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Utilisation of invertebrates discarded from the *Nephrops* fishery by variously selective benthic scavengers in the west of Scotland

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ABSTRACT: Demersal trawl fisheries generate large quantities of discards which temporarily increase the amount of carrion available to benthic communities and lead to a faster energetic turnover. This study examines the availability of discarded material to the benthos, assesses consumption times of different items and identifies scavengers attracted to those invertebrates most frequently discarded from Clyde Sea *Nephrops* trawlers. In field and laboratory trials, heavy-shelled dead whelks (*Buccinum undatum*, *Neptunea antiqua*) sank faster than softer-bodied species like cephalopods (*Allotheuthis subulata*, *Rossia macrosoma*) or echinoderms (*Ophiura ophiura*, *Asterias rubens*), making most discards available to the benthos (at ca. –60 m CD [chart datum]) within minutes after discarding. SCUBA and time-lapse camera observations in the Clyde Sea and Loch Sween indicated bait utilisation times between 24 and 48 h. Fast-moving animals like brachyuran crabs were the first to arrive at discard bait piles whose composition mimicked typical discards from the Clyde Sea *Nephrops* fishery. Bimonthly deployments of traps baited with invertebrate discards in the north of the Clyde Sea showed that *A. rubens*, followed by *Pagurus bernhardus*, *Liocarcinus depurator* and whelks, were the most abundant megafaunal scavengers. Fine-meshed funnel traps deployed inside those creels yielded up to 2819 amphipods per trap, with *Scopelocheirus hopei* and *Orchomene nanus* accounting for most of the catch. Together with whelks, *A. rubens* and *Carcinus maenas*, *O. nanus* showed a clear preference for crustacean bait. By contrast, *Pagurus bernhardus* was more attracted to *A. rubens* and, in 1 trial, to *O. ophiura* bait. Traps deployed in the south of the Clyde Sea yielded generally lower numbers and species diversity in the catch, with *Nephrops* being the most abundant megafaunal scavenger. It showed a preference for *L. depurator* and conspecific bait. While the results show that a range of epibenthic species readily utilise invertebrates discarded from Clyde Sea *Nephrops* trawlers, it is unknown to what extent discards subsidise benthic communities as information on the ecological energetics of the species involved locally is currently lacking.

KEY WORDS: Carrion · Discards · *Nephrops norvegicus* · Scavengers · Trawling · Scotland

INTRODUCTION

The environmental effects of fishing have received increasing attention recently (see reviews by Jennings & Kaiser 1998, Hall 1999, Moore & Jennings 2000). Demersal fishing gear such as otter trawls are designed to capture bottom dwelling target species but also modify habitat structure and inevitably catch or damage benthic non-target species that occur in the same habitat. Alverson et al. (1994) estimated that commercial fisheries produce 27 million t yr^{-1} discards worldwide, representing some 27% of the global marine landings. Discards are by-catch organisms that are returned to the sea because, for various reasons, they are considered undesirable. They are either unmarketable species, below minimum landing size (MLS), of inferior quality, or surplus to quota. The highest rates of discarding have been attributed to shrimp

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trawl fisheries, with an estimate of 9.5 million t yr^{-1} (Alverson et al. 1994).

The Norway lobster or 'scampi' *Nephrops norvegicus* (L.) (hereafter referred to by genus alone) is the most important commercial shellfish resource in UK waters, being worth over 72 million Euro at first sale value, and is extensively exploited throughout Europe (Marrs et al. in press). The NE Atlantic *Nephrops* trawl fishery ranks as number 5 among the top 20 world fisheries with the highest recorded discard ratios (number of discards per targeted landings = 1.7) (Alverson et al. 1994). The Clyde Sea (Scotland) *Nephrops* fishery alone generates 25 000 t yr^{-1} of discards, with 9 kg produced per kg of *Nephrops* landed (Wieczorek et al. 1999, Bergmann et al. 2000). Invertebrates account for up to 90% of the discards, of which crustaceans and echinoderms are the major groups (Bergmann et al. 2000). Exposure to air, temperature changes and sunlight results in physiological stress and injury of many of the discarded organisms (Fonds 1994, Kaiser & Spencer 1995, Bergmann & Moore 2001a,b, Bergmann et al. 2001a,b).

At the water surface, discarded animals are consumed by scavenging seabirds, notably gulls (Garthe et al. 1996, Furness et al. 1997). Wieczorek et al. (1999) estimated that 25% of discards from the Clyde Sea *Nephrops* fishery are consumed by seabirds. Scavenging fish and invertebrates may intercept sinking discards or scavenge sedimented discards (Hill & Wassenberg 1990). It is now well established that discards and damaged fauna left in the wake of towed trawls attract a number of piscivorous and invertebrate scavengers (e.g. Britton & Morton 1994, Kaiser & Spencer 1994, Evans et al. 1996, Ramsay et al. 1997, 1998, Kaiser et al. 1998, Groenewold & Fonds 2000, Veale et al. 2000a). Although Castro et al. (1999) and Demestre et al. (2000) have studied the fate of damaged fauna left exposed to predators in tracks from otter trawlers on muddy sea beds in the Mediterranean, little is known about the fate of discarded carrion on similar sea beds elsewhere.

While previous work has highlighted the ecological importance of several facultative and obligate scavenger species in the Clyde Sea area (Nickell & Moore 1991, Moore & Wong 1995a,b, Wong & Moore 1995), no inference has been made regarding the ecological effects of the increased availability of carrion, i.e. energy subsidies, due to local trawling and discarding practices. In this study, the term 'scavengers' refers to facultative scavengers unless stated otherwise.

Between 1998 and 1999, almost 70% of the mud substratum in the Clyde Sea was trawled more than once by only 18 trawlers out of a *Nephrops* fleet of between 40 and 80 (Marrs et al. in press). As fishermen discard animals from the previous catch whilst towing, it can be assumed that the majority of the Clyde Sea area is in frequent receipt of an extra input of carrion and this could affect benthic community structure and food webs. Here, we study the fate of invertebrates that are frequently discarded by *Nephrops* trawlers once they reach the sea bed. The sinking rates of typical discard components of Clyde Sea trawls (Bergmann et al. 2000) were assessed in order to evaluate the availability of discards to animals at the sea bed. Baited time-lapse camera and divers' observations were used to establish utilisation times and to study the succession of scavengers. The composition of benthic scavengers that is responsible for the reprocessing of discards was studied by seasonal deployments of baited traps.

MATERIALS AND METHODS

Four field experiments were carried out: (1) to establish the sinking rates of invertebrate discards; (2) to identify the consumers of 4 important discard species; and (3) to determine the utilisation time of discards *in situ* in the Clyde Sea area and Loch Sween (Fig. 1).

