Infection Dynamics of Sea Lice, *Lepeophtheirus salmonis* (Copepoda:Caligidae) Parasitic on Atlantic Salmon (*Salmo salar*) Cultured in Marine Waters of the Lower Bay of Fundy

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October 1995

Canadian Technical Report of Fisheries and Aquatic Sciences No. 2067

Fisheries and Oceans Pêches et Océans

Canada

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Fisheries and Aquatic Sciences 2067

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This is the two hundred and twentieth Technical Report of
the Biological Station, St. Andrews, N. B.

Cat. No. Fs 97-6/2067 ISSN 0706-6457

Correct citation for this publication:

Hogans, W. E. 1995. Infection dynamics of sea lice, *Lepeophtheirus salmonis* (Copepoda:Caligidae) parasitic on Atlantic salmon (*Salmo salar*) cultured in marine waters of the lower Bay of Fundy. Can. Tech. Rep. Fish. Aquat. Sci. 2067: iv + 10 p.

ABSTRACT

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The infection dynamics of *L. salmonis* on cultured Atlantic salmon in the lower Bay of Fundy were determined by field observations in the fall of 1994 and by field and laboratory studies during the winter months of 1995. Atlantic salmon from nineteen sea cage sites from around the lower Bay of Fundy were examined periodically between August and December 1995 and three sites in Lime Kiln and Back Bays were monitored intensively during the winter months (January, February and March) of 1995. Sea lice became epidemic on salmon in the Lime Kiln and Back Bay areas in October 1994. As many as 317 *L. salmonis* were found on individual fish at the most heavily impacted sites. Infection levels on salmon were initially recorded as two parasites per fish in late September 1994, and increased to an overall intensity (all sites combined) of 85 lice per fish before treatments in late November 1994. Heavy infections caused significant pathology of fish, resulting in direct mortalities and market down-grades for fish with tissue loss. Sea lice infections were treated with Ivermectin (in feed) and hydrogen peroxide baths at several sites. Each compound was efficacious in removing a portion of the existing infections. A combination of both compounds was more effective at reducing infection level than use of either compound exclusively. Salmon from sites examined for *L. salmonis* outside Lime Kiln and Back Bays (sites from Eastport, Campobello, Deer Island, St. Andrews Bay, Beaver Harbour) were found to have low (mean 5.2 parasites per fish) intensities of infection, but prevalence (percent fish infected) was high, with 97% of all fish examined from these sites (combined) infected.

Monitoring of *L. salmonis* populations in Lime Kiln and Back Bays in the winter of 1995 showed an overall increase in the number of sea lice present on salmon in the study area between initial counts in January and final observations in March. Field results showed that market-size fish had the highest levels of infection, followed by fall 1993 introduction and spring 1994 introduction smolts. Smolts introduced in the fall of 1994 had the lowest infection rate. Water temperatures influenced infection rate of salmon by sea lice and *L. salmonis* numbers declined slightly during periods of coldest recorded water temperatures in late February. The intensity of infection of sea lice increased with the advent of warmer temperatures in mid to late March. Re-infection rates of cage-cultured salmon were very low throughout winter and only a few infective stages (copepodids) were found on any fish examined during that period. Those that were found occurred on fish examined at the end of the study in late March. Little or no molting to successive stages by chalimus larvae or pre-adults was exhibited by *L. salmonis* during the study period until mid March. Laboratory studies indicated that nauplii II rarely molted successfully into copepodids below 3°C. Unusually prolonged high water temperatures in fall 1994 and winter 1995 were probably responsible for the fall epidemic and the high residual infection found on cultured salmon at all sites examined through the winter of 1995.

RÉSUMÉ

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Nous avons étudié la dynamique de l'infestation par le pou de poisson *L. salmonis* des saumons atlantiques éléves en mariculture dans la partie inférieure de la baie de Fundy en effectuant des observations sur le terrain à l'automne 1994 et des travaux de terrain et de laboratoire pendant les mois de l'hiver 1995. Les saumons atlantiques de 19 établissements d'élevage en cages marines situées sur le pourtour de la partie inférieure de la baie de Fundy ont été examinés périodiquement entre août et décembre 1994, et trois sites de la baie Lime Kiln et de la baie Back ont été surveillés de près pendant les mois d'hiver (janvier, février et mars) 1995. L'infestation par les poux de poisson est devenue épidémique dans les régions des baies Lime Kiln et Back en octobre 1994. On a compté jusqu'à 317 *L. salmonis* sur un seul saumon aux endroits les plus infestés. Le niveau d'infestation de départ, relevé à la fin

septembre, était de deux parasites par poisson, et il a monté jusqu'à une intensité globale (tous sites confondus) de 85 poux par poisson avant le traitement, qui a commencé à la fin novembre. Les fortes infestations causaient de graves pathologies chez les poissons, ce qui se traduisait par une augmentation directe de la mortalité et par un déclassement commercial des poissons souffrant d'une déperdition de tissu. Les infestations ont été traitées par l'administration d'Ivermectin (dans la mourriture) et par la balnéation au peroxyde d'hydrogène à plusieurs sites. Chacun des composés était partiellement efficace contre l'infestation. La combinaison des deux traitements réduisait plus efficacement l'infestation que l'emploi d'un seul des deux. Les saumons de sites autres que ceux des baies Lime Kiln et Back (Eastport, Campobello, île Deer, baie de St. Andrews, Beaver Harbour) présentaient une infestation plus faible (5,2 parasites par poisson en moyenne) mais une prévalence plus forte de poissons infestés (97% de tous les poissons) pour tous les sites combinés.

