



The effect of sublethal predation on the biology of echinoderms

Disturbance
Predation
Sublethal predation
Echinoderms

Perturbation
Prédation
Prédation sublétale
Echinoderme

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ABSTRACT

In contrast to plants, predation on animals is usually lethal. Analysis of the effect of predation on animal populations and on predator-prey dynamics typically assumes this is the case. However, sublethal predation occurs in echinoderms, primarily on the arms of crinoids, asteroids, and ophiuroids. Sublethal predation is important in these echinoderms as it meets one of Harris' (1989) major criteria, affecting basic biological processes such as acquisition of food and allocation of nutrients to growth and reproduction. Sublethal predation would have an effect on their ecological role. It is essential to consider sublethal predation in the analysis of the life-histories of these species.

RÉSUMÉ

Les effets de la prédation sublétale sur la biologie des échinodermes.

A l'inverse de la plante, l'animal subit une prédation qui lui est habituellement mortelle. Ceci est confirmé par la plupart des analyses de prédation au sein des populations animales et de la dynamique prédateur/proie. Cependant une prédation sublétale c'est-à-dire sans effet fatal, existe chez les échinodermes, principalement chez les crinoïdes, astéries et ophiures. Pour répondre à cette définition, ce genre de prédation doit répondre au critère de Harris (1989) c'est-à-dire influencer les processus de base tels que la croissance et la reproduction et varier en fonction de la densité de la population en cause. L'existence de cette prédation et ses conséquences chez les échinodermes ont été rarement étudiées. Pour certaines espèces, cette prédation peut avoir un impact important sur leur biologie et donc sur leur rôle écologique. Il est essentiel de prendre en compte ce genre de prédation lors d'une analyse des cycles de vie des échinodermes.

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INTRODUCTION

Predation can be lethal or sublethal. Sublethal predation is the consumption by a predator of a portion of the prey's biomass that does not result in death. The loss of biomass is defined as *disturbance* (Grime, 1977; Sousa, 1984; Witman, 1985; Tilman, 1988; Pickett *et al.*, 1989). In the case of carnivory, predation is usually lethal (Taylor, 1984).

This contrasts to herbivory, which is usually sublethal (Harper, 1977).

Is sublethal predation important? The costs of sublethal predation are direct in the loss of biomass and indirect in the loss of function. Thus both the amount of a structure lost and the importance of the structure in the function of the organism are important (Harper, 1977). Regeneration of the lost parts may follow sublethal predation and would

be an additional cost. Regeneration implies the structure involved is important but not essential according to Goss' (1969) paradigm, and that the benefits of regeneration exceed the cost. Reichman's (1984) support of Goss's paradigm did not consider the consequences of allocation of resources to regeneration on other functions of the organism, which provides the potential for a classical trade-off between the use of limited resources for competing uses.

Although the effect of herbivory on the biology of plants and the dynamics of animal-plant interactions has long been studied (Crawley, 1983), the effect of sublethal predation on the biology of animals has not. It affects growth in crustaceans (Bennett, 1973; Kuris and Mager, 1975; Smith, 1990), bivalves (Peterson and Quammen, 1982; Trevallion, 1971; Trevallion *et al.*, 1970; Kamermans and Huitema, 1994), and polychaetes (de Vlas, 1979), and reproduction in polychaetes (Zajac, 1985).

Harris (1989) proposed sublethal predation is an important factor regulating population size, providing the criteria of density-dependency and depression of long-term survival and reproduction are met. If so, it would be expected to have evolutionary consequences as Vermeij (1982, 1987; Aronson, 1994) suggested.

Sublethal predation in echinoderms has been documented in relatively few studies; it has been presumed in a number of studies (Tab. 1). It is most common in the stellate classes whose arms are both susceptible to predation and capable of wound healing. Although these data indicate sublethal predation occurs, they should not be taken as evidence that it occurs in all taxa in these groups. Arm loss and regeneration have never been found in some asteroid species (Lawrence, 1992). Some have extremely protective body-walls (Blake, 1991) and others have large coelomic cavities that cannot be sealed. The incidence of arm loss can be extremely variable in those species in which it does occur (Lawrence, 1992). The large coelomic cavity and rigid tests eliminate the possibility of sublethal predation in regular echinoids or spatangoids (Emson and Wilkie, 1980) as any substantial rupture of the test should result in death. However, sublethal predation of the edges of the tests of clypeasteroids occurs. Sublethal predation on the tube feet and pedicellariae have been reported.

