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The population dynamics of the parasitic copepode *Lernaeocera lusci* (Bassett-Smith, 1896) on its definitive host

P. A. Van Damme[1], O. Hamerlynck[2, 3] & F. Ollevier[1]

[1]*Laboratory of Ecology, University of Leuven, Zoological Institute; Naamsestraat 59, B-3000 Leuven, Belgium*
[2]*Marine Biology Section, University of Ghent; Ledeganckstraat 35, B-9000 Gent, Belgium and*
[3]*Center for Estuarine and Coastal Ecology; Vierstraat 28, NL-4401 EA Yerseke, The Netherlands*

ABSTRACT: The mesoparasitic copepod *Lernaeocera lusci* (Bassett-Smith, 1896) was recovered from first-year bib (*Trisopterus luscus* L.) in the Voordelta (Southern Bight of the North Sea) from May until December 1989. Analysis of the seasonal abundance and of the population structure showed that transmission of infective stages to bib mainly occurred from June to September. From September to December the overall prevalence fluctuated around 70 %. Maximum parasite population size ($47/10^4 m^2$) and the highest total egg number were recorded in September and October, respectively. It was found that total parasite mortality was significantly influenced by mortality of hosts carrying parasites. Natural mortality probably contributed a small percentage to total parasite mortality. Calculation of the temporal mean-variance regression equation revealed that the parasites were aggregated within the definitive host population.

INTRODUCTION

Some of the most conspicuous parasite species of the North Sea belong to the genus *Lernaeocera* (Pennellidae, Crustacea). Several authors have studied the population dynamics of *Lernaeocera branchialis*, a pathogenic parasite which infects economically important gadoid species such as whiting (*Merlangius merlangus*) and cod (*Gadus morhua*) (e.g. Whitfield et al., 1988; Pilcher et al., 1989). In contrast, comparatively little information is available on a related species, *Lernaeocera lusci*, which infects the bib (*Trisopterus luscus*). Some authors even doubted the validity of the latter parasite species (Heegaard, 1947; Bastide-Guillaume et al., 1985). Recently, Tirard (1991) studied both species by enzyme electrophoresis and decisively confirmed both *L. branchialis* and *L. lusci* as valid species. She also proposed a morphological distinguishing characteristic: antennary processi are absent in *L. branchialis* but are present in *L. lusci*.

Aspects of the biology of *L. lusci* have been studied by Evans et al. (1983), Eiras (1986) and Tirard (1991). The life cycle of this species was studied in detail by Slinn (1971), who found that sole *Solea solea* (L.) is the typical intermediate host in the North Sea. Several authors reported on the (broad) host specificity towards the definitive host

(Kabata, 1963; Boxshall, 1974; Kabata, 1979; Van Damme, 1993) and on the site specificity (Evans et al., 1983; Eiras, 1984) of *L. lusci*. However, the population dynamics of this species have received little attention.

The seasonal abundance of *L. lusci* was studied in the Voordelta, a coastal area in the Southern Bight of the North Sea (Fig. 1). Within this area, 0+ bib (*T. luscus*) is the most important host of *L. lusci*. The specific objectives of this study are to (1) investigate seasonal variations in prevalence and mean intensity, (2) study the seasonal variations in population structure of *L. lusci*, and (3) discuss observed dispersion patterns of *L. lusci* on 0+ *T. luscus*.

MATERIAL AND METHODS

First-year bib, which entered the Dutch coastal area in spring, were captured using a 3-m beam trawl equipped with a shrimp net. Eight samples of 0+ bib were collected monthly from May 1989 to December 1989. Samples were taken in the ebb tidal delta of the former Grevelingen estuary and in the ebb tidal delta of the Oosterschelde (Fig. 1). Water surface temperatures are given in Figure 2. On board, fish were anaesthetised in a benzocaine solution and preserved in 7 % formalin immediately after capture. After 3 months, fish were transferred to 70 % ethanol, and their total length (TL) was measured. The gill cavity was then checked for parasites. The number of fish examined for the occurrence of *L. lusci* and the mean total length of the 0+ bib cohort are given in Figure 3.