La surveillance des populations de *L. salmonis* dans les baies Lime Kiln et Back pendant l'hiver 1995 a montré une hausse globale du nombre de poux de poisson présents sur les saumons entre les premiers dénombrements de janvier et les observations finales du mois de mars. Les études de terrain ont révélé que l'infestation était la plus forte chez les saumons de taille marchande, suivis par les smolts introduits à l'automne 1993 et au printemps 1994. Les smolts introduits à l'automne 1994 présentaient le plus faible taux d'infestation. La température de l'eau avait un effet sur le taux d'infestation des saumons, et l'effectif de *L. salmonis* a baissé légèrement pendant les périodes où l'eau était la plus froide, à la fin de février. L'intensité de l'infestation a augmenté avec la hausse des températures vers le milieu et la fin de mars. Les taux de réinfestation des saumons en cages étaient très faibles tout au long de l'hiver, et on n'a trouvé que quelques stades infestants (copépodites) sur les poissons examinés pendant cette période; les parasites ont été trouvés à la fin de l'étude, c'est-à-dire à la fin de mars. On n'a pratiquement pas observé de mues vers les stades suivants chez les larves chalimus ne chez les pré-adultes de *L. salmonis* pendant la période d'étude, jusqu'à la mi-mars. Les études de laboratoire ont indiqué que les nauplii II réussissent rarement à muer pour se transformer en copépodites à une température inférieure à 3°C. Il est probable que l'allongement inhabituel de la période où la température de l'eau était élevée, pendant l'automne 1994 et l'hiver 1995, ets responsable de l'épidémie de l'automne et de la forte infestation résiduelle observée chez les saumons d'élevage à tous les sites examinés pendent l'hiver 1995.

INTRODUCTION

Sea lice, *Lepeophtheirus salmonis* and *Caligus elongatus*, are known pathogens of farmed Atlantic salmon in the lower Bay of Fundy (Hogans and Trudeau 1989). Since the initiation of salmon farming in the lower Bay of Fundy, sea lice, particularly *C. elongatus*, have been frequently seen on the fish grown in sea cages, but intensities of infections of these parasites have generally been at low levels. Sea lice populations have been monitored at some sites since 1987 and the percentage of fish infected by *L. salmonis* had historically been low and relatively constant (Fig. 1). However, in fall 1994, *L. salmonis* became epidemic on salmon in the Lime Kiln and Back Bay areas of southwestern New Brunswick (Fig. 1). Beginning in late August 1994, *L. salmonis* began to be noticed in small numbers on the farmed salmon in these areas. Within 40 d, the majority of cage sites had salmon with infection levels sufficient to cause direct mortalities of fish or impacted the fish pathologically to a degree which resulted in large scale downgrades during marketing. Hydrogen peroxide and Ivermectin treatments were utilized extensively in late November and throughout December 1994 to limit the impact of infections. Hydrogen peroxide, in particular, was successful in removing a large portion of the pre-adult and mature lice from heavily infected fish in those cages treated with the compound.

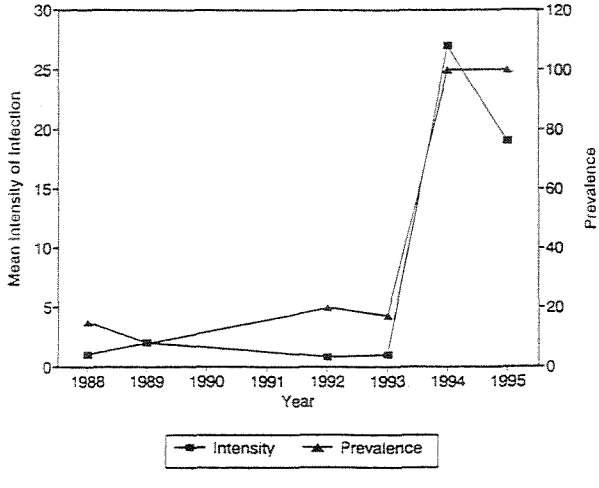

Fig. 1. Annual infection rate of *L. salmonis* on cultured Atlantic salmon in the lower Bay of Fundy from 1988-95.

With the advent of colder water temperatures in late December, the pathology of the sea lice infections was significantly reduced. However, the infection rate remained at high levels, even on fish which had been treated with either Ivermectin or hydrogen peroxide or a combination of both. Considering the large base population of lice which remained on salmon in the study area at the beginning of January 1995, it was considered necessary to intensively monitor the population dynamics of *L. salmonis* during the winter months (January, February, March) of 1995 to determine the progression of sea lice infections. The results of monitoring sea lice infections on salmon in the lower Bay of Fundy during 1994 and 1995 are presented herein.

MATERIALS and METHODS

FALL 1994 STUDY

The fall 1994 study consisted of examination of cultured salmon at various sites. Generally the sites were not chosen beforehand, but were visited, at least initially, because salmon farmers requested a visit by the author to assess a "lice problem." Most of these sites were re-visited at least once every other month after the initial examinations. Visits were made to three sites in Lime Kiln Bay, three sites in Back Bay, three sites in St. Andrews Bay, one site in Beaver Harbour, five sites around Deer Island, one site near Campobello Island and six sites in the Eastport, Maine area (Fig. 2).

Counts of sea lice were made by removing five fish per cage by dipnet and recording number of visible *L. salmonis* on each. The size of the lice dictated that visible lice consisted of mature adults, pre-adults and chalimus III and IV larva. Smaller chalimus stages and newly attached copepodids were difficult to discern and accurately enumerate with the unaided eye and were not counted. Mature lice were categorized as male, non-gravid female and gravid female. At each site, lice were counted on three types of smolts (those introduced in fall 1993, spring 1994 and fall 1994) and market size fish.

