and after 9 days found nematode species richness remained similar, but there were changes in the vertical distribution of nematode species, and community structure. Mangano *et al.* (2013) found significantly lower numbers of individuals and species and a shift in the community composition (i.e. more worms, bivalves, and scavengers) in areas of higher trawl frequency on the shelf, but not on the slope (although the latter result may have been confounded by illegal fishing activity).

The vertical penetration of various parts of trawl gear into the seabed can be significant, at least 30 cm for doors, and several centimetres for the groundgear (Buhl-Mortensen *et al.*, 2013) (and see other papers in this issue). This can affect infaunal composition and distribution (Leduc *et al.*, 2012) but also potentially epifauna that are adapted to a certain substrate mix of bedrock, boulders, pebbles, or gravel. Mixing of the upper sediment layers can also alter the chemical composition, especially in the more stable waters of the deep sea (Rumohr, 1998). Chemical release from the sediment can also be enhanced, especially if enriched nodules or sediments containing elements such as phosphorites are broken up or disturbed by trawling (ICES, 1992). In a detailed study of the sedimentary environment of a canyon in the western Mediterranean Sea, affected by intensive and regular trawling at depths of 200–800 m, Pusceddu *et al.* (2014) found substantial decreases in organic matter content of the sediments, slower organic carbon turnover, and reduced meiofauna diversity and abundance. They concluded that the majority of the daily organic carbon input could be removed by trawling, causing a general degradation of sedimentary habitats, and infaunal depauperation.

Offal discards from fisheries may result in localized organic enrichment of the sediment, and provide a trophic subsidy to deep-sea consumers. Discarded catch and processing waste that is not taken at the surface by seabirds or scavenged in the water column, can result in localized, and relatively large, food falls (Connolly and Kelly, 1996). This can lead to an influx of scavengers and predators (Britton and Morton, 1994; Clark and Koslow, 2007; Williams *et al.*, 2009; Dannheim *et al.*, 2014); but where deep-sea communities are already well adapted to a scavenging role for natural flux of dead animals, it is unclear how significant the supply of fishing discards might be (Gage *et al.*, 2005). A single study on discards from the hoki (*Macruronus novaezelandaie*) fishery off New Zealand suggested that there might be oxygen depletion (Livingston and Rutherford, 1988), although this has not been confirmed. Dannheim *et al.* (2014) observed that the trophic level of soft bottom communities in fished areas was higher than in unfished areas, and Shephard *et al.* (2014) noted increased scavenging by some fish in trawled areas affecting size structure of communities.

Smothering impacts on infauna by a sediment cloud are likely to be less severe than for epifauna. There are few deep-sea studies, but Trannum *et al.* (2010) experimented with sediment obtained from 40 m depth off Norway. Sediment thicknesses between 3 and 24 mm were applied, and no changes were found in number of taxa, abundance, biomass, or diversity of macrofauna. However, *in situ* studies at depth are required to improve our understanding of sedimentation processes and biological impacts.

Changes in community characteristics

The direct impacts on fauna through dislodgement or damage of individuals are the most obvious effects caused by fishing gear, but the range of biological changes extends well beyond these physical impacts and can significantly alter the community composition and foodweb architecture in the ecosystems subjected to fishing disturbance. On the shelf high levels of trawling results in changes to overall community composition through substantial habitat alterations, removal of non-target species, and through attraction of scavengers and predators to trawled areas (Tillin *et al.*, 2006; Hinz *et al.*, 2009).

Removal of structural engineers and homogenizing of sediments alters the benthic habitat in ways that may not be suitable for settlement of recruits from the original community, leading to long-term or potentially permanent changes in community composition and structure. Such shifts are well documented in shelf communities as a result of fishing (Kaiser *et al.*, 2000). In deeper water, trawling with heavy bottom gear has removed habitat forming stony coral from seamounts and offshore reef areas (Koslow *et al.*, 2001; Fossa *et al.*, 2002; Hall-Spencer *et al.*, 2002; Althaus *et al.*, 2009; Clark and Rowden, 2009; Buhl-Mortensen and Buhl-Mortensen, 2014) which is implicated in changes in community structure (Koslow *et al.*, 2001; Althaus *et al.*, 2009; Clark and Rowden, 2009) whereby the species composition and relative abundances have changed with removal of the coral habitat. Such shifts have yet to, or may never, recover to a pre-impact state (Williams *et al.*, 2010). Other deep-sea environments dominated by vulnerable structural species include bryozoans that consolidate soft substrates to provide habitats and attachment points for other sessile fauna, forming species rich communities on the continental slope (Schlacher *et al.*, 2010). Williams *et al.* (2009) observed that trawling has impacted such bryozoan habitat off Australia, where there is a high overlap with bottom trawling, and bryozoan turf was observed to be vulnerable to damage by a relatively light research sled.

