



Predation rates of nemertean predators: the case of a rocky shore hoplonemertean feeding on amphipods

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

Abstract

Estimates of the predation rates of benthic nemerteans are often based on observations of single individuals, and consequently they may not be representative for all members of a population of these predators. Herein we conducted controlled and repeatable laboratory experiments on the predation rate of the hoplonemertean *Amphiporus nelsoni* Sánchez 1973, which is common at exposed rocky shores along the central Chilean coast. During the austral fall (April, May 2000), nemerteans were observed in relatively high numbers crawling in the intertidal zone during early morning or late-afternoon low tides. When these nemerteans were offered living amphipods held by a forceps, they immediately attacked the amphipods and fed on them. In the laboratory experiments, nemerteans preferred the amphipod *Hyale maroubrae* Stebbing, 1899, which is also very common in the natural habitat of *A. nelsoni*. The nemerteans preyed to a higher extent on small males and non-ovigerous females than would have been expected from their abundance. We suggest that these (non-reproductive) stages of *H. maroubrae* are very mobile and therefore have a high likelihood of encounters with nemerteans. Predation rates reached maxima when nemerteans were provided prey densities of four or more of their preferred prey species, *H. maroubrae*, furthermore indicating that encounter rates with prey may affect predation rates. In long-term laboratory experiments, *A. nelsoni* consumed more amphipods during low tide conditions than during high tide conditions. Many nemerteans in the field prefer particular environmental conditions (e.g. nocturnal low tides), which restricts the time available for successful feeding. In the long-term experiment, predation rates of *A. nelsoni* never exceeded 0.5 amphipods nemertean⁻¹ d⁻¹. Maximum feeding events were 3 or 4 amphipods nemertean⁻¹ d⁻¹, but this only occurred during 10 out of a possible 2634 occasions. Nemerteans that had consumed 3 or 4 amphipods during 1 day, consumed substantially less prey during the following days. Towards the end of the long-term experiment, average predation rates decreased to ~0.2 amphipods nemertean⁻¹ d⁻¹, corresponding to predation rates reported for other nemertean species (0.1–0.3 prey items nemertean⁻¹ d⁻¹). We suggest that predation rates from laboratory experiments represent maximum estimates that may not be directly transferable to field populations. Additionally, low predator–prey encounter rates with preferred prey in the field may further limit the predation impact of nemertean predators in natural habitats.

Introduction

Hoplonemerteans are important predators on small crustaceans, particularly peracarids (amphipods and isopods) (McDermott & Roe, 1985). Several studies from seagrass and intertidal soft-bottom habitats have demonstrated that these nemertean predators can exert a substantial impact either on the individual behaviour or on the distribution pattern and abundance

of potential prey organisms (McDermott, 1988, 1993; Thiel & Reise, 1993; Kruse & Buhs, 2000; Chernyshev, 2000). In a review on the importance of infaunal predators, Ambrose (1991) revealed that nemerteans apparently have the potential to reduce the standing stock of their preferred prey organisms by up to 50%. Yet, he also cautioned that “not all laboratory derived feeding rates are easily extrapolated to the field”. In order to evaluate the role of nemerteans in macro-

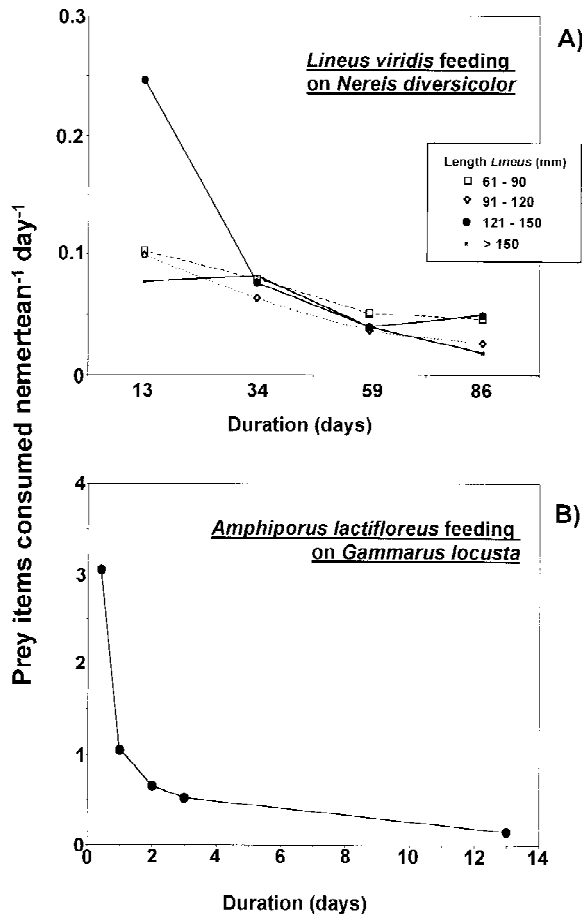


Figure 1. Predation rates of a heteronemertean and a hoplonemertean on their preferred prey organisms. Values recalculated after (A) Nordhausen (1987), and (B) Thiel (1992); in the study with *Lineus viridis* four different size classes of nemerteans were considered.

invertebrate assemblages correctly, knowledge of their prey preferences as well as of their feeding rates is essential.

Many studies reporting feeding rates of nemerteans are based on single observations or on short-term laboratory experiments using nemerteans that have recently been taken from the field. These individuals may be very hungry, and will readily attack any prey item offered to them. Indeed it has been reported that nemerteans may attack up to five prey items within a very short time period (24 h) in laboratory experiments (Bartsch, 1973, 1975, 1977; McDermott, 1976). However, following such a feeding frenzy, nemerteans possibly will not attack any additional prey items for a long time thereafter. Consequently, predation rates based on observations of only a few days duration may represent unrealistically high values. Long-term ex-

periments have indicated that the initially high predation rates of nemerteans rapidly diminish approaching values that are substantially lower than those reported from short-term experiments (Fig. 1).

