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IMPORTANCE OF SUBLETHAL PREDATION IN NON-MIGRATORY MEGAFaUNAL AND MACROFaUNAL ASSEMBLAGES IN SOFT SEDIMENTS

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Abstract Sublethal predation on non-migratory megafaunal and macrofaunal assemblages at the organismic level has been described in a wide range of autecological studies for six higher taxa over the past 90 years. However, these important data have been virtually absent from synecological discussions of infaunal communities or analyses. This is especially important when considering secondary production, where sublethal predation likely plays a highly significant role.

In this study, I examine 77 species for which investigators have described sublethal predation on non-migratory megafaunal (larger longer-lived but less common) and macrofaunal (small shorter-lived and far more abundant) infaunal invertebrates living in or on soft sediments. The review focuses on the importance of sublethal predation in infaunal assemblages, its effects on the target species and its contributions to higher trophic levels. Most research has been conducted on non-migratory megafauna but a considerable body of data for macrofauna is available. The review presents examples based on (1) observed or documented sublethal predation or regeneration of structures in prey species; (2) analysis based on gut contents of predators; and (3) the wide variety of effects observed in these studies. I also provide (4) examples that provide insight into the substantial importance of sublethal predation on non-migratory megafauna to secondary production. The volume of research conducted varies widely among these topics. The discussion makes clear that, while largely overlooked in previous discussions of ecology and ecosystem dynamics for infaunal ecosystems, sublethal predation is an activity of major importance in the energy dynamics of these ecosystems, especially for non-migratory megafauna and the higher trophic levels that prey on them.

Keywords: Predation; Sublethal; Nonlethal; Behaviour; Regeneration; Infauna; Megafauna; Macrofauna; Secondary Production

Introduction

In most discussions of benthic ecosystem dynamics, predation generally has been considered a lethal interaction in which prey animals are killed, consumed and removed from prey standing stocks as the consumed energy is transferred to higher trophic levels (Lawrence & Vasquez 1996). Thus, trophic studies for infaunal assemblages, which generally have focused on macrofaunal assemblages, assumed that lethal predation (1) predominates in energy transfer from lower to higher trophic levels (Virnstein 1977) and (2) is the major component of secondary production on soft sediments (e.g., Zahoreczak et al. 2000). Nevertheless, a wide range of autecological and feeding studies document sublethal predation, an interaction analogous to herbivory on plants in terrestrial ecosystems. Most

of these studies focus on non-migratory megafauna [the much larger longer-lived but less common ‘trees’ *sensu* Lees (2021)] as opposed to macrofauna (the much smaller, shorter-lived and relatively far more abundant weeds). Harris (1989) pointed out that nonlethal injury, i.e., sublethal predation, also may play an important role in the regulatory biology of population size in many species.

Non-migratory megafaunal organisms as defined herein are large, relatively long-lived basically non-migratory infaunal organisms that live on or in the sediments, i.e., they live out their lives within several metres of where their recruits settle out of the plankton. They do not exhibit seasonal or other types of migration like many crab or shrimp species (e.g., Boddeke 1976) or sea stars. Bivalves like *Macoma balthica* are included even though juveniles often relocate several metres up or down a beach as they mature. Sand dollars are included even though they may move tens of metres onshore or offshore to accommodate for variations in seasonal swell activity (Merrill & Hobson 1970, Morin et al. 1988). Although they are motile, epibenthic snails and brittle stars are included because their range of movements is limited to tens of metres.

In terms of longevity, typically the life span considered herein for non-migratory megafauna averages over 18 years and ranges from 3 to 4 years to over 150 years (Orensanz et al. 2004); in contrast, the life span for macrofauna is typically less than 3 years. In this framework, macrofaunal species are considered opportunistic, i.e., they recruit to disturbed areas, whereas non-migratory megafauna are considered relatively stable perennials. Generally, macrofaunal organisms live within a few centimetres of the sediment/water interface, whereas most of the non-migratory megafauna bury up to metres into the sediment, often creating complex burrow systems (Dworschak 2001). Thus, macrofauna are easy to sample, whereas non-migratory megafaunal organisms are somewhat more difficult to census. In terms of biomass, standing stocks for macrofauna are generally in tens of grams wet weight m^{-2} , whereas standing stocks for non-migratory megafauna often exceed a $kg\ m^{-2}$ (Lees et al. 1980; unpublished results).

De Vlas (1981) noted that many infaunal animals must expose parts of their bodies to predators to feed, access oxygen, defecate, or relocate. Moreover, many burrowing predators intercept their prey beneath the sediment/water interface and nip off buried parts. These interactions can lead to appreciable sublethal energy transfer from prey species to higher trophic levels (Lindsay 2010).

The number of studies for non-migratory megafauna and macrofaunal polychaetes and the variety and importance of the organisms studied indicate that sublethal predation is a major pathway for energy transfer from these assemblages to higher trophic levels and is a normal and widespread occurrence in infaunal assemblages. Ansell (1995) used underwater television to document the cues that some clams and polychaetes provide to predators that graze on exposed parts of the prey and how some predators use those cues for grazing. Nevertheless, the interaction has been ignored in traditional models and in estimates of energy flow or secondary production (Pape-Lindstrom et al. 1997).

Three reviews on this topic have been published previously. Lawrence and Vasquez (1996) described sublethal predation for epifaunal and infaunal echinoderms. They noted ca. 85 taxa among the five classes comprising Echinodermata. Ophiuroids, with 32 taxa listed, were by far the most well-researched echinoderm. They discussed the effects of sublethal predation on growth, reproduction, acquisition and distribution of nutrient reserves, movement, survivorship, tissue production, regeneration of body parts and relationships between the effects of sublethal predation and life-history strategies. They noted that sublethal predation has been only occasionally considered in discussions of marine communities, which have focused on lethal predation. They concluded that sublethal predation exerts effects on behaviour, morphology and physiology of individuals of a prey species but also reaches far beyond those effects on an individual to both population and community levels.

Lindsay (2010) covered injury for a much wider range of epifaunal and infaunal invertebrate taxa and approached the topic from different perspectives. A listing of >130 species was provided in which sublethal predation has been reported. It included cnidarians, polychaetes, brachiopods,

bivalves, gastropods, crustaceans, crinoids, ophiuroids, echinoids and sea stars. Focusing on frequency and types of injury and regeneration, she provided a broad summary of studies describing types of injury, their frequency and the source of the injuries. She discussed how effects can modify ecological patterns and processes. She concluded that a large percentage of the injuries resulted from sublethal predation, but that frequency of injury appears to vary substantially seasonally, indicating that single samplings do not suffice, especially when related to estimating energy flow.

She stated [in the supplementary table], “If the minimum and maximum incidences of injury are averaged across all taxa, types of injury, and records (i.e., each reported estimate of the incidence of injury for a given species), the proportion of injured individuals in marine benthic invertebrate populations ranged from 33% to 47%”. She pointed out many ways this interaction is important in the ecology of many non-migratory megafaunal and macrofaunal polychaete taxa living in unconsolidated sediments throughout the world and to the epibenthic browsers such as demersal fish species or invertebrate predators associated with these assemblages. In an earlier paper, Lindsay and Woodin (1992) opined that sublethal predation changes both the condition of the individual and the cost or risk associated with further predation.

Most recently, Rennolds and Bely (2023) provided a comprehensive review of injury in animals in general. They covered terrestrial, aquatic and marine organisms, including molecular, cellular, behavioural and ecological effects of injury; they included some of the examples provided below in this review. One of their final conclusions was that greater taxonomic coverage of injury needs to be conducted to expand our ability to predict how injury influences animal biology, and how injury acts as a variable in ecosystems and influences evolution.

The concept of sublethal predation likely applies to a broad variety of other non-migratory megafaunal and macrofaunal organisms, at least sea pens, nemerteans, sipunculids, echiurids and enteropneusts. However, as Pape-Lindstrom et al. (1997) pointed out, the process of sublethal predation by epibenthic or infaunal browsers is rarely mentioned or woven into the fabric of infaunal community dynamics. For example, the text by Gray and Elliott (2009, p. 101) provided a single unreferenced mention of “sublethal browsers”, following epibenthic and infaunal predators.

The intent of the review is to consolidate a substantial amount of the literature available for injury experienced by infaunal organisms. The major objectives are to describe (1) the importance of sublethal predation to ecosystem dynamics for non-migratory megafauna and macrofauna living in unconsolidated sediments; (2) the wide variety of predators that depend on these unevenly studied infaunal sub-assemblages; (3) the wide variety of effects occurring in prey organisms and populations resulting from sublethal predation; and (4) the value of the resulting energy transfer to higher trophic levels. The discussion focuses on observed injury, regeneration, structures of infaunal organisms reported in gut contents of predators (mainly fishes) and effects of this injury on the prey species. In addition, I have included a short discussion of the contributions from sublethal predation to secondary production.

It is likely that sublethal predation is a major component of secondary production, perhaps even more important than lethal predation in some ecosystems. Its importance will be described in separate chapters by providing examples of sublethal predation based on (1) documented observed injury or regeneration/recovery for injured megafauna; (2) gut contents of predators; (3) effects of sublethal predation on the prey activities and associated sediments; and (4) secondary production of the prey. Most of these examples refer to a broad range of megafauna but some examples are cited for macrofaunal polychaetes and a gammarid amphipod. While the assessment provides a wide variety of examples, it should not be considered complete. Many other examples likely will be discovered.

Species in the appendices are listed alphabetically, by higher taxon (phylum or class) or family or a functional trait. Higher taxa are listed for organisational purposes. Subordinate taxa are listed separately as an aid to understanding taxonomic diversity within higher taxa. Reports in the text are listed chronologically within species to demonstrate evolution in thinking by investigators based on earlier studies. However, reports are listed alphabetically by species within subordinate taxa

(mainly family) and then chronologically in the appendices for ease of finding reports. Indicators of variation indicated in the text, tables and appendices for species are standard deviations but where summarising for major taxa, they represent standard errors.

Initial references for this review were part of a discussion in Lees (2021) of differences between what I refer to herein as non-migratory megafauna and macrofauna. That discussion included a broad range of ecological and behavioural papers on specific infaunal organisms that included reports of sublethal predation. I also included references from the Lawrence and Vasquez (1996) and Lindsay (2010) reviews. Further references were obtained by intensive searches on the internet using the terms “sublethal” and “nonlethal” combined with “predation” and “injury”, “regeneration”, “recovery” and by examining reference sections of papers that were found in those searches for relevant papers.

Sublethal predation based on observed injury or regeneration

This section covers reports of observed injuries or regenerating structures (recovery) from nipping or cropping of (1) feeding structures of cnidarians; (2) anterior or posterior ends of polychaetes; (3) clam siphons and feet; (4) claws or legs of crabs, (5) arms or discs of ophiuroids; or (6) cropping the ambiti of sand dollars. It also includes many lab studies initiated by investigators to study regeneration.

Regeneration is a process that is of paramount importance for infaunal organisms that experience sublethal predation. Reports on regeneration associated with sublethal predation appear to be limited to polychaetes, bivalves, gammarid amphipods and ophiuroids. In many cases, investigators reported on field observations of injury and later followed up with lab studies to observe regeneration.

In most cases, injured individuals retreat into the sediment or their tubes or burrows, where the wound heals and, over time, the cropped structure regenerates. Following a few to several weeks of recovery, they return to their normal mode of life to feed and be fed upon again. In many cases, individuals may be preyed upon numerous times during their lives. Data for observed losses or regeneration from sublethal predation on the various taxa are summarised in Table 1 and detailed in Supplementary Appendix 1.

Non-migratory Megafauna

Cnidaria: Pennatulacea

In a study of the effects of man-made structures on adjacent benthic assemblages, Davis et al. (1982) reported that fish species inhabiting a newly placed artificial reef grazed on the leaves bearing the feeding polyps of nearshore sea pens (*Stylatula elongata*), progressing from the tip down the rachis of a sea pen until eventually no feeding polyps remained. The sea pens within 30m of the reef survived for months but eventually disappeared, presumably succumbing to injury and starvation.

Polychaeta

In polychaetes, external scars are not visible after lost tissue has been regenerated. Therefore, researchers have estimated the incidence of injury by counting the number of individuals with visibly regenerating segments and appendages or counting and weighing segments. In many cases, these methods almost certainly underestimate the actual frequency of injury sustained by worms as a result of rapid recovery.

Arenicolidae: Arenicolid worms are deposit feeders that burrow head-down in sediments to feed; they extend their posteriors out of the sediment to defecate and spawn (Fauchald & Jumars 1979). De Vlas (1979a,b) reported sublethal predation for posterior segments of *Arenicola marina*

Table 1 Species of Non-migratory Megafauna or Macrofauna in Which Sublethal Predation or Regeneration of Injured Structures Was Observed and Numbers of Predators Reported

Higher Taxon	Subordinate Taxon	Number of Prey Species	Type of Structure Affected	Percent of Structures Lost or Population Affected	Number of Regenerating Structure Types	% of Population Regenerating	Time Required for Recovery	Number of Predators	Number of Reports
Non-migratory Megafauna									
Cnidaria	Pennatulacea								
	Virgulariidae	1	Feeding leaves	100% of population ultimately lost	0	0		Several fishes	1
Polychaeta		26						>23	34
		15						16	23
	Arenicolidae	1	Posterior segments	20% of total weight; 40%–50% of available tail segments/year	1	0	No regeneration but tail segments swell to compensate	3	9
	Maldanidae	6	Anterior & posterior segments	Anterior: 8.8 ± 8.2 Posterior: 35.0 ± 23.2	2	Anterior: 11.0 ± 14.1 Posterior: 38.4 ± 23.4	15–45 days	3	8
	Onuphidae	8	Antennae, heads, anterior & posterior segments	Antennae: 38.5 ± 18.0 Head & anterior segments: 17.5 ± 21.5 Posterior segments: 3.9 ± 3.5	4	36.5% ± 33.7%	50–70 days	9	6
Macrofauna		11						6	11
Polychaeta									
	Capitellidae	1	Posterior segments	100% within 3 days due to natural predation	1			1	1
	Spionidae	10	Palps & posterior segments	Palps: 23.3% ± 15.2 Anterior segments: 7% Posterior segments: 14.9	2			5	10

(Continued)

Table 1 (Continued) Species of Non-migratory Megafauna or Macrofauna in Which Sublethal Predation or Regeneration of Injured Structures Was Observed and Numbers of Predators Reported

Higher Taxon	Subordinate Taxon	Number of Prey Species	Type of Structure Affected	Percent of Structures Lost or Population Affected	Number of Regenerating Structure Types	% of Population Regenerating	Time Required for Recovery	Number of Predators	Number of Reports
Crustacea		1							
	Ampeliscidae	1	Feeding antennae & urosomal appendages	Antennae: 84 Urosomal appendages: 12	2		1 or more moults	>4	1
Bivalvia		19						29	28
	Pectinidae	1	Unid. Tissue					2	1
	Tellinoidea	10	Siphons & feet	Siphons: 37.9 ± 43.5 Feet: 15.0 ± 9.8	2	25.7 ± 29.6	Prob. within 10 days	13	16
	Mesodesmatidae	1							1
	Veneridae	5	Siphons & feet	Siphons: 10%–37% Feet: 14%–34%		21.5 ± 17.2		7	7
	Myidae	1	Siphons			0		1	2
	Hiatellidae	1	Siphons					3	1
Arthropoda: Crustacea/ Decapoda		2						2	2
	Ocypodidae	1	Feeding claws	38				1	1
	Portunidae	1	Chelipeds & legs	28.0 ± 15.6				1	1
Ophiuroida		22						9	21

(Continued)

Table 1 (Continued) Species of Non-migratory Megafauna or Macrofauna in Which Sublethal Predation or Regeneration of Injured Structures Was Observed and Numbers of Predators Reported

Higher Taxon	Subordinate Taxon	Number of Prey Species	Type of Structure Affected	Percent of Structures Lost or Population Affected	Number of Regenerating Structure Types	% of Population Regenerating	Time Required for Recovery	Number of Predators	Number of Reports
	<u>Burrowing</u>	8			4			5	16
	Amphiuridae	8	Arms, disks, & body weight	Arms: 72.0 ± 32.0 Disks: 16.2 ± 27.3 Body weight: 44.3 ± 17.2		Arms: 70.0 ± 21.0 Disk: 1.8% + 1.4 % of arm population: 54.0% ± 5.6 % Body weight: 38.0 ± 45.3	Est. during growth season, 100–120 days for tissue. 135 days for skeletal regeneration, 160 days for complete replacement	5	16
	<u>Epibenthic</u>	14			2			4	6
	Ophiocanthidae	1	Arms	<0.1					1
	Ophiocomidae	4	Arms	37.2±14.4	1		521 days for 1 arm; 1158 days for 3 arms	1	3
	Ophiidermatidae	3	Arms & disks	Arms: 47.7±21.0 Disks: 1.1±0.6	1			2	2
	Ophiolepididae	1	Arms	28	1				1
	Ophiomyxidae	1	Arms	49	1				1
	Ophionereidae	1	Arms	83.3±12.6	1	92.2; ca. 3.52 arms/individual		1	2
	Ophiothricidae	1	Arms	46	46				1
	Ophiuridae	2	Arms	20.0±9.9	1				1
Echinoidea		4						4	5
	Clypeasteridae	1	Ambitus	21				1	2
	Dendrasteridae	1	Ambitus	<5				4	3
	Mellitidae	2	Ambitus	76.5 ± 16.3				1	2

Note: Range of variation is standard deviation.

in tidal-flat populations in the Dutch Wadden Sea. He reported the worm contributed about 120 mg ash-free dry weight (AFDW) per lugworm annually or about 20% of total weight and 40%–50% of available tail segments to a variety of juvenile flatfishes. He estimated that the number of tail-nippings by juvenile plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) ranged from 2.2 to 3.8 per month per individual worm in the Balgzand tidal flat and that flatfish removed only one or a few tail segments per attack. From March to December, he estimated consumption of lugworm tail segments by plaice and flounder at two sites accounted for most of the estimated loss of tail segments in field populations. Biomass of cropped tail-tips almost equaled the standing stock of lugworms in the area. At one site, the loss rate of *Arenicola* tail tips was about twice the flatfish consumption rate and de Vlas suggested that a large predatory polychaete, *Nereis* sp., was the likely predator. De Vlas (1979b) reported that posterior segments of the lugworm, *A. marina*, nipped by flatfish in the Dutch Wadden Sea, were not replaced with new segments, i.e., regeneration of nipped structures did not occur. Instead, lugworms restored the weight of their tails by lengthening the remaining tail segments and keeping their weight almost constant. Therefore, the number of tail segments declined from about 100 in adult worms to “some tens or even less” over a worm’s life. He found this kept tail size in balance with trunk size.