WINTER 1995 STUDY

The winter survey consisted of field monitoring of cage sites in the study area and comparative laboratory experiments. Field observations were made at three sites: two in Lime Kiln Bay (Aqua Fish Farms and the Salmonid

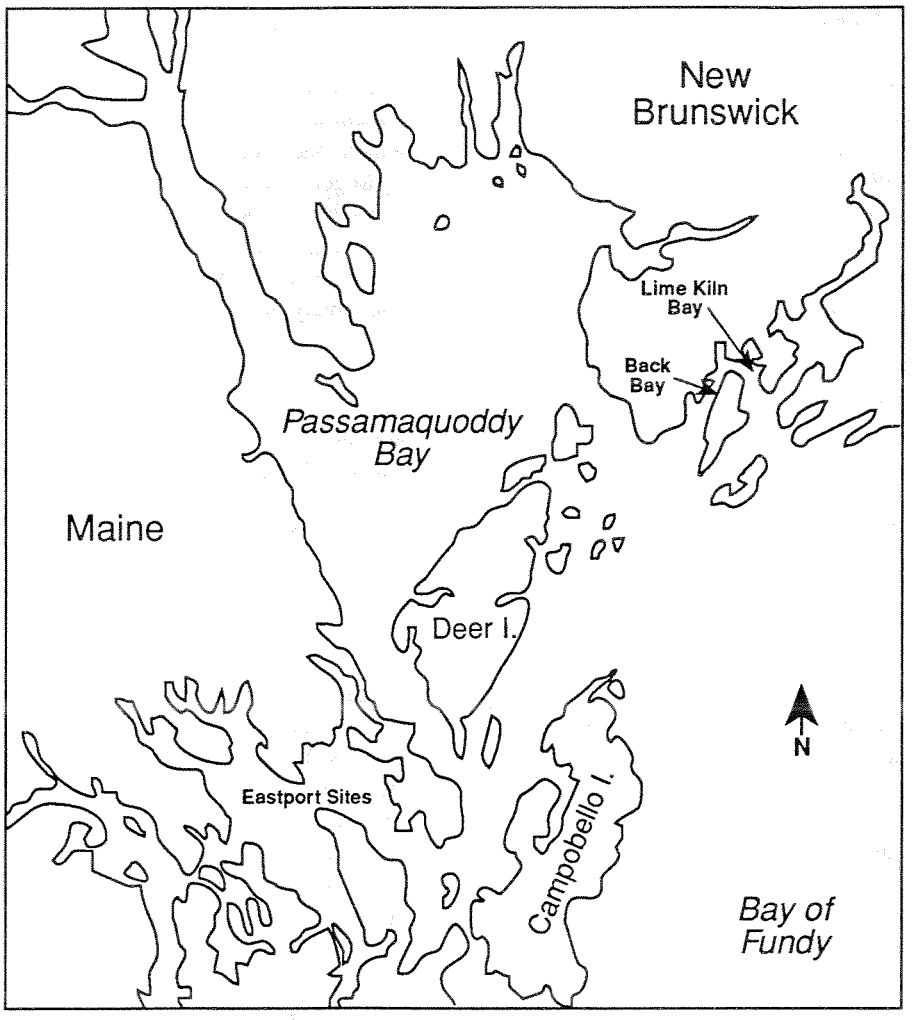

Fig. 2. Map of the survey area showing locations of cage sites where salmon were examined for sea lice in 1994-95.

Demonstration Farm) and one site in the Narrows of Back Bay (Fig. 2). Once each week starting on 19 January 1995, five salmon were removed from each of four cages at each site, lightly anesthetized with MS 222 (tricaine methanosulfate), examined for lice and returned to the water. Sea lice were counted on smolts introduced in fall 1993, spring 1994, fall 1994 and on market size salmon. Cage selection was based on size class of fish and previous treatment history. An additional five smolts were removed once each week from a pre-selected cage at the Aqua Fish site, killed and returned to the laboratory. These fish were examined microscopically for the presence of small chalimus larva and copepodid stages which were difficult to detect with the naked eye and were not recorded during the scheduled field examinations. During each weekly visit, water temperatures were recorded at each site.

Laboratory trials consisted of the following: to assess variability of field results, daily counts of sea lice on salmon held in a large aquarium were recorded. Five spring 1994 smolts were infected with sea lice adults and pre-adults and placed in a 350-L glass aquarium and held in ambient temperature Bay of Fundy marine waters (flow-through system) for the duration of the study. To determine the effects of winter marine water temperatures on the reproductive capacity and molting success of larval *L. salmonis*, several *in vitro* laboratory experiments were completed. The first consisted of placing several gravid females in separate beakers. Seawater in these containers was changed 5-8 times per day to maintain water temperatures at or near temperature levels characteristic of the cage sites. Twice each day the number of nauplii hatching from the known number of egg strings in each beaker was recorded. Counts of the number of nauplii II and/or copepodids which had

molted on successive days were also made daily. Survival rates of naupliar and copepodid stages which were present in the beakers were recorded twice each day. Egg production was determined from counts of eggs in single egg strings of similar lengths. The numbers of egg strings and the lengths of each produced by individual adult females were documented daily in separate experiments. To observe the survival rate of adult sea lice away from the fish host we collected several dozen gravid females from cage-cultured salmon in Lime Kiln Bay and held these in 5-L, aerated beakers. Percent mortality of the introduced parasites was determined and recorded each day. Detailed water temperatures in all experiments were made with a digital thermometer and recorded twice each day at 9:00 am and 3:00 pm.

