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Discard composition of the *Nephrops* fishery in the Clyde Sea area, Scotland

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Abstract

Demersal fishing gear such as otter-trawls generate large amounts of unwanted by-catch. The Norway lobster (*Nephrops norvegicus*) is the most important shellfish resource in UK waters and although the fishing effort has increased considerably over past decades the ecosystem effects of this fishery have yet to be evaluated. This study provides the first assessment of the catch and discard composition from *Nephrops* trawls in the Clyde Sea area with particular emphasis on invertebrate discards. *Nephrops* constituted only between 14 and 23% of the total catch (volume); other invertebrates and fish accounted for the remainder of the catch. On an average, 9 kg of discards were produced per kilogram of *Nephrops*. The catch composition differed markedly between samples from the north and south Clyde Sea areas. Trawls from the south yielded a significantly higher biomass of *Nephrops* (30% cf. 4% in the north) and fish discards (55% cf. 36% in the north) whereas catches from the north contained more invertebrates (60% cf. 15% in the south). Crustaceans and echinoderms accounted for up to 83 and 73% of the discards, respectively. Samples from the north also contained a greater variety of invertebrate species (93 taxa cf. 51 taxa in the south). The differences between the two study areas are likely to be a reflection of differing bathymetries, hydrographic conditions and ground types in each area.

Keywords: By-catch; Clyde Sea area; Discards; Invertebrates; *Nephrops norvegicus*; Trawling

1. Introduction

Commercial fishing has been estimated to produce 27 million tons of discards per year, equivalent to 25% the weight of the reported marine landings world-wide (Alverson et al., 1994). Discards are by-catch organisms that are returned to the sea because, for various reasons, they are considered undesirable; either they are unmarketable species, are below minimum landing size (MLS), are of inferior quality or surplus to quota. The biological, conservation and socio-economic issues related to discarding practices have recently received increasing attention (Jennings and Kaiser, 1998; Hall, 1999; Kaiser and de Groot, 2000; Moore and Jennings, 2000) with a view to finding ways to reduce such wastage of resources.

The highest rates of discarding have been attributed to shrimp trawl fisheries, with an estimate of 9.5 million tons per year (Alverson et al., 1994). The Norway lobster or prawn, *Nephrops norvegicus* (L.) (hereafter referred to by genus alone) is one of the most valuable commercial shellfish resources in European waters. Annual official landings are around 60 000 t worldwide, a third of which is landed in Scotland, being worth over 72 million EURO at first-sale value. The

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NE Atlantic *Nephrops* trawl fishery ranks as number eight among the top 20 fisheries with the highest recorded discard ratios and as number five when ordered by gear type. However, when examining the FAO report (Alverson et al., 1994) as well as the studies that it is based upon, it appears that the main emphasis is on discarded commercial fish or shellfish species. Non-target species of high public appeal such as marine mammals, turtles and sharks have helped to raise the public awareness of non-commercial discards. However, it has only been in recent years that the significance of the less charismatic invertebrate and non-commercial fish discards has been addressed.

Nephrops excavate burrows in soft substrata at depths between 14 and 200 m and are mainly fished by otter-trawling. In the Clyde Sea area, *Nephrops* trawls (mesh size $\geq$70 mm for single-rigged trawlers, and $\geq$80 mm for multirigged *Nephrops* trawlers) disturb wide areas of the seabed and benthic fauna as weighted ground lines and heavy otter doors are dragged across the sediment. The Clyde Sea area represents one of the main grounds of the Scottish prawn fishery with estimated landings currently of some 4000 tons per year (N. Bailey, pers. comm.). Between 1998 and 1999, almost 70% of the area (assessed as pixels) was trawled more than once by just 20% of the whole fishing fleet (Dr Sue Marrs,[1] in press). Trawling for *Nephrops* is restricted to vessels of lengths <22 m, and fishing is prohibited at weekends. These restrictions, along with technical measures (e.g. fitting of an 80 mm square mesh panel into the top sheet of the cod-end or the extension of a net to allow the escape of juvenile gadoids; see Briggs, 1992), and a quota system are thought to help to reduce by-catch. The MLS for *Nephrops* is currently 20 mm carapace length and landing of fish by-catch of regulated species (i.e. those with a MLS) is restricted to $\leq$60% by weight of the total catch and *Nephrops* must exceed 30% of the catch. Such measures notwithstanding, the proportion of material discarded still often accounts for 50–90% of the total catch (Edwards and Bennett, 1980; Evans et al., 1994).

The (by-)catch composition from the *Nephrops* fishery in the Irish Sea and the Farn Deeps (North Sea) have been described by Briggs (1985), Evans et al. (1994) and Craeymeersch (1994), but in these studies, emphasis was mainly on undersized *Nephrops* and commercial fish species. The discarded material in the Clyde Sea area consists primarily of invertebrates (including undersized *Nephrops* and *Nephrops* 'heads') but includes small round- and flatfish. Small *Nephrops* have their 'tails'(abdomen) removed at sea (scampi), and the unwanted 'head' (cephalothorax) is subsequently discarded.

Owing to sedimentological and hydrographic differences, *Nephrops* populations (in most years), as well as associated benthic fauna of the northern and southern parts of the Clyde Sea area, are quite distinct. In general, *Nephrops* burrow density is higher in the south, whereas the average size of prawns is usually larger in the north Clyde Sea area (Tuck et al., 1997).

The present study provides the first assessment of the catch and discard composition from *Nephrops* trawls in the north and south Clyde Sea area with particular emphasis on invertebrate discards.

2. Material and methods

To compare trawl samples taken within the north and south Clyde Sea areas, the area was divided into two sectors north and south of an arbitrary line drawn between Troon (ca. 55°33′N and 4°40′W) and the northern tip of Holy Island (ca. 55°32′N and 5°04′W) (Fig. 1).

Monthly survey trips were undertaken on three local commercial *Nephrops* trawlers and RV *Aora* between October 1997 and October 1998. For logistic reasons, the more distant south Clyde Sea area could only be sampled quarterly. Position, tow duration, average trawling depth, towing speed, fishing gear used and total catch volume were recorded for each tow (Table 1). It was attempted to sample three tows on each trip. Upon hauling, the whole catch was shovelled into standard fish baskets (44 l) to estimate total catch volume. While the catch was sorted, a subsample was taken randomly by periodically filling one basket with discards from the sorting table. After sorting of the catch, the marketable fraction of the catch was weighed and measured in baskets and the

[1] Marrs, S.J., Tuck, I.D., Atkinson, R.J.A., Stevenson, T.D.I., Hall, C., 2002. Position of data loggers and logbooks as tools in fisheries research: results of a pilot study and some recommendations. Fish. Res., in press.

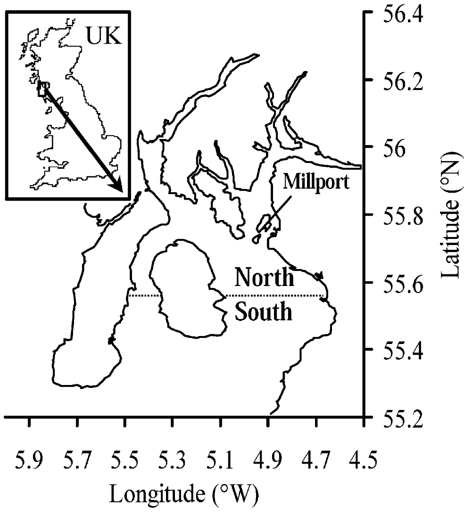

Fig. 1. North and south Clyde Sea areas.

catch composition determined by subtracting the marketable proportion from the total catch volume. Where possible, the taxonomic composition of the sub-samples was determined to species in terms of abundance and biomass (wet weight) on return to the laboratory.

