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Activity patterns and predatory behavior of an intertidal nemertean from rocky shores: *Prosorhochmus nelsoni* (Hoplonemertea) from the Southeast Pacific

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Abstract Understanding the impact of environmental stressors on predator activity is a prerequisite to understanding the underlying mechanisms shaping community structure. The nemertean *Prosorhochmus nelsoni* is a common predator in the mid-intertidal zone on rocky shores along the Chilean coast, where it can reach very high abundances (up to 260 ind m^{-2}) in algal turfs, algal crusts, barnacle crusts, and mixed substrata. Tidal and diurnal scans revealed that the activity of *P. nelsoni* is primarily restricted to night and early-morning low tides and is relatively low when air temperatures are high. On average, larger worms crawled faster than smaller worms, with their maximum velocity being influenced by substratum type. Their estimated rate of predation is 0.092 prey items $nemertean^{-1}$ day^{-1}, just below the laboratory rate of $\sim$0.2 amphipods $nemertean^{-1}$ day^{-1} previously estimated for this species. *P. nelsoni* consumes a diverse spectrum of prey items (i.e., amphipods, isopods, decapods, barnacles, and dipterans) and is possibly exerting a significant influence on its prey populations. We suggest that the opportunistic predatory behavior of this intertidal predator is caused by the trade-off between immediate persistence (e.g., avoidance of desiccation) and long-term survival through successful foraging.

Introduction

Intertidal hard-bottom habitats are highly heterogeneous environments shaped by abiotic (e.g., wave action, tidal, and diurnal conditions) and biotic factors (Dayton 1971; Sousa 1979; Steger 1987). Predation has long been identified as a key factor influencing intertidal community dynamics, and the behaviors of many predators and scavengers are heavily influenced by abiotic conditions (Menge and Sutherland 1976, 1987), with many benthic predators restricting their activity to low tides when prey escape into the water column is precluded and prey location may be facilitated through chemoreception in unidirectional currents (see Rochette et al. 1994). Temperature (ambient and seawater) has also been implicated in dictating activity patterns of intertidal predators (Sanford 1999; Tomanek and Helmuth 2002) and has been shown to dominate over the light:dark cycle, for example, influencing the activity patterns of supratidal amphipod crustaceans (Forward et al. 2009). Additionally, changes in spatial heterogeneity may cause a shift in foraging behavior and prey preference, causing changes in prey-handling time (Gaymer et al. 2004). Prey-handling time can in turn be critical in determining the success of a predation event and can lead to specific patterns of zonation (Connell 1970). Rocky shore

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environments thus provide an ideal system in which to explore the interplay between environmental stress and biological interactions and their impact on community structure (Monaco and Helmuth 2011).

Nemertean worms are important predators in intertidal communities and, through laboratory and field-based investigations, have been shown potentially capable of exerting a significant influence on their prey populations when their abundances are high (Roe 1976; McDermott 1984; Nordhausen 1988; Ambrose 1991; Kruse and Buhs 2000). However, relatively few field-based studies of nemertean feeding ecology have been conducted, with the majority taking place in soft-bottom habitats (McDermott 1976, 1984; Thiel and Reise 1993; Thiel 1998; Kruse and Buhs 2000; Bourque et al. 2002). With the exception of the field studies of Roe (1970, 1976) who examined both soft-bottom (mud flats) and hard-bottom (a rocky outcropping and a ferry landing with boulders) habitats of *Paranemertes peregrina*, our knowledge of the feeding ecology of nemerteans from hard-bottom habitats remains largely limited to laboratory observations (McDermott 1998; Thiel et al. 2001; Caplins and Turbeville 2011).

Nemerteans from intertidal rocky shore communities are especially susceptible to being swept away by waves because of their limited ability to adhere to the substratum surface and to hold on to their recently captured prey items (Roe 1976; McDermott and Roe 1985; Thiel et al. 2001). Intertidal nemerteans typically exhibit higher levels of activity during evening (Kruse and Buhs 2000) or night low tides when the risk of desiccation is low (Nordhausen 1988; Thiel et al. 1995). Foraging behavior has also been documented during mid-day low tides (Roe 1976), albeit in a climate zone where, on average, the monthly maximum temperatures rarely exceed 20 °C. Many different nemertean species from both hard- and soft-bottom intertidal habitats have been observed actively foraging and/or scavenging for prey (Roe 1970; Thiel et al. 1995; Thiel 1998; Kruse and Buhs 2000). Limited foraging time due to abiotic restrictions may result in less-specific prey selection by nemertean predators. Several studies suggest that nemerteans are opportunistic foragers, consuming specific prey items preferentially when those species are available, but switching to a wider range of prey items when necessary (McDermott and Roe 1985; Thiel and Kruse 2001). Observations of predation under natural conditions will help to identify the full range of possible prey organisms, which might include prey not being consumed in laboratory feeding assays.

As slow-moving predators, most nemerteans rely on neurotoxins (Kem 1985) administered by a rapidly everting proboscis to immobilize and capture their prey. Some nemerteans have been observed actively foraging for prey and will follow chemotactic cues to find their prey items (Amerongen and Chia 1982; Thiel 1998; Kruse and Buhs 2000), while others exhibit a sit-and-wait strategy, relying on moving prey to come within striking distance (see Christy et al. 1998; Thiel and Kruse 2001). Measuring the velocity of a foraging nemertean may allow a clearer delimitation between active and sit-and-wait foraging. Furthermore, the employed foraging strategy may affect the prey spectrum of intertidal (nemertean) predators. Additionally, in habitats such as the rocky intertidal zone, the substratum encountered by foraging nemerteans is heterogeneous, but whether the foraging strategy employed and the prey spectrum is correlated with substratum type remains to be elucidated.

