

Establishing the relative importance of sympatric definitive hosts in the transmission of the sealworm, *Pseudoterranova decipiens*: a host-community approach

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ABSTRACT

The importance of a given host to a particular parasite can be determined according to three different criteria: host preference, host physiological suitability and host contribution to transmission. Most studies on the sealworm *Pseudoterranova decipiens* have focussed on the latter factor, but few attempts have been made to develop a quantitative transmission model evaluating the relative importance of each host. The purpose of this study was to propose a flow-chart model to study sealworm transmission within a seal community. The model was applied to hypothetical data of four seal species acting as definitive hosts of *P. decipiens sensu stricto* in eastern Canada: harp seal *Phoca groenlandica*, harbour seal *P. vitulina*, grey seal *Halichoerus grypus* and hooded seal *Cystophora cristata*. The dynamics of the model was studied using population estimates from 1990 to 1996. To illustrate the interrelationship of the seal populations in the flow dynamics, the model's behaviour was explored by manipulation of the harp seal population size. The results showed that grey seals accounted by far for most transmission from and to the seals. The harbour seal population also sustained a biologically significant proportion of the flow, whereas the role of hooded and harp seals seemed negligible despite their large population sizes. The hypothetical removal of the harp seal population resulted in small increases in the relative flows to the other seals. These results conform to previous qualitative assessments on the relative importance of these seal species in sealworm transmission. The model provided some heuristic rules useful to understand transmission patterns. The data suggested that the harbour seal population should be about twice that of the grey seals to account for a larger share of transmission than grey seals. Although this is unlikely to occur at a large geographic scale, harbour seals outnumber grey seals in some areas and, therefore, the role of each host may change locally. To make this approach more realistic, further work should seek accurate estimates of parasite population parameters, better definition of the host community boundaries (at a local scale) and improved control of confounding variables.

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INTRODUCTION

It has been long realised that different host species are not equally important for a given parasite. References to the main host(s) of a particular parasite species abound in the literature, but often the term is not explicitly defined. This can cause confusion because what it is meant by 'main host' depends on the conceptual framework considered. For instance, host importance can be assessed by classifying hosts according to some measure of preference by the parasite, i.e., the extent to which a particular species of host is used by a population or taxon of parasites. Therefore, the measurement should deal with some kind of ratio between host use by the parasite and host availability in the environment (Lymbery 1989).

A second view of host importance refers to differences in physiological suitability for the parasite (Poulin 1998). In this case, measures of reproductive potential, such as relative proportion of mature worms, fecundity estimates, or parasite body size, can be used to determine host importance. To mention one example based on anisakinae nematodes, Kuramochi *et al.* (1996) surveyed four cetacean species in the NW North Pacific for the nematode *Anisakis simplex*. The higher proportion of adult worms and larger body size of *A. simplex* in minke whales *Balaenoptera acutorostrata* led the authors to suggest that this species represented the main host in the study area. Note that there is usually, but not necessarily, a correlation between host preference and physiological suitability. In some sense, each concept refers to each of the main forces determining specificity, namely, probability of encounter and physiological compatibility (Poulin 1998).

Finally, a third way to assess host importance focuses on parasite transmission and attempts to evaluate the contribution of each host, within a host community, to the parasite's total reproductive output. Following this approach, Holmes *et al.* (1977) developed a model to calculate the relative rate of flow of parasites through each population of sympatric hosts. Flows are estimated by calculating the turnover of parasites through each host population, which involves consideration of parasite abundance, proportion of mature female worms, fe-

cundity and life-span in each host, corrected for the hosts' relative population sizes (see below). Holmes *et al.* (1977) provided the following example to reveal interesting insights of their approach. Fecundity of the trematode *Schistosoma japonicum* seems to be lower in field rats than in other mammals in the Philippines, but rats are essential to maintain the *S. japonicum* population due to their larger population size relative to the other hosts. Interestingly, *S. japonicum* has the greatest life span and fecundity in humans, i.e., humans seem to be the most suitable hosts in physiological terms. This example illustrates two fundamental points: first, host preference and host significance for transmission are not synonymous; second, the same host species can play different roles in the maintenance of a parasite population depending on the host community structure (Olson and Nickol 1996).

