Marine Biology (2001) 138: 527–536

K. Ramsay · M. Bergmann · L. O. Veale
C. A. Richardson · M. J. Kaiser
S. J. Vize · S. W. Feist

Damage, autotomy and arm regeneration in starfish caught by towed demersal fishing gears

Received: 16 August 2000 / Accepted: 20 October 2000

Abstract Arm damage and loss were examined in the starfish *Asterias rubens* that had been caught in a variety of towed commercial fishing gears deployed on different sea bed types. Between 7% and 38% of the starfish in each catch lost one or more arms, and arm loss was positively correlated with the volume of the catch for two of the fishing gears examined. Subsequent monitoring of damaged animals showed that arms were autotomised for at least 3 weeks following capture. Mortality was highest in starfish with damaged or missing arms, compared with those that appeared intact after fishing. Arm regeneration was delayed in a small proportion of the animals caught by commercial gears. In a parallel study, 17% of starfish caught by a 4 m beam trawl had a damaged ambulacral ossicle at the point of autotomy (cf. none from a control group that were induced to autotomise under controlled conditions). There was no difference in regeneration rates between the animals caught by commercial gears and a control set (caught by a small trawl and forced to autotomise an arm in the laboratory) once the animals that delayed regeneration were excluded from the dataset. After 1 year under laboratory conditions the starfish had, on average, regenerated the missing arm to 75% of the length of the other four arms. During this time period the lengths of the undamaged arms increased by ca. 50%. The implications of this study for using arm loss in starfish as an indicator of fishing disturbance are discussed.

Communicated by J. P. Thorpe, Port Erin

K. Ramsay (✉) · C. A. Richardson
M. J. Kaiser · S. J. Vize
School of Ocean Sciences, University of Wales Bangor,
Menai Bridge, Anglesey LL59 5EY, UK

M. Bergmann
University Marine Biological Station, Millport,
Isle of Cumbrae, Scotland KA28 0EG, UK

L. O. Veale
Port Erin Marine Laboratory, University of Liverpool,
Port Erin, Isle of Man IM9 6JA, UK

S. W. Feist
The Centre for Environment,
Fisheries and Aquaculture Science,
Weymouth Laboratory, Barrack Road,
The Nothe, Weymouth, Dorset, DT4 8UB, UK

Present address:
K. Ramsay
Countryside Council for Wales, Plas Penrhos,
Ffordd Penrhos, Bangor, Gwynedd LL57 2LQ, UK
e-mail: k.ramsay@ccw.gov.uk

Introduction

Several animal groups have evolved the ability to autotomise and subsequently regenerate body parts. Lizards, salamanders and slow-worms can autotomise and regenerate the tail or rear portion of the body (Pratt 1946; Wake and Dresner 1967; Sheppard and Bellairs 1972) and crustaceans can regenerate limbs (Emmel 1910). Autotomy and regeneration are common in echinoderms (Emson and Wilkie 1980; Lawrence 1992) and were documented in *Asterias vulgaris* over 100 years ago (King 1898).

Fredericq (1883, 1887) defined autotomy as a nervously mediated shedding of a limb or other body part that has a defensive function. Several authors have hypothesised on the adaptive significance of autotomy and regeneration, and it is generally thought to have evolved as a predator avoidance mechanism. Hancock (1955, 1974) demonstrated that autotomy in *Asterias rubens* was effective in escaping two predators, *Hyas araneus* and *Crossaster papposus*. In a study of the frequency of arm regeneration in four species of *Asterias*, Lawrence et al. (1999) suggest that predation was the main factor responsible for the arm loss observed in the field. However, autotomy may also be a mechanism for shedding damaged or diseased limbs (Emson and Wilkie 1980) or limbs infested with parasites (Stasek 1967).

King (1898) described autotomy and regeneration in *A. vulgaris* (a species morphologically indistinguishable from *A. rubens*, Clark and Downey 1993). Autotomy occurred between the fourth and fifth or the fifth and sixth ambulacral ossicles, and, following autotomy, the aboral body wall folded down to cover the wound within 5–10 min. Regenerating tissue became apparent after ca. 10 days, but King (1898) gives no information on the growth rate of the regenerating arm. Cuénot (1966) reported that autotomy in *A. rubens* occurred between the third and fourth ambulacral ossicles. Surprisingly, there is no published information available concerning the time taken for arm regeneration in either *A. vulgaris* or *A. rubens*.

In addition to natural causes of arm autotomy, anthropogenic disturbances may also cause arm loss in starfish. Various studies of the impacts of towed, bottom-fishing gears have noted that starfish lose arms as a result of capture by, or contact with, these gears (de Graaf and de Veen 1973; Kaiser and Spencer 1995; Lindeboom and de Groot 1998). Kaiser (1996) examined the incidence of regenerating arms in two species of starfish (*A. rubens* and *Astropecten irregularis*) collected from areas of the Irish Sea subject to different fishing intensities. For both species, the incidence of animals with regenerating arms increased significantly with increasing fishing intensity. From these results Kaiser (1996) suggested that arm damage in starfish might be used over short time scales (1–2 years) as an indicator of fishing intensity. This could be valuable in many areas where the low scale of resolution and poor accuracy of fishing effort data are hampering efforts to ascertain the long-term ecological effects of fishing activities (Kaiser 1998).

