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Damage sustained by epibenthic invertebrates discarded in the *Nephrops* fishery of the Clyde Sea area, Scotland

M. Bergmann[a,*], D.J. Beare[b], P.G. Moore[a]

[a]*University Marine Biological Station, Millport, Isle of Cumbrae KA28 0EG, UK*
[b]*Fisheries Research Services, Marine Laboratory, Aberdeen AB11 9DB, UK*

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The Clyde Sea *Nephrops* fishery produces ca. 25 000 t y^{-1} discards with invertebrates accounting for up to 90% of the number of animals discarded. Trawling and handling of the (by-)catch often results in physical injury, the extent of which was previously unknown. Damage sustained by invertebrate discards was assessed following commercial trawling (of 62–270 min duration) and sorting on deck. Brittlestars *Ophiura ophiura* were most vulnerable with 100% incurring damage, followed by squat lobsters *Munida rugosa* (57%) and starfish *Astropecten irregularis* (56%). Harder-shelled species such as hermit crabs *Pagurus bernhardus* and queen scallops *Aequipecten opercularis* sustained fewer injuries (14 and 2%, respectively). Shell chipping, loss and damage of limbs were the most frequent types of injury incurred. The severity and frequency of damage was mainly correlated with species-specific morphological and behavioural characteristics. Vessel type, tow duration and animal size had a major influence on damage to the epibenthic invertebrates caught. While damage may potentially be repaired, survival is adversely affected and sublethal effects might significantly impair fitness of frequently trawled individuals and populations. © 2001 Elsevier Science B.V. All rights reserved.

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In recent years, the ecological effects of fishing have become a global environmental concern resulting in a large number of studies (see reviews by Hall (1999), Jennings and Kaiser (1998) and Moore and Jennings (2000)). Demersal fishing gears are designed to catch the maximum amount of bottom-dwelling target species. Inevitably, they also catch or damage organisms that inhabit the same ground and modify habitat and community structure (Jennings and Kaiser, 1998). Commercial fishing has been estimated to produce 27 million t y^{-1} discards worldwide (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 MLS, are of inferior quality or surplus to quota.

The Norway lobster (*Nephrops norvegicus* (L.), hereafter referred to by genus alone) is the most valuable invertebrate in Scottish waters. Official landings are around 60 000 t y^{-1} worldwide, a third of which is landed in Scotland (Marrs et al., 2000). *Nephrops* live

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* Corresponding author. Present address: School of Ocean Sciences, Menai Bridge, LL59 5EY, UK.

E-mail address: m.bergmann@bangor.ac.uk (M. Bergmann).

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on soft substrata and are mainly fished by otter-trawling. In the Clyde Sea area, *Nephrops* trawls (mesh size ≥70 mm) disturb wide areas of the sea bed and benthos as weighted ground lines and heavy otter doors are dragged across the sediment. Between 1998 and 1999, almost 70% of the Clyde Sea was trawled more than once by only 18 trawlers out of a *Nephrops* fleet of 40–80 (Marrs et al., 2000).

The highest rates of discarding have been attributed to shrimp trawl fisheries, with an estimate of 9.5 million t y^{-1} excluding non-target invertebrates (Alverson et al., 1994). In the local *Nephrops* fishery, 50–90% of the catch (volume) is discarded (Bergmann et al, 2001). Invertebrates account numerically for up to 90% of the animals discarded. However, little is known about the fate of this important component of the catch as most previous studies of this fishery have focused on commercially important discard species, such as undersized target species and roundfish (e.g. Bennett, 1973; Davis, 1981; Shirley and Shirley, 1988; Evans et al., 1994; Wileman et al., 1999). As it has been recognised that large proportions of the catch are discarded, the fate of non-target invertebrates has recently received increasing attention (Wassenberg and Hill, 1989; Craeymeersch, 1994; Fonds, 1994; Kaiser and Spencer, 1995; Bergman et al., 1998; Ramsay and Kaiser, 1998; Franceschini et al., 1999). Although the NE Atlantic *Nephrops* trawl fishery ranks as number eight among the world's top twenty fisheries with the highest recorded discard ratios, and as number five when ordered by gear type (Alverson et al., 1994), the consequences of using such trawls on non-target species have not yet been investigated.

Post-fishing survival of invertebrates is affected by a range of factors. First, trawling characteristics such as tow duration, speed, fishing depth, substratum type, catch size and composition all affect damage and mortality (Bergman et al., 1998; Wileman et al., 1999). Second, on-deck exposure can exacerbate mortality as animals endure hypoxia, temperature changes and physical damage due to handling and compression by the weight of the catch (Wileman et al., 1999). Physical damage due to trawling and handling has been shown to have a critical effect on survival of decapod crustaceans and echinoderms (Bergmann and Moore, 2001a,b).

The present study provides a first assessment of damage sustained by important epibenthic invertebrates that are routinely discarded from *Nephrops* trawls. We have also attempted to separate alternative sources of injury by comparing damage incurred to invertebrates from a series of trawls throughout the year. This has been done using non-parametric regression techniques (e.g. Venables and Ripley, 1994).