Bergman et al. (1988) conducted lab studies into the effects of tail amputation on *A. marina*. Across a wide range of nipping frequencies, loss of body weight or reduced reproduction due to amputation was compensated for by increased growth rather than regeneration until the frequency of amputation rose to once per week. Beyond that point, mortality rates increased, and reproductive effort decreased.

Maldanidae: Maldanids typically are tubicolous deposit-feeders that live head down in tubes they construct (Fauchald & Jumars 1979) and, as in arenicolids, they expose their posterior segments to defecate and spawn.

Sayles conducted two studies of external features in *Clymenella torquata* at Woods Hole, Massachusetts, USA. In the first, Sayles (1932) reported that 8.8%–78.6% of the populations surveyed exhibited loss of posterior segments but only 0.5%–5.5% had lost anterior segments. In the second, Sayles (1934) reported that 25.6% were regenerating posterior segments whereas only 1.4% were regenerating anterior segments. These patterns fit well with expected structure exposure related to the head-down feeding mode of maldanid polychaetes.

Based on lab studies at Woods Hole, MA, USA, Sayles (1932) reported that *C. torquata* regenerated from the loss of 5 anterior segments in about 15 days. In a subsequent study, he observed similar patterns after the removal of 1–6 anterior segments. About 85% of the injured worms survived 10 days or longer.

Mangum (1964) reported sublethal predation in five species of maldanid worms in Beaufort Harbor, North Carolina, USA. She reported minimal [*Branchioasychis americana* (0%–8%) and *Petaloproctus socialis* (12%)] to substantial [*Clymenella mucosa* (47%–50%), *C. torquata* (23%–56%), *C. zonalis* (48%–54%)] losses of posterior segments in the sampled populations. These differences suggest behavioural differences among the genera.

In a study of the regulation of species density of seagrass-associated macrobenthos in the Indian River estuary, Florida, USA, Young and Young (1978) observed that 46% of a population of *C. mucosa* was regenerating tails. They regenerated up to the normal 22 posterior segments. Reported predators were blue crabs (*Callinectes sapidus*) and pinfish (*Lagodon rhomboides*).

In a study of community structure on sedimentary reefs constructed by *P. socialis* near Cape Lookout, North Carolina, USA, Wilson (1979) reported that 11.8% of the worms were regenerating heads and 5.2% were regenerating tails. Considering that maldanids typically reside head-down in their tubes and significantly more worms had lost their heads, he concluded that infaunal predators, possibly a predatory worm (*Glycera* sp.), were more important than epibenthic predators or shorebirds.

Clavier (1984) reported populations of *Euclymene oerstedii* were regenerating posterior (41%) or anterior (22%) ends of their bodies. Losses ranged from 3 to 18 segments. Based on caging

experiments, it appeared that, because of normal head-down behaviour of maldanid worms in their tubes, exposure of posterior segments was a greater risk. He postulated that posterior loss was due to epibenthic predation whereas anterior loss likely was due to infaunal predators. He reported that 22% were regenerating anterior ends of their bodies and 41%, posterior ends, i.e., infaunal predators were more important in this population. Mean recovery times were 1.5 and 1 month, respectively.

These data suggest substantial differences among genera but relative similarity between losses of anterior and posterior structures in maldanids. Mean losses for *Clymenella* were $3.0\% \pm 3.5\%$ for anteriors and $45.7\% \pm 19.9\%$ for posteriors. For the five species of maldanids overall, the mean loss of posteriors was $38.4\% \pm 23.4\%$.

Onuphidae: Most onuphids live in self-constructed parchment tubes, sometimes extending more than a metre into the sediment (Emerson 1975, Fauchald & Jumars 1979). They have varied feeding strategies but generally feed with the head extending out the top of the tube and with antennae (palpi) waving in the water column and exposed to potential predators.

Sublethal predation has been reported for eight species by six investigators. Head and antenna nipping were commonly reported but tail nipping was uncommon. Emerson (1975) reported that 2%–4% of the population of *Diopatra ornata* at Big Fisherman's Cove, Santa Catalina Island, CA, USA, was undergoing anterior regeneration at any time during his 18 monthly surveys. He noted that some animals in marked tubes would not be seen for ≈ 60 days. He assumed they disappeared after losing their heads. He surmised the losses were due to predatory fishes, especially California sheepshead (*Pimelometopon pulchrum*) and senorita (*Oxyjulis californica*), which often picked up and masticated tube segments discarded by divers. Complete field-collected specimens showed no evidence of posterior regeneration although he noted in the lab that posterior regeneration can occur. He conducted lab and field experiments on *Diopatra ornata* to determine the time required to regenerate the anterior and posterior ends of the worm. In the lab, he found that worms with the head and several anterior segments clipped off completely regenerated the head and segments within 5 or 6 weeks, but feeding was not observed until the seventh week. He also found regeneration in specimens that lost posterior segments during collection but did not indicate the time required.

In their description of *Diopatra dexiospira* in the nearshore sand flats on the south side of Oahu, Hawaii, USA, Paxton and Bailey-Brock (1986) indicated the worms were subject to sublethal predation. They reported that a large number of worms were damaged and regenerating anterior and posterior segments.

When describing a new species, *Diopatra tuberculantennata*, in Belize, Budaeva and Fauchald (2008) noted that 18.5% of the specimens examined were regenerating anterior ends of the body. They described five stages of regeneration, indicating that loss had been recurrent in the sampled population.

In describing the ecology of mound-forming populations of *Diopatra leuckarti* in Oahu, Hawaii, USA, Bailey-Brock (2008) reported that 11.8% of the worms were regenerating heads and 7.2% were regenerating tails. She tentatively attributed these losses to sublethal grazing by crustaceans, fishes, or birds, but indicated they could result from bait digging by fishermen.

Nipped heads were observed in $12.8\% \pm 8.5\%$ of *Diopatra cuprea* populations in a summer month in Florida and Virginia (Berke et al. 2009). About 40%–60% of these populations (mean $38.1\% \pm 19.0\%$) experienced antenna nipping. Possible sublethal predators include several fishes [Atlantic croaker (*Micropogonias undulatus*), windowpane flounder (*Scophthalmus aquosus*) and spot (*Leiostomus xanthurus*)]. Estimated loss in nipped individuals averaged 30 mg dry weight (≈ 420 mg wet weight, based on a conversion factor from Ricciardi & Bourget (1998)). In lab experiments, 80% of specimens of *D. cuprea* for which 5–10 anterior segments had been experimentally ablated showed significant recovery of the head within 7 days; 80% recovered within 14 days at 28°C.

They also reported sublethal predation for the sympatric onuphid, *Americanuphis magna*, in Florida, USA. The species experienced more antennal loss (ca. 80%) than sympatric *D. cuprea*; 40% regenerated antennae within 14 days at 28°C. However, *A. magna* was incapable of regenerating heads and died.

In a study to assess regeneration from sublethal predation or bait digging on *Diopatra neopolitana* and *Diopatra marocensis* in Portugal, Pires et al. (2012) found tissue loss in field-collected specimens of both species. For *D. neopolitana*, they reported that 77 of 1246 specimens (6.2%) were regenerating the anterior end and 4.2% the posterior end. For *D. marocensis*, 13.6% were regenerating the anterior and 0.3% the posterior end. These species were regenerating, on average, 9.0 ± 2.5 and 7.5 ± 1.9 chaetigers, respectively. The proportion of the population regenerating was substantially higher in summer than in winter for both species.

In lab experiments of regeneration for *Diopatra neopolitana*, Pires et al. (2012) found that when posterior portions were amputated at the 15th chaetiger, which is in the brachial region, to emulate predation by fish, etc., those segments were able to regenerate the anterior of the worm, but the anterior part of the worm did not survive. With amputation at chaetiger 20 (middle of the brachial region), neither piece was able to regenerate and did not survive. For specimens amputated at or beyond chaetiger 25, the anterior portion regenerated the posterior segments, but the posterior part was unable to regenerate the anterior and succumbed. Full recovery required 60–70 days. This is relatively consistent with Emerson's (1975) findings on *Diopatra ornata*.

In summary for Polychaeta, sublethal predation has been reported for macrofaunal and non-migratory megafaunal species of mostly tubicolous or burrowing polychaetes (Table 1). Most data for non-migratory megafauna are available for maldanids and onuphids, both tubicolous. For *Diopatra* spp., on average, $11.8\% \pm 7.3\%$ (3%–23%) exhibited loss of heads, $2.9\% \pm 1.7\%$ (0%–7.2%) loss of tails, and time required to recover heads averaged 51.0 ± 12.5 (14–70 days). Reports of sublethal predation on macrofaunal polychaetes are limited to one capitellid and eight spionid species. Again, most are tubicolous.

Lost structures and regeneration varied considerably by family. Loss patterns depended upon which structure was most exposed to predators. *Arenicola* lost 40%–50% of tail segments and up to 20% of total weight annually. Tail segments were not regenerated. For maldanid populations, which live head-down in constructed tubes, loss of posterior segments was distinctly greater than anterior loss ($38.4\% \pm 23.4\%$ vs. $3.0\% \pm 3.5\%$); frequency of observed regeneration of lost structures was comparable. Time required for maldanids to regenerate lost structures ranged from 15 to 45 days. Onuphids exhibited $42.5\% \pm 21.5\%$ loss of antennae, $11.8\% \pm 7.3\%$ of populations lost heads and anterior segments, and only $3.9\% \pm 3.5\%$ lost tail segments. Regeneration was observed in $36.5\% \pm 33.7\%$ of the populations. Full regeneration of the head and return to feeding required 50–70 day. Time required for regeneration varied from no regeneration for *Arenicola* and *Americonuphis* to 50–70 days for onuphids. A wide variety of predators was reported but fish dominated.

Bivalvia

Sublethal predation and regeneration have been reported for a wide variety of bivalve taxa, especially Tellinoidea and Veneridae. Most reported lost structures are siphon or siphon tips and feet.

Pectinidae: Members of this family typically live at the sediment/water interface. Only their very short siphons and mantle are accessible to sublethal predators in the water column. Data are available for only one species, bay scallops (*Argopecten irradians concentricus*). Irlandi and Mehlich (1996) reported that scallops caged with browsing fishes in the fall resulted in lighter siphons, an injury, and less shell growth, an effect, but no differences in summer. When caged with seven browsers per cage, juvenile scallops grew about 25% faster than those with ≈ 16 fish per cage.

*Tellinoidea*¹: Tellinoid clams typically have long separate incurrent and excurrent siphons. Depending on size, they generally burrow as far below the sediment/water interface as their siphon

¹ This order designation includes families Donacidae, Psammobiidae, Semelidae, and Tellinidae, which are characterized by exposure of long thin siphons that extend above the surface of the sediments to facilitate feeding, respiration, reproduction, and defecation (Coan et al. 2000).

length and feeding mode allow. Feeding modes include suspension- and surficial deposit-feeding. Eleven investigators reported sublethal predation for nine species in this order.

During studies of growth rates of 0-year class plaice, Edwards et al. (1970) observed sublethal predation on siphons of the shallow-burrowing tellinoid clam, *Tellina tenuis*, stocked in outdoor tanks. Reporting further on that study, Trevallion (1971) observed the longer inhalant siphons of the clam were preyed upon by 0-year class plaice. Rate of predation varied by year partly due to changes in relative density of predator and prey and the abundance of other prey such as polychaetes. She measured a rate of regeneration of the inhalant siphon of ca. 0.3 mg dry tissue/week/individual. Frequency of siphon predation and regeneration varied widely by season, weather, abundance of alternate prey and abundance of the plaice.

Hodgson (1982a) reported from lab experiments that wound healing of siphon tips of the inhalant siphons of the bean clam, *Donax serra*, which lives on wave-swept beaches in South Africa is complete within 48 hours of amputation. After the wound is sealed to prevent blood loss, regeneration of the siphon tentacles commences. The siphon tentacles grow to their original size within 5 days. Alacrity is necessary because the clam is unable to respire or feed until it can reopen the inhalant siphon.

Based on studies at West Sands beach, St. Andrews, Scotland, Ansell et al. (1999) reported that between 2.5% and 18% of *Donax vittatus* showed damage to inhalant and/or exhalant siphons as a result of predation by 0- and 1-year class flatfish such as plaice. Those removed from sand by sublethal predation rapidly reburied. He further reported wound healing and regeneration of siphonal tentacles following experimental amputation of siphonal tips of *D. vittatus* on the beach at West Sands, St. Andrews, Scotland. Siphonal tips include tentacle crowns formed by siphonal tentacles. Newly formed tentacles appeared almost normal after 10 days. Siphonal tentacles included the full complement of ciliated sensory organs.

Luzzatto and Penchaszadeh (2001) conducted *in vivo* studies to examine the process of regeneration of the inhalant siphon of an Argentinian bean clam (*Donax hanleyanus*), which live in the surf zone on exposed beaches. They noted that the siphon is a complex organ with a tip bearing branched tentacles (Figure 1A). Following amputation of the tip, rudiments of the primary tentacles were observed within 24 hours. Subsequently, a very intensive process of regeneration of the primary, secondary and tertiary tentacles occurred over a period of 5 days. They observed the ramification process for 10 days after amputation, but the siphons were still less complex than those of control clams.

Complexity of siphon tips varies substantially, as is demonstrated by Figures 1A, 1B and C. It varies likely according to response to exposure to suspended particles and detrital material to which a species is exposed. Genera like *Donax* (Figure 1A) live in or near the swash zone, in which large quantities of sand are suspended by wave action. Genera like *Tresus* (Figure 1B) generally inhabit habitats with lower quantities of suspended sediment and detrital material but still require protection. Finally, genera like *Panopea* (Figure 1C) live in habitats where suspended particles are rare and therefore require no protection. However, all of these taxa likely experience sublethal predation.

Salas et al. (2001) studied sublethal foot predation in four donacid clams in Malaga, Spain and Ré Island in the French Atlantic. In Malaga, an average of 18.3% *Donax trunculus* individuals were nipped with up to 48% in September. On Ré Island, the average was 27%. Overall, nipping was observed in 10.6% of *D. venustus*, 8.4% of *D. vittatus* and 4.2% in *D. semistriatus*. Likely predators were carcinid and cancriid crabs, viz. *Portumnus latipes*, *Liocarcinus vernalis* and *Atelecyclus undecimdentatus*).

To study the rate of regeneration in the Venezuelan *Donax denticulatus* under laboratory conditions, Miloslavich et al. (2004) amputated their inhalant siphons and placed them into aquaria. They then sacrificed two individuals twice a day for microscopic examination of regeneration over a 9-day period. Initially, regeneration was slow, with only rudiments of the primary tentacle showing. However, between the second and third day, the secondary and tertiary tentacles became

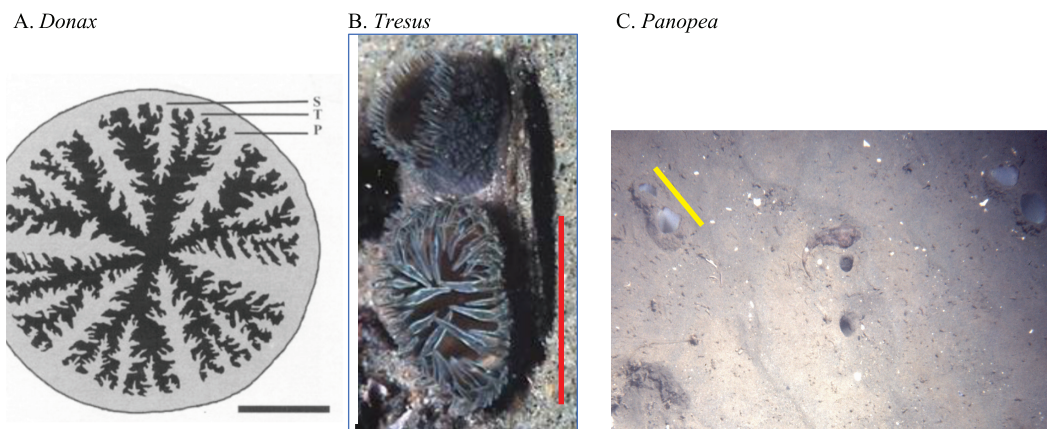


Figure 1 Variation in siphonal tentacles that exists in bivalve siphons, likely in response to differences in exposure to suspended sand particles. (A) Highly developed tentacles in a bean clam (*Donax hanleyanus*) in the surf zone; black scale bar=0.5 mm; P, S and T=primary, secondary and tertiary tentacles. (B) Moderate developed tentacles in a gaper clam (*Tresus nuttallii*) inhabiting mud flats or shallow subtidal areas; red scale bar=2.5 cm. (C) Absence of tentacles in the geoduck (*Panopea abrupta*) inhabiting deep water or mud flats; yellow scale bar=8 cm. Sources: A, Luzzatto and Penchaszadeh (2001); B, Lovell and Libby Langstroth © California Academy of Sciences; C, personal photo.

conspicuous. The siphons were fully regenerated on the fifth day after amputation, showing no difference a month later. They concluded that development of primary and secondary tentacles must be very important to basic functionality of the inhalant siphon.

