Body size and segmentation patterns in free-living and parasitic polychaetes

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Abstract: Taxa that include both free-living and parasitic lineages present opportunities to examine if and how the life-history traits of parasitic organisms have diverged from those of their free-living relatives. In a comparative analysis the body sizes and numbers of body segments of parasitic polychaetes of the family Oenonidae were compared with those of free-living polychaetes from closely related families. There was no difference in body length between oenonids and free-living polychaetes. However, the parasitic oenonids attain, on average, a much higher number of body segments than their free-living counterparts. The number of segments per unit body length is also much higher in oenonids than in related free-living polychaetes. This suggests that new segments are produced at a higher rate or for longer periods in oenonids than in free-living polychaetes, in which the proliferation of new segments slows down over time to allow for the segments to grow in size. Given that each segment can produce gametes late in the life of the worm, the proliferation of segments in oenonids may be an adaptation to their parasitic life-style.

Résumé : Les taxons qui comptent des lignées libres et des lignées parasites permettent d'examiner si et comment les caractéristiques du cycle biiologique des organismes parasites ont pu diverger de celles des formes libres qui leur sont apparentées. Nous avons comparé la taille du corps et le nombre de segments corporels de polychètes parasites de la famille des Oenonidae à ceux de polychètes libres de familles très apparentées. Il n'y a pas de différence entre les polychètes libres et les Oenonidae quant à la taille du corps. Cependant, chez les Oenonidae parasites, les segments du corps sont beaucoup plus nombreux que chez les polychètes libres. Le nombre de segments par unité de longueur du corps est aussi bien supérieur chez les Oenonidae, ce qui indique que la segmentation se fait à un rythme plus rapide et sur une plus longue période chez les Oenonidae que chez les polychètes libres chez lesquels la prolifération des segments ralentit avec le temps, permettant aux segments de croître. Comme chaque segment peut produire des gamètes jusque tard dans la vie de l'animal, la prolifération des segments chez les Oenonidae peut être une adaptation à leur mode de vie parasitaire.

[Traduit par la Rédaction]

Introduction

The life-history strategies of parasitic animals are widely believed to differ somewhat from those of free-living animals because parasites face slightly different selection pressures. On the one hand, space restrictions within the host are believed to physically constrain the body size of endoparasites, leading to a reduction in their size over evolutionary time (Price 1980; Hanken and Wake 1993). On the other hand, the abundant resources available to parasites and the huge losses incurred by their larval stages during transmission are believed to favour the evolution of high growth rates, early maturity, and mainly high reproductive output (Price 1974; Jennings and Calow 1975; Calow 1983). The available comparative evidence, however, suggests that these trends are not the rule, and that parasitic lineages can diverge from their free-living relatives in many directions (Poulin 1995, 1998). To date, this evidence comes from only a few taxa (mainly crustaceans), including both parasitic and free-living representatives; studies on other taxa are necessary to determine the evolutionary consequences of adopting a parasitic life-style for an animal's life history.

The polychaete annelids are good candidates for a study of this nature. The majority of polychaete worms are free-living in marine habitats. Nonetheless, commensalism and parasitism occur in several polychaete families, and both are usually associated with only minor morphological adaptations, such as reduced setae (Clark 1956; Pettibone 1957; Blake 1990; Dean 1992). Endoparasitism occurs almost exclusively in members of the family Oenonidae (formerly Arabellidae). The majority of oenonids are parasitic in other polychaetes, mainly of the families Onuphidae and Syllidae, one species being parasitic in echinoderms and one in bivalves (Dean 1992; Hernández-Alcántara and Solís-Weiss 1998). Other oenonids are known only as free-living forms. However, there may be a parasitic phase in the life of all oenonids. Three genera (*Arabella*, *Drilonereis*, and *Notocirrus*) of oenonids contain both parasitic and "free-living" species, suggesting that the parasitic phase of the free-living species has simply not been observed. How the young parasitic worms penetrate their host is unknown, but large worms are often found protruding from their host, apparently in the process of exiting. The fact that eggs are never found in parasitic oenonids suggests that reproduction takes place later in life, during a postparasitic free-living phase (Uebelacker 1978; Hernández-Alcántara and Solís-Weiss 1998).

It has been pointed out that parasitic oenonids can be lon-

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ger than their hosts (Hernández-Alcántara and Solís-Weiss 1998). Determining how the body sizes of parasitic oenonids compare with those of their closest free-living relatives could shed light on how a transition to parasitism has influenced the life-history strategies of polychaetes. Furthermore, in this taxon, body segmentation can be used as another measure of growth rate and (or) body size. The number of segments typically varies very little, if at all, among conspecific adult polychaetes (Dales 1967; Barnes et al. 1988), making it a true species characteristic. This number varies greatly among species, however, and the extent of segmentation in polychaetes may be associated with different life-styles. For instance, tubicolous polychaetes (order Sedentaria in older taxonomic schemes), which are deposit- or filter-feeders, generally have many fewer body segments than the free-living, predaceous polychaetes (formerly order Errantia) (Fauchald 1977). Whether adoption of a parasitic life-style is associated with a change in segmentation in polychaetes is not known.