The hoplonemertean *Prosorhochmus nelsoni* (previously *Amphiporus nelsoni*, Sanchez 1973) is a common inhabitant of intertidal rocky shores along the Pacific coast of Chile. A laboratory investigation revealed that these nemerteans preferentially feed under low-tide conditions on the amphipod *Hyale maroubrae*, which they consume at a rate of $\sim$0.2 amphipods nemertean^{-1} day^{-1} (Thiel et al. 2001). This feeding rate lies within the range of other rates measured in the laboratory (McDermott 1984; Caplins and Turbeville 2011) but likely represents a maximum for these animals reared under optimal conditions (e.g., amphipod density and environmental conditions kept constant in artificial laboratory settings). Understanding how prey availability and foraging success influence the feeding rates under field conditions will provide more accurate estimates of the potential impact of nemertean predators on prey populations.

In this study, our primary objectives are to determine (1) habitats where *P. nelsoni* forages, (2) the diurnal and low-tide activity patterns of *P. nelsoni,* (3) the behavior of *P. nelsoni* during periods of activity including the predation strategy they utilize (i.e., sit-and-wait or active foraging), (4) their foraging success rate, and (5) the range of prey items consumed under natural conditions.

Methods and materials

Site description

Observations of nemertean activity were conducted in early January through early March 2011 along a rocky shore in northern-central Chile, near Coquimbo (29°57′S/71°21′W). The shore is composed of granite boulders and rocky outcroppings that, in the intertidal zone, are colonized by diverse sessile organisms including turf algae, crustose algae, barnacles, and kelp, and that provide three-dimensional substrata for a wide variety of marine invertebrates. During the study period (austral summer), the air temperatures in the intertidal zone ranged between $\sim$13 and

~35 °C (Bernardo Broitman, unpubl data), with the highest temperatures being reached during afternoon low tides.

All observations of nemerteans were made within the same area approximately 100 m along the shore. Nocturnal observations of nemertean activity were aided with the use of LED headlamps and flashlights, which did not seem to affect nemerteans negatively.

Habitat characteristics and nemertean abundance

Surveys were conducted between January and March 2011 during early-morning, evening, and night low tides using 0.25-m^2 quadrats that were placed haphazardly along the intertidal zone. For each quadrat, we measured the following variables: orientation of the shore (by using a compass), inclination, tidal height, composition of substrata, number of nemerteans, and number of cracks in the underlying rock. The orientation of the shore was recorded because the orientation of a quadrat will determine the amount and duration of sun exposure. The composition of the substrata was recorded by assigning a percentage to the amount of space occupied within the quadrat by different biota (e.g., turf algae, crustose algae, barnacles, and *Ulva* spp. algae) and bare rock.

We conducted multiple regression analyses with the number of nemerteans as the dependent variable and orientation, inclination, tidal height, number of cracks, and the percent coverage of bare rock, turf algae, crustose algae, barnacles, and *Ulva* spp. algae, as predictor variables. Data were square-root transformed in order to reduce interactive effects of predictor variables; this made an additive model a more appropriate fit than a multiplicative model (Quinn and Keough 2002). In addition, data were standardized to variance units.

A scatter plot matrix (SPLOM) revealed weak collinearity among predictors, which was confirmed by the variance inflation factor (VIF). VIF values greater than 10 suggest strong collinearity (Quinn and Keough 2002). In our analysis, VIF values ranged from 1.11 (orientation) to 3.66 (turf algae). SPLOM also revealed nonlinear relationships between the number of nemerteans and inclination and tidal height. Consequently, we used second-order orthogonal polynomials to fit inclination and tidal height.

The Bayesian Information Criterion (BIC, Schwartz 1978) was used to find the smallest subset of predictors that provided the best fit to the number of nemerteans. This allowed us to identify the predictors that were most important in explaining the variation in the number of nemerteans. We compared all possible regression models (i.e., 511 combinations of predictions) using the meifly package in the R environment version 2.13 (R Development Core Team 2011; packages are available at http://cran.r-project.org/web/packages/). The model with the lowest BIC value was selected as the best fit. This analysis was complemented with a hierarchical partitioning of r^2 coefficients. We used the hier.part package in R to partition the contribution of each predictor to the r^2 of the full model with all predictor variables. Each independent contribution was expressed as percentage of the full model r^2 (see Burnham and Anderson 2002 for further details on multiple regression and model selection procedures).

Low-tide activity pattern

Nemertean surface abundance relative to tidal state was measured throughout the low-tide cycle on three separate occasions at three sites. Each site varied in wave exposure, tidal height, and substratum composition. Several areas ($n = 6$, 5, and 3) within each site were marked by push pins to allow consistent placement of 0.25-m^2 quadrats. Each quadrat was scanned for nemerteans every 15 min. Scans began ~2.5 h before low tide and ceased when there were no more nemerteans to count or the tide was at a height that prevented scanning. Only quadrats that had at least 10 nemerteans at any given time during the scan were plotted on a percent scale ($n = 3$, 3, and 1, respectively), with the highest count representing the assumed total number of nemerteans in that area, which was thus set to 100 %. All other counts from a tidal scan are then shown as the percentage of this maximum count. This standardization method allows comparison of activity patterns in areas with varying numbers of nemerteans.

Diurnal activity patterns

To determine the diurnal activity pattern of *P. nelsoni* during low tide, fifteen 0.25-m^2 quadrats were positioned in fixed locations in the intertidal zone and nemerteans within each quadrat were counted once during each low tide for 14 days (February 22–March 8, 2011). In this way, nemertean activity was monitored over a complete tidal cycle.

