Mortality of *Asterias rubens* and *Ophiura ophiura* discarded in the *Nephrops* fishery of the Clyde Sea area, Scotland

M. Bergmann and P. G. Moore


The Clyde Sea *Nephrops* fishery produces large amounts of invertebrate discards. Of these, up to 80% (by numbers) are echinoderms, including the starfish *Asterias rubens* and the brittlestar *Ophiura ophiura*. The short- and longer-term mortality of these species was determined after trawling in order to gain reliable estimates of trawl-induced mortality. Short-term mortality was assessed after trawling and periods of aerial exposure on deck, and ranged from 0–31%, with *A. rubens* showing lower mortality. Mortality of haphazardly collected echinoderms of various sizes and degrees of damage was monitored over one month to determine longer-term mortality. The effects of injury on starfish survival were also examined, as were the effects of trawling and aerial exposure on *O. ophiura* survival and *A. rubens* righting time. Injured *A. rubens* had a significantly higher long-term mortality (22–96%) than controls (4%). Trawling and aerial exposure significantly increased righting times of *A. rubens*, implying susceptibility to stress and an increased risk of predation. Moribund *A. rubens* developed white lesions containing bacteria (*Vibrio metschnikovii* and *Acinetobacter* sp.) and mortality rates only stabilised in the third week after trawling. In contrast, all trawled *O. ophiura* died within 14 d. Immediate re-immersion in sea water resulted in lower, but nevertheless high, mortality (91%). Our results suggest that post-trawling mortality of discarded echinoderms has been underestimated in the past.

Key words: *Asterias rubens*, autotomy, discard mortality, injury, *Ophiura ophiura*, trawling.

Received 27 July 2000; accepted 23 February 2001.

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Introduction

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; Moore and Jennings, 2000). The global commercial fishery has been conservatively estimated to generate 27 million tonnes per year of discards (range 17.9–39.5 million tonnes), by-catch organisms that are returned to the sea for various reasons (Alverson et al., 1994). This is equivalent to ca. 25% the weight of the reported marine landings worldwide. The highest rates of discarding have been attributed to shrimp/prawn trawl fisheries, with an estimate of 9.5 million tonnes per year (Alverson et al., 1994). The Norway lobster (*Nephrops norvegicus* (L.)) hereafter referred to by genus alone) supports the most valuable shellfish fishery in Scottish waters. Annual official landings worldwide are around 60 000 t, a third of which is landed in Scotland (Marrs et al., 2000). *Nephrops* live on soft substrata and are mainly fished by otter trawling. In the Clyde Sea area single-rigged (mesh size ≥70 mm) and twin-rigged (mesh size ≥80 mm) *Nephrops* trawls disturb wide areas of the sea bed and benthic fauna as weighted ground lines and heavy otter doors are dragged across the sediment (Marrs et al., 2000). The northeast Atlantic *Nephrops* trawl fishery ranks as number five among the world’s fisheries with the highest recorded discard ratios when ordered by gear type (Alverson et al., 1994). In the Clyde *Nephrops* fishery, 50–90% of the catch (by volume) is discarded (Bergmann et al., 2001a). Invertebrates account for up to 90% of the numbers of animals discarded with up to 73% of these being echinoderms. Starfish (*Asterias rubens* L.) and brittlestars...
(Ophiura ophiura (L.)) are the most abundant echinoderm species discarded in the Clyde Sea area, concurring with findings from the Irish and North Seas (Fonds, 1994; Kaiser & Spencer, 1995; Bergman et al., 1998). A recent survey by Ellis & Rogers (2000) in the eastern English Channel, the Bristol Channel and the Irish Sea has shown that echinoderms account for 29% of the epifaunal biomass captured with a 4-m beam trawl, with *A. rubens* and *O. ophiura* being amongst the most common species. However, little is known about the fate of this important component of the catch. Recent investigations have dealt with the post-trawling mortality of non-target invertebrates (Wassenberg and Hill, 1993; Craeymeersch, 1994; Fonds, 1994; Kaiser and Spencer, 1995; Bergman et al., 1998; Ramsay and Kaiser, 1998; Bergmann and Moore, 2001; Ramsay et al., 2001). However, little information is available on the fate of discarded non-target invertebrates from the *Nephrops* fishery as previous studies of this fishery have focused on commercially important discards species, such as undersized *Nephrops* and roundfish (e.g. Evans et al., 1994; Wileman et al., 1999). Post-fishing survival is affected by many 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.

