



Status of the Nemertea as predators in marine ecosystems

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Key words: nemertean, foraging, feeding rate, predation, prey selection, benthos

Abstract

The ecology of nemertean predators in marine ecosystems is reviewed. Nemerteans occur in most marine environments although usually in low abundances. Some species, particularly in intertidal habitats, may reach locally high densities. During specific time periods appropriate for hunting, nemerteans roam about in search of prey. Upon receiving a stimulus (usually chemical cues), many nemertean species actively pursue their prey and follow them into their dwellings or in their tracks. Other species (many hoplonemerteans) adopt a sit-and-wait strategy, awaiting prey items in strategic locations. Nemerteans possess potent neurotoxins, killing even highly mobile prey species within a few seconds and within the activity range of its attacker. Most nemertean species prey on live marine invertebrates, but some also gather on recently dead organisms to feed on them. Heteronemerteans preferentially feed on polychaetes, while most hoplonemerteans prey on small crustaceans. The species examined to date show strong preferences for selected prey species, but will attack a variety of alternative prey organisms when deprived of their favourite species. Ontogenetic changes in prey selection appear to occur, but no further information about, e.g. size selection, is available. Feeding rates as revealed from short-term laboratory experiments range on the order of 1–5 prey items d^{-1} . These values apparently are overestimates, since long-term experiments report substantially lower values (0.05–0.3 prey items d^{-1}). Nemerteans have been reported to exert a strong impact on the population size of their prey organisms through their predation activity. Considering low predation rates, these effects may primarily be a result of indirect and additive interactions. We propose future investigations on these interactive effects in combination with other predators. Another main avenue of nemertean ecological research appears to be the examination of their role in highly structured habitats such as intertidal rocky shore and coral reef environments.

Introduction

Nemerteans are common predators in a wide variety of marine habitats. Benthic nemerteans prey on many different prey organisms, primarily polychaetes and crustaceans (McDermott & Roe, 1985), but some species also scavenge on recently dead organisms (Heine et al., 1991; Thiel, 1998). Pelagic nemerteans occur in all major oceans but apart from recent studies on their reproductive biology and distribution pattern (Norenburg & Roe, 1998; Roe & Norenburg, 1999) very little is known about their general ecology. In this present review, we will primarily focus on benthic nemertean species with a strong bias towards nemerteans from shallow subtidal and intertidal habitats.

Modern studies focussing on the ecology of marine nemerteans started with the contribution by Roe

(1970) on the intertidal hoplonemertean *Paranemertes peregrina* (Coe, 1901). Thereafter, several other studies on the food and feeding biology, primarily of intertidal nemertean species, have been conducted (Bartsch, 1973, 1975, 1977; McDermott, 1976, 1988, 1993; Reise, 1985; Nordhausen, 1988; Thiel & Reise, 1993; Kruse & Buhs, 2000). These studies have revealed that most nemertean species are highly selective with respect to their prey species. Reported feeding rates and the results of experimental studies have indicated that nemertean predators have the capacity to exert a significant impact on the populations of their preferred prey organisms (McDermott, 1984, 1988; Nordhausen, 1988; Rowell & Woo, 1990; Thiel & Reise, 1993; Kruse & Buhs, 2000).

Among marine predators, nemerteans are quite unique in that they are very slow-moving primarily

relying on their rapidly everted proboscis and highly potent toxins. Furthermore, their chemosensory system is strongly developed permitting them to remain on the trail of a prey item once 'smelled the rat' (Amerongen & Chia, 1982). It is for these unique features that nemerteans may play a crucial role in marine habitats in which they occur in high abundance.

The main objective of this review, is to synthesise the information on the ecology of nemerteans that has been accumulated during the past three decades. Rather than providing a detailed overview summarising all the information available, we attempted to put together the pieces and direct attention to points that still require further research attention.

Results and discussion

Habitats

Nemerteans occur in almost all marine habitats from the benthos to the pelagial, from the tropics to the polar seas, and from the shallow intertidal zone to the deep sea. However, most studies that report nemerteans as important predators have been conducted in benthic habitats of temperate and polar regions (e.g. *Paranemertes peregrina*, *Nipponemertes pulcher* (Johnston, 1837), *Lineus viridis* (Müller, 1774), *Amphiporus lactifloreus* (Johnston, 1827–28), *Micrura lactea* (Hubrecht, 1879) and *Parborlasia corrugatus* (McIntosh, 1887), all from latitudes $>40^\circ$ N or S), yet they are not restricted to these higher latitudes. The nemertean *P. peregrina* is also a common predator in the rocky intertidal of California (Roe, 1979). Recently, Christy et al. (1998) reported a new species that was frequently observed to prey on fiddler crabs from Panama. Nemerteans appear to be most abundant in intertidal and shallow subtidal habitats. This result

may be biased since these habitats allow easy access to researchers. On the other hand, there is good indication that nemerteans have a relatively high foraging success in intertidal and shallow subtidal habitats, and thus, these habitats may be most suitable to nemertean predators. Many studies on nemertean predators have been conducted in soft-bottom habitats. Undoubtedly nemerteans play an important role as predators in these environments and there is no reason to believe that they are of less importance in (intertidal) hard-bottom habitats.

