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INTRODUCTION

Discards are target or non-target animals that are not retained onboard commercial fishing vessels, but are returned to the sea, either alive or dead. Organisms may be discarded for a variety of reasons including lack of fisheries quota, lack of demand, or where the organisms are unmarketable due to other reasons such as size, damage, or disease (Catchpole et al. 2005a, b). The problem of discarding in European fisheries has been widely discussed from ecological, economic, ethical, and environmental perspectives (Eliasen et al. 2014), and received increasing public attention in the run-up to the 2013 reforms of the European Union’s Common Fisheries Policy (CFP) (Borges 2015). As a result, a “landing obligation” was introduced and is being sequentially applied across European Union fisheries. The aims of this policy change are to reduce waste, encourage uptake of more selective fishing practices, and to improve data recording of actual catches. Consequences on fisheries management of the recent United Kingdom vote to exit the European Union are unclear but it is possible the “landing obligation” will be retained as various forms of discard bans are applied in other non-European Union countries such as Norway and Iceland.

Under the CFP landing obligation, discarding can potentially continue where there is evidence that the species has a high rate of post-discard survival. Forcing landing of these discards, and their subsequent disposal, would only increase economic costs for little overall conservation benefit. The prawn Nephrops norvegicus has been identified as having potentially high post-release survival and a landing obligation exemption has been approved by the European Union for creel-caught Nephrops (Ungfors et al. 2013, Fox 2014, Marine Scotland 2015). On the other hand, scientific studies suggest that trawl-caught Nephrops do not necessarily survive as well as creel-caught animals. Despite having a hardened exoskeleton, Nephrops seem to be quite vulnerable to physical damage, particularly puncture wounds to the carapace, which can lead to a loss of hemolymph and eventual mortality (Wileman et al. 1999). Levels of physical damage will be affected by factors such as gear type, volume and composition of the catch, trawling time, locations of animals within the cod-end, the care with which the catch is hauled and handled on board, as well as the size and condition of the animals (Milligan et al. 2009). The eyes of Nephrops are also particularly vulnerable to light exposure at levels typically found at the sea surface, although there is no evidence linking such damage with subsequent reduced survival (Gaten et al. 2013). From a physiological perspective, the process of being caught in a trawl is stressful with anaerobic metabolism being activated in an attempt to maintain energy levels (Ridgway et al. 2006b, Albalat et al. 2009). Nevertheless, Nephrops do show considerable ability to recover from such stress if postharvest practices are optimized and aerial exposure is minimized (Albalat et al. 2010). In such situations, key physiological parameters, such as the replenishment of muscle adenosine 5′-triphosphate (ATP), have been reported to recover to unstressed levels within 6 h post-capture with other anaerobic
metabolites (i.e., L-lactate and muscle glycogen) returning to rested conditions within 24–48 h (Albalat et al. 2010). The potential of Nephrops to recover from trawling is also influenced by season (Lund et al. 2009, Albalat et al. 2010), although it is not clear if this is mainly due to temperature or other seasonally varying factors, such as animal size, sex, and molt status (Milligan et al. 2009).

Most post-release survival studies conducted to date have monitored the recovery of animals in tubes or cages, for example Harris and Andrews (2005). These approaches provide estimates of physiological recovery, but because the recovering Nephrops are protected from predation they may underestimate true post-discard mortality (STECF 2015). In behavioral terms, survival will be related to (1) the length of time taken to regain normal predator avoidance behavior, (2) the abundance of potential predators in the immediate area, (3) the ability of the animals to escape predators using their tail-flip response, and (4) whether the animals are discarded over suitable muddy habitat allowing them to find burrows in which to hide.

In the Firth of Clyde, there are around 18 registered under 10 m Nephrops trawlers, the majority of which fish locally (Fox et al. 2015) and supply the live market. Fishing is typified by relatively short tows (~2.5 h) using single-rig trawls fishing relatively close to port. The Nephrops are generally sorted from the catches within 60–90 min of hauling, and placed into boxes of tubes according to size (Fig. 1). The tubed animals are then held in seawater tanks on-board before being transferred to shore-based tanks where they are stored for up to 3 days before being shipped by truck, mainly to continental Europe. Prawns unfit for market are discarded during sorting over muddy grounds as the vessels prepare for the next tow. Using a commercial day vessel operating in this fishery, this study analyzed (1) composition of retained and discarded Nephrops, (2) the physiological condition and short-term survival of captive Nephrops, (3) predator avoidance behavior using underwater video, and (4) which variables are linked to survival.