*Asterias rubens* has been reported from a wide range of habitats from Iceland to Senegal at depths from the intertidal zone to 650 m (Vevers, 1949). Its biology has been studied in detail (e.g. Vevers, 1949; Allen, 1983; Nichols and Barker, 1984), especially with respect to its commercial significance when predating on mussel and oyster beds (Sloan and Aldridge, 1981), and competing for food with commercial fish species (Anger et al., 1977). Although geographically widely distributed from East Finmark to the Azores and also in the Mediterranean from the intertidal to 850 m (Tyler, 1977) *O. ophiura* is less well-known (e.g. Gorzula, 1976; Feder, 1981; Dahm, 1993). Almost 60% of *A. rubens* and 100% of *O. ophiura* caught by commercial trawls in the Clyde Sea area show signs of recent injury such as punctures in the epidermis, loss of arms, broken arms and damage to the oral disc (Bergmann et al., 2001b). Such injuries may be caused by physical contact with the fishing gear, other species in the catch or handling. Alternatively, parts of arms or whole arms can be autotomized deliberately in attempts to escape or in order to reduce adverse effects after injury has occurred (Emson and Wilkie, 1980). Thus, the manner of arm loss, i.e. voluntarily or involuntarily, could have an important effect on subsequent mortality rates and regeneration. Furthermore, loss of epidermis, autotomy and trauma due to trawling can render starfish more susceptible to bacterial infection (Bang and Lemma, 1962).

The object of the present study was to assess, short- and longer-term mortality of two echinoderm species, *A. rubens* and *O. ophiura* that are routinely discarded in significant numbers during commercial fishing for *Nephrops* in the Clyde Sea area. Particular attention was paid to the effects of aerial exposure, injury and infection.

### Materials and Methods

#### Short-term mortality

Short-term mortality (mortality following trawling, sorting and exposure to air) was assessed after discards had been separated from commercial species, exposed to air on deck for 16–90 min (to imitate commercial practice) then transferred to standard fish boxes (75 × 40 cm) supplied with running seawater (25-cm water depth). The air temperature was measured, and the size of each individual was determined to the nearest mm with dial callipers (*A. rubens*: length of the longest arm, *O. ophiura*: disc diameter). Where possible, damage assessments were carried out and counts made of the number of dead vs. live animals, with individuals considered alive using the following criteria: *A. rubens*: movement of tube feet; *O. ophiura*: movement of arms, spines and mouth podia.

Longer-term mortality of invertebrates haphazardly sampled from commercial trawls

In May 1999, a commercial tow was made from a local fishing vessel (FV “Red Baron”, 12 m, 110 hp) in Fintry Bay (Figure 1). A standard commercial rock-hopper otter trawl with 80-mm (stretched) diamond-shaped mesh, fitted with a square mesh panel was used, reflecting local fishing practice. Tow variables such as average water depth, position, trawling speed and tow duration were recorded. The catch volume was measured in baskets (44 l) and note made of the by-catch species present as the catch was sorted. The two most common echinoderms (*A. rubens*, *O. ophiura*) were collected to monitor longer-term mortality. Live individuals of various sizes and of differing degrees of damage were used. Sorting times on Clyde fishing boats range from 45–300 min with a median of 90 min (M. Bergmann, unpubl. data). Therefore, selected animals were exposed to air for 90 min before placing them into on-deck fish boxes supplied with running seawater. Single *A. rubens* were measured and transferred into plastic mesh containers (Bergmann and Moore, 2001), which were then put individually into modified *Nephrops* creels in order to exclude large predators. These creels were deployed on the seabed in Fintry Bay at 35–40 m depth. On return to the laboratory, *O. ophiura* were
measured and transferred into large outdoor holding tanks (325 × 100 cm, water depth 30 cm) supplied with running seawater.

