

2002-03-07

Trawling damage to Northeast Atlantic ancient coral reefs

Hall-Spencer, JM

<http://hdl.handle.net/10026.1/1361>

10.1098/rspb.2001.1910

PROCEEDINGS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES

The Royal Society

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

Trawling damage to Northeast Atlantic ancient coral reefs

Jason Hall-Spencer^{1*}, Valerie Allain^{2†} and Jan Helge Fosså³

¹University Marine Biological Station, Millport, Isle of Cumbrae KA28 0EG, UK

²IUEM, Ressources halieutiques-Poissons marins, Pl. N. Copernic, Technopôle Brest-Iroise, 29280 Plouzané, France

³Institute of Marine Research, PO Box 1870 Nordnes, N-5817 Bergen, Norway

This contribution documents widespread trawling damage to cold-water coral reefs at 840–1300 m depth along the West Ireland continental shelf break and at 200 m off West Norway. These reefs are spectacular but poorly known. By-catches from commercial trawls for deep-water fish off West Ireland included large pieces (up to 1 m²) of coral that had been broken from reefs and a diverse array of coral-associated benthos. Five azooxanthellate scleractinian corals were identified in these by-catches, *viz.* *Desmophyllum cristagalli*, *Enallopsammia rostrata*, *Lophelia pertusa*, *Madrepora oculata* and *Solenosmilia variabilis*. Dating of carbonate skeletons using ¹⁴C accelerator mass spectrometry showed that the trawled coral matrix was at least 4550 years old. Surveys by remotely operated vehicles in Norway showed extensive fishing damage to *L. pertusa* reefs. The urgent need for deep-water coral conservation measures is discussed in a Northeast Atlantic context.

Keywords: deep-water coral; fishery impact; accelerator mass spectrometry radiocarbon dating; Northeast Atlantic

1. INTRODUCTION

In the late 1980s, large-scale fishing operations began to expand along the Northeast Atlantic continental shelf break as traditional stocks of shelf-dwelling species (e.g. cod) declined and markets were developed for deep-water species such as roundnose grenadier (*Coryphaenoides rupestris*), orange roughy (*Hoplostethus atlanticus*), black scabbard fish (*Aphanopus carbo*) and deep-sea sharks (leafscale gulper shark (*Centrophorus squamosus*) and Portuguese dogfish (*Centroscymnus coelolepis*)) (Allain 1999, 2001; Gordon 2001). Efforts to achieve sustainable exploitation of fisheries have led to major advances in our understanding of the effects of fishing on shallow marine ecosystems (Hall 1999; Kaiser & De Groot 2000) but the expense and difficulty of conducting research into resources along the upper bathyal margin means that impacts in this zone remain poorly known.

Although our knowledge of the effects of deep-sea fishing is in its infancy, photographic and acoustic surveys have recently located trawl marks at 200–1400 m depth all along the Northeast Atlantic shelf-break area from Ireland, Scotland and Norway (Rogers 1999; Fosså *et al.* 2000; Roberts *et al.* 2000). These trawl scars are up to 4 km long and characterized by parallel trenches where otter doors, rockhopper gear and nets have damaged epifauna, dragged rocks and turned-over sediment. Recent studies emphasize the need for improved management of offshore areas worldwide as there have been rapid declines in target fish stocks and widespread degradation of deep-water habitats by the fishing industry (Collie *et al.* 1997;

Probert *et al.* 1997; Watling & Norse 1998; Koslow *et al.* 2000, 2001).

The potential impact of towed demersal gear on European deep-water coral reefs has become a major concern (Rogers 1999; Duncan 2001). In 1999, the UK High Court ruled that the EC Habitats Directive (92/43/EEC), that covers reefs in Annex 1, applies to the UK continental shelf waters up to a limit of 200 nautical miles. However, the offshore deep-water reefs of all EU countries remain unprotected from current industrial fishing practices. Towed gear has had long-lasting detrimental effects on biogenic reefs in shallow European waters (Hall-Spencer & Moore 2000) and has caused extensive damage to deep-water coral reefs off Norway and Tasmania (Fosså *et al.* 2000; Koslow *et al.* 2000, 2001).