2.1. Assessment of damage sustained by discarded invertebrates

Samples of invertebrate discards were taken from 42 trawls made on three local commercial *Nephrops* trawlers and RV *Aora* between November 1997 and August 1998. Position, tow duration, average trawling depth, towing speed, total catch volume, sorting time and fishing gear were recorded for each tow. Sorting procedures varied between fishing boats as follows:

- 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. These rock hopper nets have a series of large bobbins (ca. 25 cm in diameter) attached to the groundrope to help prevent the net from snagging and becoming damaged on harder grounds. When fishing in the south Clyde Sea area, she trawled with a 'clean' net similar to that used by Vessel 3 (see below). After emptying the cod-end into the sorting pound, the catch was shovelled into standard fish baskets (44 dm^3) in order to estimate the total catch volume. Each basket was emptied onto a sorting table and, while the marketable component was separated, sub-samples of ca. 60 invertebrates per species were randomly collected from different parts of the catch and stored into buckets (3 and 6 dm^3) prior to damage assessment. Bias towards larger or more badly damaged animals was avoided by taking care to collect all animals present in one section of the sorting table. Buckets containing starfish and brittlestars were filled with seawater to minimise further damage as echinoderms often autotomize (parts of) arms when stressed.
- Vessel 2 (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, however, this vessel used a clean net with one tickler chain similar to that described below since the rock hopper net had been snagged. The sorting procedure was similar to that of RV *Aora*.

- Vessel 3 (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 the clean 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. The content of the cod-end was released into a hopper, the door of which was opened periodically, releasing the catch onto a conveyor belt where it was sorted. Invertebrates were collected from the conveyor belt in the same manner as above.
- Vessel 4 (14 m, 261 kW, 22 t) operated a twin-rigged net, comprising two nets rigged together and towed by a single boat. 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 attached to the groundrope. Upon hauling, the catch of each cod-end was released successively into a sorting pound, shovelled into baskets, then emptied onto a sorting table. Invertebrate discards were collected from the sorting table as described above.

On return to the laboratory, size and visible damage was assessed and the sex of swimming crabs and squat lobsters determined. Furthermore, note was made of the presence of regenerating limbs. Damage was assessed on a four point scale (intact, mild, medium and severe damage, as detailed in Table 1 and Fig. 1) and expressed in a standardised form for each species studied, i.e. as percentage frequency of each damage category.

2.2. Separating the effects of predictors on damage sustained

Stochastic models were built for these data because damage to invertebrates by fishing depends simultaneously on a complicated range of factors. In order to assess the variability due to any single factor in

Table 1
Criteria used to categorise and summarise damage sustained by epibenthic invertebrates caught in the Clyde Sea *Nephrops* fishery

Damage	Crustaceans	Asteroids	*O. ophiura*	*A. opercularis*	Whelks
Intact	–	–	–	–	–
Mild	1 Limb lost, broken rostrum	Punctured	Parts of arms lost	Damaged outer margin	Slight lip chipping
Medium	1–3 Limbs lost	1–2 (parts of) Arms lost	1–3 Whole arms lost	Cracked margin	Cracked base/lips, damaged apex
Severe	> 3 Limbs lost, carapace damage, abdominal injuries	> 2 (parts of) Arms lost	> 3 Arms lost, damage to the disc	Crushed valve	Holes in shell, crushed shell

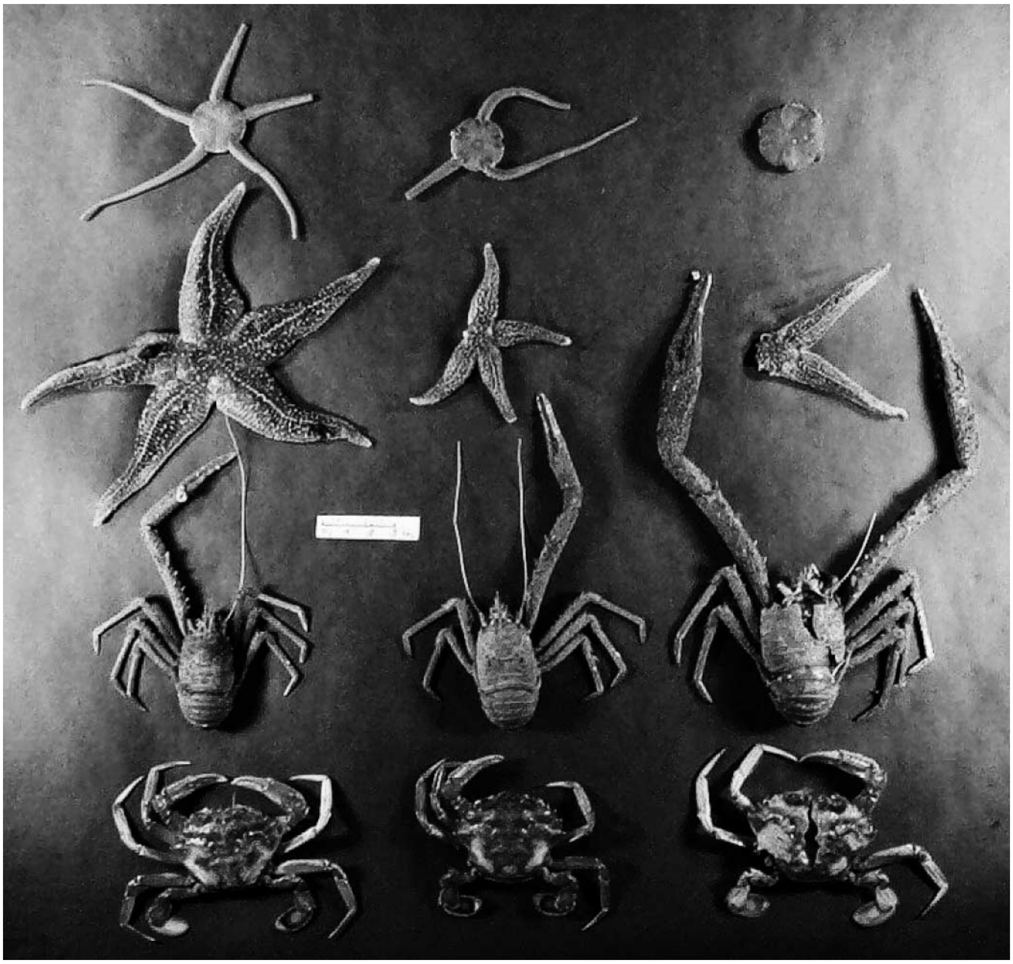

Fig. 1. Damage sustained by trawled invertebrates (from top to bottom): *Ophiura ophiura*, *Asterias rubens*, *Munida rugosa*, *Liocarcinus depurator*. Each column represents a damage category (from left to right) from mild to medium and severe damage.