When Pekkarinen (1984) amputated one-third of the inhalant and exhalant siphons of *Macoma balthica*, muscles at the cut end of the siphons were observed to contract to close the wound. Traces of tentacles were observed forming, usually within 48 hours. Tentacles were fully reformed by a week later. Siphons had regenerated to normal size and configuration under laboratory conditions within 3 months. When half the siphons were removed twice within 3 months, regeneration was slower; siphons were smaller than normal 6 months later.

De Vlas (1985) reported that regeneration of the siphons of *M. balthica* was rapid under simulated tidal flat conditions, hardly depended on temperature and season, and was faster in smaller (lighter) siphons.

In a study to determine the secondary production of *M. balthica* in the Wadden Sea, de Vlas (1985) found that only about 13% of the of siphon tips lost were consumed by flatfish. He estimated that individual clams lost unregenerated tips of siphons on average several times per day. He estimated the amount of *Macoma* siphon tissue lost during 1975 at four tidal-flat transects varied from 0.31 to 1.66 g AFDW $m^{-2} yr^{-1}$ (2.0–10.4 g shell-free wet weight), based on a conversion factor in Ricciardi and Bourget (1998). Other epibenthic predators like gobies, shrimps and shore crabs cropped the other 87%.

Peterson and Skilleter (1994) reported on siphon cropping in *M. balthica* by juvenile demersal fishes in the Neuse River estuary in North Carolina. Effects of croppers were more substantial in early to midsummer when juvenile fish were abundant. As part of the same study, Skilleter and Peterson (1994) reported that the presence of cropping fish resulted in $\approx 35\%$ loss of ash-free dry weight for *M. balthica* siphons at a density of 110 clams m^{-2} and $\approx 14\%$ at 370 clams m^{-2} .

Bonsdorff et al. (1995) observed siphon cropping of *M. balthica*, the dominant infaunal animal in the north Baltic Sea, by large predatory isopods (*Saduria entomon*) and brown shrimp (*Crangon crangon*). The regression between *Macoma* shell length and dry weight was significantly stronger

in control treatments than in *Saduria* and *Crangon* treatments, indicating greater tissue loss in the siphon cropping experiments.

De Goeij et al. (2001) conducted lab enclosure experiments with *M. balthica*. Some clams were exposed to siphon nipping by plaice and others were not. Those exposed to nipping were buried less deeply, which the investigators concluded made them more susceptible to lethal predation by predators such as shorebirds.

Although considerable effort has been invested in studies of sublethal predation in *M. balthica*, most examined recovery rates in lab studies. Few studies have quantified siphon loss rates in nature.

Tomiyama and Ito (2006) studied the rate of siphon regeneration in *Nuttallia olivacea* with shell lengths >30 mm in laboratory and field experiments in the Natori River estuary, Japan. Treatment clams had ca. 15% of their siphons amputated. In the lab, amputated clams were sampled periodically for a month. At a temperature of 15°C or 25°C, estimated siphon production was quite high within a few days of amputation but decreased greatly thereafter and was incomplete after a month. Considerable regeneration was observed in 3 months in field caging experiments but siphon weight was significantly less in the amputated clams than in the controls, indicating that regeneration was still incomplete.

Zwarts (1986) reported that Eurasian Curlews (*Numenius arquata*) graze siphons of *Scrobicularia plana* at a rate of 1–10 per minute and indicated that Eurasian Oystercatchers (*Haematopus ostralegus*) are another major predator.

Similar to his findings with the tellinid *D. serra* in South Africa, Hodgson (1982b) found that after siphon tips of the semelid, *Scrobicularia plana*, were amputated in the lab, they sealed up within 48 hours and epithelial tissue began to grow. Subsequent regeneration of the siphons, complete with siphon tentacles, was accomplished within 5 days. Regeneration rate is $\approx 6 \text{ mg week}^{-1}$, or about 20% of the siphon weight, until the original weight of the siphon is attained.

Mesodesmatidae: Noting bivalve siphons as a renewable resource, Nuñez et al. (2010) investigated the seasonal regeneration response of inhalant siphonal tips of *Mesodesma mactroides* on a beach in Punta Mogotes, Argentina. Siphons had been clipped in the laboratory at 1 and 5 cm from the distal ends. Generally, siphons recovered fastest in the spring. Length of primary siphonal tentacles on nipped siphons grew significantly faster in winter than in summer until after 12 days after nipping, after which they grew at the same rate. Length of primary siphonal tentacles on nipped siphons with 1-cm cuts consistently recovered faster for 2 weeks than those with 5-cm cuts but the rate of regeneration between 1-cm and 5-cm cuts was not significantly different.

Veneridae: Siphon length in venerid clams varies from relatively short to moderately long and the depth to which they burrow varies accordingly. Four investigators have reported observing sublethal predation on four species of venerid clams.

Based on field caging experiments, Irlandi and Mehlich (1996) examined the effects of tissue cropping and disturbance on the shallow-burrowing suspension feeding *Mercenaria mercenaria*. During fall experiments, hard clams caged with potential siphon nipping fishes had lighter siphon weight and less shell growth than clams caged without siphon-nipping fishes. During summer experiments, clams in cages exhibited no difference in siphon weight but added 3.0 mm of new shell, whether or not siphon-nipping pinfish (*Lagodon rhomboides*) and filefish (*Monacanthus hispidus*) were present. This indicates the absence of siphon nipping in summer.

Whitlatch et al. (1997) and Mouritsen and Poulin (2003) reported that 11%–37% and 14%–34% ($24.2\% \pm 8.9\%$) of *Austrovenus* populations suffered partial loss of feet, respectively. Whitlatch et al. (1997) found that the density of nipped *Austrovenus* ranged from 11.5 to 26.9 individuals m^{-2} (17%–31%), depending on the area surveyed (0.25–9.0 m^2) but that mean nipping rate ($24.1\% \pm 6.2\%$) did not vary significantly with major differences in density (0–1200 clam/1.0 m^2 treatment plot. Mouritsen and Poulin (2005) later reported that the frequency of cropped cockles declined significantly at lower elevations, from 52% to 4% because high levels of echinosome trematode parasitism

reduce the ability of the clam to bury. Predators included a variety of siphon-nipping fishes such as soles (*Rhombosolea leporina*, *Rhombosolea plebeia*) and a wrasse (*Notolabrus celidotus*).

Meyer and Byers (2005) observed siphons of the venerid clams, *Protothaca* (now *Leukoma*) *staminea* and *Venerupis philippinarum*, were cropped by two fish species (sculpins *Leptocottus armatus* and *Myoxocephalus polyacanthocephalus*) around San Juan Islands, WA, USA. They found siphons in 25% and 31% of the stomachs of the respective fishes. In a field experiment, they excised 40% of *P. staminea* and *V. philippinarum* siphons, retaining one group of each species in the lab as controls and placing another group in appropriate sediment in the field. After a month, both treatments were regenerating siphon tissue, exhibited orange coloration, but not the typical black tips seen in uncropped specimens. All had regenerated up to 65% of the lost siphon tissue in that period.

To investigate the effect of temperature on siphon regeneration, Nuñez et al. (2013) examined growth rates of tentacle crowns for ca. 1-cm long inhalant siphons of *Amiantis purpurata*, from which 0.5 cm had been snipped. Clams were exposed to seawater temperatures of 12°C, 15°C, 20°C and 22°C in the laboratory. Regeneration was most rapid at 22°C. Regeneration experiments for the tentacle crowns ran until long siphonal tentacles were between 0.6 mm and 0.7 mm long. The siphons were all still growing at an appreciable rate at the end of the respective experiments, which ranged from 18 days at 22°C to 36 days at 12°C. They stated, "Regeneration was slower than in any other species previously reported in the literature and decreasing temperature slowed down the process."

Tomiya (2016) conducted field experiments in Matsukawaura Lagoon, Japan, with caged siphon-clipped Manila clams (*Ruditapes philippinarum*), which have short siphons. Based on his observations on the clipped clams, he concluded that clams with short siphons regenerated their siphons at a slower rate than rates in literature for venerid clams with longer siphons. He suggested that regeneration may be less important for clams with short siphons.

Myidae: Softshell clams have long joined siphons and tend to bury as deeply as the siphon length permits in relatively consolidated sediments. The tubular chamber formed in the sediment by the siphon usually persists when the siphon is retracted.

Welch and Martin-Bergmann (1990) reported that, based on stomach contents, walrus (*Odobenus rosmarus*) feed on siphons of truncate soft-shell clams (*Mya truncata*) in the western Arctic. To assess the regeneration of lost siphons, they excised various lengths of the siphon from 27 clams and placed them in plastic cylinders which they backfilled with sand and mud. They placed other similarly arranged uninjured clams alternately in a tray and placed the tray in the ocean at a depth of 10 m for a year. After a year, all excised clams were dead and 31 of the 33 unexcised clams remained alive. They concluded that *M. truncata* is not capable of regenerating from loss of the siphon due to walrus predation. However, based on design issues with this experiment, their conclusion cannot be considered definitive for *M. truncata*.

Smith et al. (1999) conducted a field study of the foraging behaviour of red rock crabs (*Cancer productus*) on soft-shell clams (*Mya arenaria*), a commercially valuable species. During these studies, they observed a crab digging out, pinching off and eating a soft-shell clam siphon but presented no data on survival or regeneration. Consequently, no studies have confirmed that *Mya* spp. experience regeneration from predation, i.e., sublethal predation. This comprises a major data gap.

Hiatellidae: Geoducks (*Panopea abrupta*), one of the largest clams, have the largest siphon of all burying clams and bury deeply in sand or muddy sand on the west coast of the USA. The species is commercially important. Andersen (1971) reported that live geoducks are occasionally collected in Puget Sound, WA, USA, with pieces of their siphons missing but studies have not demonstrated regeneration. However, despite the absence of reports of regeneration, in view of the reported number of injured individuals, it seems safe to assume injured clams have survived and are recovering. Gut studies indicate several large natural predators that might cause partial siphon removal. Species include spiny dogfish (*Squalus acanthias*), Pacific halibut (*Hippoglossus stenolepis*), great sculpin

(*M. polyacanthocephalus*) and sea otters (*Enhydra lutris*). It is doubtful that the geoduck fishery would result in siphon removal.

In summary for Bivalvia, siphon or foot nipping and regeneration have been observed in many types of bivalve. Injuries have been observed in the families Pectinidae, Veneridae, Myidae, Hiatellidae and a broad range of the superfamily Tellinoidea, all of which expose a pair of long siphons above the sediment/water interface. Most studies have been conducted on siphon loss in tellinids and venerids but reports of foot loss are also common, especially in tellinoids, many of which are often awash in the swash zone.

Lost structures varied considerably by higher taxon. For Tellinoidea, predation is reported for siphon tips, siphons and feet for *Donax* spp. Siphons were lost in 37.9% ± 43.5% of the Tellinoidea and feet were lost in 15.0% ± 9.8%. Siphons were lost in 30.6% ± 46.4% (4.2%–48%) of the *Donax* populations sampled and 28.2% ± 14.0% had injured feet. Loss of siphon biomass in *Macoma* populations ranged from 4% to 25% after 10-day exposure in enclosures with predatory species. Lindsay (2010) commented on the repeated nature of siphon loss in tellinoid bivalves and suggested these clams contribute substantially to local food webs. Venerid populations lost 10% of siphons and feet were injured in 25.3% ± 18.5%. The wide variety of predators includes large isopods (*Saduria*), shrimp (*Crangon*), a variety of crabs, gobies and flatfish. Greatest observed loss occurred in summer when juvenile flatfish were occupying bays or tidal flats. However, it is likely that similar or greater losses occur in subtidal sedimentary ecosystems.

Regeneration was studied for 13 species in ten bivalve genera, including Tellinoidea, Mesodesmatidae, Veneridae and one myid. Regenerated structures included siphons and feet. Regeneration of siphonal tips (tentacle crowns), a critical structure in respiration, feeding and defecation, is a complex process. Percent of populations regenerating siphons or feet ranged from 25.6% ± 28.1% (Tellinoidea; $n=11$) to 21.5% ± 17.2% (Veneridae; $n=8$). Some research indicated that regeneration rates vary directly with water temperature, among and within the families, and between clam species with short and long siphons. Rates can range from 5 days to over 10 weeks. However, while *M. truncata* siphons were observed in walrus gut contents, it is unclear whether they can regenerate; experiments to investigate regeneration were inconclusive.

Arthropoda: Crustacea: Decapoda

Although capabilities for regeneration of lost appendages by crustaceans are well known, reports on sublethal predation in these animals are uncommon. Only two reports were found for two mega-faunal crustaceans.

In a study of autotomy in blue crab in Chesapeake Bay, Smith and Hines (1991) reported that 28.0% ± 15.6% (17%–39%) of the crabs in various populations were missing or regenerating one or more limbs. Most frequently, the crabs were missing a cheliped but seldom a swimming leg. Loss of more than a single limb was uncommon. They surmised that intraspecific aggression and cannibalism were major causes of limb loss.

Oliveira et al. (2000) found that ≈38% of the large feeding claw for adult fiddler crabs in Ria Formosa, southern Portugal, were missing or had regenerating claws. The predators were fishermen that take the large claws for consumption as a delicacy. Male fiddler crabs in an unexploited population at a remote site were not missing large claws.

Echinodermata

Sublethal predation in echinoderms has been reported for a wide variety of ophiuroids, but only a few echinoids (Table 1; Supplementary Appendix 1). Losses in ophiuroids were predominantly arms.

Ophiuroidea: I have separated ophiuroids into two categories, burrowing and epibenthic, on the basis of life-style to facilitate comparison. Family Amphiuroidae has been categorised as burrowing. The remaining ophiuroid families studied, all somewhat motile, are categorised as epibenthic.

Missing arms and disks in specimens observed in the field and structures in gut contents are the basis for enumeration.

Burrowing Ophiuroids: Amphiuridae: Several investigators have reported that 70-97% of individuals in populations of these species exhibited arm regeneration. Martin (1968) reported that 80% of the viviparous *Axiognathus squamata* collected in pooled intertidal areas in the vicinity of Auckland, New Zealand, were partially regenerating up to four arms, with an average of 1.6 regenerating arms per individual. The substrate comprised coarse shell fragments with loose stones and the calcareous red alga, *Corallina*. Only three specimens were found that had lost the complete aboral part of the disk, the stomach and gonads. The role of sublethal predation was mentioned but not quantified.

Several investigators have reported that up to 96% of individuals in populations of *Amphiura chiajei* and *A. filiformis* exhibited arm regeneration. Bowmer and Keegan (1983) reported consistent signs of recent recovery from arm damage in *Amphiura filiformis* in Galway Bay, Ireland; 96% of the population exhibited regenerating arms. Roughly 3% of the population was regenerating the disk cap or covering. Based on the frequency of scars on arms and biomass assay over 2 years, an average of $\approx 25\%$, and up to 50%, of total body weight may be regenerated tissue. Indications of arm breakage (scars) were more frequent in the proximal or mid-arm areas than in the distal ends of the arms. They reported that plaice and dabs were among the principal sublethal predators.

The proportion of total production allocated to regeneration was estimated to be 16% in Galway Bay (O'Connor et al. 1986) whereas respiration accounted for 77.4% and gonad output accounted for only 6.6% of energy flow. They reported that for a stable, high-density population of *A. filiformis* in Galway Bay, somatic growth is almost entirely restricted to regeneration.

Reporting on *A. filiformis* sampled on the Oyster Ground in the southern North Sea, Duineveld and Van Noort (1986) reported that 96% of individuals had lost arms; 55% had one or more recent losses, which equated to 20% of all arms. They reported that common dab (*Limanda limanda*) was an important predator for this brittle star.

Based on SCUBA studies in Killary Harbour, Ireland, Munday (1993) found that 99.1% of the dense (≈ 700 individuals m^{-2}) population of burrowing *A. chiajei* was regenerating arms but only 0.5% was regenerating disks. Over 21 months, the overall estimated mean length of regenerated arms was 33.5 ± 6.5 mm per individual. He estimated 4.2 arms per individual and 57.9% of total body weight were lost. Arm loss appeared to be seasonal and due to fishes, especially pleuronectid flatfish, but bottom trawling may have been a factor.

