

Field survey of the occurrence and significance of regeneration in *Amphiura chiajei* (Echinodermata: Ophiuroidea) from Killary Harbour, west coast of Ireland

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Abstract. The boreo-Mediterranean amphiuroid *Amphiura chiajei* Forbes occurs in high numbers (~ 700 individuals/m²) in Killary Harbour, a fjordic inlet on the west coast of Ireland. 99.1% of the adult individuals show signs of arm regeneration, while 0.5% show regeneration of the disc. A study of the phenomenon commenced in November 1987 and continued on a seasonal basis until July 1989. Specimens were collected by SCUBA. The overall mean length of regenerated arm tissue over the 21 mo sampling period was 33.5 ± 6.5 mm. Regeneration points were most common in the proximal and in the distal one-third of each arm. An overall mean of 4.21 ± 0.3 arms per individual showed evidence of regeneration, while biomass assays revealed that regenerated tissue accounted for up to 57.9% of the total body weight. Anthropogenic activity (e.g. bottom trawling) may contribute to regeneration, although sub-lethal predation appears to be the main causative factor of regeneration. Gut analyses of potential predators at the sampling station revealed that fish species (especially the Pleuronectidae) are particularly implicated. This predation seems to vary seasonally, being greatest in the summer months. Since the larger individuals showed the greatest evidence of arm regeneration, it is assumed that such sub-lethal damage is a persistent experience. Whatever the causality, the population of *A. chiajei* in Killary Harbour is deemed to be highly resilient.

Introduction

The phenomenon of regeneration within the phylum Echinodermata is well documented (e.g. Hyman 1955). In the case of the Ophiuroidea, it is most pronounced in the form of arm regeneration. Early studies of such arm regeneration tended to concentrate on the rate of regeneration under differing experimental conditions, e.g. Zeleny (1903) for *Ophiura texturata* (Lamarck), Morgulis (1909)

for *Ophiocoma pumila* Lutken, Milligan (1915) for *Ophiothrix fragilis* (Abildgaard), and Salzwedel (1974) for *Amphiura filiformis* (O. F. Müller). Dawydoff (1901) carried out an histological investigation of the phenomenon of ophiuroid arm-regeneration. Recent studies have tended to concentrate on the effects of external factors on arm regeneration. For example, Donachy and Watabe (1986) studied the effects of salinity and calcium on the process, while Clements et al. (1988) examined the influences of various concentrations of dissolved organic matter. Fielman et al. (1991) investigated the pattern of regeneration in the absence of external nutrient supplies.

The frequency of this phenomenon among different ophiuroids has been commented on by Buchanan (1964) inter alia; while most of the above studies focused on the regenerative capacity of given individuals, a number of investigations on the importance of regeneration at the population level, have also been undertaken. With regard to the Amphiuroidae, Buchanan evaluated the importance of regeneration in populations of *Amphiura filiformis* and *A. chiajei* off the Northumberland coast (UK), while Singletary (1980), looked at regeneration in populations of *Amphioplus coniertodes* H. L. Clark, *Ophionephthys limicola* Lütken, and *Microphiopholis gracillima* (Stimpson) off the coast of Florida (USA). Bowmer and Keegan (1983) confined their observations to a single population of *Amphiura filiformis* on the west coast of Ireland, while Bourgoin (1987) directed his study at two populations of *Acrocnida brachiata* (Montagu) in French coastal waters.

Rather than restricting the investigation of regeneration to effects on single individuals, this study considered the role of arm regeneration in the *Amphiura chiajei* population of Killary Harbour as a whole, with a view to determining its overall ecological importance. The incidence of the less frequently observed disc regeneration was also investigated.

Materials and methods

Killary Harbour (53°57'N; 9°42'W; Fig. 1) is a shallow, sheltered fjordic inlet situated some 50 km north of Galway Bay, on the west