The fishing gear used varied between trawlers:

- RV *Aora* (15 m, 194 KW, 49 t) usually operated a commercial 'rock hopper' otter-trawl with 70 mm diamond-shaped mesh, reflecting local fishing practice. Rock hopper nets have a series of large rubber bobbins (ca. 25 cm in diameter) attached to the groundrope to help to prevent the net snagging and becoming damaged on harder grounds. When fishing in the south Clyde Sea area, RV *Aora* trawled with a 'clean' net similar to that used by FV *Andrias* (see below).
- FV *Red Baron* (12 m, 82 kW, 19 t) used a standard commercial 'rock hopper' otter-trawl with a 70 mm diamond-shaped mesh fitted with a square mesh panel in the cod-end when trawling in the north Clyde Sea area. In May 1998, this vessel used a clean net with a tickler chain similar to that described below, as the 'rock hopper' net became snagged.
- FV *Andrias* (17 m, 149 kW, 33 t) operated in the south Clyde Sea area on softer grounds which necessitated the use of a 'clean' net (mesh size 70 mm). The groundrope of this dual-purpose net had small discs (ca. 6 cm in diameter) and a series of tickler chains attached to it, causing it to dig into the top sediment layer.
- FV *Tricia Anne* (14 m, 261 kW, 22 t) operated a twin-rigged net, comprising two nets rigged together with a 225 kg weight between them to hold the mouths of the nets open. The two nets were 'rock hopper' otter-trawls with 80 mm diamond-shaped mesh, fitted with a square mesh panel in the cod-end and pieces of chain were wound into the groundrope.

Comparisons between total catch weight, discard weight, and the weights of fish and *Nephrops* landed from the north and south Clyde Sea areas were done by fitting general linear models (GLM) to data using MINITAB software. All weights were wet weights and all percentage data were arcsine transformed prior to analysis. Other data transformations, such as $\sqrt{(x+1)}$, and $\log_{10}(x+1)$ were undertaken to meet the criteria for analysis of variance (ANOVA), where the analysis involved data means. The significance level for all tests was $P \leq 0.05$.

Following identification of species, the abundance and biomass of groups such as echinoderms and fish was calculated and after $\log_{10}$ transformation samples from the north were compared with samples from the south by ANOVA. The taxonomic composition of the discard sub-samples was assessed by multivariate analysis using the PRIMER software package (Clarke and Warwick, 1994). All species abundance and biomass data were fourth root transformed to counteract the effect of extremely abundant or high biomass groups and taxa that occurred in <10% of the samples were eliminated. Similarities were calculated between every pair of samples resulting in a triangular similarity matrix based on the Bray–Curtis coefficient of similarity. This enabled the classification of the data into groups of ranked similar entities. Cluster analysis was undertaken by linking the samples in hierarchical groups on the basis of the similarity between each cluster in a dendrogram. Multidimensional scaling (MDS) ordination was carried out to examine gradation trends in space and/or time without defining hierarchical groups. MDS techniques attempt to plot samples on a 'map' in two dimensions so that the rank order of the distances between samples on the map reflects the rank order of the matching similarities

Table 1
Description of hauls used for the analysis of catch composition: (Aa) RV *Aora*; (RB) FV *Red Baron*; (As) FV *Andrias*; (TA) FV *Tricia Anne*; (CN) clean net; (RH) rock hopper; (twRH) twin rock hopper; (S) south Clyde and (N) north Clyde Sea area; total catch was measured in baskets (44 l) and expressed as catch per hour fishing; discards are given as % of the total catch; (n.a.) not available

Date	Vessel	Depth (m)	Net	Tow time (min)	Area	Latitude (N)	Longitude (W)	Total catch	Catch (h^{-1})	Discards (%)	Haul
30 October 1997	As	94	CN	250	S	n.a.	n.a.	20.25	4.9	74	a11
30 October 1997	As	75	CN	185	S	55°25′	5°00′	20.4	6.6	77	a12
30 October 1997	As	53	CN	160	S	55°23′	5°01′	15.08	5.7	73	a13
12 November 1997	Aa	92	RH	80	N	55°41′	5°00′	11.5	8.6	85	A11
12 November 1997	Aa	83	RH	109	N	55°46′	4°58′	8.125	4.5	88	A12
12 November 1997	Aa	73	RH	97	N	55°51′	4°54′	6.5	4.0	98	A13
25 November 1997	RB	51	RH	145	N	55°46′	4°57′	n.a.	n.a.	n.a.	R11
25 November 1997	RB	51	RH	70	N	55°45′	4°57′	n.a.	n.a.	n.a.	R12
25 November 1997	RB	42	RH	152	N	55°45′	4°57′	16	6.3	87	R13
2 December 1997	Aa	54	CN	205	S	55°15′	5°13′	6	1.8	63	s11
3 December 1997	Aa	56	CN	180	S	55°13′	5°13′	8	2.7	49	s12
15 December 1997	Aa	82	RH	120	N	55°41′	4°57′	13	6.5	58	A21
15 December 1997	Aa	81	RH	120	N	55°41′	4°59′	10	5.0	88	A22
14 January 1998	Aa	80	RH	120	N	55°41′	4°57′	11.2	5.6	46	A31
14 January 1998	Aa	87	RH	120	N	55°41′	4°59′	8.5	4.3	85	A32
20 January 1998	As	45	CN	190	S	55°10′	5°04′	14.8	4.7	62	a21
20 January 1998	As	38	CN	200	S	55°09′	5°01′	16	4.8	56	a22
20 January 1998	As	39	CN	155	S	55°08′	5°04′	10.5	4.1	47	a23
3 February 1998	RB	36	RH	67	N	55°44′	4°55′	9	8.1	83	R21
3 February 1998	RB	102	RH	170	N	55°43′	4°59′	8	2.8	70	R22
3 February 1998	RB	74	RH	125	N	55°43′	4°58′	19	9.1	93	R23
23 February 1998	Aa	77	RH	62	N	55°46′	4°58′	4.5	4.4	61	A41
23 February 1998	Aa	83	RH	120	N	55°48′	4°58′	7	3.5	68	A42
1 March 1998	RB	54	RH	120	N	55°46′	4°53′	13.5	6.8	93	R31
1 March 1998	RB	71	RH	150	N	55°51′	4°52′	11.75	4.7	81	R32
1 March 1998	RB	52	RH	155	N	55°52′	4°54′	12	4.6	88	R33
1 April 1998	RB	56	RH	180	N	55°45′	4°58′	11	3.7	87	R41
1 April 1998	RB	89	RH	270	N	55°45′	4°58′	10	2.2	81	R42
1 April 1998	RB	66	RH	230	N	55°42′	4°59′	11	2.9	77	R43
14 April 1998	Aa	52	CN	179	S	55°20′	5°20′	10	3.4	n.a.	s21
15 April 1998	Aa	55	CN	240	S	55°20′	5°19′	9	2.3	n.a.	s22
15 April 1998	Aa	52	CN	240	S	55°19′	5°19′	4.75	1.2	n.a.	s23
21 April 1998	RB	50	CN	180	S	55°14′	5°01′	28	9.3	86	r11
11 May 1998	RB	56	RH	162	N	55°45′	4°57′	11.66	4.3	91	R51
11 May 1998	RB	78	CN	210	N	55°41′	4°56′	14.33	4.1	87	R52
11 May 1998	RB	65	CN	198	N	55°39′	4°56′	21.5	6.5	88	R53
9 June 1998	RB	44	RH	160	N	55°45′	4°57′	18	6.8	81	R61
9 June 1998	RB	44	RH	162	N	55°47′	4°57′	16.33	6.0	83	R62
9 June 1998	RB	46	RH	145	N	55°44′	4°58′	10	4.1	82	R63
10 July 1998	As	45	CN	235	S	55°09′	5°02′	32	8.2	84	a31
10 July 1998	As	87	CN	137	S	55°03′	5°11′	18	7.9	78	a32
14 July 1998	Aa	n.a.	CN	n.a.	S	n.a.	n.a.	7.75	n.a.	79	s31
20 July 1998	RB	44	RH	127	N	55°46′	4°57′	13	6.1	85	R71
20 July 1998	RB	64	RH	117	N	55°48′	4°53′	16	8.2	90	R72
5 August 1998	TA	45	twRH	145	N	55°49′	5°00′	28	11.6	79	T11
5 August 1998	TA	96	twRH	125	N	55°44′	4°59′	24	11.5	69	T12
5 August 1998	TA	96	twRH	130	N	55°40′	4°58′	21	9.7	70	T13
11 August 1998	Aa	n.a.	RH	180	N	n.a.	n.a.	9	3.0	61	A51
2 September 1998	RB	49	RH	145	N	55°45′	4°57′	16	6.6	92	R81
2 September 1998	RB	65	RH	100	N	55°47′	4°53	15.5	9.3	91	R82