RESULTS AND DISCUSSION

FALL 1994 STUDY

Examination of Sites in Lime Kiln and Back Bays

Sea cage sites from these areas were characterized by salmon which averaged only 2-3 *L. salmonis* per fish during August and September. During periods of increasing and peak water temperatures (mid-September through late October), the number of lice on fish in the Bays increased significantly. By late October, the intensity of infection on salmon from six sites averaged 84 parasites per fish. Untreated market-size salmon had the highest intensities of infection (Fig. 3) with a

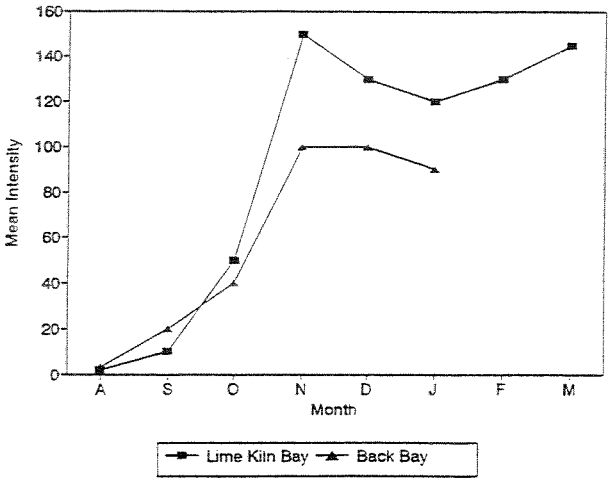

Fig. 3. Infection rate of *L. salmonis* on untreated market-size salmon in Lime Kiln and Back Bays in 1994-95.

mean infection load of 117 lice per fish. Fall 1993 and spring 1994 smolts had similar infection levels, but less than market fish, and averaged 69 parasites per fish. Fall 1994 smolts were introduced relatively late in the epidemic (late October-early November) and acquired only a few parasites, an average of six per fish, by mid-December.

Because of heavy infection levels, many thousands of salmon suffered direct mortalities or extensive tissue damage. In the worst cases of pathology, the cranial bones of the skull were exposed through gross tissue loss. Salmon affected in this fashion rarely survived. Market fish, because of the high intensities of infection, suffered more mortalities than smolts. However, smolts in many cages showed head damage. On badly impacted sites, nearly every spring 1994 smolt in certain cages had some head tissue damage which was evident even when the fish were viewed from above the waters' surface.

As a result of the infections and tissue damage, treatments with Ivermectin (standard dosage 0.5 $mg \cdot kg^{-1}$ fish body weight) and hydrogen peroxide (target treatment concentration of 1800-2000 ppm) were performed at several sites in November and December of 1994. The efficacy of the treatments was generally good and, had it not been for the applications of these compounds, many more thousands of salmon would have perished before water temperatures began to decline significantly in mid-December.

Ivermectin was used only on smolts and removed an average of 35-50% of the pre-adults and mature lice. Its efficacy in causing mortalities of chalimus larva was not observed. These are attached by a frontal filament and are generally unharmed by many of the compounds currently in use for sea lice control (Tully 1989). Hydrogen peroxide was more efficacious than Ivermectin, removing between 60-90% of pre-adults and mature lice from treated fish. Hydrogen peroxide did not appear, from preliminary observations, to cause any mortalities of chalimus larvae.

Because Ivermectin removed only about one-half of the infection load on treated fish, additional peroxide treatments were sometimes required. Salmon treated with a combination of these two compounds had fewer lice at the ends of treatment than fish which had been treated with either compound exclusively. A comparison of pre- and post-infection

levels of spring 1994 smolts from three cages at the Aqua Fish site, based on treatment method, is as follows:

Treatment method	Pre-treatment intensity	Post-treatment intensity
Ivermectin	76.2	29.7
Peroxide	59.7	13.9
Combination	74.5	7.70

The progression of infection of smolts from seven cages in Lime Kiln and Back Bays through the fall-winter 1994-95 and the efficacy of two treatments of three of these cages is shown in Fig. 4. This figure represents data collected at cages where treatments were considered to have had the most favourable results. The combined treatment of Ivermectin and peroxide reduced the intensity of infection from approximately 80 to 4 parasites per fish.

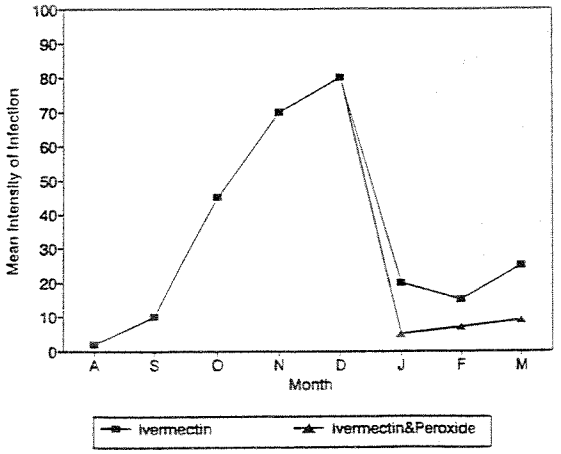

Fig. 4. Efficacy of hydrogen peroxide and combined treatments of Ivermectin and hydrogen peroxide against *L. salmonis* on spring 1994 salmon smolts in Lime Kiln and Back Bays in fall 1994.

