

The suprapopulation dynamics of *Lernaeocera branchialis* and *L. lusci* in the Oosterschelde: seasonal abundance on three definitive host species

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Quantitative samples of the demersal fish fauna of the Oosterschelde were taken between May 1988 and July 1989. The instantaneous mortality rates of the 1988 year classes of whiting (*Merlangius merlangus* L.), sand goby (*Pomatoschistus minutus* Pallas) and bib (*Trisopterus luscus* L.) were estimated at 0.017 d^{-1} , 0.014 d^{-1} and 0.018 d^{-1} , respectively. These three species were examined for the presence of mesoparasitic pennellid copepods. Combination of host population densities and parasite infection intensities allowed for estimation of parasite population densities. Whiting were infected with *Lernaeocera branchialis* shortly after their arrival (April–May) in the Oosterschelde. By the end of the year approximately 80% of the first year class whiting were infected. Spawning sand gobies were infected with *Lernaeocera lusci* in May and June. Though the prevalence of *L. lusci* on juvenile sand gobies in autumn was low, the parasite population density in this period was high. First year class bib were mainly infected by *L. lusci* after their transition from a pelagic to a demersal behaviour in August. It is suggested that *L. branchialis* has one generation each year, whereas *L. lusci* has two. A biological model of the life cycle of both parasite species is presented.

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Introduction

Lernaeocera branchialis and *L. lusci* are common mesoparasites of a number of flatfish and gadoid species in the North Sea and adjacent areas (Kabata, 1979; Evans *et al.*, 1983). The typical host species of *L. branchialis* in the Dutch coastal area are the flounder *Pleuronectes flesus* (intermediate host) and the whiting *Merlangius merlangus* (definitive host). Sole *Solea solea* and bib *Trisopterus luscus* are the intermediate and definitive hosts, respectively, for *L. lusci*. Other fish species (sand goby *Pomatoschistus minutus*, dragonet *Callionymus lyra*) can occasionally act as definitive hosts for *L. lusci*. The metapopulation dynamics of *L. lusci* and *L. branchialis* on intermediate flatfish host species were

recently studied by Van Damme and Ollevier (1996). These authors found some evidence that *L. branchialis* has only one generation each year, whereas *L. lusci* has two generations each year. The temporal patterns in occurrence of *Lernaeocera* species on definitive host species in the Delta area (the Netherlands) were studied by Hamerlynck *et al.* (1989) and Van Damme and Hamerlynck (1992).

The transmission of infective stages (pre-metamorphosis females) of *Lernaeocera* species depends on a subtle synchronisation of (intermediate and definitive) host and parasite life cycles, which are probably simultaneously influenced by temperature. According to Hamerlynck and Hostens (1993) the new year-classes of bib and whiting arrive and remain in