Predation rates may also depend on the quality and numbers of the offered prey items. For example, in turbellarian predators, feeding rates increased positively with prey densities (Menn & Armonies, 1999). Similarly, Abrams et al. (1990) had reported the predatory polychaete *Harmothoe sarsi* (Malmgren, 1865) to reduce its prey intake when offered low numbers of its preferred prey, the amphipod *Pontoporeia affinis* Lindström, 1855. Predation rates of hoplonemerteans, many of which are sit-and-wait predators feeding on highly mobile amphipods, may also strongly depend on prey densities. With increasing numbers of prey organism, the likelihood of encounters between predator and prey will also increase. In addition to prey density, the size and species composition of potential prey items will also affect the predation rate of nemerteans. Thus, replicated experiments with different numbers and species of potential prey items appear essential in order to obtain reliable estimates of nemertean predation rates.

Along the Pacific coast of Chile, the nemertean *Amphiporus nelsoni* Sánchez, 1973 is common among turf algae and mussel beds growing on intertidal hard-bottoms (Sánchez, 1973). In these habitats, also its potential prey organisms, peracarid crustaceans, are very abundant (see e.g. Taylor, 1998) yet nothing is known about the prey preference of *A. nelsoni*. Given the large numbers of *A. nelsoni* that can be observed in its intertidal habitat, this nemertean could possibly have a strong predatory impact on its prey species. The objectives of this study were therefore, to identify the preferred prey species of *A. nelsoni* and determine the predation rate of this nemertean. After revealing the preferred prey species of nemerteans, we employed replicated and long-term experiments in order to obtain estimates of their predation rates. We used our results to critically discuss previous estimates of nemertean predation rates.

Materials and methods

Study site

All nemerteans used in this study were collected at La Pampilla Beach, a hard-bottom shore near Coquimbo, (29° 57' S/71° 21' W), Chile. Many rock and boulder

surfaces at La Pampilla Beach are covered by algal turf that is inhabited by a wide variety of marine invertebrates (polychaetes, bivalves, crustaceans representing the most abundant groups). At a station of about 1 km distance from the study site, the water temperatures varied between 13 °C and 20 °C throughout the year (Moraga & Olivares, 1993).

Nemertean activity

Large numbers of *Amphiporus nelsoni* were observed during low tides in April and May 2000. Herein, we describe occasional observations on nemertean behavior in the field that we made during collecting trips to La Pampilla Beach. During these trips, we collected nemerteans as well as potential prey organisms to be used in the laboratory experiments.

Nemertean feeding rates and prey preferences

We conducted two experiments, one which lasted 8 days (short-term experiment) and a second one which lasted 75 days (long-term experiment). The general set-up was the same in both experiments: one nemertean each was placed together with prey items in small petri dishes (diameter: 8.8 cm, height: 1.4 cm) completely filled with seawater (90 ml). Each dish contained a small piece (2 cm²) of *Ulva rigida* C. Agardh 1822 as food for the peracarids. Additionally, in the long-term experiment we provided an empty and slightly eroded shell of *Calyptreaa radians* (Lamarck, 1816) as shelter for both nemerteans and peracarids. The dishes were checked twice every day, and all peracarids encountered dead during these controls were recorded and replaced. Every morning, at about 10.00 h, all dishes were checked and thereafter left without water in order to simulate low tide conditions. In the afternoon, at about 16.00 h (i.e. 6 h later), all dishes were revised again and then filled to the top with seawater in order to simulate high tide conditions. Following this second daily control, the dishes were left at a dark place in the laboratory until the following morning (i.e. 18 h later). Cause of death was determined for all amphipods that were found dead during the revision utilising a dissecting microscope. We distinguished amphipods that had been consumed by nemerteans (complete exoskeleton, remaining tissue in extremities, particularly in the gnathopods, mucus adhering to empty exoskeleton), amphipods that had been attacked and cannibalised by conspecifics (ruptured exoskeleton, tissue only partly removed where exoskeleton was broken), amphipods that had died of

unknown causes (dead, apparently untouched amphipods), and amphipod moults (exoskeleton very thin, ruptured anteriorly, extremities completely empty, no mucus adhering to empty exoskeleton). All dead amphipods were sexed and their size determined by measuring the length of the head segment. Each time we collected fresh amphipods as prey for the short-term experiment, we also preserved a representative field sample, which was used to find out whether nemerteans preferred a certain size spectrum of prey in the experiment (see below). Additional information on the condition of amphipods killed by nemerteans (recently moulted, ovigerous females, etc.) was noted whenever available.

The short-term experiment (8 days duration) was designed first to reveal the preferred prey item of *A. nelsoni*, and the optimal prey density that subsequently would be used for the long-term experiment (75 days duration). Treatments containing 1, 5, 10 and 20 randomly selected individuals of *Hyale maroubrae* Stebbing, 1899, a treatment with five mated pairs of *H. maroubrae*, and another treatment containing 2 *H. maroubrae*+2 *H. hirtipalma* (Dana, 1852)+2 isopods *Exosphaeroma* sp. were left with nemertean predators. The eight replicates of each treatment were maintained and revised as described above.

Based on the results from the above experiments, we then started a long-term experiment designed to investigate the long-term predation rate of nemerteans. For this experiment, nemerteans and their prey were maintained and checked in the same way as described above. For 75 days, we maintained one *A. nelsoni* in each dish together with two (20 replicates) and four (10 replicates) amphipods *H. maroubrae*. In each replicate, equal numbers of male and female amphipods were offered to the nemerteans. Replicates were maintained and revised as described above.