**MATERIALS AND METHODS**

**Trawling and Data Collection**

Trials were conducted in the Firth of Clyde, Scotland, using a commercial vessel (Eilidh Anne GK2), which targets Nephrops for the live market. Fishing was undertaken using a single-rig Harkess (Prestonpans, Scotland), rock-hopper trawl fitted with an 85-mm diamond mesh net and a square mesh 120-mm Cod Recovery Zone Panel (standard commercial net and rig). Two sets of Nephrops recovery trials were conducted in February, three sets in March and June, and a behavioral trial in July 2015. Environmental conditions and trawling coordinates were recorded for each tow (Table 1). Temperature and salinity profiles were recorded in February and March using an YSI Castaway CTD. In the June trial surface temperature readings were obtained from the vessel but no salinity measures could be taken due to instrument failure.

The skipper was asked to follow his normal fishing practices and once the catch was on board he began sorting the Nephrops into four commercial size categories: large, medium, small, and extra small. In this fishery animals in the first three categories are destined for the live market, whereas the extra small Nephrops are marketed as whole fresh or frozen langoustines. Animals below the Minimum Conservation Reference Size (carapace length (CL) <20 mm) or not fit for market according to the skipper’s criteria were placed in a separate basket as “discards.” After sorting of each tow was completed, animals in the large, medium, and small categories were counted and their CL recorded using digital calipers. Because of the numbers of animals in the extra small and discarded grades, size profiles were based on measuring animals within a weighed subsample, which was then raised by the total catch weight of that grade.
Physiological Condition and Short-Term Survival of Captive Discarded Nephrops

Fifteen Nephrops were taken from the discard category as soon as practical after the skipper had begun sorting the catch and sampled to provide baseline physical and physiological condition (time = 0). This generally took place within 15 min of the catch being hauled aboard. For each individual, CL, sex, damage (described in next paragraph), vigor index (described in next paragraph), molting stage, the presence of mature gonads in females (green gonads), and any obvious Hematodinium symptoms were recorded.

Visible damage was scored against the three levels (0 = no damage, 1 = slight damage, 2 = severe damage) as introduced by Ridgway et al. (2006a). Injuries were not counted if there was evidence of tissue regeneration, indicative of an old injury. Vigor was assigned to five categories: A, B, C, moribund, or dead according to the posture of the animal when held mid-air, the position of the antennae and claws, the degree of tail tension, the position of the antennae and claws, the degree of tail tension, and quantifying the parasites in the hemolymph (Beevers et al. 2012). Carapace hardness was used as a straightforward measure of the molting stage of individual Nephrops. Animals were classified as “soft” if gentle squeezing just behind the eyes gave a clear distortion (Milligan et al. 2009). “Soft” animals included those recently molted and at late intermolt (i.e., with calcium withdrawn from exoskeleton). For consistency, visual indices (vigor, damage, body color, and carapace hardness) were recorded by same observers in all trips.

Around 200 µl of hemolymph was then extracted to establish baseline physiological condition using 1-ml syringes coupled with 25G needles. A subsample of 100 µl of hemolymph was then deproteinized in 100 µl of 6 M perchloric acid, mixed, and stored on dry ice. Muscle samples were excised and immediately frozen in liquid nitrogen.

Thereafter, another 150 animals were sequentially selected from the discard category and damage and vigor indexes scored as above as they were placed into indexed tube sets (Fig. 1) for the short-term survival trial of captive specimens. Sex and length were not recorded at this stage so as not to delay returning these animals to the sea. Air temperatures during catch sorting and sampling procedures were recorded, as well as the overall time taken for the sampling and stocking of the tube sets to be completed (Tables 1 and 3). Tube-sets containing 150 discarded animals per tow were enclosed in perforated plastic boxes and returned to the sea suspended on a rope mooring at a depth (usually around 30 m) below the upper lower salinity layer.

The Nephrops stocked in the suspended tube-sets were left to recover for 48 h and after this time the boxes were collected. Sex, CL, damage index, and vigor index were then recorded for all these animals. A random subsample of 30 animals per tow was then sampled for physiology as described in the next two sections.

**Measurement of Physiological Parameters—Hemolymph and Muscle L-lactate**

L-lactate concentration was measured following Bergmeyer and Bernt (1974) and modified by Hill et al. (1991). Samples
TABLE 2. Characteristics of the different vigor index categories used in the trials.

