J. mar. biol. Ass. U.K. (1991), **71**, 425-436
Printed in Great Britain

DEVELOPMENT, GROWTH, AND SURVIVAL OF *LEPEOPHTHEIRUS SALMONIS* (COPEPODA: CALIGIDAE) UNDER LABORATORY CONDITIONS

S.C. JOHNSON* AND L.J. ALBRIGHT

Institute for Aquaculture Research, Simon Fraser University, Burnaby, British Columbia, V5A 1S6, Canada
* Present address: Department of Fisheries and Oceans, Biological Sciences Branch, Pacific Biological Station, Nanaimo, British Columbia, V9R 5K6, Canada

Development, growth, and survival data derived from laboratory experiments are provided for *Lepeophtheirus salmonis*, a common ectoparasite of wild and sea-farmed salmonids. The mean development time of eggs was 419·1 hours (17·5 days) at 5°C, 207·1 hours (8·6 days) at 10°C, and 130·8 hours (5·5 days) at 15°C. Development from the first nauplius to the infectious copepodid stage took 222·3 hours (9·3 days) at 5°C, 87·4 hours (3·6 days) at 10°C, and 44·8 (1·9 days) hours at 15°C. Development from the egg to the adult male took 40 days, and from the egg to the adult female 52 days at 10°C. No egg development occurred at 10‰ salinity. At 15‰ eggs developed but failed to produce active nauplii. At higher salinities (20-30‰) active nauplii were produced, but copepodids were only obtained at 30‰. Copepodids survived for less than 1 day in waters with a salinity of 10‰ or less. At higher salinities (15-30‰) and temperatures of 5, 10, and 15°C average survival times ranged between 2 and 8 days.

INTRODUCTION

The salmon louse *Lepeophtheirus salmonis* (Krøyer) is a common marine ectoparasitic copepod of most salmonids belonging to the genera *Oncorhynchus*, *Salmo*, and *Salvelinus* in the northern hemisphere (Kabata, 1979; 1988). In wild populations *L. salmonis* is common, generally present in low numbers on individual salmonids, and rarely reported to cause severe pathological effects (White, 1940; Wootten *et al.*, 1982; Nagasawa, 1987). However, in sea-farmed salmonids serious epizootics of *L. salmonis* do occur and result in heavy fish losses if untreated (Brandal & Egidius, 1979; Wootten *et al.*, 1982; Pike, 1989).

The life cycle of *L. salmonis* consists of ten stages. These stages include two free-living planktonic naupliar stages, one free-swimming infectious copepodid stage, four attached chalimus stages, two preadult stages, and an adult stage (Johnson & Albright, in press). Both of the nauplius stages and the copepodid stage prior to its attachment to the host are non-feeding. Attached copepodids, chalimus larvae, preadults, and adults feed on host mucus, skin, and blood (Kabata, 1974; Brandal *et al.*, 1976).

Although *L. salmonis* is an economically important parasite most aspects of its basic biology have been poorly documented. The effects of temperature on the duration of the egg bearing period (Johannessen, 1978), the duration of the naupliar stages, and survival of the infectious copepodid stage (Johannessen, 1978; Wootten *et al.*, 1982) have been

previously studied. However, these investigations were limited by the poor survival of *L. salmonis* larvae in the laboratory. The effects of temperature on the duration of the copepodid, chalimus, preadult, and the adult stages are unknown. Berger (1970) investigated the salinity tolerance of *L. salmonis* nauplii and adults, and surprisingly reports that nauplii are more tolerant to changes in salinity than are the adults.

This paper reports the effects of temperature and salinity on development, growth, and survival of *L. salmonis* under laboratory conditions. This information is important to our understanding of the dynamics of epizootics of *L. salmonis*.

MATERIALS AND METHODS

Ovigerous *L. salmonis* were collected from sea-farmed and wild chinook (*Oncorhynchus tschawytscha* (Walbaum)) and sea-farmed Atlantic salmon (*Salmo salar* (Linnaeus)) from Quadra Island and Departure Bay on the east coast of Vancouver Island, Canada. Where possible copepods were collected when the water temperature corresponded to the experimental temperature at which they were to be incubated. Possible maternal effects were minimized by using eggs or nauplii from several females in each stage of our investigations.

In most experiments eggs and developing nauplii were cultured in glass jars (250 ml to 3·5 l) covered with 100 μm Nitex mesh. The jars were suspended in tanks of flowing sea-water (28·5-30·5‰ salinity) and set temperatures (±0·5°C). Water exchange and circulation within the jars was maintained by gentle aeration.

Egg development times were determined using the indirect regression technique of Edmondson (1965). Entire collections of ovigerous females were divided into groups of five and cultured at either 5, 10, or 15°C in flowing sea water. Cultures were monitored daily from 0800-2300 h at two-hour intervals. Time to hatching for each female was recorded and the number of ovigerous females remaining at each time plotted against time from the start of the experiment. The least-squares regression of numbers of ovigerous females against time was calculated for each temperature. The point of intersection on the time axis is taken to be the mean development time. This technique is based on the assumption that the age distribution of the eggs is uniform within the sample. Although selective predation on females with eggs or embryos has been shown to result in a violation of this assumption for some free-living zooplankton species (see Threlkeld, 1979), we feel that this assumption is valid for the eggs of *L. salmonis* as the females are not free-swimming and no natural predators are known.