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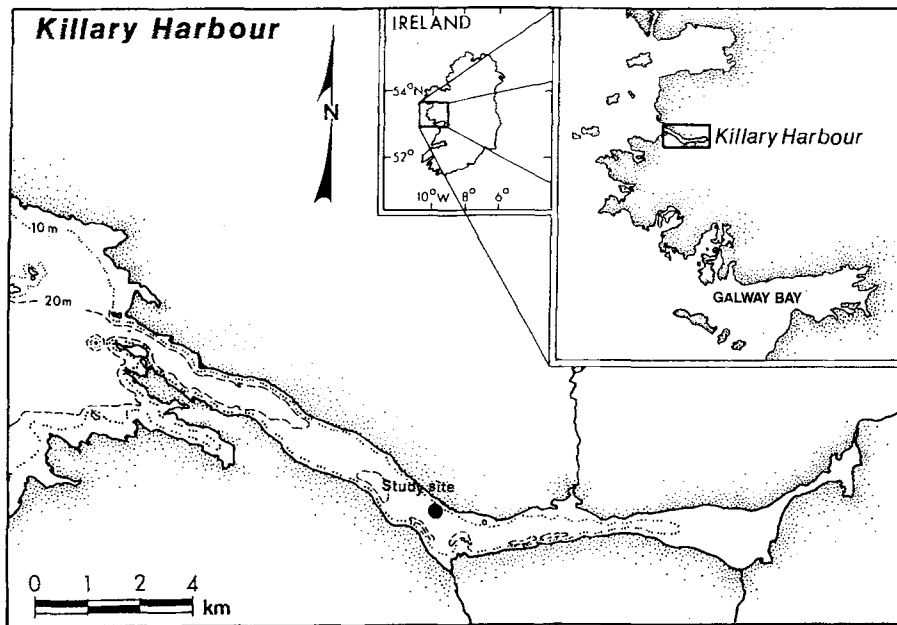


Fig. 1. Location of Killary Harbour and study site

coast of Ireland, and is largely protected from wind and wave action. Samples were collected from approximately half way down the Harbour, immediately off the north shore at a depth of ~ 14 m, on a gently sloping bottom.

The various methods of estimating the regenerative capacity of *Amphiura chiajei* Forbes in this study were based on those employed by Bowmer and Keegan (1983) for *A. filiformis*.

For their analyses, Bowmer and Keegan (1983) collected each animal individually. However, the typically close application of its arms against the muddy substrate, and the very nature of the sediment itself, made collection of individual specimens of *Amphiura chiajei* difficult. Accordingly, the samples were collected, on a seasonal basis from November 1987 to July 1989, using a diver-operated steel box-like scoop. In the laboratory, the collected sample was carefully washed through a 1.0 mm sieve in seawater. All intact adults (≥ 5.0 mm disc diam) were collected and relaxed in a 0.9 M magnesium sulphate ($Mg_2SO_4 \cdot 7H_2O$) solution before being preserved in individual glass jars with 70% ethanol. While the 0.9 M magnesium sulphate is not necessarily required to prevent arm autotomy, it aided in restricting excessive curling of the arms, facilitating subsequent examination. In this way, 15 (27 November 1987), 17 (23 February 1988), 19 (15 June 1988), 21 (20 October 1988), 18 (21 February 1989) and 17 (14 July 1989) amphiuroids were collected for detailed analysis from each seasonal sample. However, the method proved less than completely satisfactory, as unavoidable injury occurred to some individuals.

The disc diameter and oral width of the preserved amphiuroids were examined under a binocular microscope at $\times 10$ magnification to register evidence of disc loss and subsequent regeneration. This would be indicated in the "pairing" of an adult oral width with a juvenile or medium-sized disc diameter and a lighter colouration than the usual ochre pigmentation commonly found in the epidermis of burrowing individuals (Bowmer and Keegan 1983). Disc regeneration is also recognisable by the fact that the most proximal dorsal arm surfaces, originally covered by the disc, tend to be exposed during the regrowth of the new disc. Where there was any suggestion of doubt, the amphiuroid was considered undamaged. This, coupled with the lack of data on the length of time before the natural colour is resumed, may have led to an underestimation of the occurrence of disc regeneration. In addition to the individuals collected specifically for this aspect of the study, amphiuroids used for size-frequency analysis were also investigated for the occurrence and frequency of disc regeneration.

For comparison with Singletary's (1980) results, the initial investigation of the extent of arm regeneration involved the measurement

of the total length of each arm as well as the length of the regenerated portion of each arm, which were then expressed as mean lengths per sample. The number of regenerating arms per amphiuroid were then recorded, as was the number of regeneration points and their position. It had been previously noted by Singletary and by Bowmer and Keegan (1983) that regenerating arms could be identified with relative ease due to a discontinuity in thickness at the point of regeneration and by the lighter colour of the regenerated portion of the arm. These criteria also appear to hold true for *Amphiura chiajei*. Where there was any question of doubt, the arm was considered whole. The lack of data available on the time taken for a damaged arm to resume its natural pigmentation may have led to an underestimation of the regenerative capacity of each amphiuroid.

Once these initial examinations had been completed, each individual was dissected to separate the following elements: (i) the disc; (ii) the undamaged portion of the arms, and (iii) the regenerated portion of each arm in order to allow a comparison with the work of Bowmer and Keegan (1983). Each element was placed in an individual container and dried at $60^\circ C$ for 3 d. Once dried, they were weighed separately with a torsion balance to within ± 0.0002 g. The weight of regenerated material was expressed as a percentage of the total body weight.

