Modelling infection of Baltic herring (Clupea harengus membras) by larval Anisakis simplex

Jan Horbowy and Magdalena Podolska

Anisakis simplex larvae were counted in the body cavities of Baltic herring collected in the southern Baltic in 1992–1993, 1995–1996 and 1997. Mean infection intensity in infected fish was generally <10 in fish <30 cm in length but increased sharply to 20–50 in larger fish. Intensities recorded in 1997 were 30–40% higher than those documented in 1992–1993 and 1995–1996.

Models relating infection intensity to fish length and weight were developed and used to estimate the asymptotic size of herring. The \( L_{96} \) estimates ranged from 32.8–34.0 cm, and the \( W_{96} \) varied from 335.4 to 356.0 g. Estimates of asymptotic length and weight from models of infection intensity were more stable and generally were more precise than those determined from length and weight-at-age data.

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Key words: herring, Anisakis simplex, Baltic, model, asymptotic size.

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Introduction

Local stocks of herring in the Baltic Sea can be divided into spring- and autumn-spawning groups. Kompowski (1971), identified coastal and open-sea populations of spring spawners on the basis of the otolith structure. Some individuals of coastal spring herring undertake feeding migrations out of the Baltic through the Öresund to the Danish Straits (Kattegat and Skagerrak). An extensive review of herring migration is given by Aro (1989).

Baltic Sea herring are often heavily infected with the larval ascaridoid nematode Anisakis simplex which they presumably acquire from their prey (e.g. Grabda, 1974; Strzyżewska and Popiel, 1974; Weber and Neudecker, 1988; Lang et al., 1990; Myjak et al., 1993). To date, it has not been confirmed that herring become infected in the Baltic. Euphausiids, the main source of infection in herring, do not occur in the Baltic Sea. Moreover, cetaceans, the definitive hosts for A. simplex, are rare in the Baltic, where the only porpoise Phocaena phocaena is regularly noted (Skóra, 1992). The Baltic porpoises have been examined by Rokicki and Berland (1995) and Rokicki et al. (1997), but A. simplex were not noted. Thus, coastal spring herring must become infected during their annual feeding migrations to the Danish Straits and, perhaps, to the North Sea (Grabda, 1974). Hence, A. simplex larvae could be used as a population marker for herring spawning in Baltic coastal waters each spring. Since they accumulate A. simplex during the annual migrations to the feeding grounds, prevalence and intensity of infection increases with size and age (e.g. Grabda, 1974; Friess, 1977; Kühlmorgen-Hille, 1983; Weber and Neudecker, 1988; Lang et al., 1990; Myjak et al., 1993).

A model relating the parasite intensity to fish length was developed by des Clerfs (1989) for cod infected with another anisakine parasite, Pseudoterranova decipiens. Gibson and Jones (1993) estimated asymptotic length of orange roughy, albacore tuna and New Zealand southern arrow squid from intensities of A. simplex infection.

The objectives of the present study were to model the intensity of A. simplex infection in Baltic Sea herring as a function of fish length and weight and thereby estimate asymptotic length and weight of the host. Des Clerfs (1989) approach was modified here to reflect the specific feeding migration of Baltic herring, and a model describing the relation between the weight of fish and the infection intensity was developed.
Materials and methods

Samples of coastal spring herring *Clupea harengus membras* were collected from the Polish zone of the Baltic Sea (24, 25 and 26 ICES Subdivisions) and the Vistula Lagoon (Figure 1) between January 1992 and December 1993 (2667 individuals), January 1995 and April 1996 (5325 individuals) and between January and December 1997 (2840 individuals). The total body length (in half-centimetre classes) and weight (g) of each fish were recorded and viable *A. simplex* larvae in the body cavity of the fish were counted. Only a few necrotic larvae were noted, but they were not identified to species. The spawning populations and the age of the herring were classified according to the otolith method of Kompowski (1971). The number of fish examined by length class and the percentage of fish infected is presented in Table 1. The intensity of infection is defined as number of individuals of a particular parasite species in each infected host and mean intensity is mean number of individuals of a particular parasite species per infected host in a sample (Margolis et al., 1982).