Data evaluation and statistical analysis

For each prey item, it was determined whether the predation event occurred with or without water coverage. The obtained values of total predation events that occurred with or without water were compared with expected values using a χ^2 goodness of fit test. Expected values were calculated based on the assumption that nemerteans were 25% of their time without water and 75% of the time with water, i.e. if a total of four predation events was recorded during an experiment, then according to the time-dependent water coverage one predation event should have happened

without water and the other three predation events with water coverage. For this analysis, all replicates and all days from one particular treatment were pooled at the end of the experiment.

The sex of all amphipods preyed upon by nemerteans was recorded and compared to expected values. In the short-term experiment, amphipods taken from the field population had been introduced at random to the dishes, and thus the number of females and males found in the preserved field sample was taken as expected values. Similarly, the proportion of ovigerous and non-ovigerous females preyed upon by nemerteans was compared to their proportion found in the field population. In the long-term experiment, males and females were supplied at equal numbers, and thus it was assumed that nemerteans should have preyed upon the same number of females and males (=expected values).

In order to compare among treatments with different numbers of prey items, we calculated average daily predation rates for the entire duration of the short-term experiment (8 days) and for the first 8 days of the long-term experiment. For the short-term experiment, we compared among the six different treatments using a Kruskal–Wallis one-way ANOVA, and for the first 8 days of the long-term experiment we compared between the two treatments using a Mann–Whitney *U*-test. We also employed the Mann–Whitney *U*-test to examine whether significant differences between the two treatments existed for the total predation rates measured during the entire long-term experiment.

We also examined the effects of the feeding history of nemerteans on their predation rates for all nemerteans during the first 8 days of the experiments (encompassing the entire short-term experiment). Additionally, we analysed the predation rate of selected nemertean individuals during the 8 days following maximum predation events. In order to reveal long-term trends of predation rates during the long-term experiment we calculated the 8-day running mean. The running mean was used, since predation rates of individual nemerteans may be affected for several days following maximum (or minimum) feeding events. This procedure furthermore was employed in order to smoothen extreme values that resulted from the high variability in predation rates among nemerteans.

Results

Observations on the feeding behaviour of Amphiporus nelsoni

In the field, nemerteans were found primarily in the mid intertidal zone. During morning and evening low tides, large numbers of nemerteans were crawling over the rocks apparently in search of prey. Occasionally, these nemerteans were observed consuming freshly killed amphipods, either *H. hirtipalma* (one occasion) or *H. maroubrae* (several occasions). One nemertean was found to feed on an insect larva, which also occur abundantly on algal-covered rocks in the habitat of the nemerteans. Observations of nemerteans in the process of feeding were few compared to the number of nemerteans that were searching for prey. When we offered a live amphipod held by forceps to these searching nemerteans, they immediately everted their proboscis, killing and subsequently feeding on the amphipod.

In the laboratory experiments, *Amphiporus nelsoni* captured amphipods both with and without water coverage in the petri dishes. Nemerteans in the short-term experiments did not consume more amphipods during low tide conditions (dishes without water) than during high tide conditions (dishes with water) (Table 1a). However, in the long-term experiments, significantly more predation events occurred during low tide conditions (Table 1b).

Several nemerteans had overtaken amphipods shortly after these had moulted as was revealed by the presence of empty exuviae that had not yet completely hardened. Also, on one occasion, shortly after draining the seawater from a petri dish, we observed how a nemertean apparently hit two amphipods in one strike: immediately following a successful attack on a male amphipod that held a female in amplexus, the nemertean stroke again with its proboscis, this time killing the female. The exuviae of both amphipods were later (after 6 h) found empty in the dish. Occasionally amphipods were only consumed partly by their nemertean predators.

Prey organisms attacked by nemerteans

In the choice experiments, the nemerteans exclusively fed on amphipods with preference for *H. maroubrae*. Only one of the eight nemerteans that had a choice between *H. maroubrae* and *H. hirtipalma* killed and consumed the latter species. This individual first consumed one *H. hirtipalma* and 2 days later a second

Table 1. Predation events on amphipods *Hyale maroubrae* by nemertean *Amphiporus nelsoni* in dishes while covered and uncovered with water during the (a) short-term and (b) long-term experiments. Expected values based on the assumption that each day dishes were 6 h without water while they were 18 h with water; * $p < 0.05$; for further details see 'Materials and methods'

	Without water	With water	Total	χ^2
(a) Short term experiment				
1-amphipod treatment				
Consumed (after 8 days)	1	4	5	
Expected	1.25	3.75	5	0.08
5-amphipod treatment				
Consumed (after 8 days)	2	16	18	
Expected	4.5	13.5	18	3.52
10-amphipod treatment				
Consumed (after 8 days)	4	12	16	
Expected	4	12	16	0
20-amphipod treatment				
Consumed (after 8 days)	4	12	16	
Expected	4	12	16	0
(b) Long-term experiment				
2-amphipod treatment				
Consumed (after 75 days)	112	118	230	
Expected	57.5	172.5	230	68.88*
4-amphipod treatment				
Consumed (after 75 days)	109	119	228	
Expected	57	171	228	63.25*

Table 2. Total predation events of male and female amphipods *Hyale maroubrae* by nemertean *Amphiporus nelsoni* in the (a) short-term and (b) long-term experiments; and total of predation events on ovigerous and non-ovigerous female amphipods *H. maroubrae* in the (c) short-term experiment; expected values based on amphipod samples taken from the field for the short-term experiment, and on equal ratios of the two sexes offered in the long-term experiment; * $p < 0.05$; for further details see 'Materials and methods'

	Females	Males	Total	χ^2
(a) Short-term expmt.				
Consumed (after 8 days)	21	27	48	
Expected (sample from field)	213	170	383	5.70*
(b) Long-term expmt.				
Consumed (after 75 days)	219	239	458	
Expected (offered at equality)	229	229	458	0.19
(c) Short-term expmt.				
	Females		Total	χ^2
	Ovigerous	Non-ovigerous		
Consumed (after 8 days)	11	10	21	
Expected (sample from field)	45	168	213	58.62*