isolation, e.g. sex, the signal due to other factors, such as tow duration, ought first to be removed. Regression models are the natural tool for tackling such problems and were used here. Standard linear regression models are unsuitable in this particular instance because invertebrate damage was measured using a categorical system (Table 1) and standard statistical summaries (e.g. averages, sums, medians) have no clear interpretation. This problem was circumvented by analysing the damage data using generalised linear models (GLMs) for Bernoulli data. The data were transformed into a simple binary variable prior to analysis ($0 = \text{no damage}$ and $1 = \text{damage}$), which can then be modelled as a function of various predictor variables (e.g. body size, time of year, towing depth, vessel, tow duration and total catch) (Table 2). The procedure results in a loss of information since there is no distinction between higher levels of damage, but it is nevertheless a useful procedure because the quantity of interest (probability of damage) now has a clear statistical interpretation. Since all *O. ophiura* incurred damage, we explored the binary split between medium and severe injury, i.e. the probability of an individual being severely damaged versus individuals that sustain only medium damage. To select suitable subsets of predictors, the below ‘full’ model was fitted to the data separately for all species.

$$\ln\left(\frac{1}{1-P}\right) = \text{size} + \text{month} + \text{depth} + \text{vessel} + \text{tow duration} + \text{total catch}$$

[Key: size = body size; month = month of year (1:12); depth = towing depth (m); vessel = a discrete factor denoting which boat caught each individual; tow duration (min) and total catch (number of baskets)]. Best subsets of the above predictors were chosen using a backward and forward stepwise selection procedure, which discriminates between all possible models using the Akaike Information Criteria (AIC). The objective was to find the most economical models in terms of numbers of covariates used, which nevertheless explain highest quantities of variability.

It will be noted that neither non-linear nor interaction terms were assessed during the model-selection process. Strictly, this omission is difficult to defend since it is very likely that mean probability of damage, for example, varies non-linearly with season; or that multiple combinations of the other predictors co-vary with each other in respect of their influence on damage. We defend the model-selection protocol, however, by noting that the data analysed were observational and not from a designed experiment. This problem is inevitable, given that much of the sampling was done onboard commercial fishing vessels where any attempt to randomise sampling activity in space and time is impossible. The result is that the data are autocorrelated and in many cases the competing effects are inseparable from each other. By fitting only linear, independent (no interactions) terms, the results are simpler and erroneous conclusions less likely, but nevertheless remain possible. Additionally, the χ^2 statistic, used to assess the adequacy of the model’s fit to the data (McCullagh and Nelder, 1989; Beare and McKenzie, 1999), indicated that the models are, in some cases, ‘overfitted’ to the data. [$0.05 < P$-value < 0.95 = model that ‘fits’; P-value < 0.05 = poor model; and P-value > 0.95 = ‘overfitted’ model]. ‘Overfitting’ implies that all the variation is explained, hence, no significant reductions in variance would be anticipated by including non-linear and interaction terms.

The regression coefficients from the ‘best’ subsets selected for each species were used to plot probability of damage as functions of likely ranges of the various other predictor variables. To do this calculation, the other predictors selected in the model must be kept at a constant level, i.e. the average. Where a vessel effect was found to be statistically significant, the value of the other coefficients were presented as contrasts relative to RV *Aora* (Lindsey, 1995).

3.1. Assessment of damage sustained by discarded invertebrates

Damage was assessed in a range of invertebrate species but here we only refer to the eleven species that were caught frequently and in sufficient numbers for statistical analysis.

3.1.1. Damage to crustaceans

The maximal frequency of damage sustained by individual animals was 57% in squat lobsters *Munida rugosa* (Fabricius), 53% in swimming crabs *Liocarcinus depurator* (L.), 43% in *L. holsatus* (Fabricius), 35% in hermit crabs *Pagurus prideaux* Leach and 14% in *P. bernhardus* (L.) (Fig. 2). Loss of one chela was the most frequent damage sustained by all these species, particularly *M. rugosa* (37%) (Table 3). *L. holsatus* and *M. rugosa* also often lost the second pereiopod (ca. 20%). Injury to the carapace was most frequent in *M. rugosa* (9%) and *L. depurator* (8%) (Table 3). There were no obvious differences in the severity of damage between female and male *M. rugosa* and *L. depurator*, although ovigerous crabs did appear to sustain less damage than males and females without eggs. By contrast, unberried female *L. holsatus* incurred more damage than male or berried conspecifics. They also seemed to be smaller than males but larger than berried females (Kruskal–Wallis test, $n = 1110$; df = 2; $P < 0.001$).