Sinking rates. Sinking rates were established by SCUBA divers off Keppel Pier at the University Marine Biological Station, Millport (UMBSM), UK, in ca. –3 m

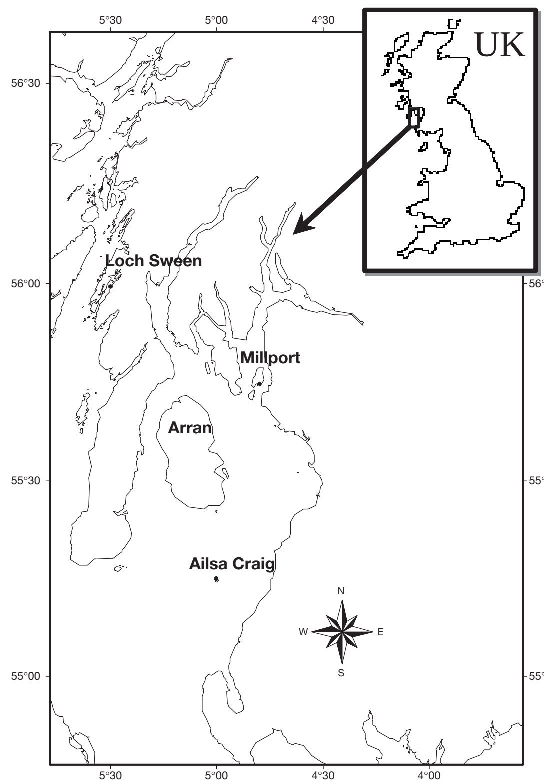


Fig. 1. Map of the Clyde Sea area showing experimental sites

CD (chart datum) at slack water, as well as under static water conditions in an aquarium (0.85 m water depth). Where possible 20 (but a minimum of 6) individuals per species of haphazardly selected size were used. All organisms were frozen dead, and defrosted unless stated otherwise. Where individual items floated, a sinking rate of 0 was assumed in the calculations.

Utilisation time. Discard utilisation times were established using a baited time-lapse camera (TLC) (Kongsberg-Simrad) deployed at ca. –7 m CD off Keppel Pier (UMBSM). The camera system consisted of a remote-controlled colour camera (no. OE1366) with a zoom lens, a modified surface control unit (no. OE1232), and 30 m of umbilical cable (type NC-13). A far-red light (Kongsberg-Simrad) and a Panasonic S-VHS time-lapse VCR were used for filming at night. The system was mounted on a cradle constructed from galvanised Dexion angle-frame. Standardised batches of bait of a representative Clyde Sea discard composition (Bergmann et al. 2000) (Table 1) were placed by SCUBA divers at the base of the TLC frame, filling the camera's field of view. The time taken for all discards to be consumed or removed from the field of view was recorded as utilisation time in 2 such deployments in September 1998. The TLC recordings were terminated when scavengers had processed most of the bait.

Succession of benthic scavengers. In October 1998, discard utilisation time and the role of individual scavenger species in discard processing were investigated by SCUBA diving. Batches of discards of a standardised representative composition (Bergmann et al. 2000) (Table 2) were placed inside the centres of 6 replicate metal rings (2.5 m in diameter), each fixed to 4 legs with flat bases to allow them to sit approximately 20 cm above the muddy substratum of a *Nephrops* ground in Loch Sween, Argyll (56° 01′ N, 05° 36′ W), at ca. –15 m CD. The bait composition varied slightly from that used in the 'utilisation time' experiment as the same species composition was not available for both experiments. At the beginning of the experiment (t_0), the megafauna present in each ring was recorded as background density. On 4 successive dives (2, 4, 6 and 24 h after deployment) each ring was visited by divers and note taken of animals present, scavengers feeding on discards and the state of the remaining bait. The $\log_{10}(x+1)$ transformed data (to achieve a normal distribution) were analysed for differences in abundance between visits for each species by analysis of variance (ANOVA) and a post hoc Tukey-Kramer multiple comparison test (Minitab). The significance criterion in all tests was $p < 0.05$.

Baited trap experiments. Two fleets of 30 standard *Nephrops* creels (mesh size 18 mm) each containing 1 baited funnel trap (Fig. 2) (see Nickell & Moore 1991, Moore & Wong 1995b) were deployed bimonthly between October 1998 and August 1999 in the Fairlie Channel off Clashfarland Point (ca. 55° 45′ N, 04° 53′ W), Isle of Cumbrae, on a muddy bottom. Traps were set out at ca. –45 m CD halfway through the lunar cycle to control for lunar phase and left for 48 h to allow for changing tidal currents or diel effects. Whilst larger scavengers were trapped in the creels, smaller organisms, such as isopods and amphipods, were captured in the funnel traps, which each contained a single bait bag.

The bait included 2 crustacean (*Liocarcinus depurator* [L.], *Munida rugosa* [Fabricius]) and echinoderm

Table 1. Standardised composition of discard bait used in time-lapse camera deployments, representative of north Clyde Sea trawls (for taxonomic authorities see Howson & Picton 1997)

Species	n
Nephrops 'heads'	40
Nephrops whole animals	10
Munida rugosa	2
Liocarcinus depurator	9
Pagurus bernhardus (without shell)	1
Crangon allmanni	9
Pandalus sp.	1
Asterias rubens	7
Astropecten irregularis	1
Ophiura ophiura	26
Sepietta oweniana	1
Merlangius merlangus	3
Eutrigla gurnardus	1
Pleuronectes platessa	4
Limanda limanda	1
Hippoglossoides platessoides	1
Glyptocephalus cynoglossus	1
Total	108

Table 2. Standardised composition of discard bait used in SCUBA experiment, representative of north Clyde Sea trawls (for taxonomic authorities see Howson & Picton 1997)

Species	n
Asterias rubens	2
Crangon allmanni	18
Limanda limanda	1
Liocarcinus depurator	17
Merlangius merlangus	1
Munida rugosa	1
Nephrops 'heads'	24
Nephrops whole animals	20
Ophiura ophiura	8
Pleuronectes platessa	2
Rossia macrosoma	4
Total	98

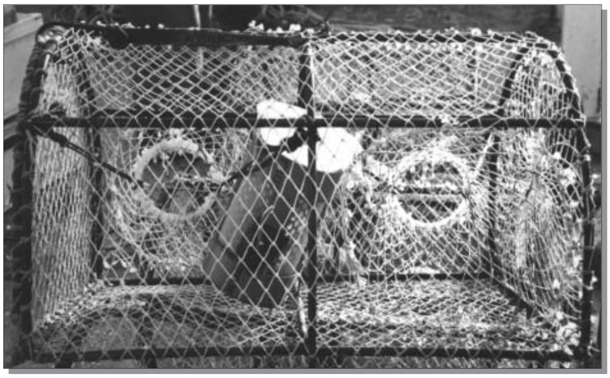


Fig. 2. Set-up used in baited trap experiments: commercial *Nephrops* creel containing a funnel trap with a bait bag inside (Nickell & Moore 1991, Moore & Wong 1995b)

species (*Asterias rubens* L., *Ophiura ophiura* [L.]) that proved to be the most abundant invertebrates discarded from Clyde Sea *Nephrops* trawlers in earlier studies (Bergmann et al. 2000). Animals obtained from recent trawls were weighed (100 g crustaceans or *A. rubens* and 80 g *O. ophiura* per bag) and injured in a standard manner by puncturing each (dead) individual before transferring animals into velcro-sealed bait bags (13×16 cm) made of plankton net (mesh size 0.5 mm) and stored in a freezer. Identical empty bait bags were used as controls in each trial. Two fleets of creels were shot in parallel lines at an angle of 45° to the predominant current to ensure an even distribution of bait odour without exposing the creels to the hazards of trawling in the adjacent channel. To assess the effects of creel position within fleets, each fleet was divided into 3 sections (blocks) of 10 creels each. Each block contained 2 replicate treatments arranged in randomised positions within the block, giving a total of 12 traps per treatment.