| Vigor A | Vigor B | Vigor C | Moribund | Dead |
|---------|---------|---------|-----------|-------|
| Animal displays defensive posture, and or vigorous and possibly prolonged (>10 flips) tail flipping. Antennae and claws are held high and may be "waved" by the animal. Tail is held rigid upright in an angle (when animal is not tail flipping). Antennae and claws are drooped and animal can raise them (for short periods) but it will not be able to right itself. Walking legs are very slowly moved very slowly, and animal is unable to reflex response. | Bouts of tail flipping are frequent and vigorous, lasting for shorter periods (<10 flips approximately). Animal is less likely to adopt defensive posture. Antennae and claws are raised but moved less vigorously. Tail is held horizontally retains some tension. Related to reflex response. Walking legs are moved but animal normally cannot right itself | Bouts of tail flipping are infrequent and do not normally exceed five flips per bout approximately. Animal can raise them (for short periods) Antennae and claws are drooped but animal can raise them (for short periods) | Tail flips are very infrequent and weak. Antennae and claws are drooped and animal can raise them (for short periods) Tail is limp. Related to reflex response. Walking legs are moved very slowly | No limb movements even if animal is stimulated. Antennae and claws are drooped and animal can raise them (occasionally). Tail is limp. Related to reflex response. Walking legs are moved very slowly |

Measurement of Physiological Parameters—ATP and Its Breakdown Products

Nucleotide analysis was performed using high-performance liquid chromatography as described by Ryder (1985) and modified by Albalat et al. (2009). The system consisted of a Spectra system P4000 pump coupled to a SN4000 autosampler and a UV1000 detector set at 254 nm. A Kinetex 5 µm 100A column 250 × 4.6 mm with an internal particle of 5 μm was used to conduct the separations (Phenomenex, Cheshire, United Kingdom). Standard curves were prepared from ATP, adenosine 5'-diphosphate, adenosine 5'-monophosphate, inosine 5'-monophosphate, inosine, and hypoxanthine using concentrations ranging from 0.1 to 1.0 mM (Sigma-Aldrich, Dorset, United Kingdom). The Adenylate Energy Charge (AEC) was calculated based on the nucleotide profiling of the muscle samples following Atkinson (1968).

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\text{AEC} = \frac{[\text{ATP}] + 0.5 \times [\text{ADP}]}{[\text{ATP}] + [\text{ADP}] + [\text{AMP}]} 
\]

Statistical Analyses of Physiological Data

Differences of L-lactate (in hemolymph and muscle) and AEC ratios between trials (February, March, and June) at 0 and time 48 h were analyzed using analysis of variance following homogeneity of variance checks using Levene's test. Post-hoc multiple comparisons (Tukey post hoc or Games–Howell test according to outcome Levene's test) were applied to determine statistical differences between samples. Differences between time 0 and 48 h within each trial were analyzed by independent sample t tests. In all cases, P values lower than 0.05 were considered statistically significant.

Predator Avoidance Behavioral Trials Using Video Surveillance

Six, 50-m depth submersible 12-V cameras (VN37CSHR-W36, Visionhitech Co., Ltd., Korea) were mounted on a custom-built lander frame in a grid layout so that they would cover a larger area of seabed (Fig. 1C). The cameras were connected to a multichannel Digital Video Recorder (Hybrid 16 DVR, Huviron Ltd., Korea) on board the research vessel “Calanus”, which was anchored next to the rig. The rig was deployed on July 29, 2015 at 55.805°N 004.882°W at a depth of just under 30 m. Temperature and salinity profiles were recorded using a YSI Castaway CTD (Fig. 2). The bottom type was sandy mud with some shell debris. Discard category Nephrops were sorted on board the commercial fishing vessel following the normal commercial procedures described in section ‘Trawling and Data Collection’ and were transferred to the research vessel as soon as possible once catch sorting was completed. Ten animals were

were thawed, deproteinized, and homogenized using an Ultra Turrax T25 homogeniser. Homogenates (50 µl) were added to microcentrifuge tubes (Eppendorf) containing 50 µl NAD⁺ (50 mM), 0.85 ml hydrazine buffer (0.6 M hydrazine hydrate, 5.6 mM ethylenediaminetetraacetic acid, 1 M glycine) at pH 9.5, and 1 unit of lactate dehydrogenase (Sigma), and incubated for 2 h at 37°C. Absorbance readings at 340 nm (Shimadzu, UV Mini 1240) were converted to concentrations of L-lactate using a calibration curve constructed from lactic acid standards (0.5–10.0 mM).
selected at random and placed in a perforated plastic container and taken directly to the camera rig by diver. Five deployments were made with animals having been exposed to varying total air times and recovery intervals (Table 4). The recorded videos were subsequently transferred from the DVR and individual video streams merged into a composite montage using a custom script written in MATLAB. Behavior of *Nephrops* and interactions with other organisms were then summarized based on visual analysis.

