

The population dynamics of *Lernaeocera lusci* and *L. branchialis* on intermediate hosts

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ABSTRACT: The metapopulation dynamics of *Lernaeocera lusci* and *L. branchialis* on sole *Solea solea* and flounder *Pleuronectes flesus* were studied in the Dutch coastal area. Both fish species harboured large numbers of parasites when they arrived in the coastal area in the spring. Between April and June all parasites detached from the intermediate hosts and infected the definitive hosts (0+ whiting *Merlangius merlangus* for *L. branchialis*, and possibly sand goby *Pomatoschistus minutus* for *L. lusci*). Thereafter, flounder remained almost parasite-free until autumn. This suggests that *L. branchialis* has only 1 generation per year. However, soles were infested again with *L. lusci* (in June and July), which detached to infest 0+ bib *Trisopterus luscus*, the typical definitive host for this parasite species. Thus, it appears that *L. lusci* has 2 generations per year. The flounder length and the infection intensity of *L. branchialis* were not correlated throughout the study period. Significant positive correlations were found between the sole length and infection intensity of *L. lusci* in late spring, but not in the summer or autumn. Throughout the year, both *L. lusci* and *L. branchialis* were aggregated within their intermediate host populations (variance \gg abundance).

INTRODUCTION

The life cycles of both *Lernaeocera branchialis* and *L. lusci* comprise two nauplius stages, a free-living copepodite stage and four chalimus stages on the intermediate host. After mating, the adult female leaves the intermediate host and infects the definitive host, usually a gadoid. In the southern North Sea, the typical definitive host species are bib (for *L. lusci*) and whiting (for *L. branchialis*). The population dynamics of both parasites on their definitive host species were recently studied in the Dutch coastal area (Van Damme & Hamerlynck, 1992; Van Damme et al., 1996).

Whereas the post-metamorphosis females of *L. branchialis* and *L. lusci* have received particular attention from fish parasitologists because of their size, their prominent position in the gill chamber of their definitive hosts and their pathogenicity, there is no comprehensive information available on the population dynamics of the parasitic stages on the intermediate hosts. Slinn (1970) found that the intermediate host of *L. lusci* is the sole *Solea solea*. The intermediate host of *L. branchialis* in the southern North Sea is the flounder *Pleuronectes flesus* (Kabata, 1979). Some quantitative data were provided by Stekhoven (1936), Sproston & Hartley (1941), Kabata (1958), Slinn (1970), Van den Broek (1979) and Whitfield et al. (1988). Anstensrud (1989, 1990a, 1990b, 1992) presented detailed accounts of the reproductive behaviour of *L. branchialis*; however, a thorough investigation of all population processes has never been undertaken. This study presents

a comparison of the population dynamics of *L. lusci* and *L. branchialis* on intermediate hosts. The metapopulation dynamics of *L. lusci* on the sole is treated in more detail.

MATERIAL AND METHODS

Sole samples were obtained monthly from April 1991 to October 1991 in the Dutch coastal area (locality A in Fig. 1). The sampling dates and corresponding water surface temperatures were 17th April (9 °C), 15th May (11 °C), 16th June (13 °C), 18th July (19 °C), 28th August (19 °C), 23rd September (16 °C) and 15th October (16 °C). Sampling was carried out with a commercial shrimp trawler. On board, the heads of the sampled soles were removed and transferred to formalin 10 %. A regression equation describing the relationship between total length (TL) and head length (HL) (distance from the anterior end to the base of the pectoral fin) allowed for back-calculation of total length:

$$TL = 12.6 + 6.2 HL \quad (r^2 = 0.97, n = 30) \quad (\text{Fig. 2}).$$

Four samples of sole were obtained on 6th April, 8th June, 12th August and 28th October 1992 from an area called Roompot in the Oosterschelde (locality B in Fig. 1). The water surface temperatures on these sampling dates were 7 °C, 15 °C, 19 °C and 14 °C, respectively. The procedure on board and in the laboratory was similar to the procedure used in the Voordelta. The same regression equation was used for back-calculation of the total length of the fish.

Samples of flounder were obtained in April, June, August and October 1992 from the same area. The procedure was similar to the procedure used for sole. The linear regression equation describing the relationship between total length (TL) and head length (HL) was $TL = 7.3 + 4.2 HL$ ($r^2 = 0.87, n = 30$) (Fig. 2).

