



SYMPOSIUM

Energetic Costs of Loss and Regeneration of Arms in Stellate Echinoderms

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Synopsis Loss of arms has energetic consequences for stellate echinoderms (crinoids, ophiuroids, and asteroids). The energetic cost of losing an arm includes loss of investment, decrease in ability to obtain nutrients and allocation of nutrients to regeneration of the lost arms at a cost to other body compartments. The cost to other body compartments is low when food availability is very low or very high. The cost becomes apparent when food availability is sufficient to support production but not high enough that the cost of regeneration has no effect on production of other body compartments. Loss of investment is greater in asteroids than in crinoids and ophiuroids because of greater development of the body wall and presence of gonads and pyloric caeca in the arms. The cost of regeneration of organic matter in an arm can be estimated from the amount of organic matter present in intact arms and the cost of anabolism. Protein production is the primary cost of regeneration of an arm because of the high concentration of protein in the regenerated arm and the high anabolic cost of protein production. A major energetic cost of loss of arms that affects regeneration is decrease in food consumption. It is necessary to separate cost of decrease in consumption from cost of regeneration. Comparison of intact and regenerating individuals requires they consume the same amount of food. The cost of regeneration will also be affected by the quality of food because of the nutrient requirements for growth. Because the quantity and quality of the food ingested is not known, it is not possible to quantify the cost of regeneration in the field. Asteroids appear to be a good model for the study of regeneration in the laboratory because it is possible to control the quantity and quality of food they ingest. They are also a good model for the study of the evolutionary significance of regeneration by comparing individuals that have lost arms and are regenerating them to those that have lost arms and are not. The difference in the frequency of loss of arms of species is related to the difference in availability of food and the ability to feed that affect the capacity for re-investment in the lost arm. This is important in considering life-history strategies.

Introduction

The cost of loss of appendages include decreased locomotory performance, loss of nutrient reserves, reduced reproductive output and growth, and altered social interaction (Fleming et al. 2007; Bateman and Fleming 2009). The energetic cost of loss of arms in stellate echinoderms (crinoids, ophiuroids, and asteroids) is considered here.

Stellate echinoderms have arms that extend from a central body. Loss of arms occurs from autotomy or predation (Lawrence, in press). Although other structures of echinoderms can be lost and regenerated (e.g., the spines of echinoids, the disc of

crinoids and ophiuroids, the viscera of holothuroids) (Emson and Wilkie 1980), I restrict myself to the arms of stellate echinoderms because they have a distinct similar function in the three classes.

Because the arms can function in feeding, locomotion, and reproduction (Lawrence 1987), the direct cost of their loss can be considered in terms of the reduction of these functions that have important consequences for the organism. An additional, indirect cost is that of re-investment in regeneration. Because regeneration is growth, it is affected by the quantity and quality of food consumed. It is essential

to know these for the study of regeneration. I focus on four areas: (i) the characteristics of the arms and their loss, (ii) the loss of investment by the loss of arms, (iii) the effect of loss of arms and regeneration on other body compartments, and (iv) the relation between arm loss and regeneration and life history strategies. I consider loss of investment, the effect on other body components, and cost of regeneration in terms of energy, which provides a means to relate them to life history strategies.

Characteristics of loss of an arm

It is important to know the characteristics of the arm and its loss in order to understand the cost of loss and regeneration of arms. Although the arms of crinoids, ophiuroids, and asteroids are all extensions from the body, they differ in structure (Cuénot 1948; Hyman 1955; Lawrence 1987). The arms of crinoids and ophiuroids are supported by internal column of ossicles and have little development of a coelom in the arm. The proximal pinnules of crinoids are reproductive. The gonads of ophiuroids are in the disk except in some families (Euryalidae, Asteroschematidae, and Ophiocanopidae) where they extend into the proximal part of the arm. Loss of arms occurs at autotomy planes spaced at intervals along the arms of crinoids and between each pair of vertebral ossicles in ophiuroids. Because loss of the arm is usually distal, it is unlikely loss of the arm in crinoids and ophiuroids results in loss of gonads. Loss of the arm of the euryalinid *Astrobrachioin constrictum*, which has gonads in the proximal part of the arm, does not cause loss of gonads (Stewart 1996). In contrast to the arms of crinoids and ophiuroids, the arms of asteroids are supported by the