The discard composition from trawls in the south of the Clyde Sea is different to that from the northern Clyde Sea in that the catch contains significantly higher quantities of undersized *Nephrops* and *Nephrops* 'heads' (cephalothoraces) (Bergmann et al. 2000). Therefore, an additional trial was carried out in the south of the Clyde Sea off Ailsa Craig (55° 20′ N, 05° 20′ W) at ca. – 45 m CD in November 1998. Each of the 2 fleets contained 6 replicate creels each baited to correspond with the local discard composition, either with *Nephrops* 'heads', whole *Nephrops*, *Liocarcinus depurator*, *Asterias rubens* or empty bait bags (control). After 48 h, the creels were lifted and megafauna present in each creel recorded. On return to the laboratory, the funnel traps were transferred into tanks supplied with running seawater and organisms were preserved in formalin within 2 d. All scavenger count data were $\log_{10}(x + 1)$ transformed prior to analysis to achieve a normal distribution. The data were examined for differences in the numbers of individuals (per species) caught in traps baited with different discard species by multi-factorial ANOVA with 'block', 'fleet' and 'treatment' as fixed factors or general linear models (GLM) and a post hoc Tukey-Kramer test.

RESULTS

Sinking rates

Sinking rates of invertebrate species measured by SCUBA divers matched those recorded in aquarium trials (Table 3), with heavy-shelled species, such as whelks (*Buccinum undatum* L., *Neptunea antiqua* [L.])

Table 3. Mean sinking rates of dead frozen then defrosted invertebrates most frequently discarded from Clyde Sea *Nephrops* trawlers measured *in situ* and *in aquaria*. na = not available

Species	Mean sinking rate laboratory (cm s^{-1})	n	Mean sinking rate field (cm s^{-1})	n
Nephrops whole animals	11.6	20	10.6	18
Nephrops 'heads'	10.3	19	na	
Munida rugosa	10.5	19	11.2	5
Munida rugosa (alive)	na		34.1	6
Liocarcinus depurator	10.9	20	12.4	8
Liocarcinus holsatus	11	21	na	
Alloteuthis subulata	6.1	21	4.9	3
Rossia macrosoma	8	8	na	
Buccinum undatum/*Neptunea antiqua*	25.8	8/2	36.2	11/10
Aequipecten opercularis	na		23.2	9
Aphrodita aculeata	11	20	11.8	6
Ophiura ophiura	9	20	na	
Asterias rubens	na		8.3	19

sinking faster (25.8 and 36.2 cm s^{-1}, respectively), than softer-bodied species like *Allotheuthis subulata* (Lamarck), *Rossia macrosoma* (delle Chiaje), *Ophiura ophiura* or *Asterias rubens* (4.9 to 9.0 cm s^{-1}). Sinking rates recorded for live *Munida rugosa* were 3 times higher (34.1 cm s^{-1}) than those of dead squat lobsters (11.2 cm s^{-1}), probably due to the live animal's active tail flipping.

Utilisation time

The first deployment was completed after 48 h, with only some pieces of empty *Nephrops* exoskeleton, claws and *Ophiura ophiura* oral discs remaining. The first bait items utilised were roundfish discards that were fed upon and dragged away by brachyuran crabs. The second TLC deployment was completed within only 28 h as the bait was utilised much faster than in the previous experiment. The predominant scavengers observed in both deployments were *Asterias rubens* and *Carcinus maenas*.

Succession of benthic scavengers

Bait items were processed as soon as they were placed inside the experimental rings, with crangonid shrimps and brachyurans (such as *Carcinus maenas* and *Liocarcinus depurator*) being the first scavengers to arrive (Figs. 3 & 4). Merely 6 h after deployment, all fish and most of the crustacean bait had been removed and after 24 h only fragments such as crustacean limbs and ophiuroid discs remained.

Figs. 3 & 4 illustrate the abundance of the dominant scavengers recorded over a 24 h observation period. The total number of scavengers recorded on successive dives did not differ statistically between observations ($p = 0.222$) although numbers increased until 6 h after the start of the experiment (reaching mean densities of 11 to 12 animals per ring) and decreased thereafter (Fig. 4).

Small numbers of gobies (*Pomatoschistus minutus* (Pallas) and *Gobius niger L.*) and *Asterias rubens* were present around the bait throughout the experiment, and showed a similar pattern to that of the total number of scavengers: population densities increased over the first 3 visits following deployment, peaked at 6 h and decreased after 24 h (Fig. 4). Crangonid shrimps were first observed in the baited rings 2 h after deployment and numbers decreased thereafter. Differences in their densities were significant between the 2 and 24 h visit only. Notably, mean numbers of the opisthobranch *Philine aperta* (L.) decreased significantly 2 h after deployment ($p < 0.001$), with densities declining to 0 thereafter (Fig. 4) although present in the vicinity of the experimental rings.

Brachyuran crabs (total number of *Carcinus maenas*, *Liocarcinus depurator* and *Cancer pagurus* L.) increased significantly in mean density following bait deployment ($p < 0.001$), reaching a peak after 6 h. Numbers were still significantly elevated after 24 h cf. t_0 (Fig. 3). The densities of *C. maenas* followed a similar pattern, although differences among sampling intervals were not significant ($p = 0.061$). While a similar trend was found for *L. depurator* during the first 3 visits ($p = 0.002$), density decreased to a level lower than the pre-deployment level after 24 h (Fig. 3).

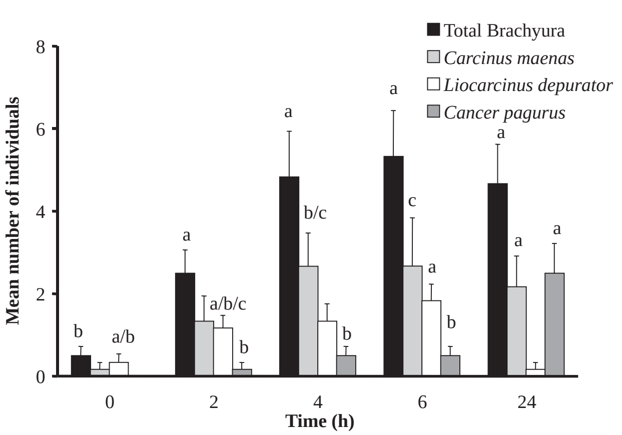


Fig. 3. Mean numbers of brachyuran species recorded in baited 2.5 m rings (n = 6) over 24 h (+SE). Groupings of 'visit' established as significantly different in a Tukey-Kramer test are denoted thus (a), (b) and (c). (a/b) indicates a mean not significantly different from (a) or (b)

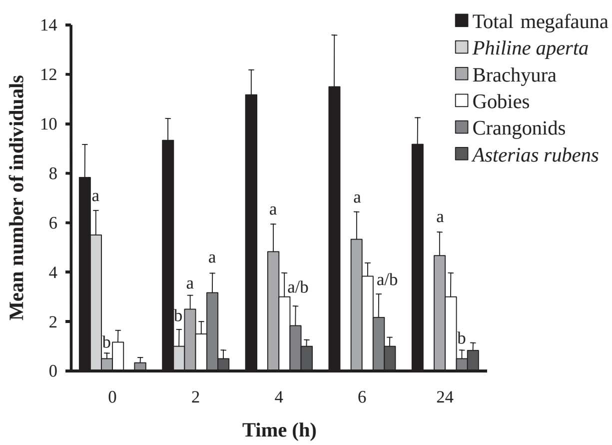


Fig. 4. Mean numbers of megafaunal scavengers recorded in baited 2.5 m rings (n = 6) over 24 h (+SE). Groupings of 'visit' established as significantly different in a Tukey-Kramer test are denoted thus (a), (b) and (c). (a/b) indicates a mean not significantly different from (a) or (b)

Low numbers of *C. pagurus* were first recorded after 2 h, and reached peak numbers 24 h after deployment ($p < 0.001$), i.e. a long time after most of the bait had been removed from the experimental ring. Inter- and intraspecific interactions among scavengers were common, particularly agonistic behaviour between brachyurans.