The present paper examines the extent and severity of damage and arm loss in *A. rubens* caught by towed, bottom-fishing gears. The study did not examine arm loss or damage in animals that were in the path of a dredge or trawl but not captured (e.g. animals that passed beneath the gear or through the mesh of a net). Post-capture mortality and autotomy were examined over longer time-scales than previously reported (2–4 weeks in this study, cf. 3–6 days previously, Fonds 1994; Kaiser and Spencer 1995), and the time taken for arms to regenerate was investigated. We also consider the implications of these data for using arm loss in *A. rubens* as an indicator of fishing effort.

Materials and methods

Arm loss in starfish caught by fishing gears

Starfish (*Asterias rubens* L.) were collected using a variety of commercial fishing gears (Table 1) at several different locations around the UK (Fig. 1) and were examined for signs of recent damage and arm loss. The fishing gears were deployed on the types of ground on which they would typically be used (e.g. beam trawls on sand and scallop dredges on harder ground).

On each sampling occasion either the entire catch or a haphazard subsample of starfish was examined for damage. For each starfish, a record was made of the numbers of arms that recently had been lost, as indicated by fresh open wounds (through which internal tissues could be seen) as opposed to older healed wounds. The term "lost" has been adopted throughout the text rather than "autotomised" as it was impossible to know whether the starfish had autotomised the arm in the manner described in King (1898) and as defined by Fredericq (1883, 1887) or whether the arm had been forcibly detached from the body whilst in the trawl or dredge. To allow for multiple arm loss, data are presented as the proportions of the total number of arms lost or damaged in the whole sample, assuming that each starfish would normally have five arms [i.e. total number of arms lost/(number of individuals × 5)]. The occurrence of damaged arms was also recorded; these had one or more open wounds in the body wall from which internal tissues often were protruding. Regenerating (but otherwise undamaged) arms were classed as intact. To improve statistical rigour, data were pooled from several tows where catch numbers were low, if those tows had been carried out on the same day and in close proximity to one another. The data were investigated to determine which variables significantly affected the frequency of arm loss in starfish. The data on percentage of arms lost were arcsine transformed (to achieve homogeneity of variance) and examined using a General Linear Model (GLM) for the relationship between arm loss and some or all of the following variables and combinations of these variables: vessel, sediment type (grouped to mud, sand and gravel), time of year (grouped to quarters: January–March, April–June, etc.), tow duration (min) and total volume of the catch (l). Each gear type was examined separately. Because the data did not fall into a balanced design, care had to be taken to ensure that inappropriate tests were not carried out. For example, although seven tows were carried out using an otter trawl clean net, these tows varied in the vessel used, the sediment type, time of year, tow

Table 1 Technical details of the fishing gears used

Gear type (location of experiments)	Width	Mesh	Towing speed (knots)	Other details
Beam trawl (Margate)	4 m beam width	80 mm diamond mesh cod-end	4	Fitted with chain matrix and flip-up ropes
Scallop dredge (Red Wharf Bay)	2 × 0.76 m dredges	Ring diameter 90 mm, liner 10 mm mesh	3	Newhaven (spring toothed) type dredges. Teeth 110 mm long
Scallop dredge (Isle of Man)	4 × 0.76 m dredges	Ring diameter 70 mm	2.5	Newhaven (spring toothed) type dredges. Teeth 110 mm long
Queen dredge (Isle of Man)	4 × 0.76 m dredges	Ring diameter 57 mm	2.5	Newhaven (spring toothed) type dredges. Teeth 75 mm long
Rockhopper otter trawl (Clyde)	13.7–15.2 m	70 mm diamond mesh cod-end	2.3–3	Square mesh panel, except for the net used by R.V. "Aora"
Clean net otter trawl (Clyde)	15.2–18.3 m	70 mm diamond mesh cod-end	2.3–3	Square mesh panel. No bobbins or tickler chains

Fig. 1 Positions of the sites fished

duration and catch size. Therefore, it was impossible to test the effect of any one of these variables, as no single variable changed without one or more of the others changing at the same time. Tests were not carried out unless there were five or more replicates of categorical variables (e.g. vessel, sediment).

Survival and subsequent arm loss following beam trawling and scallop dredging

A subsample of the starfish caught in April 1998 by a 4 m commercial beam trawl (tow duration 45 min) were transferred to a tank system supplied with running seawater on board ship (see Kaiser and Spencer 1995). The subsample was divided into three groups according to levels of damage and comprised 50 intact individuals (i.e. with no visible signs of damage), 37 damaged individuals (i.e. with one or more open wounds in the body wall but still possessing all five arms) and 72 starfish with one or more arms that recently had been lost. A control group of 40 visibly intact starfish was collected ca. 30 min after the first beam trawl tow, by a light 2 m beam trawl towed for only 5 min, to minimise stress and damage. All animals were monitored daily for subsequent mortality or autotomy over the next 8 days.

The above experiment was repeated in August 1998 using a scallop dredge (tow duration 30 min), and a subsample of starfish was transferred to a nearby laboratory aquarium. This subsample comprised 46 intact individuals, 49 damaged and 36 with lost arms. A control group of 40 animals was also collected, once again using a light 2 m beam trawl, towed for 5 min. Animals were maintained in tanks with running seawater and monitored daily for subsequent mortality and autotomy over the next 14 days.