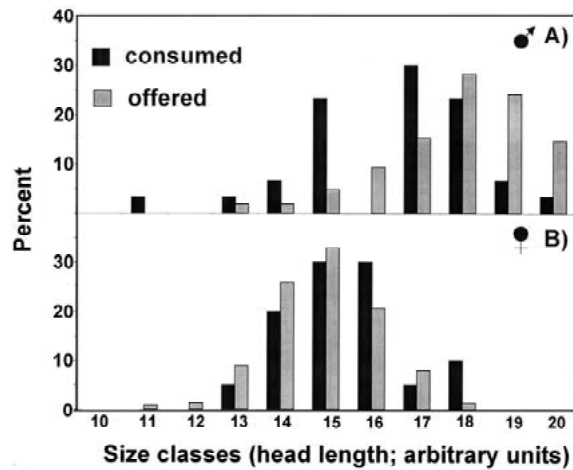


Figure 2. Size frequency distributions of (A) male and (B) female amphipods *Hyale maroubrae* consumed by *Amphiporus nelsoni* and offered during the short-term experiment (based on amphipods from the field population which were preserved simultaneously with stocking the experiments); all amphipods preyed upon by *A. nelsoni* in the short-term experiment were pooled regardless of day and treatment.

one. Nemerteans preyed upon both male and female *H. maroubrae*. In the short-term experiment, significantly more male than female amphipods were consumed while in the long-term experiment no such difference was found (Table 2a,b). Non-ovigerous females were fed upon to a significantly larger proportion than would have been expected from their frequency of occurrence in the field (Table 2c). In the short-term experiment, nemerteans fed more on small males than on large males (Fig. 2a). By contrast, nemerteans fed on all sizes of female *H. maroubrae* (Fig. 2b).

Predation rates and prey densities

Nemerteans were found to prey intensively on the amphipod *Hyale maroubrae*. After the 8 days of the short-term experiment, no significant difference in predation rates were found in treatments with different prey densities (Fig. 3a) (Kruskal–Wallis, one-way ANOVA, $df=5$; $p>0.05$). However, average predation rates in treatments with at least five *H. maroubrae* were usually higher than in those with only one or two *H. maroubrae* (Fig. 3a). This may primarily be due to the fact that nemerteans in the low density treatments repeatedly consumed all *H. maroubrae* present in a dish after which there were no more amphipods left to be consumed until we replaced them again during the next control. By contrast, in high density treatments, nemerteans occasionally consumed several

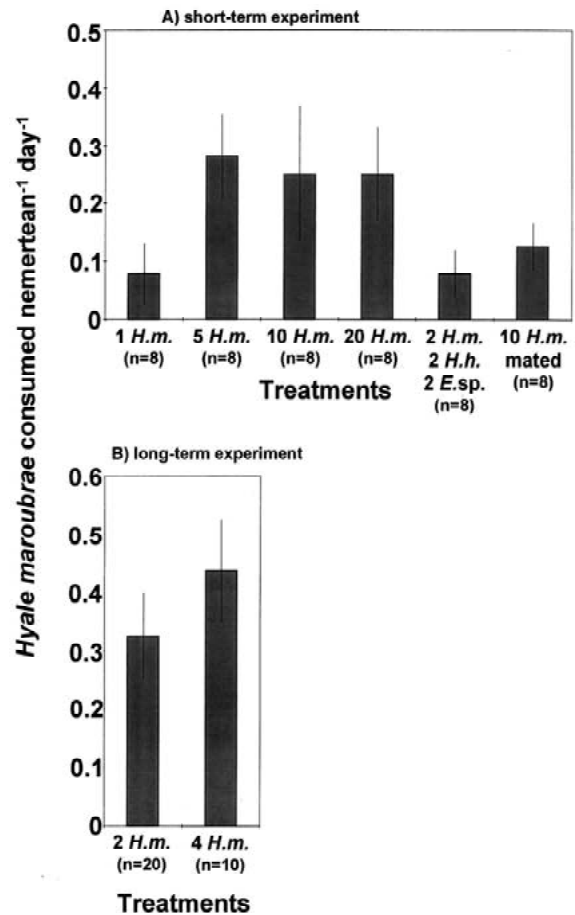


Figure 3. Average predation rates of *Amphiporus nelsoni* on its preferred prey organism, the amphipod *Hyale maroubrae* during (A) the short-term experiment, and (B) the first 8 days of the long-term experiment; individual nemerteans were held in treatments with different numbers of prey items in small plastic dishes filled with seawater; of each treatment; n =number of replicates; *H.m.* – *Hyale maroubrae*, *H.h.* – *Hyale hirtipalma*, *E. sp.* – *Exosphaeroma sp.*; for further details see ‘Materials and methods’.

amphipods, albeit never all the amphipods that were present in a dish.