The sealworm *Pseudoterranova decipiens* typically uses three types of host in its life cycle, namely, benthic invertebrates, fish and pinnipeds (McClelland *et al.* 1990). Transmission operates through food webs allowing the parasite to infect a diverse array of intermediate and definitive hosts depending on the geographic area. For instance, *P. decipiens sensu stricto* (Paggi *et al.* 2000) has been reported in at least five species of seals in the North Atlantic: grey seal *Halichoerus grypus*, harbour seal *Phoca vitulina* (Fig. 1), harp seal *Phoca groenlandica*, hooded seal *Cystophora cristata* and ringed seal *Phoca hispida* (Bratney and Ni 1992, Bratney and Stenson 1993, Marcogliese *et al.* 1996 and references therein). Given the economic importance of the sealworm, it is not surprising that most studies of host importance have focused on differences of transmission. However, the other dimensions of host importance should also receive some attention. For instance, it would be interesting to study the evolutionary processes behind the apparent high suitability of grey seals as hosts of *P. decipiens sensu stricto* (McClelland 1980). Most attempts to rank the relative host importance for sealworm transmission are based on intuitive arguments based on comparisons of (i) abundance in each host species in the study area (Young 1972, Hauksson and Ólafsdóttir 1995), (ii) parasite abundance and seal population



Fig. 1
The harbour seal
(Phoca vitulina).
 Photo: D. Marcogliese

sizes (Myers 1960, Mansfield 1968, Mansfield and Beck 1977) and (iii) in addition to (ii), data of host physiological suitability obtained from either field observations, e.g., number of adult worms or proportion of mature females (Scott and Fisher 1958, Young 1972, Stobo *et al.* 1990a, Bratney and Ni 1992, Bratney and Stenson 1993, Burt 1994) or experimental infections, e.g., development rate, worm size, fecundity or life-span of the parasite in different host species (McClelland 1980 and references therein). However, few studies have hitherto tried to draw together all these data in a quantitative transmission flow model, although some incipient attempts can be found in Mansfield (1968) and Mansfield and Beck (1977).

In this paper, we apply the flow-chart model of Holmes *et al.* (1977) to the sealworm using hypothetical data. Our aim is to illustrate the potential utility of this approach to study the relative importance of several sympatric seal species in the transmission of the sealworm. For heuristic purposes, we also explore the interrelationships among the variables used in the model, drawing some useful rules. We acknowledge at the outset that the model is very simple and based on limited data and broad assumptions. However, it represents a preliminary attempt to deal quantitatively with sealworm transmission within a seal community, since

previous models of the population dynamics of the sealworm (e.g., des Clers 1990, Mohn 1990) considered only a single definitive host. (Nonetheless, these models seem, in principle, suitable for the inclusion of several definitive hosts). A second caveat is that this paper is not intended as a major review of the literature about the biology of the sealworm and seals, but only as an exercise suggesting future research areas.

MATERIALS AND METHODS

The flow-chart model of Holmes *et al.* (1977) analyses the relative flow of parasites to and from sympatric definitive hosts based on estimates of population parameters. The relative flow of the parasite to the i^{th} definitive host (RF_i) can be calculated as

$$RF_i = A_i \cdot P_i \cdot W, \quad (1)$$

where A_i is the mean abundance of the parasite in the host, P_i is the host population size and W is a coefficient to adjust to a proportion of the total flow to all host species, i.e.,

$$W = \frac{1}{\sum_{i=1}^{i=n} A_i \cdot P_i}, \quad (2)$$

where n is the number of host species. Likewise, the flow from the i^{th} host is defined as

Table 1. Parameters used for calculations of the relative flows of *Pseudoterranova decipiens sensu stricto* in four seal species. The mean abundance and proportion of gravid females of the sealworm were obtained from Bratley and Ni (1993) (harp seal) and Bratley and Stenson (1993) (other seals) and estimates of seal population size and rates of annual population growth, from Hammill and Stenson (2000).

Seal species	Mean abundance	Proportion of gravid females	Population size estimates						Rate of annual population growth (%)	
			1990	1991	1992	1993	1994	1995		1996
Harp seal	0.50	0.000	4,193,200	4,355,000	4,556,200	4,694,200	4,915,800	5,075,600	5,236,800	3.9
Hooded seal	0.71	0.065	469,900	493,000	517,200	542,700	569,400	597,300	626,700	4.8
Grey seal	217.08	0.089	96,900	106,600	117,400	129,000	142,400	156,100	173,500	9.7
Harbour seal	126.96	0.117	22,800	24,100	25,500	27,000	28,500	30,100	31,900	5.6

the parasite's relative egg output (REO_i) and can be estimated as

$$REO_i = A_i \cdot P_i \cdot F_i \cdot W', \quad (3)$$

where F_i is the proportion of gravid females in the host and W' is a coefficient analogous to W , i.e.,

$$W' = \frac{I}{\sum_{i=1}^{i=n} A_i \cdot P_i \cdot F_i} \quad (4)$$

Note that although Holmes *et al.* (1977) used relative instead of absolute population sizes, the resulting RF and REO values would be identical in both cases, providing that the appropriate P_i 's relative to either the absolute or relative population size are used to compute W and W' .