To determine the duration of the naupliar stages, eggs were hatched in tanks of flowing sea water with a temperature of 5, 10, or 15°C. Actively swimming first nauplii that hatched over the preceding two-hour period were pipetted into 250 ml culture jars and returned to their respective tanks. Moulting activity was monitored every two hours from 0800-2300 h. Time of development is defined as the time from hatching to the first observation of either the second nauplius or copepodid stage.

Copepodids that developed at 10°C and had moulted within the previous 12 h were used to infect previously uninfected Atlantic salmon. Infections were carried out in dark aerated tanks with no water flow. Exposure times ranged between 8 and 12 h. The fish

were maintained in 10°C flowing sea water, killed at intervals and examined for parasites. All developmental stages of the copepod were identified and their position on the host recorded. For each copepod measurements were made of total length (anterior margin to the base of furca), and maximum cephalothorax width (excluding marginal membrane). Time of development is measured from the time at which the eggs were extruded. The duration of the chalimus and preadult stages was determined from observed changes in stage frequency following the methods of Landry (1983). Time of development is defined as the time when 50% of the population had moulted to the next stage, as estimated from least-squares regression of the proportion of the population which had completed a given moult versus time. The data were arcsine square root transformed to meet the assumptions of the regression model (Zar, 1984).

To determine the effect of salinity on hatching success and survival to the copepodid stage, ten ovigerous females with non-pigmented eggs were placed in individual 250 ml culture containers and incubated at 9-10°C in static sea-water baths of 10, 15, 20, 25, and 30‰ salinity, and a flowing sea-water bath of 30-30·5‰ salinity. Water in the static baths was changed every second day. Salinities were adjusted by adding distilled water. Cultures were checked at one day post-hatching when unhatched eggs, and dead and moribund nauplii were counted and removed. At 5 d post-hatching the remaining nauplii and copepodids were counted.

Actively swimming copepodids which had moulted within the previous 12 h were transferred to individual test tubes containing 20 ml of 0.45 μm filtered sea water of various salinities (15, 20, 25, or 30‰) and the temperature at which they were reared (5, 10, or 15°C). Tubes were incubated at their respective temperatures and mortality was assessed daily. Copepodids were considered dead when they failed to respond to mechanical stimulation. Best transformation of the survival data was estimated using the procedure of Box *et al.*, (1978). All data were log (x+1) transformed and differences in survival investigated by a two-way analysis of variance. Multiple comparisons of survival times at each temperature were made using a Scheffé's test.

RESULTS

For each of the three experimental temperatures, the number of ovigerous females plotted against time, the least squares regression equation, and the calculated mean egg development times are presented in Figure 1. Mean egg development times were 419·1 h (17·5 d) at 5°C, 207·1 h (8·6 d) at 10°C, and 130·8 h (5·5 d) at 15°C.

The time from first to last nauplius hatched was highly variable, ranging from 18 to 65 h (mean=31·7±13·0 h; N=16) for egg strings maintained at 10°C in 30‰ static water. Egg numbers ranged between 251 and 423 (mean=344·6±79·8; N=16). There was no correlation between number of eggs and duration of hatching. Egg strings attached to the female began hatching from the posterior end. Those released by the female began hatching at any point along their length.

The duration of the first nauplius stage was shorter than that of the second nauplius stage at all temperatures (Table 1). The average duration of the first nauplius stage varied from 52 h (2·2 d) at 5°C to 9·2 h at 15°C. The average duration from hatching to the

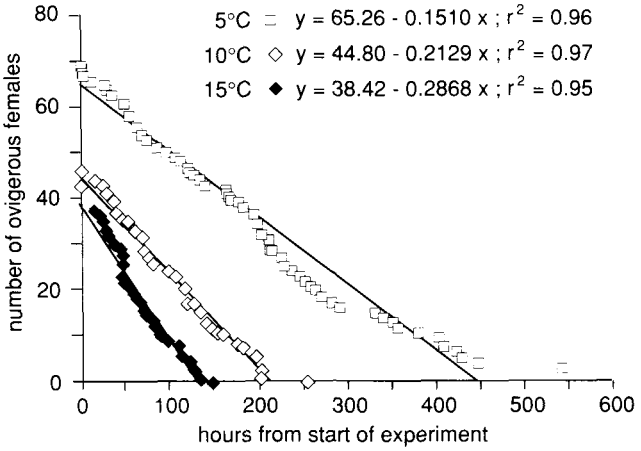

Figure 1. Mean development time of eggs of *Lepeophtheirus salmonis* at various temperatures and ambient salinity. Mean egg development times: at 5°C 419·1 h (17·5 d), at 10°C 207·1 h (8·6 d), at 15°C 130·8 h (5·5 d).