Infection of Salmon Outside the Epidemic Areas

Infection rates of *L. salmonis* on salmon outside Lime Kiln and Back Bays were recorded at several sites between November 1994 and March 1995. Figures 5 and 6 show the infection levels of mature and pre-adult lice present on smolt and market size salmon, respectively, at sites from six areas. The overall intensity of infection at all of these sites was generally low, although the prevalence (97%) was such that nearly every fish examined was infected

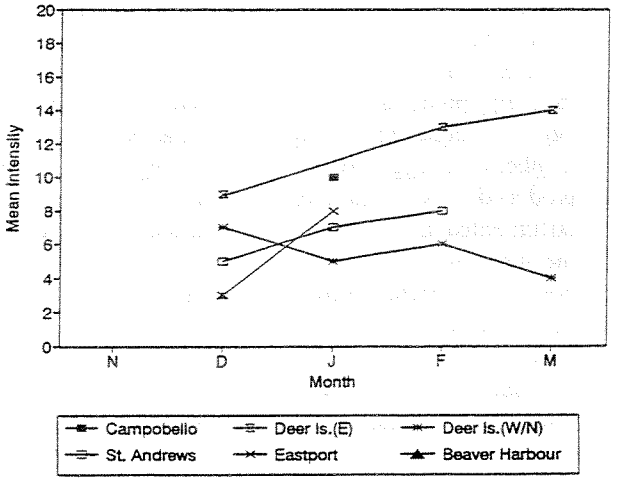

Fig. 5. Infection rate of *L. salmonis* on market-size salmon from cage sites outside of the epidemic areas of Lime Kiln and Back Bays in 1994-95.

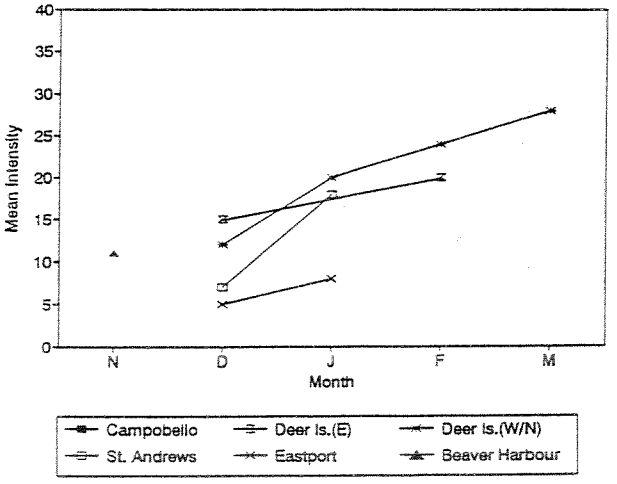

Fig. 6. Abundance of *L. salmonis* on smolts from cage sites outside of the epidemic areas of Lime Kiln and Back Bays in 1994-95.

with some *L. salmonis*. As was characteristic of sites in Lime Kiln and Back Bays, market-size fish from the outside areas had the highest numbers of *L. salmonis* and smolts were less heavily parasitized. The area with the highest intensity of infection was the East side of Deer Island (9.1 parasites per fish at both sites combined). The sites around Eastport, Maine had salmon with the lowest recorded prevalence (82.9%) and intensity of infection (2.9 parasites per fish) of any area examined.

WINTER 1995 STUDY

Prevalence and Intensity of *L. salmonis* in the Study Area

To determine abundance of sea lice in the study area, counts were made of as many kinds (year-classes) of salmon as possible, and we also attempted to examine both treated and untreated fish. However, only a very few cages of untreated salmon were present in the study area and these were market salmon which were continually being removed from the cages for sale. The only cage with untreated salmon examined (in a 70-m Polar Cerkel-type cage at the Aqua Fish site) were marketed during the first month of the study. Consequently, our results on abundance of sea lice in the study area are based predominately on fish which had been previously treated with Ivermectin, hydrogen peroxide or a combination of both.

The number of lice counted on market fish in the untreated cage was much higher than on any fish which had been treated. Before these untreated fish were marketed the number of *L. salmonis* ranged from 87-165 pre-adults and adults (combined) per fish. All of the untreated fish also had chalimus loads of at least 50-100 attached larvae each. The only reason that these fish were able to survive this very heavy infection was that water temperatures began to drop significantly at about the same time lice abundance was greatest in early December 1995. The colder temperatures possibly reduced the metabolic rate of the lice and curtailed their feeding rate, reducing the overall pathological impact of the infection.

The number of pre-adults and mature lice on salmon from all sites examined was higher at the end of the monitoring period than was found initially in late January. As a result, there was an overall increase in abundance of sea lice in the study area during the survey. Additionally, the proportion of gravid to non-gravid females was also higher at the end of the study than at the beginning. The production of egg strings by mature females was relatively constant until the end of March, when a significant increase was noted, particularly at the Lime Kiln Bay sites. At all three sites examined, the average number of lice per fish at the end of the study (26) was considered as a moderate to heavy infection load.

Winter Water Temperature Effect on Sea Lice Abundance

The numbers of pre-adult sea lice on fish at all sites did not change significantly on salmon throughout the study period until the middle of March, when numbers of this stage of parasite began to increase. Numbers of adult females from fish at all the sites changed considerably between months, and there was a positive relationship between water temperature and an increase in intensity of infection ($r^2 = 0.71$). As water temperatures fell through late January and early February, the abundance of *L. salmonis* adults decreased within the study area. Temperatures were lowest in mid-February (lowest reported 0.8°C) and the lowest number of both mature stages (including gravid females) and pre-adults were recorded during this period. As water temperatures began to rise at the end of February through early March, the numbers of visible lice on salmon increased.