Several nemertean species apparently have distinct preferences for microhabitats such as mussel clumps or sea-grass patches on intertidal soft-bottoms, the underside of boulders or even polychaete burrows (Bartsch, 1977; McDermott, 1988; Roe, 1993; Thiel & Reise, 1993; Table 1). While pursuing prey, they may leave their shelters, but, following a foraging trip, nemerteans apparently retreat into these microhabitats.

Various nemerteans also live symbiotically on, or in other organisms. Nemertean egg predators and their impacts on the host's reproductive success are well known (Shields & Kuris, 1988; Kuris, 1993). Other nemerteans inhabit the interior parts of bivalves (Gibson & Jennings, 1969; Gibson & Junoy, 1991), or ascidians (Dalby, 1996), microhabitats which they share with a variety of potential prey organisms. *Malacobdella grossa* (Müller, 1776) feeds both commensally with its bivalve hosts and as a predator on small crustacean larvae entering the mantle cavity of their hosts (Gibson & Jennings, 1969). Other nemertean species in these symbiont-assemblages may also pursue a predatory habit foraging on parasites of their hosts. Multiple infestation of, e.g., bivalves with various metazoan species, is not uncommon (Cáceres-Martínez & Vásquez-Yeomans, 1999). Possibly distinct interactions occur between different associate species as had earlier been suggested for the hoplone-

Table 1. Particular microhabitats reported for some nemertean species

Nemertine species	Microhabitat	Refs.
<i>Tetrastemma melanocephalum</i>	burrows of <i>Nereis diversicolor</i>	Bartsch, 1977
<i>Tetrastemma fozensis</i>	<i>Scrobicularia plana</i>	Gibson & Junoy, 1991
<i>Gonemertes australiensis</i>	<i>Pyura stolonifera</i>	Dalby, 1996
<i>Amphiporus lactifloreus</i>	mussel clumps	Thiel & Reise, 1993
<i>Lineus viridis</i>	mussel clumps	Thiel & Reise, 1993
<i>Cephalotrix linearis</i>	holdfasts of <i>Laminaria</i> spp.	Gibson, 1994

Table 2 Abundances of nemerteans (Nemertea spp.) reported from various marine environments (Sb soft-bottoms; Hb hard-bottoms)

Habitat	Location	Water depth [m below MLW]	Abundance [ind.m ⁻²]	Ref.
Sb	37.01 S/174.49 E	0	~60	Hewitt et al., 1997
Sb	37.02 S/174.41 E	0	~630	Thrush et al., 1992
Sb	43.56 N/69.35 W	0	~300	Thiel & Watling, 1998
Sb	36.30 N/6.10 W	0	15–80	Arias & Drake, 1994
Sb	28.00 N/48.00 E	0	~6	Prena, 1996
Sb	40.35 N/0.40 E	3	16–56	Palacín et al., 1991
Sb	30.00 N/90.00 W	~5?	105	Gaston et al., 1997
Sb	69.42 N/18.50 E	20	403 (max.)	Oug, 1998
Sb	42.45 N/9.00 W	~20?	50–200	López-Jamar & Mejuto, 1986
Sb	42.35 N/8.50 W	~20?	20–100	López-Jamar & Mejuto, 1986
Sb	54.10 N/11.28 E	23	0–3	Prena et al. 1997
Sb	62.05 S/58.28 W	30	70	Jazdzewski et al., 1986
Sb	59.40 N/10.35 E	60	~50	Olsgard, 1999
Sb	36.45 S/73.10 W	8–65	8–64	Carrasco et al., 1988
Sb	36.40 S/73.05 W	11–61	~2	Carrasco et al., 1988
Sb	58.18 N/6.10 E	50–170	~300	Olsgard & Hasle, 1993
Sb	62.43 S/60.30 W	32–421	4.4	Saiz-Salinas et al., 1998
Sb	64.00 S/61.00 W	42–671	5.5	Saiz-Salinas et al., 1997
Sb	67.30 N/6.00 W	1200–1500	1.2	Romero-Wetzel & Gerlach, 1991
Sb	55.58 N/12.41 E	27	122	McDermott, 1984
Sb	20.30 N/18.30 W	1590–2040	111	Cosson et al., 1997
Sb (mesotrophic)	18.30 N/21.02 W	3095–3128	10	Cosson et al., 1997
Sb (oligotrophic)	21.04 N/31.10 W	4580–4647	2.4	Cosson et al., 1997
Hb	32.18 S/28.50 E	0	~45	Lasiak & Field, 1995
Hb	40.55 N/140.50 E	0	~200	Tsuchiya & Nishihira, 1985
Hb	53.10 N/4.30 W	0	~16 000	Lintas & Seed, 1994
Hb	30.00 S/70.00 W	0	~10 000 (max.)	Thiel & Ullrich, in press