During the first 8 days of the long-term experiment, predation rates were of similar magnitude as those from the short-term experiments (Fig. 3). During these first 8 days no significant differences were found between the 2- and the 4-amphipod treatments (Mann–Whitney U -test; $p>0.05$). However, when considering the entire duration of the long-term experiment (75 days), nemerteans from the 4-amphipod treatments consumed significantly more amphipods than those from the 2-amphipod treatments (Mann–Whitney U -test; $p<0.05$) (Fig. 4). Similarly as in the short-term experiments, this may be due to the fact that nemer-

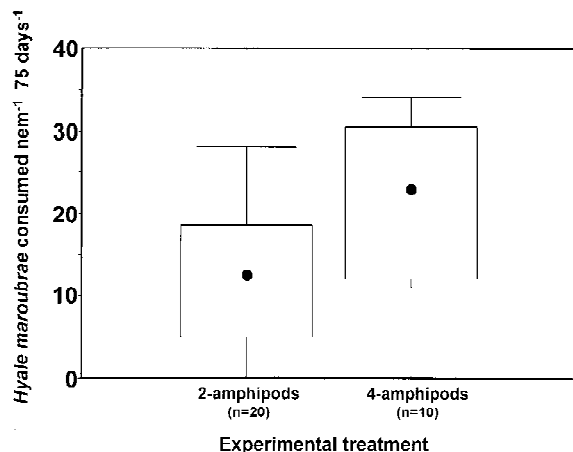


Figure 4. Total numbers of amphipods *Hyale maroubrae* consumed by individual *Amphiporus nelsoni* during the entire 75 days of the long-term experiment in the experimental treatments with 2 and 4 amphipods; shown are the median (dot), the 25% and 75% limits (box), and the range of values (whiskers).

teans in 4-amphipod treatments rarely consumed all amphipods available in their dish: this occurred only in one out of 1500 checks (10 replicates with two daily checks each during the 75 days of the experiment) which represents <0.07% of all possible occasions. In contrast, nemerteans in the 2-amphipod treatments had consumed all amphipods in 29 out of 3000 checks (~1% of all possible occasions). Thus, predation rates in the 2-amphipod treatment may have been artificially suppressed since nemerteans repeatedly had no more prey available.

Predation rates and feeding history of *Amphiporus nelsoni*

The predation rates of *A. nelsoni* both in short-term and in the long-term experiments were highly variable (Fig. 4). In the long-term experiment, one nemertean did not feed at all during the entire duration of the experiment (75 days) while others consumed >30 amphipods during this time period (Fig. 4).

Throughout our entire study, we recorded 10 occasions where individual nemerteans had consumed >2 amphipods in 1 day, but no nemertean ever killed five or more amphipods during 1 day (Fig. 5). Following days during which nemerteans had consumed three or four amphipods (i.e. maximum feeding days), they rarely consumed more than one amphipod per day (Fig. 5). During the 8-day period following and including these maximum feeding days, their average daily predation rate usually did never exceed 1.0

amphipod nemertean⁻¹ d⁻¹ (Fig. 5 – it should be emphasised that these data include the 10 maximum feeding days out of a total of 2634 ‘nemertean-days’ recorded during the entire study).

During the short-term experiment and the first 8 days of the long-term experiment, the average predation rates were highly variable (Fig. 6). No clear temporal trend with high predation rates during the first days and decreasing rates were discernible in our experiments (Fig. 6).

In contrast, a long-term decline was observed in average daily predation rates both in the 2- and in the 4-amphipod treatments (Fig. 7). This decline persisted more or less continuously throughout the study period. The average daily predation rate never exceeded 0.5 amphipods nemertean⁻¹ d⁻¹ and treatments declined to ~0.2 amphipods nemertean⁻¹ d⁻¹ in the 4-amphipod treatment and to ~0.1 amphipods nemertean⁻¹ d⁻¹ in the 2-amphipod treatment (Fig. 7).

Discussion

During our occasional observations in the field, we recorded a high searching activity of *Amphiporus nelsoni*, yet surprisingly few nemerteans were observed feeding, suggesting that predation success and consumption rate in the field may be low. In the laboratory, where we provided nemerteans with prey items *ad libitum*, nemerteans rarely attacked more than one amphipod per day. Average predation rates did not exceed 0.5 prey items nemertean⁻¹ d⁻¹. These results indicate that nemerteans may not be as voracious predators as has been suggested by previous field and laboratory experiments.

Nemertean activity

Many benthic nemerteans come occasionally to the substrate surface where they can be observed in large numbers during periods of high activity (Roe, 1976; Nordhausen, 1988; Thiel et al., 1995; Kruse & Buhs, 2000). Nemerteans are active at the substrate surface in pursuit of prey (e.g. Roe, 1970; Nordhausen, 1987; Thiel et al., 1995; Kruse & Buhs, 2000) or in search of mating partners (Bartolomaeus, 1984). During periods when nemerteans are searching for mates, feeding activity is low or absent (Thiel et al., 1995).

Most studies have revealed high foraging activity of nemertean predators during low tides, especially at