The samples were transferred after 2 months to ethanol 70 %. In the laboratory, individual parasites were removed from the gill filaments of flounder (*Lernaecera*

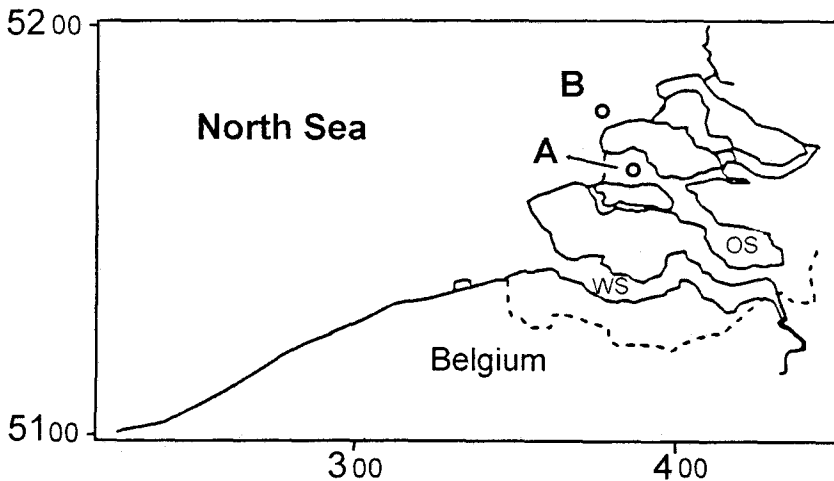


Fig. 1. Study area indicating the sampling localities A and B. WS = Westerschelde; OS = Oosterschelde

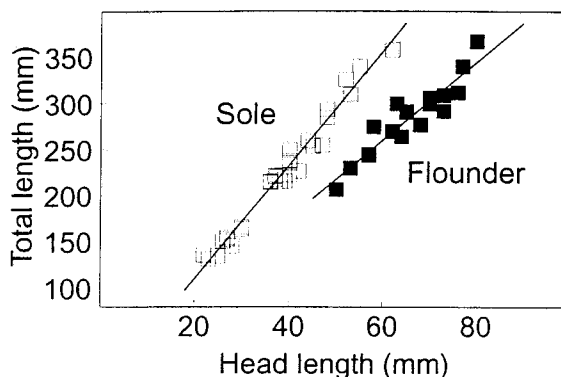


Fig. 2. Relationship between fish length and head length for flounder and sole. For regression equations see text

branchialis) and from the internal folds of the operculum of sole (*L. lusci*). The parasite life cycle stages were determined and the number of parasites was counted. The stages were abbreviated as C (copepodite), CI (chalimus I), CII (chalimus II), CIII (chalimus III), CIV (chalimus IV), AM (adult male) and AF (adult female).

The parasite dispersion pattern was studied by calculating the variance-to-abundance ratio ($I = s^2/a_t$) (cf. Elliot, 1977). For small samples, agreement with the Poisson series was tested by calculating the χ^2 value, which was compared with the appropriate 5% significance level of n degrees of freedom

$$\chi^2 = s^2n/a_t$$

RESULTS

Voordelta

The number of fish examined and the mean lengths of the soles from the Voordelta in each month are shown in Table 1. A large proportion of the soles harboured larval or adult *Lernaeocera lusci* (Fig. 3); about 96% of the soles which entered the Dutch coastal area in early spring were infected with 1 to 300 parasites. The prevalence decreased to a minimum of 45% in May, and then gradually increased to 100% infection in July. A second decline was observed in August, followed by a gradual increase to 100% infection in October. Similar seasonal patterns were observed for the parasite abundances. Maximum abundances were recorded in April and July, and minimum abundances were recorded in May and August (Table 1).

The correlations between parasite infestation intensity and the total length of the fish host are shown in Figure 4. There was a significant positive correlation in April, May and June 1991 (Spearman Rank Correlation test, $P < 0.05$). Comparison between the host size classes revealed significantly lower abundances in the smaller size class (< 175 mm) in April and May 1991 (Table 2).