3.1.2. Damage to echinoderms

All brittlestars *Ophiura ophiura* (L.) were damaged (Fig. 2). More than 70% incurred medium to severe injury. The most frequent injury recorded was broken arms (95%) but 13% of the brittlestars also sustained

Table 2
Description of tows used for damage assessments: (Aa) RV *Aora*; (FV2–4) fishery vessels 2–4; (CN) clean net; (RH) rock hopper; (twRH) twin rock hopper; latitude and longitudes represent the start position of each tow; total catch was measured in baskets (44 dm^3); (N.a.) not available

Date	Vessel	Depth (m)	Net	Tow time (min)	Latitude	Longitude	Total catch
30/10/97	FV3	94	CN	250	N.a.	N.a.	20.25
30/10/97	FV3	75	CN	185	55°25′	005°00′	20.4
30/10/97	FV3	53	CN	160	55°23′	005°01′	15.08
12/11/97	Aa	92	RH	80	55°41′	05°00′	11.5
12/11/97	Aa	83	RH	109	55°46′	04°58′	8.125
12/11/97	Aa	73	RH	97	55°51′	04°54′	6.5
25/11/97	FV2	51	RH	145	55°46′	04°57′	7.5
25/11/97	FV2	51	RH	70	55°45′	04°57′	7.5
25/11/97	FV2	42	RH	152	55°45′	04°57′	16
02/12/97	Aa	54	CN	205	55°15′	05°13′	6
03/12/97	Aa	56	CN	180	55°13′	05°13′	8
15/12/97	Aa	82	RH	120	55°41′	04°57′	13
15/12/97	Aa	81	RH	120	55°41′	04°59′	10
14/01/98	Aa	80	RH	120	55°41′	04°57′	14.8
14/01/98	Aa	87	RH	120	55°41′	04°59′	8.5
20/01/98	FV3	45	CN	190	55°10′	05°04′	14.8
20/01/98	FV3	38	CN	200	55°09′	05°01′	16
20/01/98	FV3	39	CN	155	55°08′	05°04′	10.5
03/02/98	FV2	36	RH	67	55°44′	04°55′	9
03/02/98	FV2	102	RH	170	55°43′	04°59′	8
03/02/98	FV2	74	RH	125	55°43′	04°58′	19
23/02/98	Aa	77	RH	62	55°46′	04°58′	4.5
23/02/98	Aa	83	RH	120	55°48′	04°58′	7
01/03/98	FV2	54	RH	120	55°46′	04°53′	13.5
01/03/98	FV2	71	RH	150	55°51′	04°52′	11.75
01/03/98	FV2	52	RH	155	55°52′	04°54′	12
01/04/98	FV2	56	RH	180	55°45′	04°58′	11
01/04/98	FV2	89	RH	270	55°45′	04°58′	10
01/04/98	FV2	66	RH	230	55°42′	04°59′	11
21/04/98	FV2	50	CN	180	55°14′	05°01′	28
11/05/98	FV2	56	RH	162	55°45′	04°57′	11.66
11/05/98	FV2	78	CN	210	55°41′	04°56′	14.33
11/05/98	FV2	65	CN	198	55°39′	04°56′	21.5
09/06/98	FV2	44	RH	160	55°45′	04°57′	18
09/06/98	FV2	44	RH	162	55°47′	04°57′	16.33
09/06/98	FV2	46	RH	145	55°44′	04°58′	10
10/07/98	FV3	45	CN	235	55°09′	05°02′	32
10/07/98	FV3	87	CN	137	55°03′	05°11′	18
05/08/98	FV4	45	twRH	145	55°49′	05°00′	28
05/08/98	FV4	96	twRH	125	55°44′	04°59′	24
05/08/98	FV4	96	twRH	130	55°40′	04°58′	21
11/08/98	Aa	N.a.	RH	180	N.a.	N.a.	9

damage to the disc and 5% had lost all arms (Table 4). More than 50% of the sand star *Astropecten irregularis* (Pennant) showed signs of injury (Fig. 2), the most frequent being punctures (26%) and broken arms (35%) (Table 4). By contrast, only 31% of the common starfish *Asterias rubens* L. sustained damage (Fig. 2) with loss of one arm (16%) and puncture wounds (9%) as the most common injuries (Table 4).

3.1.3. Damage to molluscs

Almost all queen scallops *Aequipecten opercularis* (L.) were undamaged with only 2% showing signs of

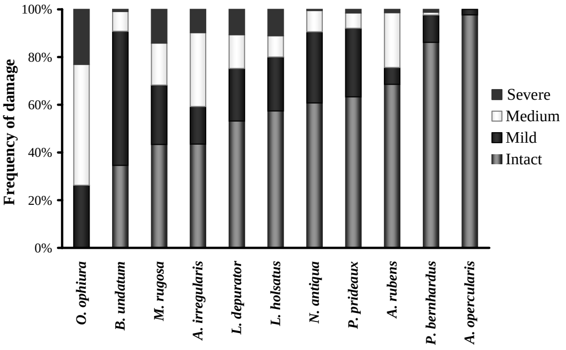

Fig. 2. Frequency of degrees of damage sustained by trawled invertebrates.

chipping at the outer margin of the shell (Table 5). Half of the red whelks *Neptunea antiqua* (L.) caught were damaged (Fig. 2), with slight chipping of the outer lip of the shell aperture being the most common injury encountered (34%) (Table 5). Edible whelks *Buccinum undatum* L. sustained higher degrees of damage (Fig. 2), again mostly involving chipping of the outer lip (64%) (Table 5).

3.2. Separating the effects of predictors on damage sustained

First it should be acknowledged that the models (Table 6) were selected using purely statistical criteria and, confounding features notwithstanding, may not all have ready biological interpretation. Consider, for example, the effect of month on the probability of damage, which we included because of its statistical significance. If month is selected in a model, it does not mean that 'June' *causes* or *prevents* damage; but rather that 'June' is a convenient proxy which economically includes information relating to *bona fide* causative information (e.g. tow duration and total catch). It may also contain other potentially useful information that was not assessed such as light intensity, food availability or sea temperature.