Table 1 (*Continued*)

Date	Vessel	Depth (m)	Net	Tow time (min)	Area	Latitude (N)	Longitude (W)	Total catch	Catch (h^{-1})	Discards (%)	Haul
2 September 1998	RB	59	RH	135	N	55°48′	4°54′	15	6.7	87	R83
29 September 1998	Aa	77	RH	91	N	55°41′	4°56′	8.33	5.5	72	A61
30 September 1998	Aa	92	RH	90	N	55°42	4°58	10	6.7	94	A71
6 October 1998	RB	65	RH	255	N	55°41	4°55	15.5	3.6	82	R91

taken from the similarity matrix. A stress coefficient indicates the fit of the graphic representation similar to R^2 in regression analyses. Variables such as depth, net type, haul duration and sorting time were linked to the discard composition by superimposing the values of the variables on the MDS configuration. The contribution of individual species to the Bray–Curtis similarity was analysed using SIMPER (Clarke and Warwick, 1994).

3. Results

The catch composition of *Nephrops* trawls ($n = 54$) in the Clyde Sea area was characterised by a large proportion of discards. Fig. 2 illustrates a typical catch from the north Clyde Sea area. A comparison of samples from the north and south Clyde Sea areas revealed significant differences in the composition of both the total catch and the discarded material. All hauls used in the analysis of the catch composition are described in Table 1 and species identified in the trawls from the two sample areas are listed in Table 2. Species of commercial importance were discarded because they were below the MLS of inferior quality or surplus to quota.

The total catch compositions of north and south Clyde Sea *Nephrops* trawls were found to be very different (Fig. 3). Whilst the overall weight of *Nephrops* landed did not vary significantly between trawls from the two areas ($P = 0.106$), the biomass of landed fish was more than twice as high in the south

Fig. 2. A typical catch of a north Clyde Sea area *Nephrops* trawl.

Table 2
List of species/taxonomic groups and their mean abundance per tow caught in *Nephrops* trawls from the north and south Clyde Sea area (for taxonomic authorities see Howson and Picton, 1997)[a]

North Clyde Sea area	Mean abundance per tow	South Clyde Sea area	Mean abundance per tow
Porifera			
Unidentified sponge	0.18		
Cnidaria			
Cyanea capillata	0.1	*C. capillata*	0.07
Aurelia aurita	0.15	*A. aurita*	0.13
Rhizostoma octopus	0.05	*R. octopus*	0.07
Unidentified colonial hydroid	1.59	Unidentified colonial hydroid	0.53
Alcyonium digitatum	1.54	*A. digitatum*	0.53
P. phosphorea	0.36	*P. phosphorea*	0.2
V. mirabilis	0.21		
Urticina felina	1.08		
Urticina eques	0.05		
Metridium senile	0.21	*M. senile*	0.13
Adamsia carciniopados	3.64	*A. carciniopados*	10.47
Unidentified anemone	0.15		
Nemertea			
Lineus longissimus	0.03		
Priapulida			
Priapulus caudatus	0.08		
Annelida			
Aphrodita aculeata	4	*A. aculeata*	7.87
Neanthes fucata	0.26	*N. fucata*	0.8
Platynereis dumerilii	0.21	*P. dumerilii*	0.07
Crustacea			
		Lepas anatifera	2.33
Natatolana borealis	0.03		
Palaemon elegans	0.08		
Palaemon serratus	0.05		
Spirontocaris lilljeborgi	0.49		
Processa spp.	3.87	*Processa* spp.	0.6
Pandalus spp.	5.18		
Pandalina brevirostris	0.08		
Dichelopandalus bonnieri	1.59	*D. bonnieri*	0.13
Pandalus montagui	4.13	*P. montagui*	0.33
Atlantopandalus propinqvus (=*Pandalus proqinquus*)	0.44		
C. allmanni	142.13	*C. allmanni*	73.47
Pontophilus spinosus	1.56	*P. spinosus*	0.07
N. norvegicus	**107.46**	***N. norvegicus***	**860.47**
Calocaris macandreae	0.26		
P. bernhardus	7.85	*P. bernhardus*	2.8
Pagurus prideaux	3.87	*P. prideaux*	10.6
M. rugosa	193.64	*M. rugosa*	0.4
Munida sarsi	0.77		
Galathea dispersa	0.08		
Galathea intermedia	0.03		
Pisidia longicornis	0.36	*P. longicornis*	0.2
Hyas araneus	1.72		
Hyas coarctatus	0.67		

Table 2 (*Continued*)