external ambulacral ossicles and the body wall and contain gonads and digestive/nutrient reserve organs (pyloric caeca). There is a single autotomy plane in asteroids that is located proximal to the disc, except in the Luididae and Archasteridae where autotomy planes occur the length of the arm. Consequently loss of arms in asteroids except these two families results in the loss of the entire arm including gonads and pyloric caeca. These differences have important consequences for energetic cost of arm loss and regeneration in the three classes.

Cost by loss of investment

The immediate cost of arm loss is loss of investment. The amount of arm loss by ophiuroids and asteroids in terms of length of arm lost has been reported for ophiuroids (Bowmer and Keegan 1983; Aronson 1991; Munday 1993; Bourgoïn and Guillou 1994; Pape-Lindstrom et al. 1997) and for an asteroid (Marrs et al. 2000). Although the length of arm lost has important implications for the functioning of the organism, it does not quantify the amount of loss of organic matter and overestimates the amount of energy lost (Fig. 1).

The amount of arm loss can be expressed in terms of dry weight, organic matter or energy. Although all are directly correlated, only the amount of energy lost provides information on the energetic loss of investment. Dry weight includes calcium carbonate, which is particularly important in the vertebrae of crinoids and ophiuroids and the body wall of asteroids. Organic matter and energy are of nutritional importance because they are involved in trophic transfer and metabolism, and are the best indicators of investment, particularly in terms of proximate composition (protein, carbohydrate, and lipid).

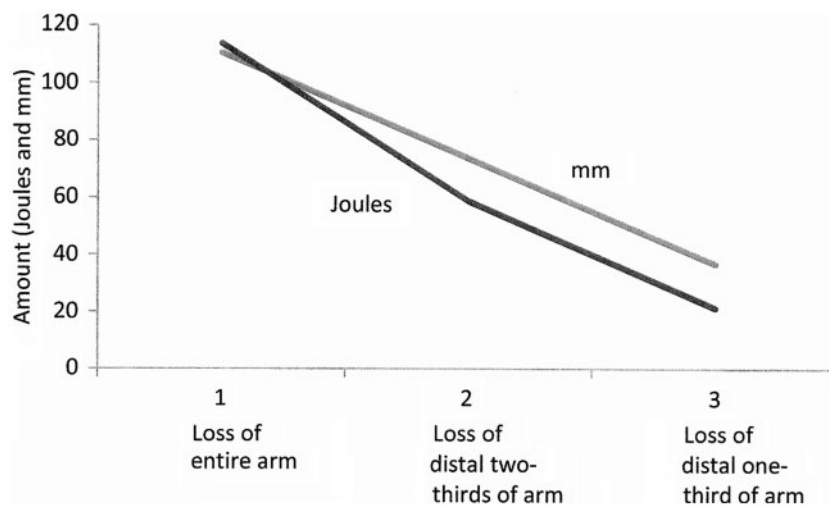


Fig. 1 *Ophiophragmus filigraneus*: Relation between length of arm lost (mm) and amount of energy lost (J).

Calcium carbonate is not of nutritional importance because it is not involved in trophic transfer or metabolism. The proximate composition of ophiuroid arms (Lawrence and Guille 1982; Pomory and Lawrence 1999, 2001) and the body wall of asteroid arms (Lawrence 1973; Lawrence and Guille 1982; Lawrence and Moran 1992; Lares and Lawrence 1994; Diaz-Guisado et al. 2006; Barrios et al. 2008) differ greatly. Ash is 60–70% dry weight⁻¹ of asteroid arms and 75–95% dry weight⁻¹ of ophiuroid arms. Most of the organic matter is protein, 21–37% dry weight⁻¹ of asteroid arms and 11–23% dry weight⁻¹ in ophiuroid arms. Very little carbohydrate or lipid is present. The proximate composition of the pyloric caeca and gonads of asteroids differs greatly from that of the body wall because of the low concentration of ash. The proximate composition of the pyloric caeca of *Luidia clathrata* and *Acanthaster planci* is ~10% carbohydrate dry weight⁻¹, 30% lipid dry weight⁻¹, and 60% protein dry weight⁻¹ (Lawrence 1973; Lawrence and Moran 1992, respectively).