Foraging and predatory behavior

Timed scans of nemertean behavior were performed during early-morning and night low tides by randomly selecting one individual that was exposed on the surface of the respective substratum (e.g., bare rock, turf algae, crustose algae, and barnacles) and monitoring its behavior for 5 min. During this time, the length of the nemertean, distance the nemertean traveled, direction of movement, substrata on which the worm occurred, and predatory behavior (e.g., proboscis eversion) were recorded. Velocity (mm min^{-1}) was calculated for individual worms and average velocities were calculated according to the substrata over which the worms traveled. Special attention was given to nemerteans involved in a predation attempt (eversion of the proboscis toward a potential prey item). If the predation attempt led to the immobilization and subsequent consumption of the prey item, the timed scan was extended past the 5-min period, and the predation event was monitored for its entire duration. Following a predation event, we continued to monitor the behavior of the nemertean until it disappeared from view (e.g., crawled into a crack or disappeared in the turf algae). Care was taken not to perform a timed scan on the same worm twice. Photographs of several predation events were obtained with a handheld digital camera (Panasonic DMC-FX37 or Olympus STYLUS TOUGH-8000).

To characterize nemertean behavior according to substratum type, the substrata over which the worms traveled during the timed scans were grouped into four main categories: bare rock, turf algae, mixed substrata (a combination of turf algae plus any of the other substrata, that is, bare rock, crustose algae, and barnacles), and other biotic substrata (i.e., crustose algae, *Ulva* spp. algae, and barnacles). Additional observations of predation events were made apart from those that occurred during the timed scans, but these are not included in the total number of scans, or calculations of the foraging success rate. For each of these predation events, the prey item, nemertean length, duration of feeding event, distance traveled after the predation event, and the substrata on which predation took place were recorded.

The effect of nemertean length on velocity was examined through a general linear model, with velocity as the response variable, substrata (bare rock, turf algae, mixed substrata, and other biotic substrata) as a nominal variable, and nemertean length as a continuous variable. Data sets containing velocity and nemertean length were square-root transformed to achieve homoscedasticity, as determined through examination of quantile-comparison plots and confirmed by Levene's test. Velocities with a value of zero (nemerteans that did not move at all during the entire scan) were not used in the velocity calculations or analyses. Three data points in the velocity data set (values of 72, 73, and 75 mm min^{-1}) were identified as outliers from quantile-comparison plots of the untransformed data and were removed to achieve a near normal distribution. Statistical analyses were performed in the R environment version 2.13 (R Development Core Team 2011).

Estimates of per capita predation rates

We used the data from the tidal, diurnal, and timed scans to construct a model estimating the average rate of nemertean activity per tidal period, the average hours of low tide per day, and the foraging success rate per nemertean. The individual rate of predation per nemertean per day was calculated using the equation: Predation rate = predation events per hour × rate of activity × low tide (hours per day), where predation events per hour represent the number of predation events observed during the 5-min timed scans, the rate of activity refers to an estimated dimensionless value of activity across the tidal and diurnal cycles, and the low-tide hours per day is the number of hours each day that the tide can be considered "low" (encompassing the ebb, flow, and mean low tide).

Results

Habitat characteristics and nemertean abundance

Prosorhochmus nelsoni occurred throughout the intertidal zone and was found on a variety of substrata (e.g., bare rock, turf algae, crustose algae, barnacles, and *Ulva* spp. algae). Bayesian Information criterion (BIC) selected a model with 3 habitat characteristics (algal crusts and the quadratic terms of inclination and tidal height; adjusted $r^2 = 0.31$). Hierarchical partitioning of r^2 confirmed that inclination, crustose algae, and tidal height contributed most to the explained variance in the number of nemerteans, with some contribution also by *Ulva* spp. (Fig. 1a). The number of nemerteans was negatively affected by the percent cover of algal crusts ($t = -3.17$, $P < 0.01$; Table 1; Fig. 1b) and positively by the coverage of *Ulva* spp. ($t = 2.78$, $P < 0.01$; Table 1, Fig. 1c). Significant second-order polynomial regressions indicated that most nemerteans were found on rocks where the inclination was between 30° and 100° (Fig. 1d, $t = -3.28$, $P < 0.01$) and in the mid-intertidal zone where tidal height ranged from 30 to 120 cm above the mean low-tide line (Fig. 1e, $t = -2.57$, $P = 0.01$).

Low-tide activity pattern

At all three study sites, surface abundances of *P. nelsoni* reached their highest values approximately 1–2 h before mean low tide (Fig. 2). The highest number of nemerteans was 45 individuals 0.25 m^{-2}, and the average across all three sites was 10.4 (SD ± 10) ind 0.25 m^{-2}. Following mean low tide, nemertean abundances began to decrease, rising again slightly approximately 1 h after mean low tide, before decreasing completely 2–3 h after mean low tide (Fig. 2). Nemerteans disappeared into cracks in the bedrock, where they gathered from the surrounding area. Some of these sites were within the quadrats, while other quadrats contained no aggregation sites.