Des Cleris (1989) modelled *P. decipiens* intensity as a function of host length *L* using the following equation

\[
N_i = A \left[ L_x^2 \ln \left( \frac{L_x}{L_x - 1} \right) - L_x \left( \frac{L_x}{2} - \frac{1}{2} \right) \right]
\]  

(1)

Figure 1. ICES Subdivisions and Polish Fishery Zone in the Baltic Sea.
where

\[ A = \frac{ab}{K} \]

\( N_l \) – mean intensity of infection at length \( l \),

\( L_\infty \) – asymptotic length,

\( K \) – growth rate,

\( a, b \) – parameters with meanings described below.

Equation (1) was derived assuming that (des Cler, 1989):

1. A fish grows in length according to the von Bertalanffy growth equation,

\[ l_t = L_\infty (1 - \exp(-Kt)) \]

where \( t \) is the age.

2. The amount of food \( F \) consumed by a fish of length \( l \) is proportional to the square of fish length,

\[ F = a l^2 \]

where \( a \) is a parameter specifying the feeding requirements of the fish.

3. The infection intensity at length \( l \) is proportional to the total amount of food \( TFC \) consumed by a fish until it has reached length \( l \),

\[ N_l = b \ TFC_l \]

where \( b \) is a constant average density of parasites per unit weight of food consumed.

4. The parasite death rate in the host is constant over time.

In addition, it was assumed that the parasites or their remains are not lost from the host.

In model (1) the total amount of food eaten by fish until it has reached length \( l \), \( TFC \), is obtained by integrating the food consumed over length from zero to \( l \). Thus, it is assumed that cod feed on infected food from the beginning of their lives. This is not the case, however, with the Baltic herring, which first become infected at age two and older when some of them undertake feeding migrations to the Danish Straits and the North Sea (Kühlmorgen-Hille, 1979, 1983). Thus, in the present approach, the total quantity of food consumed which may contain...
A. *simplex*, TFC is obtained by integrating the food consumed over length from the length at first contact with infected food, \( l=0 \), to the current length \( l \):

\[
TFC = \int_{0}^{l} \frac{a}{K(L_{\infty} - l)} \, dl
\]

This yields

\[
TFC = \frac{a}{K} \left[ \ln \left( \frac{L_{\infty} - 10}{L_{\infty} - 1} \right) + L_{\infty} (10 - 1) \right]
\]

Finally, in the present approach, the mean intensity is simulated by the model

\[
N_{\infty} = A \left[ \ln \left( \frac{L_{\infty} - 10}{L_{\infty} - 1} \right) + L_{\infty} (10 - 1) \right]
\]  

(2)

where \( A \) has the meaning given above. Letting \( l=0 \) simplifies the above equation to the form presented by des Cler (1989).

The model can be further modified to describe *A. simplex* intensity as a function of weight. Following Andersen and Ursin (1977), the amount of food consumed may be related to the weight \( w \) by

\[
F = hw^{2/3},
\]

and the change in weight may be given as

\[
dw/dt = vhw^{2/3} - kw,
\]

where \( v \) is a parameter representing the fraction of consumed food assimilated for growth and \( h \) is a species-specific parameter reflecting the food requirements of the fish. The asymptotic weight, \( W_{\infty} \), is thus equal to \((vh/k)^{3}\). Then, the total food consumed from the time the animal has reached weight \( w_0 \) to the moment it achieves weight \( w \) is:

\[
TFC = \int_{w_0}^{w} \frac{hw^{2/3}}{vhw^{2/3} - kw} \, dw,
\]

which, after integrating, yields

\[
TFC = TFC_0(w) - TFC_0(w_0),
\]

where

\[
TFC_0(w) = -h \ln \left( \frac{(W_{\infty} - w)^{2}(W_{\infty}^{1/3} - w^{1/3})^{4}}{(W_{\infty}^{2/3} + W_{\infty}^{1/3}w^{1/3} + w^{2/3})^{2}} \right) + 6W_{\infty}^{1/3}w^{1/3} + 3w^{2/3} \right] / (2k)
\]

The integral TFC was arrived at using a mathematical manipulation language MAPLE V (1991). Finally the mean infection intensity is modelled by:

\[
N_{w} = A \left[ W_{\infty}^{2/3} \ln \left( \frac{(W_{\infty} - w)^{2}(W_{\infty}^{1/3} - w^{1/3})^{4}}{(W_{\infty}^{2/3} + W_{\infty}^{1/3}w^{1/3} + w^{2/3})^{2}} \right) + 6W_{\infty}^{1/3}w^{1/3} + 3w^{2/3} \right] - W_{\infty}^{2/3} \ln \left( \frac{(W_{\infty} - w)^{2}(W_{\infty}^{1/3} - w^{1/3})^{4}}{(W_{\infty}^{2/3} + W_{\infty}^{1/3}w^{1/3} + w^{2/3})^{2}} \right) - 6W_{\infty}^{1/3}w^{1/3} - 3w^{2/3} \right] / (2k)
\]

(3)

where \( A = bh/(2k) \).