Survival and subsequent arm loss following capture by rockhopper otter trawl gear

Starfish were caught by a commercial otter trawl (tow duration of 2.5 h) in May 1999, and a subsample was haphazardly selected from the sorting table. In order to simulate commercial practice, starfish were exposed to air for ca. 90 min, before being placed in tubs with running seawater. In this respect this study differed from the investigations of the mortality of animals caught by a beam trawl or a scallop dredge where animals were placed in water within minutes of capture. Starfish were subsequently transferred to small cages (constructed of plastic netlon, ca. 0.8 cm mesh), which were placed inside creels (traps) and returned to the sea at 30–40 m water depth. As a control, starfish caught using baited creels were kept under identical conditions. Specimens were monitored for arm loss and mortality on a weekly basis for 4 weeks. Damage other than arm loss was not recorded, as this would have involved opening the cages, imposing further stress on the animals.

Arm regeneration

The rate at which arms were regenerated was compared between individuals that had lost an arm as a result of dredging and individuals that were induced to autotomise an arm. Starfish caught with the scallop dredge in August 1998 were transferred to a laboratory aquarium with running seawater at ambient temperature. A control group of 40 starfish was collected ca. 30 min after the last scallop dredge tow, by a light 2 m beam trawl, towed for 5 min. One day after capture starfish in the control group were induced to autotomise an arm by trapping them under a heavy weight whilst exposed to air. In most cases the arm was autotomised within 10 min, after which individuals were returned to the aquarium. After completion of the survival experiment detailed above a subset of those starfish that had lost a single arm as a result of experimental fishing ($n = 15$), and the control starfish ($n = 21$) were transferred to a laboratory aquarium. Initially starfish were left undisturbed for 1 month to recover from the stresses of capture and transfer to the laboratory aquarium (handling may increase stress in *A. rubens*, P.G. Moore, personal communication). Animals were kept individually in separate tanks and fed an excess of live mussels (*Mytilus edulis*) of varying sizes (feeding started immediately after the animals were transferred to the laboratory). After 1 month starfish were examined weekly at first, and then every 2 weeks, when the length of each arm was measured (from the point where the arm joins the body to the arm tip). Arm regeneration was expressed as the percentage ratio between the length of the regenerating arm and the average length of the other four arms. The starfish used were of similar sizes (average length of intact arms at the start of the experiment: dredge set 56 ± 4 mm, control set 56 ± 5 mm).

Histological examination of autotomised arms

To examine the possibility that arms were autotomised in response to bacterial infection of tissues damaged during capture, recently autotomised arms were sectioned and examined for evidence of an inflammatory response. Five recently autotomised arms (from animals caught by the 4 m beam trawl) and five arms removed from apparently healthy starfish were placed in Davidson's fixative. Tissues were then trimmed to produce transverse and longitudinal sections (4–5 mm width) from the proximal and the distal regions, respectively, and these were placed into processing cassettes. A vacuum infiltration processor was used with a standard processing schedule to process tissues to paraffin wax. Sections of 4–5 μm were obtained using a rotary microtome and were stained using haematoxylin and eosin. Mounted sections were examined using a Nikon E800 photomicroscope.

Point of arm autotomy

The possibility that some of the beam-trawled starfish had lost arms through forcible removal rather than normal autotomy was investigated by examining the point of autotomy in starfish caught by a beam trawl and a control set. A subsample ($n = 18$) of the starfish that had lost an arm as a result of being caught with the 4 m beam trawl during April 1998 was frozen. These animals were later examined under a dissecting microscope to establish the point at which the arm had been lost. A control group of intact animals ($n = 20$) were collected from the lower shore of the Menai Strait, Anglesey, induced to autotomise an arm by trapping under a heavy weight and also examined for the point of autotomy.

Predicting arm loss in populations subjected to different levels of fishing intensity

To examine the accuracy of using arm loss in starfish as an indicator of fishing disturbance, data obtained from this study were compared with data given in Kaiser (1996). Results from the current study were used to predict arm loss in areas subjected to the different levels of fishing intensity described by Kaiser (1996), and these were compared with reported values of the frequency of arm regeneration from Fig. 2 of the same study. The proportion of the sea bed swept by trawlers (from Kaiser 1996) was multiplied by the estimated arm loss per tow (from the present study), and an estimate of background arm loss due to natural causes was added to this figure. Therefore the calculation was as follows: predicted arm loss per area (%) $= [(a \times b) + c] \times 100$, where a is the area swept (proportion) for each area, as given in Kaiser (1996) and b is the predicted arm loss per tow (proportion), from the current study. A range of 2.6–18.2% was used, as in 50% of tows the percentage arm loss was between 2% and 7% and subsequent monitoring demonstrated that this could increase by a factor of between 1.3 and 2.6 in the laboratory and field experiments. In the equation, c is the background arm loss (proportion), using a range of 0.035–0.04 from Ramsay et al. (2000). This value assumes a low level of predation, as the main predators of *A. rubens*, e.g. *Luidia ciliaris* and *Crossaster papposus*, were rarely found during the study by Kaiser (1996).

This calculation assumes that all starfish in the path of a trawl or dredge will be affected in the same way (in terms of arm loss) as those animals that are actually caught by the gear.

Results

Arm loss in starfish caught by fishing gears

Starfish that had recently lost arms were observed in every catch. The percentage of arms lost varied from 1% to 26% and the percentage of intact (undamaged) starfish varied from 47% to 95% (Table 2). There was a significant positive correlation between volume of the catch and arm loss for the rockhopper trawl ($F_{1,13} = 7.6$, $P = 0.017$) and the queen dredge ($F_{1,9} = 7.2$, $P = 0.028$) but no similar relationship for the beam trawl (Table 3). There were insufficient data available to test the effect of catch size on arm loss for the clean net or scallop dredge.