The adult females of *L. lusci* were classified according to a nomenclature proposed by Van Damme & Hamerlynck (1992), which is a modification of the staging system initially proposed by Sproston & Hartley (1941). Table 1 summarizes the diagnostic characters of the substages. This nomenclature is based on the distinction between subadult (P, U, W), adult stages (X) and dead parasites (Z).

The terms prevalence (% fish infected), abundance (number of parasites/fish) and mean intensity (number of parasites/infected fish) were used according to the recommendations of Margolis et al. (1982). The Z substage was included in the calculations only when explicitly stated.

Spearman Rank Correlations between parasite intensity and total length were calculated, and a non-parametric test (Kruskal-Wallis) was used to investigate whether seasonal differences in parasite abundance occurred.

Fish densities are given as $n/10^4m^2$. No corrections were made for net efficiency. Parasite population density at each sampling date was calculated 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 = mortality coefficient

The mortality coefficient m ($0.0077\ day^{-1}$) was taken from Hamerlynck & Hostens (1993). Because the juvenile bib were sampled inefficiently in May (due to mesh size selection), the host density in this month was backcalculated. To calculate the density of mature

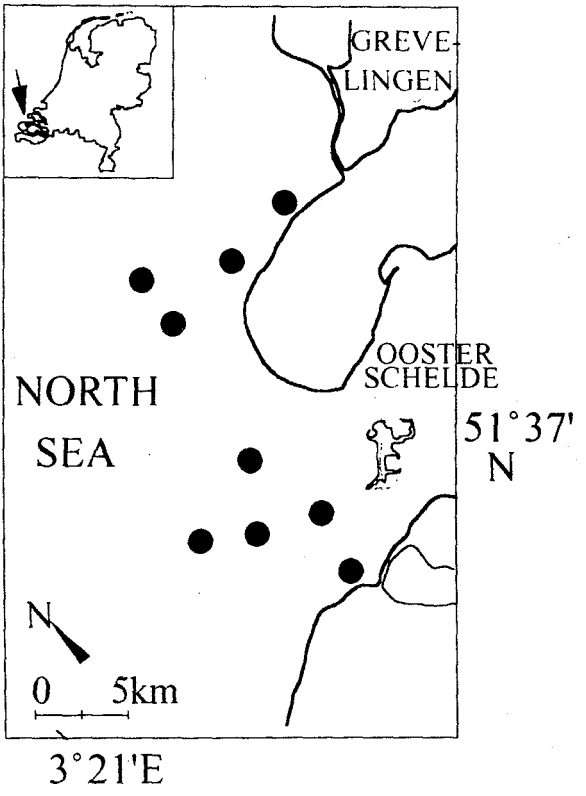

Fig. 1. Map of the study area. The sampling localities are indicated by solid circles

(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. Egg density at time t was calculated by multiplying parasite density ($P_t[X]$) with the mean number of eggs per egg-string pair at time t (z_t).

The parasite dispersion patterns were studied by calculating the variance-to-abundance ($I = s^2/a_t$) ratio (Elliot, 1977). If the individuals are randomly distributed among the samples, a value for this ratio of 1.0 is expected. Statistically significant deviations from 1.0 are termed aggregated ($I > 1$) or even ($I < 1$) distributions. Deviations from randomness were examined using the test statistic d (Elliot, 1977),