meritean *Tetrastemma fozensis* Gibson & Junoy (1991) and copepod parasites of its bivalve hosts (Thiel & Francés-Zubillaga, 1998).

Nemertean abundances

In many habitats, nemerteans are the most abundant representatives of the predator guild while in others they only occur in low numbers. Possibly as a consequence of difficulties with the species identification and their relatively low numbers, many community studies only list nemerteans among 'others', so that their true abundance often cannot be inferred. Locally, nemerteans may reach very high densities of several hundred individuals m⁻², and the highest densities have been reported from intertidal habitats (Table 2). Since studies that provide complete species lists, report numbers of a few individuals m⁻² it ap-

pears relatively safe to assume that for most species the abundance does not exceed 10 individuals m⁻² (Table 3). Few data are available on the abundances of nemerteans in hard-bottom environments but also in these habitats they have been found in very high numbers (Table 2). In a recent study on the fauna associated with kelp holdfasts, high numbers of nemerteans holdfast⁻¹ were revealed (Thiel & Vásquez, 2000), supporting the notion that these predators can be abundant in these highly structured habitats.

Few data are available on the abundance of nemerteans in coral reef environments where both, diversity and abundances may reach locally very high values (Sundberg, Norenburg, Schwartz, personal communications).

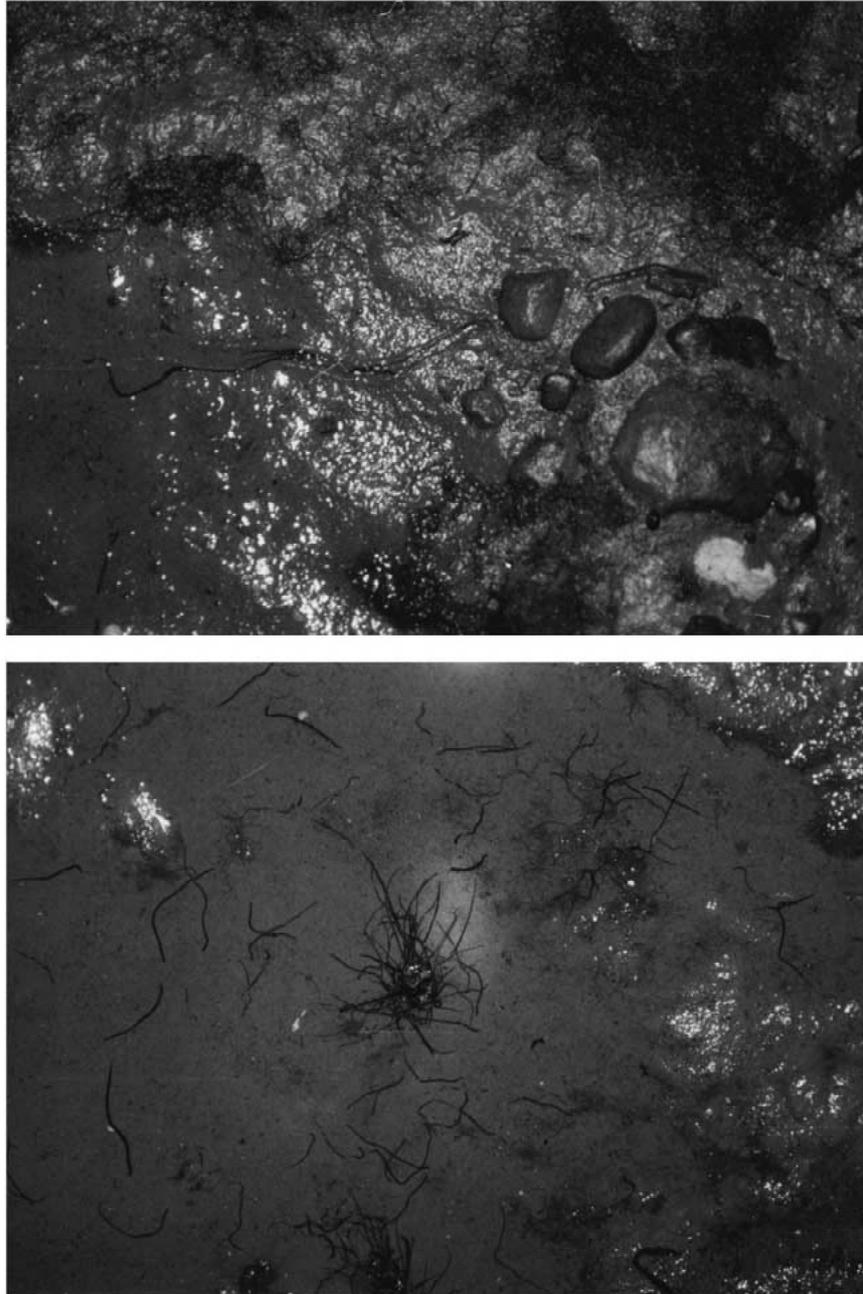


Figure 1 *Lineus viridis* foraging on polychaetes *Nereis virens* during night low tides. Several nemerteans following in the track of an escaping *N. virens* (top): nemerteans repeatedly attacked the polychaete during this pursuit; occasionally polychaetes autotomized the posterior part of their body around which nemerteans accumulated for short time periods before some nemerteans continued to follow the escaping polychaete. At the end of such a collective hunt (bottom), when the polychaete was finally overtaken, many nemerteans gathered around the carcass to feed on it. Photographs taken on intertidal mudflats in Lubec, Maine where these events were repeatedly observed during summer and fall of 1993.