For *A. filiformis* in the Skagerrak, west Sweden, 13% (0.34 g AFDW m^{-2} yr^{-1}) was allocated to regeneration, primarily of arms, indicating that this ophiuran is an important food source (Skold et al. 1994). Mean regenerated biomass ranged from 12% to 30% of total biomass and the annual P/B ratio was 0.46 yr^{-1} .

Sköld and Rosenberg (1996) observed that burrowing deposit feeders such as *A. filiformis* and *A. chiajei* had significantly more scars per arm and greater tissue loss than more exposed epibenthic suspension feeders, carnivores, or deposit feeders. Based on their other finding that arm tissue for *Amphura* spp. had higher ash-free dry weight and nitrogen content, they proposed that demersal fishes were cropping selectively on more nutritious prey.

In laboratory studies, Nilsson and Sköld (1996) and Nilsson (2000) assessed the effects of differences in normoxia ($>80\%$ O_2) and hypoxia and low and moderate flow rates on regeneration rates for suspension-feeding ophiuran, *A. filiformis*, after amputation of one or three arms or the disk. Nilsson and Sköld observed reduced arm growth in hypoxic conditions (19% and 29% O_2 saturation). Nilsson (2000) found that arm regeneration rates were higher in normoxic than in hypoxic conditions (18% saturation) at both flow velocities and that mean arm regeneration rates were significantly higher at moderate flow rates. He further reported that in normoxia, arm regeneration rates did not exhibit a response to differences in flow velocity, indicating that *A. filiformis* is able to

adequately ventilate its burrow at low flow velocities. The number of arms amputated did not affect mean arm regeneration rates. A significant interaction in regeneration rates for both arms and disks was observed between oxygen concentration and disk amputation, indicating that the disk is the major organ for gas exchange in this species.

Noting substantial variation in regeneration rates of grazed arms for *A. filiformis* in Sweden, Dupont and Thorndyke (2006) assessed how the species allocates energy between increasing arm length (growth) and developing function for feeding in regenerating arms. They commented: “There is a trade-off between regeneration in length and functional recovery for feeding”, reporting that the amount of tissue lost determines whether priority will go to regeneration or differentiation of feeding structures.

Reporting on *Amphioplus coniertodes* in the Caribbean Sea, Singletary and Moore (1974) and Singletary (1980) reported observing regeneration of arms in 87% of the population and regeneration of disks in 3%.

In a study of the ophiuroid *Acrocnida brachiata* in the Bay of Douarnenez, France, Bourgoin and Guillou (1994) reported that nearly 70% of the total arm population (i.e., number of ophiuroids times five) exhibited arm regeneration in intertidal and subtidal sampling areas. Breakages occurred in the mid-arm area intertidally and on the distal third subtidally. Actively feeding arms appeared to be the least damaged, suggesting that nipped arms were held underground while healing. Biomass of regenerating tissue accounted for 11.1% and 6.4% of total biomass in intertidal and subtidal areas, respectively. Subtidal production of regenerating tissue was estimated to be 33 g dry weight (19 g AFDW) m⁻² yr⁻¹.

Between 52% and 94% of *Ophiophragmus filigraneus* burrowing in natural and planted seagrass beds in Florida exhibited arm regeneration, sometimes on two or more arms (Clements et al. 1994). Approximately one-third of the total individuals collected were regenerating only one arm with smaller numbers regenerating more arms. Rates of soft tissue regeneration did not differ between planted and natural beds. However, rate of skeletal regeneration was three times greater in planted than in natural beds, suggesting that burrowing was less successful in sediments that were disturbed by replanting activities. Rate of regeneration was greater overall for specimens that had lost more tissue but the rate per arm was greater in specimens that had lost one arm than in specimens that had lost three arms. Regeneration rates were lower than has been reported for other burrowing ophiuroids.

In natural populations of *Microphiopholis gracillima*, Singletary and Moore (1974) found that 77.0% of the individuals had lost arms. Subsequently, Stancyk et al. (1994) reported that arms removed in lab experiments did not exhibit regeneration during cooler months of the year. Only 15.1% of the individuals collected in 13 monthly surveys from subtidal mud flats in North Inlet, South Carolina, exhibited regeneration, mainly in spring and in summer. Disk loss was substantial in 1985 and 1986 (40%–70%) but substantially lower in 1990 (20%–40%). A smaller proportion of the population showed disk regeneration in the summer. They estimated skeletal regeneration would take 135 days in the field and nearly 200 days in the lab; complete replacement of arm tissue would take 160 days under May conditions. Between 70.9% and 91.8% of the 2405 arms observed in monthly collections over 13 months were regenerating at least one arm. Greater than 50% had one scar; some arms had up to 4 scars, indicating at least four attacks. Between 20% and 70% of the individuals examined were regenerating disks. Disk predation appeared more frequent in warmer months but no such pattern was observed for arms. The species appears capable of regenerating at least 50% of its total body weight during a single growing season. In a subsequent study, Pape-Lindstrom et al. (1997) estimated the species was losing ca. 4% of total arm tissue/day but regenerating up to 3%/day. They stated the population, “can probably regenerate arm tissue almost as rapidly as it is lost to sublethal predation”.

Ophiuroida: Epibenthic Ophiuroids

Sides (1987) reported that arm loss indicating sublethal predation varied significantly among eight species of epibenthic ophiuroids, i.e., *Ophiomyxa flaccida*, *Ophionereis reticulata*, *Ophiocoma echinata*, *Ophiocoma pumila*, *Ophiocoma wendtii*, *Ophioderma appressum*, *Ophioderma cinereum* and *Ophiolepis impressa* in back-reef populations in Jamaica. Rates, ranging from 74% for *O. reticulata* to 28% for *O. impressa*, varied significantly among species. Injury rates did not appear to be simply relatable to palatability or behaviour. He also compared regeneration rates for a single arm loss for these eight species. Regeneration rates ranged from 55% replacement of its mean maximum arm length over a 3-month period for *Ophiocoma wendtii* to 23% for *Ophiolepis impressa*. Highest levels of injury were observed for *Ophiocoma pumila* and *Ophionereis reticulata*; *O. impressa* suffered the least injury. Injury rates did not appear related to either palatability or behaviour.

In a study of *Ophiocoma echinata* in the Florida Keys, Pomory and Lawrence (2001) observed that 18% and 47% of two populations exhibited regeneration. They reported that regeneration was estimated to require $0.07 \text{ kJ m}^{-2} \text{ day}^{-1}$ on average. Based on this energy budget calculation, they estimated it took, on average, ca. 720 days for individuals to completely regenerate three arms (521 days at summer rates and 1158 days at winter rates).

Aronson (1991) compared sublethal arm damage in lagoonal populations of the epibenthic ophiuroids, *Ophioderma brevispinum* in Belize and back-reef populations of *Ophioderma appressum* over 3 years in Belize and Jamaica to museum specimens of fossils of two ophiodermatid species living during the Lower Jurassic period. Arm injuries were significantly more common in the two living populations of *O. appressum* in Belize and Jamaica (30%–74%) and *O. brevispinum* in Belize (46%–57%) than in the two fossil species (0%). The differences were not significant. Disk injuries were uncommon in populations of both ophiodermatids (0%–6%) but absent in the two fossil species. Since predation is the primary source of arm damage in living *Ophioderma* spp., Aronson hypothesised that the evolution of durophagous fishes and decapod crustaceans in the late Mesozoic is the cause of current arm damage in these species. He also examined arm and disk injury in *O. appressum* and *O. brevispinum*, in Jamaica and Belize in four surveys over 3 years. Based on the difference in regenerating arms between extant and fossil ophiodermatids, he concluded that “predation on ophiuroids increased when durophagous teleostean fishes and decapod crustaceans diversified in the late Mesozoic”, where ‘durophagous’ refers to animals capable of feeding on and crushing hard structures in prey such as clams, snails and brittle stars. He noted that injured disks were rare in all populations.

To investigate the effects of different feeding strategies, Sköld and Rosenberg (1996) observed the effects of arm nipping on six ophiuran species in the northern Kattegat-eastern Skagerrak and three species in the northern Adriatic Sea. These included burrowing deposit feeders (*Amphiura filiformis* and *A. chiajei*), which had significantly more scars per arm than epibenthic suspension feeders (*Ophiothrix fragilis* and *Ophiocomina nigra*), epibenthic carnivores and deposit feeders (*Ophiura ophiura* and *Ophiura albida*). Greatest tissue loss was in *Amphiura* spp. and the least in *Ophiura* spp. Based on their finding that arm tissue of burrowing suspension- and deposit-feeding *Amphiura* spp. had the highest arm loss, highest AFDW and nitrogen content in their arms, they proposed that demersal fishes were cropping selectively more nutritious prey.

Based on ROV surveys, Metaxas and Giffin (2004) described dense aggregations of *Ophiacantha abyssicola* at depths between 430m and 498 m in Northeast Channel on the continental shelf of Nova Scotia, Canada. Such dense beds of ophiuroids are rare in the bathyal and abyssal environments. They found only two individuals with evidence of arm regeneration out of 50 examined per dive in more than six dives. They concluded predation intensity is low in these deep exposed brittle star beds, suggesting that abyssal fishes have not adapted to feeding on brittle stars.

Yokoyama and Amaral (2010) compared the frequency of arm regeneration in intertidal epibenthic populations of *Ophionereis reticulata* between two beaches in Southeast Brazil. The beaches were mixed boulder and sand with different wave exposure. Arm regeneration, observed in 92.2%

IMPORTANCE OF SUBLETHAL PREDATION

of the 1170 individuals sampled, was slightly higher on the more exposed beach. The number of regenerating arms, ca. 3.5 arms per individual, was similar between sexes. They surmised the main cause of arm loss was sublethal predation but suggested hydrodynamic factors might contribute.

In summary, many reports are available describing sublethal predation for a wide variety of ophiuroids. Specimens that are regenerating arms or disks potentially provide indirect evidence that sublethal predation has occurred. However, physical disturbances can also cause arm or disk loss that does not represent sublethal predation, especially in epibenthic brittle stars that are more exposed to physical disturbance. The different causes of arm loss generally cannot be identified.

Arm loss in burrowing ophiuroids (Amphiuridae) is far more common than in epibenthic species. Loss of arms was observed in $83.7\% \pm 11.8\%$ of the populations of burrowing ophiuroids. Observed loss of disks in populations where reported was $16.1\% \pm 27.4\%$. Average body weight reported by three investigators in observed populations declined $37.5\% \pm 19.6\%$. Relative to the five-arm arm population, $51.3\% \pm 39.5\%$ of arms were regenerating. Regeneration of arms was observed in $70.0\% \pm 21.0\%$ of the populations but disk regeneration was minimal ($1.8\% \pm 1.4\%$), suggesting that loss of disk is often fatal. Estimated time required for full recovery was 160 days, depending on the number of arms regenerating. Burrowing ophiuroids generally keep arms that are regenerating in a cavity in the sediment. Predators for burrowing ophiuroids included penaeid shrimp, blue crabs, Norwegian lobster, dab, plaice, sand gobies and haddock.

Loss of arms observed in epibenthic ophiuroids was $39.0\% \pm 18.2$, excluding *Ophiocantha abyssicola*, which apparently lives below depths where ophiuroid grazers thrive. For that species, $<0.1\%$ of the observed population suffered arm loss. Regeneration for the 5-arm population averaged $40.4\% \pm 19.2$, quite comparable to arm loss. Time required for full recovery, reported only once, was estimated to be 523 days for one arm and 1158 days for three arms. The few reports of predators for epibenthic ophiuroids included “durophagous” fishes such as labrids and gobies and decapod crustaceans.

Arm loss in epibenthic ophiuroids was significantly lower than in burrowing species (Figure 2; $44\% \pm 21\%$ vs. $82\% \pm 13\%$; $p < 0.0001$, one-way resampling comparison of means). A likely reason is selective feeding by predators. Investigators have concluded that burrowing species, with higher AFDW and nitrogen content, are more nutritious and attractive to predators, even though arms are less accessible than for epibenthic species, especially the highly mobile types.

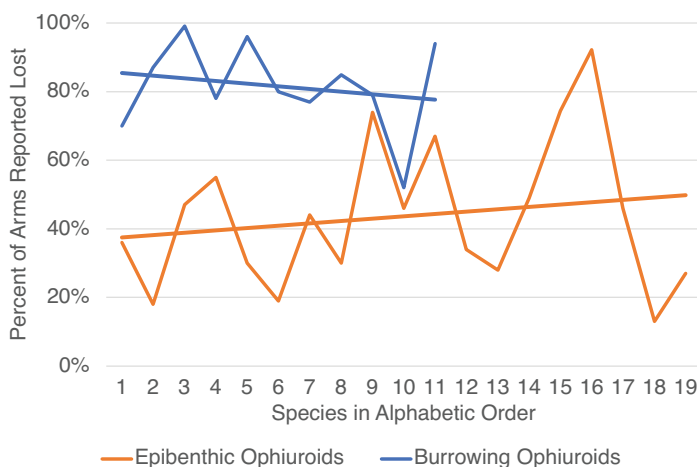


Figure 2 Comparison of percentage of brittle star arms lost by burrowing and epibenthic ophiuroids in sublethal predation reports.

Echinoidea

Because of their globular structure and open coelomic cavity, regular echinoids do not survive predatory attacks. Therefore, all reports of sublethal predation are for irregular discoid species of echinoids with a flat or thickened ambitus.

Birkeland and Chia (1971) reported <5% of the populations of the sand dollar, *Dendraster excentricus*, at Alki Point, Seattle, WA, USA, had a broken and healed ambitus, possibly due to crab grazing. I also observed grazing on the ambitus of this sand dollar in Mission Bay, San Diego, CA, USA, by white sea urchins (*Lytechinus pictus*; unpublished results, 1970).

Tennakoon et al. (2019) and Negron et al. (2020) reported on indications of sublethal predation on recent and fossil sand dollars by triggerfish. They observed cusped-shaped marks along the ambitus of the tests of notched sand dollars (*Encope michelini*), keyhole sand dollars (*Mellita tenuis*) and sea biscuit (*Clypeaster subdepressus*) in the northeastern Gulf of Mexico. These marks extended only as deep as the lunules. They were observed in 88% of *E. michelini*, 65% of *M. tenuis* and 21% of *C. subdepressus*. Injuries in the tropical species were observed in $58\% \pm 34\%$ of the populations.

In addition, they observed similar healed traces of nipping in fossil sand dollars from the Pliocene portion of the Tamiami Formation in specimens of *Encope tamiamiensis*, *Mellita acclinensis* and *Clypeaster sunnilandensis*. Durophagous fish and crustaceans evolved during this period. Negron et al. (2020) noted that traces were more frequent on flatter sand dollars (e.g., *Encope* spp.) than on the biscuit urchins (*Clypeaster*). These were attributed to gray triggerfish (*Ballistes capricus*). Injuries to *Dendraster*, observed in <5% of the populations, were attributed to large majid or cancrid crabs and a sea urchin (*Lytechinus pictus*).

Asterozoa

I considered including some sea stars in this review but concluded they are too mobile to truly be considered non-migratory megafauna. Sublethal predation is common among members of this taxon both among and within species. As described above, Lawrence and Vasquez (1996) provided a good review of this topic and several papers have been published since then.

Macrofauna

Although macrofaunal assemblages include many taxa besides polychaetes and amphipods, all are quite small and fragile. Specimens are often damaged by sampling and sieving. Moreover, they are quickly digested as gut contents following consumption. Consequently, little observational research has been conducted on sublethal predation for macrofaunal organisms in the lab or field except on polychaetes. Regeneration has been reported for four species of spionid polychaete and one species of gammarid amphipod by four investigators.

Polychaeta

Capitellidae: Bonsdorff and Pearson (1997) conducted laboratory experiments on *Capitella capitata* to examine its response to (1) sublethal predation of the worms' posterior by shrimp (*Crangon crangon*) and (2) mechanical disturbance of the sediments in which the worm tubes were constructed. Tubes at the sediment/water interface disappeared immediately when the sediment was disturbed mechanically but reappeared within 3 days in the shrimp browsing treatment (Supplementary Appendix 1). Recovery from sublethal predation took longer than from disturbance, likely because regeneration of the grazed posterior structures required more time and energy than reconstructing tubes.

Spionidae: Many spionids are tubicolous whereas others, like *Scolelepis*, are relatively free-living but with some constructing temporary tubes and remaining stationary for a period (Fauchald and Jumars 1979). They have varied feeding strategies but expose their palpi to potential predators

to feed by sweeping the sediment/water interface or waving them in the water column. Regeneration of feeding palps has been observed for 11 species by several investigators (Table 1).

Woodin (1982) reported that regenerating individuals were common in all populations of the tubicolous spionid worms that she had observed on the northwest coast of the U.S. and in the U.K. These included *Pygospio elegans*, *Rhyncospio glutaeus*, *Malacoceros fuliginosus*, *Spiophanes bombyx* and *Pseudopolydora kempi*. Lindsay and Woodin (1992) reported that, in field populations, twice as many *Rhyncospio* were found regenerating one palp as *Pseudopolydora* (17% vs 8%) but the percentage observed missing two palps was the same (10%).

Zajac (1995) found that the percentage of adult *Polydora cornuta* regenerating feeding palps or posterior segments in southeast Connecticut, USA, varied seasonally from May to November. On average, 14.9% were regenerating posterior segments and 7% were regenerating palps. Worms lost, on average, 19.1% of their posterior segments. Larger worms lost more segments. The incidence of regeneration increased directly with the density of adult worms in a population. Part of the loss was due to predatory activities by a phyllodocid polychaete (*Eteone heteropoda*). Demographic modeling suggested that up to 25% of the population could be subjected to sublethal predation before population growth would fall below population maintenance levels.