$$d = \sqrt{2\chi^2} - \sqrt{2\upsilon\text{-}1}$$

with

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

where

υ = degrees of freedom
a_t = abundance at time t
s^2 = variance

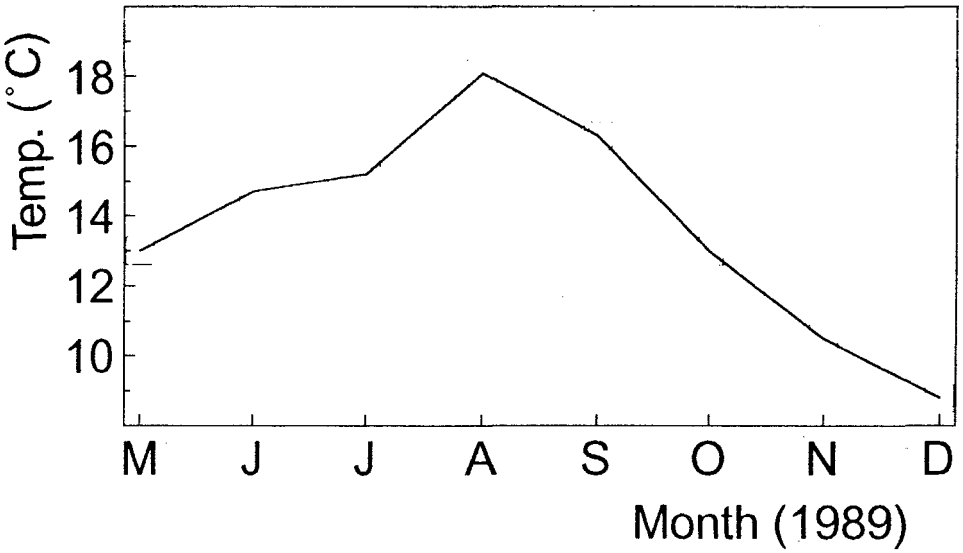

Fig. 2. Water surface temperatures in the Voordelta from May to December 1989

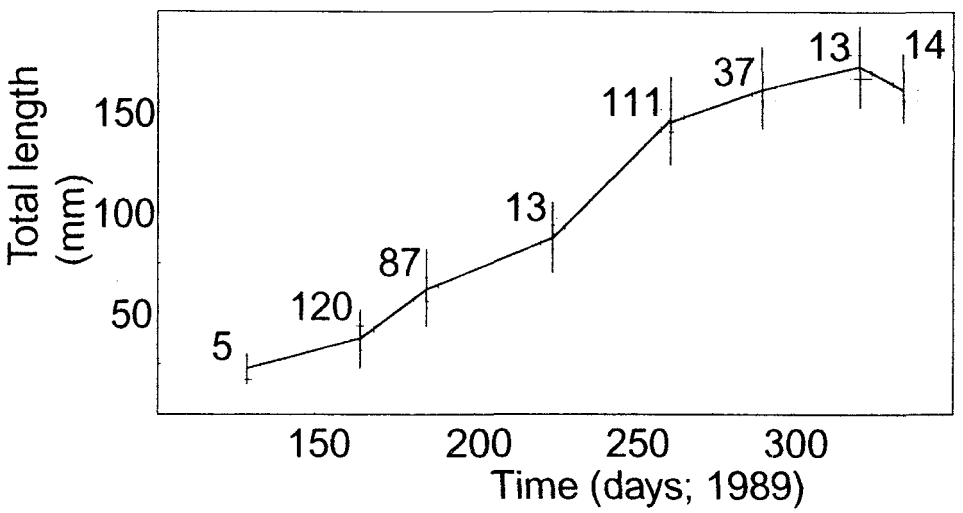

Fig. 3. Increase in mean total length of 0+ bib in the Voordelta. The standard deviations are indicated by vertical bars. The number of fish examined (n) is shown (after Hamerlynck & Hostens, 1993)

Table 1. Classification of adult female *Lernaeocera lusci* (Bassett-Smith, 1896) on *Trisopterus luscus* (L.) (after Van Damme & Hamerlynck, 1992)

Substage	Definition
Pennella (P1)	Straight body, no flexure
Pennella (P2)	One point of flexure
Immature (U)	Two or three points of flexure
Mature pregravid (W)	Genital region fully swollen
Mature gravid (X)	External egg strings present
X1	Immature eggs
X2	Mature pigmented eggs
Y	External egg strings partly or completely spent
Dead parasite (Z)	Remains of holdfast embedded in host tissue

At a level of significance of $p = 0.05$, values of $-1.96 < d < 1.96$ indicate a random distribution, and $d > 1.96$ indicates an aggregated distribution. Test statistic d was calculated only for large samples ($n > 30$). For small samples ($n < 30$), the χ^2 value was compared with the appropriate 5 % significance levels for υ degrees of freedom. Furthermore, agreement of the observed frequencies with the Poisson series and with the negative binomial was tested. The parameters of the latter distribution are the abundance a_t and parameter k. A rough estimate of parameter k was derived from the equation

$$a_t = \frac{a_t^2}{s^2 - a_t}$$

For $k < 4$ a better estimate was obtained by the method of maximum likelihood (Elliot, 1977)

$$n\ln(1 + a_t/k') = \sum \frac{A(x)}{k' + x}$$

where

x = particular count
n = number of fish
A(x) = total number of counts exceeding x

