Distribution of gill parasite (*Lernaeocera branchialis*) infection in Northwest Atlantic cod (*Gadus morhua*) and parasite-induced host mortality: inferences from tagging data

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Abstract: We describe geographic and host size related trends in the prevalence of the gill parasite *Lernaeocera branchialis* (Copepoda, Pennellidae) infecting Atlantic cod (*Gadus morhua*) in coastal Newfoundland and Labrador and assess the effect of parasitism on cod survival in the wild. Using cod-tagging studies conducted between 1962 and 1989, we test three null hypotheses: (1) parasite prevalence in the Northwest Atlantic is latitudinally invariant, (2) infected cod have the same survival probability as parasite-free cod, and (3) parasite prevalence is independent of fish length. The first hypothesis is rejected given a significantly negative relationship between prevalence and latitude. The second hypothesis is rejected in one geographic region where 8% fewer infected cod from northeast Newfoundland were recaptured relative to uninfected cod. This implies that parasitized cod can suffer an 8% differentially higher mortality relative to nonparasitized cod. The third hypothesis is rejected because the proportion of cod infected was generally greatest in the 43–49 cm length-class and decreased significantly with increasing length. Differential survival between infected and uninfected cod within length-classes was not observed. The use of *L. branchialis* as a population marker warrants caution. The parasite has the potential to affect the recovery of depleted Northwest Atlantic cod stocks in a geographically differential manner.

Résumé : Nous décrivons les tendances dues à des facteurs géographiques et à la taille de l'hôte qui caractérisent la prévalence du parasite des branchies *Lernaeocera branchialis* (Copepoda, Pennellidae), qui infecte la morue franche (*Gadus morhua*) de la côte de Terre-Neuve et du Labrador, et nous évaluons l'effet du parasitisme sur la survie de la morue en milieu naturel. Nous avons utilisé les résultats d'études d'étiquetage réalisées de 1962 à 1989 pour vérifier trois hypothèses nulles : 1) la prévalence du parasite dans l'Atlantique nord-ouest ne varie pas en fonction de la latitude, 2) la probabilité de survie de la morue parasitée est la même que celle de la morue non parasitéeet 3) la prévalence du parasite est indépendante de la longueur des poissons. Nous avons rejeté la première de ces trois hypothèses car nous avons mis en évidence une relation négative significative entre la prévalence du parasite et la latitude. Quant à la deuxième hypothèse, nous l'avons rejetée pour une région géographique où les morues du nord-est de Terre-Neuve recapturées qui étaient parasitées étaient 8 % moins nombreuses que les morues non parasitées : ce chiffre signifie que la mortalité des morues parasitées peut être de 8 % supérieure à celle des morues non parasitées. Enfin, la troisième hypothèse a été rejetée parce que la proportion de morues parasitées était généralement plus forte dans la classe de longueur de 43–49 cm et décroissait dans une mesure significative plus la longueur augmentait. Aucune différence de survie n'a été mise en évidence entre les morues parasitées et non parasitées d'une même classe de longueur. Il faut être prudent lorsqu'on utilise *L. branchialis* comme marqueur de population. Ce parasite peut influer sur le rétablissement des stocks de morue franche de l'Atlantique nord-ouest d'une manière différente selon la situation géographique.
[Traduit par la Rédaction]

Introduction

Knowledge of parasite–host relationships in fish stocks is of practical importance for at least two reasons: (*i*) parasites are used as markers for stock discrimination and as inferential descriptors of migration patterns (Sindermann 1961; Platt 1976; Templeman et al. 1976; MacKenzie 1983; Jones 1991) and (*ii*) parasites generally have deleterious effects on their hosts and can thus influence host survival and abundance. *Lernaeocera branchialis* (Copepoda, Pennellidae), a hematophagous gill parasite infecting Atlantic cod (*Gadus morhua*) and other gadoid stocks throughout the North Atlantic Ocean, has been used as a stock marker, but its influence on cod survival in natural conditions in the Northwest Atlantic has not been quantified.

Parasites can be used as biological markers if infection is not exchanged among host populations. If the frequency of parasite occurrence is treated as a characteristic of host populations from separate areas, it can be used to estimate the degree of intermixing (Sindermann 1961). Hence, a major criterion for assessing a parasite's utility as a population marker is that it exhibit spatial variation in prevalence, i.e., being