In areas in which populations of the errant spionid, *Scolecopsis squamata*, and the predatory phyllodocid, *Eteone longa*, overlap, the latter preyed on the former (Michaelis and Vennemann 2005). *Eteone* does not ingest whole prey individuals but only feeds on parts of the body that *S. squamata* can regenerate. Predatory behaviour follows a distinct pattern that leaves distinctive tracks in the sand.

From lab studies, Hentschel and Harper (2006) reported that *Polydora cornuta* can complete regeneration of feeding palps in 3 days, and the palps of recovered individuals were larger than their initial size. Worms for which both palps were excised grew significantly more slowly than those that lost one palp or none, but those that lost only one palp, or none, grew at the same rate. In another experiment, the investigators removed ca. 18% of body volume from the posterior of the worms. At the end of the 3-day flume experiment, these worms were six times larger than at the start of the experiment. They commented that since regeneration in this species is so rapid, rates of sublethal predation are likely underestimated.

Lindsay et al. (2007) studied regeneration following ablation of various lengths for anterior structures or the anterior end of the body of two spionids (*Dipolydora quadrilobata* and *Pygospio elegans*). In various laboratory treatments, they amputated palps only, anterior tissue through the first setiger, the fifth setiger, half of the gill-bearing setigers and through the last gill-bearing setiger. Treated specimens of both species regenerated lost tissues over time regardless of how much tissue was lost. Following amputation of the first setiger, palp growth did not commence for 3 days following amputation. First, the wounds healed. This was followed by the formation of the prostomium and the peristomium, i.e., the head, within about 6 days. Worms appeared to have grown 'normal' but smaller heads and palps within 9–12 days. *Pygospio* added segments at a similar rate regardless of whether 50% or 70% of the original segments were amputated. In contrast, the rate of segment addition in *Dipolydora* was directly related to the degree of tissue loss.

Whitford and Williams (2016) reported that 7% of specimens of the deep-burrowing tubicolous *Marenzelleria viridis* collected in Long Island Sound, New York, USA, were regenerating their anterior ends. Likely predators include fishes, birds and crabs (https://invasions.si.edu/nemesis/species_summary/-47). To examine regenerative capacity, they documented regeneration in worms for which from the 10th to the 50th chaetigers had been ablated. Anterior morphogenesis was similar to that observed in other spionids and was completed within 14 days. Up to ten segments were replaced normally but increasingly fewer segments were replaced than the number ablated when greater numbers of segments were removed. Survival and growth decreased when more chaetigers were removed.

In summary, observed examples of sublethal predation involving macrofaunal polychaetes have been conducted on a deposit-feeding capitellid and eight deposit- or suspension-feeding spionids. Lost structures varied considerably between the two families of macrofaunal polychaete and among the polychaete genera. Deposit-feeding capitellids live head down in tubes in the sediment and extend their posteriors out into the water column for respiration, reproduction, or defecation. In contrast, spionids live in tubes with the heads and tentacles extending out to feed but expose their posterior ends to defecate or reproduce. Consequently, capitellid lost only posterior segments. These segments were restored within 3 days. For the spionids, which expose both heads and posterior segments, $27.8\% \pm 36.5$ of the populations lost one or both palps, 7% lost anterior segments (single observation) and $31.2\% \pm 29.8$ lost posterior segments. Recovery occurred within 3–14 days. However, because macrofaunal polychaetes recover so rapidly, it is likely that rates of loss are underestimated (Hentschel & Harper 2005). Predators include phyllodocid polychaetes (e.g., *Eteone* spp.), crustaceans, fishes and birds.

Arthropoda: Crustacea; Amphipoda

Only one report was found for sublethal predation on macrofaunal crustaceans. Shearer (1998) conducted a comprehensive study of the effects of grazing predation on the tubicolous gammarid amphipod, *Ampelisca tenuicornis*, off the east coast of the Isle of Wight, England, U.K. When immature, this amphipod spends most of its time in a tube partially buried in the sediment. In this situation, its antennae are waving in the water column collecting food and are available to predators. In his study, 84% of the benthic populations of *A. tenuicornis* lost antennae. After maturity, individuals spend an appreciable amount of time in the water column, where their urosomal appendages are subject to predation; 12% lost urosomal appendages. Regeneration occurs over one or more moult cycles. Potential predators accounting for antennal loss during the benthic stage include small epibenthic predators such as peracarid crustaceans, polychaetes, post-larval fish and juvenile decapods. During the pelagic phase, small nektonic predators account for urosomal losses.

Summary for observed injury and regeneration

Earliest reports of sublethal predation based on observation were by Sayles (1932) for the maldanid polychaete, *Clymenella torquata* (Supplementary Appendix 1). Injured structures were those most frequently exposed and accessible to predators. Burrowing ophiuroids, which have arms extending from subterranean burrows onto the sediment/water interface or into the water column, exhibited the highest percentages of observed evidence of sublethal predation within populations (82%—13%); average for epibenthic ophiuroids, which live on the surface of the sediment, was $44\% \pm 21\%$. Sköld and Rosenberg (1996) reported that amphiuroid brittle stars have higher AFDW and nitrogen content in their arms than epibenthic species, possibly leading to selective predation.

Observed evidence of predation was considerably less among polychaetes, bivalves and crustaceans than in burrowing ophiuroids. Most observations have been made on non-migratory megafaunal and macrofaunal polychaete worms (32 species; Supplementary Appendix 1). Non-migratory megafaunal polychaetes, especially maldanids and onuphids, dominated the reports for worms but macrofaunal polychaetes were well represented. Ophiuroids (22 species) and bivalves (20 species) were also well represented.

Among the bivalves, sublethal predation was most frequently reported for Tellinoidea and venerids. A wide range of predators has been reported (Supplementary Appendix 1). These range from polychaetes through sea otters and humans. Fish, especially flatfish, dominated. Crabs and other crustaceans also were common predators. The greatest number of predators has been reported for bivalves and non-migratory megafaunal polychaetes.

Sublethal predation based on predator gut contents

This section discusses sublethal predation on non-migratory megafaunal polychaetes, bivalves, decapods and ophiuroids, and macrofaunal polychaetes based on prey structures observed in the gut contents of captured predators. The types of structures identified are the same as those identified in the previous section. Data for sublethal predation among the various taxa based on stomach contents are summarised in Table 2 and detailed in Supplementary Appendix 2.

Non-migratory Megafauna

Polychaeta

Arenicolidae: As indicated above, lugworms live buried heads down in sediment and extend their posterior segments out to defecate and spawn. De Vlas (1979a,b) and Beyst et al. (1999) reported that appreciable quantities of posterior segments of *Arenicola marina* were observed in gut contents of dabs, flounder, plaice and sole in the Dutch Wadden Sea and Belgium.

Magelonidae: In their study, Beyst et al. (1999) also observed that palps of *Magelona papillicornis*, a sessile burrower (Encyclopedia of Life) or motile surface deposit-feeder (Fauchald & Jumars 1979), were common (52.9% by count, 13.5% by weight) in the stomachs of juvenile plaice.

Bivalvia

In samples from the surf zone on sandy beaches on the Belgian coast, Beyst et al. (1999) reported finding bivalve siphons in 38% of stomachs of juvenile plaice (15.9% by count, 2.1% by weight) and 7.4% of sole.

Cardiidae: Members of this family typically live buried near the surface of sediments and mainly only their short siphons are apparent to nektonic predators. In a study of annual consumption

Table 2 Summary of Structures for Non-Migratory Megafaunal Species Observed in Gut Contents of Predators as Evidence of Sublethal Predation

Higher Taxon	Subordinate Taxa	Number of Prey Species	Number of Predator Species	Number of Structures Injured	Number of Reports
<i>Non-migratory Megafauna</i>		20	24	6	25
Polychaeta		2	5		8
	Arenicolidae	1	2	1	3
	Magelonidae	1	1	1	1
Bivalvia		15	19	2	23
	Cardiidae	1	2	2	1
	Pharidae	1	1	1	1
	Tellinoidea	7	8	1	13
	Veneridae	3	6	2	4
	Myidae	2	3	1	3
	Hiatellidae	1	4	1	3
Ophiuroida					
	Burrowing	3	6	2	4
	Amphiuridae	3	6	2	4
Macrofauna		5	7	3	6
Polychaeta					
	Capitellidae	2	3	1	2
	Spionidae	3	4	3	5

of benthic prey by plaice and flounder in a tidal flat in the Dutch Wadden Sea, de Vlas (1979a) reported that, in addition to tails of lugworms, these flatfish fed on siphons or foot tips of the cockle, *Cerastoderma edule*. He observed that about one-third of the total food intake of these fish consisted of siphon tips of bivalves and tentacles, tail ends and heads of polychaetes.

Pharidae: Pharid razor clams have long conjoined siphons, can burrow deeply into the sediment and move rapidly up and down semi-permanent burrows in relatively consolidated sediments. Depth of burrowing depends on the size of the clam. When feeding, their siphons are subject to nipping by predators, especially flatfish. Data on sublethal predation are available for only one species, California tagelus (*Tagelus californianus*). The predator is the diamond turbot (*Hypsopsetta guttulata*). In Anaheim Bay, California, USA, Lane (1975) estimated 3500 turbot in the middle arm of the bay consumed nearly 4.4 kg wet weight of clam siphons day⁻¹, or ≈1600 kg yr⁻¹. This comprised 10%–35% of the diet of the turbot. *Tagelus* siphons comprised 9.1% of total food weight for turbot weighing <25 g whole weight and 24.2% for those ≥25 g. Contribution of siphons from other clams was 7.35% for all turbot sizes.

Tellinoidea: In describing the ecology of 0-year class plaice and common dabs in Loch Ewe, Scotland, Edwards and Steele (1968) reported the food of these species overlapped but differed quantitatively. From 1964 to 1966, plaice focused on siphons of *Tellina* (probably *Tellina tenuis*) and dabs focused on polychaete feeding palps. However, in 1967, plaice began feeding mainly on polychaete palps. As the species grew larger, it began feeding on whole polychaetes, amphipods and cumaceans, i.e., lethal predation.

De Vlas (1979a) reported that plaice and flounder fed on siphons tips of *Macoma balthica* and the semelid *Scrobicularia plana*. Total annual consumption for plaice averaged 5.6 g shell-free wet tissue m⁻². About 36% of this comprised regenerable parts of megafaunal species. Annual consumption for flounder averaged 0.9 g wet tissue m⁻², 12% comprising regenerable parts, including tail tips of *Arenicola marina* and *Heteromastus filiformis*, heads and feeding palps of *Pygospio elegans* and other spionids, siphons and foot tips of *C. edule*, siphons of *Mya arenaria* and *S. plana*, and siphon tips of *M. balthica*.

Based on gut studies of fishes obtained in frequent seining surveys in Mugu Lagoon, CA, USA, Peterson and Quammen (1982) reported siphons of *Macoma nasuta* and *Macoma secta* were abundant in gut contents of several fish species, especially in muddy sand habitats. Important predatory fishes included a sculpin (*Leptocottus armatus*) and two flatfish (*Hypsopsetta guttulata* and *Paralichthys californicus*). Among these fishes, *Macoma* spp. siphons were observed in more *Hypsopsetta* stomachs (86%) but *Leptocottus* contained more pieces of *Macoma* spp. in their stomachs (55.9% of all pieces).

Poxton et al. (1983) reported that in early summer, young plaice and common dab in the Clyde Sea area fed on *Tellina* siphons, eating progressively larger siphons as the plaice grew. Growth rates of the plaice in the various areas surveyed appeared to be correlated to the benthic productivity of the specific areas.

In a study to determine the secondary production of *M. balthica* in the Wadden Sea, de Vlas (1985) found that only about 13% of siphon tips lost were consumed by flatfish. Other epibenthic predators included shrimp, shore crabs and gobies, which cropped the other 87%.

Based on studies on St. Andrew's Beach, Scotland, Ansell and Gibson (1990) reported finding parts of exhalant and inhalant siphons and feet of *Donax vittatus* in the guts of 0-year class flatfish such as plaice. This provided evidence of attacks while the clams were swash-riding (where the clams leave the sand to "ride" the swash to a higher or lower level on the beach, depending on the tide stage (Ellers 1995) or secondary attacks as they attempted to rebury after initial attacks on siphons removed them from the sand. They typically were able to quickly rebury.

In laboratory studies by Kamermans and Huitema (1994), after *M. balthica* had been exposed to shrimp (*Crangon*), siphon tissue of the clam was identified immunologically in shrimp stomachs, confirming the shrimp had preyed upon siphon tips.

Moreira (1995) reported that Black-headed Gulls (*Larus ridibundus*) fed largely on siphons of *S. plana* during winter in Tagus estuary in Portugal. Clam siphons represented >80% of the total ingested biomass. Average rate of siphon consumption ranged from 7.9 to 17.0 siphons per minute. Estimated length of ingested siphons ranged from 6.5 to 32 mm.

In a series of papers, Tomiyama et al. reported that juvenile stone flounder (*Platichthys bicoloratus*) was an important sublethal predator in several estuarine nurseries in Sendai Bay, Japan. Tomiyama et al. (2007) observed that the maximum width of siphon tips of the deep-burrowing psammobiid clam (*Nuttallia olivacea*) was smaller in 0-year class fish than in 1-year class fish. They concluded that the size of fish rather than clam size availability determined the intensity of predation on clam size classes. While the shell length of grazed clams ranged from 5 mm to 30 mm, highest predation intensity was in the range of 10–25 mm, even though that size class comprised only 25% of the population. Tomiyama et al. (2005) showed that juvenile stone flounder in several estuarine nurseries fed selectively on palps of the spionid polychaete, *P. kempfi* in March, but switched to siphon tips of *N. olivacea* in April through June. They concluded that sublethal predation on highly abundant infaunal prey is important in achieving the stone flounders' high growth rate. They indicated that sublethal tissue cropping of benthic invertebrates is thought to contribute to the high growth rates in the flounder in these nursery areas. Tomiyama et al. (2005) suggested that morphological development of the predator and prey vulnerability might induce the prey shift.

In another study of *N. olivacea*, Sasaki et al. (2008) described a detailed study of siphon loss to juvenile stone flounder in the Natori River estuary, Japan. They reported that clams at one station were cropped, on average, 25.8 times over four months (“22.1 mg [shell-free] wet weight) in a [≈120-day] season by fishes”). The cropped pieces are equal to approximately 1/3 of the total siphon tip weight. The interval between croppings, ranging from 2.36 to 60.1 days, averaged 17.3 ± 14.4 days and depended on location. Stone flounders accounted for 75% of cropping. The authors indicated that individual stone flounder juveniles preyed on more than 56 siphon tips per day from March to early June. This approximated the total siphon tip weight for 370 clams. They further indicated that, besides the juvenile flounder, three goby species that inhabit the estuary year-round likely accounted for 2.6 mg of the total loss of siphon tips.

Veneridae

Substantial research has been reported on venerid clams. Based on gut studies of fishes obtained in frequent seining surveys in Mugu Lagoon, CA, USA, siphons of *Protothaca staminea* were abundant in gut contents of several important predatory fish species (e.g., a sculpin (*Leptocottus armatus*) and two flatfish (*Hypsopsetta guttulata* and *Paralichthys californicus*), especially in sandy and muddy habitats (Peterson & Quammen 1982). *Hypsopsetta* were the most important grazers on *Protothaca* in terms of percent of stomachs containing *Protothaca* siphons (25.1% of stomachs) but *Leptocottus* stomachs contained more siphons than flatfish (27.8% of total items). They concluded that cropping per individual was 30%–92% lower in muddy habitats, possibly because predator attention changed to the more accessible siphons of *Macoma* spp. in that habitat.

Arrighetti et al. (2005) reported that the electric ray (*Discopyge tschudii*) fed heavily on the purple clam (*Amiantis purpurata*) on sand plains at 10–18 m depths off Argentina from June to November. Siphon tips, observed in 90% of the stomachs containing items, were the main food item. A total of 5921 siphon tips weighing 85.5 g wet weight was collected from 62 rays, i.e., 95.5 siphons per ray. Small rays ingested small siphons and large rays ingested larger siphons. While describing siphon regeneration for this species, Nuñez et al. (2013) reported these rays derive considerable nutrition from the siphons of this clam from specimens living in beaches in this region.

Meyer and Byers (2005) observed siphons of two venerid clams [*P. staminea* and *Venerupis* (now *Ruditapes philippinarum*)] were cropped by two sculpin species (*L. armatus* and *Myoxocephalus polyacanthocephalus*) around San Juan Islands, WA, USA. They found siphons in 25% and 31% of stomachs of the respective fishes.

Myidae: De Vlas (1979a) reported that plaice and flounder in the Dutch Wadden Sea fed on *Mya arenaria* siphons as well as siphons of other bivalve and several polychaete species. Parts of various prey, all assumed by de Vlas to be regenerating, made up about 36% of the stomach contents of these flatfish. However, regeneration was not confirmed.