**Modeling Overall Survival of Discarded Nephrops**

Survival proportions of all discarded *Nephrops* were analyzed using binomial logistic regression, with resulting coefficients converted to 95% confidence intervals. Three analyses were performed: (1) modeling actual survival at 48 h with trawl date, CL, sex, vigor, damage, infection status, molting status, and females showing mature gonads as explanatory variables; (2) modeling actual survival at 48 h using only date, sex, and CL as explanatory variables (to create a model that can be extrapolated to other catch compositions in each season); and (3) modeling probable survival using the same explanatory variables as in model 2, where it was assumed that all infected or damaged (class 1 or 2) animals after 48-h recovery would die shortly after in order to produce a more conservative survival estimate as studies such as Wileman et al. 1999 have suggested mortality in recovering trawled *Nephrops* can take longer than 48 h to stabilize. For each of these models, stepwise regression was performed with non-significant explanatory variables being removed. All statistical analyses were conducted using R version 3.2.3.

**RESULTS**

**General Information and Fractions of Retained and Discarded Nephrops**

Air temperatures during the trials in February and March were between 7°C and 8.5°C, whereas in June temperatures ranged from 12.5°C in the early morning to 15°C by the afternoon. The time taken to sort the catches on board the fishing vessel was 83 ± 9 min. Sorting times in February and June were slightly longer (between 95 and 103 min) compared with March, where the sorting time was around 60 min due to the smaller catches. The visual impression was that total catch volumes (*Nephrops* plus bycatch) were largest in February. The total numbers of *Nephrops* caught were noticeably lower during the March trial (234–739/tow) compared with February (1,180–1,830/tow) and June (763–1,478/tow). This was due to the stronger tides during the March trial, conditions that are often associated with reduced catches of *Nephrops* in this fishery (Skipper, personal communication).

![Figure 2. Temperature and salinity water column profiles from the camera deployment locations.](image)

**TABLE 3. General information and environmental conditions during the recovery of tubed animals.**

| Month             | February 13, 2015 | March 26, 2015 | June 18, 2015 |
|-------------------|-------------------|----------------|--------------|
| Tow               | 1 2              | 1 2            | 1 2          |
| Air temperature (°C) | 6.5 7.5         | 6.4 8.3        | 9.7 12.0     | 11.5 11.0 |
| Water temperature surface (°C) | 7.5 7.5     | 7.5 7.5        | 7.5 7.5      | 11.5 11.0 |
| Water temperature bottom (°C) | 8.1 8.1 | 7.4 7.4       | 7.4 – –       | – – – – |
| Salinity water surface (PSS) | 32.6 32.6 | 31.3 31.3     | 31.3 – –     | – – – – |
| Salinity water bottom (PSS) | 33.2 33.2 | 32.9 32.9     | 32.9 – –     | – – – – |
| Time animals arrive onboard (UTC) | 10:09 10:07 | 09:45 13:04 | 13:04 09:51 | 11:30 14:25 |
| Time start sampling (UTC) | 10:15 11:42 | 09:50 13:23 | 14:04 09:53 | 11:30 14:28 |
| Time finish sampling (UTC) | 11:40 13:15 | 11:26 14:02 | 14:55 11:22 | 12:50 15:37 |
| Total time aerial exposure (minutes) | 91 188 | 101 58 | 111 89 | 80 69 |
females in the discard fraction was higher in June and the majority of these animals was soft and had mature gonads (Fig. 3B). These animals have low market value and are, therefore, normally discarded (Skipper, personal communication).

Physiological Condition and Short-Term Survival of Captive Discarded Nephrops

Overall, discard fraction Nephrops were predominantly in vigor category "C" (51%) immediately after trawling (Fig. 4A), whereas animals in top vigor categories A + B accounted for around 25%. After a 48-h recovery period, the proportion of discarded animals in the top vigor categories (A + B) had increased to 64%, whereas 12% were moribund or dead. From a seasonal perspective, a higher proportion of the Nephrops were classified as being in vigor category A after the 48-h recovery period in February (Fig. 4B). Moreover, the number of moribund animals was lowest although the numbers of prawns dying was actually higher. In June, more animals were in vigor categories B + C after 48-h recovery but the number which had died was lower than in other months.