North Clyde Sea area	Mean abundance per tow	South Clyde Sea area	Mean abundance per tow
Inachus dorsettensis	2.1	*I. dorsettensis*	0.33
Inachus leptochirus	0.51	*I. leptochirus*	0.13
Macropodia rostrata	0.31		
Macropodia tenuirostris	2.23	*M. tenuirostris*	0.07
Atelecyclus rotundatus	0.13	*A. rotundatus*	0.2
Cancer pagurus	0.03	*C. pagurus*	0.13
Necora puber	0.05		
Liocarcinus arcuatus	0.05		
L. depurator	181.56	*L. depurator*	77
L. holsatus	47.33	*L. holsatus*	0.27
Monodaeus couchi	0.03		
Goneplax rhomboides	0.03	*G. rhomboides*	0.93
Echinodermata			
Antedon bifida	0.1		
Astropecten irregularis	3.05	*A. irregularis*	9.67
Porania pulvillus	0.13	*P. pulvillus*	0.07
Crossaster papposus	0.03	*C. papposus*	0.07
A. rubens	74.05	*A. rubens*	68.87
Marthasterias glacialis	0.1	*M. glacialis*	0.07
O. ophiura	156.05	*O. ophiura*	35.73
Ophiura albida	11.05		
Ophiothrix fragilis	19.92	*O. fragilis*	0.07
Psammechinus miliaris	7.85		
Echinus esculentus	1.72		
Echinocardium cordatum	0.05		
Brissopsis lyrifera	0.03	*B. lyrifera*	0.4
Paracucumaria hyndmani	0.13		
Thyone fusus	0.23		
Mollusca			
		Turritella communis	0.33
Aporrhais pespelecani	0.26	*A. pespelecani*	1
Colus gracilis	0.1		
N. antiqua	2.13	*N. antiqua*	0.93
B. undatum	2.15	*B. undatum*	1.67
Pleurobranchus membranacea	0.18	*P. membranacea*	0.27
Tritonia hombergii	0.03		
Nucula nitidosa	1.1		
Nucula nucleus	0.03		
Mytilus edulis	0.26		
Modiolus modiolus	0.1		
A. opercularis	46.33	***A. opercularis***	0.13
Chlamys varia	0.1		
Pseudamussium septemradiatum	0.41		
Astarte sulcata	0.03		
Arctica islandica	0.05	*A. islandica*	0.13
Abra alba	0.41		
Solenidae	0.03		
Mya truncata	0.03		
Corbula gibba	0.18		
Rossia macrosoma	1.44	*R. macrosoma*	0.73
Sepietta oweniana	3.51	*S. oweniana*	2.87
		Loligo vulgaris	**0.2**

Table 2 (*Continued*)

North Clyde Sea area	Mean abundance per tow	South Clyde Sea area	Mean abundance per tow
		Aloteuthis subulata	5.6
Eledone cirrhosa	0.03	*E. cirrhosa*	1.8
Tunicata			
Dendrodoa grossularia	0.74	*D. grossularia*	4.87
Chondrichthyes			
Scyliorhinus canicula	0.95	*S. canicula*	0.13
Scyliorhinus stellaris	0.08	*S. stellaris*	0.07
		Raja clavata	**0.2**
Osteichthyes			
Clupea harengus	**0.67**	***C. harengus***	**5.2**
		Sardina pilchardus	0.67
Argentina sphyraena	0.08	*A. sphyraena*	3.13
Lophius piscatorius	**0.03**	***L. piscatorius***	**0.07**
Gadus morhua	**9.5**	***G. morhua***	**0.67**
Gaidropsarus vulgaris	0.26		
Melanogrammus aeglefinus	**23.15**	***M. aeglefinus***	**22.87**
M. merlangus	**35.05**	***M. merlangus***	**172.67**
Molva molva	**0.03**		
Pollachius virens	0.21	*P. virens*	0.07
Enchelyopus cimbrius	0.64		
Trisopterus esmarki	0.26	*T. esmarki*	2
Trisopterus luscus	8.82	*T. luscus*	14.6
Merluccius merluccius	**1.46**	***M. merluccius***	**3.27**
		Zeus faber	**0.13**
Aspitrigla cuculus	0.26	*A. cuculus*	3.47
Eutrigla gurnardus	0.1	*E. gurnardus*	2.27
Myoxocephalus scorpius	0.03		
Taurulus bubalis	1.51	*T. bubalis*	0.33
Agonus cataphractus	3.72	*A. cataphractus*	0.2
Cyclopterus lumpus	0.15		
Trachurus trachurus	0.05		
		Cepola rubescens	0.27
Chirolophis ascani	0.03		
Lumpenus lampretaeformis	0.03		
Zoarces viviparus	1.08	*Z. viviparus*	0.27
Pholis gunnellus	0.23		
Callionymus lyra	1.97	*C. lyra*	2
Lesueurigobius friesii	0.33	*L. friesii*	1.67
Pomatoschistus minutus	2.44	*P. minutus*	1.4
Scomber scombrus	**0.05**		
Lepidorhombus whiffiagonis	0.26	*L. whiffiagonis*	0.07
Glyptocephalus cynoglossus	**2**	***G. cynoglossus***	**21.87**
Hippoglossoides platessoides	26.21	*H. platessoides*	12.87
Limanda limanda	8.62	*L. limanda*	6.8
Microstomus kitt	**0.21**	***M. kitt***	**0.4**
Platichthys flesus	0.36	*Platichthys flesus*	0.2
Pleuronectes platessa	**13.85**	***P. platessa***	**10.4**
Solea solea	**0.03**		

[a] Commercially harvested groups are indicated by bold face.

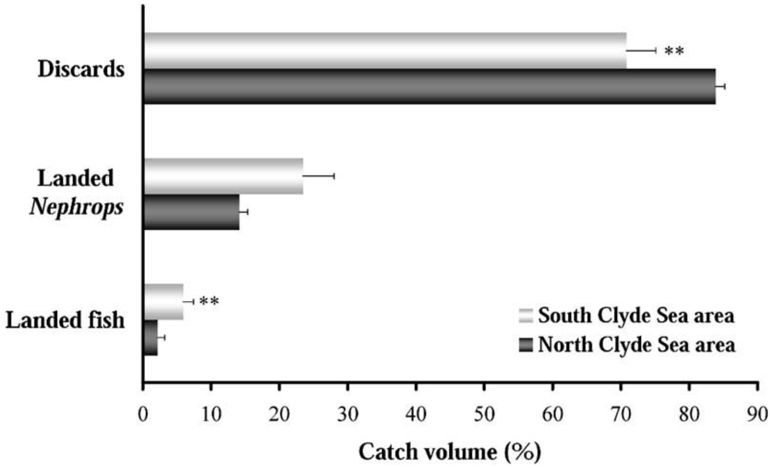

Fig. 3. Mean catch composition (±S.E.) in *Nephrops* trawls from the south and north Clyde Sea areas. Proportions are given as a percentage of the total catch volume. Significant differences are indicated thus: (*) $P < 0.05$; (**) $P < 0.01$; (***) $P < 0.001$.

($P = 0.001$). The mean proportion of discards was significantly higher in the north (84%) than in the south Clyde trawls (71%) ($P = 0.001$). The weight of discards per kg *Nephrops* is shown in Table 3. On average, 9 kg of discards were produced per kilogram of *Nephrops* across the whole Clyde Sea area (Table 3). Samples from the north were characterised by a greater variety of species; 93 taxa were identified in the north cf. 51 taxa in the south Clyde Sea discard samples (Table 2). Figs. 4 and 5 show the mean abundance and biomass of different categories of the catch as a percentage of the discards. In general, the proportion of invertebrate species in the north was much higher than in the south, with crustaceans and echinoderms accounting, on average, for 52 and 20%, respectively, of the total discard abundances (Fig. 3). In some trawls, crustaceans and echinoderms accounted for up to 83 and 73% of the discards, respectively. By contrast, the mean numbers of *Nephrops* discarded were eight times higher in samples from the south cf. the north Clyde Sea area (Fig. 4). In addition, the number of discarded individuals of commercial fish species was also approximately twice as high in samples from the south. While the proportion of fish was more important in terms of biomass (36 and 55% in the north and south, respectively) than in terms of abundance (14 and 22% in the north and south, respectively), invertebrates accounted for a higher proportion in terms of abundance (78 and 22% in the north and south, respectively) rather than biomass (60 and 15% in the north and south, respectively) (Figs. 4 and 5).