Since *P. decipiens* represents a complex of sibling species (Paggi *et al.* 2000), the dynamics of each of them should be studied separately. The present exercise is based on *P. decipiens sensu stricto* in four sympatric seal species (harp seal, harbour seal, grey seal and hooded seal) in eastern Canada. The parasite's mean abundance and proportion of gravid females in each seal species used in eqs 1 and 3 were obtained from Bratley and Ni (1992) for harp seals in the south coast of Newfoundland, and from Bratley and Stenson (1993) for the other seal species in Newfoundland and Labrador (Table 1). The population sizes also needed in eqs 1 and 3 were taken from the population estimates of the four seal species in Atlantic Canada provided by Hammill and Stenson (2000) (Table 1). Since these authors provide estimates from 1990 to 1996, the temporal dynamics of the RF s and REO s of each seal species during this period could be analysed assuming that the abundance and maturity estimates of Bratley and Ni (1992) and Bratley and Stenson (1993) did not fluctuate over time and were representative of the whole study area. Whether this is realistic or not is not relevant here because the assumption is useful only for the heuristic purpose of the exercise. In addition, the relative differences in mean abundance and fecundity estimates between the four seal species in other localities

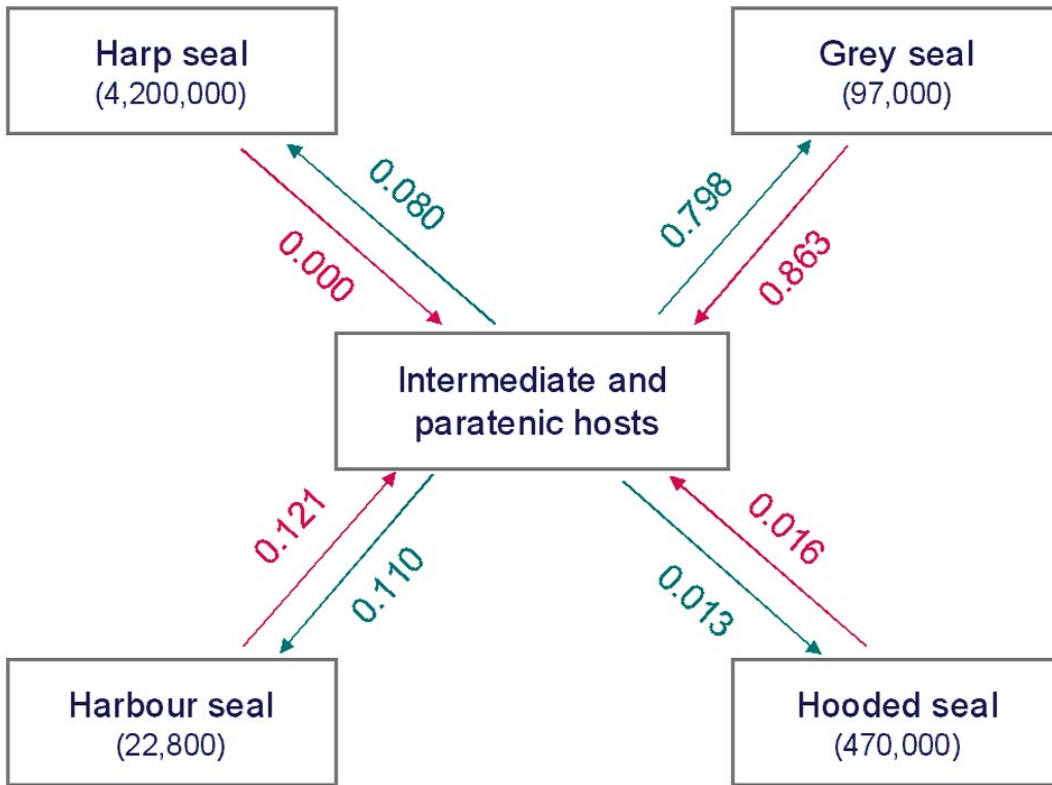


Fig. 2
Hypothetical flow chart for *Pseudo-terranova decipiens sensu stricto* in a community of four seal species in eastern Canada. Values on outwardly directed arrows indicate transfer of ingested sealworm larvae and values on inwardly directed arrows, transfer of sealworm eggs to intermediate hosts. Numbers below seal names represent the population size estimates of 1990 (Table 1) used to calculate the flows.

are quite similar to those used here (See for instance Bratley *et al.* (1990) and Marcogliese *et al.* (1996)).