The amount of energy varies with proximate composition. Paine (1971) noted the value of proximate analysis because the amount of energy of organic matter varies with its proximate composition. The importance of knowing proximate composition is indicated by the use by O'Connor et al. (1984) of Crisp's conversion value of 4.7 kcal g organic matter⁻¹. The value calculated from the proximate composition of the arm of *Amphiura filiformis* (Lawrence and Guille 1982) is 5.84 kcal g organic matter⁻¹ (24.4 kJ g organic matter⁻¹). I know of no studies that have measured the amount of organic matter or of energy in the arms in crinoids. The loss of investment is 4.48 kJ arm⁻¹ for *Ophiocoma echinata* (90% protein) (Pomory and Lawrence 2001). For *A. planci* in the non-reproductive season, the investment lost is 1675 kJ arm⁻¹ (84% protein) for the body wall and 1220 kJ arm⁻¹ (45% protein, 50% lipid) for the pyloric caeca (Lawrence and Moran 1992). The loss from the pyloric caeca is 42% of the total. Because loss of arms by asteroids involves the loss of energy of the viscera as well as the body wall, it is greater than the loss of investment in organic matter and energy in ophiuroids where this does not occur.

Cost of regeneration of arms

Increase in the length of the arm is the most sensitive measure of regeneration because the regenerating arm first increases in length and then in differentiation of appendages (Dupont and Thorndyke 2006).

It is important as an indicator of development of function but it does not measure production. Biological production is the biomass produced by chemosynthesis (USGS Biological Resources Glossary). Increase in dry weight includes the inorganic component, which is particularly important in the arms of crinoids and ophiuroids and in the body wall of asteroids. Deposition of calcium carbonate does not increase the amount of organic matter or energy although it does require energy. Calcification in echinoderms involves membrane systems that produce supersaturating concentrations by active ion transport (Dubois and Chen 1989). Emson (1985) suggested the energetic requirement for precipitation of calcium carbonate would be less than for anabolism of organic matter but pointed out no studies have been done to verify this.

The increase in the amount of organic matter or energy is important for two reasons. First, it indicates the trophic transfer of organic matter and energy. Second, it indicates the amount of organic matter or energy that is unavailable to other organs in the body. Total organic matter and energy do not consider differences in properties and functions of proximate constituents (protein, lipid, carbohydrate) that affect production. The proximate constituents of body compartments differ greatly in *L. clathrata* (Lawrence 1973) *A. planci* (Lawrence and Moran 1992), *O. echinata* (Pomory and Lawrence 1999), *Stichaster striatus* (Diaz-Guisado et al. 2006), and *Heliaster helianthus* (Barrios et al. 2008).

The production of organic matter or energy in the regenerated arm is not the total cost of regeneration because it does not include the cost of anabolism. This varies with the proximate constituent. Cost of carbohydrate and protein anabolism can be estimated by using energy equivalents (0.42 J mg glycogen⁻¹ and 13 J mg protein⁻¹; Marsh and Watts 2007). Cost of lipid anabolism is probably low compared to that of carbohydrate and protein because most single fatty-acid chains are readily absorbed from the diet intact (Marsh and Watts 2007). Using these values and the proximate composition of an intact arm of *O. echinata* (Pomory and Lawrence 1999), the energy for anabolism of organic matter in a completely regenerated arm of *O. echinata* containing 6.14 kJ is 4.3 kJ, 68% of the total. Because of the high concentration of protein in the arm (23% dry weight) and the low concentration of carbohydrate and lipid (0.26 and 0.98% dry weight, respectively) and the high cost of anabolism of protein, protein accounts for nearly all of the anabolic cost of production of organic matter.