In line with previous experimental work (i.e., Wilkie 1978, Emson and Wilkie 1980 and Bowmer and Keegan 1983) some observations were made on the voluntary, or autotomous shedding of arms. However, since the preliminary findings on the extent of regeneration within the *Amphiura chiajei* population had suggested that predation was the predominant cause of arm loss, a visual examination was conducted of the gut contents of possible predator species. A 3 m beam trawl was employed in the vicinity of the study area to catch possible predators of *A. chiajei* living on, or near, the seabed. All asteroid and fish species captured in this manner were immediately frozen and, on return to the laboratory, their gut contents were investigated under a binocular microscope at $\times 10$ magnification for any remains of the amphiuroid.

Results

Disc regeneration

During the early part of this study of disc regeneration, it soon became apparent that the complete disc autotomy and its subsequent regeneration noted by Bowmer and

Table 1. *Amphiura chiajei*. Summary of mean arm ($\bar{x}L$) and regenerated arm lengths ($\bar{x}L$ reg.) in six samples, together with number and position of arm regenerations. No of individuals examined are shown in parentheses below datas

	27 Nov. 1987 (15)	23 Feb. 1988 (17)	15 June 1988 (19)	20 Oct. 1988 (21)	21 Feb. 1989 (18)	14 July 1989 (17)	Total (107)	Mean (\pm SD) (17.8)
$\bar{x}L$ (mm)	76.6 \pm 15.5	77.0 \pm 14.2	52.0 \pm 16.0	66.8 \pm 13.8	71.1 \pm 16.1	70.9 \pm 14.0		69.1 (\pm 9.2)
$\bar{x}L$ reg. (mm)	36.6 \pm 28.2	40.7 \pm 27.7	22.9 \pm 17.3	30.2 \pm 23.5	38.6 \pm 22.8	31.8 \pm 23.8		33.5 (\pm 6.5)
Total no. arms	75.0	85.0	95.0	105.0	90.0	85.0	535.0	89.2
% reg. arms	76.0	85.9	83.2	84.8	93.3	81.2		84.1 (\pm 5.7)
% reg. points/arm ^a								
1	58.6	42.4	65.8	60.7	58.3	55.9		56.7 (\pm 7.9)
2	16.0	29.4	29.1	25.8	34.5	30.1		27.5 (\pm 6.3)
3	1.3	12.9	3.9	10.1	6.0	10.3		7.4 (\pm 4.4)
4	0.0	0.0	0.0	3.4	1.2	2.9		2.5 (\pm 1.5)
No. reg. points	70.0	121.0	108.0	137.0	126.0	109.0	671.0	111.8 (\pm 23.2)
x reg. points/ amphiurid	4.6 \pm 2.6	7.1 \pm 2.9	5.9 \pm 2.8	6.5 \pm 3.4	7.0 \pm 2.2	6.4 \pm 3.6		6.3 (\pm 0.8)
Position of reg. points on arm								
proximal one-third	24 (34.3%)	45 (37.2%)	52 (47.7%)	55 (40.2%)	51 (40.5%)	36 (33.0%)	263 (39.2%)	43.8 (11.8)
middle one-third	19 (26.1%)	31 (25.6%)	20 (18.5%)	38 (27.7%)	31 (24.6%)	27 (24.8%)	166 (24.7%)	27.7 (7.2)
distal one-third	27 (36.0%)	45 (37.2%)	36 (33.3%)	44 (32.1%)	44 (34.9%)	46 (42.2%)	242 (36.1%)	40.3 (7.5)

^a 1, 2, 3, 4: no. of regeneration points per arm

Keegan (1983) for *Amphiura filiformis* was rare in *A. chiajei*.

This phenomenon was only observed in one individual, and even stressful conditions, e.g. low oxygen concentrations and removal from the sediment for extended periods of time in the laboratory, failed to induce disc autotomy in the species. While such disc autotomy appeared to be rare, disc damage and the subsequent regeneration of the injured area, were somewhat more common. Such partial disc regeneration was distinguishable by the lighter, whiteish-grey colour of the regenerating portion of the disc compared to the more normal ochre pigmentation. These areas of regeneration commonly included a complete regenerating arm.

Of the many thousands of adult *Amphiura chiajei* examined for size-frequency analysis in a separate study (Munday 1991), only 0.5% (22 individuals) showed any evidence of complete or partial regeneration of the disc.