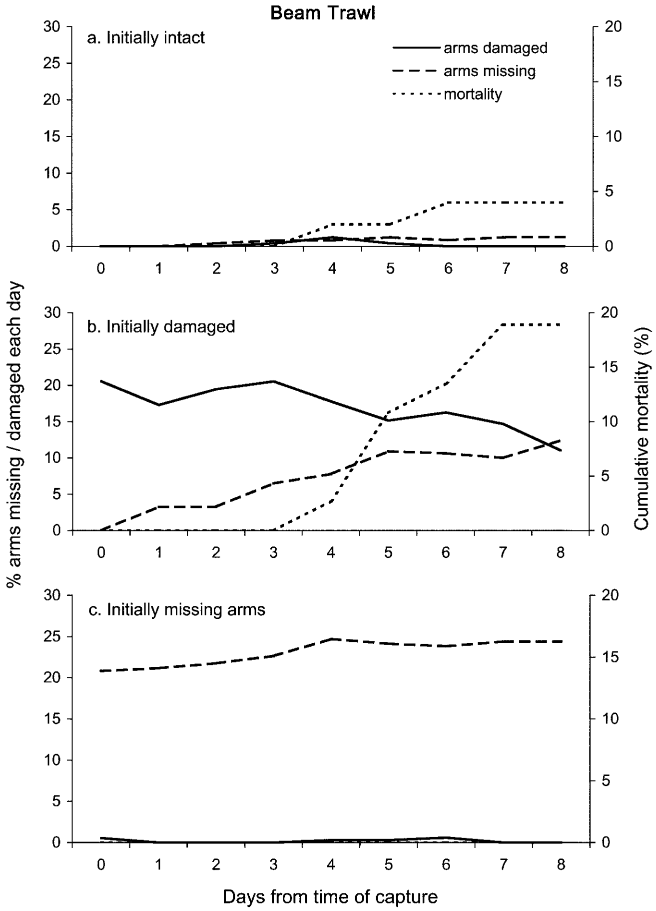

Fig. 2a–c *Asterias rubens*. Daily records of damage (live starfish with visible damage) and arm loss (live starfish with arms missing) and cumulative mortality of starfish caught by a beam trawl. **a** Starfish that were initially intact ($n = 50$), **b** initially damaged ($n = 37$), and **c** initially with arms missing ($n = 72$)

Table 2 *Asterias rubens*. Damage and arm loss of starfish caught using different gears at different sites. *Arms lost* is the percentage arms lost in the whole sample [i.e. total number of arms lost/(number of individuals × 5)]. Numbers (*in parentheses*) for the Isle of Man sites refer to sites shown on Fig. 1

Site	No. of tows	Gear	Sediment type	Month	Tow duration (min)	Volume of catch (litres)	Intact starfish (%)	Arms lost (%)	
								Range	Mean
Off Margate	6	Beam trawl	Medium sand	Apr	30–120	40–520	68–93	1–7	3
Clyde	7	Clean net	Mud, muddy sand, sand	Jan, May, Jul	137–235	560–1280	63–78	3–9	6
Clyde	19	Rockhopper	Mud, sandy mud	Jan–Jun, Aug, Sep, Nov, Dec	67–270	300–720	60–90	2–11	5
Isle of Man (1–10)	10	Queen dredge	Coarse sand, gravelly sand, sandy gravel, gravel	Oct	50	40–140	47–95	2–17	8
Red Wharf Bay, Isle of Man (1, 2, 7)	5	Scallop dredge	Medium sand, coarse sand, gravelly sand, sandy gravel	Aug, Oct	30–50	12–40	62–90	1–26	6

Adding other variables to models incorporating volume of catch did not significantly improve the model. The queen dredge appeared to be the gear most likely to cause starfish arm loss (average 8% arms lost), whilst the beam trawl appeared the least damaging (average 3% arms lost) (Table 2). When the scallop dredge was excluded from the analysis (on the grounds that there were too few replicates), there was a significant difference in the percentage arm loss between different gears ($F_{3,41} = 3.1$, $P = 0.040$). There was, however, no significant difference in percentage arm loss between the rockhopper, clean net and queen dredge ($F_{2,35} = 1.7$, $P = 0.208$).

Survival and subsequent arm loss following beam trawling and scallop dredging

Starfish caught by experimental beam trawling showed further autotomy, damage and mortality for at least 8 days after capture (Fig. 2). Two days after capture, damage became apparent on starfish that had hitherto been scored as intact, although this affected no more than 1% of arms. In addition to this, 1% of arms were autotomised in this "intact" group (Fig. 2a). The incidence of post-capture autotomy was higher (12%) in starfish that showed signs of damage when caught (Fig. 2b). In this group the percentage of damaged arms decreased with time as the percentage of autotomised arms increased, suggesting that damaged arms were subsequently autotomised. Mortality was also highest in this group, with a total mortality of 19% over 8 days (cf. 4% in the "intact" group and no mortality in the "lost arms" or the control group). In the "lost arms" group of starfish, 21% of arms had been lost at the time of the initial examination (as a direct result of capture by the beam trawl) and this rose to 24% after 8 days (Fig. 2c). There was no mortality in this group, and few arms (0.6%) showed signs of damage at any point during the monitoring period. In the control group (caught using a 2 m beam trawl, with 5 min tows) there was no arm loss, mortality or signs of damage.