Multivariate analyses of discard compositions from commercial trawls and those collected by RV *Aora* showed very similar patterns, hence the data from all trips were pooled. As the results from biomass and numerical data were very similar, we refer mainly to abundances and consider biomass data only where important differences occurred. Cluster analysis showed a clear segregation of the north and south Clyde Sea samples at a Bray–Curtis similarity of only 38% (Fig. 6). No clear seasonal trends in the species

Table 3
Mean weight of discards (kg) produced per kilogram of *N. norvegicus* and total catch landed (±S.E.)

	n	Mean weight of discards produced per kilogram of *Nephrops* landed	Mean weight of discards per kilogram of total catch landed
North Clyde Sea area	39	10.4 ± 1.3	6.7 ± 0.8
South Clyde Sea area	15	6.2 ± 1.2	2.7 ± 0.4
Clyde Sea area total	54	9.2 ± 1.0	5.6 ± 0.6

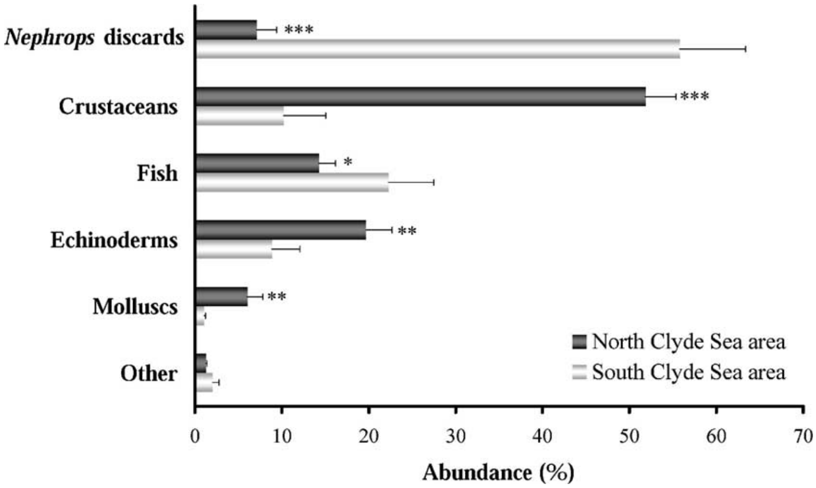

Fig. 4. Mean discard composition (±S.E.) of catches from the south and north Clyde Sea areas. Proportions are given as percentage abundance of the discard fraction. Significant differences are indicated thus: (*) $P < 0.05$; (**) $P < 0.01$; (***) $P < 0.001$.

composition could be deduced from the cluster analysis (Fig. 6). MDS of the abundance data showed a similar pattern, at a stress of 0.15, indicating a reasonable representation of the data (Fig. 7). Similarity percentages of the abundance data (SIMPER, 13 taxonomic groups) showed a within-area Bray–Curtis similarity of 75% for both north and south Clyde Sea samples. The average dissimilarity between the species abundances of samples from the two areas was 48%. The invertebrates *Munida rugosa* (squat lobster), *Liocarcinus holsatus* (swimming crab), *Crangon allmanni* (shrimp) and *Aequipecten opercularis* (queen scallop) all occurred in higher numbers in the north Clyde samples whereas *Nephrops* 'heads', whole undersized *Nephrops*, *Liocarcinus depurator* (swimming crab), *Ophiura ophiura* (brittlestar) and *Merlangius merlangus* (whiting) were more abundant in the south (Table 4).

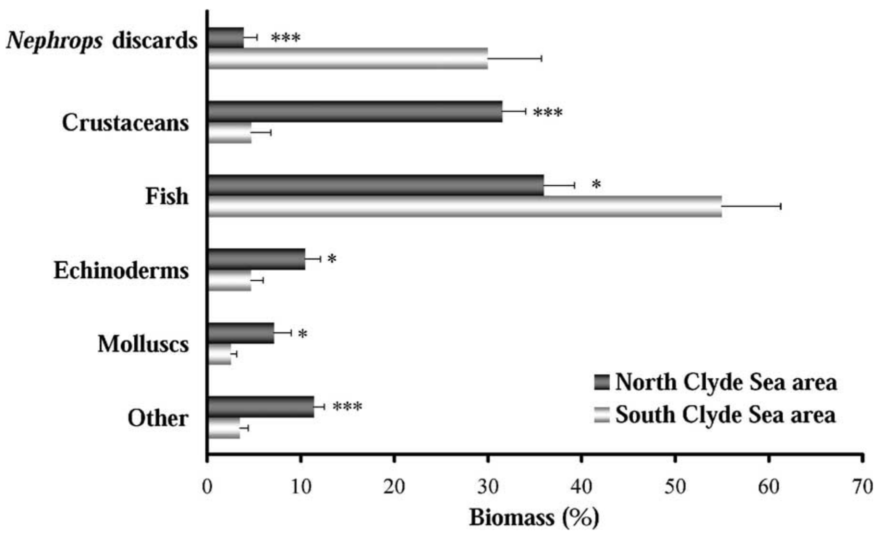

Fig. 5. Mean discard composition (±S.E.) of catches from the south and north Clyde Sea areas. Proportions are given as percentage biomass of the discard fraction. Significant differences are indicated thus: (*) $P < 0.05$; (**) $P < 0.01$; (***) $P < 0.001$.

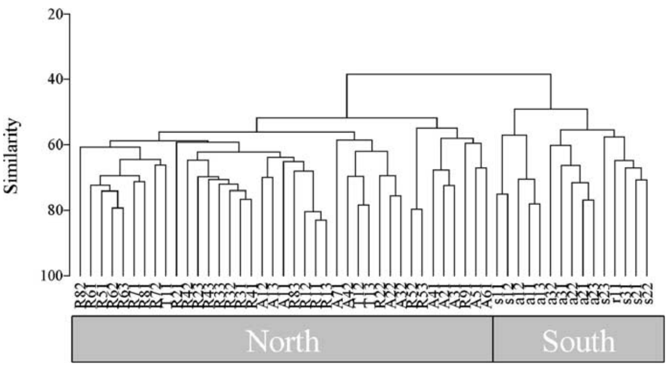

Fig. 6. Cluster analysis of the discard composition of samples from the south and north Clyde Sea area. Trawls from the two study areas are distinguished by the use of capitalised or lower case initials, respectively (see Table 1 for a list of abbreviations used).

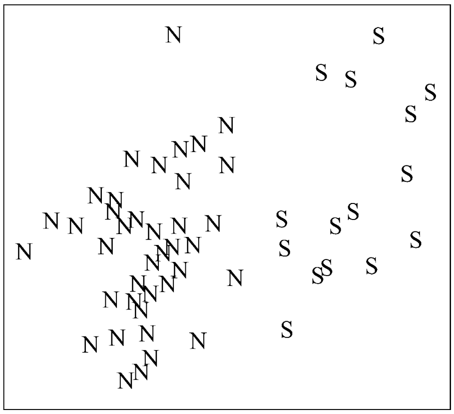

Fig. 7. MDS plot of the discard composition of samples from the south (S) and north (N) Clyde Sea area (stress = 0.15).