In soft-sediment slope environments without significant habitat structure, epifauna community structure has also been demonstrated to be markedly different between lightly and heavily trawled areas off southwest Africa (Atkinson *et al.*, 2011). In the same study, infaunal community structure was reported as very different between two of the four pairs of lightly and heavily trawled sites (Atkinson *et al.*, 2011). An extensive study of the effects of trawling on deep-sea infaunal communities was conducted using data from research trawls from a 2400 km^2 area of slope off New Zealand (Cryer *et al.*, 2002). This study demonstrated that 11–40% of variation in infaunal community structure was attributable to fishing (over many years for both finfish and scampi), and inferred that trawling probably changes benthic community structure over broad spatial scales on the continental slope as well as in coastal systems (Cryer *et al.*, 2002).

Changes in community structure include alterations in the proportions of ecological or trophic "types" of fauna. Marked differences in both epi- and infaunal communities away from larger slow-growing species, such as echinoderms, towards smaller fast-growing species such as worms and scavengers, have been observed in deep-sea environments subject to regular trawling (Atkinson *et al.*, 2011; Mangano *et al.*, 2013). Denisenko (2007) (cited in Lyubin *et al.* (2011) observed changes in Barents Sea communities down to 300 m due to demersal trawling, and a shift from abundance of large and long-lived suspension-feeders to smaller deposit feeders.

Changes may also occur through an altered balance in the composition of fish species associated with benthic habitat. Cold-water coral reef structures often have high diversity or abundance of fish species (Costello *et al.*, 2005; Auster, 2007) and may provide nursery ground, spawning, and protective habitat (Husebo *et al.*, 2002; D'Onghia *et al.*, 2010; Clark and Dunn, 2012). Hence, there could be potential flow-on effects into deep-sea fish communities, and subsequently predator–prey interactions with benthic invertebrates.

Faunal sensitivity

The impacts of fishing on benthic communities are determined by interactions between the physical, behavioural, and life history characteristics of individual taxa and the nature of the disturbance itself (Thrush and Dayton, 2002; Gray *et al.*, 2006; Hewitt *et al.*, 2011). Sensitivity can be thought of as the balance between *intolerance*—impairment or death of individuals, populations, or communities in response to disturbance, and *recoverability*—the re-colonization or re-growth following disturbance (Hiscock and Tyler-Walters, 2006). Alternative but equivalent terms, such as *ecological resistance* and *resilience*, have also been applied to these concepts (Bax and Williams, 2001; Halpern *et al.*, 2007; Williams *et al.*, 2010); in these cases, *vulnerability* accounts for the exposure of the ecological unit to fishing disturbance. Sensitivity is typically applied at the level of individual taxa by reference to a suite of relevant biological attributes or traits (MacDonald *et al.*, 1996; Bremner, 2008; Tyler-Walters *et al.*, 2009; de Juan and Demestre, 2012), but the concept can also be applied at the level of populations, habitats, biotopes, or ecosystem functions (e.g. Hiddink *et al.*, 2007; Tyler-Walters *et al.*, 2009; Bolam *et al.*, 2014; Lambert *et al.*, 2014). Estimating the relative sensitivity of fauna is important because it provides a basis for identifying the potential vulnerability of ecological units, and for assessing the risk stemming from impacts. But for management uptake of this information, for example to prioritize areas for protection or designing monitoring programmes, metrics of sensitivity are needed.

Sensitivity is necessarily defined in relation to the characteristics of a specific fishing method because the intensity, spatial scale, and frequency of disturbance can vary greatly between methods (e.g. bottom trawling vs. longlining) (MacDonald *et al.*, 1996). The principal characteristics of fishing disturbance relevant to direct impacts on benthic organisms are the gear's spatial extent, speed, degree of penetration into the substratum, and the frequency of the disturbance (Thrush and Dayton, 2002; Hewitt *et al.*, 2011). Spatial extent and speed influence whether or not mobile organisms will be able to avoid the disturbance. Spatial scale will also influence which taxa are able to benefit from exploiting food resources, such as carrion and exposed infauna, caused by the disturbance. The frequency of disturbance will influence recoverability

Table 4. List of biological attributes and corresponding traits used to define sensitivity of individual and colonial deep-sea benthic taxa to along-surface disturbance from mobile fishing gears (modified from Hewitt *et al.*, 2011).

