

PATHOGENS OF WILD AND FARMED FISH

Sea Lice

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Comparative life history of two species of sea lice

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ABSTRACT

In the Mediterranean, the parasitic copepod *Lepeophtheirus thompsoni* specifically parasitizes turbot, a marine scophthalmid, on which female copepods are haematophagous. The congeneric *Lepeophtheirus europaensis* infects brill (a marine scophthalmid) and flounder (a pleuronectid inhabiting lagoons) on which females are mucophagous like the other parasitic stages of both caligid species. The study of some life history traits such as female fertility, life span, developmental success and duration of early development reveals the probable influence of the diet and of the host species utilized. The importance of such studies in the understanding of the epidemiology of sea lice in general is discussed.

INTRODUCTION

In the Gulf of Lions (Mediterranean,, France), *Lepeophtheirus thompsoni* Baird, 1850 and *Lepeophtheirus europaensis* Zeddham, Berrebi, Renaud, Raibaut & Gabrion, 1988 parasitize three different species of flatfish (Heterosomata). *L. thompsoni* is specific to one host, the turbot (*Psetta maxima* L. 1758), a marine scophthalmid, and *L. europaensis* is found on both brill (*Scophthalmus rhombus* L. 1758), a marine scophthalmid, and flounder (*Platichthys flesus* L. 1758), a pleuronectid inhabiting lagoons. For these parasites, egg laying takes place within the gill chamber of their host. There, *L. thompsoni* females attach to the gill filaments and become haematophagous, whereas *L. europaensis* females are mucophagous like the other stages (Zeddham *et al.* 1988). De Meeûs *et al.* (Chapter I 1) describe other differences in specialization between the two copepod species studied (experimental host specificity and salinity tolerance) and reveal the existence of some heterogeneities within the Mediterranean populations of *L. europaensis* with respect to the host species parasitized (brill versus flounder).

Little is known about sea lice life history and, in particular, even basic information

about life span and fecundity of adults and survival characteristics of free-living stages is unavailable (Pike 1989). This chapter is intended to emphasize the life history traits of *L. thompsoni* and *L. europaensis* that can be correlated with the observed differences in specialization, host species parasitized and diet. For this purpose the numbers of eggs per egg sac are analysed for females sampled on each of the three host species. Experimental infections provide complementary data on the number of clutches (i.e. two egg sacs) produced, on development times and on life span of attached stages. The developmental success of eggs and of free stages, and the survivalship of infective stages (copepodids) in the absence of a host are also studied.

The results reveal that haematophagy appears to be correlated with higher female fertility. The exploitation of two different hosts (brill and flounder) by *L. europaensis* is associated with heterogeneities in female fertility and in development time of free stages. These observations are discussed and compared with what can be found on similar organisms. This work provides new data on the poorly known life history of sea lice in general.

MATERIAL AND METHODS

Ovigerous female copepods and natural clutches

Ovigerous females were collected in fishing ports (Sète and Grau-du-Roi, France) from the gill cavities of their hosts. Flounder copepods were collected on hosts caught in lagoons (Etang d'Ingril, Etang de Manguio, Etang du Ponant) by craft fishermen. *L. thompsoni* females are found attached to gill filaments, while *L. europaensis* females are found on the wall of the gill chamber and on the inner surface of the operculum (Zeddiam *et al.* 1988). Eggs contained in one egg sac per pair and per female were counted using a binocular microscope.

Experimental hosts

Some parasite-free turbot were bought **from** fish farms. **The** different flatfish species used for experimental infections were caught along the Languedoc coast (Mediterranean, France) and in lagoons (flounders). Turbot and brill were caught at sea by craft fishermen, or inshore, and flounder were caught in lagoons by craft fishermen. In the laboratory and under a binocular microscope, these fish, anaesthetized with 3-aminobenzoic acid ethyl ester (Sigma A 5040), were observed and only the parasite-free hosts were kept for experiments.

Experimental clutches

Sampled eggs were incubated at 15°C in filtered sea water. After hatching and development through the nauplius phase, the infective stages (copepodids) were isolated, counted and placed in a 50-litre tank containing fish to be infected. After development and mating, all parasites except females were removed. Observations of the anaesthetized infected fish took place every 3 days. Ovigerous females were regularly removed from the host, relieved of their egg sacs and reintroduced into the gill chamber of the host until the next egg laying. Eggs contained in these egg sacs

were then counted. The experiment stopped at the disappearance of the last female from the experimental host.