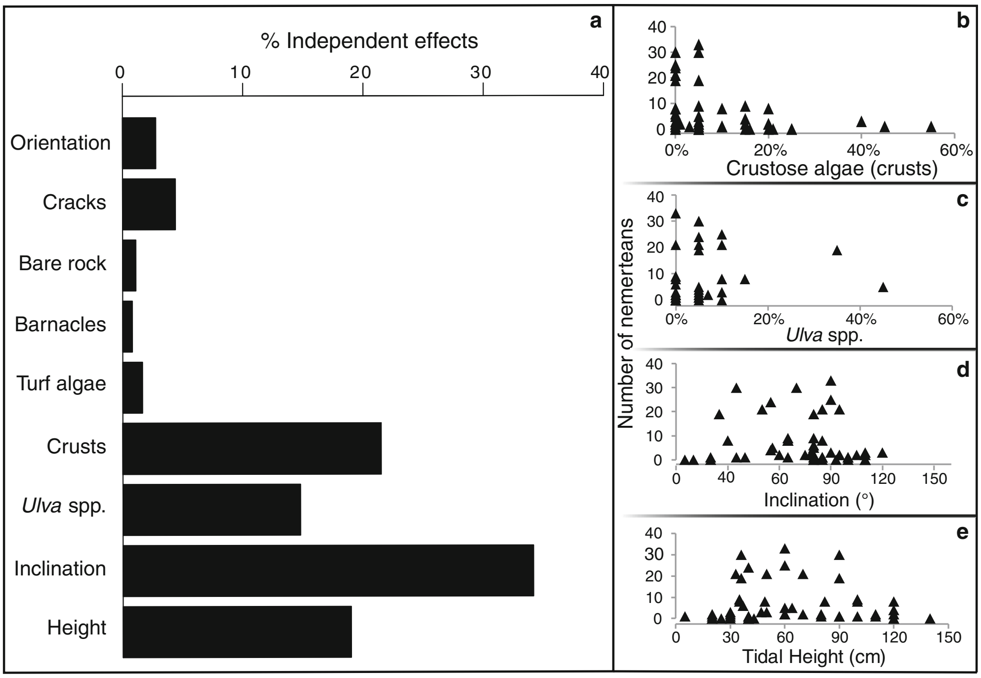

Fig. 1 **a** Proportion of independent contribution of each predictor to the variance in number of nemerteans. Inserts show scatter plots with the number of nemerteans on the *y*-axis and **b** percent cover of crustose algae, **c** percent cover of *Ulva* spp., **d** inclination, and **e** tidal height, on the *x*-axis

Table 1 Variables explaining abundances of *P. nelsoni* obtained from hierarchical partitioning of r^2 values

Variable	*t* value	*P* value
Orientation	1.108	0.273
Cracks	1.5808	0.12
Bare rock	−0.1518	0.88
Barnacles	0.4231	0.6739
Turf algae	0.6443	0.5222
Crustose algae	−3.168	0.0026
Ulva spp.	2.7828	0.0075
Inclination	−3.2792	0.0019
Height	−2.5716	0.013

Inclination and height showed a nonlinear relationship with the number of nemerteans and were thus analyzed using second-order polynomials, and the remaining variables were analyzed using linear regressions

Diurnal activity patterns

An analysis of the diurnal activity pattern over a complete (14 days) tidal cycle revealed that the nemerteans exhibit a window of activity between 19:00 and 10:00 the next day, with the main peak of activity from 3:00 until 6:30, and another smaller peak about 1 h before dusk (Fig. 3). A period of inactivity was apparent during daylight hours between 11:00 and 17:00. The maximum number of nemerteans per quadrat was 65 with an average of 6 (SD ± 9) nemerteans per quadrat.

Foraging behavior

A total of 375 timed scans (each of 5 min duration) of *P. nelsoni* behavior were performed across the four substratum categories: bare rock ($n = 79$, 21 %), turf algae ($n = 155$, 41 %), mixed substrata ($n = 76$, 20 %), and other biotic substrata (including barnacle substrata; $n = 65$, 17 %). Predation attempts (e.g., nemerteans everting their proboscis toward a prey item) were observed in only fourteen scans (3.7 %) and of these only three (0.8 %) resulted in the immobilization and consumption of the prey item (Table 2). Most predation attempts were observed on bare rock and in turf algae, with two of the three successful predation attempts (resulting in prey consumption) occurring on the bare rock (Table 2). Additionally, nemerteans were occasionally observed to evert their proboscis when there were no prey items in view, a behavior that was recorded four times, three occurring on the bare rock and one on the other biotic substrata (Table 2; listed with predation attempts). This behavior was not seen for worms in the turf algae or mixed substrata. In the turf algae, mixed substrata, and other biotic substrata, nemerteans were often found motionless and occasionally (8.8 % of all 375 scans) remained motionless for the entire 5-min scan (Table 2).

Most of the nemerteans (91.2 %) were actively crawling during our observation period, but the range of velocities varied widely across the different substrata, ranging from 2 to 75 mm min^{-1} ($n = 325$; see Table 2) with a significantly lower velocity on turf algae (Fig. 4a; Tukey's test,

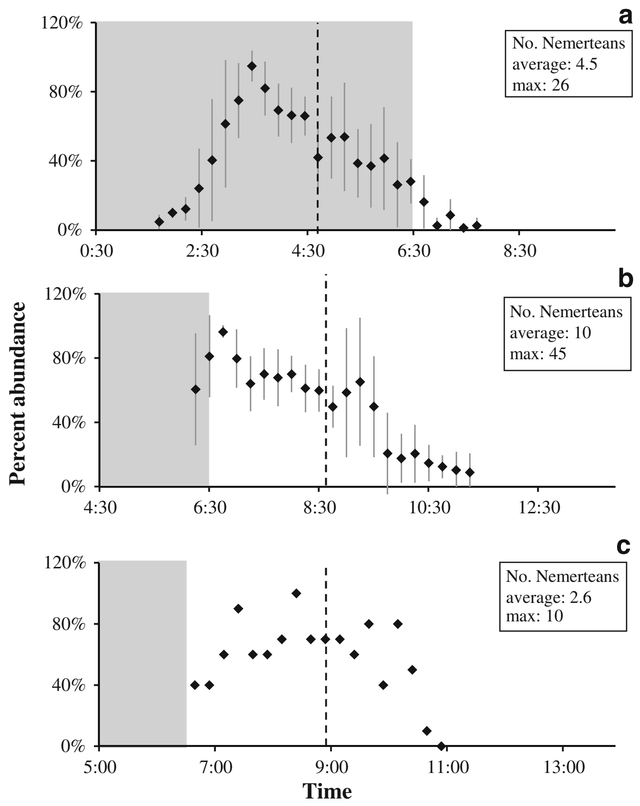

Fig. 2 Nemertean abundance (expressed as a percent of the maximum value) during low tide at three different sites. Only sites with a total count of 10 or more nemerteans during at least one count were used. Data collected on **a** March 3, 2011 ($n = 3$ sites); **b** January 9, 2011 ($n = 3$ sites); **c** January 10, 2011 ($n = 1$ site). Standard deviation is indicated by the *error bars*. Mean low tide is indicated by the *vertical line*, and darkness is shown by the *shaded region*. The average and maximum number of nemerteans for each site is shown in each *upper-right box*

$P < 0.001$). Nemertean length also varied across a broad range (10–65 mm) and was significantly different between the bare rock and turf algae (Fig. 4b; Tukey's test, $P < 0.01$). The results of the linear model revealed a significant effect of nemertean size ($P < 0.001$) and substratum type ($P < 0.01$) on velocity, with a significant interaction between size and substratum ($P < 0.01$; see Fig. S1 in supplemental material).