As noted above, the number of lice with egg strings increased significantly towards the end of the study. There was a relationship between this increase and the late winter rise in water temperature ($r^2 = 0.69$). There was also a positive relationship between rate of infection by copepodids and increasing water temperature. This relationship was highly correlated ($r^2 = 0.82$).

Relationship Between Fish Size and Sea Lice Abundance

As was evident before treatments in fall 1994, market fish had greater numbers of lice than spring or fall 1994 smolts. Figure 7 shows the progression of infection on market fish from the three study sites. The numbers of lice on market fish were relatively similar between the initiation and end of monitoring at Aqua Fish and the Narrows site and would probably have been at the Demonstration farm as well, had it not been for a hydrogen peroxide treatment completed during late January, which removed about 35-40% of the visible lice on one cage of market-size salmon. On spring 1994 smolts the numbers of both pre-adults and adults (Fig. 8) remained consistent for most of the study period and only increased at the end of the survey. At the Narrows site, the number of lice on 1994 spring smolts increased significantly on those treated with Ivermectin (only) during the January-March period, with the greatest increase in lice numbers seen in

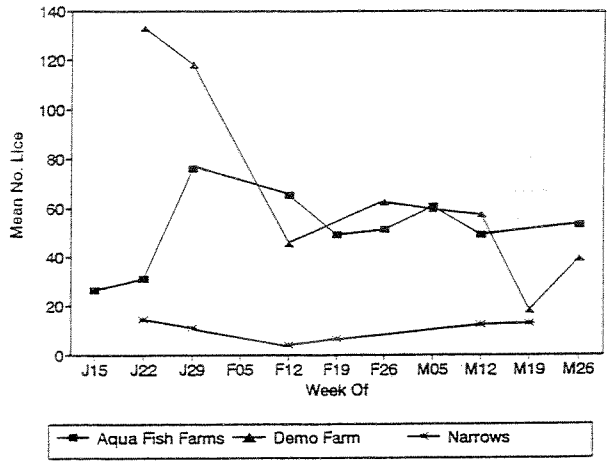

Fig. 7. Infection rate of *L. salmonis* on market fish, by site, in Lime Kiln and Back Bays in winter 1995.

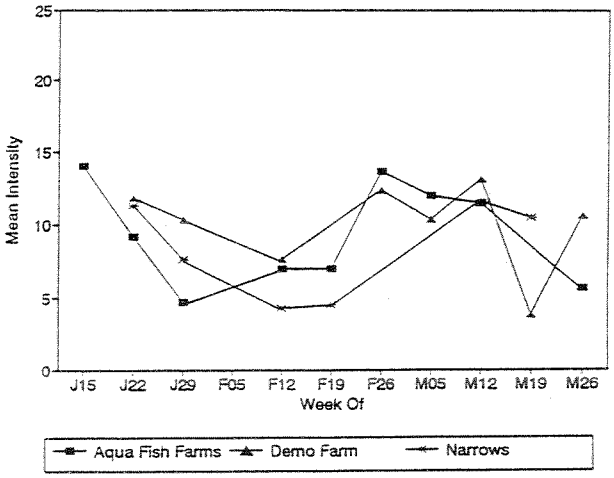

Fig. 8. Infection rate of *L. salmonis* on spring 1994 smolts, by site, in Lime Kiln and Back Bays in winter 1995.

mid to late March. Fall 1994 smolts at the Aqua Fish site in Lime Kiln Bay generally had a low level of infection (intensity 3.3 parasites per fish) throughout the winter. Mature lice were never found on these fish, all of the sea lice observed were pre-adults, chalimus and a few copepodids (found on fish in late March). As was evident on the larger year-class salmon, the number of sea lice on fall smolts was greater at the end of the study than at the beginning.

Developmental Stages of Sea Lice on Salmon in the Study Area

The majority of lice on market fish were mature. Pre-adults constituted only about 40% of the lice load. The reverse was true for spring smolts, on which mature lice generally constituted only about 10% of the infection level. The Aqua Fish farm smolts had the highest numbers of pre-adults of any farm examined, although the numbers were only slightly higher than at the Demonstration farm site.

There was little infection of salmon with copepodid larvae at the field study sites until late in March. Chalimus larvae (I-IV) were found on fishes from all sites throughout the study, but recently attached copepodids were only found once between the beginning of the monitoring program in January and the end of February. Once water temperatures began to rise in early March the proportion of infective copepodids to total lice load on fish (returned to the lab for microscopic examination) began to increase (see Table 1).

Whereas we found only two copepodids on killed and collected fish in January-February during the periods of coldest water temperatures, as many as 6 copepodids were found on some individual collected fish in mid to late March when water temperatures were at the highest recorded winter values. In the sea cages, production of infective copepodid stages appeared to be limited or non-existent at water temperatures below about 3°C. This result was corroborated by the laboratory experiments (see below). Chalimus larvae which were present on both fish returned to the water after examination and on those killed for the lab did not or molted very slowly through to successive stages during the winter periods when water temperatures averaged below about 2.5°C. The occurrence of greater numbers of visible lice (late stage chalimus, pre-adults and recently metamorphosed adults) in mid to late March, than had been recorded in January-February, indicated that temperatures had reached levels sufficient to allow for successful moltings of some developmental stages of *L. salmonis*.

Table 1. Proportion (percentage of total sample) of developmental stages of *L. salmonis* on spring and fall smolts from Lime Kiln Bay, winter 1995.