Baited trap experiments

A minimum of 41 megafaunal species were caught in creels with a total number of individuals per creel that ranged from 0 to 34 (see Appendix 1 for summary of all taxa recorded). Funnel traps yielded higher numbers both in terms of the number of species (minimum of 98) and abundance (1 to 2823 individuals). Here, Crustacea dominated with at least 80 species. Although patterns were shown by a number of species, an account of the most common species only is given here.

Creels

Crustacean bait attracted significantly higher numbers of individuals compared to creels baited with *Ophiura ophiura* and controls during most months (Fig. 5a). While creels deployed in June yielded the highest creel catches (maximum of 538 individuals), funnel trap catches peaked in October with 30 425 animals in total. There was a strong block effect in the June deployment, meaning that more animals were attracted to creels at one end of the fleet.

The mean contribution of *Asterias rubens* to total megafauna catch throughout the year varied from 27 to 44%, and it was the predominant megafaunal scavenger. *A. rubens* had a significant preference for crustacean bait (Fig. 5b). In all but the April deployment, *A. rubens* was caught in significantly higher numbers ($p < 0.001$) in creels baited with crustacean material compared to all other treatments. There were significant block effects in December, February, June and August as starfish were generally attracted more to one end of the fleet of creels while numbers decreased towards the middle and the other end of the fleet. To avoid interference with trawling activities, the creels had to be shot across a slope (ca. 5 to 6 m difference in depth), which could account for the higher catches observed at 1 end of the fleets of creels.

The second most abundant megafaunal scavenger species was *Pagurus bernhardus* (L.), which accounted for mean proportions from 10 to 27% of the total creel catch throughout the year. In the majority of deployments, this species showed a preference for *Asterias rubens* bait although this was only significant in 3 trials (Fig. 5c). It is noteworthy that *P. bernhardus* was the only scavenger recorded in traps baited with *Ophiura ophiura* although this was only statistically significant in February 1999.

Brachyurans, including *Liocarcinus depurator*, *Carcinus maenas* (L.) and *Necora puber* (L.), formed another important group of scavengers that accounted for 16 to 37% of the megafauna that were caught throughout the year. Of all brachyurans, only *C. maenas* (shore crabs) showed a clear and consistent bait preference. Shore crabs were recorded in significantly higher number in creels baited with crustaceans compared to those baited with echinoderms or controls (Fig. 5d). A weak, but significant, block effect ($p = 0.039$) was found in February.

Whelks, *Buccinum undatum* and *Neptunea antiqua*, accounted for a mean proportion that ranged from 5 to 12% of the megafauna throughout the year and were pooled for analysis as both species showed similar trends in their bait preference. They showed a clear preference for crustacean over echinoderm bait and unbaited controls ($p < 0.001$), and higher numbers were found in creels baited with *Munida rugosa* than with *Liocarcinus depurator* although this was not a statistically significant difference (Fig. 5e). Significant block effects were apparent in February, June and August. Deployments in June and April yielded the highest total counts of whelk, of which the majority were *B. undatum* ($n = 143$), whereas *N. antiqua* catches peaked in October ($n = 58$).

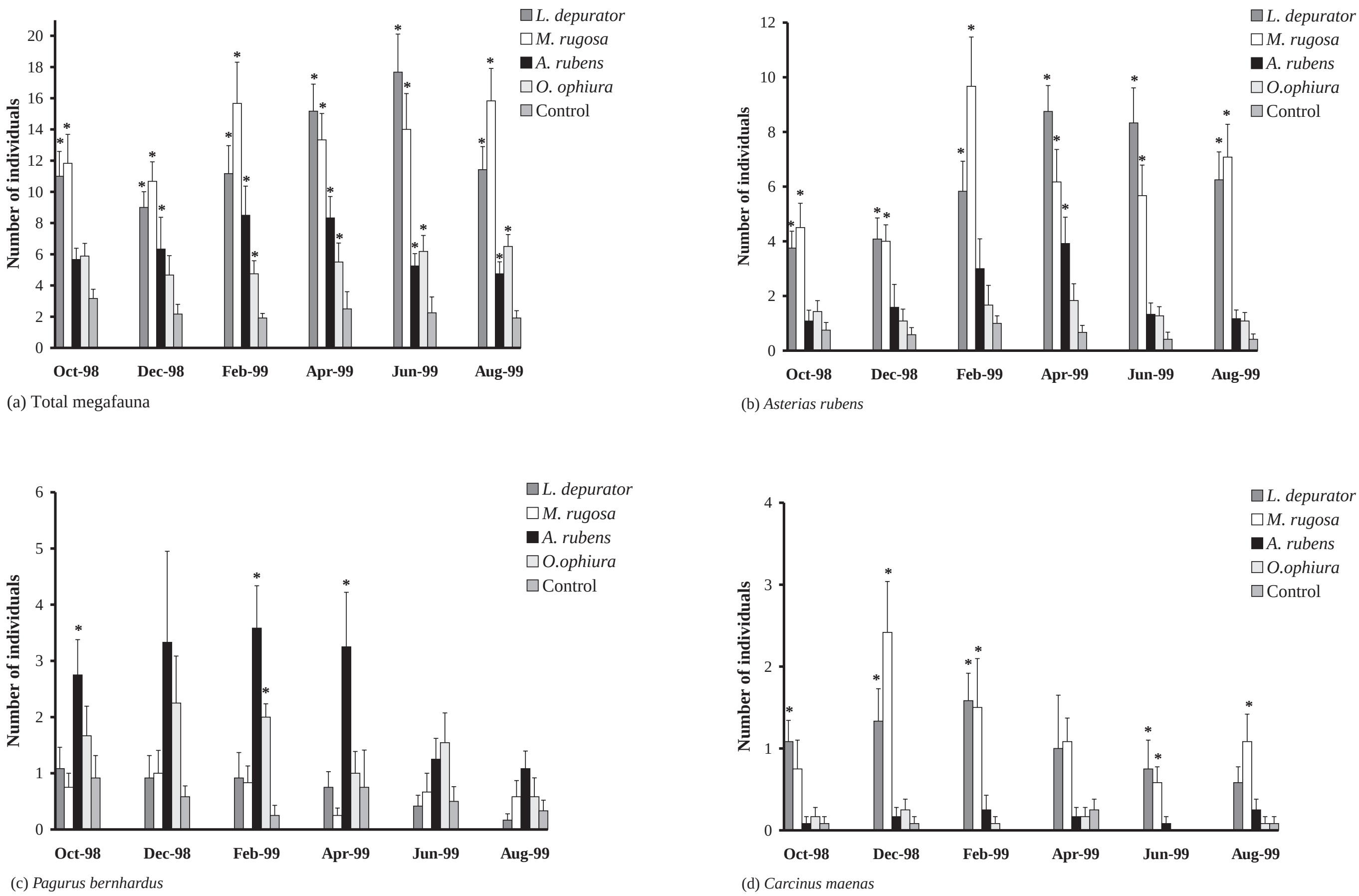
Demersal fish, such as *Myoxocephalus scorpius* (L.) and *Ciliata mustela* (L.), were caught sporadically in creels but formed only about 5% of the creel catches and showed no significant bait preference.