Broadly similar results were obtained for starfish caught by the scallop dredge (Fig. 3). Once again

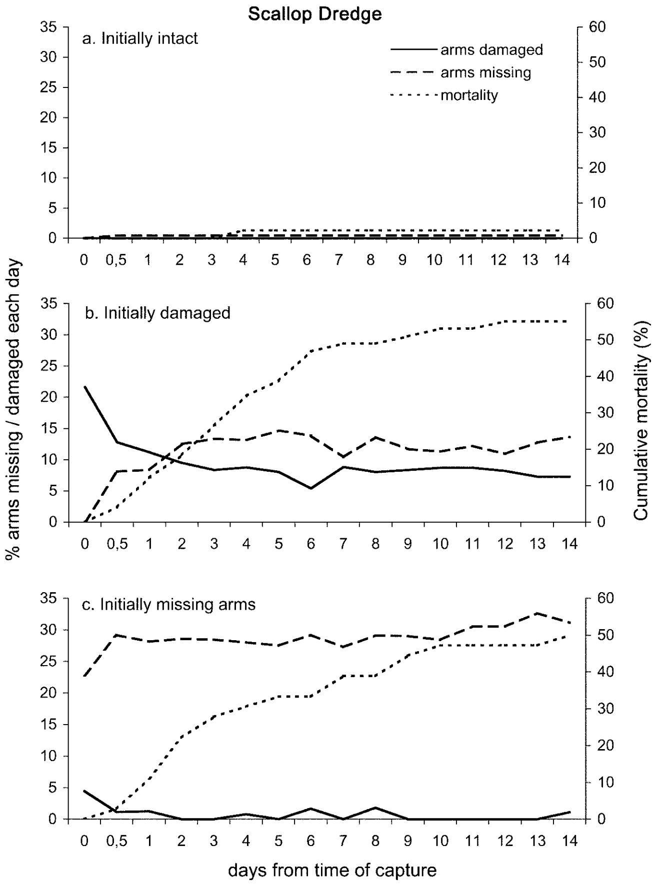

Fig. 3a–c *Asterias rubens*. Daily records of damage (live starfish with visible damage) and arm loss (live starfish with arms missing) and cumulative mortality of starfish caught by a scallop dredge. **a** Starfish that were initially intact ($n = 46$), **b** initially damaged ($n = 49$), and **c** initially with arms missing ($n = 36$)

mortality was highest in the group of starfish with damaged arms (55%, cf. "lost arms" group 50%, intact group 2%, control group 0%), as was the incidence of post-capture autotomy (Fig. 3b). There was no damage, arm loss or mortality in the control set of starfish. The monitoring results were used to predict total mortality and arm loss in a single catch from the 4 m beam trawl or scallop dredge (Table 4).

Table 3 *Asterias rubens*. Results of tests carried out to investigate the effects of different variables on percentage starfish arm loss. Constant variables are those that were the same for all data points (e.g. all beam trawl tows were carried out from the R.V. "Corystes", hence vessel is a constant variable for the beam trawl analysis). *Insufficient data* refers to a situation where there were a large number of non-constant categorical variables but too few replicates (< 5) to test these. *Quarter* refers to the quarter of the year (i.e. January–March, April–June, etc.). Sediments were grouped to mud, sand and gravel

Gear	Constant variables	Variables tested	Significant results
Beam trawl	Vessel, sediment, quarter	Tow duration, catch size	None
Clean net	None	(Insufficient data)	
Rockhopper	Sediment	Vessel	Vessel: $F_{1,18} = 5.75$, $P = 0.028$
	Vessel (F.V. "Red Baron" only: 14 tows), sediment	Quarter, tow duration, catch size	Catch size: $F_{1,13} = 7.6$, $P = 0.017$
Queen dredge	Vessel, quarter, tow duration	Sediment, catch size	Catch size: $F_{1,9} = 7.2$, $P = 0.028$
Scallop dredge	Quarter	(Insufficient data)	

Table 4 *Asterias rubens*. Estimates of total mortality in a single catch and percentages of arms lost as a result of being caught by the 4 m beam trawl or scallop dredge over time. Experimental data have been used to calculate mortality, damage and arm loss in a single catch. *Percentage starfish undamaged* and *percentage arms lost in the sample* represent percentages of the remaining live population of starfish

Gear	Days after capture	Cumulative mortality (%)	% Starfish undamaged	% Arms lost in sample
Beam trawl	0	0.1	92.7	1.0
	8	4.2	89.0	2.6
Dredge	0	0	89.6	1.3
	8	6.1	89.6	2.4
	14	6.9	89.8	2.6

Survival and subsequent arm loss following capture by an otter trawl

Starfish caught by an otter trawl showed highest mortality between 2 and 3 weeks after capture (Table 5). Arm loss occurred throughout the 29 day monitoring period (Table 5). There was no mortality or arm loss in the control group of starfish. Mortality and arm loss was higher in this experiment than in the experiments using either the beam trawl or the scallop dredge.

Histological examination of autotomised arms

No evidence of an inflammatory response was found in either the autotomised arms or the control (apparently healthy) arms.