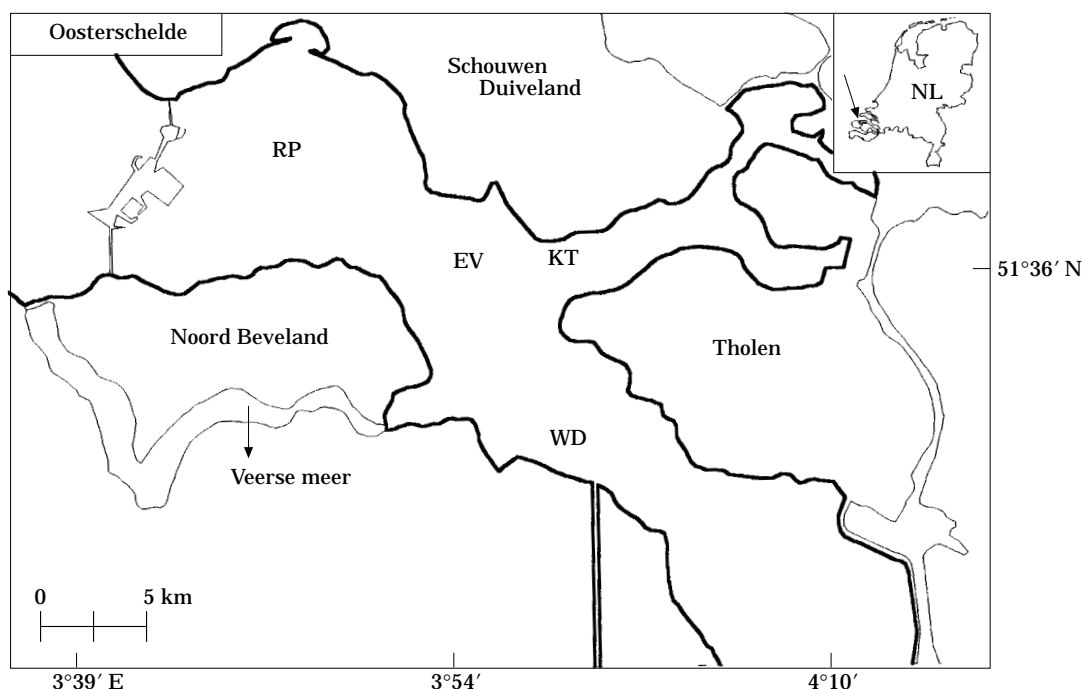


Figure 1. Map of the study area, with indications of the sampling sites Engels Vaarwater (EV), Wemeldinge (WD) and Keeten (KT). RP=locality Roompot (see text).

the coastal area until migration occurs to deeper waters in late autumn and winter, not to reappear in the following spring. Sand gobies, however, are permanent residents in the coastal area. Most adults die after breeding in spring, after which a new year class of recruits, susceptible to new infection by parasites, appears in the catches. *Lernaeocera* species profit maximally from these ephemeral host resources. Besides being affected by intensity-independent factors, adult female *Lernaeocera* populations may also be affected by intensity-dependent factors. For example there are some indications that parasite-induced host mortality may affect parasite population size (Khan, 1988; Van Damme *et al.*, 1994).

The aim of this paper is to present information on the role of demersal fish in the Oosterschelde, a marine bay, as definitive hosts in the life cycle of *Lernaeocera* species. Until now, the biology of the two known species of *Lernaeocera* has hardly been compared. A detailed and comparative study of the seasonal abundance and age structure may increase our understanding of evolutionary adaptations of the different *Lernaeocera* species to their respective hosts.

Materials and methods

Biweekly samples were collected with a research vessel using a 3 m beam trawl and a small-meshed net (10 mm).

The samples were taken between May 1988 and June 1989 at three different localities in the Oosterschelde (Fig. 1): Engels Vaarwater (EV), Wemeldinge (WD) and Keeten (KT). Sand goby, whiting and bib were sampled quantitatively and transferred to the laboratory. Collection of samples, procedures of analysis and classification of stages of *Lernaeocera* were performed as described by Van Damme and Hamerlynck (1992). The presence of *L. lusci* on other species (Lozano's goby *Pomatoschistus lozanoi*, small cod *Trisopterus minutus*, five bearded rockling *Ciliata mustela*) was recorded. Collection of samples, procedures of analysis and classification of parasite stages were carried out as described by Van Damme and Hamerlynck (1992). The frequency of developmental stages was calculated for both *L. lusci* and *L. branchialis* on bib and whiting. *L. lusci* collected from sand goby at successive sampling dates were pooled to calculate stage frequencies. Water temperatures were minimal in February 1988 (5°C) and January 1989 (5°C) and maximal in August 1988 (19.5°C) and July 1989 (20.5°C).

Lernaeocera lusci was distinguished from *L. branchialis* by the antennary processes, which are absent in the latter species (Kabata, 1979; Tirard, 1991; Van Damme and Ollevier, 1995). The numbers of fish of the 1988 year classes which were examined for parasites are shown in Figure 2. Some whiting and bib of the 1989 year class were also examined in May and June 1989.