Attribute	Traits	Response to disturbance and rationale
Fragility	Very fragile	Strongly negative; will be damaged/killed if disturbed
	Fragile	Negative; will be damaged if disturbed
	Robust or not known	Neutral
Living position	Sediment surface	Strongly negative; will be disturbed
	In top 2 cm of sediment	Negative or neutral dependent on depth of disturbance;
	Deeper than 2 cm in sediment	Negative or neutral dependent on depth of disturbance;
Mobility	Sedentary	Strongly negative; unable to move away from approaching disturbance
	Limited	Negative; may be able to move away
	High	Neutral; able to move away from (or bury below) approaching disturbance
Habit	Erect	Negative; liable to breakage
	All others	Neutral; other habits are encompassed in the analysis by attributes related to living position
Feeding	Scavengers and predators	Positive; provision of additional food source
	Suspension, deposit, and grazers	Neutral; this is a conservative interpretation as variability in the magnitude of positive or negative effects is likely to be dependent on location, disturbance regime, and individual traits

(re-growth, migration, or re-colonisation), with higher frequencies having greater impact on taxa that are less tolerant and/or with lower recoverability. In soft sediments, the degree of penetration of the fishing gear will strongly influence the range of taxa affected, with fewer taxa being tolerant of deeper penetration (Thrush *et al.* 1998).

Attributes useful for defining the sensitivities of individual benthic taxa to fishing disturbances can be separated broadly into two categories: (i) physical and behavioural attributes including feeding mode (e.g. deposit-feeding vs. suspension-feeding), living position (e.g. infaunal vs. epifaunal), growth form (e.g. encrusting vs. erect), and mobility (e.g. sessile vs. mobile) and (ii) life-history attributes such as growth rate, capacity to regenerate, reproductive mode, and dispersal potential (Bremner *et al.*, 2006; de Juan *et al.*, 2009). For deep-sea studies, an important practical issue is the availability of reliable data to inform these categories. Thus, while knowledge of life history characteristics of shallow-water benthic taxa may be derived through observation and experimentation (e.g. MacDonald *et al.*, 1996), the difficulty of applying an experimental framework in deep-sea studies leads to relatively sparse ecological knowledge for benthic fauna, particularly their reproductive and growth characteristics. Estimates of relative sensitivity or vulnerability incorporating life history attributes have been generally undertaken by expert consensus where such data are sparse (CCAMLR, 2009; Halpern *et al.*, 2007; Williams *et al.*, 2010). However, these assessments for deep-sea taxa rely heavily on the more obvious physical and behavioural characteristics, particularly living position, growth form, mobility, and fragility, which are simpler in concept and more robust in practice because the data underlying them are readily accessible. Because estimates of recoverability depend on often unknown life-history attributes, it is more conservative to assess impacts and risk of disturbance to benthic fauna and habitats in the deep-sea context by considering intolerance separately (Thrush *et al.*, 2009; Tyler-Walters *et al.*, 2009; Lambert *et al.*, 2014).

In a simple biological traits scheme developed for categorizing sensitivities of deep-sea benthic fauna Hewitt *et al.* (2011) assigned taxa to one or more 'traits' in each of five physical attributes. This was based on their expected responses to an along-surface disturbance, such as that resulting from bottom trawling (Table 4). Traits associated with fragility, living position, mobility, and habit had negative or neutral responses to disturbance; responses were greater for fragile compared with robust taxa, surface-living compared with deep burrowing taxa, sedentary compared with highly mobile taxa, and erect compared with non-erect taxa (Table 4). Only feeding had a possible positive response through the provision of additional food sources to mobile scavengers and predators (Table 4). The focus on effects at the individual, rather than population or community, level is a conservative approach, because the response of an individual exposed to bottom trawling can be predicted with greater confidence than the response of the population of which the individual is part. Rules for allocating traits can also be formulated to be conservative, such as if feeding mode is unknown, a taxon can be equally allotted to all possible traits (Chevenet *et al.*, 1994). By combining scores across all attributes, individual taxa can be ranked in sensitivity categories (Table 5 and Figure 2). In the example from Hewitt *et al.* (2011), taxa were ranked based on the degree of mortality resulting from exposure to disturbance. The highest ranked were sedentary, erect, and fragile forms, with sensitivity decreasing either as the degree of fragility decreased or there was greater mobility or a living position deeper in sediment. Thus, taxa living mainly subsurface with high burrowing capacity were considered tolerant, whereas mobile scavengers with potential to benefit from moving into a disturbed area with increased food availability were considered "favoured". Highly sensitive taxa in the deep sea include those with erect and fragile forms such as arborescent octocorals and thicket-forming stony corals (Figure 2)—taxa that typically also have correspondingly highly sensitive life history characteristics including slow growth.

In management applications, for example to prioritize areas for protection, sensitivity estimates are needed for broader ecological units—populations, communities, or ecosystems. Aggregate metrics can be developed from the traits of their constituent species using a number of methods: (i) basing higher-level sensitivity on the taxon with the highest sensitivity rank (Tyler-Walters *et al.*, 2009); (ii) rank-weighted average sensitivity, based on the product of sensitivity rank and abundance for all taxa at a site (de Juan *et al.*, 2009); and (iii) the number or proportion of taxa present in each sensitivity category defined from biological traits (Hewitt *et al.*, 2011). Ideally, knowledge of population dynamics and density-dependent effects would be incorporated into metrics scaled to population levels, but this is not

Table 5. Categories of sensitivity of deep-sea benthic taxa (individuals and colonies) to along-surface disturbance from mobile fishing gears (modified from Hewitt *et al.*, 2011).