The aims of this study were to determine whether parasitic oenonid polychaetes differ in body size and segmentation pattern from their free-living relatives, and if so, in what way. In addition, I examined whether these parameters are influenced by the body size of the hosts of oenonids.

Methods

Body lengths and numbers of segments were obtained from compilations of species descriptions of free-living polychaetes either with a worldwide distribution or from the southern hemisphere (Day 1967; Orensanz 1990). Data were not available for all species, but came from a large enough number of species to provide a representative sample. Data on parasitic Oenonidae were obtained from the latter as well as from other sources (Allen 1952; Pettibone 1957; Emerson 1974; Uebelacker 1978; Dean 1992; Hernández-Alcántara and Solís-Weiss 1998). If a range of body lengths or numbers of segments was provided, the median was used as a species value. When available, the name, body length, and number of segments of the host species of parasitic oenonids were also recorded.

The phylogenetic relationships among polychaete families have been resolved to some extent, whereas those within families are unknown. In an effort to eliminate confounding phylogenetic influences from the analyses as much as possible (Harvey and Pagel 1991), the Oenonidae were only contrasted with the polychaete families believed to be most closely related to them. Rouse and Fauchald (1997) place the Oenonidae within the clade Eunicida, along with six families of free-living polychaetes (Amphinomidae, Euphrosinidae, Dorvilleidae, Lumbrineridae, Eunicidae, and Onuphidae). They could not determine the exact phylogenetic position of the Oenonidae within the clade, and therefore in the first analysis, the Oenonidae were compared with the six free-living families of eunicidan polychaetes. Earlier, however, Orensanz (1990) had proposed that the Oenonidae may be the sister-group of the Lumbrineridae, so in a second analysis, the Oenonidae were compared only with the Lumbrineridae.

Body lengths and numbers of segments were all log-transformed prior to analysis. Skewness in the frequency distributions of body lengths or numbers of segments was estimated by computing the standard coefficient of skewness, g_1, which is scaled to equal 0 in symmetric, nonskewed distributions, and its standard error (Sokal and Rohlf 1995, pp. 111–115 and 138). To obtain an index of the extent of segmentation in each polychaete species independent of its body length, I regressed number of segments against body length and used the residuals of the relationship; positive residual values indicate species with more segments than expected, based on their length, whereas negative residuals indicate species with fewer segments than expected. All comparisons between the Oenonidae and their free-living relatives were performed using two-tailed *t* tests.

Results

The analysis is based on data from 104 species of free-living eunicidan polychaetes and 23 species of parasitic oenonids (Table 1). For some species, data were not available for both variables (body length and number of segments), but for only one.

There is no difference between oenonids and free-living Eunicida with respect to body length (t = 0.468, df = 123, P = 0.6404). For both groups, the majority of species are small-bodied, with a length not exceeding 100 mm (Fig. 1). Both groups show log left-skewed body length distributions, but the skew is significantly more pronounced in oenonids (Oenonidae: g_1 = –0.855; free-living Eunicida: g_1 = –0.482; t = 5.260, df = 123, P = 0.0001). However, the number of segments in oenonids is significantly greater than in free-living Eunicida (t = 4.349, df = 47, P = 0.0001) because a large proportion of oenonids display a very high number of segments compared with their free-living relatives (Fig. 1). In fact, the frequency distribution of segment numbers in oenonids is log right-skewed, whereas it is left-skewed in their free-living relatives (Oenonidae: g_1 = 0.391; free-living Eunicida: g_1 = –0.459; t = 6.093, df = 47, P = 0.0001).

Across all species for which data are available, the number of segments covaries positively with body length (Fig. 2). The observed number of segments in oenonids, however, tends to be greater than expected, based on their body size, as indicated by the fact that most data points for oenonids lie above the regression line, whereas those for free-living Eunicida tend to fall below the line (Fig. 2). Indeed, the residual values for oenonid parasites (0.224 ± 0.051 (mean ± SE)) are greater than those for the free-living Eunicida (–0.105 ± 0.032), and the difference is highly significant (t = 5.654, df = 45, P = 0.0001).

The results are essentially the same when only the Lumbrineridae are used as free-living relatives in a comparison with oenonids. Species of the two families do not differ in body length (t = 0.336, df = 39, P = 0.739), but oenonids tend to have more segments than lumbrinerids, although the difference is not quite significant (t = 1.851, df = 23, P = 0.077). The number of segments increases with body length across all lumbrinerid and oenonid species for which data are available ($y = 0.471x + 1.455$; r^2 = 0.516, P = 0.0001; n = 8 free-living lumbrinerids and n = 15 parasitic oenonids). Again, a comparison using the residuals of this regression shows that oenonids have more segments per unit body length than lumbrinerids (t = 3.525, df = 21, P = 0.002).