Table 3 Abundances of particular nemertean species reported from various marine environments (Sb soft-bottoms; Hb hard-bottoms)

Habitat	Species	Location	Water depth [m below MLW]	Abundance [ind.m ⁻²]	Ref.
Sb	<i>Tetrastemma melanocephalum</i>	54.22 N/8.39 E	0	max. 8	Kruse & Buhs, 2000
Sb	<i>T. melanocephalum</i>	55 N/8.25 E	0	19	Reise, 1985
Sb	<i>T. elegans</i>	39 N/74 E	0	max. 157	McDermott, 1988
Sb	<i>Amphiporus lactifloreus</i>	55 N/8.25 E	0	max. 25	Reise, 1985
Sb	<i>A. lactifloreus</i>	55 N/8.25 E	0	2	Thiel, 1992
Sb	<i>A. bioculatus</i>	55.58 N/12.41 E	27	10	McDermott, 1984
Sb	<i>A. dissimilans</i>	55.58 N/12.41 E	27	5	McDermott, 1984
Sb	<i>Prostomatella arenicola</i>	5 N/8.25 E	0	6	Reise, 1985
Sb	<i>Lineus viridis</i>	55 N/8.25 E	0	max. 88	Reise, 1985
Sb	<i>L. viridis</i>	55 N/8.25 E	0	6	Thiel, 1992
Sb	<i>Zygonemertes virescens</i>	39 N/74 E	0	max. 175	McDermott, 1988
Sb	<i>Pantionemertes californiensis</i>	40 N/124 E	0	4	Roe, 1993
Sb	<i>Nipponemertes pulcher</i>	56 N/12 E	20–50	12	Petersen, 1918; McDermott 1984
Sb	<i>N. pulcher</i>	55.58 N/12.41 E	27	74/68	McDermott, 1984, 1993
Sb	<i>Paranemertes peregrina</i>	48.34 N/123.9 E	0	max. 7	Roe, 1976
Sb	<i>P. peregrina</i>	48.34 N/123.9 E	0	max. 9	Roe, 1976
Hb	<i>Tetrastemma phyllospadicola</i>	48 N/123 W	0	>50	Stricker, 1985

Foraging behaviour

As a consequence of their locomotory system, nemerteans are not able to reach high speeds. Many species appear to use the sit-and-wait strategy expecting the prey in strategic locations where these organisms retreat during, e.g. low tide or when sheltering from water column predators. Hoplonemerteans may use this sit-and-wait strategy (for a particularly impressive example see Christy et al., 1998), but some species also actively search for prey (Roe, 1971, 1976; McDermott, 1976; Amerongen & Chia, 1982; Kruse & Buhs, 2000). Many heteronemerteans actively forage for prey and they primarily follow chemical signals in order to locate their prey (Thiel, 1998). Nemerteans also have a limited capability to pursue their prey actively. Some species can (and do) attack a prey item repeatedly if the first strike was not successful (Fig. 1).