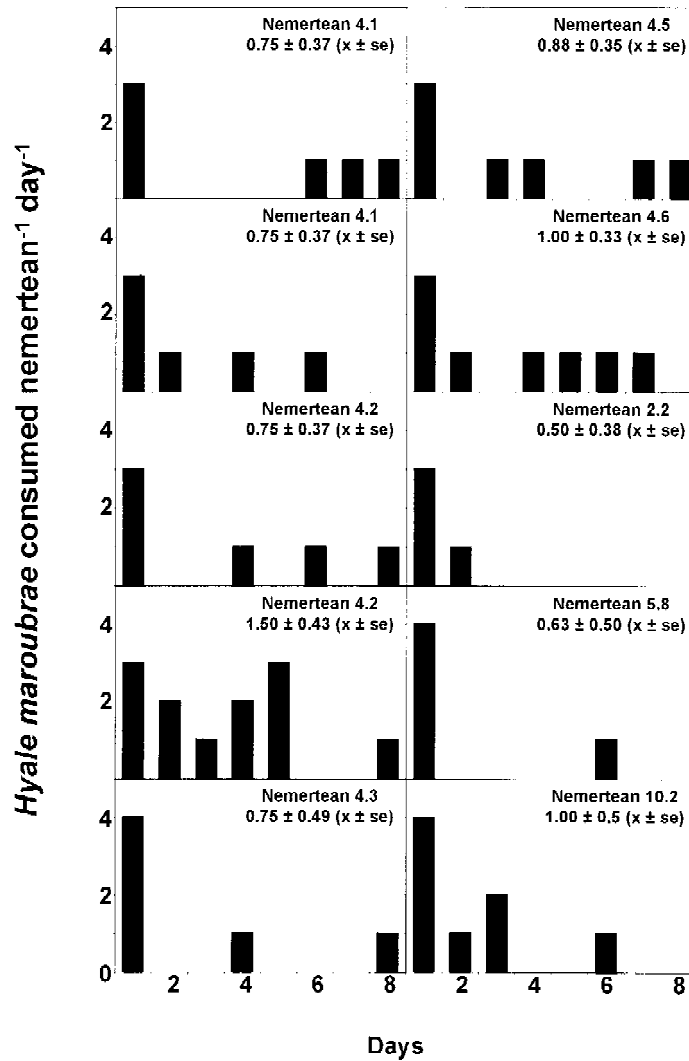


Figure 5. Daily predation events of selected nemerteans *Amphiporus nelsoni* following the days during which maximum values of predation events on the amphipod *Hyale maroubrae* were observed, starting with the day of maximum predation; shown are only nemertean individuals that consumed at least three or four amphipods (maximum numbers recorded herein) during 1 day of the experiments; the average predation rate nemertean⁻¹ d⁻¹ (mean±S.E.) has been calculated for each respective nemertean individual for the time period shown; two nemertean individuals (4.1 and 4.2) consumed a maximum of three amphipods d⁻¹ during two occasions.

night (Roe, 1970; Thiel et al., 1995). During nocturnal low tides, prey escape is largely restricted, and furthermore competition with visual competitors may be diminished (Thiel, 1998). In the present study, large numbers of *Amphiporus nelsoni* were observed during early morning and later afternoon low tides. We did not conduct observations on nemertean behaviour at night, but we consider it likely that many nemerteans were also active at night low tides. Kruse & Buhs (2000) remarked that the hoplonemertean *Tetramma melanocephalum* (Johnston, 1837), when in

active pursuit of its amphipod prey, showed highest foraging activity during evening low tides but not during night low tides – they discuss that temperatures during summer evenings coincide with the temperature preference of these actively foraging nemerteans.

Nemerteans *A. nelsoni* were actively crawling on algal-covered rocks and boulders in the mid intertidal zone. In this habitat, amphipods from the genus *Hyale* hide in large numbers between the algae growing on intertidal rocks (Buschmann, 1990; Lancellotti & Trucco, 1993). Thus, there exists a good probabil-

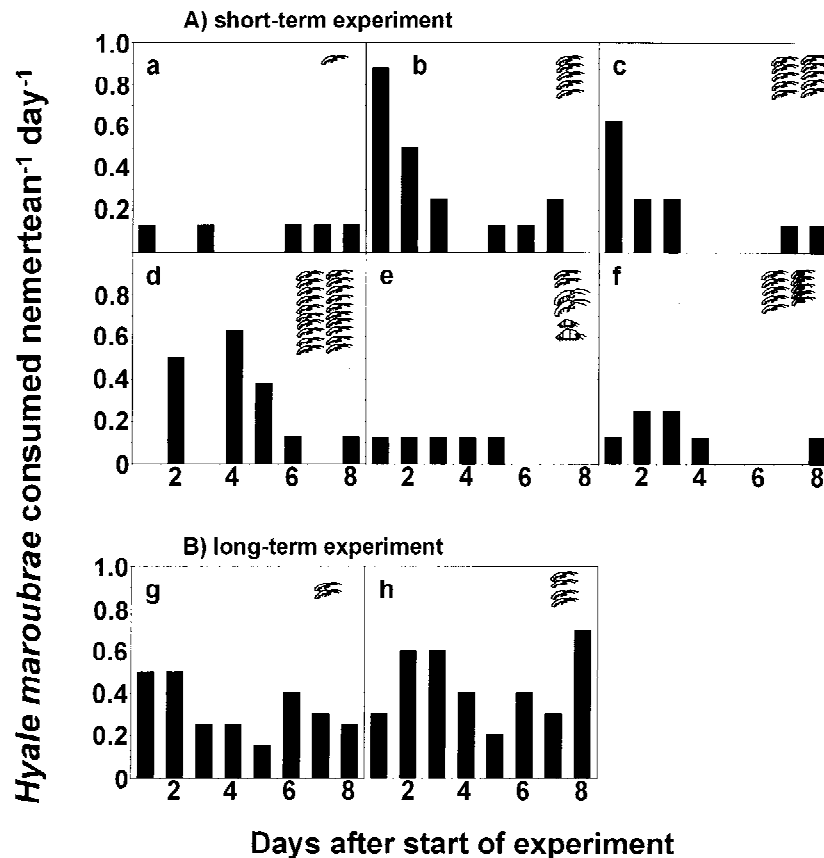


Figure 6. Daily predation rates of *Amphiporus nelsoni* on its preferred prey organism, the amphipod *Hyale maroubrae* during (A) the short-term experiment, and (B) the first 8 days of the long-term experiment; individual nemerteans were held in treatments with (a) 1 *Hyale maroubrae*, (b) 5 *H. maroubrae*, (c) 10 *H. maroubrae*, (d) 20 *H. maroubrae*, (e) 2 *H. maroubrae*+2 *H. hirtipalma*+2 *Exosphaeroma* sp., (f) 5 pairs of *H. maroubrae*, (g) 2 *H. maroubrae*, and (h) 4 *H. maroubrae*; for further details see 'Materials and methods'.

ity that *A. nelsoni* will encounter its amphipod prey during these foraging trips. At low tide, these amphipods are not able to escape into the water column when pursued by their nemertean predators. Furthermore, it must be considered that hoplonemerteans require substantial time to ingest prey, and hoplonemerteans that are feeding on crustaceans (such as *A. nelsoni*) have no means of holding their prey effectively during uptake of pre-digested prey substances. Rock surfaces in the habitat of *A. nelsoni* are exposed to strong wave action. While nemerteans themselves may be able to withstand moderate wave-action, even weak waves immediately carry away any amphipod carcass previously captured by a nemertean (own observations). Thus, in its habitat, *A. nelsoni* can only effectively capture and feed on amphipods *Hyale* spp. during low tides. The result from the long-term experiment, namely that *A. nelsoni* captured significantly more amphipods during low tide than during high tide

conditions support the notion that hoplonemerteans from wave-swept intertidal habitats preferentially forage during low tides. Taken the apparent preference of *A. nelsoni* for morning or evening low tides, the potential foraging period of this nemertean species is further restricted to particular days.