Physiological Condition and Short-Term Survival of Captive Discarded Nephrops

| Deployment 1 | Trawl began | 06:00 |
| Trawl tow ended | 07:30 |
| Prawns transferred to Calanus | 07:45 |
| Prawns placed under camera | 09:09 |
| Posttrawl treatment | around 90 min in air |
| Air temperature (°C) | 9.5 |
| Vigor | Individual vigor not recorded but a mix of C and moribund |
| Comments | Test dive (sizes of animals not recorded) |

| Deployment 2 | Trawl began | 07:45 |
| Trawl tow ended | 09:45 |
| Prawns transferred to Calanus | 10:00 |
| Prawns placed under camera | 10:50 |
| Posttrawl treatment | −60 min in air |
| Air temperature (°C) | 16.5 |
| Size (mm) | 28 30 30 28 28 30 30 31 29 |
| Vigor | B A/B A A/B B B A/B B |
| Comments | Spare animals were sunk in tubes at 20 m and also used in deployment 3 |

| Deployment 3 | Trawl began | As above |
| Trawl tow ended | As above |
| Prawns transferred to Calanus | 11:20 |
| Prawns placed under camera | −30 min air, 65 min recovery at 20 m |
| Posttrawl treatment | 17.0 |
| Air temperature (°C) | 16.5 |
| Size (mm) | 25 27 28 28 29 27 28 28 31 32 |
| Vigor | B B B A A/B C B/C B B |

| Deployment 4 | Trawl began | 10:30 |
| Trawl tow ended | 12:30 |
| Prawns transferred to Calanus | 12:43 |
| Prawns placed under camera | 13:04 |
| Posttrawl treatment | −30 min air |
| Air temperature (°C) | 17.3 |
| Size (mm) | 28 26 25 26 26 29 26 27 27 |
| Vigor | A B/C B/C B A/B B B |

| Deployment 5 | Trawl began | 13:00 |
| Trawl tow ended | 14:40 |
| Prawns transferred to Calanus | 15:00 |
| Prawns placed under camera | 15:30 |
| Posttrawl treatment | −50 min air |
| Air temperature (°C) | 17.3 |
| Size (mm) | 25 25 25 25 25 25 25 25 26 22 |
| Vigor | B/C B/C* B/C B/C B/C B/C B/C B/C |

Comments: * Deployment used to diver observations and to take flash stills photographs, video not analyzed further.
48-h recovery period, there was an increase in the proportion of animals with some visible damage (13% at T0 to 18% at T48). Potential contributing factors could include handling the animals in and out of the tube-sets or moving the boxes in and out of the water. Although in this study, damage percentages were low, damage did have an impact on the recovery potential of the animals. As shown in Figure 5A, the proportion of dead and moribund animals after 48-h recovery increased with damage. Indeed, more than 50% of the Nephrops, which were classified as being in damage category 2 immediately after trawling, were dead or moribund after 48 h.

The percentages of prawns with Hematodinium infection varied seasonally; 10.2% of animals infected in February, 12.9% in March, but only 0.4% in June. Infected animals did not show as good recovery potential as uninfected animals. After 48-h recovery, more than 50% of animals classified as visually infected immediately after trawling were dead or moribund (Fig. 5B).

Baseline physiological data for prawns immediately post-catch were indicative of capture stress with elevated muscle L-lactate (Fig. 6A) and low AEC ratios indicative of anaerobic respiration (Fig. 6B). In June, muscle L-lactate values after 48 h were significantly higher than in February or March (Fig. 6A), but seasonal effects were not so obvious in post-recovery AEC ratios (Fig. 6B). Despite some indications that physiological recovery was poorer in June (lower percentage of animals in vigor category A and significantly higher muscle L-lactate concentration), the percentage of dead animals after 48 h was actually lowest in that month (Fig. 4B).

**Predator Avoidance Behavioral Observations on Released Discard Fraction Nephrops**

During the behavioral trial, the air temperature rose from 9.5°C in the early morning to around 17°C by 10:00, whereas
CTD casts showed a layer of lower salinity water reaching down to around 5-m depth (Fig. 2). All animals used were in the discard size class (22–32 mm CL) and all test animals, except one, were in damage category 0. Prawns caught in the morning were all in vigor index A, B, or C after transfer to the research vessel. The vigor indices of *Nephrops* caught in the afternoon were slightly lower (mainly B/C) (Table 4). In the main deployments (2–5), delays in returning the animals to the sea were relatively short (30–45 min to reimmersion). The exposure to seawater during their descent seemed to act as a stimulant and nearly all the *Nephrops* (38/40) exhibited almost immediate righting action and began moving around when placed on the seabed (Table 5). The majority of these animals appeared to exhibit normal locomotory behavior and dispersed out of the camera view within a few minutes. In the initial test deployment, the animals had been held on the research vessel in air for around 90 min, while the equipment and dive team were being prepared. These *Nephrops* were mostly in vigor category C or were moribund when taken down to the camera rig. Some of these animals took up to 10 min to recover and this period was sufficient to attract several shore crabs (*Carcinus maenas*) and squat lobsters (likely *Munida rugosa*), which attacked any unrighted *Nephrops*. Although several prawns exhibited tail-flip escape responses, this tended to be a single or double flip rather than a series, which would have carried them away from the predators. At least one prawn would probably have failed to survive [the individual in question being attacked by two crabs and eventually dragged out of the observation arena (Table 5)].