Expected frequencies of the negative binomial were calculated by means of the SAS procedure PROC NGBIN = (p, k, n) where $p = 1/(1 + a_t/k)$ and n = number of parasites. Expected frequencies of the Poisson model were calculated by means of the SAS procedure PROC POISSON = (a_t,n). The observed distributions were compared with the Poisson series and with the negative binomial by χ^2 (*goodness-of-fit*) tests (Elliot, 1977); Taylor (1961) presented a formula where variance is proportional to a fractional power of the abundance. The exponent b from Taylor's power function

$$s^2 = a(a_t)^b$$

was used as an index of dispersion and varies from 0 for an even distribution to $+\infty$ for an aggregated distribution.

RESULTS

A small number of bib (4 %) in June were infected with *Lernaeocera lusci*. The prevalence then gradually increased in July and August, followed by a sharp increase in September. From September to December the overall prevalences (Fig. 4A) fluctuated between 68 % (Oct) and 77 % (Nov).

The parasite abundance changed as the prevalence changed (Table 2). Overall temporal changes in abundance were highly significant (Kruskal-Wallis, $P < 0.001$). In all months from June to September, significant increases in parasite abundance were found (Kruskal-Wallis; $P < 0.05$). The changes in the abundance scores from September to December were not significant (Kruskal-Wallis on paired means; $P > 0.05$) (cf. Table 2). The mean intensity increased gradually from about 1 (June/July) to a maximum of 4.8 in December.

The Spearman Rank Correlations between parasite intensity and total length of bib are shown in Table 3. A significant positive correlation was only found in June. Although all other correlations were not significant ($P > 0.05$), opposite trends seem to be present in summer versus autumn: from June to August large fish harboured more parasites, and from September to November the largest numbers of parasites were found on smaller fish.

Seasonal patterns in the population densities of both host and parasite are presented in Figure 4. Whereas maximum host population density in the study area was probably highest in May ($150/10^4\,m^2$), maximal parasite population density ($47/10^4\,m^2$) was recorded in September. In winter, parasite density decreased to a minimum of $15/10^4\,m^2$ (December). The corresponding densities of mature parasites exhibited a similar pattern. Maximum density was found in September ($30/10^4 m^2$).

Pennella larvae (mainly P1) were found from June to October 1989 (Fig. 5). Only a single P1 stage was found in June. The X stages were recorded for the first time in July and were found with an increasing frequency from August to December. The Z stages were recorded in low numbers from September to December. The relative occurrences of X1, X2 and Y substages are presented in Table 4. In July, only X1 stages were found. From August to December both X2 and Y stages were found, and the frequency of occurrence of the latter substages fluctuated between 19 % (Nov.) and 29 % (Sep.). The mean number of eggs in the consecutive months (z_t) is shown in Table 2. The maximum number of eggs found in one individual was 2504 (December 1989). The highest total egg number within the Voordelta area was found in October 1989 ($35\,000/10^4\,m^2$) (Fig. 4C).

The variance-to-abundance ratios ($I = s^2/a_t$) were significantly different from 1, except in June and July when they approached unity. Highly aggregated patterns were recorded in November ($I = 4.9$) and in December ($I = 3.9$). The highest number of parasites collected from one fish (14) was found in November 1989. The observed frequencies and the corresponding expected frequencies according to a negative binomial (to which best agreement was found, see Table 2) are shown in Figure 6. The parameter k, estimated by the maximum-likelihood method, and the results of the χ^2 test for agreement with the negative binomial are shown in Table 2. Between August und December this model fits well to the observed frequencies. Agreement with the Poisson series was only accepted in 3 months. The temporal regression equation describing the relation between variance (y) and abundance (x) is $\log y = 0.4 + 1.4 \log x$ ($n = 7$, $r^2 = 0.98$).