Arm regeneration

Regenerated arm lengths

In estimating the regenerated arm length, each sample was treated as a population of arms rather than of individuals. When each sample is considered separately, it can be seen that the total mean arm length varied between 52.0 \pm 16.0 mm (15 June 1988) and 77.0 \pm 14.2 mm (23 February 1988), while the overall mean length was 69.1 \pm 9.2 mm (Table 1). The mean length of the regenerated arm portion varied between 22.9 \pm 17.3 mm (15 June 1988) and 40.7 \pm 27.7 mm (23 February 1988), while the overall mean of regenerated tissue length was

33.5 \pm 6.5 mm (Table 1). Table 1 shows that the highest and lowest mean total arm lengths were recorded in two consecutive samples (i.e., 23 February 1988 and 15 June 1988, respectively), as were the highest and lowest mean regenerated arm lengths.

Occurrence and position of points of arm regeneration

In studying the occurrence and position of points of regeneration along each arm, each sample was also considered as a population of arms rather than of individuals, because of the large number of permutations and combinations presented by the number and position of the regeneration points.

Over the course of the study, 107 amphiurids were collected with 535 arms between them. Of these, 451 arms were undergoing regeneration. The percentage of regenerating arms in each sample collected varied from 76.0 to 93.3% (mean = 84.1 \pm 5.7%). Of these, between 42.4 and 65.8% (mean = 56.7 \pm 7.9%) showed evidence of one regeneration point per arm, 16.0 and 34.5% (mean = 27.5 \pm 6.3%) showed evidence of two points, while between 1.3 and 12.9% (mean = 7.4 \pm 4.4%) showed evidence of three regenerating points per arm. Of the samples taken, only the last three showed evidence of four regeneration points per arm, at between 1.2 and 3.4% (mean = 2.5 \pm 1.5%; Table 1).

There were a total of 671 regenerating points, with an overall mean of 6.3 \pm 0.8 points per individual. To qualify these results further, each arm was divided roughly into three equal portions: (1) a proximal one-third; (2) a middle one-third, and (3) a distal one-third. Of the 671 regeneration points, the majority were located in the proximal

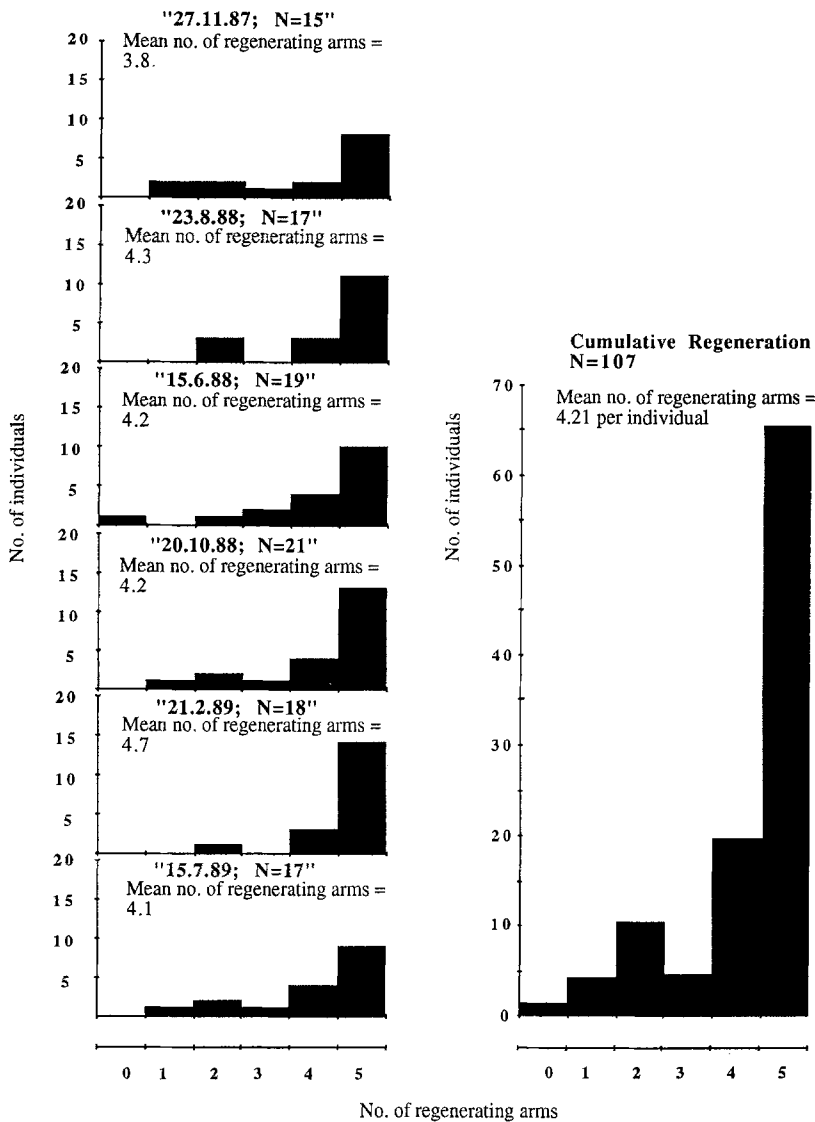


Fig. 2. *Amphiura chiajei*. Number of regenerating arms per individual

(mean = 43.8 ± 11.8) and in the distal (mean = 40.3 ± 7.5) one-thirds, while a mean of 27.7 ± 7.2 regeneration points was found for the middle portion of each arm.