As is illustrated by the high variance-to-abundance ratios ($I > 1$, $P < 0.05$; cf. Table 1), *L. lusci* was highly aggregated within populations of sole. Within all size classes (except

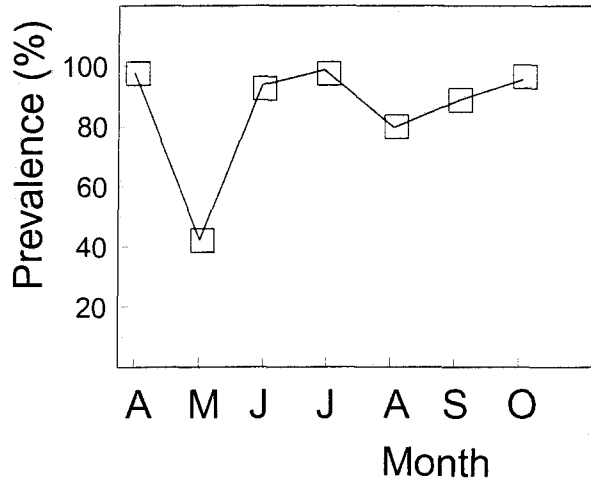


Fig. 3. Prevalence of *Lernaocera lusci* on sole *Solea solea* in the Dutch coastal area (Voordelta) (1991)

for size class $175 < x < 250$ mm in July 1991) there were no positive correlations (Spearman Rank Correlation test, $P > 0.05$) between host length and infection intensity (Table 2). All variance-to-abundance ratios within size classes were significantly larger than 1 ($P < 0.05$) (Table 2).

Two waves of transmission to the intermediate host could be distinguished for *L. lusci* (Fig. 5). The first transmission wave, characterized by high numbers of free copepodites on the intermediate host, occurred in June. A second transmission wave occurred between August and October 1991. Copepodites were predominant in June–July and in September–October. High numbers of adult males were found in April, June and July 1991. Adult pre-metamorphosis females on the other hand were mostly found in July 1991. The samples of September and October 1991 were characterized by low numbers of chalimus I–IV stages and adult individuals.

Oosterschelde

Both *Lernaocera* species were characterized by high prevalences on their intermediate hosts in the Oosterschelde: all 86 soles collected between April and October

Table 1. Number of fish (n), mean fish length (TL), abundance (a_t) and variance-to-abundance ratio ($I = s^2/a_t$) of *Lernaocera lusci* on sole in the Voordelta (1991)

	Apr.	May	June	July	Aug.	Sept.	Oct.
n	55	42	41	19	16	20	2
TL (mm)	194	178	201	216	178	224	188
a_t	61	4	40	88	5	11	24
I	76	14	84	114	4	5	–

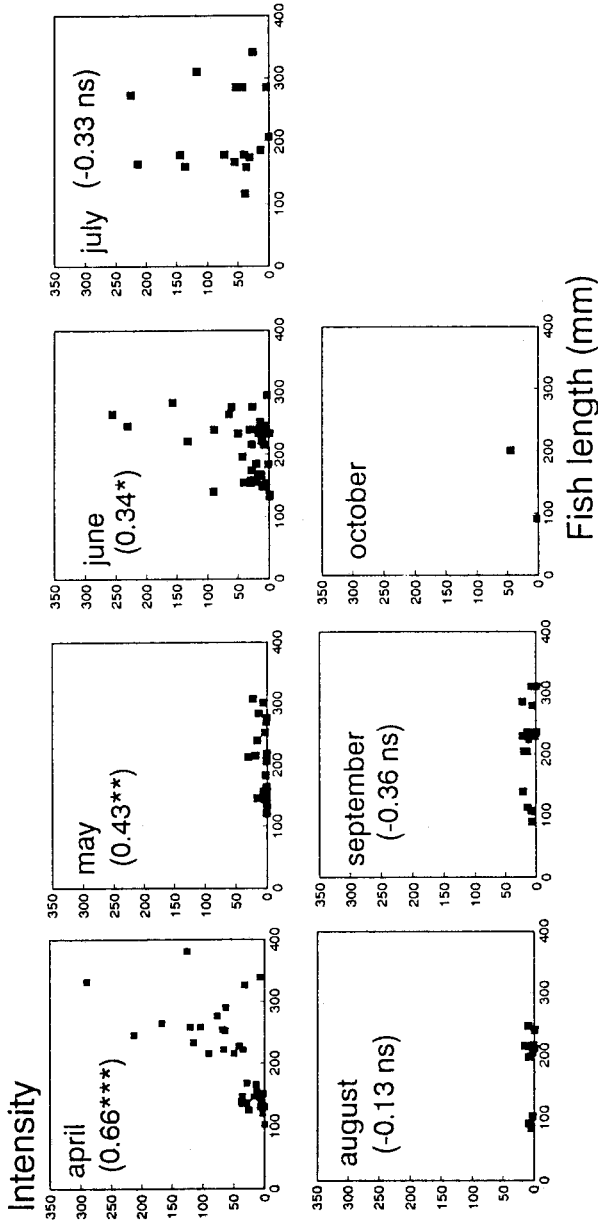


Fig. 4. Relationship between parasite (*Lernaeocera lusci*) infestation intensity and sole length in the Dutch coastal area (Voordelta) between April and October 1991. The Spearman Rank Correlation coefficients (rs) are given in brackets