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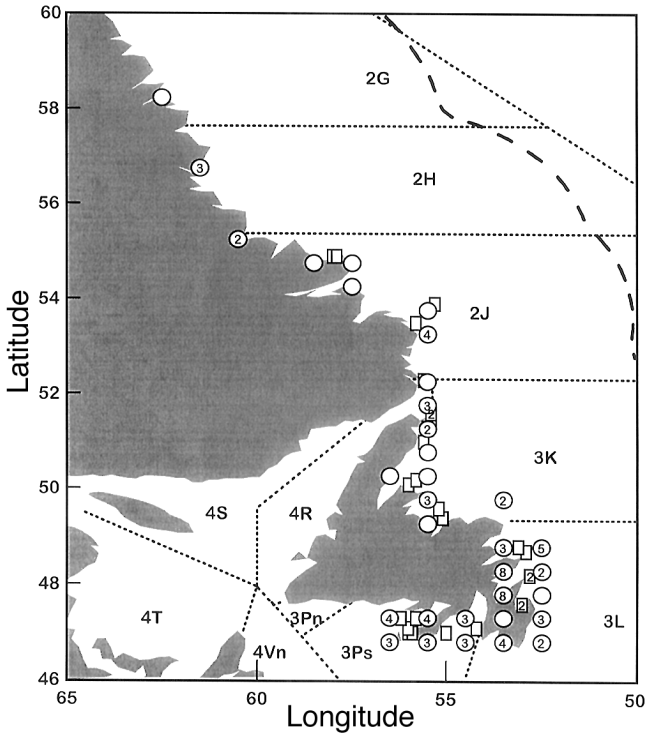
Fig. 1. Northwest Atlantic Fisheries Organization (NAFO) management divisions (dotted lines) in the Newfoundland and Labrador region and the location of coastal cod-tagging experiments used in the analyses. The Canadian exclusive economic zone is marked by the dashed line. Circles mark the geographic mean locations of 86 tagging substudies used in the latitudinal analyses, and rectangles represent the geographic mean locations of the 27 studies used in the mortality and length analyses. The number of independent studies conducted at any one location is indicated where more than one study occurred.



prevalent in one population and less so, or absent, in another (Sindermann 1983). Equally important is the parasite's effect on host survival (Sindermann 1961; Platt 1976; MacKenzie 1983). If variation in parasite prevalence induces differential survival within a stock complex, it can differentially influence the abundance, distribution, and age structure of the populations within the complex that it was intended to clarify. Such an effect introduces a direct bias into the stock discrimination measure. Age- or length-related patterns in parasite prevalence can also bias stock inferences, as some parasites do not infect certain host age- or size-classes.

Lernaeocera branchialis has been used as a cod stock marker in the Northwest Atlantic (Templeman and Fleming 1963; Khan and Tuck 1995), and experimental studies have indicated its potential as a significant mortality factor, especially in juvenile cod (Khan 1988). Despite numerous tagging, parasite, and genetic studies, cod population structure in the Northwest Atlantic remains subject to debate (Bentzen et al. 1996). The Northwest Atlantic cod fishery has historically been managed on a geographic basis, according to the Northwest Atlantic Fisheries Organization (NAFO) divisions (Fig. 1). While the divisions were originally designed to correspond to the (then) known distribution of fish stocks (not only cod), nonbiological factors such as topography and uniformity of spatial area were also incorporated (Halliday and Pinhorn 1990). Thus, the current management divisions may not be biologically appropriate. For example, the northern cod stock complex (ranging from north of Hamilton Bank to the northern half of the Grand Bank (NAFO divisions 2J, 3K, and 3L) from both coastal and offshore areas is assessed and managed as one unit (Taggart et al. 1994). However, genetic and tagging data suggest the existence of distinct breeding components within the stock complex (Lear 1984; Taggart et al. 1995; Bentzen et al.1996; Ruzzante et al. 1996*a*, 1997; Wroblewski et al. 1996; Taggart 1997). Biological parameters should be estimated separately for distinct populations, as differences among them could render some more vulnerable than others to overexploitation (Angel et al. 1994; Ruzzante et al. 1996*b*). Differences in the prevalence of *L. branchialis* among Atlantic cod populations may represent another metric to refine the management units to better reflect stock structure.

Parasite-induced mortality is either direct, through pathogenic parasites, or indirect, through the increased energetic demands of infection (Poulin and FitzGerald 1987; Rohde 1993). If *L. branchialis* induces mortality in its host (directly or indirectly), then it has the potential to influence the recovery of depleted cod stocks in the Northwest Atlantic. The size of the northern cod stock complex is estimated to be at an unprecedented low (Hutchings and Myers 1994), and evidence also shows that the average size, age, and possibly condition estimates for northern cod have decreased over the last decade (Taggart et al. 1994). Several studies demonstrate that *L. branchialis* is most prevalent in smaller, juvenile cod (Sundnes 1970; Templeman et al. 1976; Khan and Lacey 1986; Khan 1988). Thus, given the current abundance and age structure of northern cod, the ramifications of infection on stock rebuilding may be more profound than historically considered.