Toxins

Nemerteans have very potent neurotoxins which they utilise to immobilise and kill their prey (Kem, 1985; McDermott, 1993). These toxins have almost instantaneous effects leaving the prey motionless and at the site of attack within seconds. Prey organisms of similar size and weight as their nemertean pred-

ators are successfully attacked by nemerteans. Kem (1985) suggested that pyridine alkaloid proteins found in enoplans serve both in prey capture and in predator deterrence while protein toxins from anoplans exclusively serve the latter function. These defence toxins are highly efficient in rendering nemerteans unattractive to most predators (see McDermott, 2001).

Food items

Nemerteans feed on a variety of prey organisms (for a detailed overview see the excellent summary by McDermott & Roe, 1985). Heteronemerteans primarily feed on polychaetes, but they have also been observed to feed on bivalves and crustaceans. Hoplonemerteans usually feed exclusively on crustaceans primarily amphipods but some species also feed on polychaetes (e.g. *Paranemertes peregrina* on nereid polychaetes – Roe, 1976).

Several species also feed on recently dead organisms. The antarctic nemertean *Parborlasia corrugatus* gathers in large numbers around bait traps (Heine et al., 1991). The intertidal nemertean *Lineus viridis* that usually prefers live nereids has also been observed to feed on spent *Nereis (Neanthes) virens* Sars, 1835 after these have spawned (Thiel, 1998).

Table 4 Preferred and alternative prey organisms of common nemertean predators; only experiments are considered in which nemerteans were enclosed with potential prey organisms that had no possibility to escape

Nemertean species	Preferred prey	Alternative prey	Refs.
<i>Paranemertes peregrina</i>	<i>Platynereis bicaniculata</i>	<i>Nereis vexillosa</i> , <i>Armandia brevis</i>	1
<i>Tetrastemma melanocephalum</i>	<i>Corophium</i> spp.	<i>Talorchestia brito</i> , <i>Bathyporeia</i> sp.	2
<i>Tetrastemma elegans</i>	<i>Corophium acherusicum</i>	<i>Caprella penantis</i> , <i>Gammarus mucronatus</i>	3
<i>Amphiporus ochraceus</i>	<i>Ampithoe longimana</i>	<i>Corophium acherusicum</i> <i>Gammarus mucronatus</i>	3
<i>Amphiporus lactifloreus</i>	<i>Gammarus locusta</i>	<i>Idotea chelipes</i>	4
<i>Amphiporus nelsoni</i>	<i>Hyale maroubrae</i>	<i>Hyale hirtipalma</i>	5
<i>Nipponemertes pulcher</i>	<i>Haploops tubicola</i> , <i>H. tenuis</i>	<i>Corophium volutator</i>	6
<i>Lineus viridis</i>	<i>Nereis diversicolor</i>	<i>Heteromastus filiformis</i> , <i>Nephtys hombergii</i>	4
<i>Lineus sanguineus</i>	<i>Phyllodoce (Anaitides) maculata</i>	Syllids	7
<i>Oerstedtia dorsalis</i>	<i>Corophium acherusicum</i>	<i>Ampelisca vadorum</i>	8
<i>Pantionemertes californiensis</i>	<i>Traskorchestia traskania</i> <i>Armadilloniscus holmesi</i>	<i>Ligia (Megaligia) occidentalis</i>	9
<i>Zygonemertes virescens</i>	<i>Corophium acherusicum</i> <i>Ampithoe longimana</i>	<i>Ampelisca vadorum</i> , <i>Idotea baltica</i>	10

1: Roe, 1970, 1976. Amerongen & Chia, 1982. 2: Kruse & Buhs, 2000. 3: McDermott, 1976. 4: Thiel, 1992. 5: Thiel et al., 2001. 6: McDermott, 1984. 7: Jennings & Gibson, 1969. 8: Mc Dermott & Snyder, 1988. 9: Roe, 1993. 10: McDermott, 1988.

Table 5 Feeding rates of nemerteans reported from various studies; only experiments are considered in which nemerteans were enclosed with a given number of prey individuals which had no possibility to escape

Nemertean species	Prey species	Pred. rate (individuals d ⁻¹)	Duration (d)	Ref.
<i>Paranemertes peregrina</i>	<i>Platynereis bicaniculata</i>	0.83–0.95	varying time spans	1
<i>Tetrastemma melanocephalum</i>	<i>Corophium</i> spp.	1–4	30	2
		2–3	11	3
<i>Nipponemertes pulcher</i>	<i>Haploops</i> spp.	0.2	8	4
<i>Amphiporus lactifloreus</i>	<i>Gammarus locusta</i>	0.15	13	5
<i>Amphiporus nelsoni</i>	<i>Hyale maroubrae</i>	0.1–0.2	75	6
<i>Lineus viridis</i>	<i>Nereis diversicolor</i>	0.02–0.1	86	7
<i>Pantionemertes californiensis</i>	<i>Ligia (Megaligia) occidentalis</i> , <i>Armadilloniscus holmesi</i> , <i>Traskorchestia traskania</i>	0.09–0.16	8–171	8

1: Roe, 1976. 2: Bartsch, 1973. 3: Kruse, 1996. 4: McDermott, 1993. 5: Thiel, 1992. 6: Thiel et al., 2001. 7: Nordhausen, 1987. 8: Roe, 1993.