Not all nemertean predators are actively pursuing their prey as *A. nelsoni* does it during low tides. Some are simply waiting in strategic positions until a prey organism passes, which is when they strike (see e.g. Christy et al., 1998). Since in our laboratory experiments, *A. nelsoni* also captured amphipods while the dishes were completely filled with water, we assume that this nemertean can also attack amphipods in the field during high tide conditions or in tide pools. However, rather than actively pursuing their prey during high tide (as they do during low tide) they will most likely hide in crevices where they may attack any amphipod that attempts to seek shelter in these crevices.

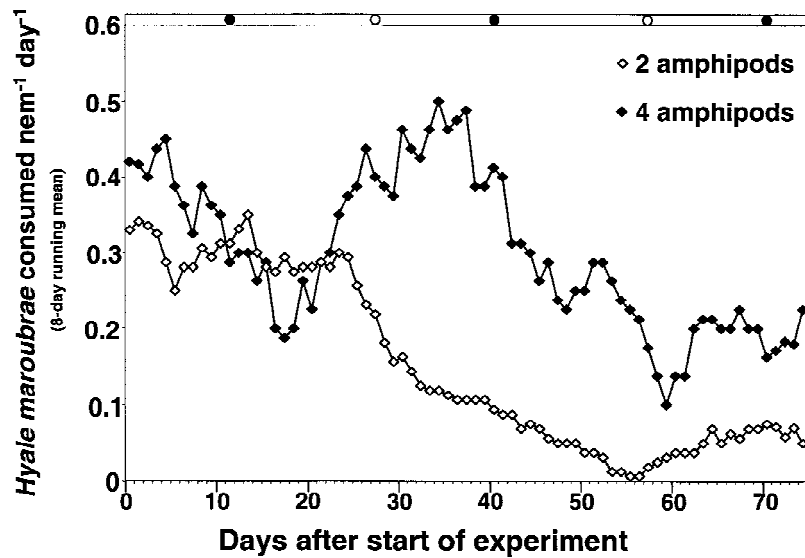


Figure 7. Average daily predation rates of *Amphiporus nelsoni* on *Hyale maroubrae* during the long-term experiment; nemerteans were held individually in treatments with two or four amphipods in small plastic dishes filled with seawater, $n=20$ and $n=10$ replicates, respectively; shown is the 8-day running mean; symbols on top of graph show days with full moon (filled dots) and days with new moon (open dots); for further details see 'Materials and methods'.

In the present study, we had a small shell in the petri-dishes during the long-term experiment but not during the short-term experiment. Both nemerteans and amphipods often hid under this shell which may explain the slightly higher predation rates of *A. nelsoni* during the first 8 days of the long-term experiment compared to the 8 days of the short-term experiment (see Fig. 4). At present, it is not known whether successful predation and prey consumption by *A. nelsoni* is possible and occurs during high tide in their natural habitat, where strong currents persist during immersion.

Nemertean prey selection and functional response to prey density

The hoplonemertean *Amphiporus nelsoni* showed a strong preference for the amphipod *Hyale maroubrae*. This species reaches a maximum length of 4 mm and is thus the smallest *Hyale* species occurring in the habitat of *A. nelsoni*. The other amphipod species that are common in this zone are *H. hirtipalma* and *H. rubra* (Thomson, 1879), which reach substantially larger sizes than *H. maroubrae*. Nemerteans are capable to attack, kill and consume *H. hirtipalma*, but they preferred *H. maroubrae* in the choice experiment. Possibly, the large *H. hirtipalma*, following the initial attack by *A. nelsoni*, may be able to escape a short distance thus increasing the possibility that nemerteans lose their prey. *Amphiporus nelsoni* may prefer *H.*

maroubrae since this small amphipod species is immediately succumbed following the initial attack by the nemertean. We therefore suggest that the higher attack rate on *H. maroubrae* as compared to *H. hirtipalma* is the result of active prey selection by the nemertean.

The fact that in the short-term experiment, nemerteans attacked large male and ovigerous female amphipods to a lesser extent than would have been expected from their natural distribution may be a result of different movement rates of these amphipod stages rather than active prey selection by the nemertean. Among amphipod males, strong competition for receptive females exists. As has been demonstrated in other studies (see for example Iribarne et al., 1996), large male amphipods are the most likely to win access to females, subsequently holding the female in the typical precopula position. Possibly, the movement rates of large male amphipods (holding females) are much lower than those of small males that are still searching for receptive females. Similarly, ovigerous females may move less than females that have recently released their broods and are now accumulating resources to produce new eggs. Given high movement rates in small males and non-ovigerous females of *H. maroubrae*, their chances of encountering nemerteans would be relatively high, and consequently, they are more susceptible to nemertean predators. Future studies investigating the movement behaviour of dif-

ferent amphipod stages and the consequences of this for their susceptibility towards nemertean predators are required.