**Modeling Overall Survival of Discarded Nephrops**

Of the available covariables (date, CL, sex, damage, vigor, softness, infection, and gonad status), only date, damage index, infection status, and molting stage were found to be statistically significant explanatory variables for 48-h survival of discarded *Nephrops*. The percentage of discarded *Nephrops* classified according to the vigor index just after trawling (time 0) and 48 h after recovery at sea from all discarded animals used in the survival trials and percentage of discarded *Nephrops* classified according to the vigor index 48 h after recovery period in each trial are shown in Figure 4 (A) and Figure 4 (B), respectively.

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Table 6 shows confidence intervals for the baseline probability of survival in each season and also the increase in the odds ratio of death according to each contributory factor. Only date was found to be statistically significant for the model of likely long-term survival (in this more conservative model, it was assumed that damaged, infected, or soft animals would all die in the longer term, Table 7).

As a caveat, it should also be noted that there was an increase in the proportion of animals with some damage during the 48-h recovery period from 12.8% at T0 to 18.0% at T48. It was not possible to correct survival estimates for this because the additional damage could have occurred at any time during the 48-h recovery, or during inspection of the animals after this time. Nevertheless, such accidentally induced additional damage would only decrease survival meaning that the estimated survival rates will be conservative.

**DISCUSSION**

Although other studies have described the annual emergence of recently molted female Nephrops in spring and early summer (Milligan et al. 2009), this is the first time that discarding of soft females as a low-quality product has been reported. Similarly, although several studies have reported the seasonal patterns of Nephrops infection by Hematodinium (Field et al. 1992, Stentiford et al. 2001, Beever et al. 2012), this is the first time that it has been observed that fishers are able to recognize symptomatic patent-infected animals (on the basis of their body color) and that these animals are then being discarded. The choice to discard soft or infected animals is driven by the fact that this particular fishery is serving the live market and prioritizing product quality over volume. Although such high grading is often considered to be an undesirable fisheries practice, the actual impacts will vary depending on the survivability of the discarded fraction.

In this study, more than 90% of the discarded Nephrops were alive after 48-h re-immersion in tube-sets. These values are higher than reported in most other post-discard studies in Nephrops trawl fisheries (Castro et al. 2003, Méhault et al. 2016). Guéguen and Charua (1975) reported a survival rate of around 25% after 3 days recovery in cages immersed at around 60 m depth, following aerial exposure of 90 min, but later studies have reported higher survival rates ranging from 31% (Charuau et al. 1982), 30%–48% (Castro et al. 2003) to 45%–65% (Méhault et al. 2016). There are multiple potential reasons for the wide disparities in estimates of post-discard survival including differences in the fishing gears and practices, differences in water and air temperatures, and the length of air exposure and differences in how the catches are handled. The higher survival rates in this study are likely related to the specific nature of this Clyde fishery that prioritizes quality over volume resulting in short tows and rapid catch sorting.

Nevertheless, the lack of standardization in experimental designs does cause problems when comparing results between studies (ICES 2014, Méhault et al. 2016). This is apparent not only in terms of the number of vessels that should be used (most survival trials conducted to date have been carried out in single vessels felt to be “representative” of the wider fleet practices), but also in relation to the length of time that experiments need to be run for (Wassenberg & Hill 1993, Castro et al. 2003, Campos et al. 2015). A report by STECF (2015) suggested observations on Nephrops recovery should be continued until mortality rates have stabilized, which in some studies took as long as 10–14 days (Wileman et al. 1999). Measurements in this study and in Albalat et al. (2010) suggest that physiological recovery to resting values occurs within 24–48 h. Delayed mortality, thus, appears to be mainly the result of physical damage (Wileman et al. 1999). Model 2 survival estimate assumed that any animals which were damaged or infected after 48-h recovery would die over the following few days and so this represents a conservative assumption of survival of around 63% (the lowest 95% confidence interval). This approach might prove useful as establishing mortality curves over 10–14 days means that recovery cages must be inspected regularly. Regular inspection requires either raising them to the surface, which causes increased aerial exposure and stress, or the use of divers (feasible down to about 30 m) or potentially inspection using remotely operated vehicles. Monitoring of recovery cages by divers has been used in some previous studies (Wileman et al. 1999) but considerably increases experimental costs. A final alternative is to allow animals to recover in tanks on board fishing vessels or ashore (Edwards and Bennett 1980, ICES 2014). Whether tanks, however, adequately replicate natural recovery conditions is debatable especially where it is difficult to control factors such as temperature and salinity. Exposure to low-salinity water in
TABLE 5.
Summary of behavioral observations.

