

Sealworm (*Pseudoterranova decipiens*) infection in the benthic cottid (*Taurulus bubalis*) in relation to population increase of harbour seal (*Phoca vitulina*) in Skagerrak, Sweden

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ABSTRACT

In Koster archipelago (northern Skagerrak, Sweden) the harbour seal population increased from approximately 350 to more than 1000 individuals between 1988 and 1998. During the same period, sealworm (*Pseudoterranova decipiens*) abundance in the most heavily infected fish species, bull-rout (*Myoxocephalus scorpius*) and sea scorpion (*Taurulus bubalis*), did not increase. Since harbour seals do not normally feed on those cottids an infection route via cod (*Gadus morhua*), which consume cottids, is proposed. The abundance of sealworm in the final host is therefore related to the probability of cod preying on infected cottids prior to being preyed upon by seals. Our model predicts that the abundance of larval sealworm in benthic fishes is not related to the number of seals when the colony is over a specific threshold size.

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INTRODUCTION

In Skagerrak, the harbour seal, (*Phoca vitulina*) (Fig. 1), is the definitive host for the nematode sealworm (*Pseudoterranova decipiens*) (Lunneryd 1991, Aspholm *et al.* 1995). The infection rate in seals collected from the northern Skagerrak during the seal-epizootic 1998 was low (abundance 22 for seals one year and older) compared with that reported in grey seals (e.g. Stobo *et al.* 1990). Grey seals (*Halichoerus grypus*) occur in the area, but in very low numbers (Härkönen and Lunneryd 1991). Most of the adult sealworm population is found in a few seal stomachs, with a skewed and heteroscedastic distribution (Lunneryd 1991, Olafsdottir and



Fig. 1
The harbour seal (*Phoca vitulina*) is a major reservoir for sealworm in European waters.
Photo: S-G. Lunneryd

Hauksson 1998). A further characteristic feature in Skagerrak is that few fish species are important as intermediate hosts (Jensen and Idås 1992, Andersen *et al.* 1995, Aspholm *et al.* 1995). Reported abundances are high only in the cottid, bullrout (*Myoxocephalus scorpius*) and cod (*Gadus morhua*), and there is a sharp decrease in infection with increasing distance from the haulout skerries (Jensen and Idås 1992, des Clers and Andersen 1995).

Based on analysis of more than 15,000 otoliths from harbour seal faeces in the Koster archipelago, it was concluded that (1) cod is the most important single prey species (approximately 20 % of the diet), and (2) cottids are not a common food since no otoliths of these species were found (Härkönen 1987, Härkönen and Heide Jørgensen 1991). Similar results are supported by studies of seals in the Hvaler archipelago, which lies 20 km north of Koster (Aspholm *et al.* 1995, Olsen and Bjørge 1995). This means that a sealworm larvae in a cottid will not reach its final host unless a fish, which is preyed upon by the seals, consumes the cottid. Aspholm *et al.* (1995) suggested that cod from deep waters might stray into the shallow areas between the seal skerries and prey upon various benthic fish species, including cottids. As a consequence some would become heavily infected with sealworm by eating cottids, and if they are subsequently eaten by seals they represent a potentially important transmission pathway to the definitive hosts.

During a seal epizootic in 1988 the harbour seal population decreased by approximately 60 % in the Koster archipelago (Dietz *et al.* 1989). Subsequent aerial censuses revealed that the colony increased from 350 to > 1000 animals between 1988 and 1998, over the course of our investigation. des Clers and Andersen (1995), by comparing abundance of sealworm in cod caught in the years 1990 to 1992, found that the infection in cod decreased after the harbour seal epizootic 1988.

In order to investigate whether the abundance of sealworm in intermediate hosts increases with the number of seals, we investigated the impact of the increasing numbers of seals on the abundance and density of sealworm in the ben-

thophagous cottid, the sea scorpion (*Taurulus bubalis*). This species is frequently caught in eel fyke-nets in Skagerrak, although not as often as its larger relative, the bullrout (Lagenfelt and Svedäng 1999). It is most abundant among rocks and seaweed in the littoral zone. The life span is four to six years, and the maximal length is 16 cm (King and Fives 1983). Our aim is to develop a model of sealworm transmission dynamics in a closed system like a typical Scandinavian archipelago where a large number of skerries and shallow grounds are surrounded by deeper water (100– 300 meters). In such systems we believe that cod plays a crucial role in transferring the larva of sealworm to the seal host.