In this paper, we use data from cod-tagging studies conducted in coastal Newfoundland and Labrador to quantify the geographic distribution of *L. branchialis* infection in cod and to quantify the influence of the parasite on the survival of cod in natural conditions. Previous studies of the pathological effects of *L. branchialis* either have been experimental (e.g., Khan 1988) or have inferred pathogenicity from physiological differences between infected and parasite-free fish in the wild and in the laboratory (Sundnes 1970; van Damme et al. 1994). Evidence of differential survival between infected and parasite-free cod has also been presented for the Northeast Atlantic (Sundnes 1970). The three hypotheses that we test in this study, using field observations, have been derived primarily from laboratory studies and secondarily from field studies in the Northeast Atlantic. First, we determine the spatial variation in parasite prevalence among inshore regions of Newfoundland and Labrador. Our working hypothesis is that the probability of cod infection increases along the coast from north to south, as indicated by Templeman et al. (1976), and as is consistent with the higher prevalence documented in more southern latitudes (e.g., Bay of Fundy, Appy 1978). Our second working hypothesis is that, in the wild, parasitized cod have lower survival probabilities than parasite-free fish. This implies that cod infected when tagged are less likely to survive from release to recapture than those that were parasite-free when tagged. We also compare temporal trends in recaptures of infected and parasite-free cod. Our third working hypothesis is that parasite prevalence is negatively related to fish length. We expect that

mortality is greater in small length-classes of cod than in large length-classes. Finally, we examine the results to determine the usefulness of *L. branchialis* as a natural tag for cod stock discrimination and to assess the potential influence of the parasite on the recovery of cod stocks in the Northwest Atlantic.

Methods

Summary of the parasite–host cycle

In the Northwest Atlantic Ocean, *L. branchialis* predominately inhabits coastal waters ranging from northern Labrador to the Gulf of Maine (Templeman et al. 1976). The parasite's life cycle requires an intermediate host during the copepodid stage and a final (definitive) host from which the adult female copepod disperses her eggs (Scott 1901; Sproston 1942). In the western Atlantic the intermediate host is almost exclusively lumpfish (*Cyclopterus lumpus*) and the most frequent definitive host is Atlantic cod. Sproston's (1942) description of the parasite's life cycle off Plymouth, England, is summarized as follows. Between late winter and early spring (January–April), adult females inhabiting the branchial arches of cod gills release their eggs into the water. The pelagic nauplius larvae are free-living until the early copepodid stage when they settle on the gills of their intermediate host. The copepods then mature on the intermediate host and copulate in the autumn. Male copepods subsequently die and the females translocate to cod where they undergo several morphological changes (see Sproston and Hartley 1941). By the time their egg strings form and enlarge, the female parasites may be found partly embedded in the aorta or the heart wall of the host. The seasonal timing of the life cycle in the Northwest Atlantic appears to be similar to that described in coastal England, with translocation to cod occurring most frequently in the autumn (Templeman et al. 1976; Khan et al. 1990). Estimates of the parasite's life span in natural conditions vary from a few weeks to over a year (Sproston and Hartley 1941; Kabata 1958; Sundnes 1970; van Damme and Hamerlynck 1992). Comprehensive reviews of *L. branchialis* and its biological effects on cod can be found in Sundnes (1970) and Kabata (1984).

Lernaeocera branchialis data from cod tagging studies

Data on *L. branchialis* infection in cod were taken from the 1954–1993 Newfoundland cod-tagging database (Taggart et al. 1995), which consists of data from 177 tagging studies conducted in the Newfoundland and Labrador region by the Canadian Department of Fisheries and Oceans (DFO). The variables recorded for the individually and uniquely tagged and released cod that are relevant here include tagging and recapture location (latitude, longitude, chart zone), dates of tagging and reported recapture, as well as fork length, and the number of *L. branchialis* parasites visually detected on the gills at the time of tagging. As of early 1995, approximately 20% of the tagged cod in the database had been reported recaptured, varying among years and regions (Taggart et al. 1995). As no tagging was conducted from 1966 to 1978 and due to inconsistent inspection for *L. branchialis* in other years, the tagging data we use are limited to the 1962–1966 and 1978–1989 periods. We further restricted our analyses to cod tagged inshore along the east coast of Labrador and the eastern and southern coasts of Newfoundland because *L. branchialis* prevalence appears to be a function of coastal proximity (Templeman et al. 1976). Here, we define inshore tagging as in Taggart et al. (1995): tagging conducted within a 30′N × 60′W grid cell (~30 nautical mile resolution) that either included a land mass or at least one third of the cell area contained an embayment. For statistical reasons, we selected only those studies in which ≥20 cod had been inspected for the parasite prior to tagging and release.

We compiled two sets of data for analysis, each subject to different constraints in addition to those defined above (although the sets shared several tagging studies). The first set was used to determine the latitudinal distribution of the parasite in cod, and the second was used to assess both the effects of the parasite on cod survival and the relationship between length and infection. Each data set is described as follows.