Table 2. Abundance (a_t), variance-to-abundance ratio ($I = s^2/a_t$) and Spearman correlations (r_s) between sole length and parasite infestation intensity for three size classes of *Lernaeocera lusci* in the Voortdelta (1991)

	<175 mm			175–250 mm			> 250 cm			
	n	a_t	r_s	n	a_t	r_s	n	a_t	r_s	I
Apr.	30	20 ^b	0.04 ^{ns}	9	93 ^a	0.14 ^{ns}	16	119 ^a	-0.12 ^{ns}	53 ⁺
May	28	2 ^b	0.12 ^{ns}	10	7 ^a	0.05 ^{ns}	4	11 ^a	0.80 ^{ns}	9 ⁺
June	17	21 ^a	0.47 ^{ns}	17	42 ^a	0.16 ^{ns}	7	84 ^a	-2.00 ^{ns}	100 ⁺
July	6	65 ^a	0.54 ^{ns}	7	82 ^a	-0.93 ^{***}	6	117 ^a	0.09 ^{ns}	212 ⁺
Aug.	5	4 ^a	-0.87 ^{ns}	11	6 ^a	0.06 ^{ns}	—	—	—	—
Sept.	4	13 ^a	1.00 ^{ns}	10	13 ^a	-0.46 ^{ns}	6	8 ^a	0.31 ^{ns}	8 ⁺

Abundances (within each month) with the same superscript are not significantly different ($P > 0.05$)
 ns = not significant; *** = $P < 0.001$
 Variance-to-abundance ratios which are significantly greater than 1 are marked by +

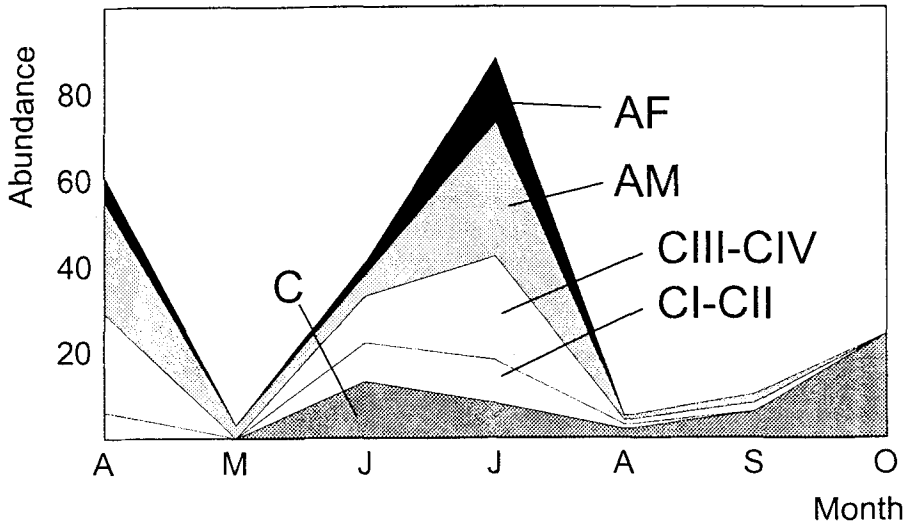


Fig. 5. Abundance of *Lernaeocera lusci* on sole *Solea solea* from April to October 1992 in the Voordelta. The abundances of the respective stages are represented by stacked areas (see text for abbreviations of stages)

1992 were infected with *L. lusci*. The maximum number found on a single host individual was 634 (on a fish with length 273 mm in April 1992). Among the 40 flounders caught in 1992, only one fish in August harboured no *L. branchialis* (Table 3). The maximum number of parasites (632) was found on a flounder, 345 mm long, in June 1992.