Deep-water corals occur worldwide and have been known by fishermen and benthic ecologists for centuries (Zibrowius 1980). However, these structures remain poorly studied and it is not until the last 5 years that video material from manned and unmanned submersibles has brought home to a wider audience just how large (≤13 km long) and spectacular these reefs can be (Freiwald *et al.* 1999; Havforskningsintitutet 2000). The sexual reproduction of deep-water corals remains unknown (Rogers 1999) and even basic information about the feeding and behaviour of these azooxanthellate corals is scarce (Mortensen 2001). There is concern over potential damage to deep-water coral reefs since they are built up over centuries to millennia (Freiwald *et al.* 1999; this study). Linear skeletal extension rates for individual *Lophelia pertusa*, one of the main North Atlantic species, range from 2 to 25 mm yr⁻¹ and slow down with increasing corallite age such that reef accumulation is extremely slow (Wilson 1979; Mortensen 2001).

As part of a study concerning the population dynamics of deep-water fish (Allain 1999), large pieces of coral were obtained aboard two French demersal trawlers working

* Author and address for correspondence: Institute of Biomedical Sciences, Department of Environmental and Evolutionary Biology, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK (gbfa20@udcf.gla.ac.uk).

† Present address: Secretariat of the Pacific Community, BP D5, 98848 Noumea Cedex, New Caledonia.

Table 1. Vertebrate catch from a coral-rich haul; trawl started on 24 March 1996 at 23.45 (54°4' N, 10°5' W, 1270 m) and ended on 25 March 1996 at 02.45 (1250 m).

common name	taxon	number	weight (kg)
roudnose grenadier ^a	<i>C. rupestris</i>	480	400
roundnose grenadier (small discards)	<i>C. rupestris</i>	902	407
orange roughy ^a	<i>H. atlanticus</i>	80	200
leafscale gulper shark ^a	<i>C. squamosus</i>	} 27	150
Portuguese dogfish ^a	<i>C. coelolepis</i>		
Baird's smooth-head	<i>Alepocephalus bairdii</i>	750	2400
North Atlantic codling	<i>Lepidion eques</i>	50	18
smalleyed rabbitfish	<i>Hydrolagus affinis</i>	37	16
spearnose chimaera	<i>Rhinochimaera atlantica</i>	4	24
roughnose grenadier	<i>Trachyrincus murrayi</i>	325	80
spearsnouted grenadier	<i>Caelorinchus labiatus</i>	125	31
dogfish sharks	Squalidae	216	351
Risso's smooth-head	<i>Alepocephalus rostratus</i>	6	—
pallid sculpin	<i>Cottunculus thomsonii</i>	2	—
pudgy cuskeel	<i>Spectrunculus grandis</i>	1	—

^a Species landed commercially.

along the continental shelf break west of Ireland between 1995 and 1997. Some of these corals were returned to the laboratory for analysis; our aims were to identify the Scleractinaria caught as by-catch and to age this material using accelerator mass spectrometry radiocarbon techniques. In addition, we illustrate trawling impacts on *L. pertusa* reefs recently surveyed by remotely operated vehicles (ROVs) in the shelf waters off western Norway.

2. MATERIAL AND METHODS

(a) Fishing by-catch

Commercial catches were analysed aboard two French trawlers (both 38 m, 883 kW) on eight quarterly trips between December 1995 and August 1997. These trawlers were typical of the fleet currently fishing the West Ireland continental shelf-break area. Both boats had trawls fitted with rockhopper gear and two 900 kg otter boards. The trawls were towed at 4.5–5.5 km h⁻¹, with the otter boards set ca. 22 m apart. On these trips, the gear was worked for ca. 4 h per haul, sweeping about 0.5 km² per haul. There were four to five hauls every 24 h and on each trip the gear was worked for ca. 15 days before returning the catch to port. The fishermen targeted sedimentary areas on the upper part of the continental slope (840–1300 m) and avoided areas with steep or rough terrain. Catches were analysed from five fishing areas: Pointe 49 (47–49° N, 8–11° W); Porcupine Seabight (50–52° N, 10°30'–14° W); West Porcupine Bank (50–53°40' N, 14–15°45' W); Rockall Trough (53°40'–56° N, 9–14°40' W); and the Hebridean Terrace (56–59° N, 7°30'–10° W) (see Allain (2001) for details). Catches (landings and discards) were examined in detail from 55 hauls. Unusual by-catches (corals, large amount of sponges, rocks) were noted from a total of 229 hauls.