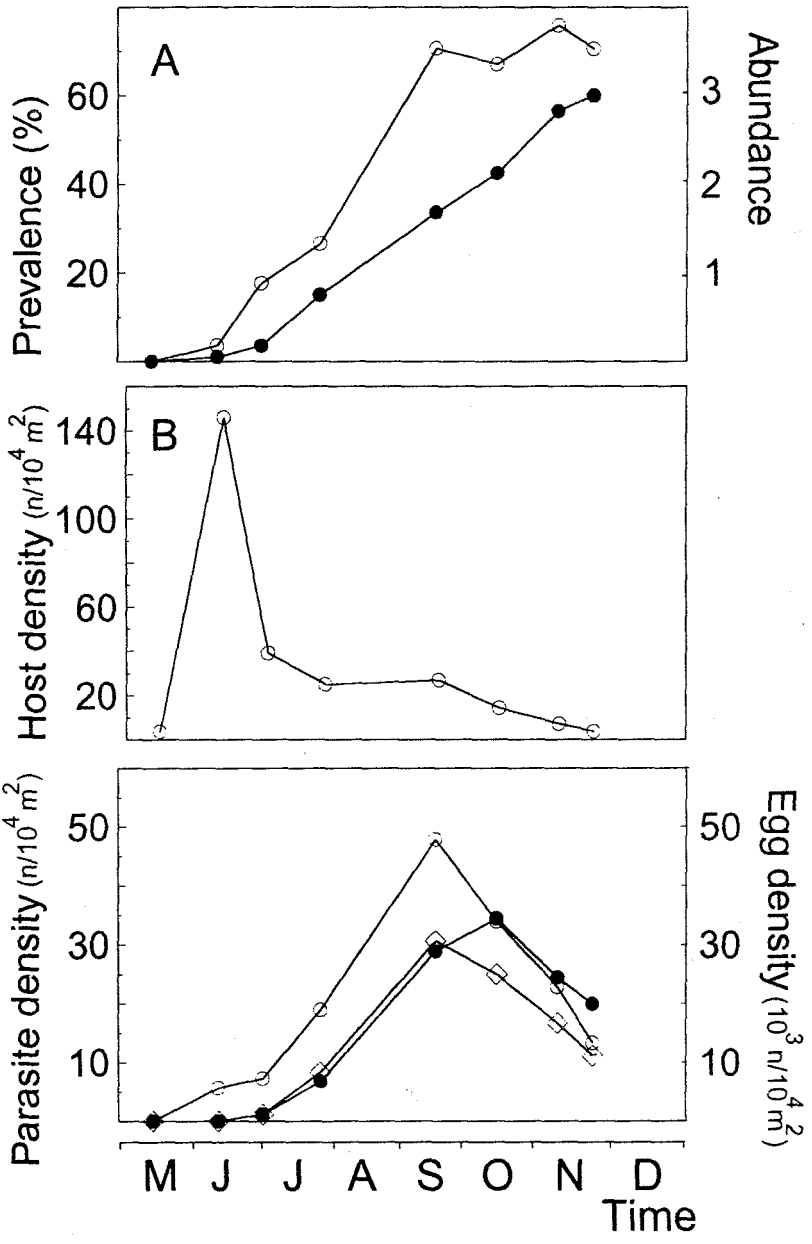

Fig. 4. Seasonal patterns in the infection of *Trisopterus luscus* by *Lernaeocera lusci*. A: Prevalence (open circles) and abundance (solid circles). B: Host population density. C: Population density of all parasites (open circles) and mature parasites (squares), and egg density (solid circles)

Table 2. Parasite abundance (a_t), variance to abundance ratio ($I = s^2/a_t$), test statistic d, parameter k of the binomial distribution, mean number of eggs (z_t) and agreement with the Poisson series (PO) and the negative binomial (NB) of *Lernaeocera lusci* on *Trisopterus luscus* from June to December 1989 in the Voordelta

	n	a_t	I	d	k	PO	NB	z_t
June	120	0.04^c	0.97	−0.29	–	PO	–	–
July	87	0.18^{bc}	1.00	−0.36	–	PO	–	873
Aug.	43	0.74^b	3.33+	7.51	0.32	PO	NB	963
Sept.	111	1.68^a	1.99+	6.03	1.71	0	NB	952
Oct.	37	2.11^a	2.87+	5.82	1.13	0	NB	1365
Nov.	13	2.85^a	4.85+	5.79	0.74	PO	NB	1447
Dec.	14	3.43^a	3.85+	4.80	1.20	0	NB	1643