Predatory behavior

Our observations revealed that *P. nelsoni* consumes a wide range of prey items including amphipods (*Hyale hirtipalma*, *H. grandicornis*, and unidentified *Hyale* sp.), isopods (*Ligia* sp.), a cirriped, decapod adults and megalopae (*Cyclograpsus cinereus*, *Petrolisthes tuberculatus*, *P. violaceus*, and *Betaeus truncatus*), and both dipteran larvae and adults (Table 3; Fig. 5). Dipteran adults were successfully attacked when they oviposited in the turf algae (pers obs; Fig. 5a).

We observed a total of 17 predation events, three of which were made during the 5-min timed scans (see above). Predation events were observed primarily in the bare rock (23 %) and turf algae (59 %) habitat zones, with the remainder taking place on the other biotic substrata (12 %). The substratum was not recorded for one observation (Table 4). No predation events were recorded on the mixed substratum. Most predation events took place in the morning after sunrise (between 6:30 and 9:30) with only three being recorded under darkness, one in the late evening (at 21:36) and two in the early morning (between 1:00 and 3:00). However, this may be due to the increased difficulty of making observations at night, when the field of view is more limited than during daytime observations. Amphipod crustaceans were the most common prey items, but dipterans (larvae and adults) and the isopod *Ligia* sp. were also consumed with relatively high frequency (Table 4). It took longer on average for nemerteans to consume the isopod crustaceans than any other prey item;

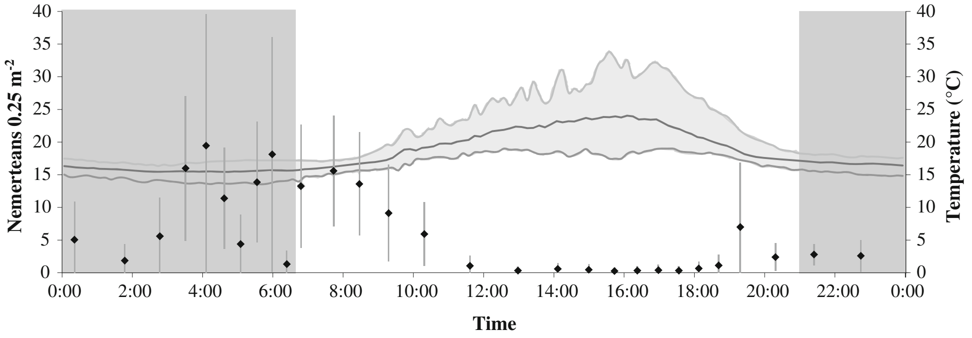

Fig. 3 Activity pattern of *P. nelsoni* as evaluated by counting the number of nemerteans in fixed quadrats ($n = 15$) at every low tide for 14 days (February 22–March 8, 2011). Each data point shows the average nemertean count for all 15 quadrats with standard deviation indicated by the *error bars*. The *dark shading* indicates periods of darkness. The air temperature of the low intertidal zone is shown as a dispersion graph indicated by the *horizontal gray lines* and was made from time intervals of 10 min for 24 h over the survey period in February/March 2011 (data kindly provided by Bernardo Broitman)

Table 2 Summary of foraging behavior of *P. nelsoni* obtained during the 5-min timed scans

Substrata	Number of scans	Average length (mm ± SD)	Average distance traveled in 5 min (mm ± SD)	Average velocity (mm/min ± SD)	Maximum velocity (mm/min ± SD)	"Sit-and-wait" worms (%)	Total predation attempts	Successful predation attempts
Turf algae	155	25 ± 7.5	67 ± 38	13 ± 8	42	16.1	2	1
Mixed	76	28 ± 10	95 ± 41	19 ± 8	49	5.3	0	0
Bare rock	79	32 ± 12	127 ± 71	25 ± 14	75	0	5	2
Other biotic substrata	65	29 ± 10	121 ± 66	24 ± 13	72	6.1	3	0
Total	375	27 ± 10	93 ± 58	19 ± 12	75	8.8	14	3

Average velocities (±standard deviation) were calculated only for scans that lasted five min and excluded the nemerteans that did not move at all during the entire scan. Values for predation attempts include those that resulted in successful predation (predation events)

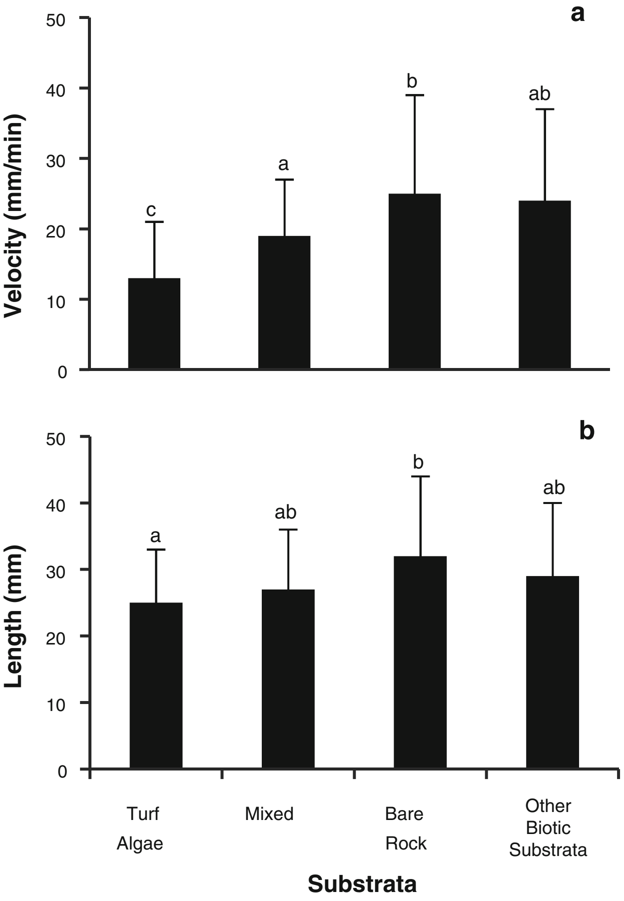

Fig. 4 **a** Mean nemertean velocity (mm min^{-1}) and **b** Mean nemertean length (mm), according to substratum type. *Error bars* show standard deviations. *Letters* that are not shared indicate a significant difference (Tukey's test, $P < 0.001$)