The mean host length and the abundance of *L. lusci* and *L. branchialis* are shown in Table 3. For both *L. branchialis* on flounder and *L. lusci* on sole, the highest abundances were found in early spring (April 1992). For both species, a significant decline in abundance was observed between April and August (Kruskal-Wallis; $P < 0.05$). A signifi-

Table 3. Number of fish (n), mean fish length (TL), prevalence (p_t), abundance (a_t) and variance-to-abundance ratio ($I = s^2/a_t$) of *Lernaeocera lusci* on sole and of *L. branchialis* on flounder in the Oosterschelde (1992)

	April	June	August	October
<i>L. branchialis</i> on flounder				
n	10	10	10	10
TL (mm)	312	308	261	290
p_t (%)	100	100	90	100
a_t	200	135	10	28
I	149	269	7	14
<i>L. lusci</i> on sole				
n	30	30	18	8
TL (mm)	201	209	231	204
p_t (%)	100	100	100	100
a_t	107	42	7	42
I	176	49	6	17

cant increase in abundance was observed between August and October for *L. lusci* (Kruskal-Wallis; $P < 0.05$), but not for *L. branchialis* (Kruskal-Wallis; $P > 0.05$). Abundances were consistently higher for *L. branchialis* than for *L. lusci* in the spring and summer, but lower in autumn.

The correlations between the parasite intensity and the length of the respective intermediate hosts are shown in Figure 6. There was a positive correlation between the

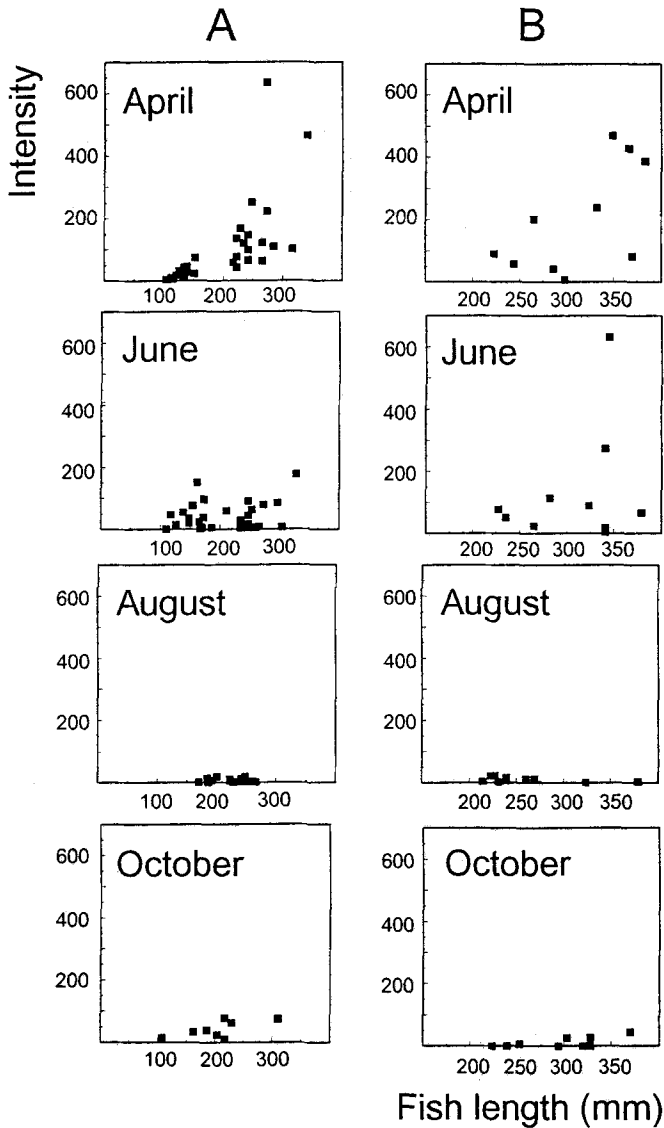


Fig. 6. Infestation intensity of *Lernaecera lusci* (A) and *L. branchialis* (B) in relation to the length of their intermediate hosts (*Solea solea* and *Pleuronectes flesus*) in the Oosterschelde (1992).

abundance of *L. lusci* and sole length in April 1992 (Spearman Rank Correlation Test; $P < 0.05$) and no significant correlation ($P > 0.05$) in June, August or October 1992 (Table 4). This was confirmed by a non-parametric Kruskal-Wallis test which was performed to test for significant differences in abundance between three size-groups in April and in June (Table 5). In April, significant differences ($P < 0.01$) were found between the largest size-groups (> 250 mm) and the other size-groups (< 250 mm). No significant differences were found among size-groups in June 1992 ($P > 0.05$). There was no correlation between intensity of *L. branchialis* and flounder length at any time of the year (Table 4).