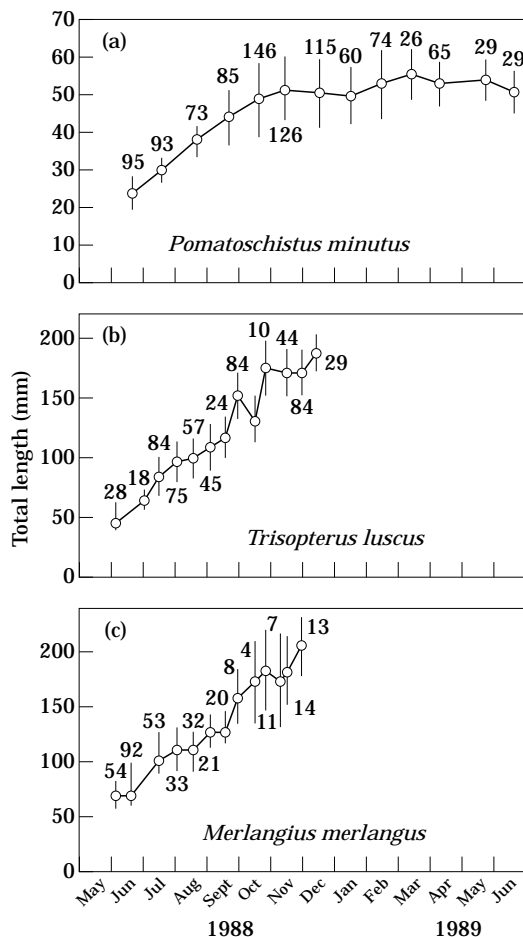


Figure 2. Increase in mean total length of (a) sand goby, (b) whiting and (c) bib (1988 year classes) in the Oosterschelde in 1988–1989. The number of fish collected is shown.

The terms prevalence (percentage of fish infected), abundance (mean number of parasites per fish) and intensity (number of parasites on one host individual in a sample) were used according to the recommendations of Margolis *et al.* (1982). A non-parametric test (Kruskal–Wallis) was used to test for significant differences in parasite abundance between samples. Parasite population density is defined as the number of parasites per unit area (10^4 m^2) and is calculated from the fish population density as follows:

$$P_t = a_t H_t = a_t H_0 e^{-mt}$$

where

P_t = parasite population density at time t

H_t = host population density at time t

H_0 = initial host population density at time 0

a_t = parasite abundance at time t

m = host mortality coefficient.

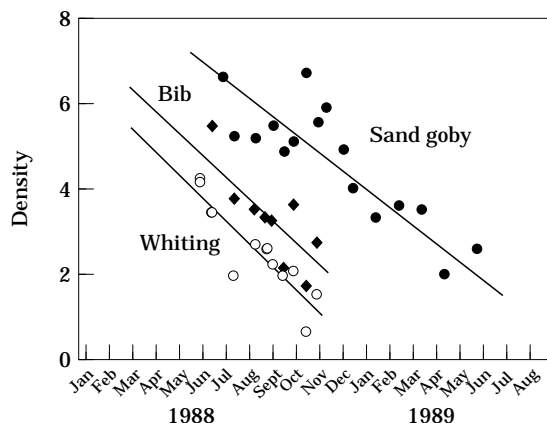


Figure 3. Relationship between density (ln transformed $n/10^4 \text{ m}^2$) of sand goby, 0+ whiting and 0+ bib (1988 year classes) and time in the Oosterschelde in 1988 and 1989.

No correction for net efficiency was made. The mortality coefficients m were obtained from the catch data. To calculate the density of mature (X stage) parasites ($P_t(X)$) at different time intervals, the same formula was used with $a_t(X)$ (abundance of X parasites) instead of a_t .

Counts of the eggs per egg-string pair (using a binocular microscope) allowed calculation of egg densities. The equations describing the relationship between egg number and time were used to estimate the (predicted) mean number of eggs at each sampling date. Egg density at time t was calculated by multiplying parasite density ($P_t(X)$) with the (predicted) mean number of eggs per egg-string pair at time t (z_t).

Results

Pomatoschistus minutus, *Trisopterus luscus* (0+) and *Merlangius merlangus* (0+) were the typical definitive host species, the former two host species for *L. lusci* and the latter species for *L. branchialis*.

Juvenile *Pomatoschistus minutus* appeared in the catches in June but were probably not efficiently caught in this month. Maximum abundance was recorded in July ($764 \text{ ind}/10^4 \text{ m}^2$). The instantaneous mortality rate was estimated at 0.014 d^{-1} (Fig. 3). They attained their maximal total length (about 54 mm) in October (Fig. 2). Spawning occurred in spring, after which they disappeared from the samples.