MATERIALS AND METHODS

The Koster archipelago (Fig. 2) is located in the northern Skagerrak close to the mainland of Sweden and is based on a plateau shelf surrounded by deep water on all sides. The archipelago consists of a large number of skerries, islets and islands with shallow areas in between, where the bottom is covered by sand, gravel, stones or shells. Seals are concentrated in four main areas in the Koster archipelago where they prefer certain skerries for haul-outs. Three of these areas constitute the main breeding haul-outs and are protected as seal sanctuaries from May to mid July. Abundance of seals at the haul-outs is greatest during the breeding, mating and moulting seasons between May and September (Härkönen *et al.* 1999). During the rest of the year the seals are more dispersed in the archipelago.

Between October 1991 and October 1998 a total of 163 sea scorpions were caught with 6 eel fyke-nets. They were caught up to 300 m from haul-out skerries in a seal sanctuary near Ursholmen in the southwest part of the archipelago. An additional sample was obtained from another seal-sanctuary 2 km southeast from Ursholmen. All fish were frozen, thawed in the laboratory, and filleted before candling. Fork length (mm) and weight (g) were recorded for each fish. Sea scorpions which were 82 to 146 mm in length were partitioned into three length groups for both study areas: (1) less than 110 mm, (2) between 111 and 120 mm, and (3) lar-

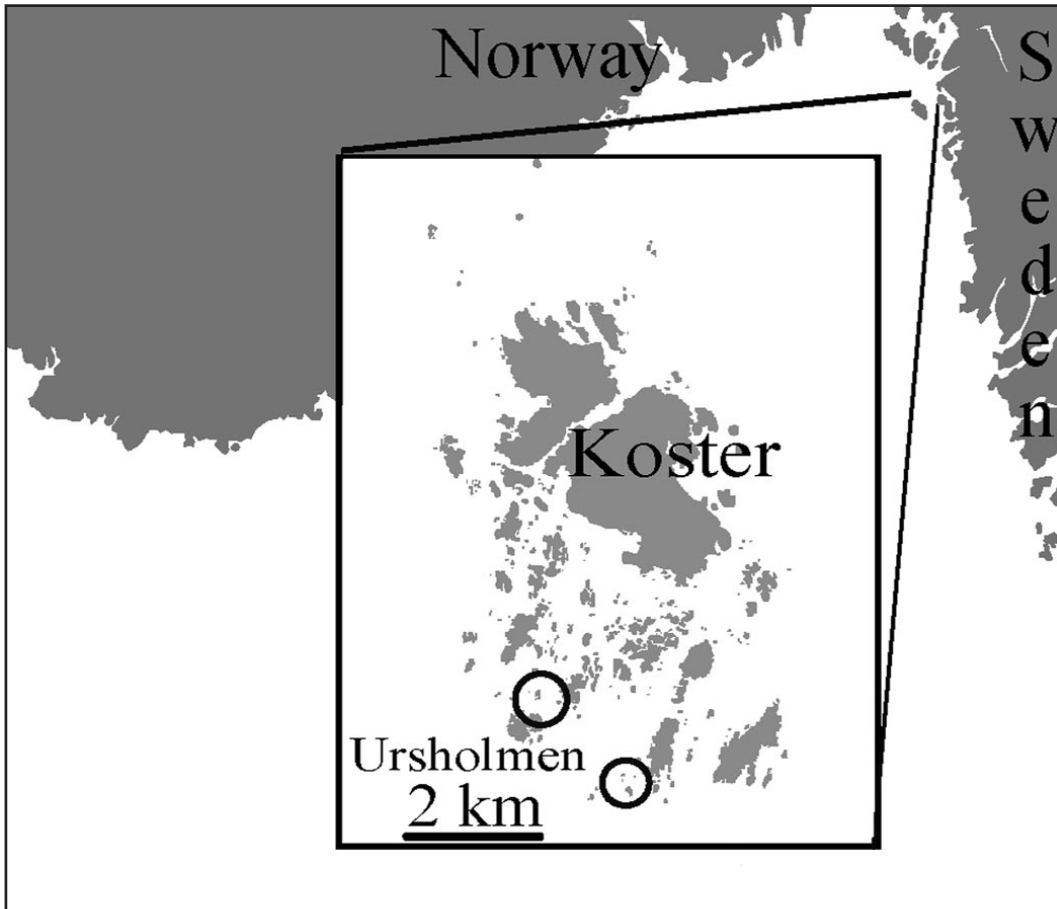


Fig. 2
 Map of the study area in the Koster archipelago, Skagerrak. Haul-out skerries are circled.