Cost to other body compartments of the loss and regeneration of arms

Allocation of nutrients and energy to regeneration could affect production associated with growth, storage of nutrient reserves or reproduction, the classic trade-off situation. Maginnis (2006) pointed out the traditional approach to this has been comparison of intact and regenerating individuals. Field studies of regenerating individuals are important because they indicate their condition in the field and can guide laboratory studies. Substantial allocation of resources to regeneration in the field has been reported for *A. filiformis* (Bowmer and Keegan 1983; O'Connor et al. 1986; Sköld et al. 1994), *Amphiura chiajei* (Munday 1993), *Acrocnida brachiata* (Bourgoin and Guillou 1994) and *O. echinata* (Pomory and Lawrence 2001) but the effect on growth, storage of nutrient reserves or reproduction were not reported.

Lawrence and Larrain (1994) found that *S. striatus* that were not regenerating arms had larger pyloric caeca with a higher content of lipid and more calories than did intact arms of those that were regenerating arms. Bourgoin and Guillou (1994) concluded that *A. brachiata* allocate energy to regeneration of the arms at the expense of somatic growth, thereby maximizing fitness. Pomory and Lares (2000) found no difference in the dry weight of the body wall or pyloric caeca between intact arms of intact or regenerating *L. clathrata*. Morgan and Jangoux (2004) calculated that regeneration of arms by *Ophiothrix fragilis* resulted in a small but significant decrease in the storage of energy and in gonadal growth. The difficulty with these studies is that they did not distinguish between the cost incurred by a decrease in the ability to feed and the cost of regeneration. They indicated the cost of arm loss but not necessarily the cost of regeneration.

Laboratory studies allow control of conditions. Bourgoin and Guillou (1994) reported that the length of regenerating arms of *A. brachiata* did not vary significantly among individuals with one to three amputated arms. Soong et al. (1997) also found no difference in the length of regenerating arms in *O. scolopendrina* with one to three amputated arms. Nilsson (1999) reported that arm regeneration and disc production by *A. filiformis* were greater in individuals with one regenerating arm than those with three regenerating arms. Pomory and Lawrence (1999) reported that *O. echinata* that were regenerating arms had reduced production of gonads as well as lower reserves of nutrients in the stomach than did intact individuals. The amount of

food consumed will affect the response to loss of arms. These studies did not measure this. Even if the availability of food was the same for both regenerating and intact individuals, it was not known whether the amount consumed was the same. Amputation of the arms could reduce feeding either through the effect of trauma or by reducing the number of feeding arms. The study of the effect of regeneration on other body components by comparison of production of intact and regenerating individuals requires that both ingest the same amount of food.

The importance of the effect of amputation of arms on food consumption can be seen in studies on asteroids. In a laboratory study Diaz-Guisado et al. (2006) reported that arm loss in small *S. striatus* resulted in a pronounced (ca. 67%) decrease in consumption of food that lasted five months. Growth as well as storage of nutrients in the pyloric caeca of intact arms decreased and the increase in length of intact arms of intact individuals was much greater than occurred in regenerating individuals. Because of the long-term decrease in food consumption, it is not possible to know whether the effect was due to regeneration or to a decrease in feeding. A similar decrease in feeding that lasted five months has been reported for *H. helianthus* (Barrios et al. 2008). When long-term decrease in food consumption occurs, three treatments (intact individuals fed *ad libitum*, regenerating individuals fed *ad libitum*, and intact individuals fed at the rate that regenerating individuals consumed food) are necessary to distinguish between the cost to production of decreased food consumption and the cost of regeneration (Fig. 2).

Piscopo et al. (2005) reported that severing the radial nerve in one arm of *Asterias rubens* had no immediate effect on appetitive behavior but that such behavior progressively decreased for up to 40 days until complete recovery after 60 days. In contrast, Lawrence et al. (1986) and Lawrence and Ellwood (1991) found that amputation of arms of *L. clathrata* did not reduce ingestion of food.