Prey selection (species, size)

Prey preference for most nemertean species is known from laboratory observations, in which nemerteans have been offered different potential prey species (Table 4). Many of these nemertean species show distinct preferences for one prey species, but when the preferred prey is not available, they have also been found to feed on alternative prey organisms (Table 4). It should be expected that nemerteans also show a preference for particular sizes of prey that most likely correspond to their own body size. However, at present it is not known whether nemerteans at the moment of

encounter are able to rapidly determine the size of a prey organism and actively select for a particular size.

Ontogenetic changes in prey selection have been reported for one nemertean species: juveniles of the hoplonemertean *Tetrastemma melanocephalum* (Johnston, 1837) have been observed to prey on harpacticoid copepods while adults apparently feed exclusively on amphipods *Corophium* spp. (Bartsch, 1973, 1975, 1977; Kruse & Buhs, 2000). It is likely that juveniles of other nemertean species may also feed on other prey organisms than the adults.

The preferred prey organisms are known for many nemertean species for which predation was observed

either in the field or in the laboratory (McDermott & Roe, 1985). However, there are many nemertean species, which cannot be easily snooped around during the act of feeding – for these species the use of immunoassay techniques is probably most promising (see Feller et al., 1998).

Feeding rates

The food intake by nemerteans may depend on a variety of factors. Numbers of available prey items probably strongly affect feeding rates of nemerteans as has been shown for polychaete or flatworm predators (Abrams et al., 1990; Menn & Armonies, 1999). Seasonal changes in prey availability may result in seasonal changes of food intake in nemerteans. In addition to prey density, the conditions to locate and successfully attack them may vary, e.g. on a diurnal or tidal basis. While these extrinsic factors are important, intrinsic factors may also affect the feeding rate of nemerteans. During the reproductive periods of the nemerteans *Lineus viridis* and *Amphiporus lactifloreus*, high surface activity of these intertidal nemerteans was observed, yet no prey attacks were recorded (Thiel et al., 1995). Nemerteans may be in a constant state of hunger – in laboratory environments nemerteans show enormous attack rates when first exposed to prey items. Several short-term laboratory experiments (a few days) report feeding rates of several prey items nemertean⁻¹ d⁻¹ (Bartsch, 1973; Kruse, 1996; Table 5). However, when held over long time periods, the feeding rates of many species appear to slow down considerably (McDermott, 1984, 1993; Nordhausen, 1987; Thiel, 1992) suggesting that after being offered a super-abundant supply of food, they may become satiated within a few days. When deprived of access to food, nemerteans are also capable of surviving without feeding for long time periods (Gibson, 1972). Feeding rate estimates, regardless of how they were obtained, could be examined in the future with the aid of physiological studies (e.g. O₂-utilization rates). This has been done for *Lineus viridis* by Nordhausen (1988), who, based on the comparison of respiration rates and feeding rates, came to the conclusion that “feeding rates estimated by the field experiment are probably too high”. We consider this as a particularly promising avenue in verifying predation rates of nemertean predators.

Comparison with other predators

Nemerteans either actively pursue their prey or they utilise a sit-and-wait strategy in particular strategic locations where prey are likely to be found. Since their toxins act very rapidly, nemerteans are capable of overwhelming even prey with a highly mobile life style. After a successful attack, prey organisms are incapable of moving large distances from the site of attack.

Nemerteans, as a consequence of their body shape and feeding strategy, are able to access habitats that are inaccessible to many other predators. They are able to squeeze themselves through the smallest openings and crevices. Thus, habitats such as seagrass beds, algal holdfasts, or mussel clumps, which offer structural protection against many important predators, provide no protective advantage against nemertean predators. To the contrary, these habitats may provide ideal predation arenas for nemerteans since crevices may actually function as traps from which prey organisms can not escape once pursued by a nemertean predator. Nemerteans often possess a highly efficient chemosensory capacity, enabling them to pursue their prey after encountering a mucus trail (Amerongen & Chia, 1982). Nemerteans preferentially prey on organisms that are well protected from other predators such as decapod crabs, fish and birds (e.g. polychaetes in deep burrows or in solid tubes, amphipods between blue mussels, sea grass plants, or algal holdfasts).