Intact *A. rubens* and *O. ophiura* captured in *Nephrops* creels baited with herring, were collected from Fintray Bay before trawling, and used as controls for the effects of trawling and on-deck damage. As it was difficult to obtain sufficient numbers of entirely intact *O. ophiura*, only those with two or fewer missing arm tips were used as controls. Aerial exposure of the creel-caught animals was minimized (<20 min) while they were carefully transferred into cages. As with the trawled animals, individual control invertebrates were placed in small plastic mesh cages in *Nephrops* creels. Mortality of control and trawled invertebrates was recorded weekly over the following month, necessitating hauling, assessment on deck and re-deployment of creels.

Longer-term mortality after trawl damage and induced autotomy

As previous work in the Clyde Sea area has shown that more than 30% of *A. rubens* caught in *Nephrops* trawls were physically damaged (*Bergmann et al.*, 2001b), the degree of injury to *A. rubens* was manipulated to quantify and distinguish between the effects of injury and autotomy on survival in this experiment (*Ramsay et al.*, 2001). Furthermore, the degree of exposure to air was manipulated for *O. ophiura*.

In January 2000, RV “Aora” (15 m, 260 hp) made a 2-h tow at 2.5–3.0 kt and 90 m depth in the Firth of
Clyde Channel, south of Little Cumbrae Island (Figure 1, 55°46′N 04°58′W) using a clean net otter trawl. The groundrope of a clean net has only small discs attached to it and is typically used on softer grounds while rockhoppers have a series of large bobbins attached to the groundrope enabling the net to “hop” over small obstructions on hard grounds. The volume of the catch and the bottom temperature were measured and starfish were exposed to air (8.5°C) for 90 min before being stored in running water from the sea surface (7.6°C). In order to assess the effects of aerial exposure on brittlestar survival, one group of O. ophiuroides (n=45) was placed in seawater immediately whereas another group (n=60) was re-immersed 90 min after hauling. On return to the laboratory, brittlestars were measured and transferred into separate communal holding tanks (110 × 65 cm, water depth ca. 30 cm) while starfish were placed in floating plastic mesh containers to prevent animal interaction within the outdoor holding tanks (325 × 100 cm, water depth 30 cm). Brittlestar mortality was recorded weekly over 21 d. All tanks were supplied with running sea water at 7–8°C, similar to the in situ bottom temperature measured on the day of capture. Starfish were measured and subjected to further treatment as follows:

- Control: creel-caught starfish (n=28).
- Trawled: trawled and intact starfish (n=29) were exposed to air for 90 min.
- Punctured: trawled and originally intact starfish (n=26) were exposed to air for 90 min and punctured with a scalpel.
- Induced autotomy: trawled and originally intact starfish (n=28) were exposed to air for 90 min and induced to autotomize by pressing and squeezing one arm by hand in a tray in air to distinguish between the effects on survival of forcible arm removal and autotomy.
- One arm removed: trawled and originally intact starfish (n=27) were exposed to air for 90 min and one arm was removed by scalpel to simulate trawl-induced arm loss.
- Three arms removed: trawled and originally intact starfish (n=23) were exposed to air for 90 min and three arms were removed by scalpel to simulate trawl-induced multiple arm loss.

Where possible, mortality was recorded daily over a period of 3 wk and notes made of incidences of white lesions and further autotomy.

Since the numbers of starfish and brittlestars varied between treatments the data were standardized as cumulative percentages. For each A. rubens treatment further autotomy was expressed as cumulative percentage arm loss, the initial total number of arms in a sample (after treatments) representing 100%. The percentage of individuals exhibiting white lesions was also standardized as cumulative percentage. The median number of additionally autotomized arms and the median incidence of lesions in different treatments was compared using Kruskal-Wallis tests and subsequent pairwise Mann-Whitney U tests. Spearman’s rank-order correlation tests were done to explore correlations between treatment, animal size, the incidence of lesions, progressing autotomy and survival time.

Righting time of A. rubens.