Sensitivity category	Expected response	Biological traits	Example taxa
High	Individuals in disturbed areas die	Sessile, erect forms that are very fragile	Gorgonian fans (e.g. *Corallium*); non-fleshy arborescent octocorals (e.g. bamboo corals); branching stony corals (e.g. *Solenosmilia*); erect branching or laminar sponges
Intermediate	Some individuals in disturbed areas die	Fragile forms with no or limited mobility that are either erect or surface dwellers	Fern-frond, non-fleshy—bushy octo- and black corals, fleshy—arborescent octocorals (e.g. Nephteidae); quills (e.g. Seapen); whiplike octocorals (e.g. Chrisogorgidae sp.); massive sponges (e.g. ball and simple forms); stalked crinoids; sea urchins
Low	A few individuals may die	More robust or small erect forms or mobile surface dwellers, or fragile dwellers or in the top 2 cm of the sediment with limited mobility	Bottle-brush octocorals (e.g. *Chrysogorgia* sp.) and black corals (Antipatharia); ophiuroids, asteroids; sea cucumbers; ascidians; large crabs; large molluscs
Tolerant	No response	Robust and/or mobile surface dwellers, or subsurface with high mobility (burrowing capacity)	Lobsters (squat, true and slipper); echiurans; polychaetes; encrusting fauna including sponges
Favoured	Individuals may move into disturbed area	Scavengers and predators which are highly mobile	Swimming crabs; some hermit crabs

yet possible for deep-sea benthos. Hewitt *et al.* (2011) applied the above three methods to data from a deep-sea fishery area in New Zealand and concluded that community sensitivity was best assessed by a combination of (ii) and (iii), both of which yielded a graduated negative relationship between sensitivity and trawl intensity (Figure 3). The number of high-sensitivity taxa at each site declined with increasing fishing intensity (a pattern which remained when numbers were converted into percentages, indicating that the decrease was not driven by decreasing species richness). Favoured taxa showed no relationship with fishing intensity (Figure 3). However, it must be stressed that metrics incorporating abundance of taxa do not overly emphasize the responses of the most abundant species and underrepresent rare and/or highly sensitive taxa. Communities will typically be composed of a mix of highly sensitive and tolerant taxa—especially when spatial units of analysis use physical environmental surrogates to map biological distributions and result in relatively larger (10s–100s km) community or population areas. Hence, interpretation of aggregate metrics should be done with caution.

Time-series observations of seamount benthic communities exposed to bottom trawl impacts (Williams *et al.*, 2010) indicated that fine-level grouping of taxa may be needed to classify their sensitivity. Relatively high abundances of sessile forms (unstalked crinoids, chrysogorid octocorals, solitary scleractinians, and gorgonians), and mobile forms (the urchin *Dermichinus horridus* and species of echinoids and prawns) occurred where trawl intensity had been relatively high. While these patterns might have contained some early signals of recolonization (including immigration by mobile species), a more detailed examination of the size and distribution of some of these taxa in still images of the seabed indicated that they were more likely to have resulted from individuals that were tolerant of the direct impacts of trawling and those that existed in natural refuges inaccessible to trawls (authors unpublished data). Tolerance of erect taxa to bottom trawling was apparent in chrysogorgid corals on account of their small size and high structural flexibility, and in solitary scleractinians and stylasterids with their small size and robust hard exoskeleton. Thus, analysis of sensitivity may need to treat hard and soft bottom separately because the expected responses of fauna to disturbance may be partially mitigated by natural refuges which are more common on complex rocky seabed.

Recovery potential from fishing impacts

A critical element in managing the environmental performance of deep-sea fisheries is to identify the capacity for impacted populations, assemblages and ecosystems to re-establish biological structures and functions after the impacts have ceased or diminished. Recovery—or the return to conditions that resemble background values in systems not damaged by fishing activities—is not unique to managing impacts in the deep sea (Paine *et al.*, 1998). It is a feature common to all ecosystems and encompasses disturbance regimes that can be natural (e.g. turbidity flows, benthic storms, and volcanic eruptions) or anthropogenic (i.e. mining, trawling, and longlining). Many studies have examined this aspect in shallow and shelf waters, where it has become evident that responses are based on a complex set of site-specific factors that are often poorly understood and difficult to estimate. Collie *et al.* (2000) documented a number of studies where results from carefully designed studies were contrary to expectations, or changes could not be detected. Severe storm events can also influence benthic communities to a depth of ~100 m (Sharma, 1974). This is much shallower than the depths considered in this paper, but it is nevertheless useful to bear in mind that such natural influences can have as large, or a greater, influence on changes in species abundance than bottom trawling (McConnaughey and Syrjala, 2014). What is, however, unique in the deep sea is (i) the rates of recovery may be much slower than in shallower systems and (ii) the almost complete lack of empirical data on faunal recovery in the deep sea means that inferences about recovery have to be made using proxies based on the longevity and growth rates of the organisms that have been damaged.