Dispersion patterns were characterized by variance-to-abundance ratios that were significantly greater than 1 in all months for both sole and flounder ($P < 0.05$; cf. Table 3). The size heterogeneity within the sole populations of April and May 1992 (which may partly be responsible for the aggregated patterns) was reduced by size-specific comparisons (Table 5). It should be noted that only within one size-group (< 175 mm in April) was

Table 4. Spearman Rank Correlations (r_s) between total fish length and number of parasites (all stages or copepodites [cop.] only) between April and October 1992 in the Oosterschelde

	n	<i>L. lusci</i>		n	<i>L. branchialis</i>	
		r_s all	r_s cop.		r_s all	r_s cop.
Apr.	30	0.87***	0.67***	10	0.48 ^{ns}	0.23 ^{ns}
June	30	0.13 ^{ns}	0.16 ^{ns}	10	0.14 ^{ns}	0.31 ^{ns}
Aug.	18	-0.24 ^{ns}	-0.07 ^{ns}	10	-0.37 ^{ns}	-0.19 ^{ns}
Oct.	8	0.54 ^{ns}	0.42 ^{ns}	10	-0.43 ^{ns}	-

ns = not significant ($P > 0.05$); *** = $P < 0.001$

Table 5. Abundance (a_t), variance-to-abundance ratio ($I = s^2/a_t$) and Spearman Rank Correlation (r_s) between host length and infestation intensity of *Lernaecera lusci* (respectively of all stages or only copepodites [cop.]) within size groups of sole in April and May 1992

Size class	n	<i>L. lusci</i>		I all	<i>L. lusci</i>	
		a_t all	r_s all		r_s cop.	I cop.
April 1992						
< 175 mm	13	26 ^b	0.76**	14 ⁺	0.44 ^{ns}	5 ⁺
175-250 mm	10	116 ^b	0.55 ^{ns}	34 ⁺	0.17 ^{ns}	12 ⁺
> 250 mm	7	245 ^a	0.24 ^{ns}	196 ⁺	-0.05 ^{ns}	37 ⁺
June 1992						
< 175 mm	13	28 ^a	0.20 ^{ns}	185 ⁺	0.05 ^{ns}	19 ⁺
175-250 mm	10	24 ^a	0.18 ^{ns}	37 ⁺	-0.07 ^{ns}	11 ⁺
> 250 mm	7	84 ^a	0.50 ^{ns}	93 ⁺	0.31 ^{ns}	29 ⁺

Abundances (within each sample) with the same superscript are not significantly different (Kruskal-Wallis, $P > 0.05$)
 ns = not significant ($P > 0.05$), ** = $P < 0.01$
 Variance-to-abundance ratios marked with + are significantly different from 1

a significant positive correlation found between sole length and parasite intensity. Further, the results displayed in Table 5 indicate that within all size-groups of sole the variance-to-abundance ratios were significantly greater than 1.

Abundance and dispersion indices within the size classes were also calculated for the free copepodids only. Table 5 indicates that for both sole and flounder no significant relationships were found between fish length and infestation intensity of free copepodids. However, dispersion indices were always significantly different from 1.

The relative percentages of parasites belonging to the respective substages of *L. branchialis* (on flounder) and of *L. lusci* (on sole) are shown in Figure 7. Clearly, the largest proportion of adult males of *L. branchialis* was found in April and mainly in June. Pre-metamorphosis females were predominantly found in June. Infective copepodites were mainly found in April, though small numbers were also present in June and October. A slightly different picture was obtained for *L. lusci*: infective copepodites, adult males and adult females were all found predominantly in April. Some adult males were still present on the intermediate host in June, but by August almost all had left. It seems as if a new recruitment wave occurred in October, which is shown by the increased number of copepodites in this month.

The positive correlations between the number of copepodites and the number of chalimus and adult stages, combined, of *L. lusci* were significant in April, June and August ($P < 0.05$) but not in October (Table 6). For *L. branchialis*, similar positive correlations were found in April and June.

DISCUSSION

Whitfield et al. (1988) experimentally determined the duration of successive development stages of *Lernaeocera branchialis* on flounder gills: at 10°C the overall development time was about 25 days. Field experiments at 16°C showed that some parasites had completed development, at the most, in 11 days. The development time of the chalimus and adult stages could not be estimated from the present study because there is recruitment of infective stages (copepodites) throughout the year. However, there is evidence that *Lernaeocera lusci* chalimus stages are passed through rapidly on sole. No parasites were found in May, and soles in July were infected with large numbers of adult males and females.