The righting time of trawled A. rubens was quantified as a convenient indicator of stress (Lawrence and Cowell, 1996) caused by trawling, hypoxia and dehydration. In June 2000, RV “Aora” made a 2-h tow at 2.5–3.0 kt and 74 m depth in the channel between the Island of Bute and Great Cumbrae Island (55°41′N 04°57′W) with a clean net otter trawl. In order to assess the effects of aerial exposure on righting time, one group of starfish (n=28) was placed in a fish box with running seawater immediately after collection whereas another group of animals (n=24) was exposed to air for 1.5 h after hauling. For comparison, a control group of A. rubens (n=52) was collected by divers at depths of 6–15 m on a rocky slope at Port Loy, Great Cumbrae Island, and left in tanks with running seawater and mud for 24 h before experimentation. Starfish were then placed oral surface uppermost in seawater tanks containing mud and the time taken to resume a normal posture and the size of each individual were recorded. A Spearman’s rank-order correlation test was done to explore correlations between starfish size and righting time. A Kruskal-Wallis and subsequent Mann-Whitney U tests were done to determine differences in the righting time of A. rubens from different treatments.

Identification of pathogenic agents

In Experiment 2 and 3, many A. rubens developed white lesions and subsequently disintegrated. In order to identify bacterial pathogens, swabs were taken from the lesions of trawled A. rubens and from the epidermis of apparently healthy starfish. The swabs were plated on Zobell’s medium, cultured at 20°C for 4 d and stored at 4°C until processed. Colonies were plated separately and analysed by Gram staining (Prescott et al., 1996). The next step was to identify bacteria according to their biochemical properties, i.e. fermentation, catalase or oxidase activity and Penicillin G and B sensitivity (as described in Prescott et al., 1996). In order to confirm those results, the colonies were analysed using the Analytical Profile Index 10 S (API), a more reliable method commonly employed to identify Entrobacteriaceae and other Gram-negative rods. The system used consisted of 12 biochemical tests using API 10 S strips and subsequent interpretation of the results by means of the API 10 S data base and the identification
Results

Short-term mortality

Short-term mortality ranged from 0–18% in *A. rubens*, and was highest after a long tow at 90 m and high air temperatures (Table 1). In brittlestars it varied from 8–31% and highest mortality occurred after a tow at 92 m with a large total catch. The mean short-term mortality for *A. rubens* and *O. ophiura* from all trawls was 4 and 16%, respectively.

Longer-term mortality of haphazardly sampled echinoderms from commercial trawls

All trawled *O. ophiura* died within 4 wk. Mortality of *A. rubens* was lower (11%, Table 2). The highest mortality rate occurred during the first week for *O. ophiura*, but in the third week for *A. rubens*. Trawled *A. rubens* lost arms throughout the monitoring period (15% arm loss in total after 29 d) often resulting in complete disintegration and death. Mortality of creel-caught controls was generally low for all species and never exceeded 5%.

Longer-term mortality after trawl damage and induced autotomy

While all *O. ophiura* that had been exposed to air died within 14 d, 9% of those that had been re-immersed immediately after hauling remained alive after 21 d (Figure 2). The temperature of the seawater in the tanks was almost identical to the bottom (47 m) temperature of 8.5°C on the date and location of collection. Since insufficient control *O. ophiura* could be obtained for this experiment, results from Experiment 1 were taken as a baseline against which these experimental results were compared. Median survival time of control *O. ophiura* was significantly higher than that of “trawled” animals which was in turn significantly higher than that of “trawled and air-exposed” starfish (p<0.001).

Figure 3 illustrates the cumulative mortality of *A. rubens* treatment groups over a period of 3 wk. The

Table 1. Percentage (short-term) mortality of *Asterias rubens* and *Ophiura ophiura* caught by *Nephrops* otter-trawls.