Funnel traps

Samples from funnel traps contained high numbers of foraminiferans, juvenile bivalves, juvenile ophiuroids, crustacean zoea larvae and nematodes that were probably washed accidentally into traps (Appendix 1).

The most significant taxon present in the funnel traps was the Amphipoda, forming 51 to 95% of individuals caught throughout the year. The large standard errors for the amphipod taxa reflect this group's ephemeral nature. The 2 lysianassoid amphipods, *Scopelocheirus hopei* (Costa) and *Orchomene nanus* (Krøyer), accounted respectively for 3 to 67 and 15 to 43% of the animals caught in funnel traps, and composed the largest fraction of the amphipods collected.

In most deployments, *Scopelocheirus hopei* was significantly more abundant in traps baited with crustacean bait, *Liocarcinus depurator* in particular, cf. *Ophiura ophiura* bait and controls (Fig. 6a).



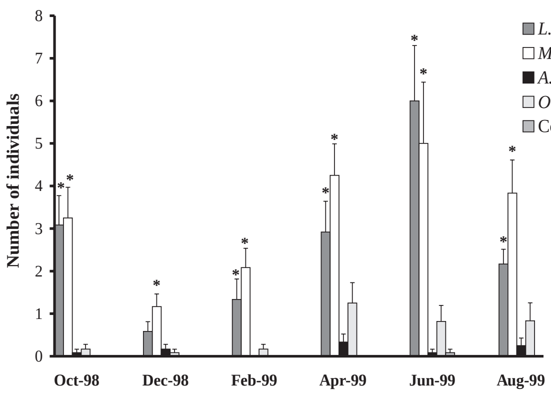


Fig. 5 (a)–(e). Mean total number of individuals caught in *Nephrops* creels baited with 5 different types of invertebrate discards throughout the year (+SE). (a) Total megafauna, (b) *Asterias rubens*, (c) *Pagurus bernhardus*, (d) *Carcinus maenas*, (e) whelks (*Buccinum undatum*, *Neptunea antiqua*). *Mean counts significantly higher than those from controls within each deployment (ANOVA, $p < 0.05$)

Furthermore, a significant preference for traps baited with *Asterias rubens* over controls or *O. ophiura* was found in trials from October to April. In October, the numbers of *S. hopei* attracted to *A. rubens* significantly outnumbered those attracted to *Munida rugosa* and also in December those attracted to any other bait.

Numbers of *Orchomene nanus* were highest in October, peaking at 12 361. This species showed a consistent preference for crustacean bait (Fig. 6b). In most trials, higher numbers were found in traps baited with *Munida rugosa* cf. *Liocarcinus depurator* but this was only statistically significant in April and December. Significant block effects were detected in August, June and a weakly significant Treatment/Fleet/Block interaction in April ($p = 0.048$).

A third amphipod species, the caprellid *Pariambus typicus* (Krøyer) var. *inermis* Mayer, occurred consist-

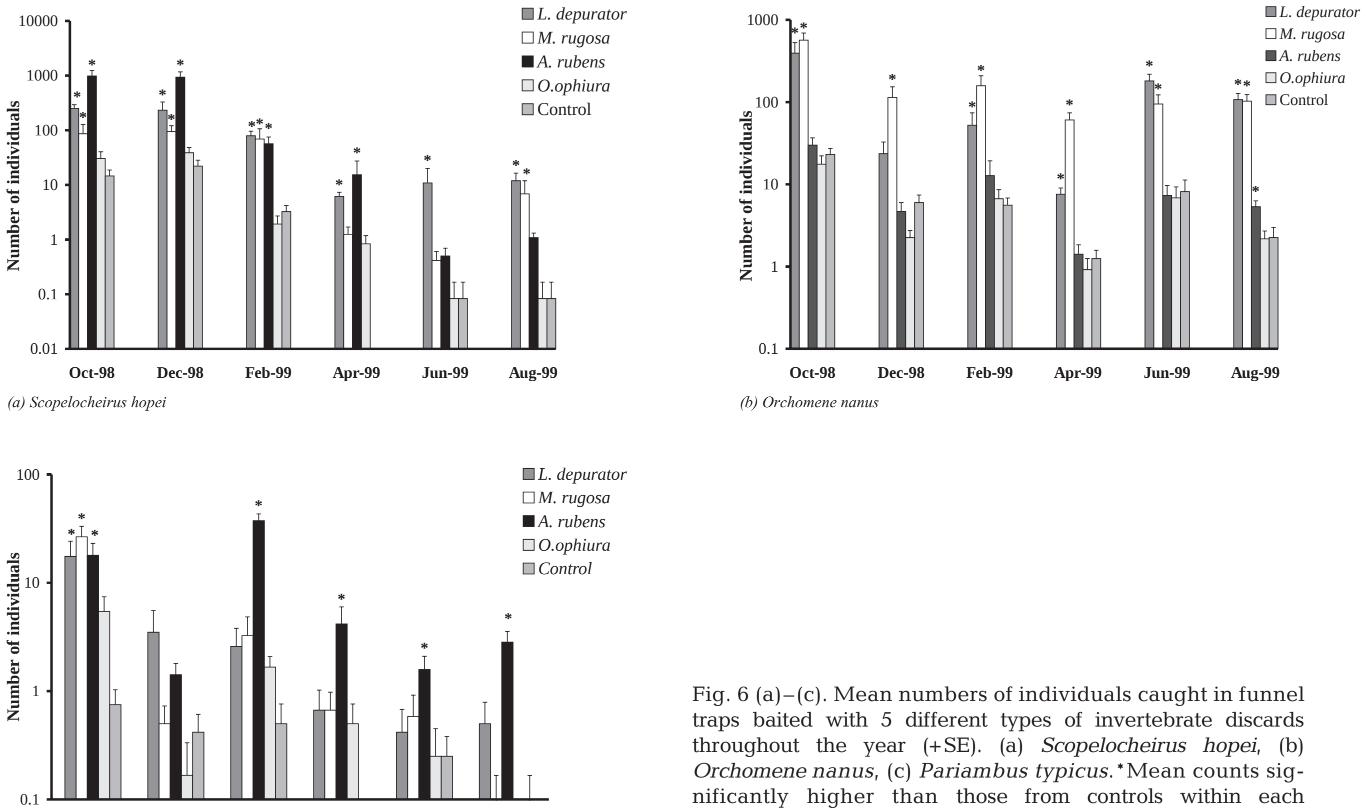


Fig. 6 (a)–(c). Mean numbers of individuals caught in funnel traps baited with 5 different types of invertebrate discards throughout the year (+SE). (a) *Scopelocheirus hopei*, (b) *Orchomene nanus*, (c) *Pariambus typicus*. *Mean counts significantly higher than those from controls within each deployment (ANOVA, $p < 0.05$). Note the logarithmic scale

ently in samples accounting for 0.6 to 12 % of the mean funnel trap counts. *Asterias rubens* bait attracted significantly higher numbers of *P. typicus* than unbaited controls. Additionally, from February onwards numbers attracted to *A. rubens* significantly exceeded those attracted to *Ophiura ophiura* bait and, in February and August, exceeded those of all other bait treatments (Fig. 6c). Significant block effects were detected in June.