0+ *Trisopterus luscus* and *Merlangius merlangus* entered the Oosterschelde in May–June. Their numbers declined rapidly during autumn. The mortality rates of bib and whiting were estimated at 0.018 d^{-1} and 0.017 d^{-1} , respectively (Fig. 3). After December, the majority of the bib and whiting migrated to deeper water and were completely absent from the shallow localities of the present study. The highest densities recorded were

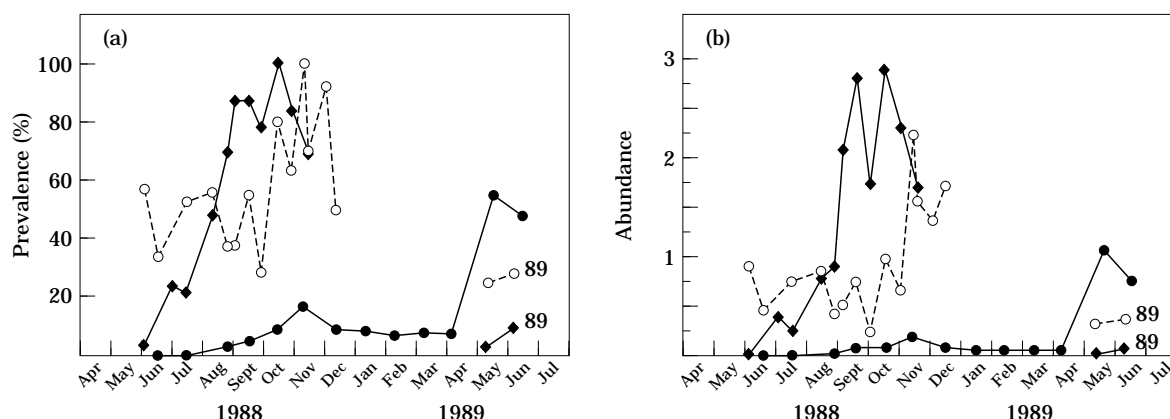


Figure 4. Prevalence (a) and abundance (b) of *Lernaeocera lusci* (◆ and ●) and *L. branchialis* (○) on three final host species (bib —◆—, whiting ···○··· and sand goby —●—) in the Oosterschelde. All fish belonged to the 1988 year class, except when indicated (year class 1989 of bib and whiting in May and June 1989).

71/10⁴ m² for whiting (June 1988) and 242/10⁴ m² for bib (July 1988). Both bib and whiting belonging to the 0+ age class grew fast, the mean total length of whiting increasing from 30 mm in June to 150 mm in November and from 30 mm in June to 130 mm in November for bib (Fig. 2).

The temporal patterns in prevalence and abundance of *Lernaeocera lusci* and *L. branchialis* are shown in Figure 4. A small proportion of the sand gobies was infected before winter (a maximum of 18% in November 1988; Kruskal–Wallis, $p < 0.05$). Transmission of infective stages occurred mainly during the next spring (prevalence of 58% in May 1989; Kruskal–Wallis, $p < 0.001$). Abundance was always lower than 0.5, except in May and July when it exceeded 0.7. Thus, two distinct transmission waves could be distinguished, the first in autumn (infection of juvenile fish) and the second in spring (infection of adult gobies).

Only a small percentage of the bib population was infected with *Lernaeocera lusci* in spring (both for the 1988 and the 1989 year class). Transmission of infective stages was highest in July and August. The highest prevalence was found in late autumn (88% in October). Abundance gradually increased from 0.3 (June) to 1.0 (July), then increased significantly (Kruskal–Wallis, $p < 0.001$) to 2.0 in August and fluctuated thereafter between 1.5 and 3.0.

Juvenile whiting had already accumulated high numbers of parasites prior to first collection in, respectively, 1988 and 1989. In May 1988, more than 50% of the whiting population was infected by juvenile *Lernaeocera*. Prevalence remained fairly constant in the summer months and then reached a peak in November 1988 (85%). A similar pattern was found for the abundance: between June and October, abundance varied between 0.2 and 1 (Kruskal–Wallis, $p > 0.05$); after

October it increased significantly (Kruskal–Wallis, $p < 0.01$) to values of 1.5 and higher.

Figure 5a shows the seasonal patterns in the frequency of developmental stages of *Lernaeocera lusci* on sand goby. Between August 1988 and April 1989 all life cycle stages were found at low frequencies. However, no pennella larvae were found in winter. In May 1989 high numbers of juvenile stages were found on the adult spawning fish. By June 1989, almost all parasites possessed egg-strings.