Scleractinian corals were collected from the hauls as the commercial catch was sorted on deck. Notes were made regarding the by-catch composition and the coral samples were then photographed and identified based on external morphology, with reference to Zibrowius (1980). Six large (more than 80 cm²) coral concretions were selected for radiocarbon analysis,

each of these lumps being a mixture of dead coral matrix with live scleractinian polyps on their upper surfaces.

(b) Radiocarbon dating

Samples were washed in distilled water and a sonicator was used to loosen compacted sediment from subfossil material. Contaminants (e.g. stones, shells, foraminiferan tests, echinoderm spines) were removed then the specimens were air dried. The corals were sectioned along the line of colony growth using a geologist's diamond saw and dissected using a Dremmel modelling drill. Skeletal carbonate was removed from the tip of a *L. pertusa* corallite that had been living at the time of collection (radiocarbon publication code AA39673) to investigate incorporation of ¹⁴C from nuclear-bomb tests and other anthropogenic sources since the 1950s. Dead *L. pertusa* material was obtained from the basal region of the same colony (AA39672). Dead material was analysed from the central basal regions of three other trawled scleractinians together with two large concretions (25 and 35 cm²) of *Desmophyllum cristagalli*. These coral fragments were stored in a desiccator prior to submission to the Natural Environment Research Council Radiocarbon Laboratory (East Kilbride, Scotland) where they were acid etched (25% of the sample was dissolved using hydrochloric acid to remove potential contaminants) and prepared to graphite. Stable isotope ($\delta^{13}\text{C}$) and ¹⁴C/¹²C enrichment was measured at the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, University of California.

(c) Seabed video

To investigate the effects of commercial trawling on the benthos of deep-water coral reefs, an 'Aglantha' ROV was used in May 1999 to survey two known *Lophelia* reefs at a depth of 200 m in West Norway (Fosså *et al.* 2000). The first site was in the Iverryggen area (65°00.0' N, 09°20.0' E) that had been intensely trawled for redfish (mostly *Sebastes marinus*) and saithe (*Pollachius virens*) during the 1990s. The second site was an unimpacted coral reef near the island of Nordleksa at the entrance to Trondheimsfjorden (63°36.4' N, 09°22.8' E) where no commercial trawling had taken place.

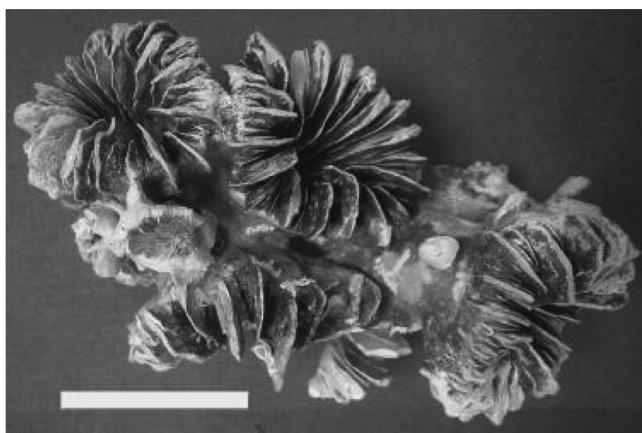


Figure 1. Dead *D. cristagalli*, one of five species of scleractinian azooxanthellate coral trawled from West Ireland at depths of 840–1300 m, between December 1995 and August 1997. Black staining caused by metal salt deposits. Scale bar, 4 cm.

3. RESULTS

(a) Fishing by-catch

On board, by-catch analysis revealed that commercial otter trawling with rockhopper gear damaged coral habitats along the West Ireland continental shelf-break area. However, the skippers of the fishing vessels actively avoided uneven ground and out of 229 trawls observed, only five were notable for large amounts of coral by-catch. This resulted in poorer catch quality and damage to the nets that had to be repaired before the gear was reused. The loss of time and the extra work involved meant that areas with abundant coral by-catch were avoided on future hauls. Table 1 lists the vertebrate catch from a haul taken in the Rockall Trough that was noted for coral by-catch. The dead portions of the by-catch corals provided substratum for a diverse array of sessile suspension feeders (including sponges, gorgonians, hydroids, anemones, serpulids, barnacles, bivalves, bryozoans, brachiopods, crinoids and tunicates). The complex three-dimensional architecture of the calcareous coral matrix trapped sediment and harboured various cryptic species such as worms (nemertines, polychaetes), crustaceans (isopods, amphipods, brachyurans), molluscs (bivalves, gastropods) and echinoderms (echinoids, ophiuroids and asteroids).