There is a long-standing and widely held belief that recovery is extraordinarily sluggish in the deep sea (Grassle, 1977). The expectation of slow recovery arises primarily from low biological rates in deep-sea species (Smith, 1994), life history traits that are predicted to delay recovery (Young, 1983), and variable larval dispersal and intermittent recruitment and settlement (Lacharité and Metaxas, 2013). While it is true that organisms in colder, deeper waters have slower turnovers, this is primarily a temperature effect: when body size and temperature are accounted for, deep-sea benthic species have similar metabolic rates (McClain *et al.*, 2012). Some deep-sea benthos also have comparatively longer lifespans and tend to grow slower as a consequence of living in food-poor and

Figure 2. Example deep-sea fauna representative of the different sensitivity categories defined in Table 5 (red, highly sensitive; orange, intermediate; yellow, low; pale green, tolerant; dark green, favoured). The shape and form of taxa can vary widely, and these examples serve to show the sensitivity characteristics of deep-sea species.

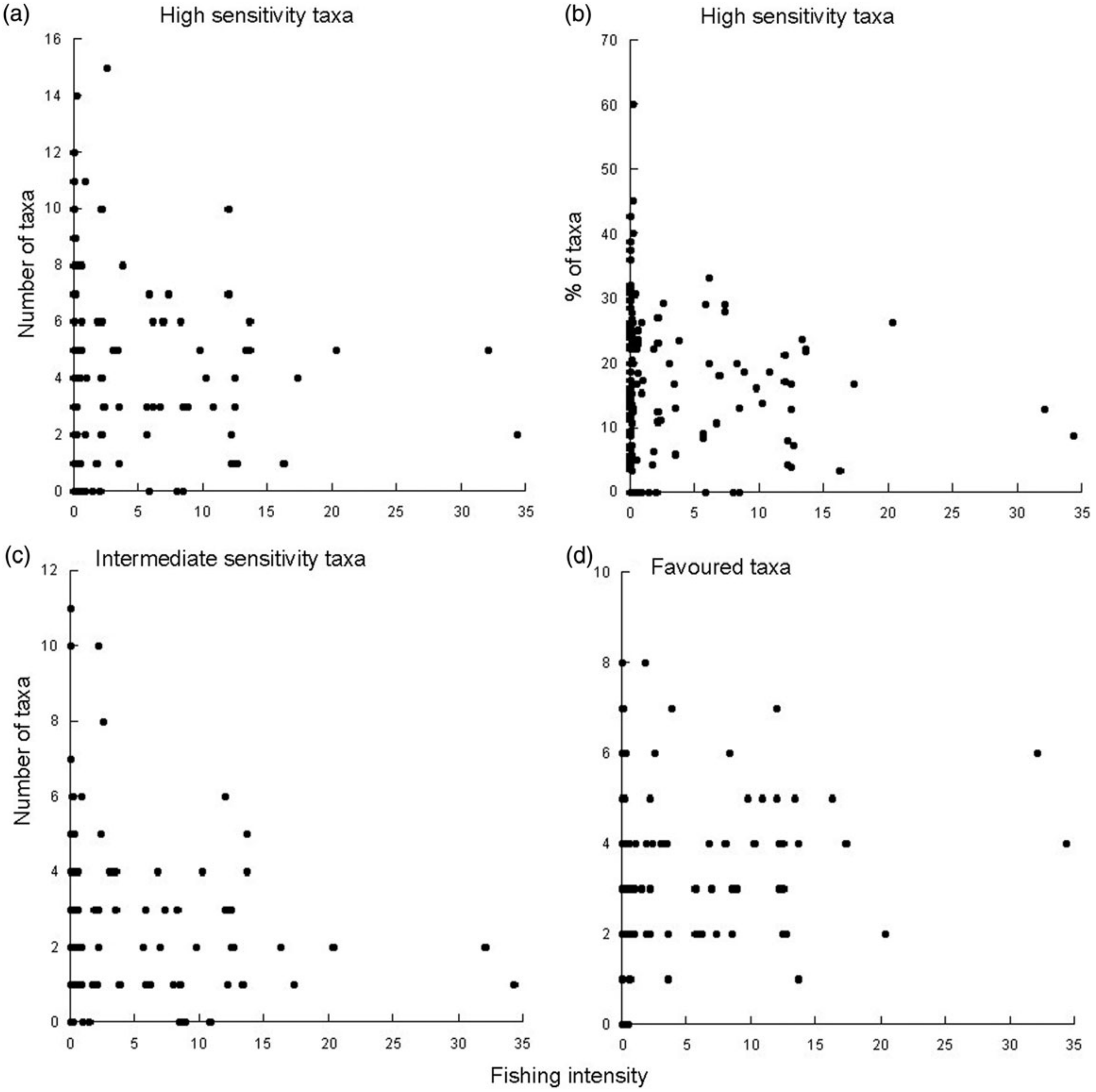

Figure 3. Relationship between fishing intensity (percentage of 25 km^2 cells trawled over 16 years) and the numbers of benthic taxa in high, intermediate, and favoured sensitivity categories (see Table 5): (a) number of high sensitivity taxa, (b) number of high sensitivity taxa converted to percentage of taxa, (c) number of intermediate sensitivity taxa, and (d) number of favoured taxa. Reproduced with permission from Hewitt *et al.* (2011).