Stekhoven (1936) inferred from field observations that the large numbers of *L. branchialis* which accumulate on flounders in spring detach in summer. His hypothesis is corroborated in the present study: the highest abundance of *L. branchialis* in the Oosterschelde was found in April and the adult females left the intermediate host en masse after June (Table 3). First-year whiting which enter the Dutch delta in early spring probably act as definitive host for the female *L. branchialis* which detach from flounders (Van Damme & Hamerlynck, 1992). Thus, *L. branchialis* probably has only one generation each year: recruitment of infective stages (copepodites) on flounders probably occurs in winter, whereas transmission to the definitive host occurs in summer. Similar observations were made by Kabata (1958) for *L. branchialis* on *Microstomus kitt*.

The population dynamics of *L. lusci* are considerably more difficult to interpret. The large numbers of adult males and females which had accumulated on soles in the Oosterschelde in April had all left the intermediate host in summer (Fig. 7). In the

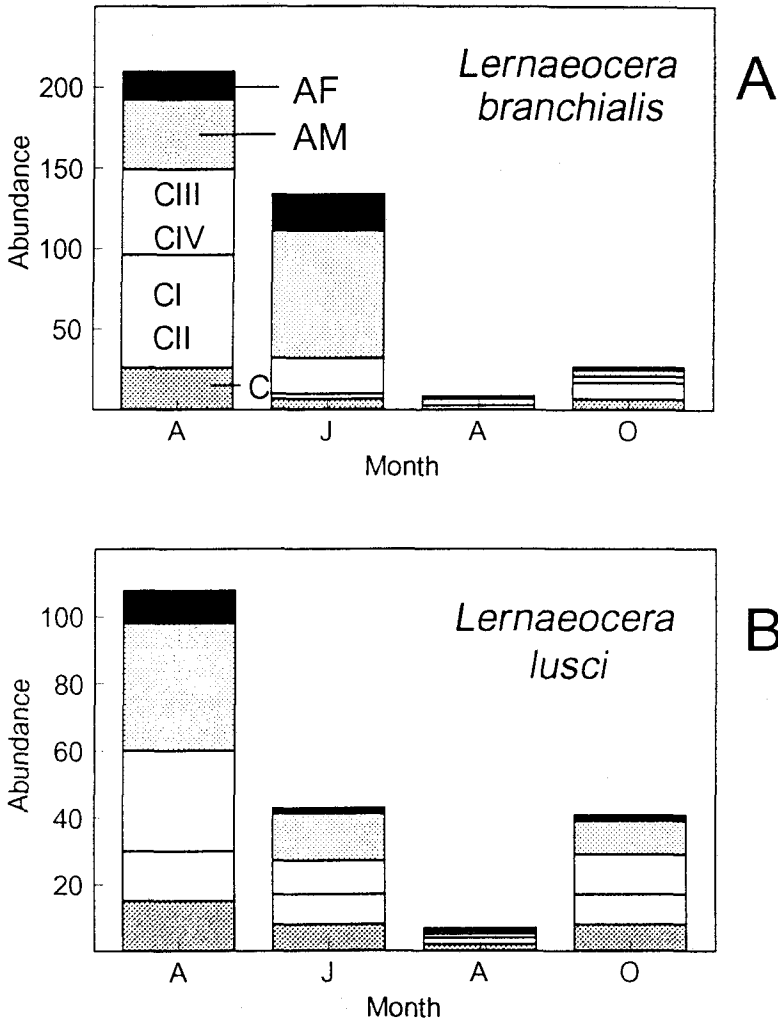


Fig. 7. Abundance of *Lernaeocera branchialis* (A) and *L. lusci* (B) on their respective host species in April, June, August and October 1992 in the Oosterschelde. The abundances of the respective (combined) substages are represented by stacked bars (see text for abbreviations of stages)

Voordelta, all parasites left sole in May, followed by new transmission of copepodites in June and July. The adult males and pre-metamorphosis females which resulted from this transmission wave had all left the intermediate host in August. Both in the Oosterschelde and in the Voordelta, new recruitment occurred in October (in contrast to *L. branchialis* on flounders). Thus, three transmission waves could be distinguished in the Voordelta: a first transmission wave (in late spring) of pennella larvae (pre-metamorphosis females) to definitive hosts, a recruitment wave (in early summer) of copepodites from definitive host to sole, and a transmission wave (in summer) of pennella larvae from sole to definitive host. The three separate transmission waves probably also occurred in the Oosterschelde

Table 6. Spearman Rank Correlations (r_s) between the number of copepodites and the number of chalimus and adult stages combined for *Lernaeocera lusci* on sole and for *L. branchialis* on flounder in the Oosterschelde (1992)

	<i>L. lusci</i> on sole		<i>L. branchialis</i> on flounder	
	n	r_s	n	r_s
April	30	0.68***	10	0.79**
June	30	0.84***	10	0.73*
August	18	0.55*	10	0.46 ^{ns}
October	8	0.41 ^{ns}	–	–

ns = not significant ($P > 0.05$) * = $P < 0.05$ ** = $P < 0.01$ *** = $P < 0.001$

but were not detected (due to the absence of a May sample). Thus, *L. lusci* probably has 2 generations each year.