Figure 1 shows part of a coral fragment that was radiocarbon dated from the trawls. This piece was typical of the trawled coral material with freshly broken, clean, sharp fractures showing points of attachment to the underlying carbonate reef. There are no quantitative data on coral by-catch but pieces up to *ca.* 1 m² were landed on deck. Much of the trawled coral matrix was dead *L. pertusa* or *D. cristagalli* with black staining caused by metal salts (figure 1). These dead corals were often encrusted with the calcareous remains of large gorgonian (Isididae) stems and overgrown by other live corals such as the matrix-forming colonial hard coral *Solenosmilia variabilis*. Five species of azooxanthellate coral contributed to complex carbonate concretions collected in by-catch from along the West Ireland shelf-break area (table 2).

(b) Radiocarbon dating

Analysis of carbonate from the corallite of a live *L. pertusa* coral tip had a low percentage of modern ¹⁴C

enrichment (values of more than 100% reflect the influence of bomb ¹⁴C in shallow waters of the British Isles (Cook *et al.* 1998)). This material had a radiocarbon age of 451 ± 36 years BP (Before Present, meaning before AD 1950) providing an indication of the ‘marine reservoir effect’ for this area (see § 4). The *L. pertusa* fragment was 340 mm long with a basal region that was 311 radiocarbon years older than the live corallite. This indicates a mean extension rate of 1.1 mm yr⁻¹; a minimum rate as the colony could have been eroded or may have died and been recolonized. Dead portions of two clumps of *D. cristagalli* had the oldest radiocarbon ages of *ca.* 4067 and 5001 ¹⁴C years BP (table 2). The other coral species (*S. variabilis*, *Enallopsammia rostrata*, *Madrepora oculata*) grew attached to dead clumps of *L. pertusa* and *D. cristagalli*. The dead bases of these attached corals were younger than the *D. cristagalli*, with radiocarbon ages in the region of 637–750 years BP.

(c) Seabed video

Remotely operated vehicle surveys of unfished and heavily trawled *Lophelia* reefs in West Norway revealed clear differences in the appearance of the benthos. The trawled area of Iverryggen had sparse living *L. pertusa* colonies that were often broken, dislodged and sometimes buried in mud. Coral rubble littered the whole area and scrape marks on the sediment surface showed where boulders and coral had been dragged along the seabed by trawl gear. Trenches (5–10 cm deep) had been left by otter boards, providing unmistakable evidence of trawling activity (figure 2). This contrasted starkly with the area at Nordleksa (figure 3) that had no trawl scars. Instead there were prominent expanses of erect, live *L. pertusa* reefs. The untrawled habitat had a greater relief and three-dimensional complexity than the trawled reef and more sessile filter-feeding macrofauna such as large *Mycale* sponges.

4. DISCUSSION

In the sea, the slow mixing of water masses of different ages results in an overall deficiency and marked spatial variation in natural ¹⁴C concentration known as the ‘marine reservoir effect’ that can give an ‘apparent age’ range from *ca.* 200 years to more than 2000 years older for marine organisms, depending upon the influence of upwelling deep water (Harkness 1983). Therefore, for chronological interpretation a geographically dependent correction factor is needed. Isotopic analysis of 19th century shell samples from throughout the British Isles indicates that an ‘apparent age’ correction of 405 ± 40 years must be subtracted in the interpretation of conventional radiocarbon ages measured for samples of shallow-water marine origin (Harkness 1983). This is in close agreement with the 430 ± 20 years value calculated by Mangerud & Gulliksen (1975) for shell samples collected from Norwegian waters south of 62° N. No study has been made of the marine reservoir effect in the deep waters off West Ireland, but our live coral tip from the Rockall Trough had an ‘apparent’ radiocarbon age of 451 ± 36 years BP. In the 1950s, nuclear-weapons testing resulted in a global increase in atmospheric ¹⁴C that has been dissolving in surface seawater, and becoming incorporated into marine