Superimposition of trawl variables (e.g. tow depth, net type and tow duration) revealed generally longer haul durations (resulting in larger bulk catches) and sorting times for the south Clyde (Fig. 8). The north Clyde trawls tended to be in deeper water and there 'rock hopper' nets were used predominantly rather than clean nets (Fig. 8), reflecting the differing bathymetry and sediment types. No coincidental pattern was apparent within the ordination with other factors, such as day-light (distinguishing between hauls taken before and after 12:00 h), day duration (splitting the year into 'short days', i.e. the months October–March; and 'long days', the months June–September), or bottom temperatures (dividing the year into 'cold months', i.e. December–May; and 'warm months'

Table 4
Analysis of dissimilarities (SIMPER) between south and north Clyde Sea trawls based on species abundance (±95% CI)[a]

	Common name	Mean abundance (south) $n = 15$	Mean abundance (north) $n = 39$	Cumulative percentage
M. rugosa	Squat lobster	0.4 ± 0.6	193.6 ± 67.3	13
Nephrops heads	Norway lobster	560 ± 205.2	065.4 ± 46.9	24.5
L. holsatus	Swimming crab	0.27 ± 0.4	047.3 ± 15.2	33.7
N. norvegicus	**Norway lobster**	300.5 ± 188.0	042.1 ± 58.9	42.7
C. allmanni	Shrimp	73.5 ± 152.8	142.1 ± 83.4	51.2
L. depurator	Harbour crab	77 ± 88.0	035.7 ± 45.9	59.5
O. ophiura	Brittlestar	156.1 ± 45.6	003.9 ± 84.7	67.5
A. opercularis	**Queen scallop**	0.1 ± 0.3	046.3 ± 25.1	75.3
M. merlangus	**Whiting**	172.7 ± 107.1	035.1 ± 19.3	80.8
A. rubens	Common starfish	68.9 ± 57.6	074.1 ± 36.7	85.2
H. platessoides	Long rough dab	12.9 ± 12.2	026.2 ± 11.5	89.4
O. fragilis	Brittlestar	0.1 ± 0.1	019.9 ± 28.1	93.2
M. aeglefinus	**Haddock**	22.9 ± 12.8	023.2 ± 9.8	96.8

[a] Species are shown in order of their contribution to dissimilarity (cumulative percentage). The average dissimilarity between groups was 48%. Commercial species are indicated by bold face.

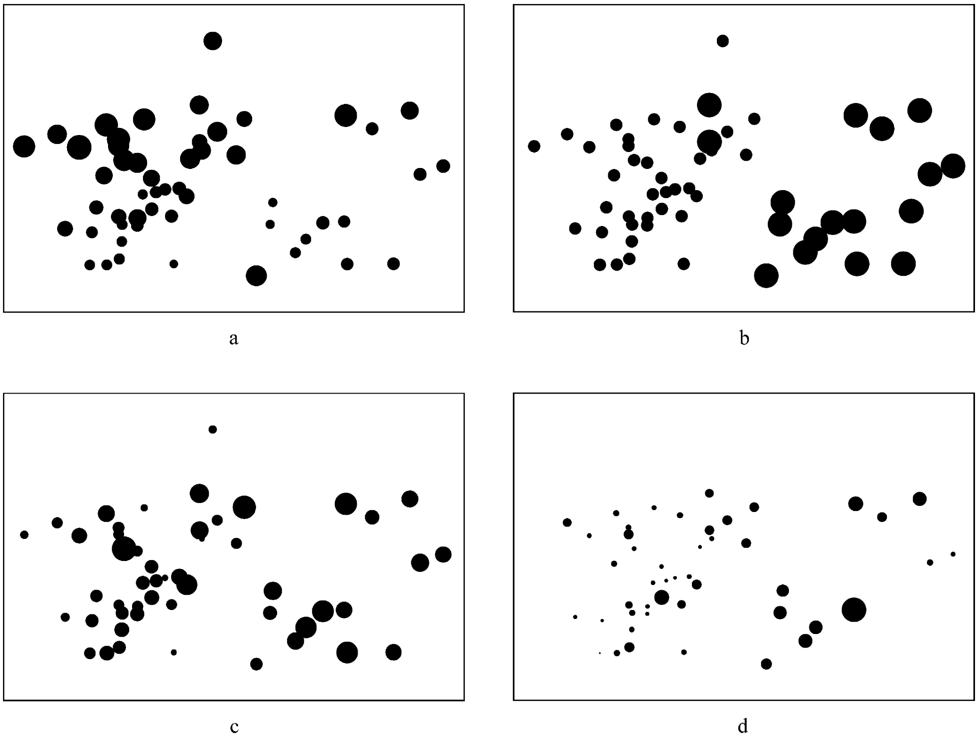

Fig. 8. Superimposition of trawl variables on the MDS ordination of the Clyde Sea discard composition (from the top to the bottom); (a) mean trawl depth (relative depth is represented by the size of the bubbles); (b) gear type: rock hopper (small bubbles) and clean net (large bubbles); (c) tow duration; (d) catch sorting time (relative times are represented by the size of the bubbles).

June–November) and graphs have therefore not been included here.

4. Discussion

In recent years, the environmental impacts of fishing have become a global concern, with particular respect to discarding practices (Jennings and Kaiser, 1998; Hall, 1999; Kaiser and de Groot, 2000; Moore and Jennings, 2000). Inevitably, discarding leads to increased mortality of undersized target species, fish (Wileman[2] et al., unpublished data) and benthos (Wassenberg and Hill, 1989; Fonds, 1994; Bergman et al., 1998; Bergmann and Moore, 2001a,b) and can be expected to have serious ecological consequences. In our study, *Nephrops* constituted only 14–23% of the total catch (biomass), while 66–80% was wasted (Fig. 3). Likewise, landings of *Nephrops* in the Farn Deeps (North Sea) and Irish Sea *Nephrops* fishery accounted only for 12 and 13% of the total catch weight (Evans et al., 1994; Craeymeersch, 1994).

The composition of discarded material was markedly different in the north and south Clyde Sea areas, with catches from the south yielding a higher proportion of small *Nephrops* (58%) resulting in large proportions of undersized *Nephrops* and *Nephrops* heads. Wileman et al. (unpublished data) found mortality rates of *Nephrops* discards held in holding pens in situ as high as 69% (see footnote 2). Wieczorek[3] et al. (unpublished data) have shown that *N. norvegicus* were also the most abundant scavengers caught in

[2] Wileman, D.A., Sangster, G.I., Breen, M., Ulmestrand, M., Soldal, A.V., Harris, R.R., 1999. Roundfish and *Nephrops* survival after escape from commercial fishing gear. Report to the EC (FAIR-CT95-0753) (difta@difta.dk).

[3] Wieczorek, S.K., Campagnuolo, S., Moore, P.G., Froglia, C., Atkinson, R.J.A., Gramitto, E.M., Bailey, N., 1999. The composition and fate of discards from *Nephrops* trawling in Scottish and Italian waters. Report (96/C75) to the EC, Millport (m.bergmann@bangor.ac.uk).

creels baited with dead conspecifics in the south of the Clyde Sea. Underwater TV observations have shown that *N. norvegicus* consumed discards of conspecifics (Wieczorek[3] et al., unpublished data) which might be an indication of food limitation experienced by the population of small, slow-growing, but densely packed individuals in the south Clyde Sea (Tuck et al., 1997). Information on the ecological energetics of *N. norvegicus* is only just beginning to emerge (Parslow-Williams, 1998). As yet, insufficient data are available to establish to what extent discarding practices subsidise the food supplies of benthic populations of this target species or any other on the soft muds of the Clyde Sea. However, Groenewold and Fonds (2000) have calculated that up to 13% of the total annual secondary production of macrobenthos becomes available, as damaged or displaced animals, to scavengers and the detritus-based food web after the passage of a single beam trawl in the southern North Sea.