Our experiments indicated some functional response of *A. nelsoni* at different prey densities. Apparently the maximum feeding rates were reached at ~4 amphipods per petri-dish. A further increase in prey density (5, 10 or 20 amphipods in dishes) did not result in any further increase of predation rates. Also the fact that no nemertean ever consumed more than four amphipods in 1 day suggests that this is the upper limit of prey items one nemertean can handle during 1 day. This value also ranges among the maximum number of prey killed during 1 day for other hoplonemerteans (Bartsch, 1973; McDermott, 1976, 1984, 1988; Thiel, 1992). Since in our present experiments, the dishes were checked twice each day and dead amphipods were replaced during these controls, nemerteans in the 4-, 5-, 10- and 20-amphipod treatments could never reach their consumption limit. Thus, predation rates recorded in these treatments (including the 4-amphipod treatment) can be considered relatively reliable estimates of the maximum predation rates of *A. nelsoni*.

Temporal development of nemertean predation rates

In our long-term experiment, we revealed that the predation rate of *A. nelsoni* approached values of 0.2 prey items nemertean⁻¹ d⁻¹. These values correspond to those reported for other nemertean species albeit only to those resulting from experiments that lasted at least 1 week (McDermott, 1984; Nordhausen, 1987; Thiel, 1992; Roe, 1993). In most of these studies, initially high predation rates rapidly decreased subsequently approaching a value of 0.2 prey items nemertean⁻¹ d⁻¹ or even lower. Clearly, laboratory experiments may not always reflect 'natural' predation rates of a predator. Organisms held for a long time under laboratory conditions may change their behaviour and their metabolism. Nemerteans, however, appear to be ideally suited to be maintained in the laboratory. Individuals of some species have reportedly been maintained in the laboratory for years (Gibson, 1972). Both Nordhausen (1987) and we were able to maintain nemerteans for time periods of >3 months without any apparent negative changes in their condition. The fact that the nemerteans continued to feed throughout these time periods indicates that they probably were in rather normal condition. The nemerteans *A. nelsoni* which we maintained in this study

even reached sexual maturity and after releasing them from intraspecific isolation in the experimental dishes and combining males and females they immediately spawned (personal observations at the end of long-term experiment). Following spawning, they immediately returned to feed in an apparently normal fashion (personal observations). We therefore conclude that the predation rates as revealed in long-term laboratory experiments reflect (or are very similar to) maximum predation rates in the field.

In the long-term experiments we observed a continuous decline in feeding rates. This decline, however, did not occur as rapidly as might have been expected given our original hypothesis that high initial feeding rates drop within a few days following saturation of the nemertean predators. We rather recorded a relatively slow decline throughout the study period. Possibly, this decline is due to the upcoming reproductive period of *A. nelsoni* towards the end of our study period. All nemerteans held during this long-term experiment accumulated reproductive products in their gonads. Interestingly, our observations revealed that *A. nelsoni* reproduces during the austral fall/winter (May–July), similar as has been observed for *A. lactifloreus* during the boreal fall/winter (October–December; Thiel & Dornedde, 1996). At present, however, it is not clear whether and how predation rates of *Amphiporus* spp. are affected by their reproductive activity.

The predation rates that we recorded during the beginning of our study range around 0.4 prey items nemertean⁻¹ d⁻¹. This predation rate is in the upper range of that reported for other nemertean species in long-term studies (McDermott, 1984; Nordhausen, 1987; Thiel, 1992; Roe, 1993), which is why we also consider this as the maximum value for *A. nelsoni*. It should also be noted that these values represent maximum predation rates revealed from laboratory experiments with *ad libitum* food supply. In their natural environment, these nemerteans may rarely experience such an easy and unhindered access to their preferred food items as in laboratory experiments. Thus, caution is advised when transferring these predation rates to the natural environment.

Conclusions

Two main approaches of revealing the predation activity of a nemertean predator can be distinguished: (a) estimate prey selection and predation rates that are

representative of those realised in a natural environment; or (b) examine prey preference and maximum predation rates that nemerteans will realise in an 'optimal' environment. While approach (a) aims to obtain data that can directly be included in community models, approach (b) aims to investigate intrinsic preferences and consumption rates of nemertean predators. Data obtained from approach (b) not necessarily can be transferred directly to the field since predator-prey encounter rates in a laboratory environment with *ad libitum* food supply may not reflect the natural situation. In our present study, we followed approach (b) aiming to identify maximum predation rates of nemerteans. Our results indicate that, when supplied with an overabundant food supply for 8 days or more, nemerteans do not consume more than 0.5 prey items nemertean⁻¹ d⁻¹. These maximum predation rates were obtained in highly artificial experiments where both predators and prey often sought shelter under the same hide and consequently predator-prey encounters may have occurred very frequently. Given that predator-prey encounters in the field may be dramatically less common than in our experiments, and that active foraging in the field is only possible during relatively short time periods of low water, average predation rates in the field probably rarely exceed 0.1 prey items nemertean⁻¹ d⁻¹. Predation rates that exceed these estimates should be re-examined before utilising them to estimate the effect of nemertean predators in natural communities.

Nemerteans have a strong preference for particular prey organisms (see Thiel & Kruse, 2001). In the present study, we also found indication that nemerteans prey more actively on certain life stages of their preferred prey. It is thus important to consider the proportion of different life stages within local populations of prey organisms before transferring predation rates from the laboratory to the field. Similarly, it became evident that temporal differences in foraging activity occur due to extrinsic factors (e.g. tidal, diurnal and lunar cycles) and to intrinsic factors (e.g. the reproductive stage of the respective nemertean predator). Thus, the impact of a nemertean predator on its prey population will also vary temporally.

Acknowledgements

We are most grateful to W. Nordhausen for kind permission to recalculate and use some of his unpublished data. A special thanks to S. Maslakova for

confirming our identification of *Amphiporus nelsoni* Sánchez, 1973. Two reviewers and I. Kruse provided many helpful comments that helped to improve the manuscript. During the writing of this article, M.T. received financial support through project FONDECYT 3980002.

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