Table 2. Summary details for radiocarbon analyses of by-catch coral samples collected from West Ireland from depths of 840–1300 m between December 1995 and August 1997.

sample code	taxon	live/dead	enrichment (% modern ^{14}C)	$\delta^{13}\text{C}$	^{14}C years BP
AA-39673	<i>Lophelia pertusa</i>	live	94.54 ± 0.44	-0.3 ± 0.1	451 ± 36
AA-39672	<i>L. pertusa</i>	dead	90.96 ± 0.49	-1.3 ± 0.1	762 ± 42
AA-39669	<i>Solenosmilia variabilis</i>	dead	92.38 ± 0.45	-7.7 ± 0.1	637 ± 39
AA-39670	<i>Enallopsammia rostrata</i>	dead	92.21 ± 0.43	-4.1 ± 0.1	651 ± 37
AA-39671	<i>Madrepora oculata</i>	dead	91.08 ± 0.58	-2.9 ± 0.1	750 ± 50
AA-39674	<i>Desmophyllum cristagalli</i>	dead	60.27 ± 0.36	-4.6 ± 0.1	4067 ± 47
AA-39668	<i>D. cristagalli</i>	dead	53.66 ± 0.34	-5.2 ± 0.1	5001 ± 50



Figure 2. Trawled *L. pertusa* grounds at a depth of 200 m in the Iverryggen area, West Norway, May 1999. Smashed coral fragments litter the sediment around a clear trench from towed fishing gear (arrow). Lower edge of photograph *ca.* 1.5 m.

organisms, ever since. For example, anthropogenic ^{14}C enrichment is clearly evident in *L. pertusa* from 300 m in Trondheimfjord, West Norway (Mikkelsen *et al.* 1982). Other sources of anthropogenic ^{14}C , such as from the Selafeld nuclear fuel reprocessing plant, have also entered organisms in shallow waters around the Northeast Atlantic (Cook *et al.* 1998). The low-percentage modern ^{14}C for live *L. pertusa* from the West Ireland continental shelf break indicates negligible contamination by anthropogenic ^{14}C . This suggests that radiocarbon levels in these corals were influenced by waters that had not been in contact with the ocean surface since the 1950s. This ties in with oceanographic data that reveal the influence of older waters below 1000 m on the West Ireland continental shelf break (New & Smythe-Wright 2001). We estimate that the concretions of *D. cristagalli* that had been broken from the reef by trawling were at least 4550 years old. This evidence adds to mounting international concern over the unprotected fate of these deep-water coral habitats (Rogers 1999; Duncan 2001; Koslow *et al.* 2001).

Over the past 20 years there has been intensive survey work along the Norwegian and Scottish shelf areas due to commercial interests in oil and gas deposits. We now know that *L. pertusa*, that was first described from the coast of Norway (Linnaeus 1758), is the main reef-forming species in the area and often occurs with *M. oculata* to form patch reefs all along the shelf and shelf-break area (Wilson 1979; Hovland & Mortensen 1999). Our video surveys of deep-water reefs in the Iverryggen and Nord-

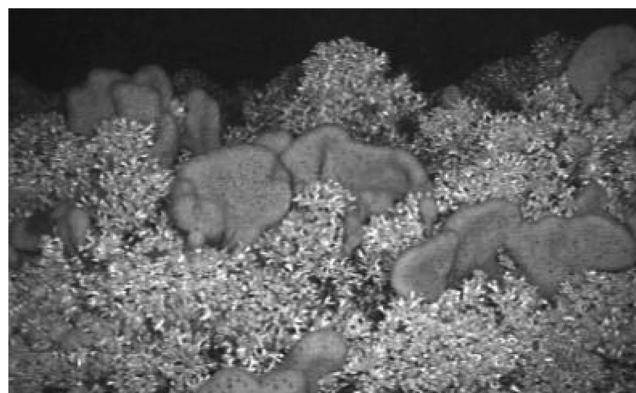


Figure 3. Untrawled *L. pertusa* interspersed with *Mycale* sponges standing erect to form a prominent reef at 200 m, Nordleksa, West Norway, May 1999. Lower edge of photograph *ca.* 2.5 m.

leksa areas of West Norway show that these deep-water coral systems are especially fragile and easily reduced to rubble by towed fishing gear. This contrasts with exposed shallow-reef systems where wave action favours corals with sturdy, compact growth forms and there is sufficient light for calcareous coralline algae to consolidate and strengthen the reef structure.