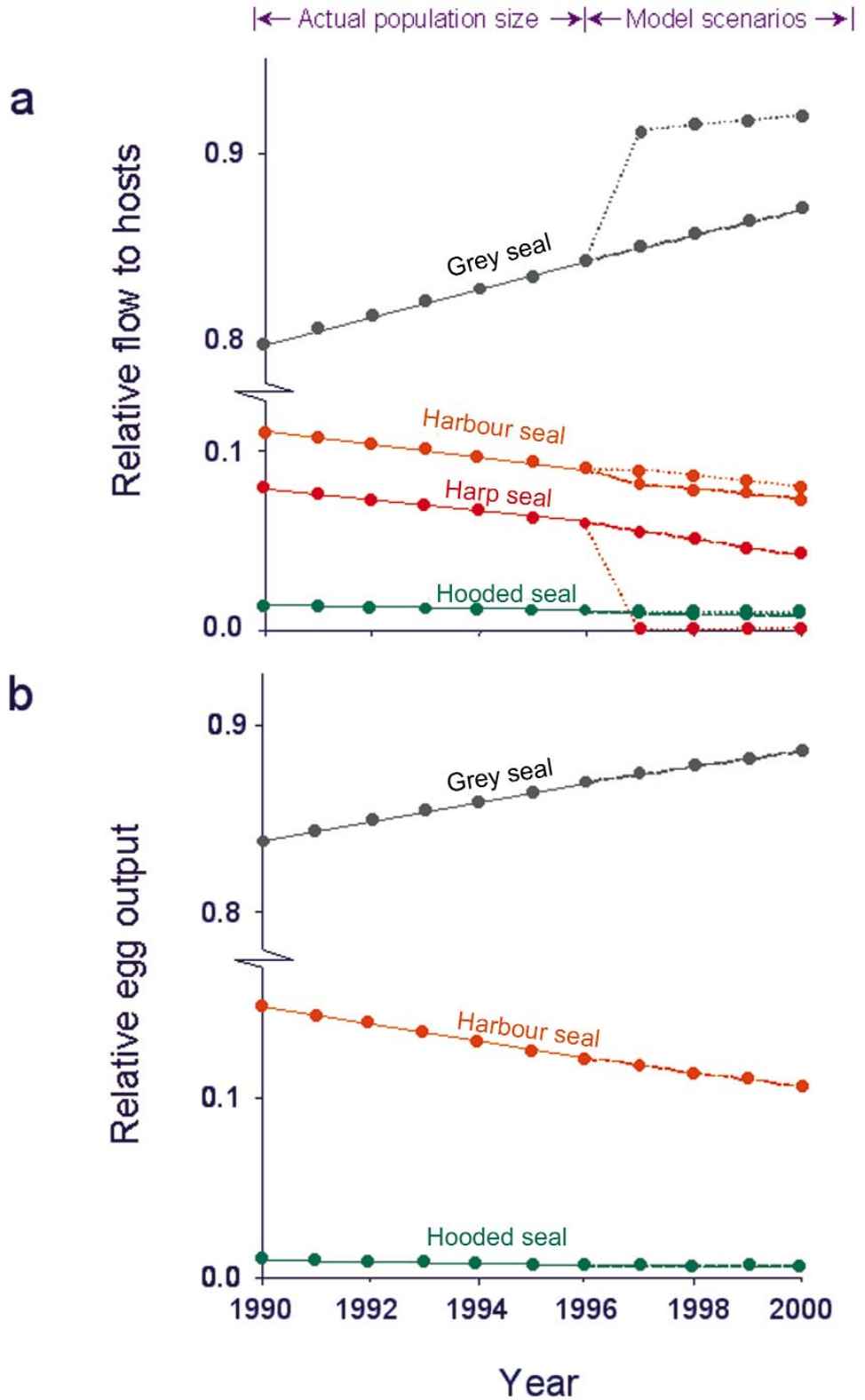
To illustrate the interrelationship of the four seal species in the flow dynamics, we also studied the behaviour of the model by manipulating the population size of harp seals. The reason for this choice is that given the abundance and fecundity estimates of the sealworm in this species (Bratley *et al.* 1990, Bratley and Ni 1992, Marcogliese *et al.* 1996), harp seals can be expected *a priori* to contribute little to the flows of the parasite. So it seemed interesting to explore the degree to which variations in population size of a host species intuitively perceived as unimportant for sealworm transmission could alter the flow dynamics of the whole system. Under the same assumption of temporal stability in abundance and fecundity of the sealworm in each seal population, we studied the flow dynamics from 1997 to 2000 considering two situations. First, since the population of harp seals seems to have stabilised from 1996 onwards (Anonymous 2000), the population size was kept constant in the model (5,200,000