Juvenile P (P1+P2) stages of *L. lusci* were found on bib between 3 June and 30 October but were most abundant in August (Fig. 5b). Between 16 August and 2 February the abundance of mature X stages fluctuated between 0.8 and 1.8. Low numbers of dead parasites (Z) were recorded between August and December.

The seasonal patterns in the occurrence of *L. branchialis* on whiting were less marked than in *L. lusci*: juvenile P stages were found erratically in all months and mature X parasites occurred infrequently (Figure 5c).

Parasite population densities of *L. lusci* and *L. branchialis* between 3 June and 12 December are shown in Figure 6a. The highest densities of *L. lusci* on sand goby were found between July and August (about 30/10⁴ m²). The second highest density (12/10⁴ m²) was found in next spring when adult sand gobies were infected. *L. lusci* on bib were most common between May and October (peak density 60/10⁴ m² in August). Adding up the data for *L. lusci* on sand goby and bib, the highest density of this species was recorded in August (130/10⁴ m²).

A high density (45/10⁴ m²) of *L. branchialis* on whiting was found in early spring. Thereafter, the densities of *L. branchialis* were on average 10 times lower than the corresponding densities of *L. lusci*.

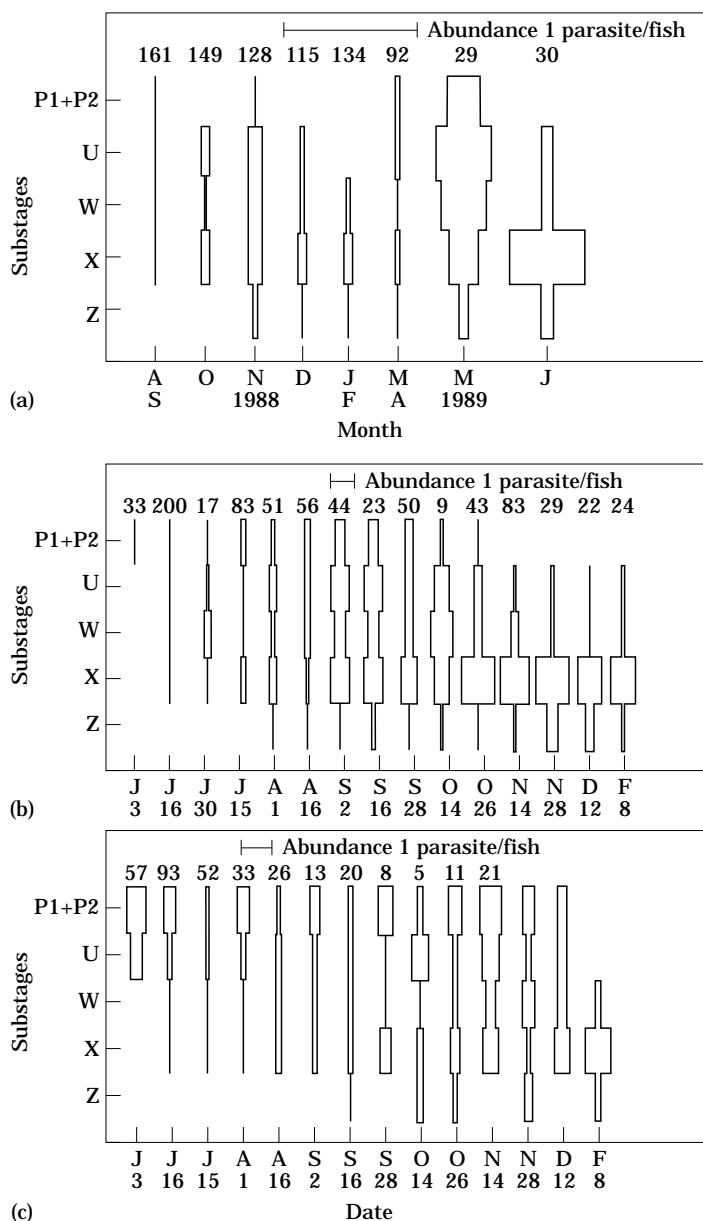


Figure 5. Frequency of developmental substages of *Lernaocera* species in the Oosterschelde in 1988 and 1989 (a) *Lernaocera lusci* on sand goby *Pomatoschistus minutus* (year class 1988), (b) *Lernaocera lusci* on bib (year class 1988), and (c) *L. branchialis* on whiting (year class 1988). The number of fish examined is indicated.