In a study to determine if the truncate soft-shell clams (*Mya truncata*) can regenerate lost siphons, Welch and Martin-Bergmann (1990) cited several reports that walrus (*Odobenus rosmarus*) fed on these clams in the western Arctic, Baffin Bay and eastern Canadian Arctic. They noted that walrus stomachs in the eastern Arctic contain both *Mya* siphons and characteristic chitinous siphon sheaths but not shells or viscera, suggesting possible sublethal predation. To assess this possibility, siphons of live specimens, which constitute 45% of its soft body dry weight, were partially excised in the lab. The excised clams were placed in containers. These containers were then filled with mud from the area and returned to the seafloor. When examined 1 year later, none of the clams had regenerated or survived so it appears the observed partial predation was lethal. However, because of flaws in the design, this experiment cannot be considered definitive.

Stehlik and Meise (2012) reported on stomach contents of winter flounder (*Pseudopleuronectes americanus*) in New Jersey, USA. Siphons were absent from stomach contents of individuals smaller than 50 mm total length. In contrast, fish between 50 and 299 mm in total length contained *M. arenaria* siphons. Again however, since regeneration has not been confirmed, it is not clear that this predation is sublethal.

Hiatellidae: In his thesis on geoduck clams (*Panopea abrupta*), Andersen (1971) cited reports of sublethal predation on this large clam in Puget Sound, WA, USA, by large fish species. He reported that stomachs of spiny dogfish (*Squalus acanthias*) contained as many as seven geoduck siphons. One cabezon (*Scorpaenichthys marmoratus*) contained 14 siphon tips. Goodwin and Pease (1989) noted that fishermen have reported finding siphons in stomachs of Pacific halibut (*Hippoglossus stenolepis*). Geoduck siphons have also been observed in the stomach contents of sea otters (*Enhydra lutris*) in southeastern Alaska (B. Weitzman, USGS, unpublished results). As with *Mya*, no research has been conducted to demonstrate regeneration of nipped siphons. However, considering that: (1) geoducks experience high rates of siphon nipping; (2) are sufficiently abundant to be commercially harvestable; and (3) are reported to live >160 years (Orensanz et al. 2004), it seems reasonable to assume that loss of siphon tips is sublethal and siphons are regenerated. Meat (i.e., siphon) weights for geoducks comprise 42.5% of total weight. Thus, considering the high individual tissue weight of these clams, often in excess of 636 g wet tissue (Andersen 1971), it is clear they contribute considerable energy to higher trophic levels in areas where they are common and preyed on.

In summary, a variety of studies on sublethal predation involving gut contents of predators has been conducted on bivalves. Tellinoidea clams are most represented; fish species were the dominant predators. The most numerous structure was siphon tips, but siphons, especially from *Mya* and *Panopea*, likely comprise the highest biomass. Commenting on the repeated nature of siphon loss in tellinoid bivalves, Lindsay (2010) suggested these clams likely contribute substantially to local food webs. Quantities of structures are substantial, ranging up to 4.4 kg or $\approx 1600 \text{ kg yr}^{-1}$ wet weight of clam siphons/day in a small bay, and comprising from 10% up to 35% of the diet for some fish species. Siphon tips comprise >80% of the stomach contents of a gull in an estuary in Portugal. Studies suggesting sublethal predation have been conducted on Pectinidae, Cardiidae, Tellinoidea, Pharidae, Myidae and Hiatellidae.

Echinodermata

Ophiuroidea: Burrowing Ophiuroids: Amphiuridae: Just three species of burrowing ophiuroids, all amphiurids, were reported in gut contents. Bowmer and Keegan (1983) reported that arms of *Amphiura filiformis* occurred at high densities within Galway Bay, Ireland, and were found in the gut contents of young plaice and dabs. Later, Duineveld and Van Noort (1986) reported that *A. filiformis* formed an important component of the diet of dab at a site in the Oyster Ground, southern

North Sea. Only 4% of the individual ophiuroids sampled had fully intact arms and 55% of the individuals (20% of the arms) had one or more distal scars from injury. Annual consumption was estimated to be 0.84 g wet weight m⁻², or 6% of the arm population. They hypothesised this had little effect on population structure.

Munday (1993) reported observing arms of the abundant brittle star, *Amphiura chiajei*, in the stomach contents of fish species, especially pleuronectid flatfish, in Killary Harbour, western Ireland, especially in summer. He reported that such grazing is the likely cause of the high rate of arm regeneration observed (99.1%).

Trophic transfer resulting from sublethal predation on another amphiuroid, *Microphiopholis gracillima* by fish, crabs and penaeid shrimp ranged from ≈13 to 39 g wet weight m⁻² yr⁻¹ (Pape-Lindstrom et al. 1997). Gut contents of 16 potential predators were tested by immunochemical analyses. Most important were macerating (durophagous) predators, viz., shrimp [*Penaeus setiferus* (88%) and *P. aztecus* (39%)], and blue crab (70%).

Macrofauna

Polychaeta

Capitellidae: Capitellid tail tips have been reported in gut contents by two investigators. De Vlas (1979a) found tail tips of *Heteromastus filiformis* in gut contents of plaice and flounder in the Dutch Wadden Sea. In the laboratory, Bonsdorff and Pearson (1997) compared impacts of predation by *Crangon* to physical disturbance of sediments on density of *Capitella capitata* tails appearing at the surface of the sediment. They reported that physical disturbance of the sediment caused worm tails to disappear immediately whereas with predation by *Crangon*, they disappeared gradually within 3 days. Examination of the gut contents of the shrimp indicated they fed mainly on worm tails. The effect of physical disturbance was to destroy the tubes; recovery from that treatment, i.e., reappearance of tubes and tails, occurred within 48 hours. In contrast, predation removed the tails and required regeneration. Consequently, reappearance at the surface of tubes containing tails following shrimp grazing required 11 days.

Spionidae: Appearance of spionids in gut contents of fishes has been reported for at least three species. Edwards and Steele (1968) observed feeding palps for an unidentified spionid in gut contents from 0-year class plaice and common dabs in Loch Ewe, Scotland. Similarly, Poxton et al. (1983) found palps of unidentified spionids in the gut contents of 0-year class plaice and flounder in the Clyde Sea area in Scotland. De Vlas (1979a) reported finding heads and palps of *Pygospio elegans* in gut contents of flounder and plaice in the Dutch Wadden Sea.

In a feeding study of juvenile stone flounder in the Natori River estuary and Sendai Bay, northern Japan, Tomiyama et al. (2005, 2007) and Tomiyama (2012) reported that juveniles frequently fed on palps of *Pseudopolydora kempii* in March but, as they grew, they switched to the siphons of a clam (*Nuttallia olivacea*) in April through June. They postulated that sublethal tissue cropping may contribute to the high growth rates for the flounder in these estuarine nursery areas.

Summary for gut contents

Earliest reports of sublethal predation based on gut contents were by Edwards and Steele (1968) for siphons of the tellinid clam, *Tellina tenuis*, and unidentified spionid polychaetes consumed by 0-year class plaice and common dabs (Supplementary Appendix 2). The types of structures observed in gut contents were limited for each major taxon. These included palps and posterior segments for polychaetes, siphon tips, siphons and foot tips for bivalves and arms for brittle stars. Several studies indicate that sublethal predation provides large percentages of the diets of juvenile as well as adult species of predators. Juvenile flatfish especially depend on feeding on clam siphons and palps of macrofaunal polychaetes to support their growth and survival. Most observations have been made

on bivalves, followed by macrofaunal polychaetes (Table 2). It is notable that amphiuroid ophiuroids are common in gut contents of predators but no reports for epibenthic ophiuroids in gut contents were found. The variety of predators ranged from walrus, sea otters and birds to a variety of fish and shrimp. Fish (70%), especially flatfish, were the dominant predator.

Effects of sublethal predation on non-migratory megafauna and macrofauna

This section deals with the direct effects of injury on non-migratory megafauna and macrofauna. The effects are quite diverse, including changes in individual and population growth rates, physiology, behaviour, reproduction and survival. Effects tend to be negative, including reduced feeding, slower growth, reduced mating success and lower fecundity and mortality. Effects can also alter sediment conditions. Only one effect, escape response, is considered positive. Data for the effects of sublethal predation among the various taxa are summarised in Table 3 and detailed in Supplementary Appendix 3.

Non-migratory Megafauna

Polychaeta

Arenicolidae and *Maldanidae*: Several polychaete species need to expose their tail tips to defecate. Woodin (1984) amputated the tail tips of the arenicolid, *Abarenicola pacifica*, and the tube-building

Table 3 Summary for Frequency of Prey Species, Types of Structure Injured, and Types of Effects of Sublethal Predation on Non-Migratory Megafaunal and Macrofaunal Species

Higher Taxon	Subordinate Taxon	Number of Prey Species	Type of Structures Injured	Number of Types of Effects	Number of Reports
<i>Non-migratory Megafauna</i>		22		10	35
Polychaeta		5	4	10	6
	Arenicolidae	2	1	8	3
	Maldanidae	1	1	3	1
	Onuphidae	2	2	5	2
Bivalvia		10	2	11	16
	Tellinoidea	5	2	6	9
	Veneridae	5	2	5	5
Arthropoda					
	Crustacea/Decapoda				
	Ocypodidae	1	1	4	1
Ophiuroida		5	2	7	7
	Burrowing				
	Amphiuridae	4	2	7	6
	Epibenthic				
	Ophiocomidae	1	1	3	2
Macrofauna		6			7
Polychaeta					
	Spionidae	5	4	10	6
Arthropoda: Crustacea: Amphipoda					
	Gammaridae	1	2	Minimal	1

maldanid, *Axiothella rubrocincta*, in the Pacific Northwest to observe the effects on defecation, burrowing, or tube building. Defecation rates were significantly reduced for both species. This also indicates that the feeding rate was reduced. Neither frequency of defecation nor weight of fecal piles had recovered after 24 days for *Abarenicola*, but amputation did not affect burrowing. Percent of specimens defecating returned to control levels by Day 8 for *Axiothella*, but tube-building was not reduced. These experiments indicate that the loss of small amounts of tissue can result in changes in feeding and defecation rates, burrowing and tube building. She concluded these changes can result in important sediment effects.

Bergman et al. (1988) studied the impacts of sublethal predation on the growth and reproduction of the lugworm, *Arenicola marina*, in the Wadden Sea by amputating tail tips in the laboratory at various rates. Although they saw differences in growth between control and treatment experiments of one or two amputations per month, the differences were not significant and the worms continued to grow. When they amputated weekly, however, differences were significant; growth became negative, mortality rates were significantly higher and sulphide concentrations in sediments increased, likely because of reduced sediment mixing (bioturbation) due to reduced feeding and burrowing.

In a modelling study to examine the interactions among browsing predators, infaunal adult activity and recruitment of the lugworm, *Abarenicola pacifica*, Lindsay et al. (1996) predicted that mortality of juvenile worms would be highest at intermediate rates of nipping. Modelling results indicated that when adult densities of *Abarenicola* were low, browsing did not affect recruitment success. However, at higher adult densities, higher grazing rates resulted in increased recruitment success.

Onuphidae: Emerson (1975) observed several effects of regeneration resulting from loss of anterior or posterior tissue in *Diopatra ornata* in lab experiments on Santa Catalina Island, CA, USA. He examined the effect of regeneration on oogenesis of mature worms and found that specimens undergoing anterior regeneration contained all sizes of oocytes and appeared to be developing in a manner similar to non-regenerating specimens over the 4–6 weeks of regeneration. Specimens with mature oocytes regenerated posterior tissue more rapidly, apparently using nutrients from the oocytes for somatic growth. Spawning of reproductively mature individuals could be delayed by both anterior and posterior regeneration, possibly desynchronising spawning within a population.

Berke et al. (2009) found that when heads of *Americanuphis magna* in Fort Pierce, Florida, USA, were lost, the worms died. When posterior segments were ablated, they were incapable of reburrowing or regenerating segments and the worms succumbed.

Bivalvia

Pectinidae: Only the very short siphons and mantle of scallops are accessible to predators in the water column. Data are available for only bay scallops (*Argopecten irradians concentricus*). Irlandi and Mehlich (1996) reported that caging scallops with browsing fishes in the fall resulted in lighter siphons (injury) and less shell growth (effect); however, they observed no differences in summer. When caged with seven browsers per cage, juvenile scallops grew about 25% faster than those with ≈16 fish per cage. In the lab, their observations indicated that scallops in tanks in contact with browsing fish spent more time with their valves closed, presumably because of siphon or mantle nipping.

Tellinoidea: Based on a study of the share of cropped *Macoma balthica* siphon tips in the secondary production in the Wadden Sea, de Vlas (1985) reported that individuals lost several siphon tips per day. He stated: “The loss and subsequent regeneration of siphon tips must be an important [negative] factor in the ecology of *Macoma*, affecting feeding behaviour, burying depth and body weight.”

Brey (1991) reported that where siphons were smaller, the potential feeding area that could be grazed by *M. balthica* was reduced. Cropping of siphons by shrimp (*Crangon*) resulted in reduced growth rates in clam populations (Kamermans & Huitema 1994). During a 4-week lab experiment in which replicated buckets each contained 10 clams, whole ash-free dry weight of the clams was

reduced by ca. 85% in replicates containing 2 shrimp. Moreover, shorter siphons led to a change from deposit feeding to suspension feeding as deposit feeding was less 'profitable' with shorter siphons. Feeding areas were smaller. They found that clams with shorter siphons buried less deeply in the sediment, increasing the risk of predation, but that exposure to browsing caused clams with same size siphons to bury more deeply.

Bonsdorff et al. (1995) demonstrated that siphon cropping by large isopods (*Saduria*) and shrimp (*Crangon*) caused changes in length/weight relationships and general condition index in *M. balthica*, which was the dominant infaunal prey in the area in terms of abundance and biomass. Siphon nipping by *Crangon* caused significantly more clams to move nearer the sediment/water interface than *Saduria* or than was observed in control plots. Cropping by both species reduced the condition index of clams significantly below that observed in controls and changed the feeding mode from deposit feeding to suspension feeding, and because siphons became more visible to predators, it increased the risk of siphon predation.

Similarly, Peterson and Skilleter (1994) reported that cropping by juvenile demersal fish on siphons of *M. balthica*, a facultative forager, reduced the length of siphons needed for effective deposit feeding. This caused the clams to change to suspension feeding. This was most prevalent in early to midsummer when juvenile fish were most abundant.

De Goeij et al. (2001) conducted lab enclosure experiments with *M. balthica* in which some were exposed to siphon nipping by plaice and others were not. They reported siphon nipping caused significant reductions in length-weight relationships and condition index for 7–17-mm long clams in addition to greater susceptibility to lethal predation.

Sandberg-Kilpi et al. (2008) studied the effects of cropping by shrimp (*Crangon*) on morphometric, somatic and biochemical condition of *M. balthica* under normoxic and moderate hypoxic conditions. They reported a significant reduction in the condition of clams under both normoxic and hypoxic conditions when exposed to cropping by *Crangon* for 3 weeks. However, exposure to hypoxia did not increase siphon cropping.

Zwarts (1986) reported that the semelid *Scrobicularia plana* reduced its burying depth when part of its siphon was experimentally amputated. With the shorter incurrent siphon, the semelid needed to burrow shallower in order to feed. The degree to which cropped *S. plana* approached the surface appeared to depend on body condition. Thus, only specimens with underweight siphons that were also in poor condition move closer to the surface and put themselves at greater risk of further predation. He then concluded that burying depth "is the outcome of conflicting demands", i.e., need to avoid predation vs. need to enhance feeding success.

Salas et al. (2001) reported that foot nipping in two species of bean clam (*Donax trunculus* and *D. vittatus*) by three species of crabs resulted in a greater than 20% loss of dry tissue weight annually. The loss of biomass accounted for up to 37% of tissue in larger clams.

Tomiyama et al. (2010) found that siphon-cropping pressure by juvenile stone flounder on *Nuttallia olivacea*, the dominant bivalve in the Natori River estuary, exerted only a minor negative influence on somatic condition, accounting for only 1.2% of the variation. In contrast, environmental variables accounted for 30.2%. They concluded that "sublethal predation is only a potential factor affecting bivalve condition".

Veneridae: With regard to growth, Peterson and Quammen (1982) reported that littleneck clams (*Protothaca staminea*) in a clean-sand habitat protected from siphon cropping by fish in control plots for 2 years exhibited 2.2 times greater average linear growth and 2.5 times greater volumetric growth than those in unprotected plots. Similar growth was not observed concurrently in muddy sand habitat, likely because co-occurring *Macoma nasuta*, which extend their siphons for deposit-feeding, were more easily available for siphon nipping to predatory fishes. Cropping of *Protothaca* siphons in the mud habitat was 30%–92% lower than in the clean-sand habitat.

Meyer and Byers (2005) amputated the top 40% of siphons of *P. staminea* and *Venerupis philipinarum*. *Venerupis* naturally has shorter siphons than *Protothaca* and so buries significantly

less deeply. In the laboratory, clipped *Venerupis* burrowed 55% shallower than unclipped specimens whereas clipped *Protothaca* burrowed 42% shallower. In field experiments, mortality rate for *Venerupis* was 37% greater than in the laboratory but did not increase for *Protothaca*.

In a comparison of experimentally excised and unexcised specimens of shallow-burrowing *Mercenaria mercenaria* in sandy unvegetated areas and areas vegetated by a subtropical seagrass, Coen and Heck (1991) reported that shell length of unexcised clams grew significantly faster than excised clams in sandy habitats (17.3% vs. 12.0%, respectively). However, growth for excised clams, 6.9% faster in sand, was not significantly different between the two habitats. They also observed that shell growth was most rapid in unexcised individuals in sand, less rapid in unexcised individuals in a seagrass bed, and least in excised individuals in grass beds. They observed no change in burrowing depth following nipping. They hypothesised that regeneration costs and reduced feeding efficiency together may explain the significant differences observed between excised and unexcised treatments where they occurred.