Having counted the numbers \( N_{w}^{\text{obs.}} \) of parasites in infected fish of length \( l \), the parameters \( A \) and \( L_{\infty} \) in model (2) can be determined by minimising the sum of the squared differences between the observed mean infection intensity and the infection intensity resulting from the model (2):

\[
SS(A, L_{\infty}) = \sum_{i} \left( \sqrt{N_{i}^{\text{obs.}}} - \sqrt{N_{i}^{\text{mod.}}} \right)^{2}
\]

(4a)

where \( N_{i}^{\text{mod.}} \) denotes the modelled number of parasites in infected fish. Similarly, the parameters \( A \) and \( W_{\infty} \) of model (3) can be estimated by minimising the sum of the squares:

\[
SS(A, W_{\infty}) = \sum_{i} \left( \sqrt{N_{w}^{\text{obs.}}} - \sqrt{N_{w}^{\text{mod.}}} \right)^{2}
\]

(4b)

where \( N_{w}^{\text{mod.}} \) is now represented by model (3) and \( N_{w}^{\text{obs.}} \) denotes the mean number of parasites in infected fish of weight \( w \), where \( w \) is the mean weight at length \( l \).

Only data referring to infected fish were used in the model since only part of the coastal spring herring undertakes feeding migration outside the Baltic. So in the presented approach the models and the growth parameters are representative of the infected part of the stock.

Parasite intensity distribution is often aggregated and best described by negative binomial distribution (e.g. review by Shaw et al., 1998). However, to estimate the model parameters the mean intensity is taken which, according to the central limit theorem of probability, is asymptotically normally distributed. In addition, the square root transformation of the modelled and observed values was used to stabilise the variance and remove the skewness in the error distribution. The \( L_{\infty} \) and \( W_{\infty} \) were also assessed from mean length and weight-at-age data, using the von Bertalanffy growth equation. In the latter approach \( L_{\infty} \) and \( W_{\infty} \) was estimated for all herring sampled and also for infected herring only, so that the estimates could be compared with those based on infection intensity. The
minimisation of the above sum of squares was performed using SOLVER in Microsoft EXCEL97. Outliers were identified on the basis of the distribution of the model residuals. The points with residuals outside the interval defined as the lower quartile – 1.5 interquartile range, upper quartile + 1.5 interquartile range were treated as outliers and omitted in the final minimisation procedure. Eventually, one point was omitted from the 1992–1993 data, four points were omitted from the 1995–1996 data, and three from the 1997 data.

The jack-knife procedure (Efron, 1982) was applied to estimate the variance of the parameters of the model.

Results

The average numbers of *A. simplex* observed and estimated from model (2) in each host length class in 1992–1993, 1995–1996 and 1997 are given in Figure 2. The error distribution is approximately normal as exemplified by the 1997 data (Figure 3). Estimated values of $L_{\infty}$, A and their coefficients of variation for parasite intensity data and for mean length-at-age data are also presented in Table 2, while the length–age relationship is shown in Figure 4 with outliers omitted. The estimates provided by the model differ between the periods analysed. Intensities estimated from the 1997 data were over 30% greater than those estimated from 1992–1993 data,

Figure 2. Relationship of mean *A. simplex* intensity to length of host Baltic herring – observed and estimated from the model. ◇, observed; ——, estimated.

![Figure 2](image)

Figure 3. An example of the error distribution in the model fit to the 1997 data as presented by normal probability plot.

Table 2. The estimated values of $L_{\infty}$, A and their coefficients of variation, CV, arrived at using different methods.