Similar foraging tactics as used by nemerteans are employed by, e.g. flatworms and leeches (Young et al., 1995; Seaby et al., 1995). These predators capture their prey in a similar manner as nemerteans. Flatworms possess a highly developed chemosensory system that is utilised to locate prey items. Their reaction times to chemical cues from crushed or recently dead prey are in the range of minutes (Seaby et al., 1995) which are comparable to those of nemerteans (Thiel, 1998). Flatworms have also been reported to pursue and feed on large prey organisms in groups (Cash et al., 1995), a behaviour that has also been observed in some nemerteans (personal observations – Fig. 1; Chernyshev, 2000). Insights from studies on these predators may be useful to gain a better understanding of the foraging behaviour of nemerteans.

Contrary to other sit-and-wait predators (such as hydrozoans), most hoplonemerteans appear incapable of holding their prey upon attack. However, their toxins are so potent that prey lose their mobility immediately after a successful attack. Intoxicated prey

thus remains within the range of a few nemertean body lengths after a successful attack, where nemerteans usually find them within seconds to minutes. Nemerteans feed on similar prey organisms as other predators. In particular, polychaetes and crustaceans that are preferred prey of nemerteans are also consumed by many fish, bird and crustacean predators.

Importance of nemerteans in marine environments

In their 1985 review on the feeding biology of nemerteans, McDermott & Roe (1985) remarked that “effects of nemerteans on community structure are almost completely unknown...”. While the role of nemerteans in marine environments still remains scarcely known, some important progress has been made during the past 15 years. Several studies have attempted to quantify the impact of nemertean predators in benthic communities (McDermott, 1984, 1988, 1993; Nordhausen, 1988; Rowell & Woo, 1990; Thiel & Reise, 1993; Kruse & Buhs, 2000). In a review focussing on endobenthic predators, Ambrose (1991) revealed that the effects of nemertean predators on their prey’s populations are significant. In addition to the immediate impact of nemertean predation activity, indirect effects have been reported: epibenthic (non-nemertean) predators fed upon juvenile *Hydrobia neglecta* Muus, 1963 in the presence but not in the absence of infaunal predators (including *Lineus ruber* (Müller, 1774)) (McArthur, 1998). Given the foraging mode of nemerteans and their ability to crawl into even the smallest crevices (see above), we suspect that these interactive effects occur in a variety of habitats and with a variety of nemertean predators and their preferred prey. Marine invertebrates commonly preyed upon by nemerteans are also consumed by a multitude of other predators. Nemerteans are relatively slow-moving predators, or even utilise a sit-and-wait strategy, while many other predators actively search for their prey. Potential prey organisms are thus exposed to predators using opposing strategies. It is thus very likely that additive interactions occur when nemerteans are present together with other more active predators. Nemerteans that are preferably sitting between algae or mussels, under stones or in crevices may ‘block’ shelters that are used by many potential prey organisms in the presence of water column predators (see Fig. 2). When benthic disturbers are present, the amphipod *Corophium volutator* (Pallas, 1766) becomes highly susceptible to epibenthic predators (Flach & de Bruin, 1994). This amphipod reacts

to the presence of its nemertean predator *Tetrastemma melanocephalum* in a similar manner as to benthic disturbers, i.e. by increased emigration (Kruse & Buhs, 2000), thereby becoming exposed to water column predators. Increased migration behaviour has also been observed for *Gammarus locusta* (Linnaeus, 1758) and *Nereis (Hediste) diversicolor* O.F. Müller, 1776 in the presence of their nemertean predators, *Amphiporus lactifloreus* and *Lineus viridis*, respectively (Thiel & Reise, 1993). More experiments approaching the natural situation with multiple predators lurking for prey should be conducted (see Sih et al., 1998). Predator manipulations in the field appear necessary in order to elucidate the impact of nemerteans on the community structure. In addition, surveys of the spatial and seasonal distribution of both predator and prey species will help to reveal interactions between them.

Future directions

Nemertean predators are locally abundant in hard-bottom habitats and in other highly structured habitats, yet little is known about their abundance and impact. This lack of knowledge most likely is due to the fact that it is difficult to quantify the abundance of macrofauna in these highly structured habitats, a task that should be approached in the future.

Until present, prey preferences have been examined only for a few large nemertean species, but there remain many nemertean species for which nothing is known about their prey preferences. Similarly, the predation rates of nemerteans appear to be highly variable and the factors influencing them need to be elucidated in order to obtain more reliable estimates. We propose that these estimates be verified by physiological studies (e.g. O₂-consumption). It would also be important to examine the predation rates of nemerteans in response to different temperatures (“What is the preferred temperature of nemertean predators?”). Interestingly, nemertean predators are reported as abundant and important predators from environments where water and air temperatures rarely exceed 5–15 °C. In these environments, large aggregations of nemerteans can frequently be observed (Fig. 3). It is possible that their physiology gives nemertean predators an advantage over their prey items in these environments. Similarly, other important predators (e.g. fish and decapods) may lose predation efficiency at low temperatures, which may increase the competitive advantage of nemertean predators.