Mouritsen and Poulin (2003) reported on widespread sublethal predation of the foot of intertidal populations of the New Zealand cockle (*Austrovenus stutchburyi*) in Otago Harbour, New Zealand. Although the injury was sublethal, it reduced the ability of the cockle to rebury and likely resulted in lethal predation or death from environmental exposure effects.

Cledón and Nuñez (2010) studied the effects of siphon nipping on subsequent sublethal predation by snipping off the top 6.6%–30% of the siphons of the clam, *Mesodesma mactroides*. This resulted in clams burrowing 25%–75% shallower than unsnipped control clams. Predation rates on artificially snipped clams were twice those of unsnipped clams.

Arthropoda: Crustacea: Decapoda

Juanes and Smith (1995) stated, “Given the prevalence of injury in decapod crustacean populations, the costs involved, and the ecological importance of many crustacean species, nonlethal injury has the potential to affect population dynamics and community processes. Convincing evidence of autotomy’s effects beyond the level of the individual, however, is, at present, lacking.” However, the study by Oliviera et al. (2000) below provides convincing evidence of the accuracy of their statement.

Ocyrodidae: Sublethal predation by humans on adult fiddler crabs (*Uca tangeri*) at Ria Formosa, southern Portugal, had major effects on population structure of the exploited population (Oliveira et al. 2000). They found that 37% of male fiddlers were missing or were regenerating large feeding claws whereas none were missing large claws in an unexploited population at a remote site. Lack of the large feeding claws precluded breeding displays and reduced feeding efficiency. The differences between the populations at the two sites were highly significant, with the unexploited site having 15% larger carapace size, 40% higher burrow density and 40% greater operational sex ratios. Nevertheless, the ratio of males to females was the same.

Echinodermata

Ophiuroidea: Burrowing Ophiuroids: Amphiuridae Bowmer and Keeegan (1983) suggested that *Amphiura filiformis* is a long-lived species that is regularly subjected to arm cropping by predators. The continual need to replace cropped tissues must be a major drain on energy that reduces growth and reproductive output. In Nilsson’s and Sköld’s (1996) study of the effects of hypoxia on *A. filiformis* in Gullmarsfjord, Sweden, they reported disturbance of spawning in addition to reduced arm regeneration rates. They also indicated that arm loss may result in an increase in sulphide concentrations in sediment under moderate and severe hypoxia.

In flume experiments, Rosenberg and Selander (2000) demonstrated that excision of arms of *A. filiformis* caused a nearly simultaneous alarm response in downstream *A. filiformis*. When dabs nipped an arm of an *A. filiformis* upstream in the flume, the downstream specimens with upstretched

arms bent them down close to the sediment/water interface or retracted them into burrows. When *Amphiura chiajei* was nipped, the response by downstream *A. filiformis* was similar but weaker. Homogenates of the two species introduced into the flume elicited similar response.

Fielman et al. (1991) studied *Microphiopholis gracillima* with different amounts of disks and arm tissue removed in North Inlet Estuary near Georgetown, South Carolina, USA. They found these brittle stars suffered frequent sublethal tissue loss in nature and have regeneration patterns that result from a complex interplay between time, quantity and quality of tissue lost, available nutrients, and risk of future damage or mortality. Depending on which and how much tissue was lost, the specimens allocated stored material to either the disk or arms until they could construct feeding and respiration burrows, i.e., either a gut or three whole arms were completed.

Based on a study of arm regeneration in a population of *Acrocnida brachiata* in a high-energy environment in Little Killary on the west coast of Ireland, Makra and Keegan (1999) concluded that, in addition to sublethal predation, physical stresses, probably due to wave action, caused considerable amount of arm loss. They found that injured arms were withdrawn inside the burrow and replaced at the sediment/water interface with less injured arms for feeding.

Ophiuroidea: Epibenthic Ophiuroids: Ophiocomidae In two studies of effects of sublethal predation for epibenthic *Ophiocoma echinata*, Pomory and Lawrence (1999) conducted laboratory studies to assess the effects of arm regeneration. They subjected one group with all arms intact and another with three arms amputated to two different food regimes for 2 months. One food regime was adequate for maintenance and the other was below the estimated maintenance level. In the adequate food regime, both treatments stored lipids, as normal, in the stomach, but the regenerating animal stored less. In the group with an inadequate ration, both treatments lost tissue. Later, Pomory and Lawrence (2001) reported that regeneration of three arms reduced storage material in the stomach of *O. echinata* of both males and females and significantly reduced gonad production by females.

Macrofauna

Polychaeta

Spionidae: In a study of predator browsing effects on activity, Woodin (1984) reported that removal of one or two feeding palps for tubicolous *Spiophanes bombyx* resulted in a reduction of defecation frequency for 7 days and 6%–35% reduction of weight of fecal pellets. Tube-building was also significantly reduced.

Zajac (1985) studied the effects of amputating two types of structures on reproduction for *Polydora ligni*. Loss of feeding palps led to mixed results in terms of changes in numbers of gametogenic segments, capsules, eggs per capsule and fecundity, with either no change or reductions. Loss of non-gametogenic posterior segments reduced fecundity significantly and increased brood development time by 100%. Nevertheless, females continued to reproduce in both cases. Cost of regeneration in terms of lost fecundity was estimated to range between 10% and 29% from palp loss and between 49% and 80% for posterior regeneration.

In a laboratory study to assess the differences in effects of palp removal on two spionid polychaetes with different feeding mechanisms, Lindsay and Woodin (1992) excised 0, 1, or 2 palps from worms. Both *Rhyncospio glutaeus* and *Pseudopolydora kempji japonica* feed at the sediment surface. During 2-hour periods of observation after palp removal, the frequency of segment exposure (2.28–7.72 exposures), maximum number of segments exposed (1.73–3.25), and frequency of palp exposure (14.27–19.17) increased significantly for *Pseudopolydora* with increasing palp loss. Also, the maximum number of segments exposed per emergence increased from 1.21 to 1.71. For *Rhyncospio*, mean number of segments exposed in 2 hours (3.70–5.32) and mean and maximum

number of segments per emergence increased significantly (3.12–4.84 and 3.72–6.52, respectively) with an increasing number of palps removed. They concluded that the loss of one or both palps significantly increased the amount and frequency of tissue exposure, but not the duration of exposure, and that the patterns were consistent with the differences in foraging behaviour.

Subsequently, Lindsay and Woodin (1995) reported on how ablation of 1 or 2 palps affects feeding mode of *R. glutaesus* and *P. kempji japonica*. Loss of both feeding palps caused both species to switch to alternative feeding modes involving mouth-feeding but did not change where the worms fed. Based on fecal output and time spent feeding, the feeding mode was effective for *Rhyncospio* but not for *Pseudopolydora*.

In further studies of effects of loss of feeding palps on disturbance of feeding areas, Lindsay and Woodin (1996) reported disturbed areas, and fecal production was reduced 30 to nearly 100% for up to a week in plots with greater numbers of regenerating *P. kempji*. Fecal production for *R. glutaesus* was reduced only when all worms were regenerating both palps. Neither species exhibited changes in rates of tube-building.

Demographic modelling suggested that sublethal predation can reduce the population growth rate of *Polydora cornuta*, but the reduction in growth rate is less than if the added predation pressure were solely lethal (Zajac 1995). It was estimated that up to 25% of the population could be subjected to sublethal predation before the potential for population growth fell below population maintenance levels.

Henschel and Harper (2006) reported that removal of feeding palps reduced growth rates significantly for *P. cornuta*. Damaged palps fully regenerated within 3 days. In contrast, removal of the posterior end of the worms (ca. 18% of body volume) did not reduce growth rates significantly. In fact, after 3 days, the damaged worms were six times larger than at the start of the experiment.

Arthropoda: Crustacea: Amphipoda

Ampeliscidae: Shearer (1998) reported that because regeneration is rapid in *Ampelisca tenuicornis* and it engages in compensatory feeding with the secondary antennae when the first antennae are lost, the effect of sublethal grazing on feeding and reproduction of this amphipod is minimal.

Summary for Effects of Sublethal Predation

The earliest report of effects of sublethal predation found in this review were for delayed and desynchronised spawning and more rapid regeneration of cropped structures in specimens with more mature oocytes for the onuphid polychaete, *Diopatra ornata* (Emerson 1975; Supplementary Appendix 3). Overall, 36 reports showed a wide variety of effects of sublethal predation for 25 species in four higher taxa (Table 3). Most observations have been made on bivalves and polychaetes. Non-migratory megafauna were represented by 23 species whereas macrofaunal polychaetes were represented by only five species. Fewer ophiuroids were studied. For brittle stars, Fielman et al. (1991) remarked about the “complex interplay between time, quantity and quality of tissue lost, available nutrients and risk of future damage or mortality” for many of these species following loss of arms. This statement applies equally to the interplay among many other effects of sublethal predation on prey species.

Overall, at least 25 types of effects have been reported. The most important effects were reduced depth of burial, which resulted in increased susceptibility to predation, and growth. The more common effects reported were for fecundity, defecation, growth and increased susceptibility to mortality. Other effects included changes in feeding mode, area, rates, regeneration rates, energy allocation and burrowing rates. Changes in defecation rates imply reduced feeding and that effect extends to altered conditions of surficial sediments and subsurface sediment chemistry. Changes in feeding behaviour were particularly important for tellinoid clams following siphon nipping.

Only one effect is positive, where nipping of an upstream individual causes an alarm response and potential escape behaviour in downstream neighbors or congeners. The remaining effects all have negative implications for the prey populations. Loss of palps or posterior segments resulted in reduced production of fecal pellets, so in cases where deposit feeders are common, sublethal predation resulted in changes to sediment quality (Rhoads & Young 1974). Loss of brittle star arms may result in increased sulphides in the sediment during moderate or severe hypoxic conditions.

Khater et al. (2016) discussed ways sublethal predation can play “crucial roles in shaping population and community dynamics”. The study of the effects of human harvesting of the feeding claw of the fiddler crab, *Uca tangeri*, demonstrated the complexity of effects of interactions that can result from sublethal predation, where removal of the male feeding claw changed operational sex ratios, male growth rates, burrow defense and colony density (Oliveira et al. 2000). This is a dramatic example of the tradeoffs in population dynamics.

Effects of sublethal predation on secondary production in sedimentary assemblages

Few investigators have provided details that facilitate estimation of mean annual rates for secondary production for non-migratory megafauna (Table 4). Data for macrofauna appear to be lacking.

Non-migratory Megafauna

Polychaeta

Arenicolidae: De Vlas (1979b) observed annual losses of about 120 mg ash-free dry weight (AFDW) per lugworm (*Arenicola marina*) or about 20% of its total weight but that loss was replaced by elongation of segments, resulting in maintenance of biomass. He estimated that number of tail-nippings per month per individual worm by juvenile plaice and flounder in two areas ranged from 2.2 to 3.8 in the Balgzand tidal flat in the Wadden Sea. From March to December, he estimated consumption of lugworm tail segments by plaice, flounder and *Nereis* sp., a predatory polychaete, at a third site almost equaled the standing stock of lugworms in the area, i.e., was likely >90% (Table 4). Thus, for lugworms in this table, the annual replacement rate due to sublethal predation averaged ≈55%. They undoubtedly constitute a major renewable energy source for higher trophic levels in the Dutch Wadden Sea.

Bivalvia

Tellinoidea: De Vlas (1985) reported that individual *Macoma balthica* lost an average of several incompletely regenerated siphon tips per day. The estimated amounts of *Macoma* siphon tissue lost during 1975 at four tidal-flat transects varied from 0.31 to 1.66 g AFDW m⁻² yr⁻¹ (Table 4), i.e., was “nearly half of the annual mean biomass of soft parts and hardly different from elimination in the form of whole *Macoma*”. He concluded that regeneration of siphon tips and other cropped body parts of *Macoma* must contribute significantly to benthic secondary production.

Veneridae: Based on the comparison of changes in size between caged and uncaged control clams over 2 years, Peterson and Quammen (1982) indicated that *Protothaca staminea* in Mugu Lagoon, CA, USA, grew more than two times faster in sandy plots protected from siphon nipping than in control plots. In sand habitat, they observed that caged clams increased 218% in length and 250% in volume more than clams exposed to grazing. An increase in volume is roughly equivalent to an increase in biomass. In mud habitat, they observed no significant differences, likely because *Macoma* spp. provided an alternative prey to *Protothaca*. Based on these figures, it appears that siphon nipping may result in ca. 58.5% annual loss of growth (basically biomass) in the sandy and muddy environments as a result of sublethal predation in these two habitats. Thus, for bivalves in

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Table 4 Percentage of Population Biomass Lost Annually to Sublethal Predation by Three Higher Taxa of Dominant Non-Migratory Megafaunal Organisms

Species	Higher Taxon	Annual Biomass Lost or Replaced (%)	Estimated Annual Tissue Loss	Structure Lost	Reference
<i>Arenicola marina</i> Intertidal	Polychaete	>20 ^a		Tail segment	de Vlas (1979b)
<i>Arenicola marina</i> Intertidal	Polychaete	>90 ^b		Tail segment	de Vlas (1979b)
<i>Macoma balthica</i> Intertidal	Bivalve	≈50	0.31–1.66 g AFDW m ⁻² yr ⁻¹	Siphon	de Vlas (1985)
<i>Protothaca staminea</i> Intertidal	Bivalve	≈58.5		Siphon	Peterson and Quammen (1982)
<i>Acrocnida brachiata</i> Subtidal	Ophiuroid	11.1		Arm	Bourgoin and Guillon (1994)
<i>Acrocnida brachiata</i> Subtidal	Ophiuroid	6.4	19 g AFDW (33 g DW) m ⁻² yr ⁻¹	Arm	Bourgoin and Guillon (1994)
<i>Amphiura chiajei</i> Subtidal	Ophiuroid	33		Arm	Munday (1993)
<i>Amphiura filiformis</i> Subtidal	Ophiuroid	25		Arm	Bowmer and Keegan (1983)
<i>Amphiura filiformis</i> Subtidal	Ophiuroid	22	0.34 g AFDW m ² yr ⁻¹	Arm	Sköld et al. (1994)
<i>Amphiura filiformis</i> Subtidal	Ophiuroid	22.6		Arm & gonad production	O'Connor et al. (1986)
<i>Microphiopholis gracillima</i> Subtidal	Ophiuroid	50		Arm	Stancyk et al. (1994)
Mean±SD		35.3±24.6			

^a Based on predation by juvenile plaice and flounder.

^b Based on predation by juvenile plaice and flounder and a polychaete, *Nereis* sp. DW, dry weight; AFDW, ash-free dry weight.

this table, the annual replacement rate due to sublethal predation averaged ca. 54%. They undoubtedly constitute a major renewable energy source for higher trophic levels.

Echinodermata

Ophiuroida: Burrowing Ophiurans: Amphiuridae: For *Acrocnida brachiata* in Brittany, France, Bourgoin and Guillon (1994) reported that nearly 70% of arms in intertidal and subtidal populations were regenerating. Biomass composed of regenerating arm tissue differed significantly annually between intertidal (11.1% ± 9.5%) and subtidal habitats (6.4% ± 8.4%). Estimated annual production for *Acrocnida* arm tissue lost subtidally was 33 g dry weight (19 g AFDW m⁻² yr⁻¹). O'Connor et al. (1986) estimated that *Amphiura filiformis* in Galway Bay, Ireland, contributed 16% of its biomass annually to higher trophic levels through loss of arms. They estimated that an additional 6.6% was contributed through gonad production, for a total of 22.6% annually. Sköld et al. (1994) reported

that *A. filiformis* in the Skagerrak, Sweden, contributed 22% of its total population biomass (0.34 g AFDW m⁻² yr⁻¹) to higher trophic levels through sublethal predation on arms. Trophic transfer resulting from sublethal predation on another amphiuroid, *Microphiopholis gracillima*, by fish, crabs, and penaeid shrimp ranged from ≈13 to 39 g wet weight m⁻² yr⁻¹ (Pape-Lindstrom et al. 1997). Based on their data, that team subsequently estimated 50% production for that species (Stancyk et al. 1994). With an estimated average of 24.3% ± 14.4% annual replacement of biomass for these four ophiuroid species, combined with high biomass, burrowing brittle stars probably constitute a significant renewable energy source for higher trophic levels in areas where they occur in dense populations.

Summary for secondary production for non-migratory megafauna

Overall, the biomass lost or replaced annually by these seven species ranged from 6.4% to >90% and averaged 35.3% ± 24.6%. This value suggests that non-migratory megafauna contribute substantial energy to higher trophic levels, especially in areas where species are abundant, and biomass is high. This tissue or energy contribution to higher trophic levels must be added as an important component to secondary production calculations for infaunal assemblages as defined by Crisp (1971). Considering that non-migratory megafaunal biomass likely is much higher than macrofaunal biomass in most sedimentary habitats (Lees et al. 1980, Lees 2021), it is highly likely this sub-assemblage contributes far more energy to higher trophic levels than macrofauna.