The costs of sublethal predation in echinoderms and, as Emson and Wilkie (1980) observed, "the effect of the burden of regeneration on growth, reproductive potential, and general viability, are not well known". Here the biological effects of sublethal predation on echinoderms will be considered. These effects must be known to fully understand the ecology and evolution of the species in which it occurs, and in the analysis of their life histories.

Effects of sublethal predation

Effect on reproduction

A direct effect on reproduction occurs if sublethal predation results in loss of gonads. This would occur with arm loss in crinoids and asteroids and with visceral-mass loss in ophiuroids. Nichols (1994) reported the average loss of pinnules of the crinoid *Antedon bifida* was 17 % and that sublethal predation was almost totally confined to the geni-

tal pinnules. The potential loss of gamete production could be calculated from these data. Similar calculations could be made for the loss of gametes with arm loss in asteroids. This has not been done.

Lane (1984) suggested the large anal sac of extinct inadunates contained the gonads, separating them from the remaining viscera. Disadvantageous as the loss of the gonad intuitively seems, Lane hypothesized it was adaptive in these crinoids by suggesting the supposed extra-thecal location of the gonad was an evolutionary adaptation to attract sublethal predation to the gonads to spare the vital organs in the theca.

In extant crinoids, the gonads are located in the arms or in genital pinnules (Hyman, 1955). Noting the high incidence of sublethal predation on the arms and pinnules of *Antedon bifida*, Nichols (1994) like Lane suggested the occurrence of the gonads on the arms was a strategy of tolerating sublethal predation of the pinnules to protect the more vital organs in the theca. Nichols stated such a strategy would be justified only if the loss and regeneration could be equated in energy terms, and that lifetime reproductive potential must be considered.

Effect on nutrient reserves

Essentially all tissues of echinoderms are used if starvation is sufficiently extensive. The pyloric caeca of asteroids are specific reserve organs (Giese, 1966; Lawrence and Lane, 1982; Lawrence, 1987). Sublethal predation on the arms of asteroids would decrease the amount of reserves. This would decrease the ability of the individual to withstand starvation and the amount of reserves that could be used for gametogenesis. As with the gonads, the amount of nutrient reserve lost with arm loss can be calculated. This has not been done.

Effect on movement

When attacked by the asteroid *Solaster dawsoni*, the asteroid *Pycnopodia helianthoides* autotomizes arms and escapes (Birkeland *et al.*, 1982). Not only is the behavior of the individual affected, but that of others as well as they show an alarm response to the presence of body and tissue fluids of their conspecifics. The asteroid *Stichaster striatus* also autotomizes arms when attacked, but does not show an alarm response (Lawrence, unpub. obs.). This may be responsible for a much higher rate of sublethal predation (Viviani, 1978).

Hiding time did not change with arm loss in *Micropholis gracillima*, as individuals usually travelled down an existing hole rather than burrowing (Clements, 1985). Grober (1988 *a*) reported that the time for withdrawal into the reef by the ophiuroid (*Ophiopsila riisei*) is significantly increased immediately following arm loss. The ophiuroid *Ophioderma brevispina* with two or three lost arms do not move as rapidly as intact individuals until arms regenerate to half the length of the intact arms (Henry, 1993).

Effect on acquisition of nutrients

Sublethal predation may decrease production by decreasing the acquisition of nutrients (feeding and digestion). As

Table 1

Studies documenting or presuming sublethal predation in echinoderms.

Class Crinoidea

Order Isocrinida

Cenocrinus asterias: Lost arms almost always few in number and partially regenerated (Messing *et al.*, 1988).

Diplocrinus wyvillethomsoni: Photographs show fish feeding on arms (Conan *et al.*, 1981).

Metacrinus fossilis: 10 % arm regeneration in specimens of this extinct species is lower than that of modern isocrinids living deeper than 100 m (Meyer, Oji, 1993).

Metacrinus rotundus: 89 % of individuals with arm regeneration (Meyer, Oji, 1993).

Order Comatulida

"comatulids": The triggerfish *Ballistoides conspicillum* observed attacking arms of partially exposed individuals. Feces contains portions of crinoid arms (Gladstone, in Vail, 1987).