Table 3 List of prey items consumed by *P. nelsoni* and the number of observations made for each (total = 25)

Prey item	No. of observations
Crustacea	
Amphipoda	
*Unidentified	2
Hyale hirtipalma	2
Hyale grandicornis	2
**Hylae* sp.	1
Hyalidae (genus,unid.)	1
Isopoda	
**Ligia* sp.	5
Decapoda	
Cyclograpsus cinereus (megalopa and juvenile)	2
*‡*Petrolisthes violaceus* (megalopa and adult‡)	2
*‡*Petrolisthes tuberculatus*	1
Betaeus truncatus	1
Maxillopoda	
Barnacle (unid.)	1
Insecta	
Diptera	
Adult (unid.)	2
*Larvae (unid.)	3

In some cases, the initial attack was not observed and instead the nemertean was found consuming an already-immobilized/dead prey item (not considered predation events). All prey items were adults, unless specified otherwise. Prey items consumed by more than one nemertean are indicated with an asterisk ($n = 6$). The double dagger symbol indicates prey items that were scavenged ($n = 2$)

however, too few observations were made to determine whether significant differences exist in feeding duration for different prey items (Table S1).

Predation events lasted between 7 and 30 min (Table 4), beginning with the initial strike of the proboscis and terminating with the satiated nemertean crawling away from the prey item. Worms involved in predation events were monitored for an average of 40.5 min (SD ± 19.7), and during this time crawled an average of 398 mm (range: 70–800 mm; note: the total distance traveled was only recorded for 9/17 observations). In most cases (14/17, 82 %), nemerteans were observed to disappear into refugia

Fig. 5 Digital images of several predation events. **a** *P. nelsoni* (*N*) feeding on adult dipteran. **b** One individual of *P. nelsoni* attempting to consume a dipteran larva (DL), while two other worms feed on a megalopa (M) concealed within an empty barnacle shell. **c** *P. nelsoni* consuming *Ligia* sp.

(e.g., cracks in the rocks, the underside of boulders, or turf algae) shortly or immediately after predation events. For the remaining predation events, the nemerteans crawled out of view (2/17, 12 %), or the behavior was not recorded (1/17, 6 %). In no case was a nemertean observed to feed more than once during an observation period.

On several occasions (4/17), multiple nemerteans (2 or more) were observed consuming a prey item that had been captured and immobilized by a single individual (Table S1, see also Table 3), and this behavior was observed for four different prey items, a *Hyale* sp. amphipod, an unidentified amphipod, *Ligia* sp., and a dipteran larva. Additionally, we observed on two occasions, apparent scavenging behavior involving multiple individuals of *P. nelsoni* feeding on portions of the carapace and/or cheliped of two species of porcellanid crabs, *P. tuberculatus* and *P. violaceus* (Table 3). As the death of the crab was not observed and only the tissue in the cheliped and portions of the carapace were being consumed, we considered these to be scavenging events and not predation events.

Rate of predation

The following formula was used to estimate the average individual rate of predation (P):

$$\mathrm{P} = \text{predation events h}^{-1} \times \text{rate of activity} \times \text{low tide}\,(\text{h day}^{-1})$$

The number of predation events per hour was calculated from the timed scan data and resulted in a value of 0.0967 predation events h^{-1} (375 timed scans × 5 min per scan/60 min per hour = 31.25 h, during which time we recorded 3 predation events: 3 predation events/31.25 h = 0.0967 events h^{-1}). The average rate of activity was estimated in two parts, using data from both the tidal and diurnal scans. For the three tidal scans, the average proportion of nemerteans was calculated for each hour around mean low tide and was then multiplied by the average proportion of nemerteans active for each of the 15 quadrats over the 14-day diurnal scans, returning a dimensionless value of 0.0798. Low tide occurs twice a day and under the assumption that the nemertean habitat is exposed for 6 h

Table 4 Summary of predation events by *P. nelsoni* according to the substrata on which they occurred. (a) The percent was obtained from the timed scan data and is likely representative of the total observation effort. (b) Average duration and nemertean length with standard deviations (±) according to prey item. Prey consumption began when the nemertean captured the prey item and ended when the nemertean pulled away from the consumed prey

Substrata	Predation event	Estimated number of observational hours (timed scans)
a		
Algal turf	10 (59 %)	13 (41 %)
Mixed	0 %	6.25 (20 %)
Bare rock	4 (23 %)	6.6 (21 %)
Other biotic substrata	2 (12 %)	5.4 (17 %)
Undocumented	1 (6 %)	0
Total	17	31.25

Prey item	Average duration of prey consumption (min ± SD)	Average worm length (mm ± SD)	Number of observations
b			
Amphipod	16 ± 7	27 ± 15	7
Isopod	37 ± 10	36 ± 13	5
Dipteran (larvae and adult)	14 ± 3	23 ± 7	4
Barnacle	10	30	1
Total	22 ± 12	30 ± 13	17

during each low tide returns a value of 12 h day^{-1}. Inserting the above values into the formula gives the average rate of predation for an individual nemertean:

$$\begin{aligned} P &= 0.0967\,\text{predation events}\,\text{h}^{-1} \times 0.0798 \times 12\,\text{h}\,\text{day}^{-1} \\ &= 0.092\,\text{predation events}\,\text{day}^{-1}. \end{aligned}$$