<table>
<thead>
<tr>
<th>Species</th>
<th>Date</th>
<th>Vessel</th>
<th>Tow duration (min)</th>
<th>Depth (m)</th>
<th>Exposure time (min)</th>
<th>Air temperature (°C)</th>
<th>Total catch (baskets)</th>
<th>n</th>
<th>Percentage damaged</th>
<th>Short-term mortality (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. rubens</em></td>
<td>11/8/98</td>
<td>Aa</td>
<td>180</td>
<td>90</td>
<td>70</td>
<td>16</td>
<td>9</td>
<td>40</td>
<td>58</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>29/9/98</td>
<td>Aa</td>
<td>90</td>
<td>76</td>
<td>60</td>
<td>15</td>
<td>8.3</td>
<td>22</td>
<td>41</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>30/9/98</td>
<td>Aa</td>
<td>90</td>
<td>92</td>
<td>60</td>
<td>n.a.</td>
<td>10</td>
<td>74</td>
<td>36</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>04/5/99</td>
<td>RB</td>
<td>154</td>
<td>46</td>
<td>70</td>
<td>12</td>
<td>8.5</td>
<td>26</td>
<td>34</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>6/200</td>
<td>Aa</td>
<td>120</td>
<td>75</td>
<td>90</td>
<td>5</td>
<td>7</td>
<td>35</td>
<td>n.a.</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>06/6/00</td>
<td>Aa</td>
<td>120</td>
<td>74</td>
<td>90</td>
<td>15</td>
<td>n.a.</td>
<td>24</td>
<td>17</td>
<td>0</td>
</tr>
<tr>
<td><em>O. ophiura</em></td>
<td>29/9/98</td>
<td>Aa</td>
<td>90</td>
<td>76</td>
<td>60</td>
<td>15</td>
<td>8.3</td>
<td>111</td>
<td>100</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>30/9/98</td>
<td>Aa</td>
<td>90</td>
<td>92</td>
<td>60</td>
<td>n.a.</td>
<td>10</td>
<td>39</td>
<td>100</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>04/5/99</td>
<td>RB</td>
<td>154</td>
<td>46</td>
<td>70</td>
<td>12</td>
<td>8.5</td>
<td>114</td>
<td>100</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>16/2/00</td>
<td>Aa</td>
<td>120</td>
<td>75</td>
<td>90</td>
<td>5</td>
<td>7</td>
<td>89</td>
<td>n.a.</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>06/6/00</td>
<td>Aa</td>
<td>120</td>
<td>74</td>
<td>90</td>
<td>15</td>
<td>n.a.</td>
<td>95</td>
<td>100</td>
<td>4</td>
</tr>
</tbody>
</table>

Each trip is shown separately as season, vessel, tow duration, average tow depth, on-deck exposure to air, temperature and the total catch varied. The proportion of individuals that sustained damage is also given (RB=FV “Red Baron”, Aa=RV “Aora”).

Table 2. Longer-term survival of *Asterias rubens* and *Ophiura ophiura* (Experiment 2, May 1999).

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>Cumulative percentage mortality (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Day: 7</td>
<td>14</td>
</tr>
<tr>
<td><em>A. rubens</em></td>
<td>Control</td>
<td>37</td>
</tr>
<tr>
<td></td>
<td>Trawled</td>
<td>35</td>
</tr>
<tr>
<td><em>O. ophiura</em></td>
<td>Control</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>Trawled</td>
<td>40</td>
</tr>
</tbody>
</table>

Intact “controls” were caught in creels; “trawled” animals were haphazardly collected trawl-caught animals that had been exposed to air for 90 min.

Table in the instruction manual (for details see Bio Merieux, 1990).
median survival time was lowest for *A. rubens* with three removed arms (p<0.001). The median survival time of starfish with induced autotomy was significantly lower than controls (p=0.0049) or intact trawled specimen (p=0.014). Punctured starfish also had a significantly lower survival time than controls (p=0.037). Starfish began to die 4 d after trawling and increasing numbers of *A. rubens* exhibited white lesions (Figure 3), often followed by autotomy and complete disintegration of the animal throughout the monitoring period. Figures 5 and 6 show, respectively, the cumulative percentage of starfish with lesions and cumulative severance of arms throughout the monitoring period. The incidence of lesions was significantly higher in trawled *A. rubens* treatments compared with controls (p<0.03), and highest in specimens with three arms removed and punctures. All treatments comprising experimental injury (including induced autotomy) had a significantly
higher number of autotomized arms (p<0.05). Additional arm severance was highest in *A. rubens* with three removed arms.