| Filename     | Timestamp (h:min:sec) | Time since release (min:sec) | Summary main events |
|--------------|-----------------------|------------------------------|---------------------|
| Montage_Deploy1 | 09:09:23             | 00:00                        | Prawns released into arena |
|              | 09:09:44             | 00:21                        | Two prawns show almost immediate recovery |
|              | 09:09:48             | 00:25                        | Diver withdraws from site |
|              | 09:10:11             | 00:48                        | Prawn at top of group exhibits a flick-tail escape response, another prawn begins to recover and move around |
|              | 09:10:53             | 01:30                        | Another prawn recovers and moves away; five unrecovered animals remain |
|              | 09:12:00             | 02:37                        | Four more prawns begin to show signs of recovery, limb movement, attempts at righting |
|              | 09:14:53             | 05:30                        | All prawns except one showing some signs of recovery although three animals have still failed to fully right themselves |
|              | 09:16:23             | 07:00                        | All prawns except two have either left the arena or are moving within the arena |
|              | 09:18:13             | 08:50                        | Prawn at top left interacts with another recovering animal and exhibits a flick-tail escape |
|              | 09:18:53             | 09:30                        | All prawns righted, all except one moving around, squat lobster enters arena and one prawn evades |
|              | 09:19:33             | 10:10                        | Prawn nips squat lobster which moves away, one prawn still only partially righted (camera 5) |
|              | 09:20:07             | 10:44                        | Squat lobster attacks partially righted prawn |
|              | 09:20:36             | 11:13                        | First crab arrives and chases off squat lobster |
|              | 09:20:39             | 11:16                        | Crab attacks recovered prawn but prawn exhibits escape response |
|              | 09:21:13             | 11:50                        | Crab attacks damaged prawn which exhibits a flick-tail response but then fails to right itself (moving from camera 5–6) |
|              | 09:21:31             | 12:08                        | Second crab then moves in to attack a separate prawn (camera 5) |
|              | 09:21:37             | 12:14                        | Both crabs then attack the prawn |
|              | 09:21:53             | 12:30                        | Prawn is dragged out of camera arena by one crab and second crab resumes searching |
| Montage_Deploy2 | 10:49:54             | 00:00                        | Prawns placed in camera arena |
|              | 10:50:01             | 00:07                        | Eight or nine prawns seem to recover almost immediately and begin to disperse |
|              | 10:50:08             | 00:14                        | Remaining prawns right themselves and begin moving around |
|              | 10:51:01             | 01:07                        | All animals appear to be moving around within, or have exited the arena, rate of tidal flow picking up compared with earlier deployment |
|              | 10:51:44             | 01:50                        | Single prawn reenters arena, moving around on seabed |
|              | 10:51:50             | 01:56                        | Second prawn reenters after exhibiting tail-flick escape response from some unseen stimulus |
|              | 10:53:05             | 03:11                        | End |
| Montage_Deploy3 | 11:20:54             | 00:00                        | Tide had picked up and diver reported that the prawns were all active but dispersed very rapidly, video of a single animal walking |
|              | 11:21:35             | 00:39                        | End |
| Montage_Deploy4 | 13:04:35             | 00:00                        | Prawns placed in arena, camera 3 not working |
|              | 13:04:40             | 00:05                        | Four animals show good recovery and move away |
|              | 13:04:45             | 00:10                        | All animals have righted themselves and are beginning to recover |
|              | 13:05:02             | 00:27                        | Three animals remain within arena |
|              | 13:05:44             | 01:09                        | Four prawns continue moving around within arena |
|              | 13:06:31             | 01:56                        | Two prawns show interaction then move apart |
|              | 13:06:49             | 02:14                        | End |
| Montage_Deploy5 | 13:10:00             | 05:25                        | Not analyzed, divers using flash still photography |
TABLE 6.
Ninety-five percent confidence intervals for results of model 1.

| Season   | 95% confidence interval of probability of survival (healthy undamaged Nephrops) |
|----------|---------------------------------------------------------------------------------|
| February | 93.4%–97.1%                                                                      |
| March    | 95.6%–98.8%                                                                      |
| June     | 98.8%–99.9%                                                                      |

| Category                  | Increase in odds ratio of death comparing undamaged and uninfected animals with other categories |
|---------------------------|-----------------------------------------------------------------------------------------------|
| Damage class 1            | 1.3–5.4 times                                                                                 |
| Damage class 2            | 2.0–3.58 times                                                                                |
| Visually infected         | 2.2–11.4 times                                                                                |
| Soft                      | 3.1–31.3 times                                                                                |

Results are expressed as baseline probability of mortality in each season, and increase in odds ratio of mortality according to each contributory factor.

particular is known to cause stress to Nephrops (Harris & Ulmestrand 2004). Because of these problems, most studies on Nephrops have not monitored individual survival over time but have used start-end comparisons in recovery cages deployed for periods of between 2 and 9 days (Castro et al. 2003, Campos et al. 2015).