cold environments (McClain *et al.*, 2012). A further critical factor in determining recovery is the supply and fitness of colonizers: dispersal in the deep sea can thus be a limiting factor if disturbed areas are widely separated from colonizer pools, resulting in potentially low larval supply to impacted areas (Lacharité and Metaxas, 2013).

The question whether deep-sea systems recover as slowly as expected cannot at present be answered with empirical data. While there exist a number of studies that have measured post-disturbance processes in the deep-sea, these are, with one exception, limited to soft-sediment habitats (Smith and Hessler, 1987; Borowski and Thiel, 1998; Bluhm, 2001; Thiel *et al.*, 2001; Khripounoff *et al.*, 2006; Miljutin *et al.*, 2011; Gates and Jones, 2012). In contrast, trawling most commonly targets hard grounds in the deep sea (e.g. seamounts) where ecological impacts are often most severe (Clark *et al.*, 2010b). On seamounts that have been the target of fisheries for several decades in New Zealand and Australia, Williams *et al.* (2010) attempted to measure actual recovery rates of the fauna: they found no consistent and clear signal of recovery in the megabenthos 5–10 years after fishing had ceased, suggesting that any recovery is likely to be very prolonged.

A complementary line of evidence that suggest limited recovery potential for the megabenthos (e.g. sponges, corals, and crinoids) impacted by trawling gear on hard bottoms in the deep sea comes from data on growth, age, and lifespans of the fauna (Table 6). Notwithstanding variations between taxa, geographic areas, depths,

Table 6. Ages and growth rates of deep-sea megabenthic animals reported to be vulnerable to bottom-contact fishing.