Abundance scores with common superscript are not significantly different (Kruskall-Wallis on paired means, $P > 0.05$)
Variance to mean ratios marked with + are significantly different from 1
PO = agreement with the Poisson series ($P > 0.05$); NB = agreement with the negative binomial ($P > 0.05$); 0 = no agreement ($P < 0.05$); the model which gave the best agreement is underlined

Table 3. Spearman Rank Correlations (r_s) between parasite intensity and total length of bib in the Voordelta (1989)

Date	n	r_s
June	119	0.27••
July	87	0.19ns
Aug.	43	0.15ns
Sept.	111	−0.08ns
Oct.	38	−0.09ns
Nov.	13	−0.28ns
Dec.	12	0.01ns

ns = not significant; •• = $P < 0.01$

DISCUSSION

The winter prevalences of *L. lusci* on 0+ *T. luscus* fluctuated between 67.4 % (October) and 76.9 % (November). The maximum mean intensity was found in December (4.8). These values are high in comparison with infection levels recorded in other localities (Boxshall, 1974; Eiras, 1984; Evans et al., 1983; Tirard & Raibaut, 1989; Tirard, 1991). It can be suggested that the Voordelta is an area where the transmission rates of *L. lusci* from intermediate host (sole) to final host (first-year class bib) are rather high. Indeed, the Voordelta area is characterized by high sole densities (Hamerlynck et al., 1993), such that significant spatial overlap of intermediate host and final host may be responsible for the high prevalences recorded.

During the winter, sole is found in deep and warmer water (more than 30 m depth). In

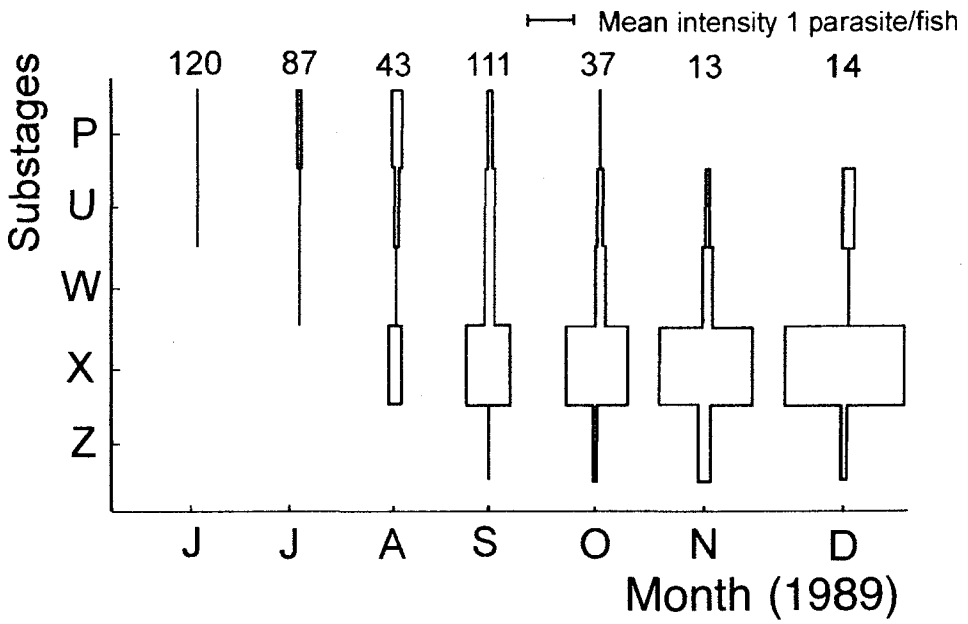

Fig. 5. Frequency of development stages of *Lernaeocera lusci* (Bassett-Smith, 1896) on *Trisopterus luscus* in the Voordelta 1989