Number of regenerating arms per amphiuroid and quantitative estimates of arm regeneration

The most common number of regenerating arms per individual among the six samples collected was 5 (Fig. 2), with an overall mean of 4.21 ± 0.3 arms per amphiuroid.

When each sample is considered separately, it can be seen that any given individual *Amphiura chiajei* has a chance of regenerating up to a mean of $27.07 \pm 16.4\%$ of its total body weight (Table 2).

If the amphiuroids are considered individually, out of a total of 107 examined, 106 (99.1%) showed some evidence of arm breakage and subsequent regeneration, with the percentage of regenerated tissue varying between 0.4 and 57.9% of the total body weight.

Although all the amphiuroids examined were adults with an overall mean disc diameter of 7.9 ± 0.89 mm and

a mean oral width of 2.94 ± 0.34 mm, the smaller individuals has less regeneration points than the larger specimens. Their regenerating points were most commonly located in the distal third of each arm, although the largest individuals showed evidence of regeneration along the length of each arm. Table 3 gives the mean number of regenerating points per individual for each sample grouped into 0.2 mm (oral width) size classes. A cumulative effect is evident, with the larger and presumably older amphiuroids displaying more evidence of arm damage and subsequent regeneration than the smaller, younger individuals. Therefore, it is assumed that such extensive arm regeneration is not due to a single isolated incident, but may represent something of a "respository" of a number of past events.

Possible causes of arm loss

During the course of this study, it was noted that under conditions of stress (i.e., rough handling) some specimens of *Amphiura chiajei*, as with other ophiuroid species, tended to lose portions of their arms.

Table 2. *Amphiura chiajei*. Summary of percentage of total body weight regenerated in six samples. \bar{x} whole wt: mean dry wt of whole individual; \bar{x} wt reg. arms/individ: mean dry wt of regenerated arms/individuals; (N): no. of individuals examined; Wt reg. (%): percentage of body weight regenerated

Date	\bar{x} whole wt (g)	\bar{x} wt reg. arms/individ (g)	(N)	Wt reg. (%)
27 Nov. 1989	0.1289 ± 0.0430	0.0276 ± 0.024	(15)	19.45 ± 14.61
23 Feb. 1988	0.1299 ± 0.0118	0.0394 ± 0.029	(17)	27.07 ± 16.37
15 June 1988	0.1107 ± 0.0141	0.0233 ± 0.023	(19)	18.04 ± 16.68
20 Oct. 1988	0.1312 ± 0.0118	0.0340 ± 0.027	(21)	23.38 ± 16.00
21 Feb. 1989	0.1302 ± 0.0177	0.0324 ± 0.020	(18)	24.65 ± 11.70
14 July 1989	0.1355 ± 0.0108	0.0277 ± 0.028	(17)	17.89 ± 15.40

Table 3. *Amphiura chiajei*. Mean number of regeneration points per individual. Data grouped in size classes of 0.2 mm oral width. nd: no data

Date	2.2–2.4 mm	2.5–2.7 mm	2.8–3.0 mm	3.1–3.3 mm	3.4+ mm
27 Nov. 1987	1	2.3	5	5	nd
23 Feb. 1988	2.7	5	8.4	8.2	nd
15 June 1988	4	2.4	6.3	6.8	8
20 Oct. 1988	2	4.8	6.4	9.3	nd
21 Feb. 1989	nd	5.5	7.2	7.4	8.5
14 July 1989	nd	3.4	6.7	7	12

Table 4. *Amphiura chiajei*. Species recorded in trawls total number of each species collected, and number of specimens with evidence of ophiuroid arms in stomach contents

Species name	Common name	Total	No. with arms in gut
<i>Asterias rubens</i> (L.)	common starfish	24	0
<i>Marthasterias glacialis</i> (L.)	spiny starfish	1	0
<i>Scyliorhinus canicula</i> (L.)	lesser spotted dogfish	1	0
<i>Raja clavata</i> (L.)	thornback ray	3	0
<i>Eutrigla gurnardus</i> (L.)	grey gurnard	2	0
<i>Lesueurigobius friesii</i> (Collett)	Fries' goby	33	7
<i>Pomatoschistus minutus</i> (Pallas)	sand goby	4	1
<i>Pleuronectes platessa</i> (L.)	plaice	8	6
<i>Platichthys flesus</i> (L.)	flounder	2	2
<i>Limanda limanda</i> (L.)	dab	5	3
<i>Solea solea</i> (L.)	sole	1	0