An alternative approach to assure equal ingestion of food is to provide an amount of food that is completely consumed by intact and regenerating individuals. Lawrence et al. (1986) fed equal amounts of a low ration of food that was completely consumed to individuals of *L. clathrata* with all arms intact and those with two amputated arms. Very little arm regeneration occurred but the increase in dry weight of the pyloric caeca per intact arm was greater in regenerating than intact individuals although the total amount for all intact arms was

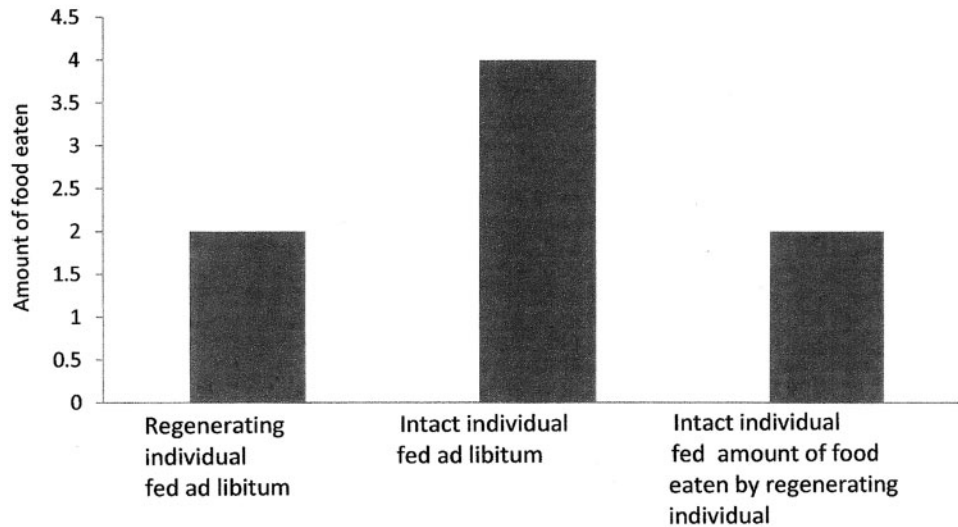


Fig. 2 Analysis of cost of regeneration. If arm loss results in a decrease in feeding, feeding intact and regenerating individuals ad libitum does not separate the cost of the decrease in feeding from the cost of regeneration. In this situation, feeding intact individuals the amount of food consumed by regenerating individuals will indicate the cost of regeneration.

slightly less. Under the conditions of this experiment, there was no cost of regeneration because little arm regeneration occurred. Lawrence and Ellwood (1991) fed equal amounts of a high ration of food that was completely consumed to individuals of *L. clathrata* with all arms intact and those with three amputated arms. In contrast to the previous experiment, these *L. clathrata* rapidly regenerated the arms and over-compensated in production of gonads and pyloric caeca in intact arms. Under the conditions of this experiment, arm loss did not result in a cost of regeneration because production in the regenerating individuals exceeded that in the intact individuals. These studies suggest that a cost of regeneration would be incurred at intermediate provision of food (Fig. 3). They indicate the importance of knowing the amount of food consumed in studies of the cost of regeneration. It is not possible to assess the effect of regeneration unless the amount of food consumed by regenerating and intact individuals is the same.

One would expect the quality of food to affect regeneration. Production involves anabolism. This requires energy that is usually supplied by carbohydrates and lipids. Production in regeneration of arms is primarily protein. If concentrations of carbohydrate and lipid in food is low, protein is used for energy and production decreases (National Research Council 1993). A formulated feed has been prepared for asteroids by A.L. Lawrence (Texas A&M System). A formulated feed is important because it is possible to vary its composition. In *L. clathrata* production, including total gonad and pyloric caeca, increased

with increasing amount of food consumed and with a higher protein:lipid ratio (Lawrence et al. unpublished). As with quantity of food consumed, the quality of the food affects the cost of regeneration. Growth factors can be added to prepared feeds to study their effect on regeneration.