Higher taxon	Species	Locality, region	DEPTH (m)	AGE (years)	RADIAL growth rate (mm year^{-1})	AXIAL growth rate mm year^{-1})	Source
Porifera, Demospongiae, and Verticillitidae							
	Vaceletia sp.	Norfolk Ridge seamounts, SW Pacific	160 – 600	600 – 740		0.11	
Porifera, Hexactinellidae, and Monorhaphididae							
	Monorhaphis sp.	Norfolk Ridge seamounts, SW Pacific	–	440 – 440			Ellwood and Kelly (2003)
Bryozoa, Cheilostomadida							
	Cellarinella margueritae	Antarctica, Southern Ocean	247 – 414	15			
	Cellarinella nodulata		247 – 414	14			
	Cellarinella rogickae		247 – 414	15			
	Cellarinella watersi		247 – 414	11			
	Melicerita obliqua		247 – 414	32			
	Stomhypselosaria watersi		247 – 414	15			
Hexacorallia and Anthipatharia							
	Leiopathes sp.	Azores seamounts, North Atlantic	293 – 366	240 – 2380	0.005 – 0.030		Carreiro-Silva *et al.* (2013)
	Leiopathes sp.	Hawaii seamounts, Pacific	400 – 500	350 – 4300	–		Roark *et al.* (2009)
Hexacorallia and Scleractinia							
	Desmophyllum cristagalli	South Pacific		150		0.5 – 2.0	Adkins *et al.* (2004)
	Desmophyllum dianthus	Tasmanian Seamounts, SW Pacific	957 – 2193	190			Thresher *et al.* (2011)
	Enallopsammia rostrata	North Bermuda Slope, North Atlantic	–	100-	0.07 – 0.07	5.0	Adkins *et al.* (2004)
	Enallopsammia rostrata	Line Islands, Equatorial Pacific	480 – 788	201 – 612	0.01 – 0.07	0.6 – 1.9	Houlbrèque *et al.* (2010)
	Lophelia pertusa	Gulf of Mexico, Atlantic	460 – 507			2.44 – 3.77	Brooke and Young (2009)
	Solenosmilia variabilis	Tasmanian Seamounts, SW Pacific	958 – 1454	75 – 120		0.84 – 1.25	Fallon *et al.* (2014)
Hexacorallia and Zoantharia							
	Gerardia sp.	Florida Straits, Atlantic	610 – 630	1500 – 2140			Druffel *et al.* (1995)
	Gerardia sp.	Hawaii Seamounts, North Pacific	400 – 500	300 – 2742	0.011 – 0.085		Roark *et al.* (2009)
Octocorallia and Corallidae							
	Corallium sp.	Davidson Seamount, NE Pacific	1482 – 1482	20 – 100	–	9 – 11	Andrews *et al.* (2005)
Octocorallia and Isididae							
	Isidella tentaculum	Gulf of Alaska, NE Pacific		43 – 63	0.084 – 0.12	11.4 – 16.7	Andrews *et al.* (2009)
	Keratoisis sp.	Davidson Seamount, Alaska		80 – 220		1.9 – 4.4	Andrews *et al.* (2005)
	Keratoisis sp.	Davidson Seamount, Alaska		89 – 282	0.039 – 0.074	1.4 – 2.8	Andrews *et al.* (2009)
	Keratoisis sp.	Gulf of Alaska, NE Pacific		87 – 146	0.044 – 0.075	8.2 – 13.8	Andrews *et al.* (2009)
	Keratoisis sp.	New Zealand, SW Pacific	200 – 2000	300 – 500			Tracey *et al.* (2003)
	Keratoisis sp.	Australia, SW Pacific	200 – 2000	100 – 150			Tracey *et al.* (2003)
	Keratoisis sp.	New Zealand, SW Pacific	935 – 935	38 – 38	0.22 – 0.22	21 – 57	Tracey *et al.* (2007)
	Lepidisis spp.	New Zealand, SW Pacific	638 – 1030	26 – 61	0.13 – 0.29		Tracey *et al.* (2007)
Octocorallia and Paragorgiidae							
	Paragorgia arborea	New Zealand, SW Pacific	200 – 800	300 – 500		–	Tracey *et al.* (2003)
	Paragorgia sp.	Davidson Seamount, NE Pacific	1313 – 1313	9 – 14		60 – 90	Andrews *et al.* (2005)
Octocorallia and Primnoidae							
	Primnoa resedaeformis	Gulf of Alaska, NE Pacific	263 – 369	105 – 112	0.36 – 0.36	16 – 23.2	Adkins *et al.* (2002)
Crinoidea and Hemicrinidae							
	Neogymnocrinus richeri	Norfolk Ridge (New Caledonia) seamounts	300 – 500	340			Samedi *et al.* (2007)

Listed values are not comprehensive of all published growth or age estimates in the deep-sea fauna, but merely serve here as examples to illustrate the range of growth and longevity in many species typical of hard-bottom seabed assemblages in the deep sea.

and other factors, the clear message from these biological data is that the overwhelming majority of species that are commonly impacted grow very slowly and have very high longevity. These traits of slow growth and great age translate into estimates of recovery times that, for many communities, are likely to span centuries to millennia. Hence, very slow recovery is expected from any disturbance, not just by fishing but also other industries (e.g. mining of ferromanganese crusts from seamounts) that removes the attached fauna (Schlacher *et al.*, 2014). Formation of new habitat could operate at geological time-scales (centuries or longer).

Limited recovery potential is a key difference between shallow-water and deep-sea benthic communities (and many fish species). Even if the sensitivity of the benthos is similar, the recovery time from any given disturbance will be much greater in the deep sea.

Management implications

This review has identified a number of studies demonstrating that direct and indirect fishing disturbances can severely impact deep-sea benthos by reducing diversity and abundance. Impacts from bottom trawling are better understood than those from other gears such as bottom-set longlines, and show that changes to benthic communities can be rapid, persistent, and occur with low levels of fishing effort. This is because many individual taxa are sessile with erect and fragile forms, can be relatively long-lived and slow-growing (especially as depths increase beyond ~500 m), and may attain large body size. Communities associated with biogenic habitats formed by deep-sea corals and sponges are among the most susceptible to fishing impacts because their tolerance (ecological resistance) and recoverability (ecological resilience) is low. The few post-impact time-series data available from the deep sea show, unsurprisingly, that recovery times of benthic communities may be very long. Deep-sea benthic communities have the collective properties of high susceptibility and low recoverability, and hence it is unrealistic to expect them to recover from ongoing fishing impacts, or in the time-spans (years) typically applied to management planning. Restoration concepts are unachievable in the short term, and will be prohibitively expensive (see Van Dover *et al.*, 2014). What then are the options for fisheries managers tasked with balancing sustainable fisheries exploitation and environmental conservation?