ger than 120 mm. The nematodes were fixed using standard techniques (Berland 1984) and identified according to Berland (1961). Most nematodes were readily identified microscopically when mounted on slides with water. However, in cases of uncertain identity, the nematodes were washed in glacial acetic acid for 2-4 minutes, then transferred to glycerol prior to microscopic examination.

Abundance is defined as the mean number of sealworms in all fish examined (i.e. un-infected fish are included), prevalence as the proportion of fish infected and density as the number of parasites kg^{-1} host round weight (Margolis *et al.* 1982).

RESULTS

In a sample of 297 fish collected during the first three years of the study, only five of 13 species were infected with sealworm: cod, five-bearded rockling (*Ciliata mustela*), bullrout, sea scorpion

and eel-pout (*Zoarces viviparus*). Table 1 shows that the highest densities were found in bullrout ($76.6 \text{ sealworms} \cdot \text{kg}^{-1}$) and sea scorpion ($33.4 \text{ sealworms} \cdot \text{kg}^{-1}$). The other infected species had much lower values. After 1993, the study focused on the two cottid species (bullrout and sea scorpion) (Fig. 3). During these eight years the ratio of sea scorpion to bullrout in the catches was one to six.

Sealworm prevalence increased with host length, from 40% in the smallest length class to 80% in the largest length class (Fig. 4a). Sealworm abundance was about one in sea scorpions < 120 mm and increased to 2.5 in fish > 120 mm in length (Fig. 4b; Kruskal-Wallis test, $P < 0.001$). All size groups had a density of approximately 50 nematodes per kg host weight (Fig. 4c), but the highest individual densities were found in the smallest size group. The most intense infection was 8 nematodes in a fish with a length of 92 mm and weight of 10 g. In order to reveal temporal trends, the abundance was

Table 1. Infection parameters of *Pseudoterranova decipiens* in a sample of 297 fish caught with fyke nets, during 1991 to 1993 in Skagerrak. Abundance is defined as the mean number of sealworms in all fish (i.e. non-infected fish are included), prevalence as the proportion of fish infected and density as number of parasites kg⁻¹ host round weight.

Species	Number of fish	Mean length (mm)	Prevalence (%)	Abundance	Density
<i>Gadus morhua</i>	31	209	13	0.8	3.0
<i>Ciliata mustela</i>	22	209	41	0.7	11.3
<i>Myoxocephalus scorpius</i>	58	167	78	12.1	76.6
<i>Taurulus bubalis</i>	33	111	42	0.9	33.4
<i>Zoarces viviparus</i>	29	220	21	0.2	2.9
*Other species	124		0	0	0

*Other species are *Pholis gunnellus* (16), *Gobius niger* (7), *Pollachius virens* (5), *Merlangius merlangus* (1), *Syngnathus typhle* (2), *Symphodus melops* (38), *Ctenolabrus rupestris* (54) and *Pleuronectes platessa* (1). Number of caught fish in brackets.

subdivided into four time periods: 1991 - 1992, 1993 - 1994, 1995 - 1996 and 1997 - 1998. Figure 5 reveals no temporal trend in any of the three size groups.

DISCUSSION

To our knowledge, this is the first report on of sealworm in sea scorpions in the Skagerrak area. Although the sea scorpion is a small fish occurring in low abundance among the skerries, it may play an important ecological role locally as prey for larger fishes such as cod (Andriyashev 1954, Salvanes and Nordeide 1993).

Examinations by pepsin-HCl digestion of benthophagous fish tissue indicate that a substantial proportion of nematodes of size 2 to 10 mm are overlooked in a normal optical investigation of sliced tissue (McClelland *et al.* 1983). This further emphasizes the role of sea scorpions as a potential reservoir of parasites to larger piscivorous fishes.