Antedon bifida: Predation on pinnules by wrasse *Crenilabrus melops* (Nichols, 1994).

Capillaster sp.: 3 % with regenerating visceral mass; 32 % with regenerating arms (Meyer, 1985).

Capillaster multiradiatus: 4 % with regenerating visceral mass; 29 % with regenerating arms (Meyer, 1985). 44 % of individuals and 6 % of all arms with regeneration (Schneider, 1988).

Cenometra bella: 6 % with regenerating visceral mass; 50 % with regenerating arms (Meyer, 1985). 10 % of individuals and 10 % of all arms regenerating (Schneider, 1988).

Colobometra perspinosa: 9 % with regenerating visceral mass; 23 % with regenerating arms (Meyer, 1985).

Comanthina sp.: 63 % with regenerating arms (Meyer, 1985).

Comanthina schlegeli: 5 % with regenerating visceral mass; 65 % with regenerating arms (Meyer, 1985). 68 % of individuals and 4 % of all arms regenerating (Schneider, 1988).

Comanthus parvicirrus: 3 % with regenerating visceral mass; 33 % with regenerating arms (Meyer, 1985).

Comaster bennetti: 1.8 % with regenerating visceral mass (Meyer, 1985). 89 % of individuals and 6 % of all arms regenerating (Schneider, 1988).

Comaster distinctus: 57 % of individuals and 10 % of all arms regenerating (Schneider, 1988).

Comaster multifidus: 63 % of individuals and 3 % of all arms regenerating (Schneider, 1988).

Comatula purpurea: 16 % of individuals and 3 % of arms regenerating (Schneider, 1988).

Comatheria briareus: 75 % of individuals and 81 % of all arms regenerating (Schneider, 1988).

Dichrometra flagellata: 83 % of individuals and 5 % of all arms regenerating (Schneider, 1988).

Florometra serratissima: 80 % with regenerating arms. Although some arm loss attributed wave action and physical factors, most attributed to predation by the asteroid *Pycnopodia helianthoides* and the crab *Oregonia gracillis* (Mladenov, 1980, 1983).

Heterometra savignyi: Suggests arm loss is the result of fish feeding on plankton trapped in mucus in food grooves. Arm loss greater in seagrass meadows than in areas where diurnal crypsis is possible (Magnus, 1963).

Himerometra magnipinna: 100 % of individuals and 24 % of all arms regenerating (Schneider, 1988).

Himerometra robustipinna: 5 % with regenerating visceral mass; 77 % with regenerating arms (Meyer, 1985).

71 % of individuals and 8 % of all arms regenerating (Schneider, 1988). Arms preyed upon by the fish *Chaetodon ephippium* (Meyer *et al.*, 1984).

Himerometra bartschi: 2 % with regenerating visceral mass; 67 % with regenerating arms (Meyer, 1985).

Lamprometra palmata: 40 % of individuals and 11 % of all arms regenerating (Schneider, 1988).

Nemaster grandis: 100 % of individuals and 13 % of all arms regenerating (Schneider, 1988).

Oligometra serripinna: ca. 30 % of population with arm loss (Vail, 1989).

Pontiometra andersoni: 100 % of individuals and 15 % of all arms regenerating (Schneider, 1988).

Reometra mariae: 100 % of individuals and 14 % of all arms regenerating (Schneider, 1988).

Stephanometra indica: 24 % of individuals and 3 % of all arms regenerating (Schneider, 1988).

Stephanometra oxyacantha: 4 % with regenerating visceral mass; 33 % with regenerating arms (Meyer, 1985).

Tropiometra afra: 21 % of individuals and 5 % of all arms regenerating (Schneider, 1988).

Class Asteroidea

Order Forcipulatida

Asterias amurensis: Arm loss possibly from predation by the crab *Paralithoides camtschatica* (Hartsock, pers. comm.).

Asterias forbesi: 10 % of the spider crab *Libinia emarginata* with arm ossicles in stomach (Aldrich, 1976).