Southern Clyde Sea deployment

The creel deployment in the southern Clyde Sea area yielded lower numbers of trapped animals, 77 individuals in total belonging to only 5 species (*Nephrops*, *Liocarcinus depurator*, *Asterias rubens*, *Trisopterus luscus* [L.] and *Merlangius merlangus* [L.]). With a mean of 48 % (±6.2 SE), *Nephrops* accounted for the majority of animals caught and was found in significantly higher numbers in creels baited with *L. depurator* compared with *Nephrops* 'heads', *A. rubens* and control treatments (Fig. 7). Bait of whole *Nephrops* discards also attracted significantly more conspecifics than controls.

High numbers of amphipods were caught in funnel traps in the southern Clyde Sea area also, *Scopelocheirus hopei* accounting for the majority of individuals (93 % ±1.2 SE) (Fig. 8). Numbers of both 'total Amphipoda' and *S. hopei* were higher in creels baited with *Asterias rubens* (with means of 657 and 653 individuals per trap, respectively), than for those baited with *Liocarcinus depurator* (403 and 398 individuals), whole *Nephrops* (368 and 357 individuals) or *Nephrops* 'heads' (319 and 311 individuals). Although highly significant overall

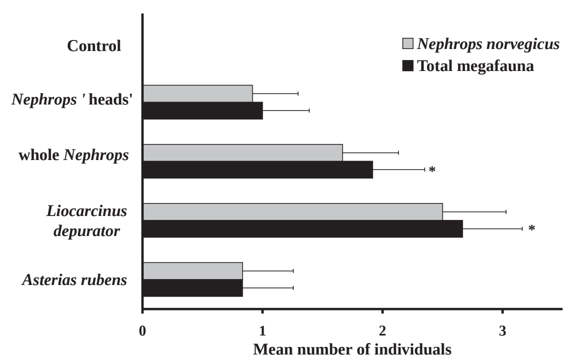


Fig. 7. Mean numbers of total megafauna and *Nephrops* caught in creels baited with 5 different types of invertebrate discards in the south of the Clyde Sea area (+SE). *Mean counts significantly higher than those from controls within each deployment (ANOVA, $p < 0.05$)

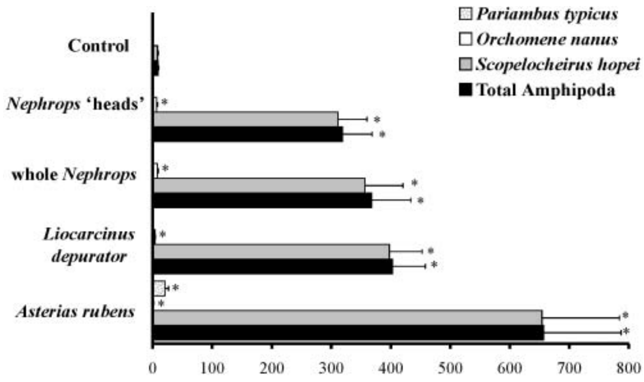


Fig. 8. Mean numbers of amphipod species caught in funnel traps baited with 5 different types of invertebrate discards in the south of the Clyde Sea area (+SE). *Means significantly higher than those from controls (ANOVA, $p < 0.05$)

treatment effects were found ($p < 0.001$), the variance was explained by differences between bait treatments versus controls alone.

Numbers of *Orchomene nanus* were low in all south Clyde Sea treatments (< 10 per trap), but were significantly higher ($p < 0.001$) in traps baited with whole *Nephrops* (7.8), *Nephrops* 'heads' (6.6) and *Liocarcinus depurator* (3.8) cf. *Asterias rubens* bait (1.3) or controls (0.3) (Fig. 8). Although only found in low numbers (mean count of 4.2 individuals per trap), *Pariambus typicus* once again showed a significant preference for *A. rubens* bait over all other treatments ($p < 0.001$), with up to 61 individuals caught per trap.

DISCUSSION

The results of this study demonstrate that invertebrate discards fall to the sea bed rapidly, where they are readily consumed by megafaunal scavengers and amphipods.

Sinking rates

The fact that live *Munida rugosa* had sinking rates 3 times higher than those of dead conspecifics has important implications as escape from predators becomes more likely. Short-term mortalities of trawled *M. rugosa* and *Liocarcinus depurator* in the Clyde Sea ranged from 2 to 25% (Bergmann & Moore 2001a), indicating that a high percentage of discarded crustaceans may be able to escape from surface predators. Although Wieczorek et al. (1999) found little evidence of mid-water scavenging (using baited long-lines), seals were frequently observed to follow Clyde Sea trawlers (M. Bergmann pers. obs.) possibly feeding on discards or organisms that passed through the mesh of the cod-end. Concurring with studies by Wassenberg & Hill (1990) in Australia, the majority of the material discarded in the Clyde Sea can be assumed to reach the sea bed within a few minutes (at depths of 50 to 60 m), where it becomes available to benthic scavengers.

Utilisation time

The rate of consumption of carrion varies with the background density of scavenging species (Ramsay et al. 1997). The shorter utilisation time in the second trial (28 h) could have been a result of the camera being deployed at the same location as in trial 1 (ca. 24 h later), i.e. an already elevated background density of scavengers may have existed (although scavengers had been scattered by SCUBA divers prior to the second trial). The siting of the camera was limited by cable length to the only power source available. The divers' observations of bait utilisation times in Loch Sween corresponded well with those found in the TLC deployments. While similar consumption rates have been found in the Mediterranean (Castro et al. 1999) with only fish bones remaining after 24 h, Ramsay et al. (1997) reported that only 60% of fish bait was utilised in 38 h, indicating longer processing times in the Irish Sea, possibly due to differences in temperature, depths or scavenger background density.

High densities of the cirolanid isopod *Natatolana borealis* reduced small gadoid fish to skeleton in 1 h in the north Adriatic Sea (Wieczorek et al. 1999). While *N. borealis* occurred only sporadically in our funnel traps, it has been recorded as a significant consumer of *Nephrops* discards, fish and other crustaceans in deeper Clyde Sea waters (Wong & Moore 1995, Wieczorek et al. 1999). During the discarding process from commercial vessels, bait items are likely to be broadcast widely in a haphazard way (Castro et al. 1999), making shorter utilisation times than those observed in the present study (using bait piles) likely as the odour is spread over a wider area.