Arm regeneration

After 1 month (when the animals were first examined) 95% of the control animals and 64% of the dredge-caught animals were visibly (to the naked eye) regenerating their lost arm (Fig. 4) and after 36 days all of the control animals had regenerating arms, compared with only 79% of the dredge-caught animals. Regeneration occurred at a rate of ca. 10% of the length of the intact arms per month for the first 3 months and ca. 4% per month for the remaining 7 months of the experiment (Fig. 5). Three of the dredge-caught animals had not begun regenerating after 46 days. When these were separated from the rest of the dataset (on the grounds that they showed major differences from the rest of the animals), there appeared to be little difference between regeneration rates of the control and the rest of the dredge-caught animals. The starfish used in this experiment continued to grow throughout the experiment; increasing their average arm length by almost 50% over the year (Fig. 6). After 10 months there were no significant differences between the control and the dredge-caught group in either percentage length of the regenerating arms (*t*-test on arcsine transformed data, excluding animals showing delayed regeneration $t = 1.1$, $df = 26$, $P = 0.27$) or length of the four intact arms ($t = -1.3$, $df = 29$, $P = 0.19$). Nineteen of the 21 control animals and 13 of the 15 dredge-caught animals survived for 10 months after capture.

Table 5 *Asterias rubens*. Mortality and arms lost in starfish caught by a rockhopper otter trawl. During the course of the experiment five animals escaped from their creels, hence the decrease in *n* is not accounted for by mortality

Days post-capture	Cumulative mortality (%)	% Arms lost in sample	*n*
0	0	15.0	40
8	0	15.8	38
14	2.7	21.6	37
22	11.1	14.3	35
29	11.1	19.4	31

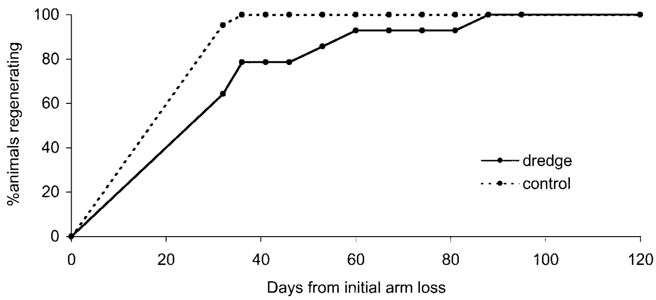

Fig. 4 *Asterias rubens*. Time taken to start regeneration in starfish caught by a scallop dredge ($n = 15$), compared with a control set ($n = 21$)

Point of arm autotomy

For the majority (95%) of control animals there was a clean break between either the 4th and 5th, or the 5th

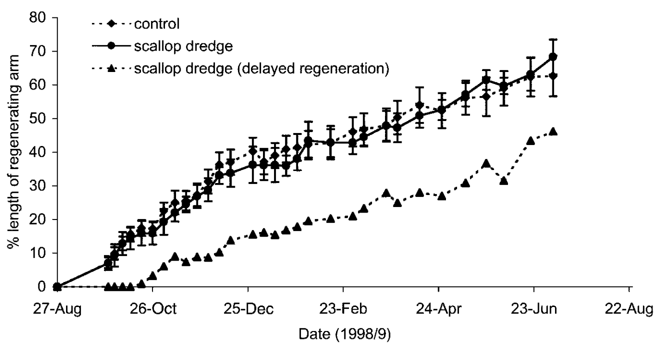

Fig. 5 *Asterias rubens*. Regeneration rates for starfish caught by a scallop dredge (excluding animals that delayed regeneration) ($n = 11$) and a control group ($n = 20$). Also showing the animals that delayed regeneration (started regeneration after >45 days) ($n = 3$). Regeneration is expressed as a percentage: i.e. (length of regenerating arm/average length of intact arms) × 100

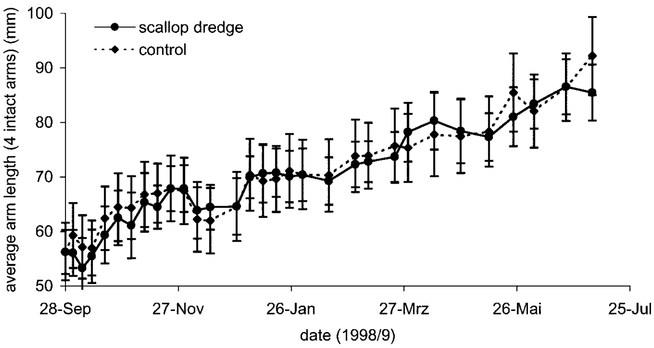

Fig. 6 *Asterias rubens*. Growth (average length of four undamaged arms) of starfish maintained in the laboratory for regeneration rate experiments, caught by a scallop dredge ($n = 14$) and a control group ($n = 20$)

and 6th ambulacral ossicles. However, for 17% of starfish caught by the 4 m beam trawl, the 5th ambulacral ossicle was broken, with only half of it remaining (Table 6; Fig. 7).

Predicting arm loss in populations subjected to different levels of fishing intensity

The actual values from Kaiser (1996) fall within the predicted values (from the current study), although the ranges of the predicted values are large (Table 7).

Discussion

These results demonstrate that capture by towed fishing gears often results in damage and arm loss in *Asterias rubens*. In total between 1% and 26% of all arms were lost. Arm loss was positively correlated with catch size for two of the gears, suggesting that starfish are more likely to be crushed or damaged as the weight of the catch in the net or bag increases. The beam trawl caused significantly less arm loss than the other gears, whilst the queen dredge was the gear most likely to cause arm loss.