Among oenonid species with a known polychaete host only, neither body length (r = 0.488, P = 0.220, n = 8) nor number of segments (r = 0.414, n = 9, P = 0.269) correlates significantly with the body length of the host species. Not enough data on host segmentation were available to determine whether this variable correlated with either body length or number of segments in the parasitic oenonids.

Table 1. Body lengths and numbers of segments in polychaetes of the clade Eunicida included in the analyses.

Family	No. of genera	No. of species	Avg. length (mm)	Avg. no. of segments
Free-living				
Amphinomidae	7	11	83 (17–250)	76 (28–120)
Dorvilleidae	5	10	14 (4–50)	66 (25–100)
Eunicidae	4	33	170 (30–560)	147 (95–200)
Euphrosinidae	1	2	20 (15–25)	—
Onuphidae	8	28	83 (7–350)	85 (32–180)
Lumbrineridae	4	20	81 (10–250)	108 (60–140)
Parasitic				
Oenonidae	9	23	88 (3–240)	250 (50–1200)

Note: Values in parentheses are ranges.

Fig. 1. Frequency distribution of body lengths and numbers of segments among free-living Eunicida and parasitic Eunicida of the family Oenonidae. Note that the scale of the *x* axis is contracted at the right-hand side.

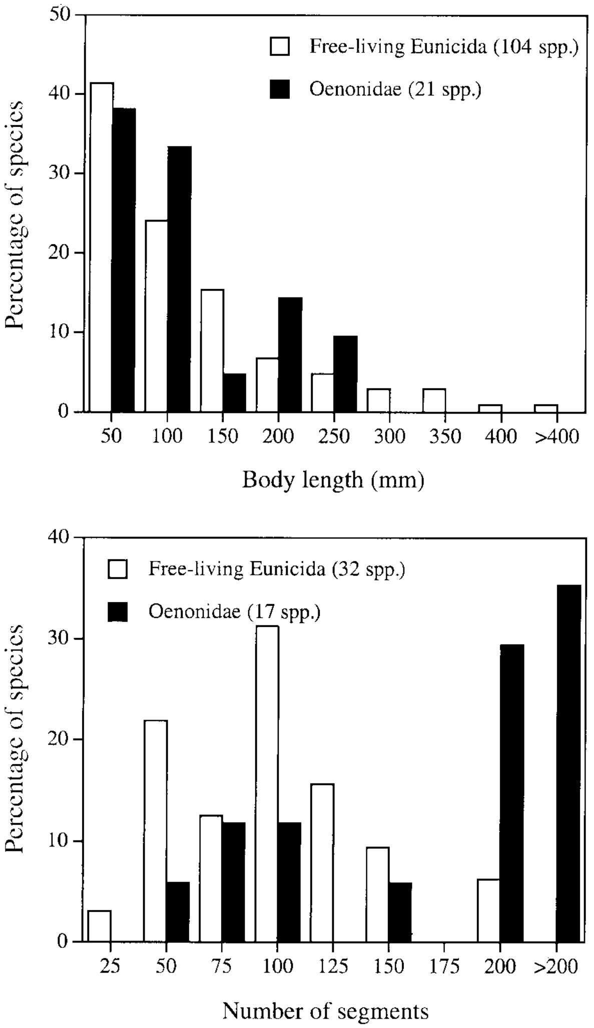
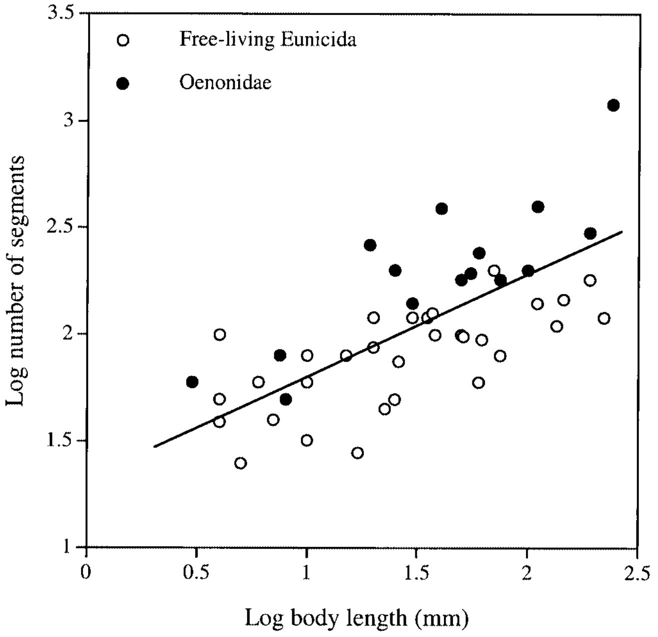


Fig. 2. Relationship between number of segments and body length among polychaete species of the clade Eunicida ($y = 0.434x + 1.385$; $r^2 = 0.464$, $P = 0.0001$; $n = 32$ free-living Eunicida and $n = 15$ parasitic oenonids).