Time	Stage									
	Gravid female	Female	Male	Pre AII	Pre AI	Chal IV	Chal III	Chal II	Chal I	Cop
Jan 15-31	8.5	11.0	11.5	52.5	13.0	2.0	1.5	0.0	0.0	0.0
Feb 1-14	6.0	17.0	16.0	38.0	18.0	2.5	0.0	1.0	0.0	1.5
Feb 15-28	4.0	9.5	18.5	56.0	12.0	0.0	0.0	0.0	0.0	0.0
Mar 1-15	9.5	8.0	18.0	42.0	14.5	3.5	2.5	0.0	0.0	2.0
Mar 16-28	19.0	6.0	12.0	36.0	16.0	3.5	1.0	0.0	0.0	6.5

Pre AII= pre adult II; Pre AI= pre adult I; chal= chalimus; cop= copepodid.

Treatment Efficacy and its Effect on Sea Lice Abundance

Salmon in the study area were treated in the fall of 1994 with Ivermectin (*in vivo*), hydrogen peroxide or with a combination of these two compounds. Due to the long withdraw period (6 mo) requirement for Ivermectin-treated salmon, market fish were treated only with hydrogen peroxide. Market salmon before treatment in November-December 1995 in the study area had an average infection level of about 80-120 parasites per fish (pre-adults and mature lice combined). After treatments market fish averaged 20-35 parasites per fish. During the winter survey the number of lice on market fish which had been hydrogen peroxide-treated changed considerably over time, but was highest at the end of the study period. Smolts introduced in the spring of 1994 were generally treated with a combination of Ivermectin and hydrogen peroxide, the bath treatment usually applied when the numbers of lice were not sufficiently reduced by the initial Ivermectin treatment. The number of mature stages on spring smolts (all sites combined) which were treated with Ivermectin only (Fig. 9) was slightly higher at the end of the survey than at the start in mid-January. The abundance of pre-adults on these same fish was

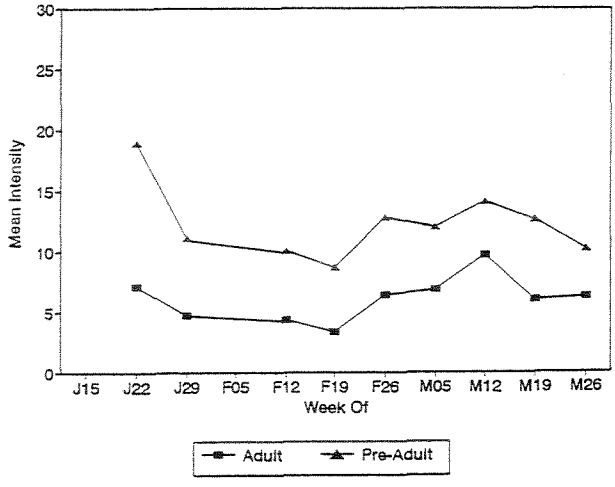

Fig. 9. Infection rate of *L. salmonis* on 1994 spring smolts treated in fall 1994 with Invermectin in Lime Kiln and Back Bays in winter 1995.

slightly less at the end of March than in January. Spring smolts from all sites which were treated with peroxide only (Fig. 10) had slightly more mature lice in late March than was recorded when observations began. The number of pre-adults however was much greater on these treated fish at the end of the winter

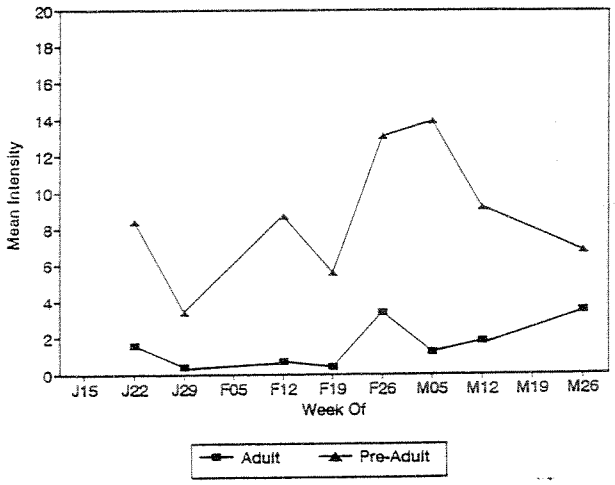

Fig. 10. Infection rate of *L. salmonis* on 1994 spring smolts treated in fall 1994 with hydrogen peroxide in Lime Kiln and Back Bays in winter 1995.

period. Two aspects of treatment were evident from these results: 1) Ivermectin was more efficacious against pre-adults than hydrogen peroxide and 2) hydrogen peroxide removed a greater proportion of adult stages than Ivermectin. A combination of both treatments on spring smolts was more effective than single uses of the compounds in reducing infections of sea lice and for maintaining these levels at constant rates through the winter (Fig. 11). The smolts which had been treated with a combination of Ivermectin and hydrogen peroxide had fewer lice initially than those treated exclusively with each, both at the beginning of the study and at the end.

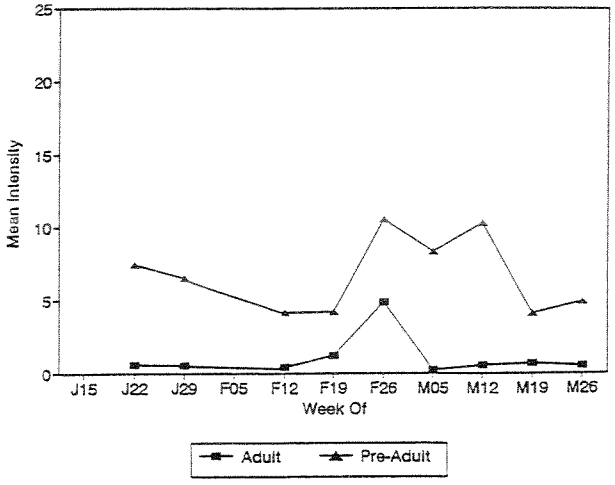

Fig. 11. Infection rate of *L. salmonis* on 1994 spring smolts treated in fall 1994 with a combination of Ivermectin and hydrogen peroxide in Lime Kiln and Back Bays in winter 1995.