Discussion

The activity patterns of nemerteans are associated with feeding and reproduction (mate searching and fertilization; Thiel et al. 1995; Kruse and Buhs 2000) and are largely limited by diurnal and tidal conditions. Roe (1976) found that the tidal activity period of the hoplonemertean *P. peregrina* peaked during the initial 2–2.5 h after the tide ebbs during morning and night low tides, respectively. Likewise, the abundances of *P. nelsoni* were highest 1–2 h before mean low tide, both before and after sunrise. We estimate that an individual *P. nelsoni* spends approximately 1 h per day (0.957 h day^{-1}) foraging (calculated by multiplying the activity rate of 0.0798 by the number of hours of low tide per day). The tidal activity pattern of nemerteans reveals that they have limited foraging time during a tidal cycle. In comparison, Connell (1970) found that snails (*Thais* spp.) feed on barnacles for ~10.7 h day^{-1} and require 8 h to consume a single barnacle. This limits *Thais* sp. predation to barnacles in the lower intertidal zone where desiccation stress is reduced (Connell 1970).

The diurnal period of activity for *P. nelsoni* spans both dark and light hours of low tides, although the peak of activity occurs before dawn. Similarly, *P. peregrina* is also active at both morning and night low tides (Roe 1976). In contrast to these species, the heteronemertean *L. viridis* is active exclusively during night low tides (Nordhausen 1988; see also Thiel et al. 1995), whereas the hoplonemertean *Tetrastemma melanocephalum* is active during the evenings for 2–4 h after the tide begins to ebb (Kruse and Buhs 2000). Additionally, an unidentified hoplonemertean that preys on fiddler crabs is active during daytime low tides (Christy et al. 1998), in accordance with the daily activity cycle of its prey (J. Christy, pers comm). Clearly, there is a range of diurnal patterns in nemerteans, but most of the species investigated thus far are active at least in part during dusk/dawn and at night.

Activity patterns of intertidal nemerteans are likely related in part to a decreased desiccation risk (Thiel et al. 1995). By limiting activity to evening, night, and early-morning hours, the worms are subjected to little or no solar irradiance, less thermal loading, and less evaporation across the body wall. Roe (1976) mentioned that increased solar irradiance resulted in reduced numbers of *P. peregrina* during low tides. It is also likely that the optimal physiological temperature range of these animals lies within their activity window. We have no microclimate data for this study period, but temperature data obtained for the rocky intertidal zone from the Coquimbo region (unpubl data from Bernardo Broitman) allow a provisional activity-temperature comparison for *P. nelsoni*, which exhibited an activity peak between 3:00 and 6:00 when the air temperature ranged from ~13 to 16 °C (Fig. 3; Bernardo Broitman, unpubl data).

Relative humidity and wind speed are also likely to impact the activity pattern of intertidal nemerteans, given that evaporation is inversely related to humidity and wind speed is roughly proportional to evaporation. Thus, less activity might be expected during periods of low relative humidity and high wind speeds. Likewise, we observed relatively few nemerteans during mid-afternoon to early evening low tides, and the rocks at this time were often dry and still warm in areas that during early-morning low tides were cool and damp. Furthermore, climate data for the region show a steady increase in wind speed from 10:00 to 17:00, rising from an average of 1.6 m s^{-1} (SD ± 0.8) to a peak of 3.5 m s^{-1} (SD ± 0.9) before gradually decreasing (data obtained from www.ceazamet.cl, Doca station from February 22 through March 8). This corroborates observations by Roe (1976), who found strong winds to be a factor limiting foraging behavior in *P. peregrina*. While there are indications that suggest temperature and wind speed influence nemertean activity, these factors were not quantified in this study at the microhabitat level.

The laboratory study of Thiel et al. (2001) found that the feeding rate of *P. nelsoni* averaged ~0.2 amphipods nemertean^{-1} day^{-1} and reached a maximum of 0.5 amphipods nemertean^{-1} day^{-1}. While the value of 0.5 likely represents a maximum feeding rate, our estimation of feeding rates based on activity patterns and observed foraging success reveal a rate of 0.092 prey items nemertean^{-1} day^{-1}, which is near the lowest rate of ~0.1 amphipods nemertean^{-1} day^{-1} measured in the laboratory (Thiel et al. 2001) and just below the range of 0.1–0.3 prey items^{-1} day^{-1} measured for other intertidal nemerteans in laboratory settings (McDermott 1984; Roe 1993; Caplins and Turbeville 2011). The corroboration of the field-estimated predation rate with the lower end of that measured in the laboratory provides some support for lab-based measures of feeding rates being a useful metric. However, the limited foraging time attributable to tidal and diurnal factors should be taken into consideration before extrapolating feeding rates to large-scale community effects.

The size of the prey item should also be considered when applying feeding rates to the field. *P. nelsoni* consumes prey items over a large range of sizes, from the large isopod *Ligia* sp. to the relatively small *H. maroubrae* (preferentially consumed in the lab) and equally small decapod megalopae. One could easily assume that the feeding rate for a nemertean would be low if they only consumed *Ligia* and possibly much higher when consuming smaller prey items. Additionally, an adaptive escape response of the prey organism may result in lower predation rates independent of predator population size (see Abrams 1993) and is a factor worthy of closer examination. Our results strengthen the assertion of Thiel et al. (2001; see also Caplins and Turbeville 2011) that field assessment of predation rates are necessary before realistic estimates of the potential impact of these predators on prey populations can be quantified.