individuals), whereas those of the other seal species were allowed to increase at the annual rates reported from 1990 to 1996 by Hammill and Stenson (2000) (Table 1). Second, we explored a more radical scenario by setting the harp seal population to zero, whereas the other seal populations increased annually at the observed rates.

RESULTS

Figure 2 shows an example of flow chart built with population estimates of 1990 (Table 1). The chart shows that most flow from and to the seals passed through grey seals, followed by harbour seals; hooded and harp seals had much larger population sizes but played a negligible role in sealworm transmission. Note that the harp seal population acted as an ecological sink for transmission (Fig. 2). The dynamics of the *RFs* and *REOs* from 1990 to 2000 are displayed in Fig. 3. All else being equal, grey seals tended to increase their share in both *RF* and *REO* at the expense of the other seal species (Fig. 3a, b) because grey seals exhibited the highest annual population growth rate (Table 1). The trajectory-

Fig. 3
 Temporal variation of the relative flow to host (a), and relative egg output (b) of *Pseudoterranova decipiens sensu stricto* in a community of four seal species in eastern Canada. Data from 1990 to 1996 (solid lines) was based on actual population size estimates (Table 1). From 1997 to 2000, dashed lines represent a scenario where the harp seal population size stabilised, whereas the remainder populations increased at constant rates, and stippled lines correspond to a situation where the harp seal population was set to zero, whereas the other kept increasing at constant rates indicated in Table 1.



ries seemed little affected by the stabilisation of the harp seal population. However, when the size of the harp seal population was set to zero, the effects were more apparent: the *RFs* of the other seals increased (Fig. 3a) due to the lower value of *W* (eq. 1), but the *REOs* were unaffected because sealworm fecundity was zero in harp seals.

DISCUSSION

This flow-chart approach, as any other based on host community analysis, conveys a holistic view of parasite transmission in situations where several host populations co-occur. This is because it evaluates the interrelationships and relative weight of each host population in parasite transmission. For instance, our analysis suggested that grey seals are likely to contribute most to parasite transmission in eastern Canada, and that only harbour seals can dispute this role. In addition, manipulation of the harp seal population altered the relative transmission flows of the other host species, but the changes seemed biologically insignificant. These results provide quantitative support to previous qualitative assessments on the importance of these seal species in sealworm transmission (Bratley and Stenson 1993, Burt 1994, Marcogliese *et al.* 1996).

In addition, the model provides a way to explore the conditions under which a particular seal species would account for higher flows than others. From equations 1 and 3, it can be deduced that for host population *a* to have greater *RF* and *REO* than *b*, the following inequalities must be satisfied, respectively:

$$P_a > \frac{A_b}{A_a} P_b \quad \text{and} \quad P_a > \frac{A_b \cdot F_b}{A_a \cdot F_a} \cdot P_b$$

Thus, considering the abundance and fecundity parameters in Table 1, the harbour seal population should be, respectively, 1.7 and 2.3 times greater than that of grey seals for a larger share of transmission. At a large geographical scale, the likelihood of harbour seals sustaining the largest *RF* and *REO* seems low since both historical and current records show that grey seals outnumber harbour seals in eastern Canada (McClelland 1980, Burt 1994, Hammill and

Stenson 2000). At a local scale, however, harbour seals are more abundant than grey seals in certain areas, particularly off the coast of mainland Nova Scotia and the Bay of Fundy (Scott and Fisher 1958, Mansfield and Beck 1977), and therefore the role of each host species in sealworm transmission may change locally.