Asterias rubens: Arms autotomized in response to predation by the stone crab *Hyas araneus* and the asteroid *Solaster papposus* (Hancock, 1955, 1974). Arms autotomized in response to predation by the asteroid *Solaster endeca* (Christensen, unpub., in Feder and Christensen 1966). Individuals in the eastern Bering Sea often missing arms, presumably from predation (possibly crab *Paralithoides camtschatica*). As often only distal portions of arms missing, probably cropping and not autotomy (F. Hartsock, pers. comm.).

Asterias vulgaris: 11 % with regenerating arms (King, 1898). Arms lost to attack by lobsters in the laboratory (Breen, 1974).

Evasterias troscheli: Arms autotomized in response to predation by the asteroid *Solaster dawsoni* (Christensen, unpub., in Feder and Christensen, 1966). Predation by *S. dawsoni* observed (Birkeland *et al.*, 1982).

Heliaster helianthoides: 0-62 % regenerating arms in different populations. Predation by the asteroid *Meyenaster gelatinosus*. Usually 3-4 adjacent arms regenerating (Viviani, 1978).

Meyenaster gelatinosus: Predation by the asteroid *Luidia magellanicum*. 10-62 % regeneration in different populations. Occurred in individuals radius from 80-220 mm, suggesting lethal predation at small size and escape from predation at large size (Viviani, 1978).

Pycnopodia helianthoides: Autotomizes arms in laboratory in response to predation by *Solaster dawsoni* (Mauzey *et al.*, 1968). Feeding by *S. dawsoni* on autotomized arms observed in field (Birkeland *et al.*, 1982). Autotomy of two adjacent arms in response to attack by *S. dawsoni* (M. Byrne, unpub. obs.).

Stichaster striatus: 2-38 % with regenerating 1-2 arms. Occurred in individuals with radius from 40-90 mm, suggesting lethal predation at small size and escape from predation at large size (Viviani, 1978).

Order Valvatidae

Acanthaster planci: Pinned individuals often responded to attack by chiton *Charonia tritonis* by autotomizing arms (Chesher, 1969). Scars on arms attributed to predation (Campbell and Ormond, 1970). Arm loss attributed to predation by the triton (Endean, pers. comm.) and fish (Ormond, 1971). Predation by shrimp *Hymenocera picta* and

crustacean defensive interactions (Glynn, 1982 b). Arm loss most common at intermediate size (McCallum *et al.*, 1989).

Order Paxillosida

Astropecten articulatus: 0-40 % individuals regenerating arms (Hopkins *et al.*, 1990).

Luidia clathrata: 12-59 % individuals regenerating arms (Hopkins *et al.*, 1990).

Luidia magellanica: Predation by the asteroid *Meyenaster gelatinosus*. 51-69 % regenerating in different populations (Viviani, 1978).

Order Velatida

Solaster stimpsoni: arm stumps or very short arms believed result of predation by *Solaster dawsoni*; variation in frequency of individuals with arms regenerating directly correlated with abundance of *S. dawsoni* (Engstrom, 1974).

Class Ophiuroidea

"ophiuroids": Freshly cropped arms of "ophiuroids" found in guts of tiger prawns *Penaeus esculentus* and *Penaeus semisulcatus* (Wassenberg and Hill, 1987). "Ophiuroid" vertebrae a dominant prey of nekto-benthic crab *Portunus pelagicus* (Williams, 1982).

Order Phrynophiurida

Asteroporpa annulata: 20 % regeneration of arms (Hendler *et al.*, 1995).

Ophiomyxa flaccida: 48 % of arms regenerating (Sides, 1987).

Order Ophiurida

Acrocnida brachiata: 70 % of all arms regenerating in intertidal and subtidal predation (Bourgoin and Guillou, 1994).

Amphipholis squamata: 80 % arm loss, 3 % disc loss in population (Martin, 1968). 61 % of population regenerating one or more arms, ca. 1 % of population regenerating one arm; autotomy of arms more likely from hydrodynamic conditions than predation (Alva and Janoux, 1990).

Amphiplus coniotodes: 87 % of population regenerating arms, 3 % regenerating discs (Singletary, 1970, 1980).

Amphiura chiajei: 93 % of adults with arm regeneration (Buchanan, 1964). Found in 58 % of guts of haddock *Melanogrammus aeglefinus*, 46 % as arms only (Mattson, 1992). 99 % of adults with arm regeneration, 0.5 % with disc regeneration; all 5 arms of individuals regenerating in 65 % of population; attributed to fish predation (gobi *Lesueur gobius friesii*, plaice *Pleuronectes platessa*, flounder *Platichthys flesus*, dab *Limanda limanda*) (Munday, 1993).