The pattern of infection in the Koster archipelago was similar to that found in fish in Hvaler, where heavily infected cod are caught occasionally, but the bullrout was the only species which was infected consistently (Jensen and

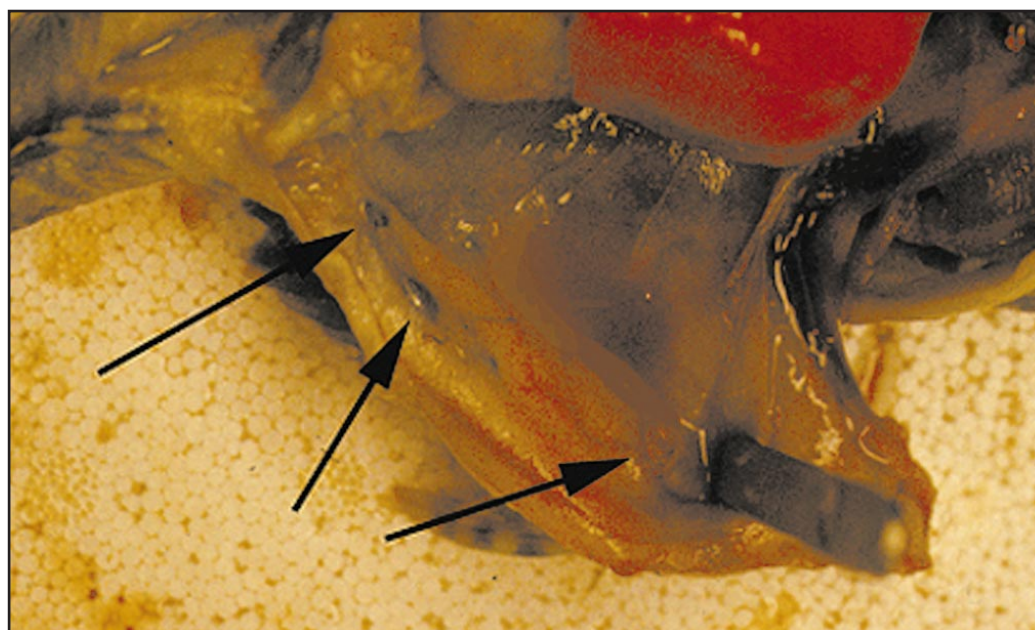


Fig. 3.
Nape of a cottid fish showing larval sealworms in the flesh.
Photo: S-G. Lunneryd

Idås 1992, Andersen *et al.* 1995, Aspholm *et al.* 1995). In our study only 5 of 13 fish species were infected with sealworm and only the cottid species had high densities of infection (Table 1).

Of the infected fish species (cod, five-bearded rockling, cottids and eelpout) from this investigation, only cod are regularly consumed by the harbour seals in Koster (Härkönen 1987, Härkönen and Heide-Jørgensen 1991). A potential source of bias in the interpretation of the harbour seal diet would be a feeding behaviour where only parts of the fish were consumed. However, a feeding experiment with dead fishes in Koster revealed that seals consumed all but the heads of codfish but refused to eat cottids (Lunneryd 2001). Tollit *et al.* (1998) suggests that harbour seals select the larger individuals of a given prey species. In a sample of 798 cod otoliths from seal faeces collected in the study area, individuals over 30 cm constituted approximately half of the total weight, and the largest fish exceeded 50 cm in length (recalculated data from Härkönen and Heide-Jørgensen (1991) and regression of cod weight and length from Härkönen (1986)). Bowen and Harrison (1996) found a mean cod length of 35.2 cm in harbour seal stomachs. Thus, harbour seals consume larger cod, which are likely to prey on bottom fishes near the seal-skerries. Since cottids do not occur in the diet of harbour seals, it is plausible that the main infection route of sealworm in the Koster archipelago is through two intermediate fish hosts, smaller benthic fish and larger demersal fishes such as cod.

Aspholm *et al.* (1995) presented a model in which uninfected cod entering shallow waters from the surrounding deep water become infected when feeding on cottids. Thus, the recruitment of sealworm to seal stomachs occurs when seals eat the recently infected cod. This mechanism is quite feasible since Burt *et al.* (1990) have shown experimentally that the sealworm larvae may be transmitted from fish to fish, although Jensen (1997) found that the survival rate was low for a larva transmitted from bullrout to cod.