**Righting time of *A. rubens***

Starfish collected by divers were significantly smaller than trawled animals [analysis of variance (ANOVA), p<0.001]. A Spearman’s rank correlation test revealed significant positive correlations between size and righting time for the “dive-collected” and the “immediately re-immersed” but not for the “air-exposed” group of starfish. Within the 40–80 mm size range, size frequency distributions of animals from all treatment groups were not significantly different (ANOVA, p=0.13), so further analysis was restricted to this subset (n=39, 10 and 13, respectively). A Kruskal-Wallis and subsequent Mann-Whitney U tests showed significant differences in the righting times of starfish from each treatment (p<0.01). Controls had the lowest median righting time (102 s).
Figure 5. Cumulative incidence of white lesions (%) in six *Asterias rubens* treatment groups over 3 wk following capture. (— ▲ —) Three arms removed (n=28); (— — ▼ —) punctured (n=26); (— —) induced autotomy (n=28); (— — □ —) one arm removed (n=27); (— — ▼ —) trawled and intact (n=29); (— — ○ —) control (n=28).

Figure 6. Cumulative arm severance (%) in six *Asterias rubens* treatment groups over 3 wk following capture. (— ▲ —) Three arms removed (n=23); (— —) induced autotomy (n=280); (— — ▼ —) punctured (n=26); (— — □ —) one arm removed (n=27); (— — ▼ —) trawled and intact (n=29); (— — ○ —) control (n=28).
followed by the immediately re-immersed group (252 s) and starfish that had been exposed to air (788 s). One individual of each trawl treatment was still lying on its aboral side after 3 h.

Identification of pathogenic agents
Cultured swabs from the epidermis of healthy *A. rubens* contained *Moraxella* sp. and *Flexibacter* sp. whereas swabs from lesions contained *Acinetobacter* sp., *Vibrio metschnikovii* and *Moraxella* sp.

Discussion

Survival and righting time of trawled *A. rubens*
There was considerable variation between hauls with respect to tow duration, vessel, tow depth, air exposure, air temperature, total catch (Table 1) and catch composition, all of which can contribute to damage and mortality of captured organisms (Craeymeersch, 1994; Bergman et al., 1998). Thus damage and mortality cannot be attributed to any single factor. Seasonal aspects also merit consideration, as longer tows with potentially larger catches in summer may contribute to higher mortality since physical injury and physiological stresses on deck due to temperature differences become more severe as indicated by the high short-term mortality of *A. rubens* in August 1998 (Table 1). Excepting that particular trawl, the short-term mortality recorded for *A. rubens* was similar to that found by others working on the same species in the North and Irish Seas (Fonds, 1994; Kaiser and Spencer, 1995; Bergman et al., 1998; Ramsay et al., 2001).

In Experiment 2, the longer-term mortality of trawled starfish was relatively low (11%), probably because the majority of the haphazardly collected individuals were intact and the animals were kept in the field. Similar figures have been reported from the North Sea and Irish Sea beam trawl fishery (Fonds, 1994; Kaiser and Spencer, 1995; Bergman et al., 1998) although post-trawling mortality was only monitored there for ≤5 d. In Experiment 3, mortality increased six- to 11-fold after day 5 of the experiment (Figure 3). Hence, it could be concluded that post-trawling mortality of *A. rubens* may have been underestimated, especially in the light of the theoretically more destructive fishing gear employed in those studies.

In Experiment 3, experimental injury (including induced autotomy) decreased the median survival time while the mortality rate of intact trawled *A. rubens* was very close to that of controls, implying that most animals soon recovered from the stresses of trawling and hypoxia. Surprisingly, starfish with induced autotomy had a 10% higher mortality rate than starfish with a surgically removed arm. Bang and Lemma (1962) reported that autotomy and trauma rendered the starfish *Asterias forbesi* susceptible to bacterial infection. Hotchkiss et al. (1991) distinguished between fast, probably neurochemical, events during autotomy that enable rapid separation of the arm, and slow muscular processes involved in subsequent wound closure. If the separation of the arm is very rapid, these slow processes follow arm severance and leave a large temporary opening into the coelom exposing the starfish to infection. Hence, our experimental practice could have favoured the fast events increasing the infection risk afterwards. Nevertheless, trawl-induced autotomy probably follows a similar pattern. Starfish arms were removed arbitrarily, but slightly distally to the breakage plane in most cases. This might have facilitated subsequent autotomy of damaged parts and better conditions for the co-ordination of fast and slow processes cf. the induced autotomy treatment. Punctures also significantly increased mortality, and it was noticeable that no wound closure occurred during the monitoring period, posing a constant threat of infection. Trawling and injury significantly increased the incidence of lesions and severance of arms (Figures 5 and 6). Dungan et al. (1982) and Eckert et al. (2000) reported the development of rapidly enlarging white lesions and progressive fragmentation, similar to our own observations, in a variety of asteroids at the Gulf of California and the Channel Islands (USA) and termed the phenomenon “sea star wasting disease”. As in our study, the lesions contained high concentrations of bacteria (Dungan et al., 1982), and similar to Delavault and Leclerc (1969), we isolated *Acinetobacter* sp. from lesions. The presence of *Vibrio metschnikovii* in the lesions of diseased *A. rubens* corresponds to findings by Crowell (cited by Eckert et al., 2000) who isolated *Vibrio* bacteria from diseased *Heliaster kubinjii*. Injection of the bacterial isolates into healthy starfish would help to establish pathogenicity. As mortality and exhibition of lesions in controls was low, we suggest that physical trauma (see Bang, 1982) rendered starfish more susceptible to infection by opportunistic bacteria. We suspect that starfish that pass through the mesh of the trawl could be affected in similar ways. *Asterias rubens* with white lesions were also observed on a sublittoral rocky slope locally (M. Bergmann, pers. obs.) indicating that starfish exhibit similar symptoms *in situ*.