Two flounder and two turbot were infected by flounder and turbot copepods, respectively. Because brill does not survive well in experimental conditions, *L. europaensis* from brill were studied on two flounder and on only one brill.

Development of eggs and survival of free stages

Clutches were incubated at 15°C in filtered sea water (35‰ salinity). After hatching and development through the nauplius phase, the infective stages (copepodids) were counted daily. The mean survival (in days) was then calculated for each clutch. These observations provided data on the developmental success of clutches, eggs and free stages, and also on the development times from egg laying to infective stage.

RESULTS

Size of natural clutches

The number of eggs per egg sac is 66 ($s^2 = 398$) for turbot copepods ($n = 247$ egg sacs examined), 52 ($s^2 = 287$) for brill copepods ($n = 251$) and 61 ($s^2 = 407$) for flounder copepods ($n = 335$). Variances are not homogeneous (F -tests for homogeneity of variances, $p < 0.01$). A non-parametric test (one-tailed Kolmogorov-Smirnov) is thus used for paired comparisons. This reveals that *L. thompsoni* lays more eggs per egg sac than *L. europaensis* from brill ($p < 0.001$) and flounder ($p < 0.02$). Moreover, flounder parasites produce larger clutches than brill parasites ($p < 0.001$).

Experimental clutches

Experimental clutches contain fewer eggs than natural ones (Fig. 1). This point is only tested for flounder copepods raised on flounder because more data are available for this experiment. The difference between these data and natural clutches is very significant ($p \ll 0.001$, one-tailed Kolmogorov-Smirnov). The experimental results must therefore be interpreted with care. Females lay a number of clutches which can be relatively large (e.g. up to 16 clutches for one flounder copepod) compared with what has been reported in the literature (Lewis 1963). First and last clutches contain fewer eggs than intermediate clutches. This may explain the large variances observed in natural clutches.

During these experiments, we obtained some data on the development times or attached stages (from copepodid to the first egg laying) and on the delay between the production of consecutive egg sacs (in 15°C sea water). For reasons given above, these results, presented in Table 1, must be considered with caution and are only presented here as a basis for discussion. In all experiments, development times of the attached phases appear homogeneous (about 36 days) as does the delay between successive clutches (6-8 days).

Developmental success and survival of free stages

The observation of clutch development in sea water revealed that 10%, 4% and 6% of clutches do not develop at all (absence of pigmentation) for turbot, brill and flounder copepods, respectively (∴ not significant, 1 d.f., $p > 0.1$). Furthermore, the