Table 1. *Mean time (SD) in hours to first moult of the second nauplius and copepodid stages of* Lepeophtheirus salmonis, *maintained at three temperatures and ambient salinity (29·0-31·0‰)*

Development stage	Temperature					
	5°C		10°C		15°C	
Nauplius I to Nauplius II	52.0 (4.5)	N=5	30.5 (2.1)	N=12	9.2 (1.8)	N=5
Nauplius I to Copepodid	222.3 (4.4)	N=5	87.4 (5.0)	N=10	44.8 (1.2)	N=5

N=number of cultures that moulted

Table 2. *Cumulative development time (CDT), time of first and last appearance, and duration of each* Lepeophtheirus salmonis *developmental stage at 10°C*

Stage	CDT (d)	First appearance (d)	Last appearance (d)	Duration (d)
Egg	-	-	-	-
N1	8.6	9	-	-
N2	9.9[a]	10	-	-
Copepodid	12.3[a]	12	22	10
Ch1	19.0[b]	19	24	5
Ch2	22.5[b]	22	27	5
Ch3	29.8[b]	23	32	9
Ch4	32.0[b]	29	35	6
Pre1	39.0[b]			
Male		32	40	8
Female		32	43	10
Pre2	47.6[b]			
Male		36	45	9
Female		40	52	12
Adult male	-	40	-	-
Adult female	-	52[c]	-	-

[a] time to first appearance (direct observation). [b] time to when 50% of the population had attained this stage (calculated from least squares regression of arcsin transformed data). [c] last copepods obtained on day 52.

copepodid stage varied from 222·3 h (9·3 d) at 5°C to 44·8 h (1·9 d) at 15°C.

The time to hatch, naupliar development times, and the calculated median development times for the chalimus and preadult stages of *L. salmonis* raised at 10°C are summarized in Table 2 and Figure 2. The two naupliar stages developed quickly compared with the copepodid stage, which required almost 7 d for 50% to moult to the first chalimus stage. The third chalimus and both preadult stages also had protracted stage durations. The first adult males were obtained 40 d after egg extrusion and two adult females were obtained at 52 d after egg extrusion.

There is a large range of variability in developmental rates between individual copepods, with the time between the first and last appearance of the stages far exceeding the initial 12-h difference in ages (Table 2, Figure 2). Although both male and female first preadults first appeared at 32 d after egg extrusion, males reached maturity before females. Both adult males and second preadult females first appeared on day 40. Of the 113 preadults and adults obtained 61% were males and 39% were females.

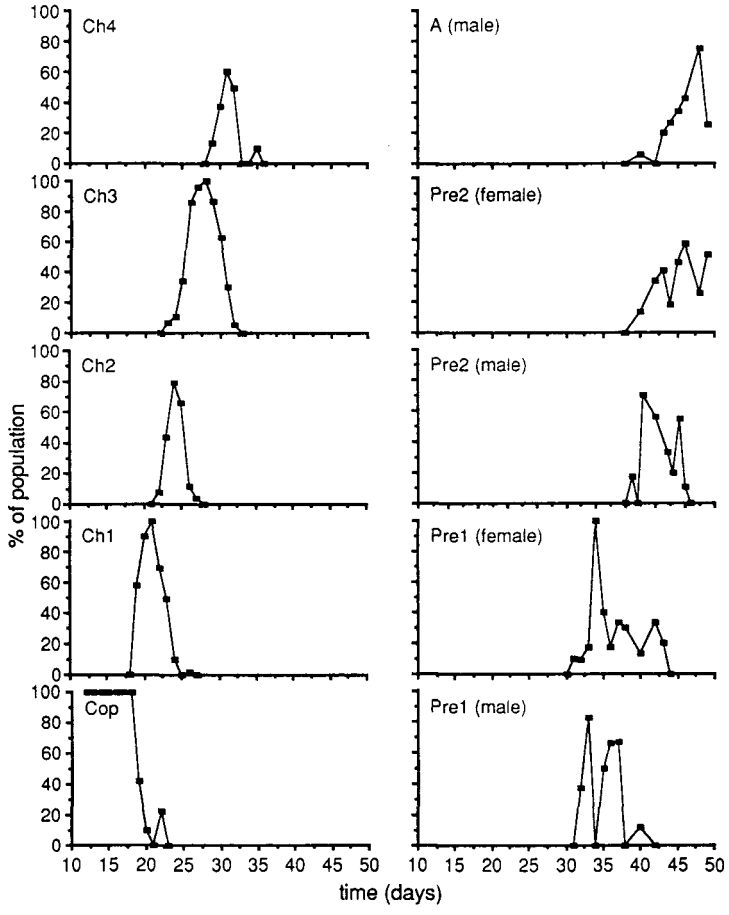

Figure 2. Development sequence of a cohort of *Lepeophtheirus salmonis* at 10°C and ambient salinity (Cop, copepodid; Ch1, first chalimus, Ch2, second chalimus; Ch3, third chalimus; Ch4, fourth chalimus; Pre1, first preadult; Pre2, second preadult, A, adult).

The percentage moult increments (*sensu* Hartnoll, 1982) calculated from the mean sizes demonstrate no consistent trends over development (Figures 3 & 4). There are marked increases in total length and cephalothorax width with the moults to the copepodid and third chalimus stages. With the moult from the second preadult to adult female there is a marked increase in total length and a relatively small increase in cephalothorax width.