The majority of the seabed in the Clyde Sea area is subject to frequent trawling disturbance (Marrs et al., 2000); so, it is not unlikely that starfish are subject to multiple-discarding events that could additionally reduce the chances of survival. Lawrence and Vasquez (1996) stated that sub-lethal predation and subsequent regeneration may lead to a reduction in the pyloric ceca, loss of gonads, decrease in locomotory abilities and nutrient acquisition, and suggested significant effects at the population and community level.
The longer righting time of trawled cf. control starfish indicates that trawled *A. rubens* suffered from stress. This corresponds to decreased activity coefficients of *Stichaster striatus* reported after experimental exposure to air (Lawrence and Cowell, 1996). Trawled starfish often had a “deflated” appearance, possibly due to fluid loss during aerial exposure. Hence, righting time might have been higher because trawled starfish needed to re-absorb water before being able to use their tube feet effectively. Damaged starfish in an inverted position could be more susceptible to additional sub-lethal predation in situ, as opportunistic scavengers are attracted to the odour of damaged fauna in trawl tracks (Ramsay et al., 1998). Field observations and behavioural experiments similar to those conducted by Ramsay and Kaiser (1998) could provide valuable information about *A. rubens* mortality in the field. Ramsay et al. (2000) found that starfish numbers increased with increasing fishing effort but declined after a threshold level of fishing intensity had been reached in the Irish and North Seas. The authors suggest that at low fishing effort artificially increased food availability, and removal of predators and competitors could lead to population growth until these benefits were outweighed by deleterious effects such as fishing mortality of starfish and their prey organisms.

Various authors have suggested using the frequency of regenerating arms in *A. rubens* as an indicator of fishing intensity (de Graaf and de Veen, 1973; Kaiser, 1996; Ramsay et al., 2001) because *A. rubens* is known to have high regenerative capabilities. Since our mortality experiments have shown that injury reduces longer-term survival cf. intact creel-caught animals, we suspect that this approach may not provide an accurate indicator of fishing intensity.

Survival of trawled *Ophiura ophiura*

Short-term mortality was greater in *O. ophiura*, probably reflecting the higher damage sustained by this fragile species cf. *A. rubens*. It was highest after a tow at 92 m with a large total catch, which had probably increased physical damage and stress. Our short-term mortality figures are higher compared with other studies from the North and Irish Seas where *O. ophiura* mortalities were reported to be around 1–5% (Fonds, 1994; Kaiser and Spencer, 1995; Bergman et al., 1998), although heavier fishing gears with tickler chains were used in those studies. Shorter tow durations with smaller catches at shallower depths in those studies may have caused lower short-term mortality compared with the study at hand.