Succession of benthic scavengers

The 2 highly mobile brachyurans *Carcinus maenas* and *Liocarcinus depurator* were typically the first species to arrive at the carrion, as was *L. depurator* in the Irish Sea (Ramsay et al. 1997). Surprisingly few *Pagurus bernhardus* were encountered in Loch Sween unlike in other studies (Ramsay et al. 1997, 1998, Kaiser et al. 1998, Wieczorek et al. 1999), or of our creel catches in the Clyde Sea. While *L. depurator*, *C. mae-*

nas and crangonid shrimps had previously been frequently observed in underwater TV surveys of the *Nephrops* grounds in Loch Sween (Atkinson 1988), the same author reported that *P. bernhardus* were not common in this area. The opisthobranch *Philine aperta* left the experimental ring as brachyurans arrived, perhaps indicating avoidance of carrion or of potential predators by this shell-less gastropod. This might be the first record of an organism actively vacating the vicinity of sea bed carrion. Slow moving *Asterias rubens* and *Buccinum undatum* were among the last species to arrive at the discard bait (Ramsay et al. 1997).

Similar to the findings of Nickell & Moore (1991), no clear seasonal trends in Clyde Sea creel catches were observed for most of the species in our study. The predominant megafaunal scavenger species attracted to invertebrate discards concur with reports from the Irish and North Seas (Kaiser & Spencer 1994, Ramsay et al. 1997, 1998, Groenewold & Fonds 2000) although higher numbers and a greater diversity of fish were recorded in those studies. Possibly, the experimental designs used here (TLC rig, creels, metal rings, diver presence) could have deterred demersal fish that have been observed feeding on exposed fauna in dredge tracks in the nearby Stravanan Bay (Hall-Spencer & Moore 2000).

Baited trap experiments

Creels

Taking all north Clyde Sea creel catches together, *Asterias rubens* was the predominant megafaunal species. It showed a clear and consistent preference for crustacean bait. Groenewold & Fonds (2000) similarly reported Manly α indices of bait preference for crustacean, molluscs or fish bait in this species. Since crustaceans represent a high proportion of the material discarded in the Clyde Sea, starfish may switch from other prey types to crustacean carrion and these discards could subsidise starfish populations. In food-limited systems, it could provide starfish with the additional nutrients required for gonad growth and gametogenesis although the reproductive benefit would need to surpass the fishing mortality of starfish (Bergmann & Moore 2001b).

The next most frequent scavenger species caught in creels was *Pagurus bernhardus*. Its preference for *Asterias rubens* and *Ophiura ophiura* bait concurs with the findings of Gorzula (1976), who observed *P. bernhardus* feeding on brittlestar arms (*Ophiocomina nigra*) (see also Groenewold & Fonds 2000). This could also explain the aggressive behaviour of *P. bernhardus* towards *A. rubens* observed in recently trawled areas by Ramsay et al. (1997).

In accordance with other studies from the Irish, Clyde and Adriatic Seas (Ramsay et al. 1997, 1998, Wieczorek et al. 1999) *Liocarcinus depurator* outnumbered all other brachyuran scavengers. While Groenewold & Fonds (2000) found that *L. depurator* showed significant bait preferences in the North Sea this was not true in our study, perhaps because neither molluscs nor fish were offered as alternative baits (present study). It should also be noted that a previous experiment using the same creels as cages for *L. depurator* indicated poor crab retention as several individuals escaped even from creels with sealed entrances (Bergmann & Moore 2001a). Similarly, smaller-sized hermit crabs might have escaped, or been washed through the relatively large mesh of the creels, so that the abundance of these species may have been underestimated in this study.

The frequent occurrence of the 2 whelks *Neptunea antiqua* and *Buccinum undatum* in traps baited with Crustacea concurs with Evans et al. (1996), who found a strong preference for *Liocarcinus depurator* bait in the Irish Sea. In the southern North Sea, however, *B. undatum* showed a strong preference for molluscan over crustacean and echinoderm bait (Groenewold & Fonds 2000). Such differences may reflect local variation; *B. undatum* may shift its preference depending on the variety of bait types available or abundance of whelk predators. Concurring with Hancock (1963), *B. undatum* counts showed something of a seasonal trend peaking in April and June. Similarly, in the Clyde Sea, creel catches increased after the breeding season in February (Nickell & Moore 1991) when animals presumably resumed feeding.

Funnel traps

The number of amphipods caught in funnel traps was variable and ranged from 0 to 2819 individuals per trap, indicating a patchy distribution of amphipods on the seabed or variations of 'wash-through' due to the position of traps in the fleet. *Orchomene nanus* peaked in traps baited with crustaceans as in the North and Irish Seas (Ramsay et al. 1997, Groenewold & Fonds 2000) and is likely to be an obligate scavenger that specialises on crustacean carrion (Moore & Wong 1995a, Kaiser & Moore 1999).

The most abundant amphipod, *Scopelocheirus hopei*, was less specialised than *Orchomene nanus* and showed preferences for both crustacean and starfish bait. High numbers were also recorded in traps baited with fish or *Nephrops* in the Clyde and Mediterranean Seas (Nickell & Moore 1991, Castro et al. 1999, Wieczorek et al. 1999). Often found in thousands, we conclude, and in this we concur with Castro et al. (1999), that these 2 amphipod species are amongst the most important scavengers responsible for the consumption of discards on the sea bed in European coastal waters. It would be interesting to investigate this in more detail (e.g. consumption rates) in future studies.

The occurrence of the caprellid *Pariambus typicus* on *Asterias rubens* bait could be a reflection of its established commensal association with this starfish species (Jones 1970) rather than a feeding preference, although Volbehr & Rachor (1997) observed *P. typicus* feeding on ophiuroid carrion. The caprellid could have been carried to the vicinity of the funnel traps by *A. rubens* caught in the creels. While Volbehr & Rachor (1997) reported an association with *Ophiura ophiura* and *O. albida* in the German Bight, numbers of *P. typicus* attracted to *O. ophiura* bait were negligible in the present study, possibly due to a preference for starfish when offered that choice, or to local differences.

Southern Clyde Sea deployment

The scavenger composition in the south of the Clyde Sea area was different from the north in that creel catches were lower both in terms of total numbers and species diversity. This corresponds with the catch composition of south Clyde Sea trawls being characterised by a lower invertebrate diversity compared with the north (Bergmann et al. 2000). *Nephrops* was the most abundant scavenger caught in creels in the south Clyde Sea. Using *Nephrops* as bait in the south Clyde Sea, Wieczorek et al. (1999) found that almost the entire catch was made up of *Nephrops* in a creel deployment in July 1998.

Information on the ecological energetics of *Nephrops* 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 other species on the soft muds of the Clyde Sea. Underwater TV observations have shown that *Nephrops* consumes discards of conspecifics (Wieczorek et al. 1999), which might be an indication of food limitation experienced by this population of small, slow-growing, but densely packed individuals in the south Clyde Sea (Tuck et al. 1997). By subsidising an expansion of crustacean scavengers, e.g. populations of hermit crabs (Ramsay et al. 1997), swimming crabs, *Natatolana borealis*, or amphipods, discarding might conceivably encourage vector transmission of diseases like the *Hematodinium* infection of *Nephrops* (Field et al. 1998), although this link is presently unproven (Stentiford 2000).