The corresponding densities of mature (X stage) parasites of both species are shown in Figure 6b. The most striking observation is the much higher density of *L. lusci* as compared to *L. branchialis*.

The egg count for *L. lusci* on sand goby was not correlated with time (Spearman Rank Correlation; $p > 0.05$). Overall, the mean number of eggs of the parasites on this host species was 593 ($n = 23$). However, there were significant positive correlations between egg

numbers and time for both *L. lusci* on bib and *L. branchialis* on whiting. The linear regression equations describing the relationship between egg number (z_t) and time (t ; in number of days after 1 January 1988) were as follows: $z_t = -737 + 6.8t$ ($n = 76$, $r^2 = 0.48$) and $z_t = -158 + 4.6t$ ($n = 26$, $r^2 = 0.25$) for *L. lusci* on bib and *L. branchialis* on whiting, respectively. The egg densities of *L. lusci* and *L. branchialis* are shown in Figure 6c. The highest overall egg density of *L. lusci*

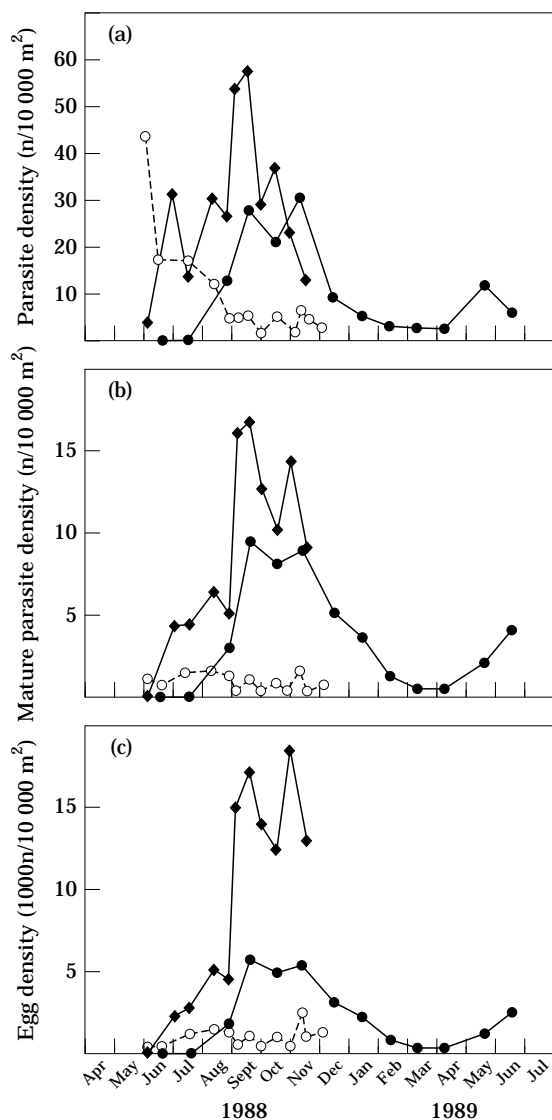


Figure 6. (a) Parasite population densities ($n/10^4 \text{ m}^2$), (b) mature parasite population densities ($n/10^4 \text{ m}^2$), and (c) egg densities ($10^3 n/10^4 \text{ m}^2$) of *Lernaeocera lusci* (\blacklozenge and \bullet) and *L. branchialis* (\circ) on three definitive host species (bib — \blacklozenge —, whiting --- \circ --- and sand goby — \bullet —) in the Oosterschelde. Only parasites that infected fish of the 1988 year class were enumerated.

(approximately $25 \cdot 10^3/10^4 \text{ m}^2$) was recorded in autumn. Between August and October, the egg density of *L. branchialis* fluctuated between $10^3/10^4 \text{ m}^2$ and $2.5 \cdot 10^3/10^4 \text{ m}^2$.