Comparison of intact and regenerating individuals to investigate the cost of regeneration requires consideration of the reduction in feeding in consequence of having lost an arm. Maginnis (2006) stated the amount of regeneration and consequently the effect on relative fitness could differ but stated that species that autotomize arms tend to be fixed in regard to their tendency to regenerate. The studies with *L. clathrata* (Lawrence et al. 1986; Lawrence and Ellwood 1991) show regeneration is not fixed but differs with the quantity of food consumed. This must be taken into account in studies of the cost of regeneration.

Cost of loss and regeneration of arms and life history strategies

Plant ecologists have considered loss of biomass and regeneration more than zoologists because predation is usually sublethal in plants and lethal in animals. Grime (1977) developed life-history strategies for plants on the basis that two external factors, stress (defined as decreased acquisition and deposition of energy, production) and disturbance (defined as removal of energy from the organism, loss of biomass) limit energy in organisms. Grime's life history theory has been used to explain differences among plants in their life history characteristics, including

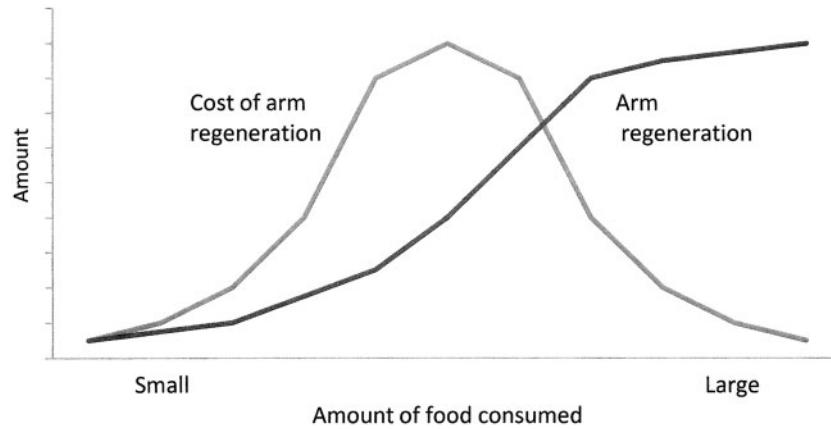


Fig. 3 Theoretical relation between cost of arm regeneration and the amount of food consumed if the amount of regeneration depends on the amount of food consumed.

regeneration. His theory predicts that regeneration following loss of parts would evolve under conditions of low disturbance and low stress, which he called the competitive strategy (Grime 1979, 2001). Another name is the capitalistic strategy, in which re-investment in regeneration of lost body parts is emphasized (Grime 1989). In human societies capitalism involves re-investment in productive units when resources are abundant or the ability to obtain them is high and society is stable. Grime (1979) stated the strategies of an organism in response to stress and disturbance should be the same in all taxa. Lawrence (1990, 1991) applied Grime's concept to echinoderms but did not consider loss (disturbance) and regeneration of arms.

Goss (1969) considered differences in the capacity to regenerate to be a characteristic of the body part lost: Vital or unimportant structures are not regenerated while non-vital but important ones are. Because arms of stellate echinoderms have many useful functions and their loss does not result in immediate death, their capacity to regenerate is expected. The generalization that stellate echinoderms frequently lose arms and regenerate them is current (Cuénot 1948; Hyman 1955; Candia Carnevali 2006; Fleming et al. 2007). However, there are species for which loss of arms and regeneration of arms have not been observed in the field (Emson and Wilkie 1980; Lawrence 1992; Schneider 1998; Lawrence et al. 1999). The question is why they are not. Different life history strategies are implied.

What are appropriate strategies for countering the cost of arm loss and regeneration? The simplest would be to decrease the frequency and amount of arm loss or avoid it altogether. The evolution of planes of autotomy in stellate echinoderms decreases the amount of loss. A solution to avoid arm loss is

deterrence of predation. Stellate echinoderms have structural and chemical protection that decreases the frequency of arm loss, as do plants, and behavioral protection as well (Lawrence, in press). Such protection has a cost. When should it occur? Comparisons between species of contrasted ecology indicate the strategy for plants in unproductive environments is to have structural or chemical adaptations that reduce predation (Grime et al. 1988). It is probable that stellate echinoderms would evolve structural, chemical or behavioral defenses against arm loss when availability of food or ability to feed is low. Many stellate echinoderms possess such defenses (Lawrence, in press). This evolutionary hypothesis could be tested by predicting these species would have low availability of food or ability to feed.