<table>
<thead>
<tr>
<th>Method</th>
<th>Year</th>
<th>$L_{\infty}$ (cm)</th>
<th>A</th>
<th>CV (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intensity of larval <em>A. simplex</em> infection</td>
<td>1992–1993</td>
<td>32.8</td>
<td>0.0083</td>
<td>58.34</td>
</tr>
<tr>
<td></td>
<td>1995–1996</td>
<td>34.0</td>
<td>0.0075</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>1997</td>
<td>33.7</td>
<td>0.0117</td>
<td>0.28</td>
</tr>
<tr>
<td>Length/age data (infected)</td>
<td>1992–1993</td>
<td>29.1</td>
<td>—</td>
<td>1.22</td>
</tr>
<tr>
<td></td>
<td>1995–1996</td>
<td>*</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>1997</td>
<td>*</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Length/age data (infected and non-infected)</td>
<td>1992–1993</td>
<td>29.1</td>
<td>—</td>
<td>0.98</td>
</tr>
<tr>
<td></td>
<td>1995–1996</td>
<td>35.7</td>
<td>—</td>
<td>1.93</td>
</tr>
<tr>
<td></td>
<td>1997</td>
<td>38.7</td>
<td>—</td>
<td>5.02</td>
</tr>
</tbody>
</table>

*Unreasonable estimate.
while estimates for 1992–1993 and 1995–1996 differed by 5–10%. Intensity was generally <10 in host <30 cm in length, but increased sharply to 20–50 in larger fish.

The estimated values of \( L_p96 \) are relatively similar, ranging as they do from 32.8–34.0 cm for the periods analysed. The CVs of the estimated \( L_p96 \) are very low (less than 1%) for estimates based on data from 1995–1996 and 1997. The estimated \( L_p96 \) derived from the 1992–1993 data has a very high CV of 58%. The 1992–1993 estimate of \( L_p96 \) is to a large extent determined by the last data point, which gives the number of parasites at a fish length of 30.5 cm. If this point is omitted from the calculations the model produces an unrealistic estimate of \( L_p96 \) of 94 cm. If this data point is not omitted in the jack-knife procedure, the CV of \( L_p96 \) is equal to about 0.1%.

Asymptotic weights, \( W_p96 \) for \( A. \) simplex intensities and weight-at-age data are given in Table 3 and Figure 5. The intensity model failed to yield realistic estimates of \( W_p96 \) for the 1992–1993 sample, whilst parameters estimated from weight at age data (Table 3, Figure 6) varied from 150–720 g for 1992–1993, 1995–1996 and 1997 data sets. When from infected fish alone were used, the estimates of \( W_p96 \) for the 1995–1996 and 1997 weight-at-age data yielded quite extraordinary values of 8–9 kg. Estimation of asymptotic weight on the basis of model (3) produced much more stable results. The CVs calculated for the estimates using the traditional method are much higher than those based on parasitic infection. The traditional estimates were very much dependent on the data point at the oldest age in the sample. When this point was not omitted in the jack-knife procedure, the CVs of the asymptotic weight were similar to the ones obtained using model (3). It can be concluded that for these data sets our model (3) provides more realistic estimates of \( W_p96 \) than the traditional method based on weight at age data.

The model was not sensitive to the assumed length of first feeding on euphausiids \( l_0 \). The estimated parameters with \( l_0=0 \) differed little from the parameters obtained
with 10=19 for the 1995–1996 and 1997 data. The difference between the estimated parameters for the 1992–1993 data was greater but still relatively low.

Discussion

The model of des Cleres (1989) assumes that infection level of the parasite in the prey of the fish is constant over the lifespan of the fish. However, our results show a marked increase in the intensity of infection in herrings collected in 1997 compared to 1995–1996 samples. Such an increase may happen when the parameter b, the average density of parasites per unit weight of food consumed (assumption 3), is not constant over time. To take this into account, one would have to develop a new model in which b would be time dependent. However, the estimates of asymptotic sizes, based on data for both periods, show only slight differences. This suggests that the model for these data is relatively robust to violation of the assumption.