Amphiura filiformis: 84 % of adults with arm regeneration; loss of an arm causes a brilliant flash and retraction of other arms (Buchanan, 1964). 78 % arm regeneration, 3 % disc regeneration attributed to predation by the young of flatfish (dab and plaice) (Bowmer and Keegan, 1983). 96 % of adults with arm regeneration attributed to fish (dab *L. limanda*) (Duinevelt and Van Noort, 1986). Found in 86 % of guts of haddock *Melanogrammus aeglefinus*, 53 % as arms only (Mattson, 1992). High percentage arm regeneration (Sköld *et al.*, 1994).

Hemipholis gracilis: At least 25 % of all arms regenerating, greater for large individuals attributed to predation by portunid crab *Callinectes arcuatus* (Lee and Lee, 1978).

Microphipholis gracillima: 77 % of population regenerating arms, (Singletary, 1970, 1980). 85 % of all arms regenerating attributed to predation (Stancyk *et al.*, 1994). (Note: Hendler *et al.*, 1995, reject *Microphipholis* and assign this species to *Amphipholis*.)

Ophiacantha fidelis: Guts of the asteroid *Meyenaster australiensis* with arm fragments only (Blaber *et al.*, 1987).

Ophiocoma pumila: Fish (wrasses *Halichoeres bivittatus*, *H. maculipinna*, *H. garnotti*) ate primarily arms of individuals exposed in the field (Hendler, 1984). 55 % of arms regenerating; loss attributed to predation (Sides, 1987).

Ophiocoma wendtii: 29 % of arms regenerating (Sides, 1987).

Ophiocoma nigra: The hermit crab *Pagurus bernhardus* eats of arm tips (Gorzula, 1976, in Warner, 1986). 30-54 % arm regeneration in different populations (Aronson, 1989).

Ophioderma appressum: 44 % of arms regenerating (Sides, 1987). 30-74 % arm regeneration in different populations, 50-85 % disc regeneration (Aronson, 1991).

Ophioderma brevispinum: 46-57 %, 68 % arm regeneration in different populations (Aronson, 1987, 1991). Regenerating arms attributed to water activity and predation (Henry, 1993).

Ophioderma cinereum: 34 % of arms regenerating (Sides, 1987).

Ophiolepis ailsae: 43 % of population regenerating arms (Hendler and Turner, 1987).

Ophiolepis gemma: high incidence of regenerating arms attributed to predation or physical factors (Hendler and Turner, 1987, Hendler *et al.*, 1995).

Ophiolepis impressa: 28 % of arms regenerating (Sides, 1987).

Ophiolepis pawsoni: Arm regeneration attributed to predation (Hendler, 1988).

Ophiomusium lymani: Predation by fish bites indicated large number with evidence of healed lesions in the interradial area over the gonad (Gage and Tyler, 1982).

Ophionephthys limnicola: 79 % of population regenerating arms (Singletary, 1970, 1980).

Ophioneis reticulata: 74 % of arms regenerating (Sides, 1987).

Ophiophragmus filigraneus: Discs in guts of 24 % of the stingray *Dasyatis sabina* (Turner *et al.*, 1982).

Ophiopsila riisei: Low level of arm loss attributed to bioluminescence that deters predation by nocturnal portunid crabs (Grober 1988 a, b, c).

Ophiothrix fragilis: Portions of arms usually found in guts of the hermit crab *Eupagurus bernhardus*, the swimming crab *Macropipus puber*, the poor cod *Gadus minutus*, *Callionymus lyra*, and *Pleuronectes platessa*. Rare for disc to be found. *Asterias rubens* also ingests arms (Warner, 1971). 27-92 % arm regeneration in different populations (Aronson, 1989).

Ophiophragmus filigraneus: 52-94 % regenerating arms (Clements *et al.*, 1994).

Ophiothrix lineata: Arm loss attributed to predation (Hendler, 1984).

Ophiothrix oerstedii: Arm fragments found in feces of polychaete *Eunice rubra*, in stomach of ophiuroid *Ophioderma brevispina*, and the crab *Mithrax* (Aronson and Harms, 1985). 30-85 % arm regeneration in different populations (Aronson, 1987, 1992).