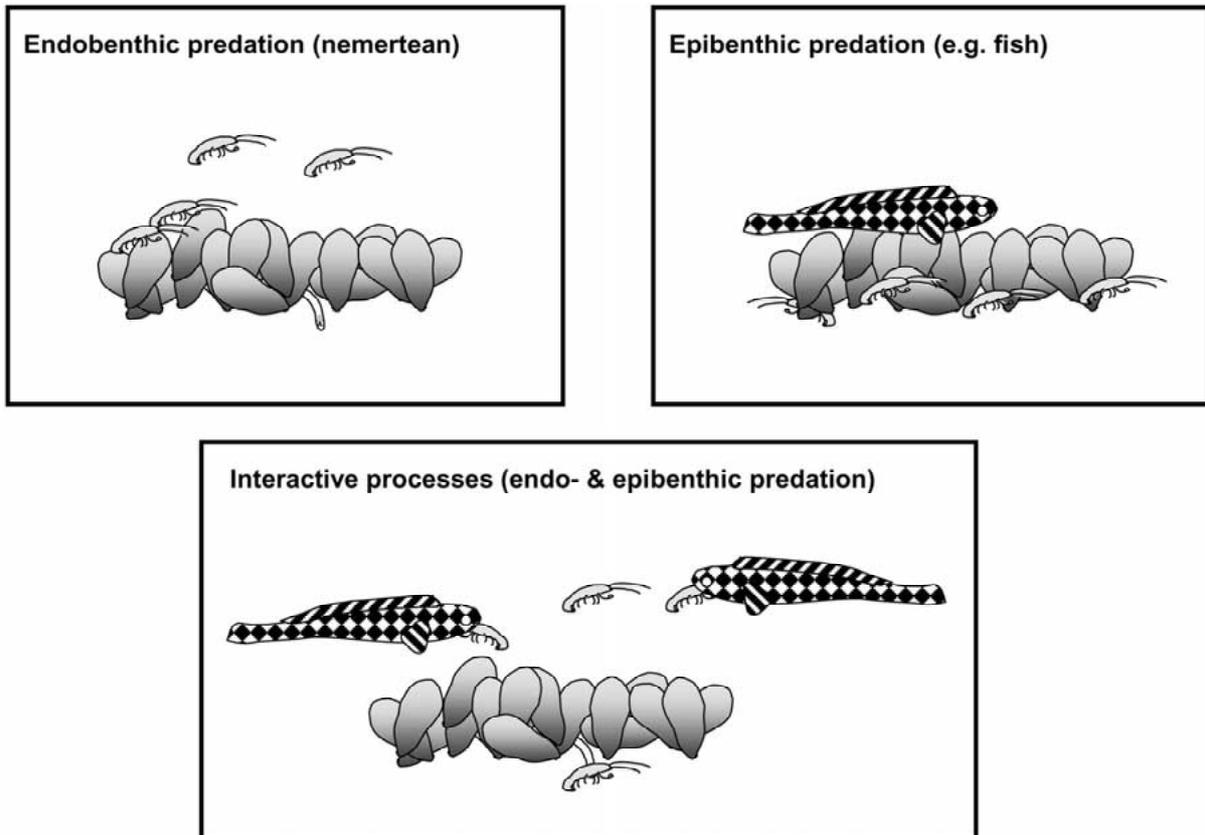


Figure 2 Exemplified reaction of prey organisms to the presence of endobenthic and epibenthic predators in highly structured habitats, and the hypothetical interactive effects of both endo- and epibenthic predators.



Figure 3 Dense assemblages of *Parborlasia corrugatus* underneath boulders in the intertidal of Magellan Street, near Punta Arenas, Chile; Photo courtesy of Jacqueline Parada Martinez, Universidad de Magallanes, Chile.

With respect to the nemertean fauna in highly structured habitats, we consider it of primary importance to identify the preferred prey organisms of the main nemertean predators in these habitats. Interactive effects are most likely to occur in these highly structured habitats. Understanding how, and under which conditions, nemertean predators are most effective, will help to better understand their role in marine ecosystems in the future.

Acknowledgements

During the writing of this article M.T. received financial support through project FONDECYT 3980002. We thank J. McDermott and two anonymous reviewers for many helpful comments.

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