Coral by-catches from West Ireland had more diverse coral assemblages than those encountered in Norway. *L. pertusa* and *M. oculata* were common, as expected from previous reports from the area (Zibrowius 1980; Hovland *et al.* 1994), but *S. variabilis*, *E. rostrata* and *D. cristagalli* were also widespread. In addition, a bathyal solitary coral of the genus *Stephanocyathus* was obtained from French commercial trawls working in the Porcupine Seabight in 1999 (J. M. Roberts, personal communication). Thus the reefs off West Ireland are ancient, having been in place for at least the last 4.5 millennia. We know very little about the ecology of these habitats, but they appear to have a more diverse coral assemblage than has been reported further north, in the colder Norwegian waters (e.g. Hovland & Mortensen 1999). The Wyville-Thompson Ridge, which separates the warmer deep Atlantic waters from the much colder Norwegian Sea water, is responsible for a major faunal division on the Atlantic Frontier (Gordon 2001) that may explain the relative paucity of scleractinian coral species off Norway.

Realization of the extent of damage to deep-water corals off Tasmania (Koslow *et al.* 2001) and Norway (Fosså *et*

al. 2000) met with a rapid response from national governments. In Norway, for example, fishers first warned of widespread reef damage by trawlers in 1994, leading to ROV surveys and then areal closures to prevent long-term ecological damage to selected coral reefs in 1999. Our findings emphasize that conservation areas are urgently needed to protect coral reefs within the Exclusive Economic Zone of EU waters, following the example set by Norway and Australia. On typical 15 day trips, otter trawlers currently sweep ca. 33 km² of continental shelf-break habitat. Although the fishers try to avoid dense coral reefs, collateral damage does occur. Areas where corals are known to be at risk of damage, such as Northwest Rockall and the recently described 'Darwin Mounds' in the Northeast Rockall Trough, should be afforded legislative protection as soon as possible (Duncan 2001). Managing such areas to minimize environmental damage will be more straightforward now that there is an agreement between EU member states, the Faroes, Iceland, Greenland, Russia and Norway to satellite track all vessels more than 24 m in length (Article 3, Regulation (EEC) 2847/93).

The authors' sincere thanks go to H. Zibrowius for helping with the coral identifications and to M. Roberts for helpful discussions aboard RV *Johan Hjort*. Thanks also to the crews and owners of the fishing vessels for their hospitality and cooperation. This work was carried out with financial support from the Natural Environment Research Council (small grant no. GR9/4089) and a Royal Society Fellowship to J.H.-S.