In 1990, des Clers and Andersen (1995) found that cod had a higher abundance of sealworm

than cod caught in the subsequent two years. They suggested that this could be explained by a lower rate of sealworm transmission from invertebrates to cod after the seal epizootic in 1988. However, this theory has a serious problem: In 1990, cod 20 to 30 cm in length had almost the same sealworm abundance (0.15) as cod 40 to 50 cm in length (abundance 0.21 and 0.20). Since cod < 20 cm in length are not infected, worms in cod 20 and 30 cm in length must have been acquired in 1990, two years after the seal epizootic. This implies a time lag of two years for the transmission of sealworm to smaller cod via local reservoir hosts. Our point is that if there is a time lag of this magnitude, it is more biologically reasonable that cod, which became infected in 1990, acquired sealworm from benthophagous fishes rather than short-lived invertebrates.

In order to explain why the abundance of sealworm in cottids seems to be independent of the number of seals, we created a simple model of the transmission dynamics, using the following assumptions: (1) the probability that a cod is caught by a seal is proportional to the number of seals and inversely proportional to the size of the area, (2) the abundance of sealworm in the invertebrates may be approximated with a linear function of the seal density (number per unit area), and (3) the cottids feeding on invertebrates is a randomly sampling. This model predicts that when the seal colony is over a certain size, the abundance of adult sealworm is not influenced by the number of seals (see Appendix). Thus when the harbour seal population is over a certain (habitat specific) threshold size, abundance of sealworm is mainly regulated by factors other than seal numbers in a closed system like that found in Skagerrak. This is what is predicted by our model, and supported by our time series (Fig 3).

We emphasise our model is probably only valid for a closed system like a typical Scandinavian archipelago where a large number of skerries and shallow grounds (less than 5 meters) of limited area are surrounded by deeper water (50 to 150 meters). It is reasonable to assume that a cod experiences a greater risk of being caught by a seal in such areas than in the surrounding deep waters.

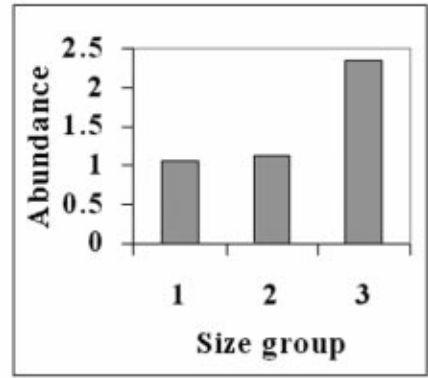
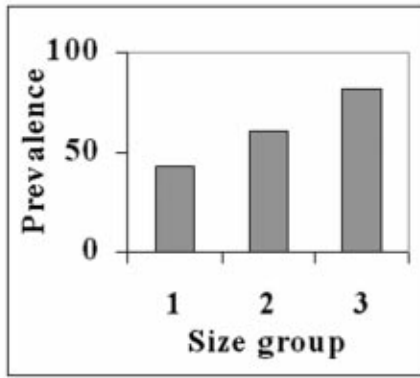


Fig. 4
Prevalence (%), abundance and density of *Pseudoterranova decipiens* in three length groups (mm) of the intermediate host sea scorpion (*Taurulus bubalis*) from 1991 to 1998.