Ophiura spp.: disc and arm fragments frequent in the guts of *Ophiura texturata*, possibly from ingestion of intact individuals (Feder, 1981).

Ophiura albida: Arm fragments in gut of hydroid *Hydractinia echinata*. Autotomizes arm to hydroid in laboratory (Christensen, 1967).

Ophiura sarsi: 39->98 % arm regeneration; arm loss not size dependent (Fujita, 1992). Arm fragments in gut of plaice *Hippoglossoides platessoides*; <10 % arm regeneration in population (Packer *et al.*, 1994).

Class Echinoidea

Order Echinoida

Echinometra lucunter: the goby *Ginsburgellus novemlineatus* feeds primarily on the tube feet and pedicellariae (Teytaud, 1971, in Shirley, 1982).

Order Clypeasteroida

Dendraster excentricus: Predation on edge of test by crabs *Loxorhynchus grandis* and *Cancer* sp. (Merrill and Hobson, 1970). < 5 % of population with broken, healed edges attributed to crab predation (Birkeland and Chia, 1971).

Mellita quinquiesperforata: Regenerating edge of test attributed to predation by crab *Callinectes sapidus* or fish, although possibly from wave damage (Weihe and Gray, 1968).

Class Holothuroidea

Order Aspidochirotida

Stichopus chloronotus: In the laboratory, escaped attack by the gastropod *Tonna perdx* by shedding a piece of the body wall and bounding away (Kropp, 1982).

Stichopus horrens: In the laboratory, escaped attack by the gastropod *Tonna perdx* by shedding a piece of the body wall and bounding away (Kropp, 1982).

Order Dendrochirotida

Athyonidium chilensis: Regenerating tentacles attributed to fish predation (Vásquez, unpub. obs.).

Eupentacta fraudatrix: Regenerating tentacles attributed to fish predation (Levin, unpub. obs.).

the amount of nutrients acquired determines the amount available for all requirements by the organism, this component of the energy budget is of paramount importance and could be a major consequence of sublethal predation.

Although dissolved organic material can contribute to these requirements (Bamford, 1982; Smith *et al.*, 1981; Clements *et al.*, 1988, 1993), the acquisition of food is of major importance. The arms of crinoids (Meyer, 1982), asteroids (Jangoux, 1982), and ophiuroids (Warner, 1982) and the tentacles of holothuroids (Massin, 1982) are used in feeding, and their loss by sublethal predation should decrease the ability to feed. The loss of the disc of crinoids and ophiuroids involves the loss of the digestive system and would eliminate the ability to obtain resources.

The trauma of arm loss can also decrease feeding behavior. The feeding posture is not assumed initially after arm loss in the comatulid *Cenometra bella* (Smith *et al.*, 1981). Removal of arm tips reduces feeding in the asteroid *Pisaster giganteus* for months, possibly by affecting the neurosensory apparatus (Harrold and Pearse, 1980).

The well-known withdrawal reflex of tentacles of dendrochirotid holothuroids indicates the probability of sublethal predation. The tentacles of the dendrochirotid holothuroids *Athyonidium chilensis* at Playae el Frances, Chile (Vásquez, unpub. obs.) and *Eupentacta fraudatrix* in Peter the Great Bay, Russia (V. Levin, unpub. obs.) are preyed upon. We know of no study on the effect of tentacle loss on feeding in holothuroids.

Ophiuroid behavior is affected by arm loss in ways that should reduce feeding. Sediment-probing and arm-waving activity by the arms is reduced in *Microphiopholis gracillima* with lost arms and/or disc (Clements, 1985). The burrowing *Acrocnida brachiata* (Bourgoin, 1987) and *Ophiopsila riisei* (Grober, 1988 *a*) tend to keep their regenerating arms below the surface and not use them for feeding.

Effect on survivorship

The effect of sublethal predation on survivorship is rarely considered. The effects of attacks by the predatory shrimp

Hymenocera picta on the asteroid *Acanthaster planci* range from minor wounds to massive wounds with arms missing (Glynn, 1982, 1984). Subsequently, the scavenging polychaete *Pherecardia striata* enters the wound and causes death of the asteroid by feeding on the internal organs. Glynn concluded the combined effect of the shrimp and polychaete can be a control of populations of *A. planci*. *Pycnopodia helianthoides* apparently damaged by partial digestion by *Solaster dawsoni* was observed scavenged by a "host" of the amphipod *Parapleustes pugettensis* (Engstrom, 1974).