REFERENCES

- Allain, V. 1999 *Écologie, biologie et exploitation des populations de poissons profonds de l'Atlantique du nord-est*. PhD thesis, Université de Bretagne Occidentale, France.
- Allain, V. 2001 Reproductive strategies of three deep-water benthopelagic fishes from the northeast Atlantic Ocean. *Fisheries Res.* **51**, 165–176.
- Collie, J. S., Escanero, G. A. & Valentine, P. C. 1997 Effects of bottom fishing on the benthic megafauna of Georges Bank. *Mar. Ecol. Prog. Ser.* **155**, 159–172.
- Cook, G. T., MacKenzie, A. B., Naysmith, P. & Anderson, R. 1998 Natural and anthropogenic ¹⁴C in the UK coastal marine environment. *J. Environ. Radioact.* **40**, 89–111.
- Duncan, C. 2001 Offshore marine conservation, 'Darwin Mounds' and beyond. *Mar. Conserv.* **5**, 14–15.
- Fosså, J. H., Mortensen, P. B. & Furevik, D. M. 2000 *Lophelia*-korallrev langs norskekysten forekomst og tilstand. *Fisken Havet* **2**, 1–94.
- Freiwald, A., Wilson, J. B. & Henrich, R. 1999 Grounding Pleistocene icebergs shape recent deep-water coral reefs. *Sediment. Geol.* **125**, 1–8.
- Gordon, J. D. M. 2001 Deep-water fisheries at the Atlantic Frontier. *Continental Shelf Res.* **21**, 987–1003.
- Hall, S. J. 1999 *The effects of fishing on marine ecosystems and communities*. Oxford: Blackwell Science.
- Hall-Spencer, J. M. & Moore, P. G. 2000 Scallop dredging has profound long-term impacts on maerl beds. *ICES J. Mar. Sci.* **57**, 1407–1415.
- Harkness, D. D. 1983 The extent of natural ¹⁴C deficiency in the coastal environment of the United Kingdom. *PACT* **8**, 351–364.
- Havforskningsintitutet (Institute of Marine Research) 2000. *Norwegian coral reefs*. Video. Bergen: Havforskningsintitutet.
- Hovland, M. & Mortensen, P. B. 1999 *Norske korallrev og prosesser i havbunnen*. Bergen: John Greig forlag.
- Hovland, M., Croker, P. F. & Martin, M. 1994 Fault-associated seabed mounds (carbonate knolls?) off western Ireland and north-west Australia. *Mar. Petrol. Geol.* **11**, 233–246.
- Kaiser, M. J. & De Groot, S. F. (eds) 2000 *Effects of fishing on non-target species and habitats, biological, conservation and socio-economic issues*. Oxford: Blackwell Science.
- Koslow, J. A., Boehlert, G. W., Gordon, J. D. M., Haedrich, R. L., Lorange, P. & Parin, N. 2000 Continental slope and deep-sea fisheries: implication for a fragile ecosystem. *ICES J. Mar. Sci.* **57**, 548–557.
- Koslow, J. A., Gowlett-Holmes, K., Lowry, J. K., O'Hara, T., Poore, G. C. B. & Williams, A. 2001 Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. *Mar. Ecol. Prog. Ser.* **213**, 111–125.
- Linnaeus, C. 1758 *Systema naturae*, 10th edn, vol. 1. Stockholm: L. Salvii.
- Mangerud, J. & Gulliksen, S. 1975 Apparent radiocarbon age of recent marine shells from Norway, Spitsbergen and Arctic Canada. *Quat. Res.* **5**, 263–273.
- Mikkelsen, N., Erlenkeuser, H., Killingley, J. S. & Berger, W. H. 1982 Norwegian corals: radiocarbon and stable isotopes in *Lophelia pertusa*. *Boreas* **11**, 163–171.
- Mortensen, P. B. 2001 Aquarium observations on the deep-water coral *Lophelia pertusa* (L., 1758) (Scleractinaria) and selected associated invertebrates. *Ophelia* **54**, 83–104.
- New, A. L. & Smythe-Wright, D. 2001 Aspects of the circulation in the Rockall Trough. *Continental Shelf Res.* **21**, 777–810.
- Probert, P. K., McKnight, D. G. & Grove, S. L. 1997 Benthic invertebrate by catch from a deep-water trawl fishery, Chatham Rise, New Zealand. *Aquat. Conserv. Mar. Freshwater Ecosystems* **7**, 27–40.
- Roberts, J. M., Harvey, S. M., Lamont, P. A. & Gage, J. D. 2000 Seabed photography, environmental assessment and evidence for deep-water trawling on the continental margin west of the Hebrides. *Hydrobiologia* **44**, 173–183.
- Rogers, A. D. 1999 The biology of *Lophelia pertusa* (Linnaeus, 1758) and other deep-water reef-forming corals and impacts from human activities. *Int. Rev. Hydrobiol.* **84**, 315–406.
- Watling, L. & Norse, E. A. 1998 Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. *Conserv. Biol.* **12**, 1180–1197.
- Wilson, J. B. 1979 'Patch' development of the deep-water coral *Lophelia pertusa* (L.) on Rockall bank. *J. Mar. Biol. Assoc. UK* **59**, 165–177.
- Zibrowius, H. 1980 Les scléactiniaires de la Méditerranée et de l'Atlantique nord-oriental. *Mem. Inst. Oceanogr.* **11**, 1–227.