In the growth experiments approximately 53% of the copepodid and chalimus larvae were attached to the tips of the gill filaments and 33% to the fins. Of those on the fins the majority were on the pelvic (14%), pectoral (9%), and anal (7%) fins. Larvae attached to the body were most commonly found along the margin of the operculum. Of the preadults collected, 15% had retained their frontal filament. Unattached preadults and adults were found on the body surfaces, but most commonly on the postero-dorsal surface of the head and postero-dorsal to the dorsal fin.

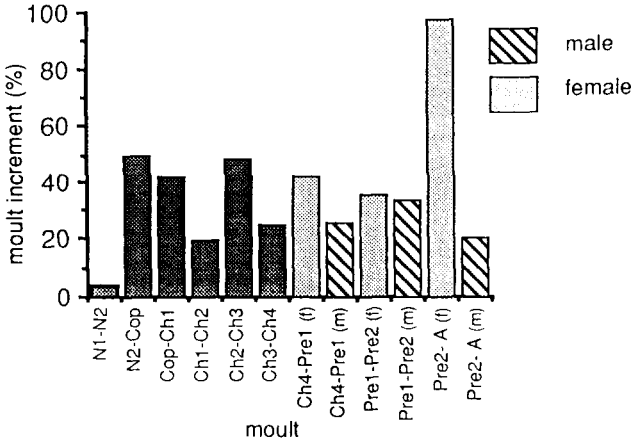

Figure 3. Percentage moult increments of total length for *Lepeophtheirus salmonis* raised at 10°C (N1, first nauplius; N2, second nauplius; other abbreviations as in Figure 2).

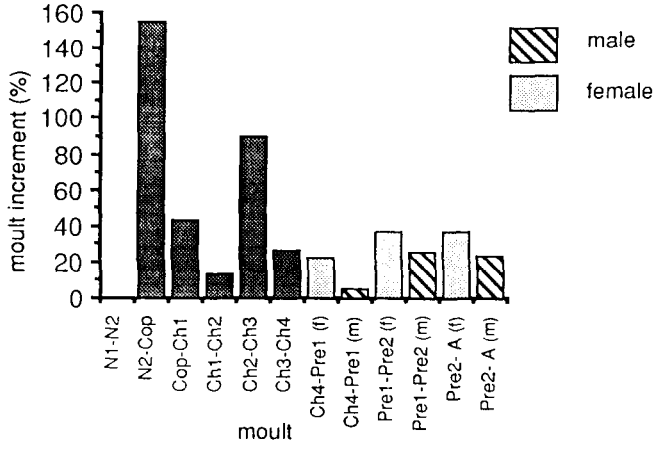

Figure 4. Percentage moult increments of cephalothorax width for *Lepeophtheirus salmonis* raised at 10°C (N1, first nauplius; N2, second nauplius; other abbreviations as in Figure 2).

Egg strings maintained at 10°C and 10‰ in static water failed to develop (Table 3). In static water of 15 and 20‰ salinity, high proportions of the egg strings hatched, but active nauplii were obtained only at 20‰. At 20‰ from 0 to 89·9% (mean=19%) of the eggs developed to the copepodid stage, but only one active copepodid was obtained. At higher salinities 100% of the egg strings hatched and the percentage of eggs that produced active nauplii ranged from 9·7 to 95%. At 25‰ from 0 to 2·9% (mean=0·9%) of the eggs developed to the copepodid stage, but only one active copepodid was obtained.

Table 3. *Hatching success of egg strings of* Lepeophtheirus salmonis, *and the mean percentage of total eggs (TE) that produced active nauplii and copepodids at 10°C and salinities of 10-30‰. Values are the mean and range (in parentheses); sample size=10, except for 25‰ where the sample size=7; nd=no development.*

Salinity (‰)	Hatching Success (%)	Active Nauplii (% TE)		Active Copepodids (% TE)	
10	nd	nd		nd	
15	70	0		0	
20	78	19.8	(0-89.9)	<0.01	(0-<0.01)
25	100	51.1	(12.0-94.1)	<0.01	(0-<0.01)
30 (static)	100	65.9	(9.7-95.0)	35.2	(0-80.6)
30 (flowing)	100	54.6	(5.6-88.4)	26.8	(0-59.5)

At 30‰ the percentage of eggs that produced active copepodids ranged from 0 to 80·6%.

In preliminary experiments at 10°C newly moulted copepodids survived for less than 3 h when transferred to 5‰ salinity water, and less than 1 d when transferred to 10‰ salinity water. At higher salinities (15-30‰) and temperatures of 5, 10, and 15°C survival was prolonged. Maximum survival time was 17 d at 10°C and 25‰ salinity, with average survival times ranging between 2 and 8 d (Figure 5). A comparison of survival times (2-way ANOVA) indicated that temperatures ($P<0·001$) and salinities ($P<0·001$) had significant effects on survival and that there was a significant interactive effect of these two factors ($P<0·001$). (A significant interaction indicates that the direction of difference among salinities varied among temperatures.) The results of multiple range tests (Scheffé's test; $P<0·05$) over each temperature showed survival times to be significantly higher at 30‰ when compared to 15‰ at all temperatures. At 10°C survival time at 25‰