Fig. 3 summarises the probability of damage to trawled invertebrates as a function of the predictor variables we examined. In five out of the ten common epibenthic species caught, animal size was an important variable affecting injury. Damage to *A. opercularis*, *O. ophiura* and *A. rubens* increased significantly with animal size while the reverse was true for *B. undatum* and *L. holsatus*. Four species showed a seasonal pattern in their susceptibility to damage by virtue of a statistical dependence on month. The probability of damage to *N. antiqua* and *A. opercularis* was lowest in November 1997 and increased through the year to August 1998 whereas the reverse was true of *L. holsatus* and *P. bernhardus.* Size–frequency histograms of *L. holsatus* revealed that those captured between January and March were smaller than those from April to August, implying autocorrelation of the covariables size and season.

The range of depths fished (36–102 m) had no significant effect on the damage sustained by eight of the commonest invertebrate species discarded. However *A. opercularis* caught in deeper waters were (weakly) more susceptible to damage, while the reverse was true for *P. prideaux*. The type of vessel used had a significant effect on damage sustained by the majority of species. Capture by the twin rigger (Vessel 4) increased the probability of damage in a number of species (Fig. 3; Table 6). Vessel 3 caused the highest levels of damage to *O. ophiura*. Unfortunately, vessels sometimes used different fishing gears (Table 2), and the models

Table 3
Percentage of decapods with missing appendages caught in *Nephrops* otter-trawls. In addition to missing appendages (P2–5: pereiopod 2–5), some decapods had a damaged carapace (CP), abdomen (AD) and/or rostrum (R). Proportions are given as percentages of the total number (*n*)

	n	Intact	Individuals with appendage loss						CP	AD	R
			Chela		P2	P3	P4	P5			
L. depurator	2182	53	17	3	14	15	16	7	8	2	–
L. holsatus	1110	57	18	3	21	11	9	12	4	1	–
M. rugosa	1715	43	25	12	20	18	17	N.a.	9	4	4
P. bernhardus	418	86	9	1	3	1	0	N.a.	1	0.7	–
P. prideaux	327	65	25	2	5	7	5	N.a.	1	0	–

Table 4
Damage sustained by the starfish *A. rubens*, *A. irregularis* and the brittlestar *O. ophiura* caught by *Nephrops* otter-trawls. Proportions are given as percentages of the total number (*n*)

	n	Intact	Puncture	Damage to the disc	Part of arm missing	Individuals with whole arm(s) lost					
						0	1	2	3	4	5
A. rubens	1643	70	9	N.a.	2	78	16	4	1	0.1	0.1
A. irregularis	184	44	26	N.a.	35	91	6	0.5	0.5	2	0.5
O. ophiura	1838	0	N.a.	13	95	28	26	19	13	8	5

should be re-fitted using fishing gear type as a factor rather than vessel (i.e. clean net, rock hopper and twin rigger). A cursory investigation of the data using aggregations (medians) by gear-type indicated that brittlestars caught by a clean net sustained higher degrees of damage compared with other fishing gears (Kruskal–Wallis test, $n = 1837$; $\mathrm{df} = 2$; $P < 0.001$). There was a positive correlation between tow duration and damage to *M. rugosa* and *A. rubens*, but the probability of higher levels of damage to *O. ophiura* decreased with tow duration. In six out of ten species, the total catch was an important variable affecting injury. There was a positive correlation between total catch and damage sustained by *L. depurator*, *P. prideaux*, *A. rubens* and *A. opercularis*. In contrast, larger catches decreased the probability of damage to *B. undatum* and *P. bernhardus*.

4.1. Damage sustained by discarded invertebrates

Our results show that otter-trawling for *Nephrops* damages a variety of important epibenthic invertebrates. Considering the scale of fishing pressure in the Clyde Sea area (Marrs et al., 2000), this may have considerable ecological implications.

4.1.1. Damage to crustaceans

The squat lobster *M. rugosa* was particularly vulnerable, with >50% incurring damage. Its fragile morphology, viz. spiny exoskeleton, long rostrum and claws, could enhance entanglement in a net or with other animals in the catch. Concurring with Juanes and Smith (1995), the most frequent damage incurred in all decapod species was the loss of a chela. Wood and Wood (1932) stated that galatheids autotomise appendages more readily than any other decapod, hence *M. rugosa* caught in trawls may autotomise appendages in attempts to escape. Bergmann and Moore (2001a) have shown that the manner of appendage loss, i.e. either voluntarily or forcible, significantly affects the survival rates of *M. rugosa* and *L. depurator*, but it was not possible to assess the proportion of limb loss due to autotomy or forcible removal in this study.

The frequency of *L. depurator* with lost appendages in the catch was in close agreement with reports from the Irish Sea (Kaiser and Spencer, 1995), even though shorter tow durations (10 min) and different gear (a beam trawl with a chain mat) was used in that study. However, the frequency of damage was much higher (85%) in *Liocarcinus* sp. caught in the Adriatic (Franceschini et al., 1999), which could be attributed to their use of toothed ‘Rapido’ trawls.

Interestingly, berried *L. depurator* sustained lower

Table 5
Damage sustained by queen scallops *A. opercularis* and whelks *B. undatum* and *N. antiqua* caught by *Nephrops* otter-trawls. Proportions are given as percentages of the total number (*n*)

	n	Intact	Damaged apex	Damaged spire	Damaged lips	Damaged base	Damaged margin
A. opercularis	729	98	–	–	–	–	2
B. undatum	217	35	0	0.9	64	5	–
N. antiqua	191	51	1	0.5	34	5	–

Table 6
Effect of size, time of year, towing depth, type of vessel, tow duration and volume of the total catch upon damage sustained by trawled invertebrates as estimated by the final GLM models. (Aa) RV *Aora*; (FV2–4) fishery vessels 2–4; (N.s.) not significant; (N.a.) not available