The longer-term mortality of “trawled and air-exposed” *O. ophiura* was 100% in both experiments cf. 5% in controls in Experiment 2. Low survivorship of animals re-immersed immediately after hauling implies that trawling (rather than aerial exposure) was the main cause of death, although aerial exposure accelerated mortality (Figure 2). This indicates that ophiuroids that pass through the mesh of the codend could also be subject to increased mortality. The extent of damage appeared not to be important as even slightly damaged individuals died within 2 wk. All previous studies on post-trawling mortality of *O. ophiura* had been terminated after a period of ≤5 d, and those brittlestars had not been subject to aerial exposure (Fonds, 1994; Kaiser and Spencer, 1995; Bergman et al., 1998). In our study, the mortality of immediately re-immersed *O. ophiura* was 11% after 7 d, in closer agreement to figures given by Fonds (1994), Kaiser and Spencer (1995) and Bergman et al. (1998). It would appear that brittlestar mortality may have been considerably underestimated in the past as a result of using only brief (<5 d) monitoring periods.

Several studies have suggested that *O. ophiura* is resilient to bottom fishing (Hill et al., 1996; Ramsay et al., 1998; Bergman and van Sanbrink, 2000) owing to its high capacity for regeneration. Yet, in the present study, almost all individuals died within 3 wk in several trials. Consequently, one could expect *O. ophiura* populations to suffer increased fishing mortality and population decline. Collie et al. (2000) found that, together with holothurians, ophiuroids were the echinoderm group most negatively affected by bottom fishing. It was predicted that chronic fishing disturbance could lead to a 93% reduction of ophiuroid densities. However, the sheer abundance of *O. ophiura* caught in trawls and recorded in underwater camera observations (Wieczorek et al., 1999) give the impression that populations have not been decimated by the last 40 years of Clyde Sea *Nephrops* trawling. Tuck et al. (1998) found a significant increase in *O. ophiura* densities after experimental trawling (without a net). *O. ophiura* is considered omnivorous, and can substantially affect benthic community structure (Thorson, 1966; Feder, 1981). Overwintering oocytes and the presence of pelagic ophioplutei from March to October, suggests that spawning can potentially take place throughout most of the year (Tyler, 1977). Hence, *O. ophiura* populations that had been exposed to trawling could be restocked with larvae from adjacent populations at the margins of fishing grounds. In summary, it would appear that increased brittlestar mortality from trawling might be outweighed at the population level by the species’ reproductive resilience and advantages attributable to fishing such as a decrease in densities of predator and competitors although further investigation is needed to substantiate this hypothesis.

There has been evidence from continuous plankton recorder (CPR) survey data in the North Sea of an increase of pluteus larvae, from the 1950s to the early 1990s and a simultaneous increase in several benthic
The removal of predators of echinoderms due to increased fishing effort, along with increased food supply owing to eutrophication, were suggested as possible causes for this increase.

Concurring with Fonds (1994), Kaiser and Spencer (1995) and Bergman et al. (1998) our results should be regarded as “broad-brush” estimates since mortality in the field depends on so many factors. Live injured individuals returned to the sea may be prone to predation (Ramsay and Kaiser, 1998), and are likely to be less successful in resource acquisition and reproduction (Lawrence and Vasquez, 1996). The seriousness of such handicap is increased, as is often the case, if echinoderms are discarded over unsuitable habitats (Evans et al., 1994).

Our study has shown that discard mortality of A. rubens and O. ophiura discards may have been underestimated in the past, probably as a result of brief monitoring periods. In contrast to Wassenberg and Hill (1993) we recommend a minimal monitoring period of 14 d for more realistic mortality estimates in prospective studies. However, we have yet to establish the consequences of discarding practices at the population level, especially since no information is available on the catch efficiency of Nephrops trawls for echinoderms. Our results may also have important implications for those echinoderms that pass through the mesh of the cod-end and sustain damage upon contact with the fishing gear or other animals in the catch. Furthermore, future experiments need to be designed to address the fate of survivors returned to the sea bed.

Acknowledgements

The authors gratefully acknowledge Steven McGuinness for help with the microbiological analysis of A. rubens swabs. Furthermore, we are indebted to Carolyn Blance, Katy Weir and the skippers and crews of FV “Red Baron”, RV “Aora” and RV “Aplysia” for their invaluable assistance on board. We would also like to thank Dr Roger Coggan, Dr Jason Hall-Spencer, Dr Mark Fonds and an anonymous referee for useful comments on earlier manuscripts. This study was funded by a Sheina Marshall studentship to M.B.

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