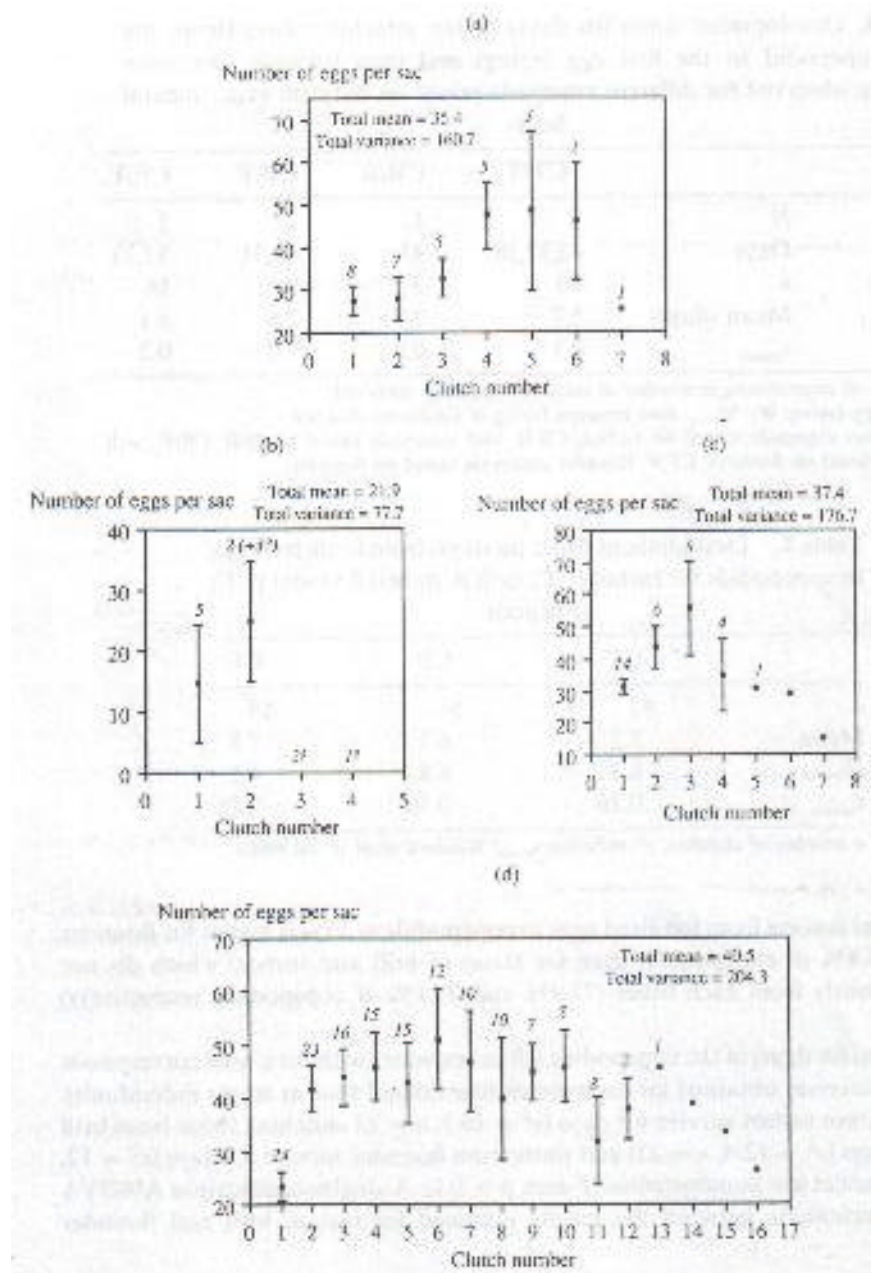


Fig. 1. Experimental clutch production observed for turbot copepods on turbot (CT/T) (a), for brill copepods on brill (CB/B) (b) or on flounder (CB/F) (c) and for flounder copepods on flounder (CF/F) (d). Successive numbers of gravid females are given within the graphs (italics).

Table 1. Development times (in days) of the attached phase (from the fixed copepodid to the first egg laying) and time between successive clutches, observed for different copepods raised on different experimental hosts

		CT/T	CB/B	CB/F	CF/F
W1	<i>N</i>	3	1	2	2
	Days	42,37.38	47	35,31	37.35
	<i>n</i>	10	3	9	16
$W_i - W_{i+1}$	Mean (days)	5.7	7.7	7.6	6.1
	S_{mean}	0.7	0.9	1.0	0.3

N: number of experiments; *n*: number of successive Clutches observed;
 W1: first egg laying; $W_i - W_{i+1}$: time between laying of successive clutches.
 CT/T: turbot copepods raised on turbot; CB/B: brill copepods raised on brill; CB/F: brill copepods raised on flounder; CF/F: flounder copepods raised on flounder.

Table 2. Development times (in days) from fertilized eggs to copepodids for turbot (CT), brill (CB) and flounder (CF) copepods

	CT	CB	CF
<i>n</i>	42	51	58
Mean	8.2	6.3	7.8
s^2	6.3	6.8	4.5
S_{mean}	0.36	0.36	0.28

n: number of clutches; s^2 : variance; S_{mean} : standard error of the mean.

developmental success from fertilized eggs to copepodids at 35‰ is higher for flounder copepods (86.4% of copepodids) than for those of brill and turbot, which do not differ significantly from each other (73.9% and 75.1% of copepodids, respectively) (Chapter 11).

The survival (in days) of the copepodids left in sea water without a host corresponds to the mean survival obtained for each clutch (considered thus as single individuals), Copepodids from turbot survive 6.8 days ($s^2 = 16.9$, $n = 27$ clutches), those from brill survive 7.5 days ($s^2 = 12.4$, $n = 23$) and those from flounder survive 5.5 days ($s^2 = 12$, $n = 20$). Variances are homogeneous (*F*-test, $p > 0.1$). A single classification ANOVA does not discriminate between the results obtained for turbot, brill and flounder ($p > 0.1$).