Species	*n*	df	*P*	Residual deviance	Intercept	Regression coefficient								
						Size	Month	Depth	Aa	FV2	FV3	FV4	Tow duration	Total catch
L. depurator	2101	2099	0.42	2895.6	−0.38	N.s.	N.s.	N.s.	N.s.	N.s.	N.s.	N.s.	N.s.	+0.017
L. holsatus	1074	1071	0.45	1453.3	+1.02	−0.270	−0.036	N.s.	N.s.	N.s.	N.s.	N.s.	N.s.	N.s.
M. rugosa	1654	1650	0.57	2250.8	−0.081	N.s.	N.s.	N.s.		−0.15	N.a	+0.18	+0.003	N.s.
P. bernhardus	414	409	1	319.1	+0.35	N.s.	−0.210	N.s.		+0.27	N.a.	+0.57	N.s.	−0.063
P. prideaux	327	321	0.45	401.6	+0.37	N.s.	N.s.	−0.035		−0.22	−0.37	+0.50	N.s.	+0.110
A. rubens	1570	1566	0.49	1917.3	−2.20	+0.006	N.s.	N.s.	N.s.	N.s.	N.s.	N.s.	+0.0028	+0.034
O. ophiura	1751	1745	0.47	1966.8	+0.40	+0.040	N.s.	N.s.		−0.1	+0.40	−0.24	−0.0025	N.s.
N. antiqua	189	184	0.11	213.8	−2.26	N.s.	+0.240	N.s.		+1.91	+1.06	+0.44	N.s.	N.s.
B. undatum	217	211	0.37	222.7	+9.85	−0.060	N.s.	N.s.		+0.29	+0.58	+2.04	N.s.	−0.140
A. opercularis	665	658	1	112.3	−12.57	+0.061	N.s.	+0.016		+1.02	N.a.	+0.04	N.s.	+0.091

levels of damage than males and non-gravid females, if we assume that samples were random in time and space, which is not likely to be true. Berried females might respond differently to trawling in that they fold away their appendages in an attempt to protect their external egg masses rather than extend appendages in attempts to flee, rendering these appendages less vulnerable. Moreover, berried females might spend more time recessed inactive in the sediment and in this position be less vulnerable to trawling. Female *L. holsatus* incurred higher degrees of damage compared with their male or berried conspecifics, and were smaller than males, but larger than berried crabs. Although small size was significantly associated with increased damage (Fig. 3), again behavioural patterns might have protected limbs of small berried *L. holsatus* from damage.

The frequency of damage sustained by hermit crabs was (expectedly) low, and is attributed to their ability to retract into protective shells when disturbed. The number of damaged individuals, however, was 20% higher in *P. prideaux*, whose foundation gastropod shell rarely provides complete protection (unlike that of *P. bernhardus*) (Hazlett, 1981).

The immediate effect of trawling is not the only concern; damage sustained in trawling has implication for the longer-term survival of discards. Bergmann and Moore (2001a) reported longer-term mortalities of injured *L. depurator* of between 26 and 53%, and the survival of crustaceans with carapace damage can be assumed to be zero (Kaiser and Spencer, 1995). Potter et al. (1991) reported low recapture rates of tagged injured or trawled sand crabs *Portunus pelagicus* compared with pot-caught individuals, also indicating a low survival in situ. Sublethal injury reduces foraging efficiency, mating success and increases the susceptibility to intra- and inter-specific attack (Juanes and Smith, 1995). The loss of limbs decreases subsequent moult increments (Bennett, 1973) and regeneration of lost appendages imposes additional energetic costs. A decrease in growth rate may in turn increase the risk of predation and delay sexual maturity, thus extending natural mortality opportunities over a longer period than normal (Davis, 1981). The seriousness of such a handicap is increased, as is often the case, if crustaceans are discarded over unsuitable habitats (Evans et al., 1994; Wileman et al., 1999) or repeatedly caught.