Discussion

Lernaeocera species infected a large proportion of the populations of 0+ whiting, 0+ bib and sand goby which were present in the Oosterschelde in 1988. Apart from

the general similarities in the life cycles of *L. branchialis* and *L. lusci*, their population dynamics differ markedly in several aspects.

About 50% of the 0+ whiting were already infected prior to first collection in May. Prevalence and abundance remained fairly constant in the summer months and then increased sharply in autumn (maximum prevalence about 90%). Thus there appears to be a consistent temporal pattern in the infection levels of whiting (see also Van Damme and Hamerlynck, 1992): an increase in spring, a plateau in summer and a further increase in autumn. To focus first on the spring increase in infection levels, it is probable that the juvenile whiting accumulate the large numbers of *Lernaeocera* soon after their arrival (April–May) in the Oosterschelde. Indeed, between March and June in the Oosterschelde the majority of the pre-metamorphosis females detach from the intermediate host (flounder) (Van Damme and Ollevier, 1996) and then infect the definitive host (0+ whiting). The following plateau in infection level probably results from a lack of overlap of intermediate and definitive host distributions and a reduced release of infective stages by the intermediate host in summer (Van Damme and Ollevier, 1996). In autumn flounders migrate again to the tidal gullies for their winter migration to the open sea. This autumn overlap in intermediate and definitive host distributions in the gullies may again increase the chances of *Lernaeocera* being transmitted and the sharp increase in prevalence and abundance observed in autumn may result from this transmission wave. However, this hypothesis is not fully corroborated by the flounder data since small numbers of infective stages detach from the intermediate hosts in autumn (Van Damme and Ollevier, 1996). The higher infection level recorded in whiting in autumn may also partly be explained by several alternative hypotheses: (a) the sample sizes in this period may have been too low, (b) infected fish may be caught more efficiently than “healthy” fish (Sprengel and Luchtenberg, 1991), and (c) the Sproston and Hartley (1941) assumption that in winter infected whiting linger in the coastal area whereas uninfected whiting migrate to deeper water. The present data confirm the earlier observations on the population dynamics of *L. lusci* made by Van Damme and Ollevier (1994). Both the spring transmission wave (of pennella larvae towards adult sand gobies) and the autumn transmission wave (of pennella larvae towards juvenile sand gobies) were observed. Both prevalence and abundance of *L. lusci* on sand goby are considerably higher in spring than in all other seasons. However, because sand gobies are more abundant in autumn (Fig. 3) the population density of *L. lusci* on this host species (*L. lusci* f. *minuta*, according to Van Damme and Ollevier, 1995) is higher in autumn than in spring. The best measure of the extent of the contribution of *L. lusci* f. *minuta* is egg density. The number of eggs produced by *L. lusci* f.