Trawls in the south also generated larger quantities of roundfish discards (35%), including important commercial species such as whiting, cod and haddock. Although trawlers are legally required to take precautionary measures such as fitting a square mesh panel to the cod-end to facilitate the escape of juvenile fish (Madsen et al., 1999), undersized commercial fish still accounted for up to 39% of the total catch in the Clyde Sea area. While proportions of fish discards in the Irish Sea (Craeymeersch, 1994) were similar, an even higher percentage (60%) was found in trawls from the Farn Deeps (Evans et al., 1994). Several studies have revealed that post-fishing survival of fish is negligible (Main and Sangster, 1990; van Beek et al., 1990; Fonds, 1994; Kaiser and Spencer, 1995; Bergman et al., 1998) especially in species with swim bladders such as cod, haddock and whiting. Wieczorek[3] et al. (1999) have shown that a substantial proportion of the discards from the *Nephrops* fishery is taken by scavenging sea birds and seals were observed on a number of occasions following trawlers (M. Bergmann, pers. obs.).

Considering the scale of the fishery in the Clyde, the discarding of juvenile fish together with alteration of the seafloor habitat by demersal fishing activity could magnify the effects of overexploitation by limiting juvenile survivorship as reported by Lindholm et al. (1999) in the USA. Wileman[2] et al. (1999) reported high survival rates for fish and *Nephrops* escaping through the mesh of a *Nephrops* cod-end but low survival rate for discarded animals. Conservation measures such as the total allowable catch (TAC) quota system, together with the MLS, may in fact encourage high-grading and discarding since larger animals fetch a higher market price (Hillis and O'Morchoe, 1994). This emphasises the benefits of developing more selective *Nephrops* trawls as an essential management tool to reduce juvenile fish by-catch in addition to the square mesh panels already in use.

In the north Clyde Sea area, invertebrates formed a high proportion ($\leq$95%) of the discards. In comparison, trawls from the Farn Deeps and the Irish Sea yielded only 17 and 5% invertebrates (respectively) and the number of invertebrate taxa reported was also four times fewer in Farn Deeps trawls (Evans et al., 1994; Craeymeersch, 1994). Although different sampling techniques and the use of different mesh sizes may have affected the number of species caught, the magnitude of the difference suggests that the Farn Deeps *Nephrops* grounds are characterised by a lower invertebrate abundance and diversity than the Clyde Sea. It should be noted that invertebrates accounted for a higher proportion of the catch in terms of abundance rather than by biomass in the present study. In most fisheries studies, however, biomass is the parameter assessed, which may have led to an underestimation of the importance of invertebrates discarded in the past.

The dissimilarities in the catch composition from trawls of the two study areas are likely to be a reflection of differing bathymetries, benthic communities and ground types. The north and south Clyde Sea areas are sedimentologically (Deegan et al., 1973) and hydrographically (Edwards et al., 1986) distinct, with the north Clyde Sea area being more muddy with a patchy distribution of sediment types, whilst the south Clyde Sea area is characterised mainly by muddy sands and sandy muds (Deegan et al., 1973). Very similar patterns were observed in a more recent study using RoxAnn® by Marrs et al. (2000).[1] Hence, the higher abundance and diversity of epibenthic invertebrates in the north could be attributed to a greater heterogeneity of bottom sediments, depths, habitats and organic enrichment (Deegan et al., 1973; Edwards et al., 1986; Pearson et al., 1986; Bock et al., 1999).

While trawling reduced the long-term survival of epibenthic invertebrates such as *O. ophiura*, *L. depurator* and *Asterias rubens*, other species (e.g. whelks *Neptunea antiqua* and *Buccinum undatum* and hermit crabs *Pagurus bernhardus*) seemed to be less sensitive (Bergmann, 2000; Bergmann and Moore, 2001a,b). Low survivorship, however, might be outweighed locally at a population level, by the benefits arising from fishing activities such as a reduction of predators and competitors and the provision of an additional food source to epibenthic scavengers (Evans et al., 1996; Ramsay et al., 1998; Wieczorek et al., 1999[3]) as well as by the reproductive resilience of some of these species, e.g. *L. depurator*, *L. holsatus*, *P. bernhardus*, *O. ophiura* (Allen, 1967; Wear, 1974; Tyler, 1977, Falk-Petersen, 1982). In general, the epibenthos appeared to be characterised by resilient organisms, possibly reflecting selection after years of increasing fishing pressure. More sensitive species like sea pens (e.g. *Pennatula phosphorea*, *Vigularia mirabilis*) and the firework anemone *Pachycerianthus multiplicatus* (MacDonald et al., 1996), on the other hand, occurred only very rarely in our trawls. The lack of quantitative historical data sets and non-fished control areas makes it difficult to evaluate the effects of fishing on the Clyde Sea benthos. However, Tuck et al. (1998) have shown infaunal community changes in a previously unfished (25 years) Clyde Sea loch following trawling persisted for over 18 months and concluded that even fishing during a restricted period of the year may be sufficient to maintain communities occupying fine muddy sediment habitats in an altered state. Chronic fishing disturbance has certainly changed the benthic community structure in certain shelf seas (Kaiser et al., 2000). Acoustic mapping of habitats in the north of the Clyde Sea at a micro-scale resolution followed by the closure of identified habitats that support highly diverse bottom communities could help to preserve biodiversity as well as providing recovering habitats for threatened commercial fish stocks and *Nephrops*.

Discarding represents a waste of biological resources and for this reason is banned in some countries (e.g. Norway). Such practices tend to characterise numerical management of fisheries based on TAC and quotas. Technical measures can play an important role in helping to alleviate discarding (van Marlen, 2000), but the challenge to integrated fisheries management is now to develop practices that are compatible with the long-term needs of the ecosystem. The current review of the Common Fisheries Policy (CFP) offers an opportunity for the development of more effective and enforceable management of fishing effort.

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References

Allen, J.A., 1967. The fauna of the Clyde Sea area. Crustacea: Euphausiacea and Decapoda, Scottish Marine Biological Association, Millport.

Alverson, D.L., Freeberg, M.H., Murawski, S.K., Pope, J.G., 1994. A global assessment of fisheries by-catch and discards. FAO, Rome.

Bergman, M.J.N., Ball, B., Bijleveld, C., Craeymeersch, J.A., Munday, B.W., Rumohr, H., van Santbrink, J.W., 1998. Direct mortality due to trawling. In: Lindeboom, H.J., de Groot, S.J. (Eds.), The Effects of Different Types of Fisheries on the North Sea and Irish Sea Benthic Ecosystems. NIOZ-Rapport 1998-1, RIVO-DLO Report C003/98. Netherlands Institute for Sea Research, Texel.

Bergmann, M., 2000. The fate of discarded invertebrates from the Clyde *Nephrops* fishery. Ph.D. Thesis. University of London.

Bergmann, M., Moore, P.G., 2001a. Survival of decapod crustaceans discarded in the *Nephrops* fishery of the Clyde Sea area. Scotland. ICES J. Mar. Sci. 58, 163–171.

Bergmann, M., Moore, P.G., 2001b. Mortality of Asterias rubens and *Ophiura ophiura* discarded in the *Nephrops* fishery of the Clyde Sea area. Scotland. ICES J. Mar. Sci. 58, 531–542.

Bock, M.T., Miller, B.S., Bowman, A.W., 1999. Assessment of eutrophication in the Firth of Clyde: analysis of coastal water data from 1982 to 1996. Mar. Pollut. Bull. 38, 222–231.