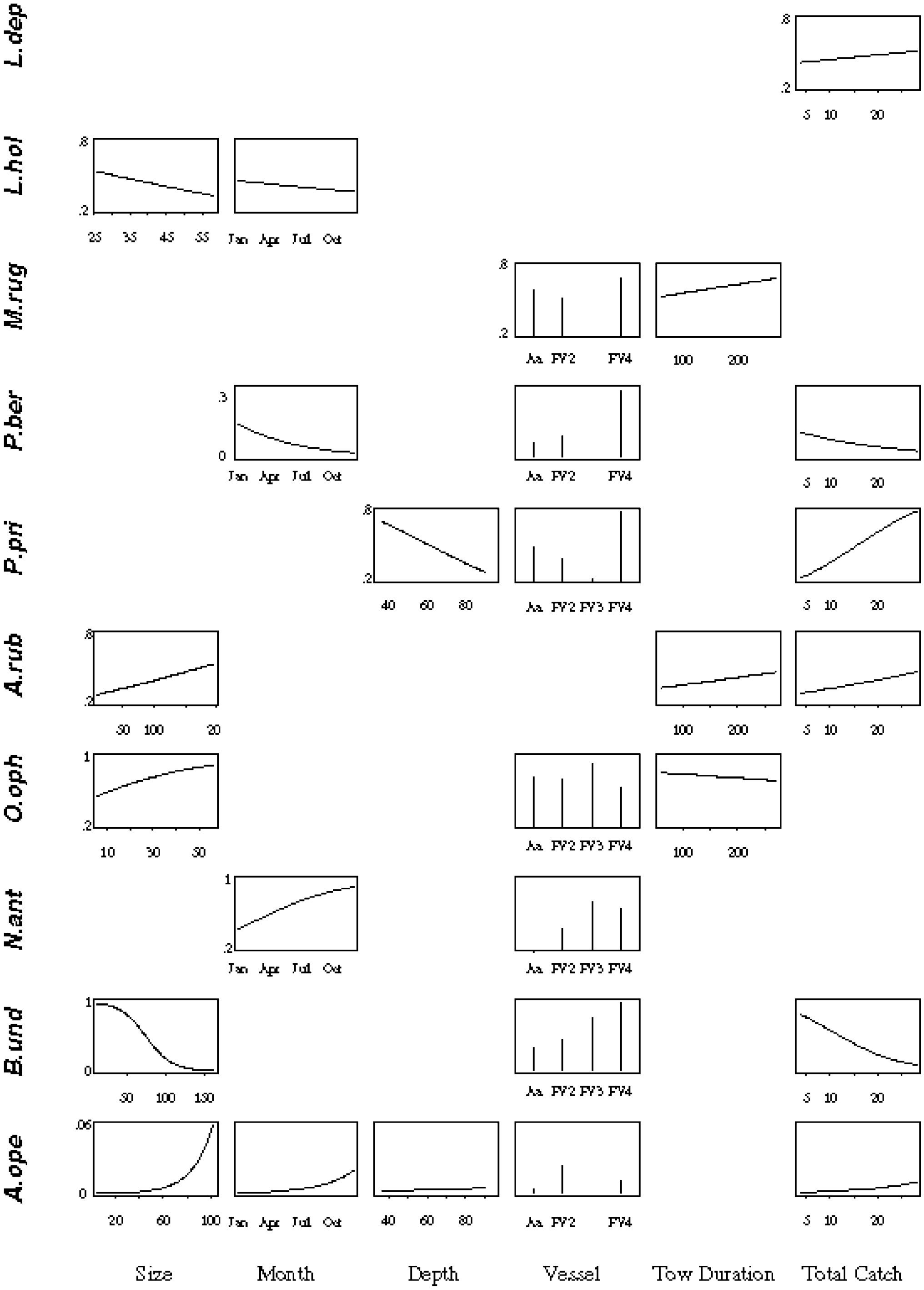

Fig. 3. Probability of damage to trawled invertebrates (*Y*-axis) as a function of significant predictors (*X*-axis): Size (mm); Month (January–October); Towing depth (m); Vessel (Aa) RV *Aora*, (FV2–4) Vessel 2–Vessel 4; Tow duration (min); Total catch (44 dm^3 baskets). Species names were abbreviated: (*A. ope.*) *Aequipecten opercularis*; (*B. und*) *Buccinum undatum*; (*N. ant*) *Neptunea antiqua*; (*O. oph*) *Ophiura ophiura*; (*A. rub*) *Asterias rubens*; (*P. pri*) *Pagurus prideaux*; (*P. ber*) *P. bernhardus*; (*M. rug*) *Munida rugosa*; (*L. hol*) *Liocarcinus holsatus*; (*L. dep*) *L. depurator*.

Given the scale of the fishery in the Clyde Sea area, (sub-) lethal injury due to trawling has the potential to affect population dynamics and community processes and this should be addressed in future research.

4.1.2. Damage to echinoderms

All trawled *O. ophiura* sustained damage, indicating that this species is particularly vulnerable to trawling. Only 5% of the individuals lost all arms, compared with 28% reported by Kaiser and Spencer (1995) (who used heavy beam trawls which penetrate the sediment deeper than otter-trawls and can be expected to cause more damage to this surface-recessed species). Experimental studies revealed 100% mortality in *O. ophiura* 14 d after trawling (Bergmann and Moore, 2001b) emphasising this species' vulnerability to trawling. Franceschini et al. (1999) also showed that *O. ophiura* passing through the mesh of the cod-end sustained more damage than those retained in the catch, indicating high mortality of cod-end escapees.

The frequency of damage to *A. irregularis* was more than 15% higher than that reported from the Irish Sea (Kaiser and Spencer, 1995) possibly as a result of longer tow durations and higher total catches in our study (62–270 min cf. 30 min). This species has a rigid morphology rendering it more susceptible to fracture (35%) than the more flexible common starfish *A. rubens* (30%) (Kaiser and Spencer, 1995). The most frequent damage sustained was loss of an arm (16%). While studies in the Irish Sea have yielded similar results (Kaiser and Spencer, 1995), the frequency of damage found in starfish from the North Sea was lower (De Graaf and De Veen, 1973), possibly as a result of different tow durations and fishing gear used. Bergmann and Moore (2001b) have shown that injury significantly reduces the survival of *A. rubens*, and Ramsay et al. (2001) also found that wounded individuals undergo further arm severance. Sub-lethal predation and regeneration may lead to a reduction in the pyloric caeca, loss of gonads, decrease in locomotory abilities and nutrient acquisition and could have significant effects at both population and community levels (Lawrence and Vasquez, 1996).

4.1.3. Damage to molluscs

Very few *A. opercularis* incurred injury, and damage was restricted to chipping of the outer shell margin. Kaiser and Spencer (1995) reported high survival rates (90%) for this well-protected species. By contrast, half of the whelks *N. antiqua* sustained damage, though this was limited to chipping of the outer lip. Seeing that it is difficult to discriminate between shell damage inflicted by trawling and predators (Ramsay et al., 2000) care was taken to assess fresh damage only. It cannot be excluded, however, that some of the whelks examined may have been recently damaged by predators or when attacking bivalves (Nielsen, 1975). The more brittle-shelled whelk species *B. undatum* sustained higher frequencies of mild and medium damage but injury was less severe than has been reported in whelks caught by beam trawls in the North Sea (Mensink et al., 2000). Since the survival of whelks discarded in the *Nephrops* fishery is high (Bergmann, 2000) and *B. undatum* can repair chipping damage within six weeks (Mensink et al., 2000), the resulting shell scars could possibly be utilised to indicate past fishing intensity, similar to an approach taken by Witbaard and Klein (1994) and Kaiser et al. (2000) using scars on bivalve shells.