Post-capture mortality occurred for 3 weeks in animals caught by an otter trawl, and arms were still being shed when the experiment was terminated after 4 weeks. Further mortality and arm loss also occurred for at least 2 weeks after starfish were caught by a beam trawl or a scallop dredge. This suggests that the relatively short experiments (3–6 days) previously carried out to estimate starfish mortality following fishing (Fonds 1994; Kaiser and Spencer 1995) may have underestimated mortality.

Post-capture mortality was higher in animals caught by the otter trawl than for those caught with the beam trawl or scallop dredge, but it is not clear whether this is a gear effect or the result of the 90 min exposure to air experienced by the starfish caught by the otter trawl. The highest rates of post-capture arm loss were in the groups of starfish with damaged arms, suggesting that damaged arms were subsequently autotomised. It is perhaps sur-

Table 6 *Asterias rubens*. Arm breakage points in starfish caught by a beam trawl and a control group (induced autotomy)

	% Breakage points between ambulacral ossicles:			Damaged 5th ossicle (%)
	3 and 4	4 and 5	5 and 6	
Beam trawl ($n = 18$)	0	72	11	17
Control ($n = 20$)	5	50	45	0

Table 7 *Asterias rubens*. Predicted values of arm loss (using data from the present study) compared with the observed values recorded in Fig. 2 of Kaiser (1996)

Site	Area of sea bed swept per year (%)	Predicted frequencies of arms lost (%)	Observed frequencies of arms lost (%)
Anglesey	4	3.6–4.7	3.6
Mersey	12	3.8–6.2	6.0
Fleetwood	50	4.8–13.1	12.0

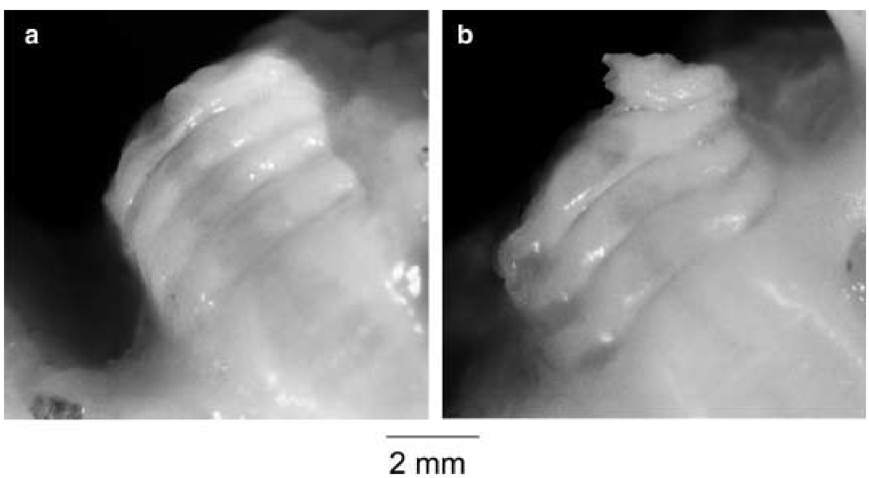

Fig. 7a, b *Asterias rubens*. Photographs of the point of arm autotomy. **a** Clean breakage point between the 5th and 6th ambulacral ossicles, and **b** damaged 5th ambulacral ossicle prising that damaged arms are autotomised rather than healed, as it seems probable that less energy would be required to heal a damaged arm than to completely regrow an arm. However, damaged arms may be susceptible to infection by pathogens or may attract predators, and it could, therefore, be advantageous for the animal to autotomise these arms. For animals caught by a beam trawl or a scallop dredge, the highest mortalities were in the groups with damaged or missing arms and mostly occurred during the first week after being caught (there was no mortality at all in the control group). Mortality was lower in the group of starfish that had lost arms immediately after being caught, compared with those that had damaged arms (beam trawl 0%, cf. 19% after 8 days; dredge 50%, cf. 55% after 14 days). If mortality was a result of infection by pathogens, this could strengthen the hypothesis that it is advantageous to autotomise damaged arms due to the high risk of infection. However, as histological examination of autotomised arms failed to produce any evidence of bacterial infection, this suggestion remains speculative.

A regenerating arm was visible to the naked eye in the control set of starfish after 36 days (when the animals were first examined). However, at this time regeneration was visible in only ca. 79% of the animals caught by the scallop dredge. Of the starfish caught by the scallop dredge three individuals delayed regeneration until 53, 60 and 88 days after capture. Thus, a small proportion of starfish caught by the scallop dredge delayed regeneration, compared to those in the control set and others caught by the scallop dredge, suggesting an effect of fishing on the time taken to start regeneration in some animals. In a separate study, several animals (17%) caught by a beam trawl had a damaged ambulacral ossicle at the point of autotomy, whereas those from the control set all had intact ossicles at the autotomy point. It is possible that this was a result of the arm being forcibly removed during fishing, rather than undergoing the normal autotomy process. This may be linked to the delayed regeneration observed in some of the starfish caught by the scallop dredge. It is likely that arm autotomy would have evolved in such a way as to produce optimal conditions for subsequent regeneration (e.g. the protective flap of skin left to cover the wound, King 1898), and, conversely, forcible removal of an arm or abnormal autotomy might result in less favourable conditions for regeneration.