Fall 1994 smolts at the Aqua Fish site which were examined regularly had been treated only with peroxide (early December 1994). They had been in the water about 5 wk before the treatment and had acquired a peak infection level of about 10-12 lice per fish of which only 1-4 were adult females. Consequently, most of these large parasites were dislodged, but a lesser proportion of the pre-adults which made up the greater part of the pre-treatment infection load were removed. There were no fall smolts on any of the sites which had been treated with compounds other than hydrogen peroxide which were available for examination.

LABORATORY EXPERIMENTS

Reproductive Success of *L. salmonis* in winter 1995

Gravid female *L. salmonis* produced eggs throughout the period of laboratory observations, regardless of water temperature values. We observed newly hatched nauplii I during periods of the coldest recorded water temperatures (0.8°C). Egg production was actually greatest at the lowest recorded water temperatures. Average number of eggs produced per temperature (based on counts of eggs in 10 single egg strings of identical length) was as follows:

Temperature (°C)	Mean number eggs per string
1.0	232
2.0	187
2.5	179
3.0	148

A relationship between a decline in water temperature and an increase in the length of egg strings on individual females was also observed. This result is corroborated by European studies on *L. salmonis* where egg numbers and egg string length increased during winter with the advent of cold temperatures (Ritchie et. al. 1993).

Water Temperature and its Effect on Molting Success and Rate

Several experiments were completed to determine development time of the various larval stages. We held nauplii I and II for extended periods at ambient temperatures. We did several individual

experiments to determine the success of molting and water temperature to determine the duration of each stage. Duration of each stage was as follows:

Stage	Water temperature (°C)	Duration (mean h)
NI	1.0	220
	2.0	125
	3.5	80
N2	1.0	289
	2.0	190
	3.5	112

The duration of the first nauplius was shorter than that of the second at all three temperatures. This result was similar to that recorded for naupliar development of *L. salmonis* by Johnson and Albright (1991). The duration of the entire naupliar stage is very slow at winter water temperatures in the lower Bay of Fundy. Additionally, there was limited molting success of nauplii at these temperatures. The percent molting success of nauplii to the second stage increased with a rise in water temperature, but was generally very low throughout the winter. At 2°C only 8-15% of the first nauplii successfully molted to second stage and only 4% of these survived for longer than 3 d after molting.

Copepodids, the infective free-swimming stage, were found only rarely in the field during the winter and were inhibited from developing by cold temperatures. In the laboratory, very few nauplii II successfully molted into copepodids at temperatures of 2-3°C, and none molted successfully below 2°C. Even at 3.5°C, the percentage of nauplii II which were able to molt into copepodids was only 2-8% of the total larvae observed. At 4°C, the molt rate increased substantially to 12% of observed larvae. The number of copepodids which survived after the initial molt was lowest at 1°C (2.5%) and increased to only 7% at 3.5-4°C.

Considering the data on reproductive rate and molting success, *L. salmonis* development was limited during the winter of 1995. Infection with copepodids in the wild was limited or did not occur at all until sometime in mid- to late March. At this time, temperatures reached levels sufficient to allow successful molting of second nauplii to copepodids. However, even successful molting did not ensure a high rate of infection, as the number of copepodids that survived to attach to salmon was probably also very low during late March.

Rate of Development of Chalimus Larva and Pre-adults

Based on the observations of aquaria-held salmon, there was limited growth and/or molting of chalimus and pre-adults during the winter. Daily counts of chalimus larva in the tanks confirmed that molting to successive stages was curtailed completely from January through mid-March by cold water temperatures. Chalimus III, IV and first and second stage pre-adults on fish in the tank remained dormant for the entire study, showing no discernable increase in size or molting to next larval stage. However, during the last 3 wk of March the growth of pre-adults did increase significantly and was evident in daily counts. The proportion of second pre-adults to total infection level on aquaria salmon was greater on the last day of observations (28 March) than on 6 March 1995. There were also more first pre-adults in evidence at the end of March on aquaria-held smolts than were seen on these fish in the first week of March 1995.

Infection Rate of *L. salmonis* on Aquaria-held Salmon

The salmon held for daily observations showed a very constant rate of infection with *L. salmonis* throughout the study period. The fish were infected in mid-December 1994 after being placed in the aquaria, and few lice were lost after initial infection on any of the five smolts. There was no significant difference between the number of pre-adults and mature lice recorded during initial counts on 22 January and at the end of the study period. The number of lice with egg strings did, however, rise by approximately 18% during the last month of observations, indicating that lice possibly produce more egg strings at higher water temperatures. This phenomenon was also seen during field observations (see above: section on water temperature and sea lice abundance, results of field studies). Re-infection of aquaria-held salmon by copepodids was limited during the study. We saw no early chalimus larva on any of the fish during the entire study. This can be attributed to: 1) the low production of copepodids and lack of molting success at the low water temperatures recorded, and 2) to the flow-through environment of the aquaria which did not allow long-term exposure of the fish to infective stages present in the tank.