4.2. Separating the effects of predictors on damage sustained

The GLMs were only partially successful because of confounding influences. The impact of autocorrelation might be lessened by more careful survey design in future studies. Nevertheless, we have shown that damage to invertebrates is dependent upon multiple factors (gear, depth, animal size), which should be assayed in more detail separately before sensible management policies can be proposed.

Damage to *A. opercularis*, *O. ophiura* and *A. rubens* increased significantly with animal size. Having a larger body surface presumably increases the probability of being damaged during the fishing process. On the other hand, small *B. undatum* and *L. holsatus* were more prone to damage, probably as a result of their thinner shells or carapaces (Kaiser and Spencer, 1995). Similarly, Gilkinson et al. (1998) suggested size-related severity of damage to trawled bivalves.

Four species showed a seasonal pattern in their susceptibility to damage, possibly due to seasonal behavioural changes. *Neptunea antiqua*, a sluggish whelk that spends much of its time partially buried in the sediment, forms breeding aggregations from February to October to deposit egg clusters on conspecifics or other hard substrata (Pearce and Thorson, 1967). During this particular time, *N. antiqua* may be more vulnerable to trawl-inflicted damage as a result of its position (Martel et al., 1986) in relation to the trawl. *L. holsatus* caught in the winter were smaller and this probably contributed to their higher frequency of damage then. It could be argued that 'month' should have been treated as a circular rather than a continuous variable as it seems surprising that, for example, damage sustained by *P. bernhardus* was highest in January and decreased over the course of the year to its lowest point in December. If a longer time-series had been available, we would have attempted this together with circular predictors, e.g. harmonics. Fitting a long-term trend (year) plus cyclical seasonality with the current data set, however, would have led to misleading results, given that factors such as depth, tow duration, etc. were also modelled.

While *A. opercularis* caught in deeper waters showed higher frequencies of damage, the reverse was true for *P. prideaux*. The increased hauling time or composition of catches from different depths could contribute to this pattern. Differing size distributions at different depths may also have led to the trend observed.

The type of vessel used had a significant effect on damage sustained by the majority of species. Capture by the twin rigger (Vessel 4) increased the damage to a range of species. This may have considerable implications since the proportion of twin riggers in the fishing fleet is increasing; but these results have to be treated with caution, as sampling was limited to one occasion only (Table 2) reducing the sample size and causing confounding errors. For instance, twin rigger catches were much larger, so that interactions between vessel type and total catch cannot be sensibly assayed. Additional sampling is needed to test these findings. Capture by Vessel 3 increased the probability of damage to *O. ophiura*. Further analysis implied that the main cause of this pattern was the use of a clean net, the groundrope of which digs deeper into soft sediments and was usually used in combination with tickler chains. The detrimental effects of tickler chains have been demonstrated by De Graaf and De Veen (1973) and Van Beek et al. (1990).

There was a positive correlation between tow duration and damage to *M. rugosa* and *A. rubens*, with longer tow durations increasing the chances of damage by direct contact with items in the catch and the fishing gear. However, Kaiser and Spencer (1995) found no such correlation. Their smaller range of tow durations tested, low number of replicate tows (with 1 and 2 h tows) and their use of a heavy beam trawl could have masked the correlation found in our study. The probability of damage to *O. ophiura* decreased slightly with tow duration and is probably an artefact caused by confounding with other variables.

In six out of ten species, total catch (volume) was an important variable affecting injury. There was a positive correlation between tow duration and damage sustained by *L. depurator*, *P. prideaux*, *A. rubens* and *A. opercularis*; large heavy catches increased the probability of injury during the tow itself as well as of compression upon hauling and whilst on deck. In contrast, larger catches decreased the probability of damage to *B. undatum* and *P. bernhardus*. A larger catch could cushion the shells, when the cod-end content is released on deck, thus limiting damage to the shells of *B. undatum* and *P. bernhardus*. Again confounding due to the survey design cannot be completely ruled out, although examination of the data along the trajectories of each covariate indicated no obvious causes for concern. Such difficulties in interpretation again highlight the need to carry out more detailed 'randomised' experiments in future so that effects can be separated more confidently.

Our study has established that *Nephrops* trawling causes extensive physical damage to epifaunal invertebrates, the extent of which is influenced largely by morphological and possibly behavioural characteristics of the invertebrates as well as by the fishing gear used and total catch volume. While much of the damage incurred is capable of repair (e.g. regeneration of limbs), injury has been shown to affect discard survival adversely and sublethal effects might significantly impair fitness in frequently trawled individuals and populations.

The sheer abundance of the species considered in our study, however, after four decades of increasing fishing effort for *Nephrops* suggests that adverse effects may be countered by advantages such as an increased mortality of predators and competitors due to trawling (Ramsay et al., 1997) and is certainly testimony to the resilience of the species remaining on the fishing grounds. Furthermore, low catch efficiency of *Nephrops* trawl for the epibenthic invertebrates studied here may have contributed to such resilience. Future studies on the catch efficiency of *Nephrops* trawls for epibenthic invertebrates and effects of injury at a population level are needed to elucidate community effects. Unfortunately, the lack of quantitative historical data sets and of unfished control areas makes it difficult to evaluate the impact of trawling on what were probably the most vulnerable species, such as erect sea pens (e.g. *Virgularia mirabilis*, *Pennatula phosphorea*), cnidarians (e.g. *Bolocera tuediae*, hydrozoans) or the starfish *Luidia ciliata*. However, while the numbers of these species caught in our trawls were too low for reliable damage assessments, their low capture rates could in itself point to their vulnerability and further emphasise the need for the establishment of no-take zones, though they would probably need to be extensive (ca. 20% of the area fished) to have any effect (Watson et al., 2000).

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