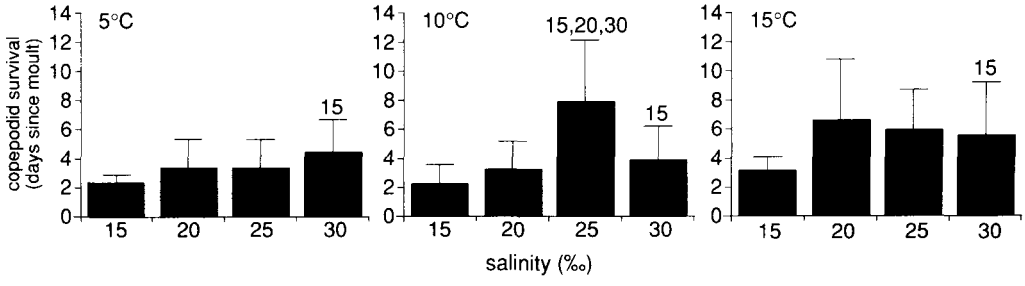

Figure 5. Mean (±SD) survival time of newly moulted copepodids of *Lepeophtheirus salmonis* at various temperatures and salinities. Values above error bars indicate which salinities have statistically significant differences in survival (Scheffé's test; $P<0.05$).

was significantly higher than survival at 15, 20, or 30‰. At all temperatures copepodids at low salinities (15 and 20‰) were generally less active than those maintained at higher salinities (25 and 30‰).

At 9-10°C adult female copepods which were removed from their fish hosts survived for a maximum of 12 d (mean=9·5±2·5; N=5) and 13 d (mean=9·3±2·3; N=10) in static water baths of 10‰ and 15‰ salinity, respectively. At higher salinities survival was prolonged with a maximum survival of 18 d (mean=13·9±3·8; N=16) at 30-31‰.

DISCUSSION

This is the first comprehensive study of development, growth, and survival of *L. salmonis* under controlled laboratory conditions. In this discussion we cite results obtained for the pennellid copepods *Lernaeocera branchialis* and *Lernaeenicus sprattae* and for the lernaeopodid copepod *Salminicola californiensis*. These species represent the only other siphonostome copepods outside the family Caligidae for which development, growth or survival data are available. We have included them to supplement the limited data available for caligid copepods.

Our time to hatch of 8·6 d at 10°C corresponds poorly with previous determinations for *L. salmonis* of 10-14, 25, and 33-39 d at 11·5°, 9·5°, and 9°C, respectively (Johannessen, 1978). At 15°C the time to hatch of 5·5 d corresponds well with the 5·7-6·1 d reported for *Lepeophtheirus kareii* (= *Lepeophtheirus hospitalis*) at 15°C (Lopez, 1976). Other determinations of time to hatch for *Lepeophtheirus* species have been made at higher temperatures. These include: 2·7 d for *Lepeophtheirus hospitalis* at 20°C (Voth, 1972), and 1·3-1·7 d for *Lepeophtheirus dissimulatus* at 23°C (Lewis, 1963). The eggs of *L. salmonis* develop faster than those of pennellid copepods at comparable temperatures. Egg development takes approximately 12·7 d at 10°C for *L. branchialis* (*cf.* Whitfield *et al.*, 1988), and 16 d at 7-9°C for *L. sprattae* (Schram, 1979).

In our experiments the hatching period of the egg strings was highly variable and longer than previously reported. Johannessen (1978) reports that the hatching period of *L. salmonis* egg strings containing 100-500 eggs was less than 40 h, with the majority of the nauplii hatching within 5-10 h. It is difficult to compare the hatching rates of *L. salmonis* with other species of parasitic copepods due to differences in egg number and rearing temperature. Izawa (1969) reports the egg strings of *Caligus spinosus*, which carry between 10 and 20 eggs per string, hatching in 3-8 h at approximately 20°C. The hatching period for a pair of egg strings of *L. branchialis*, commonly containing an average of 1145 eggs per pair, was 12 d at 10°C, although most hatched within the first 3 d (Whitfield *et al.*, 1988). Egg strings of *L. sprattae*, which contain between 50 and 600 eggs, hatch in 4-5 h at 15°C (Schram & Anstensrud, 1985).

In our experiments, the moult to the second nauplius stage took 30·5 h at 10°C and 9·2 h at 15°C. Development to the copepodid stage took 87·4 h at 10°C and 44·8 h at 15°C. These durations correspond well with previous studies on *L. salmonis*: 35 h at 9·2°C, 12 h at 15·5°C (Johannessen, 1978), and 18 h at 12°C (Wootten *et al.*, 1982) for the moult to the second nauplius stage, and 77 h at 9·2°C, 63 h at 11°C (Johannessen, 1978), and 46 h at 12°C (Wootten *et al.*, 1982) for development to the copepodid stage. In *L. hospitalis*, the

moults to the second nauplius and copepodid stages take approximately 24 h and 64 h, respectively, at 15°C (Voth, 1972). In contrast, Lopez (1976) reported development to the copepodid stage to take 120-150 h at 15°C in *L. kareii* (= *L. hospitalis*). Other determinations of naupliar development in *Lepeophtheirus* species have been made at higher temperatures. For *L. hospitalis*, the average duration of the first nauplius stage is 7·5 h (range=6-9 h), and the average duration of the second nauplius stage is 11 h (range=10·5-12 h) at 20°C (Voth, 1972). For *L. dissimulatus*, the average duration of the first nauplius stage is 6·5 h (range=4·5-13 h), and the average duration of the second nauplius stage is 14·5 h (range=9·5-19 h) at approximately 23°C (Lewis, 1963).