Grabda (1974) investigated Baltic herring from the Pomeranian Bay (ICES Subdivision 24) and found that the number of A. simplex nematodes increases in accordance with the length of a fish. The smallest herring of length 20–22 cm contained an average of 1.6 larvae per fish while in the largest individuals (30 cm in length) the average number of larvae was 15. The intensity of infection increased abruptly at 27 cm and longer. She did not find any nematodes in fish less than 20 cm in length. The curve of the dependence of infection intensity on length in Grabda’s paper is similar to ours, but the infection intensity is higher in our samples. Moreover, Myjak et al. (1996) and Podolska (1996) have also reported intensity of A. simplex infection in herring increased with host length in the Baltic. According to Lang et al. (1990) the intensity of infection in western Baltic herring (ICES Subdivisions 22 and 24) is positively correlated with the length and age of fish. They fit linear functions to intensity/host length data, but stated that the relationship was probably not a simple linear one. A relationship showing increasing intensity with age of fish has also been described by Bishop and Margolis (1955) for herring C. pallasii from the British Columbia coast.

Data presented by Khalil (1969) reveals spatial variation in the prevalence and intensity of A. simplex infection in North Sea herring from British coastal waters but also indicate that intensity in North Sea herring increased with the age and length of host irrespective of geographical origin. According to Khalil, intensity in North Sea herring usually ranged between 30–50, but the maximum intensity was 126. Mean intensity was 33.05 and prevalence, 100% near the British coast. Similar results were also presented for North Sea herring by Davey (1972) (British and adjacent waters) and by van Banning and Becker (1978). In our study, the maximum intensity of A. simplex in herring ranged between 41–87 with the highest intensity occurring in 1995–1996. Khalil (1969) reported infection even in a small herring from the North Sea (less than 12 cm in length), although this specimen was infected with only a very few larvae. In the case of the Baltic herring examined in the present study, the smallest fish infected with A. simplex was 19 cm in length.

Gibson and Jones (1993) applied model (1) to estimate the asymptotic length of other hosts of A. simplex, such as the orange roughy (Hoplostethus atlanticus), a slow-growing teleost, the albacre tuna (Thunnus alalunga), and the arrow squid (Notodarbus sloani), a fast-growing but short-lived mollusc. The confidence limits of the estimated asymptotic length are indicative of very low CV values, as was the case in our study. Thus the model works well for different species of fish and even for squid.

Estimates of \( L_\infty \) from length-at-age data vary widely for the periods under consideration, and range between 29.1–38.7 cm when both infected and non-infected herring from the samples are used in the calculations. These estimates differ substantially from the values obtained from model (2). They show an increasing trend in

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Table 3. The estimated values of \( W_\infty \), A and their coefficients of variation, CV, arrived at using different methods.

<table>
<thead>
<tr>
<th>Method</th>
<th>Year</th>
<th>( W_\infty ) (g)</th>
<th>A</th>
<th>CV (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intensity of larval A. simplex infection</td>
<td>1992–1993</td>
<td>*</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>1995–1996</td>
<td>335.4</td>
<td>0.1848</td>
<td>6.09</td>
</tr>
<tr>
<td></td>
<td>1997</td>
<td>356.0</td>
<td>0.3006</td>
<td>12.95</td>
</tr>
<tr>
<td>Weight/age data (infected)</td>
<td>1992–1993</td>
<td>190.9</td>
<td>—</td>
<td>9.07</td>
</tr>
<tr>
<td></td>
<td>1995–1996</td>
<td>*</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>1997</td>
<td>*</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Weight/age data (infected and non-infected)</td>
<td>1992–1993</td>
<td>148.2</td>
<td>—</td>
<td>0.97</td>
</tr>
<tr>
<td></td>
<td>1995–1996</td>
<td>410.0</td>
<td>—</td>
<td>75.38</td>
</tr>
<tr>
<td></td>
<td>1997</td>
<td>719.9</td>
<td>—</td>
<td>266.20</td>
</tr>
</tbody>
</table>

*Unreasonable estimate.
Asymptotic length that is inconsistent with the decreasing size and growth rate of herring observed in the Baltic (Sparholt and Jensen, 1992; Horbowy, 1997). The CVs of estimated \( L_\infty \) values are low but nevertheless higher than the CVs of \( L_\infty \) estimated using model (2) for data from 1995–1996 and 1997. Because of insufficient data in the asymptotic range 1995–1996 and 1997 length-at-age analyses for infected fish produced unrealistically high estimates of \( L_\infty \) in the order of metres. Only the 1992–1993 data produced a reasonable estimate of \( L_\infty \), 29.1 cm.