spring, when the water temperature increases, they migrate to the shallow coastal zone. In this area, they are found in the gullies (between 5 m and 20 m). The 0+ bib on the other hand migrate to the shallow coastal zone in spring and can be found from May to December in the gullies. Thus, there are indications that a significant spatial overlap exists between sole and bib from May to September, and that may explain the high transmission rates during this period (Fig. 4). Similar explanations for the observed seasonal patterns in the transmission of infective pennella stages were put forward by Van Damme & Hamerlynck (1992) for the related species *L. branchialis*. These authors assumed that the migration patterns of both intermediate (flounder) and final host (whiting) of *L. branchialis* affect the transmission success of the pennella stages.

Table 4. Seasonal variations in the number of X1, X2 and Y substages and in the ratio J=100(X2+Y)/(X1+X2+Y) for *Lernaeocera lusci* infecting 0+ bib in the Voordelta (1989)

	X1	X2	Y	J
June	–	–	–	–
July	3	–	–	0
Aug.	11	3	0	21
Sept.	47	11	8	29
Oct.	22	4	3	24
Nov.	21	5	0	19
Dec.	32	5	3	20

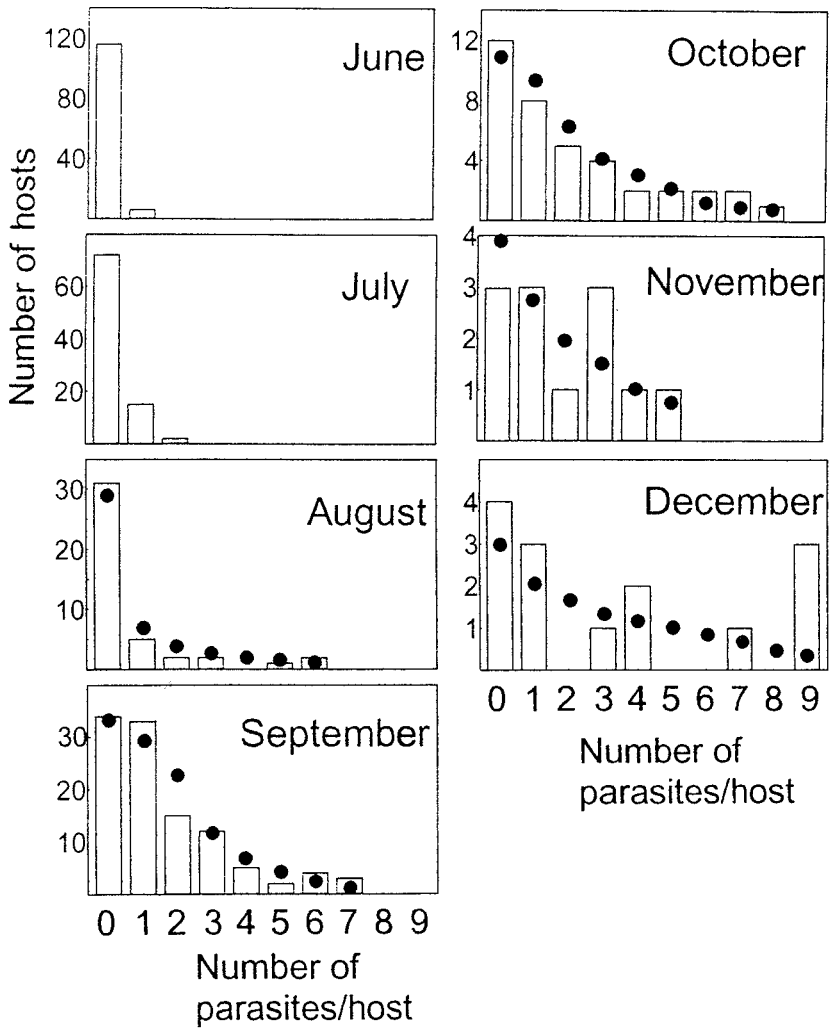

Fig. 6. Observed (bars) and expected (circles) frequencies according to the negative binomial for *Lernaeocera lusci* on 0+ bib in the Oosterschelde (1989)

Slinn (1971) estimated the duration of the substages of *L. lusci* under experimental conditions. At temperatures slightly higher than in the sea, he found that the parasites passed through substages P, U and W within about 8 weeks. This estimate is confirmed in the present study, where X substages were found as early as July and August, though the first P substages were only recovered in June. In contrast to Slinn's results, the proportion of Z substages remains relatively low up to December, indicating that the majority of parasites probably overwinters on its final host.