The variety of management actions taken to date include regulating fishing methods and gear types, specifying the depths fished, limiting the volumes of bycatch or limiting catch, move-on rules, and closing areas of particular habitat and individual seamounts (Probert *et al.*, 2007; Morato *et al.*, 2010). In terms of fishing methods and gears, various technical modifications to trawl gear such as a lighter groundrope, reduced trawl door weight, shortening the sweep wires that connect the doors to the net, using fly-wires to reduce ground contact, as well as elevating the sweep wires are possible (Mounsey and Prado, 1997; Valdemarsen *et al.*, 2007; Rose *et al.*, 2010; Skaar and Vold, 2010). However, while these can reduce fisheries bycatch and small invertebrates, they are unlikely to substantially reduce the impact on benthic communities, particularly sessile invertebrates with fragile and erect body forms. Use of midwater trawling gear close to the seabed has potential to reduce impact, and longline fishing may be appropriate in some environments—but the practicality of using these methods will vary with target species and location, and operationally will almost certainly involve a trade-off between bottom impact and catch rate of fish species. Many of the main target commercial species have a diving behaviour when disturbed (e.g. orange roughy, oroes, and alfonsino) and hence fishing clear of the seabed can leave an escape channel open that will reduce catch rates. Nevertheless, environmental management is as important in many nation's fisheries policies as target fish species catches. The "ecosystem approach" to fisheries management is now widely advocated and applied in deep-sea fisheries (Garcia *et al.*, 2003). In the deep sea, however, the inherent restrictions on obtaining sufficient stock assessment or benthic habitat data (compared with nearshore shelf/slope fisheries) mean that management regimes typically operate at a low level of knowledge, and management action must occur in a highly precautionary manner. Move-on rules have recently become a common management tool, promoted by United Nations General Assembly resolutions for high seas fisheries that force vessels to move a certain distance if a threshold catch of vulnerable marine ecosystem (VME) indicator species is exceeded (Rogers and Gianni, 2010; Auster *et al.*, 2011). However, the impacts from a single deep-sea trawl will potentially affect the benthos over a large distance (up to 150 m width along the length of a tow). The cumulative area swept by bottom trawl fisheries is typically the most extensive human impact on the seabed (Benn *et al.*, 2010; Ramirez-Llodra *et al.*, 2011), and there are further issues with move-on rules, such as threshold criteria and forcing fishing effort to spread further (Auster *et al.*, 2011; Clark and Dunn, 2012).

Spatial management is likely to be the most effective strategy, and perhaps the only approach that can be successful for protection of vulnerable benthic fauna in the deep sea (Clark and Dunn, 2012; Schlacher *et al.*, 2014). This approach is best achieved by restricting the distribution of fishing effort, and putting in place a system of zones which can allow exploitation in productive fishing areas, but protect vulnerable or sensitive species and habitats. Typically, this involves a network of open and closed areas, with closure of unfished areas where benthic communities occur in their natural state.

Management of the deep-sea lags behind that of the continental shelf, but there is a growing array of protection measures. Fishery closures are becoming common, with large areas within EEZs being closed zones for bottom trawling (e.g. New Zealand, North Atlantic, Gulf of Alaska, Bering Sea, USA waters, Azores) (Hourigan, 2009; Morato *et al.*, 2010), and there are even some closures implemented on the high seas under international fishery management agreements (e.g. South Pacific, Penney *et al.*, 2009). The effectiveness of such deep-sea fishing closures is, usually, yet to be formally established. One of the most thorough evaluations conducted to date suggests that the spatial closures instigated by New Zealand on the Louisville Seamount Chain, Lord Howe Rise, Challenger Plateau, and West Norfolk Ridge are suboptimal for the protection of VMEs and alternative closures would better balance protection against economic loss to fishers from closure of historically fished areas (Penney and Guinotte, 2013). There are increasing efforts to identify areas of importance for deep-sea benthic biodiversity, such as Ecologically or Biologically Significant Areas (CBD, 2009) and VMEs (FAO, 2009), and systematic methods are being developed (Taranto *et al.*, 2012; Ardron *et al.*, 2014; Clark *et al.*, 2014) to help incorporate them in spatial management measures. Even without extensive biological data on deep-sea communities, it is possible to use habitat suitability models to predict the likelihood of regions hosting particularly vulnerable taxa (Davies and Guinotte, 2011; Vierod *et al.*, 2014), derive risk indices to rank the threat of fishing (Clark and Tittensor 2010), and use biophysical variables as surrogates for biological assemblages (Anderson *et al.*, 2011). Such methods and techniques will always have their limitations given the paucity of hard data in the deep sea, but together with the application of planning software tools (such as Marxan (Ball and Possingham, 2000), Zonation (Moilanen, 2007)) these methods can give managers a potentially powerful array of information and scientific approaches on which to base improved management of the impacts of fishing in the deep sea.

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