Whether sublethal predation leads to infection and subsequent death has never been evaluated, although Birkeland and Lucas (1990) suggested *A. planci* may be prone to infection after damage due to its relatively large regions of soft tissues and body cavities. The relation between amount of arm loss and survivorship of stellate echinoderms in the field has not been documented.

Effect on production

The resources allocated to regeneration and other activities add another dimension to the classical growth-reproduction trade-off.

Regenerating tissue can be a large proportion of the body of ophiuroids. It averaged 25 % in *Amphiura filiformis* in Galway Bay (Bowmer and Keegan, 1983) and 22 % in the Skagerrak off Sweden (Sköld *et al.*, 1994), 59 % in *Amphiura chiajei* from Kily Harbor (Munday, 1993), and 11 % in intertidal and 6.4 % in subtidal populations of *Acrocnida brachiata* in Douarnenez Bay, Brittany (Bourgoin and Guillou, 1994). This would require considerable allocation of production to regeneration.

Duineveld and Van Noort (1986) calculated the loss of arms by *Amphiura filiformis* in the southern North Sea to be ca. 0.84 g wet weight.m⁻².a⁻¹. The proportion of total production allocated to regeneration by *A. filiformis* was estimated to be 16 % in Galway Bay (O'Connor *et al.*, 1986) and 13 % in Skagerrak (Sköld, 1994).

Singletary (1970) calculated regeneration of body parts amounts to 14-19 % of total organic production of *Amphiura coniertodes*, *Ophionephys limicola*, and *Microphiopholis gracillima*. These resources would not be available for growth or reproduction, and Singletary (1980) found a suggestive negative correlation between the amount of arm loss and gonadal development for *O. limicola*.

The asteroid *Luidia clathrata* on a maintenance diet allocates few resources to regeneration (Lawrence *et al.*, 1986) while the ophiuroid *Microphiopholis gracillima* regenerates both the disc and arms even when starved (Fielman *et al.*, 1991). Salzwedel (1974) reported at least some of the material for arm regeneration is derived from the disc in *Amphiura filiformis*.

Regeneration in the field can be quite variable. Regeneration of the visceral mass by the crinoid *Himerometra robustipinna* was completed in some individuals by nine days while it was still incomplete in others after 23 days (Meyer, 1988). The basis for this difference in these individuals that depend on reserves or dissolved organic material is difficult to understand.

Remarkable control of allocation is indicated as allocation of stored resources were allocated to the disc and/or arm regeneration until a gut and three complete arms were regenerated by *Microphiopholis gracillima* (Fielman *et al.*, 1991). This is a remarkable parallel of the initial ontogenetic production of three long and two short arms in *Ophiophragmus filigraneus* (Turner, 1974) and *Amphiura filiformis* (Muus, 1981). Salzwedel (1974) did not find this differential allocation to only a few arms in *A. filiformis*. He did report that the regenerating arms are initially thin, which he interpreted as a means to produce a functional, feeding arm with the investment of as few resources and in as short a period of time as possible.

Rates of development in pentactula larvae of *Eupentacta fraudatrix* decrease in individuals regenerating tentacles. This could be a trade-off in allocation of resources even if feeding is decreased.

Whether regeneration results in an increase in total production and in energy requirements is an intriguing question. Mead (1901) concluded the loss of two arms by *Asterias forbesi* did not decrease the rate of growth. A direct correlation between total production in arm regeneration with the amount of arm loss in crinoids and ophiuroids (Salzwedel, 1974; Singletary, 1980; Mladenov, 1980, 1983; Bourgoin, 1987; Fielman *et al.*, 1991; Clements *et al.*, 1994; Stancyk *et al.*, 1994) indicates a controlled increase. Production by *Luidia clathrata* fed below maintenance requirements was by the gonads and pyloric caeca (Lawrence *et al.*, 1986), while production by individuals fed above maintenance requirements was by both the viscera and the bodywall (Lawrence and Ellwood, 1991). Production was greater in individuals with arm loss than in those with intact arms (Lawrence and Ellwood, 1991). The greatly reduced amount of biomass, lipid, and energy in the pyloric caeca of the asteroid *Stichaster striatus* with regenerating arms suggests a reduced capacity for feeding that could affect capacity for reproduction (Lawrence and Larrain, 1994).