Gibson and Jones’ (1993) estimates of \( L_\infty \) on the basis of the parasite abundance rests upon the following assumptions: parasites or their remains are not lost from the host and the continued consumption of infected food by fish leads to the accumulation of parasites in time. The first assumption was also made in our calculations and the second one results from it and assumption 3 of the des Cleres (1989) model. After infection, \( A. \) simplex larvae may become encapsulated in the body cavity (on the mesentery, gonads and pyloric caeca) or penetrate musculature. Larvae may remain viable for a considerable time while living in a state of anabiosis (Grabda, 1976). Smith (1984) reports \( A. \) simplex larvae with a known minimum age 60 weeks and possibly as old as 3 years in a herring.

Anisakis larvae naturally occur in the flesh of herring (Huss and Drewes, 1989; Roepstorff et al., 1993) but are greatly outnumbered by those in the body cavity. Davey (1972) found that the percentage of larvae occurring in the muscles of North Sea herring herring remains practically constant at \( \sim 0.77\% \) in all host length groups. According to Roepstorff et al. (1993), larvae in viscera constituted over 95\% of the total number of larvae in the majority of samples. There is some evidence, however, of postmortem migration of Anisakis larvae from the body cavity to the flesh of herring after the fish is caught and stored on ice (van Thiel et al., 1960; Smith and Wootten, 1975). In our study, only larvae visible in the body cavity were counted in each sample examined.

Euphausiids are among the principal food organisms of herring in the North Sea (Last, 1989). Anisakis larvae have been found in five species of euphausiids, Tysanoessa inermis, T. longicaudata and Meganyctiphanes norvegica (Smith, 1971) and in Nycitphanes couchii and Tysanoessa raschii (Smith, 1983a,b) from the North Sea. Baltic herring feed on euphausiids during annual migrations to the Danish Straits or North Sea, and this leads to gradual accumulation of \( A. \) simplex larvae. Gibson and Jones (1993) suggested that their method of estimating asymptotic length from infection intensity data is not applicable to fish which prey only sporadically on infected food. Baltic herring which migrate outside the Baltic continue to consume infected prey over much of their life span.

In some cases the estimation of growth parameters on the basis of length-at-age or weight-at-age data produced unrealistically high values. This was usually not the case, however, when parasite intensity models were employed. Estimates of reasonable growth parameters result only when the range of the independent variable, i.e. age in age-length (age-weight) relationships or the length (weight) range in intensity models reaches the asymptotic phase. If the length (weight) at age relationship or parasite intensity at length (weight) relationship do not curve towards the asymptote, unrealistically high \( L_\infty (W_\infty) \) may result (e.g. Figure 4, data for 1995–1996 and 1997; Figure 5, data for 1992–1993). Similar results may be expected when there are problems in ageing older fish or when, due to poor survival, older and larger fish are not represented in the data.

The estimation of the asymptotic length and asymptotic weight from parasite intensity models differs from length (weight)-at-age procedures in that the model
estimates of $L_\infty$ and $W_\infty$ must always be higher than the highest observed length and weight, respectively. This is because the expression $(L_\infty - l)/(L_\infty - l_0)$ is an argument of the log function in model (2) and the argument of the log function in model (3) likewise contains the term $W_\infty - w$. When the asymptotic length (weight) is estimated using the length (weight)-at-age data, the estimate of $L_\infty$ ($W_\infty$) may be lower than the maximum observed length (weight). The model can be used successfully for the interpolation of the intensity of $A. simplex$ at host sizes for which there were no observations. However, the model should not be used to extrapolate the intensity of infection. The modelled values of nematode numbers at sizes close to the asymptotic size rise sharply and tend towards infinity when the length (weight) approaches $L_\infty$ ($W_\infty$) (Figures 2 and 5).

The model does not allow for the estimation of the catabolism coefficient $K$, as it is contained in $A$, and this is equal to $ab/K$. In order to estimate $K$ the estimates of $a$ and $b$ should be available, but these are probably much more difficult to obtain than the value of $K$ when length-at-age data are available. However, if the estimates of both $L_\infty$ and $K$ are available from length-at-age data, then the product of $a$ and $b$ can be estimated from data on parasitic infection. Then again, one of the parameters, $a$ or $b$, can be estimated when the other is known.

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References