We recorded nemertean abundances at a maximum of 65 ind 0.25 m^{-2} (or 260 ind m^{-2}) in a habitat composed primarily of turf algae, which is within the upper range of nemertean abundances for soft- and hard-bottom habitats (see Thiel and Kruse 2001). More events of nemertean predation were observed in the turf algae than in other habitats, which may be due to a slightly higher nemertean abundance for this zone, as well as a greater likelihood of prey encounter. Turf algae provide cover for small crustaceans and insects (Thiel 2002; pers obs), and it can be expected that the nemerteans will encounter prey more often on this substratum type. The prey item consumed most frequently on bare rock was the large semiterrestrial isopod *Ligia* sp., which appears to be preferentially active on this substratum at low tides, and relies on its speed to escape or seek shelter from predators.

Most nemertean species studied so far exhibit an active foraging behavior (Roe 1976; Thiel et al. 1995; Thiel and Kruse 2001), but some employ a sit-and-wait or ambush strategy (Thiel and Reise 1993; Christy et al. 1998). An active foraging strategy is typically correlated with consumption of unevenly distributed, clumped, or sedentary prey, whereas a sit-and-wait strategy is utilized when prey are active (Huey and Pianka 1981; Perry and Pianka 1997). Both sit-and-wait or "ambush" predators and actively foraging worms were observed during this investigation. The sit-and-wait mode would be expected to increase the chance of predation on active prey organisms (e.g., amphipods and isopods) as the nemertean is not fast enough to pursue the prey, although rapid proboscis eversion may compensate for lack of locomotory speed. Typical sit-and-wait predation has been observed for an unidentified Panamanian soft-bottom, suctorial hoplonemertean that feeds on relatively large and fast fiddler crabs (Christy et al. 1998) and for the amphipod predator *Amphiporus lactifloreus,* which waits for its prey in mussel clumps (Thiel and Reise 1993).

Ambush predation rather than active foraging would be predicted to enhance predation of the highly mobile isopod *Ligia* by *P. nelsoni* (see Huey and Pianka 1981; Perry and Pianka 1997), but the boundary between these modes is not distinct in the case of *P. nelsoni*. Active foraging by *P. nelsoni* on rocks frequented by the isopod *Ligia* sp. may increase the probability of an encounter, with the eversible proboscis serving to attack the isopod when it scurries within striking distance. The overall rate of crawling speed for actively foraging individuals of *P. nelsoni* is heavily influenced by the substrata, with large worms on the bare rock and other biotic substrata crawling faster than worms of the same size on the algal turf and mixed substrata.

However, on average, larger individuals of *P. nelsoni* crawled faster than smaller worms. The average distance covered by *P. nelsoni* is less than one-tenth the distance of 5–10 m that the larger nemertean *Lineus viridis* is able to travel in a single-foraging period over tidal flats (Thiel 1998). The more complex hard-bottom habitat, higher prey density, and the limited foraging window of *P. nelsoni* could explain the relatively short distances traveled over a foraging period.

In laboratory prey-preference experiments, *P. nelsoni* preferred the amphipod *Hyale maroubrae* over the amphipod *H. hirtipalma*, and the nemertean did not feed on the isopod *Exosphaeroma* sp. (Thiel et al. 2001). In contrast, our field observations suggest that this nemertean is opportunistic, feeding not only on various amphipod species, but also on the isopod *Ligia* sp., decapod crustaceans (including adults and recently settled megalopae), barnacles, and dipteran larvae and adults. The only preference exhibited was for crustaceans. Contrasting results of the field and laboratory investigations could be in part explained by differing seasonal abundance of prey, as the investigation of Thiel et al. (2001) was carried out in the austral fall, and we conducted our investigation in the austral summer. In fact, of the taxa offered as prey in the previous laboratory prey-preference test, only a single species (*H. hirtipalma*) was also identified as prey during the present study. Thus, we cannot discount the possibility that this nemertean adapts its prey preference to the species available in the field. The comprehensive field study of Roe (1976) indicated that *P. peregrina* in a hard-bottom community consumes representatives of five families of polychaete annelids, although this nemertean prefers nereid polychaetes when they are present (Roe 1970). Rigorous assessments of prey preference and breadth under natural conditions are lacking for other hard-bottom nemertean species, but limited field observations suggest that *Nemertopsis gracilis* feeds only on bivalve molluscs whereas, *Emplectonema gracile* may be a generalist like *P. nelsoni* (Dayton 1971; McDermott and Roe 1985). The prey spectrum of *P. nelsoni* observed in the field is substantially wider than anticipated based on the laboratory observations of Thiel et al. (2001), suggesting that these worms may play an important role in shaping the highly structured intertidal community.

Conclusion and outlook

The interplay between environmental stressors and predator–prey interactions greatly influences community structuring in hard-bottom intertidal habitats. Most intertidal predators operate within a particular tidal zone and diurnal period that are likely dependent on their own physiological tolerance to desiccation and temperature stress, the type of prey they consume (e.g., mobile or sessile prey) and the handling time associated with each prey item. Mobile prey items are able to escape during high tide and are possibly more easily caught during low tide; however, this is when the risk of desiccation is highest. Sessile prey organisms such as mussels and barnacles are afforded some protection in areas of high wave action or high desiccation stress, to which they typically have a greater tolerance than their predators (e.g., snails and sea stars). Consequently, intertidal predators face a trade-off between immediate survival and foraging success (thus longterm survival). Similarly, the foraging activity of *P. nelsoni* is limited by the risk of desiccation and temperature stress, but individuals are also susceptible to strong wave action and are unable to maintain contact with their prey items throughout the entire feeding process. The combination of these factors results in greater foraging activity during night and morning low tides, when desiccation stress is reduced, and actively moving prey is limited in its ability to escape. This trade-off and the limited available foraging time may also be responsible for the diverse prey spectrum of *P. nelsoni* and other intertidal predators, forcing these predators into opportunistic prey habits, as they attempt to capture and consume any potential prey item that comes into striking distance.

The estimated rate of predation and high abundances of *P. nelsoni* presented in this study indicates that this predator, which can be very abundant in the rocky intertidal zone, is likely capable of influencing the populations and behaviors of its prey. We strongly advocate manipulative experiments of nemertean abundances as the next step in understanding how these predators affect their prey populations and influence the structure of their community.

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