If an increase in production follows sublethal predation, it must be associated with an increase in resource acquisition or use of existing biomass and an increase in the rate of respiration would be expected. Initial increases in oxygen consumption and production in the visceral mass was found after eviscerating the crinoid *Cenometra bella* (Smith *et al.*, 1981) and initial increases in oxygen consumption and nitrogen excretion were found after amputating arms from the ophiuroid *Ophiocoma echinata* (Sullivan, 1988). Similarly, the respiration rate per unit weight of *Ophiocoma echinata* regenerating arms was much greater than that of non-regenerating individuals (C. Pomory, unpubl. obs.). In contrast, no major change in the rate of oxygen consumption was found after amputating arms from the ophiuroid *microphiopholis gracillima* (Golde, 1991), and the rates of oxygen consumption and nitrogen excretion were the same for the asteroid *Luidia clathrata* with regenerating or all intact arms (Adams, 1991). It is probable that the metabolism of regenerating individuals depends on many variables, such as the physiological state of the individuals and resource availability. Production/biomass and respiration/biomass ratios change with size, nutritional state, and reproductive state.

Correlation between effects of sublethal predation and life-history strategies

A basic tenet of life-history theory is that a suite of adaptive characteristics have evolved to environmental conditions. According to Grime's (1979) triangular model, species are adapted to combinations of stress (conditions that decrease production) and disturbance (conditions that decrease biomass). Species that are adapted to high levels of disturbance such as sublethal predation must have low levels of stress. Lawrence (1991) noted this in comparing the asteroids *Pisaster ochraceus*, *Asterias forbesi*, and *Asterias rubens*. The former species may be a stress-adapted species as it is food limited and almost never shows regeneration, while the latter two species may be disturbance-adapted species as they seem less food limited and frequently show regeneration (see Lawrence, 1992).

This concept is implicit in the suggestions that species with different degrees of sublethal predation differ in their rates of regeneration. Swan (1966) noted ophiuroids vary in the incidence of arm regeneration and that it is not known whether this is related to their ability to regenerate or to the frequency of encountering events causing arm loss. Litvinova and Zharkov (1977) found *Amphipholis kochii*, which has a high incidence of sublethal predation, has a higher capacity for regeneration than *Ophiura sarsi*, which does not. Lares and Lawrence (1994) similarly found a lower capacity for regeneration in the asteroid *Echinaster paucispina*, which rarely shows arm loss, than *Luidia clathrata*, which frequently shows arm loss.

As sublethal predation has an effect on the biology of echinoderms by affecting feeding and allocation of nutrients to growth and reproduction, does it have an effect on their ecology and evolution? Sublethal predation is common in several marine invertebrate taxa and has been considered an evolutionary factor (Vermeij, 1982, 1987). Crawley (1983) pointed out that traditional animal population dynamics usually assumes change in numbers alone is an adequate description of population behavior, while changes in size and functioning must be included with the study of plants. Most models of population dynamics of animals assume lethal predation (Wilbur, 1988; Kooijman, 1993). Harris (1989) proposed sublethal predation is an important factor in the regulation of population size providing the criteria of density-dependency and depression of long-term survival and reproduction are met. Viviani (1987) suggested sublethal predation on asteroids on the northern Chilean coast had a great effect on their populations.

Sublethal predation has been little considered in marine communities that have focused on lethal predation. Asteroids are often major factors determining community structure (Paine 1971, 1974; Menge, 1982; Paine *et al.*, 1985; Menge and Farrell, 1989). Menge and Sutherland (1987) proposed a model for community structure that depends directly on abiotic disturbance, competition and lethal predation; and indirectly on recruitment and environmental stress. The model does not consider an effect of sublethal predation on recruitment or the ability to withstand environmental stress. Sublethal predation can affect a

species' behavior, morphology and physiology and thus have an indirect effect on prey (Strauss, 1991). The biological importance of sublethal predation thus extends upwards from the organism to the population and community and warrants attention.

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