Although the model is crude, we think that its rationale is useful and future refinements will make it more realistic and amenable to local scenarios. One of these improvements concerns the estimation of population parameters of the sealworm. Mean abundance estimates, for instance, depend heavily upon host sample size and the degree of parasite aggregation (Gregory and Woolhouse 1993). Anisakids typically exhibit aggregate distributions in the definitive hosts (Stobo *et al.* 1990a, Bratley *et al.* 1990, Bratley and Ni 1992, Bratley and Stenson 1993, Marcogliese *et al.* 1996) and, therefore, adequate host sample sizes and suitable measures of central tendency (Rósza *et al.* 2000) are required to compare sample estimates in several host species. Likewise, the fecundity of the sealworm is difficult to measure (Bratley *et al.* 1990). The proportion of gravid females conveys little information of the true egg output because similar proportions of gravid females, used in this study, in several host populations may lead to different egg outputs due to differences in host physiological suitability. Additional variables, such as worm size and, particularly, uterine egg counts will result in better estimates of parasite fecundity. Determining the generation times of female worms in each host species is also essential because, egg production rates being equal, long-lived worms would have higher reproductive output than short-lived ones. Accurate data of female size, egg counts and generation time for the sealworm in all the seal species involved is still scarce and in need of replication. Evidence from experimental infections suggests significantly higher values of these parameters in grey seals than in harbour seals (McClelland 1980). This means that grey seals may actually account for a larger share of the transmission flows of *P. decipiens sensu stricto* than suggested by our model. Further research should also attempt to evaluate the effect of different variables (density dependence and differences in host responses re-

lated to species, sex, age, etc.) in fecundity estimates (See Marcogliese (1997) and references therein for examples).

The development of the present model also raises some objections about its suitability to explain real-world processes. First, unlike closed systems like ponds or lakes, for which the flow-chart model was initially developed and applied (Holmes *et al.* 1977, Ashley and Nickol 1989), the boundaries of the local host community in marine habitats are less distinct. Consequently, it is more difficult to define the spatial scale confining the local host community. The area chosen here was deliberately large to take advantage of the recent data of seal population estimates and sealworm abundance and maturity. However, the application of the model to real situations might work best and be more meaningful at a smaller, local scale, where operational boundaries for host communities can be defined, at least temporally, based on both a good knowledge of the area and the ecology of the host species involved in the cycle.

A second potential objection to the model is that it conveys a static and deterministic picture of parasite transmission, while the variables determining the actual flow rates may change dramatically over time. Seal population size at a given site, for instance, may depend on seasonal variations due to breeding or moulting. For instance, grey seals tend to concentrate around Sable Island and the Gulf of St. Lawrence during the breeding season from October to December, whereas they tend to disperse outside that period (Stobo *et al.* 1990b). Likewise, harp seals summer in the Arctic and migrate southwards in the autumn to their whelping areas in the Gulf of St. Lawrence and off eastern Newfoundland and southern Labrador (Anonymous 2000). Thus the removal of harp seals simulated in the present study might not be so unrealistic as it would roughly depict host availability during the summer months.

Seasonal and annual variations of sealworm abundance and proportion of reproductive worms have also been widely reported and much of this variation seems associated to diet changes and fasting periods of the seals (Bratley *et al.* 1990, Stobo *et al.* 1990a, Bratley and Stenson 1993, Marcogliese *et al.* 1996). An additional source of variation is the age composition of the seal population (Bratley *et al.* 1990, Marcogliese *et al.* 1996), and therefore this factor should be considered in further modelling. In conclusion, an accurate picture of the flow of the sealworm from and to the seal populations needs long-term monitoring at a local scale of size and age composition of the host population, and parasite abundance and fecundity.

Obviously, the flow-chart model can be (and should be) extended to describe the flow of parasites through intermediate and paratenic hosts. This is highly relevant because evidence suggests that non-commercial benthic fish may play a major role in sealworm transmission (Jensen and Andersen 1992, Jensen *et al.* 1994, Andersen *et al.* 1995, Aspholm *et al.* 1995, Haukson and Ólafsdóttir 1995, Martell and McClelland 1995). However, the actual contribution of these hosts has not been quantitatively evaluated. Thus, further modelling could use data of host population size, mean parasite abundances and the relative predation rates by the intermediate, paratenic and definitive hosts to provide a quantitative framework of the relative importance for transmission.

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