Autotomy

Arm autotomy commonly involves 2 to 4 segments, although as many as 6 to 7 may be involved. Bowmer and Keegan (1983) noted that the pressure exerted by forceps is similar to that which might be caused by a predatory fish, decapod or some similar species, and is thus likely to be followed by some degree of autotomy to prevent the

whole individual from being removed from the sediment. As pointed out by Emson and Wilkie (1980), there is no known way of determining whether a regeneration point has been caused by autotomy per se or by simple mechanical damage.

Predation

From the evidence of persistent regeneration noted above, and from previous studies (e.g. Bowmer and Keegan 1983, Duineveld and Van Noort 1986), sub-lethal active predation of the arms was deemed to be the most likely cause of arm loss.

The 3 m beam trawl deployed over the study was moderately successful in capturing a number of molluscan and decapod species, including 12 specimens of *Nephtys norvegicus* (L.). Two species of asteroid, *Asterias rubens* (L.) and *Marthasterias glacialis* (L.), were collected, as were a variety of fish species (Table 4). In addition to the above, large numbers of *Amphiura chiajei* were taken on the trawl runners and in the net.

All the asteroid species examined had empty guts. However, in the case of *Asterias rubens*, all specimens had portions of *Amphiura chiajei* arms along the length of their arms, entangled among the spines/tube feet. The single specimen of the more spinous *Marthasterias glacialis* from the same haul was not festooned with *A. chiajei* arms.

Clear evidence of amphiuroid predation was evident among the fish collected (Table 4), with five species having arm portions in the alimentary tract. While the remains were clearly amphiuroid, they could not be positively identified as belonging to *Amphiura chiajei*.

Of the seven specimens of Fries' goby, *Lesueurigobius friesii* (Collett), which contained some amphiuroid arms, only one specimen showed evidence of substantial amphiuroid arm cropping. The remaining six only had one or two arm portions (generally arm tips), as well as other potential food items such as juvenile *Turritella communis* Risso, *Mytrea spinifera* (Montagu) and a number of ostracods, throughout the length of the alimentary tract. The single sand goby, *Pomatoschistus minutus* (Pallas), with amphiuroid arms in its stomach had a significant quantity of remains, while the hindgut was vacant.

The most extensive evidence of active predation was exhibited by three of the four flatfish species (Table 4). The six specimens of the plaice, *Pleuronectes platessa* (L.), containing remains in their alimentary tract, were almost completely full of amphiuroid arms. In addition, three specimens also contained complete *Amphiura chiajei* discs, while one specimen had two discs. This was the only plaice which had evidence of other food items; i.e., an unidentified polychaete worm and some crustacean remains. With the exception of one specimen whose stomach was empty, but whose foregut and rectum contained arm fragments, the stomachs of the remainder were full of relatively fresh arm remains. In each case, the foregut also contained arm fragments while the rectum was packed with single vertebral plates and ossicles from which all the surrounding tissue had been removed. The

specimens of flounder, *Platichthys flesus* (L.), and dab, *Limanda limanda* (L.), also had their stomachs full of amphiuroid arm segments, while the remainder of the alimentary tract contained broken-down arm remains. One specimen of dab also contained an *A. chiajei* disc.

Discussion

Bowmer and Keegan (1983) found that 3.6% of all *Amphiura filiformis* examined in Galway Bay displayed evidence of disc regeneration and cited disc autotomy as the primary cause. Singletary (1980) reported that 5.55% of *Ophionephthys limicola*, 3.3% of *Amphioplus coniertodes*, and 1.5% of *Microphiopholis gracillima* were regenerating their discs at any given time. Stancyk (in Turner et al. 1982) found the frequency of disc regeneration in *Ophiophragmus filograneus* to range from 2.5 to 56%, with a mean of $26.7 \pm 15.1\%$. Both Singletary and Bowmer and Keegan commented on the fact that the exact causes of disc autonomy were unknown, but that hydrographic disturbance or the physical action of digging/burrowing predators may be responsible, while Turner et al. indicated that disc autonomy in *O. filograneus* may occur in response to the mechanical properties of stingray feeding activity. Exact comparison with the present study is difficult, due to the paucity of evidence of complete disc regeneration. However, the incidence of partial disc regeneration, coupled with the complete loss and subsequent regeneration of the nearest arm, may point to an active (i.e., predation) rather than a passive causality as underlying disc regeneration within the *Amphiura chiajei* population in Killary Harbour.