Development times of eggs and free stages

The different development times, from fertilized eggs to copepodids, are presented in Table 2. Variances are homogeneous (*F*-test, $p > 0.05$). A single-classification ANOVA indicates that the three samples are heterogeneous ($p < 0.001$). Paired comparisons (*t*-tests) reveal that this heterogeneity comes from brill parasites, which develop faster

(6.3 days) than turbot parasites (8.2 days) and flounder parasites (7.8 days) ($p < 0.001$). The differences between turbot and flounder parasites are not significant ($p > 0.5$).

DISCUSSION

Despite the fact that the present study is restricted to certain conditions (35‰, sea water at 15°C, experimental constraints), it provides detailed quantitative information on the life history of two sea lice species on their respective hosts. These data concern essential parameters of the fitness of those organisms: fecundity, developmental success and survival and duration of the different life cycle phases. Such data are not frequent in the literature (Pike 1989). It is nevertheless known that the concept of the 'highest possible number of eggs', postulated for parasites in general, has many exceptions in parasitic copepods (Kabata 1981). Indeed, on a basis of ten clutches laid by one *L. thompsoni* female (the most fertile), we would only have obtained 1320 eggs, a number comparable to that found in non-parasitic copepods (e.g. Uye 1981).

High survival must compensate for low fecundity (Hirschfield and Tinkle 1975). In accordance with this, the developmental success appears high for *Lepeophtheirus salmonis* (Johannessen 1978) as it does for the copepods studied in this chapter. Moreover, if we use the experimental fixation rates of copepodids on their original hosts (Chapter 11) as the ratio of successfully infective copepodids, the proportions of eggs leading to infective copepodids become 68% for *L. thompsoni* and 71% and 81% for *L. europaensis* from brill and flounder, respectively. Furthermore, copepodid survival without a host is also high. With a general mean of 7 days, some copepodids survived more than 20 days without a host, a result close to the maximum of 1 month observed for *L. salmonis* by Johannessen (1978), although this period may be exceptional. Such results can have important epidemiological and evolutionary consequences. The free-swimming phase indeed represents a critical step in parasitic life cycles. A good dispersal ability appears to be a basic necessity for organisms displaying habitat selection (De Meeûs *et al.* 1993), which in the present case may be equivalent to host specificity.

The compilation of all the results obtained on the duration of the different life cycle phases provides an approximate estimate of the life cycle duration. The period from fertilized eggs to the first egg laying is about 44 days for all the copepods studied in this chapter. The maximum life span of a single female, from fertilized egg to death, is 135 days (observed for one *L. europaensis* from flounder).

Our study also reveals important heterogeneities between the different copepods studied. Possibly as a correlation with its haematophagous diet, *L. thompsoni* appears more fertile than *L. europaensis* (mucophagous). Moreover, *L. europaensis* from flounder lay more eggs than those from brill, the free phase of which (fertilized eggs to copepodid) appears shorter, perhaps as a compensation. In the North Sea, flounder are parasitized by two different species of ectoparasitic copepods: *Lepeophtheirus pectoralis* (Müller, 1776), the adult females of which are found on the inner surface of pectoral and pelvic fins; and *Acanthochondria depressa* (Scott, 1901), which occupies the gill chamber (Boxshall 1974). In this area, Anstensrud (1990) found a maximum of 70 eggs per clutch. Such a value is just above half of the mean observed for *L.*

europaensis (122 eggs per clutch) and is far from the maximum observed for this species (218). It is possible that the gill chamber represents a more favourable environment (more oxygen, more mucus available) than the pectoral and pelvic fins. To conclude, these data obtained on the life history of *L. thompsoni* and *L. europaensis* may lead to a better understanding of sea lice epidemiology. Differences in diets (mucophagy, haematophagy), in location on the host (gill chamber, fins), in the host species parasitized (brill versus flounder for *L. europaensis*) and in external environment (sea and lagoons) appear to be correlated with important life history traits. Changes might occur within the populations of *L. salmonis*, for example the adoption of haematophagy, when faced with farmed rather than wild salmon. Such possibilities of consequential changes should be taken into account in studies dealing with such a major pathogen of farmed salmon (Pike 1989).

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