Determinations of naupliar development times have been made for several *Caligus* species. Hogans & Trudeau (1989) reported that the duration of the second naupliar stage of *Caligus elongatus* is 35 h at 10°C. Ben Hassine (1983) reports naupliar development times for *Caligus pageti* over a wide range of temperatures (16-26°C). With one exception the duration of both the first and second naupliar stages is reported to be 24 h at each of these temperatures. Based upon our studies at 15°C we feel that the observation period in Ben Hassine's study was too long to determine accurately the naupliar development times, and that development may be faster than reported.

In the pennellid copepod *L. sprattae*, development from the first to the second nauplius stage takes 23-27 h and development from the first nauplius to the copepodid stage 48-51 h at 15°C (Schram & Anstensrud, 1985).

With the exception of *C. elongatus* (*cf.* Hogans & Trudeau, 1989), the duration of the first nauplius stage is shorter than that of the second nauplius stage in all caligid species studied. In both *L. salmonis* and *L. hospitalis* the duration of the copepodid stage is relatively long. Moulting to the first chalimus stage occurred approximately 6-8 d after host contact in *L. hospitalis* at 15°C (Voth, 1972). The duration of the copepodid stage in *L. dissimulatus* is unknown. The relatively long duration of the copepodid stage may be due to the need to recover energy lost during development of the non-feeding naupliar stages, or the requirement of additional time or energy for completion of development prior to filament production and moulting. A similar trend is seen in the free-living copepods where the duration of the pre-feeding naupliar stages is relatively short (possibly due to energetic considerations), and the duration of the first feeding instars relatively long (Landry, 1983).

The earliest adult male was obtained at 32 d and the earliest adult female at 40 d after egg hatching for *L. salmonis* at 10°C. For *L. pectoralis*, Anstensrud (1990) reports development to adult males in 24-27 d and adult females in 29-32 d from eggs hatching at 10-12°C and 30-31‰ salinity. Other studies on *Lepeophtheirus* species have been conducted at higher temperatures. Development from the first chalimus stage to the second preadult stage took 21·5 d at 20°C for *L. hospitalis* (*cf.* Voth, 1972) and 8·5 d at 23°C for *L. dissimulatus* (*cf.* Lewis, 1963).

Development rates have been investigated for several species of *Caligus*. In *C. elongatus*, development from the first chalimus to newly moulted adult takes approximately 3 weeks at 12°C (Hogans & Trudeau, 1989). In *C. pageti* development from first nauplius to second preadult takes 23·5 d at 16-18°C, 16 d at 20-22°C, and 10·5-11·5 d at 24-26°C (Ben Hassine, 1983).

We estimate the generation time of *L. salmonis* to be 7·5-8 weeks at 10°C. Other estimates of the generation time of *L. salmonis* have been made based on field data. Wootten *et al.*, (1982) reported a generation time of approximately 6 weeks at 9-12°C, and Tully (1989) reported generation times between 7 and 13 weeks depending on water temperature and the development stage used for the calculation.

In the caligids *L. salmonis*, *Lepeophtheirus pectoralis*, the pennellid *L. branchialis*, the lernaeopodid *S. californiensis*, and many free living copepods, males mature faster than females (present study; Anstensrud, 1989, 1990; Kabata & Cousens, 1973; Landry, 1983). Adult males of *L. salmonis* commonly establish precopula with first and second preadult females (present study; Wootten *et al.*, 1982). In both *L. salmonis* and *L. pectoralis* copulation occurs upon moult to the adult female and results in the female genital openings being sealed by the spermatophores. It is therefore advantageous for the males of a cohort to mature first and develop reproductive products.

The percent moult increments calculated from the size data for *L. salmonis* do not decrease with increasing size as suggested for a wide variety of Crustacea (reviewed in Hartnoll, 1982). The large increase in total length with the moult to the adult female occurs after the moult when the genital complex undergoes a considerable change in size and shape with the change from the pre-ovigerous to ovigerous condition (Johnson & Albright, in press).

In our experiments the majority of the copepodid and chalimus larvae were collected from the gills. Copepodids and chalimus larvae of *L. salmonis* have not been previously reported from the gills of salmon. Wootten *et al.* (1982) reported that chalimus larvae of *L. salmonis* are most commonly found attached to the dorsal and pelvic fins and the area around the anus, although it is not clear whether the gills were examined. Gills may serve as an important site for initial attachment of copepodids.