Studies providing adequate data on the percent of population biomass lost due to sublethal predation (i.e., contributed to higher trophic levels) are sparse. Nevertheless, despite the paucity of data, it seems reasonable, when estimating secondary production for infaunal assemblages, to estimate that sublethal predation on non-migratory megafaunal organisms contributes conservatively ca. 25% biomass annually. The average for polychaetes in Table 4 is 55%, for bivalves, 54.25% and for ophiuroids, 28.4%, for the overall average cited above. Obviously, however, these are very speculative estimates for those taxa. This 25% estimate is basically a conservative place holder based on a very sparse data set. It is meant to provide some insight into a potential effect of sublethal predation on secondary production. In view of regeneration, that contribution has, on average over time, a negligible effect on standing stocks. Undoubtedly, the actual figure will vary substantially according to ecosystem and which taxa dominate, as well as addition of more data sets on production.

Unfortunately, few estimates of annual tissue loss were located. The two included from intertidal populations in this table are consistent. However, it is notable that the subtidal estimate for tissue loss (i.e., secondary production) is orders of magnitude higher. It seems reasonable to assume that this pattern is valid since subtidal populations of many prey species are denser and individuals are larger. They have more time to feed and are exposed to less stress. However, they also have more time to expose nippable structures for predators to browse on them.

Since sublethal predation has been demonstrated for numerous macrofaunal species, it seems reasonable to adopt that practice for macrofauna as well although it is likely that lethal predation will be a more important component for these much smaller organisms. Adding to the conservative nature of the 25% placeholder, estimates of secondary production or yield could be expanded to include consumable reproductive and excretory products such as eggs, sperm and mucus, which likely are substantial.

Discussion and conclusions

Eighty-eight species from six major taxa reported to have been subjected to sublethal predation or regeneration are discussed in this review. Dominant among these were polychaetes, bivalves and ophiuroids. Other higher taxa included sea pens, amphipod and decapod crustaceans, and irregular echinoids. The numbers of species observed in each of the five topics examined in this review

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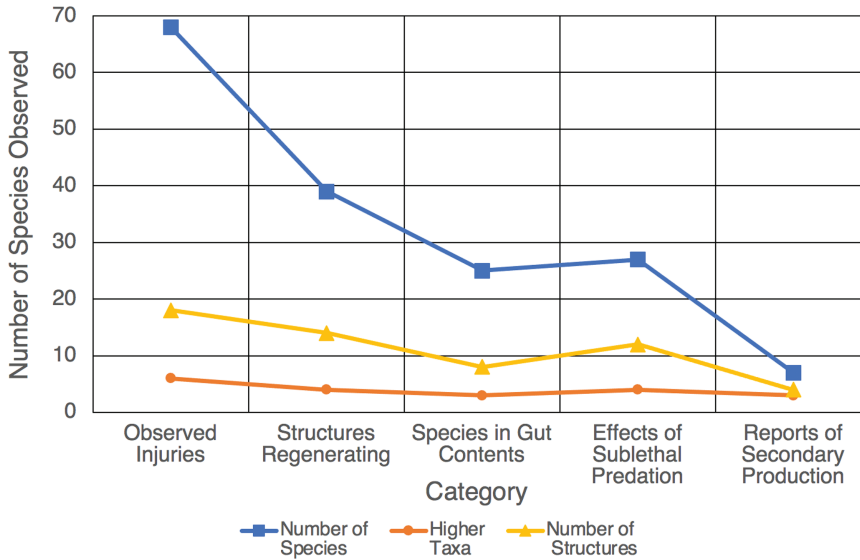


Figure 3 Distribution of research effort among the five categories of focus in this review.

vary widely by topic (Figure 3). Substantially more species were examined for observed injuries than for other categories. The least, with only about a tenth of those for observed injury, were observed for secondary production. The number observed regenerating was slightly more than half those observed with injuries. This suggests that considerably more research needs to be conducted on regeneration. Also, the number of species observed in gut contents was relatively small, suggesting that more effort is needed in studies of gut contents. The number of structures observed, generally small, declined progressively by category with a slight bump in the effects category. It is interesting that only about a third of the number of observed injured structures appeared in gut contents. Diversity of higher taxa was generally low, suggesting that a greater range of taxa should be examined.

Studies providing adequate information to determine secondary production are sparse even though that is a process of major importance for describing the value of ecosystems. Considering the importance of this topic to infaunal ecology, much more research is necessary.

Observed injuries of specific structures or their absence or observed regeneration were the basis for the initial discussion. These structures, generally exposed and accessible to predators, were reported for six higher taxa comprising 26 polychaete, 18 bivalves and 23 ophiuroids. The latter dominated studies for regeneration. The types of structure accessible to sublethal predation are unique and specific to each major taxon. The injuries were caused by at least 50 predators. Demersal fishes, from juveniles to mature adults, were the dominant predators but polychaetes, crabs, shrimp and other crustaceans, shorebirds and extending on to sea otters and humans, were also commonly reported.

Gut studies were performed on at least 24 predator species including fish, crabs, shrimp, a gull, sea otters and a walrus. Most studies of gut contents were on fish. Structures of megafaunal species suggesting sublethal predation based on examination of predator gut contents are reported here for 33 prey species from three higher taxa. Dominants among these were bivalves (17 species) and polychaetes (10 species). Macrofaunal species are likely greatly under-represented because structures resulting from sublethal predation are small, fragile and probably quickly digested in the predator.

Effects described in this review related to 27 species from four higher taxa. Most important among these are bivalves (11 species) and polychaetes (10 species), followed by ophiuroids

(6 species). Effects were complex, wide-ranging, important and mostly negative. They ranged from several individual behaviours to reproduction effects and population dynamics, 41 kinds in all. Only one of these effects, an escape response observed in downstream brittle stars, when an upstream individual is attacked, can be considered a positive effect.

The distribution of research effort varied substantially among higher taxa in terms of number of species studied and reporting effort (Figure 4). A broader range of species was studied for Polychaeta and least on Ophiuroida. Most effort on polychaetes was expended on *Arenicola marina* and *Diopatra cuprea*. Substantially more research effort was expended on Bivalvia; most studied were *Macoma balthica* and *Donax* spp. Most studied among the ophiuroids was *A. filiformis*, a burrowing species.

The number of species was evenly split among non-migratory megafaunal and macrofaunal polychaetes (16 each). *A. marina* and *D. cuprea* were the most studied megafaunal species, and *Pseudopolydora kempii japonica* was the most studied macrofauna.

Maginnis (2006) discussed how both structure loss and regeneration can result in important effects on various aspects of fitness, e.g., locomotion, foraging, survivorship, somatic growth and reproduction. In the reviewed studies, the most commonly studied of the ten general effects categories identified by Maginnis related to reproduction, somatic growth and feeding. Less frequently mentioned were effects on feeding, energy, respiration, mortality and effects on sediment quality due to changes in fecal production and foraging patterns. Because this review focuses on relatively non-migratory invertebrates, locomotion was not a factor. It is clear that the range of effects from sublethal predation is broad and complex; more research is needed.

Nine reports (polychaete-1, bivalves-2 and ophiuroids-6) provided suitable data to allow preliminary estimation of the contribution by sublethal predation to production. Types of tissue included tail segments for lugworms, siphons for bivalves and arms for ophiuroids. The reported amount of biomass lost or replaced in populations of these species ranged from 6.4% to >90% and averaged $35.3\% \pm 24.6$. Obviously, considerably more research is needed to improve our knowledge for this important process.

Based on her research on spionid worms, Woodin (1982) suggested that sublethal predation (browsing) by visual predators has been important in marine sedimentary environments “in the

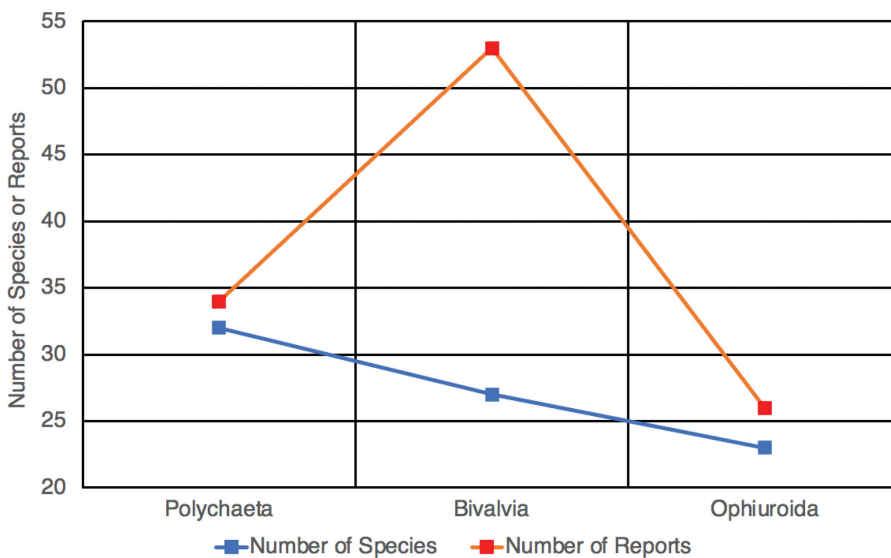


Figure 4 Distribution of research effort among the major taxonomic groups reviewed in this assessment.

evolutionary past". She reported that many spionids that expose their anterior ends to feed or defecate have evolved cryptic anteriors, likely in response to sublethal predation. In contrast, spionids not exposing their anteriors have not developed cryptic coloring. However, the importance of sublethal predation on the evolution of the affected species has received little attention.

The importance of the "evolutionary past" is also indicated by studies on fossil ophiuroids and echinoids. Aronson (1992) reported that evidence of browsing was absent in fossil ophiuroids from the Jurassic period (201–145 mya). He hypothesised that such browsing on ophiuroids did not arise until the evolution of durophagous fishes and decapod crustaceans, i.e., animals that are able to crush and digest hard skeletal parts, diversified during the late Mesozoic era (145–66 mya). Echinoids from the Pliocene epoch (5.33–2.58 mya) were also unbrowsed (Negron et al. 2020). It appears durophagous predators on sea urchins evolved much later in geologic history.

Knowledge gaps: suggested future research

Lees (2021) provided a broader description for infaunal assemblages than has been presented in more conventional research. This broader scope suggests that in order to obtain better understanding of infaunal systems, future research should focus on non-migratory megafauna and associated sublethal predation. This will require adding sampling methods that cover larger sampling areas and penetrate more deeply into the sediment (see Peterson 1977).

Two major data gaps in knowledge are suggested by these analyses. The first gap, knowledge of sublethal injury to a broad range of infaunal invertebrates, can be resolved by (1) actively documenting frequency of lost or regenerating structures in collected species, especially those previously shown to suffer partial predation (e.g., *Mya* spp. and *Panopea*) and (2) studying gut contents of more and a wider variety of predators. Resolving the second gap, a paucity of information regarding sublethal predation in a broad range of infaunal species, requires more careful assessment of sublethal predation within the many major taxa for which regeneration is possible but has not been investigated.

Major gaps for bivalves are studies demonstrating whether soft-shell clams (*Mya* spp.) or geoducks (*Panopea* spp.) are capable of regenerating partially or fully lost siphons. These clams are major inhabitants of intertidal and subtidal mudflats and nearshore sediments. Some are valuable commercial species and important sources of nutrition for several charismatic predators. Their siphons appear as major items of stomach contents of several major predators. However, studies demonstrating lost or regenerating siphons in living individuals appear to be lacking. This is an important data gap. As reported above, Welch and Martin-Bergmann (1990) reported that siphons and chitinous siphon sheaths of truncate soft-shell clams (*Mya truncata*) are common in gut contents of walrus (*Odobenus rosmarus*) in the western Arctic, Baffin Bay and eastern Canadian Arctic. Unfortunately, the design of their year-long study to assess the regeneration of experimentally excised siphons was flawed and all excised clams succumbed. *In situ* studies need to be conducted for deep-burrowing species like *Mya* spp. and *Panopea* spp., which are preyed upon by several large fish and sea otters. These studies should be conducted over a period sufficient to assess recovery and regeneration. Because of the importance of soft-shell clams as food items, they should be conducted on at least two species of *Mya*.

Taxa lacking documented sublethal predation

The species reviewed in this study are far from a complete listing of species potentially subjected to sublethal predation. For example, 27.5% of the marine genera listed in a review of segment regeneration for annelids (Bely 2006) are not included among the genera discussed in this current review. These include members of important families such as Amphinomidae, Chaetopteridae, Eunicidae, Nereididae, Oweniidae, Polynoidae, Sabellidae and Syllidae, all of which are reported by Bely to

exhibit regenerative capabilities. Many of these taxa likely are subject to sublethal predation, are important members of infaunal assemblages and thus contribute to secondary production.

This review shows clearly that little information is available for a broad range of infaunal taxa that often are important in non-migratory megafaunal assemblages in sedimentary habitats. Many of these soft-bodied invertebrates have strong regeneration capabilities. However, because of their lack of hard parts on nippable organs (e.g., setae and jaws for polychaetes or arms for ophiuroids), they are not identifiable in gut contents. Nevertheless, it is likely they are also subject to sublethal predation. Zattara et al. (2019) summarised the widespread regeneration of heads in Nemertea, especially *Lineus sanguinea*. Davis et al. (1982) reported that repeated predation on sea pens by fishes, initially sublethal, was ultimately lethal. Malecha and Stone (2009) indicate that predation of pennatulaceans by nudibranchs is possibly sublethal. Rice (1970) described regeneration in sipunculids. Walls (1982) reported on regeneration for echiurids. It is surprising that sublethal predation is not commonly reported for sabellid (feather duster) worms since regeneration is widely reported for these worms, some of which form large mound-like colonies (Bely 2006, Kolbasova et al. 2013). McKinney et al. (2003) and Jørgensen et al. (2015) reported that bryozoans, often common to abundant on mid to outer shelf sediments, can be subjected to intense predation by a broad range of predators ranging from flatworms and pycnogonids to fish. This predation is likely often sublethal in some because of their colonial fleshy growth form (e.g., *Flustrellidra* spp.) Eisapour et al. (2021) described regeneration for burrowing holothurians. Francour (1997) stated that holothurians are usually consumed whole but cited papers describing predation of viscera (Bakus 1968) and tentacle crowns (Mortensen 1927) from which the prey likely survived and regenerated the lost structures. Holothurians are known to eviscerate all internal organs in response to disturbance by potential predators (Byrne 1985); this should be considered sublethal predation. Rychel and Swalla (2009) and Arimoto and Tagawa (2018) reported regeneration in enteropneusts, a poorly studied but often important non-migratory megafaunal invertebrate.

The importance of many of these infaunal assemblages indicates that substantial increases in research on various aspects of sublethal predation and regeneration, as well as more comprehensive studies of the highly productive non-migratory megafauna, are called for. Non-migratory megafaunal organisms have routinely been undersampled or actively avoided by conventional infaunal sampling methods (Lees 2021), leading to a relatively poor understanding of the value of these ecosystems worldwide. Expanding assessment of non-migratory megafaunal assemblages will greatly increase our understanding of the importance and value of infaunal ecosystems and will increase the opportunity to inspect these organisms for lost or regenerating structures. This will lead to a better understanding of the magnitude of the contribution of these assemblages to higher trophic levels, i.e., secondary production, by sublethal predation.

Importance of sublethal predation

In view of its virtual absence in discussions of community dynamics, one can ask, “How important is sublethal predation in infaunal ecology?” The answer to that question is apparent in this review, based on the importance of the types of infaunal animals that are its focus, especially non-migratory megafaunal polychaetes, bivalves and ophiuroids, and considering the proportion of community biomass these taxa generally comprise in specific ecosystems. These three higher taxa often are among the dominants in sedimentary ecosystems in terms of biomass and ecological engineering. However, other higher taxa like echiurids, burrowing shrimp, crabs or holothurians also can be important. Their combined biomass is generally orders-of-magnitude greater than that of macrofauna (e.g., Peterson 1978, Lees et al. 1980, Lees 2021). Moreover, as is well demonstrated above, they are major targets for sublethal predation and contribute substantial amounts of energy to their predators as well as other trophic levels. Consequently, their contribution to secondary production far exceeds that of macrofauna. Since secondary production is a major factor in discussions

of infaunal ecosystem dynamics, the importance of sublethal predation is therefore quite clear. However, few studies have addressed the topic, particularly from the perspective of non-migratory megafauna.

Notably, sublethal predation has never been considered previously in calculations of infaunal secondary production. For future implementation, in view of the paucity of applicable data, I propose establishing a value of 25% as a conservative placeholder for use in estimating contributions by non-migratory megafauna to secondary production for infaunal ecosystems. All the taxa listed for the loss analysis above upon which that conservative estimate is based (Table 4) are non-migratory megafauna; such data appear to be lacking for macrofauna. In view of the variation in percentage contribution among those taxa, it is clear that contribution estimates will vary substantially within species and among assemblages depending on dominant species. Optimally, more data will be acquired, allowing refinement of that figure or providing specific values for particular studied ecosystems. Clearly, then, considerably more research into sublethal predation, especially on non-migratory megafauna, will be required to improve estimates for contributions by sublethal predation and provide more accurate and defensible estimates of the magnitude of the secondary production for these rich productive systems. But it seems quite clear that inclusion of the contributions of sublethal predation in these calculations will increase estimates of secondary production for infaunal assemblages by a substantial amount. This will demonstrate that these systems have been greatly undervalued in the past.

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