The rates of arm regeneration were similar between the starfish caught by a scallop dredge and the control group, once those animals not regenerating normally had been excluded. This suggests that, where regeneration commences normally, the stresses caused by being caught by fishing gears are not sufficiently long-lasting to affect regeneration rates. In *A. rubens* it appears that complete regeneration of an arm takes over 1 year. Published data concerning starfish regeneration rates are sparse. Donachy et al. (1990) note that *Asterias forbesi* kept in aquaria grew a regenerating arm to a length of ca. 1 cm in 60 days, although they do not state the size of the starfish. In our experiment the average length of the regenerating arm was 1.3 ± 0.1 cm after 60 days. Briggs (1983) presented data concerning a single tagged *A. rubens* that completely regenerated an arm in 7 months in the field. It is possible that rates differ between the laboratory and the field, although it is not obvious whether rates would be faster or slower. Starfish in the field may receive less food (animals in our experiments were fed to excess), although the diet may be more varied. Animals in the field will also experience a smaller range of temperatures (temperatures in the aquaria varied from 6 °C to 16 °C during the course of the 10 months), and it is thought that *A. rubens* become stressed at temperatures above 16 °C (Fonds et al. 1998). However, the starfish used in laboratory experiments continued to grow throughout the experiment, on average, increasing arm length by almost 50% over the year-long experiment, suggesting that the laboratory conditions were not excessively stressful. Water temperature and spawning may also affect regeneration rates, causing seasonal variations.

The experiments described here did not investigate the effect of multiple arm loss on regeneration. This could be caused either by animals losing more than one arm during a single fishing event, or by the animal being damaged several times in multiple fishing events. The effect of multiple arm loss on regeneration appears to be unknown at present.

Our results suggest that arm loss in starfish may be potentially useful as an indicator of fishing effort over a time period of ca. 1 year, although the variability in levels of damage and arm loss will adversely affect the precision of estimates. If rates of arm regeneration were the same between different areas (and this has not been tested) and seasonal variability had been established, it might be possible to estimate the time since damage occurred from the relative length of the regenerating limb. However, this remains highly speculative at present. The comparison between predicted values of arm loss (from data presented in this study) and actual values of arm loss in areas subjected to different levels of fishing intensity (from Kaiser 1996) revealed that the observed values fell within the predicted values. However, the range of each predicted value was large, reflecting the inaccuracies involved in the calculation. The model also assumes that all starfish in the path of a trawl or dredge suffer the same degree of arm loss as those actually caught in the fishing gear. The validity of this assumption is unknown; intuitively it seems likely that those animals not caught by the gear would suffer less damage. However, observations of areas recently fished with a scallop dredge or beam trawl have demonstrated that starfish not caught by these gears do nevertheless suffer damage (Ramsay et al. 1998). Before starfish arm loss can be used as an indicator of fishing effort, the background frequency of arm loss from natural causes has to be established. Unsuccessful predator attacks probably account for the bulk of additional arm loss (Lawrence et al. 1999), although few data are available to verify this. In a study of an unfished sea lough (Lough Hyne, SW Ireland), Ramsay et al. (2000) found a possible link between arm loss in *A. rubens* and the density of predators (the starfish *Luidia ciliaris* and the edible crab *Cancer pagurus*), with higher arm loss in an area where predators were abundant. The calculations used for the comparison between the current study and that of Kaiser (1996) use a background frequency of 3.5–4.0% arm loss (Ramsay et al. 2000). This assumes a constant low level of arm loss due to predation, based on Kaiser's (1996) observation that the main predators of *A. rubens*, e.g. *L. ciliaris* and *Crossaster papposus*, were rarely found during his study. However, were levels of arm loss due to predation to vary between areas, this could produce erroneous estimates of fishing effort if the changes in predation pressure were not accounted for.

Fishing effort around the UK can vary enormously; some areas of the North Sea may be trawled over 20 times a year (Rijnsdorp et al. 1996), whilst others are virtually unfished. Our data suggest that counts of starfish arms could successfully be used to distinguish between light (10% swept = 0.26–1.8% arm loss) and heavy (five times per year = 13–93% arm loss) fishing effort (assuming constant levels of arm loss from predation between areas). Thus, although it is unrealistic to expect to estimate precise values of fishing effort from arm counts of *A. rubens*, it appears feasible to identify areas subjected to light or heavy fishing effort. This could be useful for researchers attempting to ascertain fishing effort on a smaller spatial scale of resolution than, for example, the statistical rectangles used around Europe for reporting fishery statistics.

A. rubens is a ubiquitous predator and scavenger in northeastern Atlantic inshore waters, and the current study demonstrates that the mortality of these animals due to fishing is higher than previously estimated. In addition, many starfish that survive fishing may lose arms in the process and will therefore be forced to divert energy to regeneration. Lawrence and Larrain (1994) suggested that one cost of regeneration in starfish may be a reduced capacity for reproduction. At present, not enough is known about the ecology of starfish populations and the factors controlling population size to determine the overall impact of fishing on starfish populations.

Acknowledgements We would like to thank the officers and crew of the R.V. "Corystes", R.V. "Prince Madog", R.V. "Roagan", R.V. "Aora", R.V. "Aplysia", F.V. "Andrias" and F.V. "Red Baron". This study was partly funded by the Ministry of Agriculture Fisheries and Food, Fisheries Division III, project code MF0714 (K.R., C.A.R., M.J.K. and S.J.V.) and contract no. CSA 2332 (L.O.V.). Funding was also received from the Isle of Man Department of Agriculture, Fisheries and Forestry scallop research project (L.O.V.) and a Sheina Marshall studentship (M.B.). We would also like to thank the following for their comments on earlier drafts: Dr. C. Bradshaw, Prof. P.G. Moore, Prof. S.J. Hawkins and Dr. R. Coggan.

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