Wieczorek et al. (1999) estimated that 75 to 80% of the energy represented by *Nephrops* discards ends up on the sea bed while most of the remainder is consumed by sea birds. The energy subsidy to individual benthonts, however, can be assumed to be modest since discarded material will be dispersed over a very wide area (Castro et al. 1999) and provoke only local chance consumption by benthic scavengers (Moore & Jennings 2000), although an aggregation of fishing effort in shallower areas (Castro et al. 1999) could produce 'hotspots' of discards.

In the North Sea, the energy subsidy represented by discards to benthic scavengers has been quoted at a maximum of 10% (Lindeboom & de Groot 1998). Groenewold & 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. There has been much debate as to whether discards or damaged benthos could subsidise scavenger populations (e.g. Kaiser & Spencer 1994, Evans et al. 1996, Ramsay et al. 1996, 1997, 1998, 2000, Kaiser et al. 1998, Castro et al. 1999, Wieczorek et al. 1999, Demestre et al. 2000, Groenewold & Fonds 2000, Veale et al. 2000a,b). An emerging consensus is that while fishing temporarily augments the diet of scavengers it is unlikely to constitute its major part.

No data exist on the impact of discarding on the community structure or food web of the benthos in the area studied. The main difficulty in obtaining such information is teasing out different interacting components of a diverse community and finding suitable unfished control areas for comparison. An interesting approach which would shed light on such issues could be by comparison of exploited areas with areas that might recover after closure to fishing (although such areas have to be large to ensure that animals are not moving between closed and fished sites and must be regarded as impacted at the outset). A recent study by Marrs et al. (in press) provides invaluable background information on the micro-scale distribution of fishing effort in the Clyde Sea for future studies on the impacts of trawling at the population and community level.

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Appendix 1. List of taxa found in funnel traps (f) and creels (c) baited with discards after 48 h deployment (for taxonomic authorities see Howson & Picton 1997). * = first Clyde Sea record

Cnidaria
- *Aurelia aurita* (c)
- Hydrozoa (f/c)
- *Coryne* sp. (f)
- Actiniaria (c)
- *Urticina felina* (c)
- *Metridium senile* (c)

Platyhelminthes
- Turbellaria (f)
- Digenea (f)

Nemertea (f)

Nematoda (f)

Entoprocta
- *Loxosomella* sp. (f)

Chaetognatha (f)

Sipunculida (f)

Annelida
- *Aphrodita aculeata* (c)
- Polynoidae (f)
- Phyllodocidae (f)
- *Sphaerodoridium claparedii* (f)*
- Hesionidae (f)
- Lumbrineridae (f)
- Cirratulidae (f)
- Maldanidae (f)
- Opheliidae (f)
- *Scalibregma inflatum* (f)
- Terebellidae (f)
- Oligochaeta (f)

Chelicerata
- Pycnogonida (f)

Crustacea
- *Podon polyphemoides* (f)
- Calanoida (f)
- *Acartia* sp. (f)
- Cyclopoida (f)
- Harpacticoida (f)
- *Tisbe furcata* (f)
- *Alteutha* sp. (f)
- Thalestridae (f)
- *Lepeophtheirus* sp. (f)
- Ostracoda (f)
- *Acanthocythereis dunelmensis* (f)
- *Nebalia bipes* (f)
- *Erythrops serrata* (f)
- *Leptomysis* sp. (f)
- *Mysidopsis didelphys* (f)
- *Apherusa bispinosa* (f)
- *Apherusa jurinei* (f)
- *Eusirus longipes* (f)
- *Perioculodes longimanus* (f)
- *Westwoodilla caecula* (f)
- *Leucothoe incisa* (f)
- *Leucothoe spinicarpa* (f)
- *Stenula rubrovittata* (f)
- Lysianassidae (f)
- *Orchomene nanus* (f)
- *Scopelocheirus hopei* (f)
- *Tryphosella* sp. (f)
- *Stegocephaloides christianiensis* (f)
- *Iphimedia obesa* (f)
- *Atylus vedlomensis* (f)
- *Dexamine spinosa* (f)
- *Dexamine thea* (f)
- *Gammarus locusta* (f)
- *Melphidippella macra* (f)
- Melitidae (f)
- *Abludomelita obtusata* (f)
- *Cheirocratus* sp. (f)
- *Gammaropsis maculata* (f)
- *Gammaropsis nitida* (f)
- Ischyroceridae (f)
- *Ericthonius punctatus* (f)
- *Jassa falcata* (f)
- *Jassa marmorata* (f)
- *Parajassa pelagica* (f)
- *Aora gracilis* (f)
- *Lembos websteri* (f)
- *Leptocheirus pilosus* (f)
- *Corophium bonnellii* (f)
- *Caprella acanthifera* (f)
- *Pariambus typicus* (Krøyer) var. *inermis* Mayer (f)
- *Gnathia* sp. (f)
- *Natatolana* (= *Cirolana*) *borealis* (f)
- *Munna* sp. (f)
- Cumacea (f)
- *Diastylis* sp. (f)
- *Athanus nitescens* (f)
- *Caridion gordoni* (f)
- *Eualus occultus* (f)
- *Hippolyte varians* (f)
- *Thoralus cranchii* (f)
- *Processa* sp. (f)
- *Dichelopandalus bonnieri* (f/c)
- *Pandalina brevirostris* (f)
- *Pandalus montagui* (f)
- *Crangon allmanni* (f)
- *Pontophilus spinosus* (f)
- *Nephrops norvegicus* (c)
- *Pagurus bernhardus* (c)
- *Munida rugosa* (c)
- *Pisidia longicornis* (c)
- *Hyas araneus* (c)
- *Hyas coarctatus* (c)
- *Inachus dorsettensis* (c)
- *Macropodia rostrata* (c)
- *Macropodia tenuirostris* (c)
- *Cancer pagurus* (c)
- *Liocarcinus depurator* (c)
- *Liocarcinus holsatus* (c)
- *Necora puber* (c)
- *Carcinus maenas* (c)

Mollusca
- *Tectura testudinalis* (f)
- *Aporrhais pespelecani* (c)
- *Buccinum undatum* (f/c)
- *Neptunea antiqua*(c)
- *Odostomia* sp. (f)
- *Cylichna* sp. (f)
- *Diaphana* sp. (f)
- *Nucula nitidosa* (f)
- *Nucula nucleus* (f)
- *Nuculana* sp. (f)
- *Mytilus edulis* (f)

Appendix 1 (continued)

Abra alba (f)	Osteichthyes
Arctica islandica (f)	*Ciliata mustela* (c)
Echinodermata	*Gadus morhua* (c)
Antedon bifida (c)	*Merlangius merlangus* (c)
Astropecten irregularis (c)	*Raniceps raninus* (c)
Asterias rubens (f/c)	*Trisopterus esmarkii* (c)
Ophiothrix fragilis (f/c)	*Trisopterus luscus* (c)
Amphiura sp. (f/c)	*Myoxocephalus scorpius* (c)
Amphiura chiajei (f/c)	*Callionymus lyra* (c)
Amphiura filiformis (f/c)	*Pomatoschistus minutus* (f)
Ophiura albida (f/c)	*Hippoglossoides platessoides* (c)
Ophiura ophiura (c)	*Limanda limanda* (c)

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