Because mortality in discarded Nephrops seems to be more related to physical damage than physiological stress, changes in fishing practice aimed at reducing damage should increase post-catch survival but implementing such changes may be difficult within a commercial fishery context. For example, the use of short tows, which appears beneficial in this fishery, may not be acceptable in other métiers where catch volume is more important and tow durations are up to four hours (Milligan et al. 2009, Fox 2010). Improved survival of discarded Nephrops has also been reported with some gear modifications, such as in-trawl sorting grids and SELTRA panels (STECF 2015). This may be related to reductions in the overall bulk of catch in the cod-end leading to reduced damage (Broadhurst et al. 2009). Nevertheless, these results remain to be confirmed as the higher survivals reported could also have a seasonal, rather than gear modification, basis (STECF 2015).

Although the majority of discard survivability trials have allowed animals to recover in predator-free enclosures (Wileman et al. 1999, Bergmann & Moore 2001, Castro et al. 2003, Revill et al. 2005, Mandelman & Farrington 2007, Rulifson 2007, Enever et al. 2009, Campos et al. 2015), it is widely recognized that this may overestimate post-discard survival (Raby et al. 2014). Animals returned to the sea must escape potential predators and, in the case of Nephrops, seek protection in existing or newly excavated burrows. In this study, around 80% of the discarded Nephrops were in vigor categories A–C immediately after being trawled (Fig. 4A), and results from underwater observations suggested that these animals could right themselves, begin active movement and adopt natural defensive postures, and escape responses within a few minutes of being returned to the seabed. On the other hand, animals in a moribund condition, as a result of longer air exposure, took up to 10 min to recover on the seabed. This period was sufficient to attract predators, such as shore crabs and squat lobsters, which were observed to successfully capture at least one of these Nephrops. The metabolic capacity of moribund Nephrops, thus, appears to be compromised to the point where they struggle to make repeated escape tail-flips when attacked by predators (Gornik et al. 2008). Because moribund animals made up around 20% of the discard category immediately after trawling (Fig. 4A), these animals are likely to be more vulnerable to predation after reaching the seabed. Unfortunately, behavioral observations only extended over the immediate post-release period because fences were not used around the camera arena because this would have excluded benthic predators. The relatively rapid attraction of predators to the discarded Nephrops, as also observed by Bergmann et al. (2002), suggests that future studies need to place more emphasis on such behavioral interactions. Discarded Nephrops might also be vulnerable to predation during the descent to the seabed but based on measurements of sinking rates and estimates of midwater predation, Bergmann et al. (2002) suggested that most discards in the Firth of Clyde would reach the seabed. For longer term survival studies, STECF (2015) have suggested that tag and release programs may be required. Such programs would have to be run over extensive periods, tag loss rates evaluated, large numbers of Nephrops marked, and a large percentage of the fishing vessels in the area equipped to detect the presence of the internal tags that would have to be used. The costs involved in such large-scale discard-survival programs are such that they may only be worth undertaking for animals with higher conservation concern and which are occasionally caught in Nephrops trawls, such as the flapper skate Dipturus intermedia (Neat et al. 2015).

Given the many factors, which vary between fishing fleets, grounds, seasons, and even individual vessels, producing realistic survival estimates for animals discarded in commercial fisheries remains extremely challenging. This study was conducted in a commercial vessel thought to be representative of practices in the Firth of Clyde trawl fishery that targets the live market. Further studies may be required to confirm that the data presented are representative of the wider fleet.

The fishery studied here is characterized by day vessels that perform short tows (typically <2.5 h) and practices.

TABLE 7.
Ninety-five percent confidence interval for probability of survival for each season.

| Model                                      | February       | March        | June          |
|--------------------------------------------|----------------|--------------|---------------|
| (1) Actual survival, based on percentage of animals alive after 48-h recovery | 90.1%–95.8%    | 91.8%–96.9%  | 96.1%–98.9%   |
| (2) Likely survival, assuming damaged or infected animals will not survive in the longer term | 68.0%–77.7%    | 63.4%–73.8%  | 81.3%–88.0%   |
which prioritize the quality of the animals over catch volume (Combes 2007). This makes this fishery quite specialized compared with the majority of Nephrops trawling where tow durations and sorting times tend to be longer and the catches larger. Data from this study should, therefore, not be extrapolated to other trawl-based Nephrops fisheries where further studies will be required to estimate the survival of discarded animals.

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