Discussion

Contrary to earlier suggestions concerning the evolution of parasites (Price 1980; Hanken and Wake 1993), the results presented here provide no evidence that the body size of oenonid polychaetes was reduced following their transition to a parasitic mode of life. This conclusion reinforces the view that there are no fixed rules governing parasite evolution (Poulin 1998). In fact, using the number of body segments as a measure of body size, parasitic oenonids are much "larger," on average, than their free-living relatives. An endoparasitic life-style has clearly placed no constraints on the number of segments that a polychaete can achieve. This conclusion is based on a single evolutionary event, i.e., the one transition to an endoparasitic life-style that occurred among the ancestral Eunicida, which gave rise to the family Oenonidae, and it must be viewed with some caution. It was not possible to control for a possible confounding phylogenetic effect. The difference in segmentation pattern between the free-living and parasitic eunicidans is striking, however, and their different life-styles provide the most likely explanation.

The present comparative analysis is based on only a sample of existing polychaete species because body-size and segmentation data are not available for all known species. Nevertheless, several representatives of all eunicidan families (except Euphrosinidae) are included. Only 18 species of parasitic oenonids have been described (see Hernández-Alcántara and Solís-Weiss 1998), in addition to a few supposedly free-living species. The paucity of parasitic species currently known is no doubt due to their very low prevalence in host populations (often <1%; see Uebelacker 1978) and the fact that they are usually not visible without dissecting the host. Nevertheless, the present analysis included data from 14 of the 18 known parasitic species and from 9 "free-living" species of Oenonidae, providing a representative sample of the family.

Little is known of the ecology of oenonid parasites, although parameters such as intensity of infection could influence the growth of the parasites. In two oenonid genera, *Arabella* and *Notocirrus*, it is common to find numerous individuals within a single host (Allen 1952; Pettibone 1957). These often range in size from very small worms to adult-sized ones. In the other genera, parasites always occur singly. Excluding species of the genera *Arabella* and *Notocirrus* from the analysis had no effect on the results.

In many endoparasite groups, such as nematodes (Morand 1996; Morand et al. 1996), parasite body size correlates with host body size in comparative analyses across species. The influence of host body size is particularly important in parasitic worms that, like oenonids, live singly in an invertebrate host which is less than an order of magnitude larger than the parasites, such as mermithid nematodes and nematomorphs (Poinar 1991). No evidence for such a relationship was obtained here, although the number of oenonid species that could be included was quite small. It is possible that oenonid body length is not constrained by the size of the host species, however. In some associations, the oenonid parasite's body is folded on itself several times (e.g., Hernández-Alcántara and Solís-Weiss 1998), whereas in others it is not (e.g., Uebelacker 1978). A host worm can thus either harbour a parasite that is much shorter or much longer than itself, making host size a poor predictor of parasite size in these polychaetes.

The main finding of this study is the greater rate of segmentation per unit body length in the parasitic Oenonidae than in their free-living eunicidan relatives. Another way of stating this is that oenonids have more and smaller segments than their free-living counterparts. One explanation may be that parasitic oenonids produce new segments at a faster rate than free-living polychaetes. In polychaetes, new segments are formed in a germinal region just in front of the terminal region, or pygidium; thus, in adult worms the oldest segments are those closer to the head of the worm (Dales 1967; Barnes et al. 1988). In young worms the rate of segment proliferation is usually high, and it slows down in older individuals, to be compensated for by the enlargement of the segments as they become filled with accumulating gametes (Barnes et al. 1988). In most polychaetes, the body wall of gravid worms ruptures to release the accumulated gametes at the end of the worm's life (Barnes 1980). In the Eunicida and most other polychaetes, almost all segments produce gametes (Barnes 1980). It may thus be that the strategy adopted by parasitic oenonid polychaetes is either to maintain a higher rate of segment proliferation than in free-living polychaetes, or to keep producing new segments for a longer time. This could easily be achieved early in their life, when they are parasitic and growing in a resource-rich environment, in order to achieve high fecundity later in life after emergence from the host. The extremely low prevalence of oenonid infections in host populations (e.g., Uebelacker 1978) suggests that oenonid transmission rates are very low, a fact that would strongly favour parasitic individuals with a high reproductive potential. The proliferation of segments in oenonids may thus be an adaptation to their parasitic lifestyle, and appears to be the main difference in life-history strategy between them and their free-living relatives.

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