Briggs, R.P., 1985. Catch composition in the northern Ireland *Nephrops* fishery. Fish. Res. 3, 47–60.

Briggs, R.P., 1992. An assessment of nets with square mesh panel as a whiting conservation tool in the Irish Sea *Nephrops* fishery. Fish. Res. 13, 133–152.

Clarke, K.R., Warwick, R.M., 1994. Change in marine communities: an approach to statistical analysis and interpretation. Natural Environment Research Council, Plymouth, UK.

Craeymeersch, J.A., 1994. Effects of a 4 m beam trawl on the benthic fauna of the Belgian continental shelf (Flemish Banks). In: de Groot, S.J., Lindeboom, H.J. (Eds.), Environmental Impact of Bottom Gears on Benthic Fauna in Relation to Natural Resources Management and Protection of the North Sea. Netherlands Institute for Sea Research, Texel, pp. 209–233.

Deegan, C.E., Kirby, R., Rae, I., Floyd, R., 1973. The superficial deposits of the Firth of Clyde and its sea lochs. Institute of Geological Sciences. Report No. 73/9. Her Majesty's Stationery Office, London.

Edwards, E., Bennett, D.B., 1980. Survival of discarded *Nephrops*. CM 1980/K:10. ICES Shellfish Committee.

Edwards, A., Baxter, M.S., Ellett, D.J., Martin, J.H.A., Meldrum, D.T., Griffith, C.R., 1986. Clyde Sea hydrography. Proc. Roy. Soc. Edin. B 90, 67–83.

Evans, S.M., Hunter, J.E., Elizal, Wahju, R.I., 1994. Composition and fate of the catch and bycatch in the Farne Deep (North Sea) *Nephrops* fishery. ICES J. Mar. Sci. 51, 155–168.

Evans, P.L., Kaiser, J.M., Hughes, R.N., 1996. Behaviour and energetics of Whelks, *Buccinum undatum* (L.), feeding on animals killed by beam trawling. J. Exp. Mar. Biol. Ecol. 197, 51–62.

Falk-Petersen, I.-B., 1982. Breeding season and egg morphology of echinoderms in Balsfjorden, northern Norway. Sarsia 67, 215–221.

Fonds, M., 1994. Mortality of fish and invertebrates in beam trawl catches and the survival chances of discards. In: de Groot, S.J., Lindeboom, H.J. (Eds.), Environmental Impact of Bottom Gears on Benthic Fauna in Relation to Natural Resources Management and Protection of the North Sea. Netherlands Institute for Sea Research, Texel, pp. 131–146.

Groenewold, S., Fonds, M., 2000. The effects of discards and damaged benthos produced by beam trawl fishery on benthic scavengers in the southern North Sea. ICES J. Mar. Sci. 57, 1395–1406.

Hall, S.J., 1999. The Effect of Fishing on Marine Ecosystems and Communities. Blackwell, Oxford.

Hillis, J.P., O'Morchoe, M.O., 1994. Restoring a depleted fishery by different methods including mesh control, decommissioning and individual quota: a bio-socio-economic comparison. ICES CM 1994/T:11.

Howson, C., Picton, B.E., 1997. The species directory of the marine fauna and flora of the British Isles and surrounding seas. Ulster Museum Publication No. 276, Belfast.

Jennings, S., Kaiser, M.J., 1998. The effects of fishing on marine ecosystems. Adv. Mar. Biol. 34, 201–352.

Kaiser, M.J., de Groot, S.J., 2000. The Effects of Fishing on Non-target Species and Habitats. Biological, Conservation and Socio-economic Issues. Blackwell, Oxford.

Kaiser, M.J., Spencer, B.E., 1995. Survival of by-catch from a beam trawl. Mar. Ecol. Prog. Ser. 126, 31–38.

Kaiser, M.J., Ramsay, K., Richardson, C.A., Spence, F.E., Brand, A.R., 2000. Chronic fishing disturbance has changed shelf sea benthic community structure. J. Anim. Ecol. 69, 494–503.

Lindholm, J.B., Auster, P.J., Kaufman, L.S., 1999. Habitat-mediated survivorship of juvenile (0-year) Atlantic cod *Gadus morhua*. Mar. Ecol. Prog. Ser. 180, 247–255.

MacDonald, D.S., Little, M., Eno, C., Hiscock, K., 1996. Disturbance of benthic species by fishing activities: a sensitivity index. Aquat. Conserv.: Mar. Freshwater Ecosyst. 6, 257–268.

Madsen, N., Moth-Poulsen, T., Holst, R., Wileman, D., 1999. Selectivity experiments with escape windows in the North Sea *Nephrops* (*Nephrops norvegicus*) trawl fishery. Fish. Res. 42, 167–181.

Main, J., Sangster, G.I., 1990. An assessment of the scale damage to and survival rates of young gadoid fish escaping from the cod-end of a demersal trawl. Scott. Fish. Res. Rep. 46, 28.

Moore, P.G., Jennings, S., 2000. Commercial Fishing: The Wider Ecological Impacts. Blackwell, Cambridge.

Parslow-Williams, P.J., 1998. Nutritional limitation in populations of the Norway lobster, *Nephrops norvegicus* (L.) in the Firth of Clyde, Scotland. Ph.D. Thesis. University of Glasgow, Glasgow, UK.

Pearson, T.H., Ansell, A.D., Robb, L., 1986. The benthos of the deeper sediments of the Firth of Clyde, with particular reference to organic enrichment. Proc. Roy. Soc. Edin. B 90, 329–350.

Ramsay, K., Kaiser, M.J., Hughes, R.N., 1998. Responses of benthic scavengers to fishing disturbance by towed gears in different habitats. J. Exp. Mar. Biol. Ecol. 224, 73–89.

Tuck, I.D., Chapman, C.J., Atkinson, R.J.A., 1997. Population biology of the Norway lobster, *Nephrops norvegicus* (L.) in the Firth of Clyde, Scotland. I. Growth and density. ICES J. Mar. Sci. 54, 125–135.

Tuck, I.D., Hall, S.J., Robertson, M.R., Armstrong, E., Basford, D.A., 1998. Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea loch. Mar. Ecol. Prog. Ser. 162, 227–242.

Tyler, P.A., 1977. Seasonal variation and ecology of gametogenesis in the genus *Ophiura* (Ophiuroidea: Echinodermata) from the Bristol Channel. J. Exp. Mar. Biol. Ecol. 30, 185–197.

van Beek, F.A., Van Leeuwen, P.I., Rijnsdorp, A.D., 1990. On the survival of sole and plaice discards in the otter-trawl and beam-trawl fisheries in the North Sea. Netherlands J. Sea Res. 26, 151–160.

van Marlen, B., 2000. Technical modifications to reduce the by-catches and impacts of bottom-fishing gears. In: Kaiser, M.J., de Groot, S.J. (Eds.), Effects of Fishing on Non-target Species and Habitats: Biological, Conservation and Socio-economic Issues. Blackwell, Oxford, pp. 253–268.

Wassenberg, T.J., Hill, B.J., 1989. The effect of trawling and subsequent handling on the survival rates of the by-catch of prawn trawlers in Moreton Bay, Australia. Fish. Res. 7, 99–110.

Wear, R.G., 1974. Incubation in British decapod Crustacea, and the effects of temperature on the rate and success of embryonic development. J. Mar. Biol. Assoc. UK 54, 745–762.