The rather constant prevalence scores of *L. lusci* from September to December can be

explained by the absence of further recruitment of juvenile parasites on 0+ bib after September (Fig. 5). Yet, it can be seen in Table 3 that the abundance scores continue to increase (though non-significantly) between September and December. This may be explained by the hypothesis that heavily infected fish are more susceptible to predation and also to capture by trawlers (Van Damme & Hamerlynck, 1992). It is clear that this factor, which can hardly be quantified, can distort some of the calculations in the present study.

Whitfield et al. (1988) demonstrated the capacity of *L. branchialis* to engage in iteroparous reproduction. The possibility to produce several sets of egg-strings, which also has been demonstrated in *L. lusci* (Van Damme, unpubl.), significantly increases the reproductive potential of these pennellid species. Of the X substages collected between August and December 1988, 77 % belonged to the X1 substage, 17 % to the X2 substage and 6 % to the Y substage. As both X2 and Y substages were found until December, it may well be that eggs are released both in summer and in winter. However, in order to calculate the number of eggs released per time interval the effect of temperature on egg maturation should be available. Whitfield et al. (1988) provided estimates of the duration of the X substages of *L. branchialis* obtained in laboratory conditions (at 10 °C, artificial sea water). The durations of X1, X2 and Y substages were, respectively, 10 days, 2.7 days and 12 days. Though it may be unreliable to extrapolate from laboratory experiments to the field, these data illustrate the high reproductive output of pennellid species. A second factor which significantly influences egg production within *L. lusci* populations and which has been frequently overlooked is host mortality. It was found in the present study that the high mortality rates of first-year class bib (whether parasite-induced or caused by other factors) significantly reduce population size, hence, total reproduction potential of this parasite species. 'Natural' parasite mortality due to senescence or host immune responses (as reflected by the number of Z-stages found) (cf. Fig. 5) probably accounts only for a small part of total parasite mortality.

It is noticeable that *L. lusci* and *L. branchialis* exhibit different dispersion patterns within their respective host populations in the Dutch Delta-area. *L. branchialis* was found to be randomly distributed within 0+ whiting populations (Van Damme & Hamerlynck, 1992), whereas *L. lusci* is aggregated within 0+ bib populations (present study). This discrepancy may follow from a range of factors, including differences in parasite-induced host mortality among those two species. However, the same authors express some doubts about the use of indices to measure dispersion of marine parasites within host populations. They suggest that the differential efficiency of the nets of research vessels, host migration patterns and spatial heterogeneity within marine habitats may hinder correct interpretation of parasite dispersion indices. Anderson & Gordon (1982) add to these limitations the sample size, which should be large enough to reduce the significance of chance effects. Host immune responses (Van Damme & Hamerlynck, 1992), senescence and intraspecific competition may also have profound influences on the dispersion pattern of *Lernaeocera* spp. Can parasite dispersion patterns provide information on the impact of parasites on host population size? Anderson & Gordon (1982) have dealt in detail with this question, and they warn us not to over-interpret field data. Yet, *L. branchialis* and *L. lusci* exhibit certain characteristics which render them suitable for comparative studies (Van Damme et al., 1994). The pathogenic effects of both species are established, *L. branchialis* causing severe pathological damage to its host (e. g. Van den Broek, 1978) and *L. lusci* apparently

not being very harmful to its host (Evans et al., 1983). Besides, they are rather long-lived (e. g. Whitfield et al. 1988; present study), and eventual parasite mortality is still observable on dissection of the host (Z stages) (Evans et al., 1983; present study). Though a full discussion of the above question is beyond the scope of this paper, this study might give a new impetus to investigations on the effect of different parasite species on both host individuals and host populations in marine habitats.

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