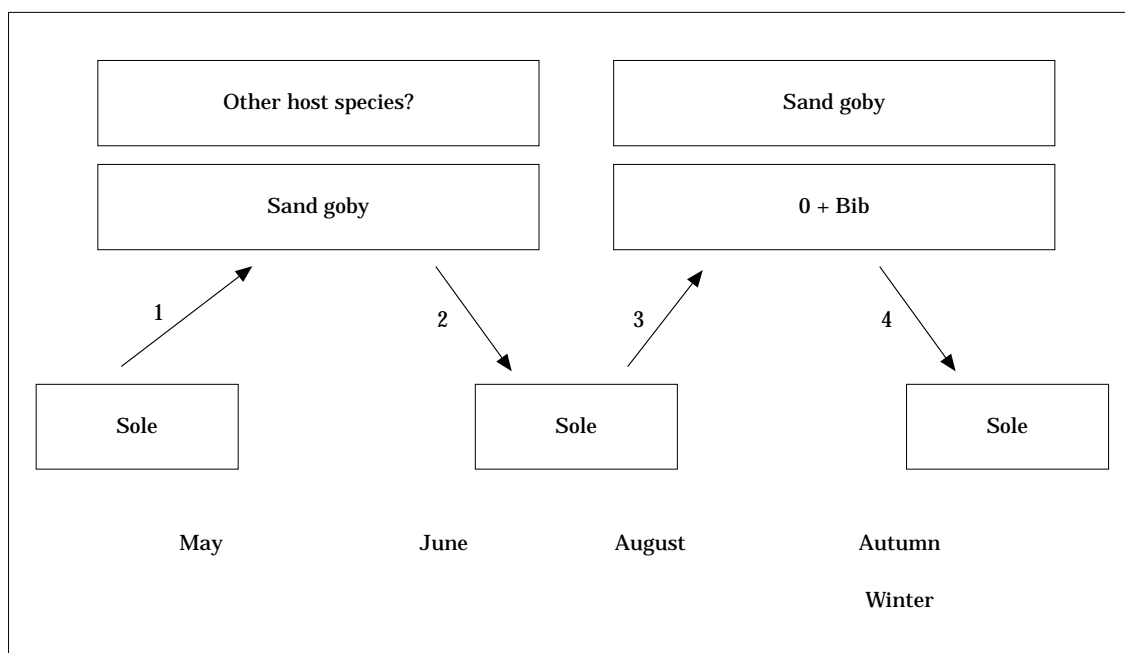


Figure 7. Schematic diagram of the hypothetical life cycle of *Lernaocera lusci* in the Oosterschelde. For explanations see text.

minuta in autumn is about 2.5 times the corresponding number produced in spring and about one third of the corresponding number produced by *L. lusci* f. *lusci* on bib. This interesting finding, that more than 25% of the eggs of *L. lusci* in autumn are produced on sand goby, illustrates perfectly the role of this host species in the life cycle of *L. lusci*.

Van Damme and Ollevier (1996) gave indications that (at least in the Delta area) two temporally distinct generations of *L. lusci* can be found. There are some arguments that support the hypothesis that sand gobies play an important role in the life cycle in *L. lusci* both in autumn and in spring. In early spring bib is rare in the shallow coastal waters while 1+ bib have migrated to deeper waters. Thus, the infective stages which detach from sole in early spring (Van Damme and Ollevier, 1996) probably infect other fish species, such as dragonet, five-bearded rockling and sand goby. The role of the two former fish species is not well studied, but in view of their low densities in the Oosterschelde (Hamerlynck et al., 1993) their role in the life cycle may be negligible in this bay. The latter species, sand goby, accumulated high numbers of *L. lusci* in May 1988. By June, the parasites had already become mature parasites releasing eggs in the environment.

Although 0+ bib arrive in the Oosterschelde in May, they are mostly infected after July. Hamerlynck and Hostens (1993) suggest that 0+ bib are pelagic initially and become demersal at a later stage. The diet of 0+ bib reflects this shift from pelagic to demersal; in May and June 0+ bib fed predominantly on pelagic calanoids,

whereas mysids and shrimps were (numerically) more important food items after June. Therefore, sand gobies may be quite important as the definitive host in May and June. A schematic diagram of the transmission windows of *L. lusci* is shown in Figure 7. Several aspects of this scheme demand further clarification. Van Damme and Ollevier (1996) suggest that transmission waves 1 and 3 (both from sole to definitive host) are temporally segregated. Transmission of copepodites from definitive host to intermediate host may be more efficient in June (transmission wave 2, mainly from sand goby to sole) than in autumn (transmission wave 4, from sand goby and bib to sole); though the density of eggs is lower in June, sole accumulate high numbers of parasites. The importance of other species or age classes in the life cycle (Fig. 7) needs further clarification. For example, it may be possible that 1+ bib plays some role in May and June but is not efficiently caught by the sampling gear. Bib were caught occasionally between December and May 1989 at a deeper locality in the Oosterschelde (Roompot) (Fig. 1) (Van Damme, unpubl. data).

Both the population densities of *L. lusci* and *L. branchialis* are strongly influenced by host mortality (and possibly parasite-induced host mortality). Parasite mortality by senescence is probably less important, as reflected by the low number of dead parasites (Z-substages) found in both species throughout the sampling period (Fig. 5).

Whereas *Lernaocera branchialis* is characterised by one generation each year, *L. lusci* has a faster development and is characterised by two generations each year.

0+ whiting and sand gobies are typically infected in spring, whereas 0+ bib are mainly infected in summer. Inclusion of sand goby in the life cycle of *L. lusci* may be a life history strategy of this parasite species to secure completion of its cycle in the Oosterschelde. Other hosts may take over the role of sand goby in other areas (e.g. dragonet in the Belgian coastal area).

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