Eggs of *L. salmonis* fail to develop in 10‰ salinity water at temperatures of 10 and 12°C (present study; Wootten *et al.*, 1982). Johannessen (1978) reported that most eggs of *L. salmonis* aborted, and that the few nauplii produced only lived for a short time at 11·5‰ salinity and temperatures of 5-12°C. Berger (1970) reported that the nauplii of *L. salmonis* survive for 32 and 48 h when transferred to water with salinities of 8 and 12‰, respectively. All nauplii of the pennellid *L. sprattae* died when transferred to 10‰ salinity water at temperatures between 5 and 25°C (Schram & Anstensrud, 1985). At 15‰ eggs of *L. salmonis* developed and hatched, but produced few active nauplii. Schram & Anstensrud (1985) report that some nauplii of *L. sprattae* moulted to the second nauplius stage, but none survived to the copepodid stage when transferred to water of 15‰ salinity. However, when transferred to salinities of 20-30‰ most nauplii (60-80% of the first nauplii) survived to the copepodid stage. The eggs of *L. salmonis* that developed and hatched at higher salinities (20, 25, and 30‰) produced active nauplii. At 20 and 25‰ the majority of the active nauplii died at the copepodid moult. With the exception of several individuals, active copepodids were obtained only at 30‰ salinity. Additional stresses imposed in the laboratory (*e.g.* handling, less than optimal water quality) may limit survival to the copepodid stage at less optimal salinities. *Lepeophtheirus salmonis*, like *Lernaeenicus sprattae*, may be excluded from low salinity areas (<15‰) due to reduced hatching success and survival of the naupliar and copepodid stages.

In our experiments, average survival of the copepodid stage ranged between 2 and 8 d, depending on temperature and salinity. Similar results were obtained by Wootten *et al.* (1982) who reported that copepodids of *L. salmonis* remained active for 4 d at 12°C. Although Johannessen (1978) reported that one copepodid of *L. salmonis* survived for 30 d it is unlikely that many copepodids are able to survive for this length of time. Voth (1972) reported an average survival time of 4·5 d (range 3-8 d) at 20°C for copepodids of *L. hospitalis*. Whitfield *et al.* (1988) reported a maximum survival time of 18 d and a 50% survival time of 7·5 d at 10°C for copepodids of the pennellid *L. branchialis*. As noted by Whitfield *et al.* (1988) copepodid infectivity is likely to decline substantially over this time.

Adult *L. salmonis* survived on average 9·5 d after removal from their host at 10°C and 10‰ salinity. In contrast, Berger (1970) reported that adult *L. salmonis* survive for less than 12 h at 12‰ salinity and 1 h at 4‰ salinity. Hahnenkamp & Fyhn (1985) demonstrated that *L. salmonis* females were able to maintain a hyperosmotic state at a salinity of 12·4‰, but started to die within 8 h when exposed to fresh water. Our reduced average survival times for adults at low salinities may be due to a higher energy requirement for maintenance of a hyperosmotic state.

We thank Drs Z. Kabata and L. Margolis for critically reviewing this manuscript. This research was funded by a Natural Sciences and Engineering Research Council of Canada Operating Grant to L.J.A., and by the Department of Fisheries and Oceans' Biological Sciences Branch, Pacific Region. S.C.J. was supported by a British Columbia Science Council GREAT scholarship and a Simon Fraser University graduate fellowship.

REFERENCES

Anstensrud, M., 1989. Experimental studies of the reproductive behaviour of the parasitic copepod *Lernaeocera branchialis* (Pennellidae). *Journal of the Marine Biological Association of the United Kingdom*, **69**, 465-476.

Anstensrud, M., 1990. Mating strategies of two parasitic copepods [(*Lernaeocera branchialis* (L.) (Pennellidae) and *Lepeophtheirus pectoralis* (Müller) (Caligidae)] on flounder: polygamy, sex-specific age at maturity and sex ratio. *Journal of Experimental Marine Biology and Ecology*, **136**, 141-158.

Ben Hassine, O.K., 1983. *Les Copépodes Parasites de Poissons Mugilidae en Mediterannée Occidentale (Côtes Françaises et Tunisiennes). Morphologie, Bio-écologie, Cycles Évolutifs.* PhD dissertation, Academie de Montpellier, Université des Sciences et Techniques du Languedoc, Montpellier, France.

Berger, V.Ja., 1970. The effect of marine water of different salinity on *Lepeophtheirus salmonis*, ectoparasite of salmon. *Parazitologiya* (Leningrad), **4**, 136-138.

Box, G.E.P., Hunter, W.G. & Hunter, J.S., 1978. *Statistics for Experimenters. An Introduction to Design, Data Analysis, and Model Building.* New York: John Wiley and Sons.

Brandal, P.O. & Egidius, E., 1979. Treatment of salmon lice (*Lepeophtheirus salmonis* Krøyer, 1838) with Neguvon® - description of method and equipment. *Aquaculture*, **18**, 183-188.

Brandal, P.O., Egidius, E. & Romslo, I., 1976. Host blood: a major food component for the parasitic copepod *Lepeophtheirus salmonis*, Krøyer, 1838 (Crustacea: Caligidae). *Norwegian Journal of Zoology*, **24**, 341-343.

Edmondson, W.T., 1965. Reproductive rate of planktonic rotifers as related to food and temperature in nature. *Ecological Monographs*, **35**, 61-111.

Hahnenkamp, L. & Fyhn, H.J., 1985. The response of salmon louse, *Lepeophtheirus salmonis* (Copepoda: Caligidae), during the transition from sea water to fresh water. *Journal of Comparative Physiology*, **155B**, 357-365.