The question remains as to which demersal fish species act as definitive hosts for *Lernaeocera* species in the Dutch delta. It is highly probable that the whiting *Merlangius merlangus* fulfills this role in the Oosterschelde. Van Damme & Hamerlynck (1992) observed that more than 50% of the 0+ whittings in this area are infected with *L. branchialis*. In offshore areas, other gadids such as cod *Gadus morhua* may also play a significant role. Bib *Trisopterus luscus* is possibly the typical definitive host for *L. lusci* in the Oosterschelde (Van Damme et al., 1996). Dragonet *Callionymus lyra*, lozano's goby *Pomatoschistus lozanoi* and sand goby *Pomatoschistus minutus* may represent important definitive hosts in the Belgian and Dutch coastal area (Hamerlynck et al., 1989; Van Damme et al., 1993). The former two species are not very common in the Oosterschelde (Hamerlynck et al., 1993), so their role may be minor in this area.

First-year bib *Trisopterus luscus*, the typical definitive host species of *L. lusci*, enter the coastal area in May and remain in shallow waters until winter, when the majority of the population migrates to deeper water (Hamerlynck & Hostens, 1993). However, juvenile bib accumulate only small numbers of adult pre-metamorphosis female *Lernaeocera* between May and July (Van Damme et al., 1996). Thus, it appears that in spring 0+ bib is excluded, for some reason, from the transmission window of *L. lusci*. Other demersal fish, such as dragonet and sand goby, are the most promising candidates to take up the role of definitive host in late spring in the Voordelta and/or Oosterschelde.

The significant positive correlations between sole length and parasite infestation intensity in April 1991 (in the Voordelta) and in April 1992 (in the Oosterschelde) indicate that, at the time of entering the Dutch delta, larger sole have acquired a larger number of parasites than smaller sole. This may be due to the fact that the larger soles occupy different winter grounds than juvenile soles and that the former may have a higher chance of being infected by *L. lusci*. For this to be true, a transmission window created by the joint occurrence of the definitive host (bib) and sole should have occurred for larger sole but not for smaller sole. On the other hand, there were no significant correlations between sole length and parasite infestation intensity in June and July 1991 (in the Voordelta) and in June 1992 (in the Oosterschelde). This may imply that sole of all size classes are equally susceptible to infective stages in summer, but not in winter. A survey of the literature shows that no information is available on the spatial winter- and summer

distributions of different age classes of sole, and this makes testing of this hypothesis impossible.

It was found that *Lernaeocera* individuals (free copepodid + chalimus I-IV + adults) were always aggregated within intermediate host populations. The transmission processes which have led to these dispersion patterns may have a temporal component: infective stages may have been accumulated over a long period, and the aggregated distributions may result from compounding Poisson distributions (Elliot, 1977). Because the development of the free copepodite to chalimus I, after attachment of the host, is completed within 2 days at 10°C (cf. Whitfield et al., 1988), the patterns of these stages on the intermediate host may provide information about the recent transmission process. The observation that copepodites are always aggregated within their host populations may suggest that the aggregation of infective stages within the aquatic habitat is one of the main factors inducing aggregated patterns within the host populations.

In the Oosterschelde, positive correlations were found between the number of copepodites and the number of parasites of other stages. This suggests that hosts which were previously infected with parasites had a greater chance to be infected with new infective stages. Many factors can be responsible for this relationship between the number of parasites already accumulated on the host and the number of parasites newly acquired. Some examples are: (1) Infective stages may actively search for hosts and are possibly guided by chemical stimuli generated by parasites already on the host (Anstensrud, 1989); (2) individual soles may be genetically predisposed for acquiring parasites; (3) infected soles may exhibit a specific behaviour (eventually parasite-induced) or may prefer certain localities, resulting in an increased risk of encountering infective stages; (4) larger soles may always accumulate more parasites than smaller soles. Detailed laboratory and field studies are needed to sort out these questions.

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