Despite the limitations of length as a measure of true regeneration (Clements et al. 1988), the mean regenerated arm lengths for *Amphiura chiajei* in Killary Harbour compare well with the results obtained by Singletary (1980), who reported mean regenerated arm lengths of 30 mm for *Amphioplus coniertodes* and *Microphiopholis gracillima* and 40 mm for the deeper burrowing *Ophionephthys limicola*. The pronounced decrease in total mean arm length, from 77.0 to 52.0 mm (in February 1988 and June 1988, respectively), may reflect some form of disturbance that resulted in massive arm damage; considering the reduced level of regenerated arm tissue, such disturbance presumably occurred in the recent past. This was followed by a period of sustained arm recovery, with a gradual increase in the mean regenerated arm length, and with the total mean arm length returning to near its "pre-disturbance" length.

The percentage regenerated body weight of *Amphiura chiajei* compares well with that recorded for *A. filiformis* by Bowmer and Keegan (1983). In Galway Bay, *A. filiformis* is reported as regenerating a mean of up to $32.5 \pm 16.3\%$ of its total body weight compared with $27.09 \pm 16.4\%$ for *A. chiajei*. If the amphiuroids are considered individually, the percentage of regenerated tissue varies from between 0.4 and 57.9% of the total body weight for *A. chiajei* and between 1 and 56% for *A. filiformis*. With regard to the number of regenerating arms, between 65 and 82.1% of all arms showed regeneration in

the *A. filiformis* population (Bowmer and Keegan 1983), compared to 76 and 93.3% of all arms in the *A. chiajei* population (Table 1).

Examination of stomach contents shows that predation of amphiuroid arms does occur. Given the locality and duration of the trawl, as well as the large numbers of *Amphiura chiajei* entangled in the beam trawl net, it seems reasonable to suggest that any arm remains would be those of *A. chiajei*. Keegan and Mercer (1986) reported that *A. chiajei* is the only amphiuroid to occur commonly throughout Killary Harbour.

As in the studies of Bowmer (1982) and Grehan (1982), who reported difficulties in identifying the gut contents of molluscan and decapod species due to the nature of their feeding techniques, members of these taxa were ignored in the present study. However, Thomas and Davidson (1962) recorded *Amphiura chiajei* as being among food items consumed by *Nephrops norvegicus* (of which there is a significant population in Killary Harbour). Therefore, *N. norvegicus* in particular, and the other decapod species in general, cannot be ruled out as potential predators.

Sloan (1980) showed that a large number of starfish species actively prey on ophiuroids. Brun (1969) stated that *Ophiura albida* arms were commonly found in *Asterias rubens* and *Marthasterias glacialis*. While no evidence of predation of *Amphiura chiajei* by *M. glacialis* was found in the present study, the possibility that *Asterias rubens* may actively use the species as a food source cannot be ignored. It was not possible to determine whether *Amphiura chiajei* arms had become accidentally entangled with *Asterias rubens*, either within the trawl or as the amphiuroids progressed across the bottom, or if the asteroids had been actively engaged in transporting them along their arms to their mouths.

Among the fish species recorded, the pleuronectid species showed the most evidence of actively preying on *Amphiura chiajei*. The Pleuronectidae are visual day feeders (Jones 1956), although plaice and flounder, more so than dab, also make use of chemosensory perception (Edwards and Steel 1968, De Groot 1971), with plaice being attracted to waterflows from *Tellina* spp. siphons (Edwards and Steel 1968). Plaice and the other pleuronectids may thus be attracted by the respiration currents from *A. chiajei* burrows. If so, it may explain the greater number of regeneration points in the proximal and distal thirds of the *A. chiajei* arms. During respiratory undulation only the arm tip is extended out of a burrow, while feeding arms are often observed to project up to 6 cm along the sediment. Attraction by the respiratory current may elicit predation of the distal arm portions, while the larger arm lengths accessible during feeding may be visually targeted. By comparison, the mainly suspension-feeding *A. filiformis* has the greatest number of regeneration points in the proximal and middle portions of each arm (Bowmer and Keegan 1983). These arms remain more or less erect in the water column, extending ~5 cm above the sediment surface during feeding and undulation (Bowmer and Keegan 1983), and thereby increasing the incidence of cropping points in the lower half of the arm. As the hunting posture of a species such as plaice is nearly hor-

izontal (Jones 1952), the full visible extent of a projecting arm may be taken.