Hartnoll, R.G., 1982. Growth. In *The Biology of Crustacea*, vol 2. *Embryology, Morphology and Genetics* (ed. L.G. Abele), pp. 111-196. New York: Academic Press.

Hogans, W.E. & Trudeau, D.J., 1989. Preliminary studies on the biology of sea lice, *Caligus elongatus*, *Caligus curtus* and *Lepeophtheirus salmonis* (Copepoda: Caligoida) parasitic on cage-cultured salmonids in the Lower Bay of Fundy. *Canadian Technical Report of Fisheries and Aquatic Sciences*, no. 1715, 14 pp.

Izawa, K., 1969. Life history of *Caligus spinosus* Yamaguti, 1939, obtained from cultured Yellow tail *Seriola quinqueradiata* T & S (Crustacea: Caligoida). *Report of the Faculty of Fisheries, Prefectural University of Mie. Tsu*, **6**, 127-157.

Johannessen, A., 1978. Early stages of *Lepeophtheirus salmonis* (Copepoda, Caligidae). *Sarsia*, **63**, 169-176.

Johnson, S.C. & Albright, L.J., in press. The developmental stages of *Lepeophtheirus salmonis* (Krøyer, 1837) (Copepoda: Caligidae). *Canadian Journal of Zoology*.

Kabata, Z. & Cousens, B., 1973. Life cycle of *Salmincola californiensis* (Dana 1852) (Copepoda: Lernaeopodidae). *Journal of the Fisheries Research Board of Canada*, **30**, 881-903.

Kabata, Z., 1974. Mouth and mode of feeding of Caligidae (Copepoda), parasites of fishes, as determined by light and scanning electron microscopy. *Journal of the Fisheries Research Board of Canada*, **31**, 1583-1588.

Kabata, Z., 1979. *Parasitic Copepoda of British Fishes*. London: The Ray Society.

Kabata, Z., 1988. Copepoda and Branchiura. In *Guide to the Parasites of Fishes of Canada*, Part II. *Crustacea* (ed. L. Margolis and Z. Kabata), *Canadian Special Publication of Fisheries and Aquatic Sciences*, **101**, 3-127.

Landry, M.R., 1983. The development of marine calanoid copepods with comment on the isochronal rule. *Limnology and Oceanography*, **28**, 614-624.

Lewis, A.G., 1963. Life history of the caligid copepod *Lepeophtheirus dissimulatus* Wilson, 1905 (Crustacea: Caligoida). *Pacific Science*, **17**, 195-242.

Lopez, G., 1976. Redescription and ontogeny of *Lepeophtheirus kareii* Yamaguti, 1936 (Copepoda, Caligoida). *Crustaceana*, **31**, 203-207.

Nagasawa, K., 1987. Prevalence and abundance of *Lepeophtheirus salmonis* (Copepoda: Caligidae) on high-seas salmon and trout in the North Pacific Ocean. *Nippon Suisan Gakkaishi* (*Bulletin of the Japanese Society of Scientific Fisheries*), **53**, 2151-2156.

Pike, A.W., 1989. Sea lice - major pathogens of farmed Atlantic salmon. *Parasitology Today*, **5**, 291-297.

Schram, T.A., 1979. The life history of the eye-maggot of the sprat, *Lernaeenicus sprattae* (Sowerby) (Copepoda, Lernaeoceridae). *Sarsia*, **64**, 279-316.

Schram, T.A. & Anstensrud, M., 1985. *Lernaeenicus sprattae* (Sowerby) larvae in the Oslofjord plankton and some laboratory experiment with the nauplius and copepodid (Copepoda, Pennellidae). *Sarsia*, **70**, 127-134.

Threlkeld, S.T., 1979. Estimating cladoceran birth rates: the importance of egg mortality and egg age distribution. *Limnology and Oceanography*, **24**, 601-612.

Tully, O., 1989. The succession of generations and growth of the caligid copepods *Caligus elongatus* and *Lepeophtheirus salmonis* parasitising farmed Atlantic salmon smolts (*Salmo salar* L.). *Journal of the Marine Biological Association of the United Kingdom*, **69**, 279-287.

Voth, D.R., 1972. *Life History of the Caligid Copepod* Lepeophtheirus hospitalis *Fraser, 1920 (Crustacea, Caligoida)*. PhD dissertation, Oregon State University, Corvallis, Oregon, USA.

White, H.C., 1940. 'Sea lice' (*Lepeophtheirus*) and death of salmon. *Journal of the Fisheries Research Board of Canada*, **5**, 172-175.

Whitfield, P.J., Pilcher, M.W., Grant, H.J. & Riley, J., 1988. Experimental studies on the development of *Lernaeocera branchialis* (Copepoda: Pennellidae): population processes from egg production to maturation on the flatfish host. *Hydrobiologia*, **167/168**, 579-586.

Wootten, R., Smith, J.W. & Needham, E.A., 1982. Aspects of the biology of the parasitic copepods *Lepeophtheirus salmonis* and *Caligus elongatus* on farmed salmonids, and their treatment. *Proceedings of the Royal Society of Edinburgh* (B), **81**, 185-197.

Zar, J.H., 1984. *Biostatistical Analysis*. New Jersey: Prentice Hall.

Submitted 24 October 1990. Accepted 8 January 1991.