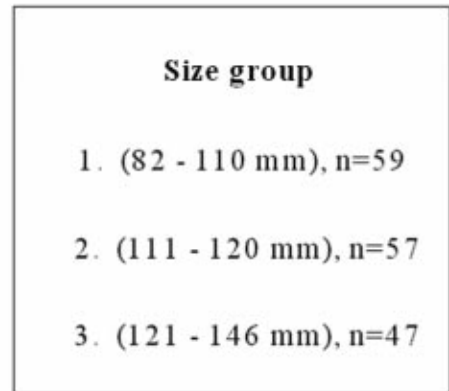
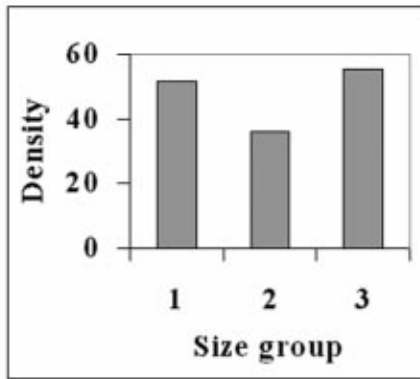
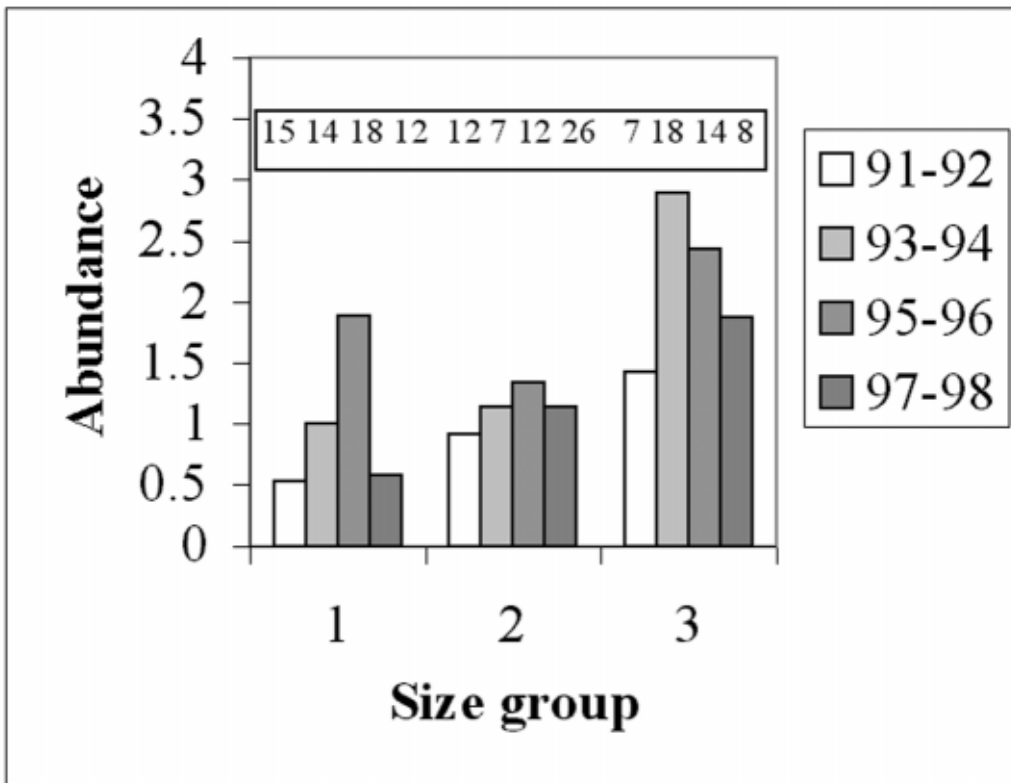


Fig. 5
Abundance of *Pseudoterranova decipiens* in three length groups (mm) of the intermediate host sea scorpion (*Taurulus bubalis*) from 1991 to 1998. Number caught fish in each group is indicated above each column.



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APPENDIX

Consider a cod entering an infectious ground of area a . Predation on this individual by a seal is assumed to be a Poisson process with intensity, λ during a small (infinitesimal) time interval, h , the probability that the cod is not eaten by a seal is

$$(1 - \lambda h)^s = 1 - s \lambda h,$$

where s is the number of seals. Thus, the probability of surviving to time t is $\exp(-s \lambda t)$. The foraging time for a cod entering the area has an exponential distribution with parameter $s\lambda$, and therefore, the expected survival time of a cod in these waters is $1/(s\lambda)$.

We next assume that the chance of being caught by a seal decreases with the size of the area. A simple quantification of this assumption is an inverse relationship between the catch intensity and area: $\lambda = q/a$, where q is a constant. It also seems reasonable to assume that when the number of seals is over some lower limit (say ten individuals), the abundance of the third stage of sealworm in the invertebrates, Inv , will increase

with the number of seals per unit area. This relationship may be complex, so we apply the first order approximation:

$$Inv = b + c s/a,$$

where b and c are constants, and the colony size s is over some lower limit.

Finally, if foraging cottids exploit the benthic community in a random manner, the average number of sealworm larvae transmitted to the seal population by a migrant cod will be proportional to

$$[1/(s\lambda)] * [b + c s/a] = (1/s * a/q) * (b + c s/a) = (b/q)/(s/a) + c/q$$

which reaches the asymptote c/q for large seal densities (s/a). Consequently, all our assumptions of average relationships predict that the total number of mature sealworm in a colony of harbour seals will fluctuate without trend when the density of seals is over a certain (habitat specific) threshold level.