Buchanan (1964) recorded a mean of 1.8 regenerating arms/individual among a population of *Amphiura chiajei* off Northumberland, with a mean population density of 12.3 ± 2.5 individuals/m². This contrasts with the mean of 4.21 regenerating arms/individual in the Killary population and a mean density of ~ 700 individuals/m². The higher numbers of individuals in the present study area may provide a greater potential food supply, as the results compare closely with those of the dense *A. filiformis*-dominated community in Galway Bay (mean = 4.01 regenerating arms per individual: Bowmer and Keegan 1983), which has a mean density of up to 1,200 individuals/m². In both these populations, sub-lethal predation is assumed to be the main cause of arm loss and subsequent regeneration. While the calorific value of the arms of *A. filiformis* is higher than that of the arms of *A. chiajei* (0.293 kJ and 0.209 kJ individuals, respectively: Lawrence and Guille, in Lawrence 1987), the high level of sub-lethal predation in Killary Harbour may be exaggerated by the overall paucity of the macrobenthic fauna in the study area (Munday 1991). For example, Jones (1952) notes that plaice select the bivalve *Cultellus pellucidus* (Pennant), in preference to *Amphiura* spp.

While these infaunal amphiuroid populations show quite extensive levels of sub-lethal predation, the population of the epifaunal ophiuroid *Ophiothrix fragilis* at the mouth of Killary Harbour (Ball 1991), with a population density as high as 10 000 individuals/m² (Keegan et al. 1985, Keegan and Mercer 1986), provides an interesting comparison. Regeneration levels for this species were recorded as 10.6% of all arms. While the population density of fish in the area is not known, Ball suggests that the low level of regeneration may be because small fish are unable to tackle the much larger and sturdier arms of *O. fragilis*. The serrated spines along its arms may also constitute a barrier to some larger potential predators, while the thin, thread-like arms of the amphiuroid species may be more accessible, leading to greater levels of sub-lethal predation.

The large potential food supply constituted by the *Amphiura chiajei* population of Killary Harbour may, therefore, be an underlying factor in the persistent nature of the phenomenon of regeneration evidenced by the accumulation of regeneration points by the larger and, presumably, older individuals. The fact that the stomachs of plaice, dab and flounder, which empty in 16 to 24 h at 10.0 to 17.4°C (De Groot 1971), were full of fresh arm portions, also points to continuous predation. The one fish with an empty stomach did have remains of amphiuroid arms in the posterior of its alimentary canal, which empties in 54 to 72 h at the same temperature (De Groot 1971).

Variation in the seasonal feeding habits of these fish species raises further speculation. Feeding activity is at a minimum from November to February among plaice in the North Sea (Jones 1952). A similar situation in Killary Harbour could account for the greater mean regenerated arm lengths and percentage regenerated dry weights recorded there during the winter months. This may indi-

cate that predation, while persistent, may vary seasonally, being greatest in the warmer summer months and least during winter, allowing a greater build-up of regenerated material. Lower light intensity at the bottom during winter may limit visual feeding and thus may compound the effect of lowered temperatures on the amount of food ingested at this time.

The June 1988 sample shows the greatest reduction in mean arm length, and a correspondingly low mean percentage of regenerated-arm dry weight. In this instance, predation pressure may have been particularly heavy or damage may have been the result of some stochastic cause, e.g. mechanical damage due to some anthropogenic activity. For example, occasional commercial trawling of the *Nephrops norvegicus* population in the vicinity of the study site must cause a significant amount of damage to the co-occurring ophiuroids.

Due to the persistent nature of predation and the possibility of mechanical damage, there must be an additional loading placed on the energy budget of individuals which introduces an imponderable element to production estimates (Buchanan 1964). In addition to the normal maintenance of basal metabolism, an amphiuroid such as *Amphiura chiajei* will require a substantial input into gonad development each year. Singletary (1980) noted that the stage of gonad development declined when arm regeneration was in progress. This was not investigated during the course of the present study but, due to the interlinked factors of regeneration, reproduction and basal metabolism, the necessity for further research in this area is recognised.

The incidence of disc regeneration was much less than arm regeneration (0.5% of the population). However, the occurrence of discs within the stomachs of some predators, and the incidence of partial disc regeneration indicates that active predation of complete individuals by fish species also takes place. Whether this is due to the atypical occurrence of such individuals on or very near the sediment surface is not known, but the phenomenon is clearly uncommon.

Therefore, it is assumed that both lethal and sub-lethal predation of the *Amphiura chiajei* population occurs, with sub-lethal pressure being the important factor in arm loss and subsequent regeneration. Such predation provides a substantial trophic link between the densely aggregated *A. chiajei* in Killary Harbour and the demersal fish species of the area, as reported for *A. filiformis* in Galway Bay (Bowmer and Keegan 1983).

While cropping of the *Amphiura chiajei* arms is clearly intensive, the population nonetheless remained very stable and became reproductively mature each year (Munday 1991). From this, it must be assumed that the stock is highly resilient and is able to contend with this sub-lethal drain on its resources.

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