Lawrence (in press) compared arm loss and life history characteristics between the closely related asteroids *A. rubens* and *Pisaster ochraceus*. *Asterias rubens* is an active predator and scavenger (Sloan and Albridge 1981; Dare 1982; Nickell and Moore 1991; Ramsay et al. 1997), which suggests a high capacity for production. In contrast, *P. ochraceus* is not an active predator. Castilla and Paine (1987) considered it to be food limited, often to an extreme degree. This suggests it has a low capacity for production. These differences in ability to feed are correlated with a relatively weak body wall in *A. rubens* and a robust one in *P. ochraceus* (Fisher 1930). This in turn can be correlated with frequency of arm loss, high in *A. rubens* and low in *P. ochraceus* (Lawrence 1992; Lawrence et al. 1999). This suggests there is a trade-off between the cost of losing an arm and the cost of defense.

That arms are not lost does not mean that the potential for it to occur has been lost. Scheibling

(R. Scheibling, Dalhousie University, personal communication) did not observe any arm loss in an estimated several thousand *Oreaster reticulatus* in the field. However, autotomy of an arm near the disc occurred when he traumatized individuals by threading a line through the arm near the disc. Because *O. reticulatus* have large, broad arms, the open wound could not be closed and the individuals died.

Maginnis (2006) noted that the traditional comparison of intact and regenerating individuals in the laboratory is appropriate to measure tradeoffs associated with the cost of regeneration as described above. She proposed comparison of individuals that had lost arms and were or were not regenerating to be appropriate for measuring the evolutionary significance of regeneration. Regeneration should evolve if the relative fitness of individuals regenerating appendages was greater than in the fitness of those that did not.

This approach is possible with stellate echinoderms. Although Morgulis (1909) reported cauterization of the radial nerve prevented regeneration of arms in *Ophiocoma pumilla*, I have not had success with this operation with *L. clathrata*. Candia Carnevalli (2006) stated the nervous system of echinoderms has a high capacity for regeneration. An alternative method to prevent regeneration of arms is repeated amputation of the tip of the regenerating arm as soon as it appears. I have had success with this operation with *L. clathrata*. I have amputated the regenerating arm bud at the end of 7–8 days when it is 2–3 mm in length after successive amputations, before substantial production had occurred. Asteroids would be an appropriate model for testing Maginnis' proposal because regeneration of arms can be prevented and the quantity and quality of food consumed can be controlled. Maginnis (2006) did not define the conditions under which regeneration would decrease or increase relative fitness. I suggest that important conditions are the amount and frequency of loss of arms and the availability of food and the capacity to feed.

Conclusion

The energetic cost of losing an arm to stellate echinoderms includes loss of investment, decrease in ability to obtain nutrients and their allocation to regeneration of the lost arms and other body compartments. These typically have not been separated in stellate echinoderms. Analysis of the cost of regeneration will be complex. A basic requirement is an appropriate measurement of regeneration.

Although increases in length and dry weight of regenerating arms indicate growth, increases in organic matter and energy are better indicators of the cost of regeneration because they involve organic material. This means that the regeneration of arms has a nutritional basis and will be affected by the quantity and quality of food consumed. Comparison of intact and regenerating individuals requires the ability to measure and control consumption of food so that the intake of nutrients is the same in both. This is difficult with crinoids and ophiuroids because of the nature of their food and feeding. In contrast, it is possible with asteroids. Use of a formulated feed for asteroids allows control of food quality and provides another avenue for investigating the cost of arm regeneration. Formulated feeds provide the opportunity to add growth factors that may affect the cost of regeneration. The ability to obtain the nutrient resources necessary for re-investment in the arm is a characteristic associated with life history strategies and may explain why frequency of arm loss and regeneration differs among species.

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