Data set 1: Latitudinal trend in parasite prevalence

To quantify latitudinal trends in infection, we included tagging data from all studies conducted inshore at locations ranging from Saglek Bay, Labrador (NAFO division 2G), in the north to Dantzic Point, Fortune Bay (subdivision 3Ps), in the south (Fig. 1). We did not restrict the data by season. We excluded studies conducted along the west and southwest coasts of Newfoundland and within the Gulf of St. Lawrence, as they were relatively rare in both regions during 1962–1966 and nonexistent during 1978–1989 (see Taggart et al. 1995). These exclusions also had the advantage of not confounding latitudinal trends with other geographical differences because the excluded studies latitudinally parallel the studies conducted on the east coast of Newfoundland. The tagging studies were subdivided if they spanned more than one 30′N × 60′W grid cell (Fig. 1, and as defined above), resulting in 86 substudies that were treated as independent. In summary, the data set used for analysis of latitudinal trends included 86 substudies conducted in all seasons in coastal areas of NAFO divisions 2G, 2H, 2J, 3K, and3L and subdivision 3Ps (Fig. 1), each of which is detailed in Taggart et al. (1995).

Data set 2: Parasite-induced mortality, temporal trends, and influence of length

To determine the parasite's effect on cod survival and the relationship between parasitism and cod length, we selected 27 cod-tagging studies from the database on the basis of seasonal and geographic constraints derived from what is known of the parasite's distribution and life cycle in Newfoundland waters. We limited the data to studies conducted between August and November (inclusive) because translocation from the intermediate host to cod is most frequent during this period**.** As these data are most likely to represent maximum annual prevalence and the largest sample size of infected fish, they are therefore expected to exhibit the most extreme and most easily detected effects of *L. branchialis* on cod. In addition, data from these presumed most recently infected fish allow for an assessment of the cumulative effects of the parasite for all stages of its life span on cod.

We did not subdivide tagging studies that spanned more than one grid cell because fine spatial resolution was not essential or, in many cases, possible. In this case, studies were defined as coastal if at least one of the grid cells in which tagging was conducted was classified as coastal as above. As few studies were conducted in autumn on the west coast of Newfoundland, in the Gulf of St. Lawrence, and north of NAFO division 2J, the tagging studies were selected from NAFO divisions 2J, 3K, 3L, and 3Ps only. In addition, studies conducted in division 3L were selected only if conducted north of 47.0°N, as this line approximates the boundary between the Labrador – east Newfoundland stock complex (northern cod) and the Avalon stock complex (Templeman 1979). Cod from this area appear to represent several distinct breeding populations with different migration patterns (Templeman 1979; Bentzen et al. 1996; Taggart 1997), so excluding these locations presumably decreased the likelihood of combining data from different populations.

In summary, the 27 tagging studies represented four NAFO divisions as follows: 2J ($N = 5$ studies, $n = 3426$ cod inspected, tagged, and released), 3K ($N = 9$, $n = 4207$), 3L ($N = 6$, $n = 4655$), and 3Ps ($N = 7$, $n = 3083$). The number of inspected and tagged cod varied among each of the 27 studies from 1152 in each of Exp. 6318 (3K) and Exp. 6309 (2J) to only 25 in Exp. 8110 (2J). Tag returns from individual studies ranged between 10.7 and 54.3% of those that had been inspected, tagged, and released. Overall, a total of 28.9% (4444) of the 15 381 cod released were recaptured (Table 1).

Temporal- and length-related trends

The analysis of temporal trends in survival required the division of

Table 1. Summary of 27 cod tagging studies (experiment No.) conducted during different periods among different NAFO divisions in the Newfoundland region as reported in Taggart et al. (1995).

Experiment No.	Tagging period	NAFO division	Total inspected and tagged, T	Total recaptured R and R/T (%)	Total infected at tagging T_i T_i/T (%)	Total recaptures infected when tagged R_i and R_i/R (%)
6503	Sept. 21 – Oct. 5, 1965	3Ps	383	208 (54.3)	18 (4.7)	10 (4.7)
6504	Oct. 23 – Nov. 11, 1965	3Ps	382	172 (45.0)	26 (6.8)	**11 (4.8)**
8609	Sept. 30, 1986	3Ps	160	39 (24.4)	15 (9.4)	**1 (2.6)**
8809	Aug. 24 – Sept. 15, 1988	3Ps	698	159 (22.8)	119 (17.0)	**23 (14.5)**
8810	Aug. 25 – Sept. 16, 1988	3Ps	421	93 (22.1)	40 (9.5)	**7 (7.5)**
8811	Aug. 29 – Sept. 15, 1988	3Ps	122	13 (10.7)	7 (5.7)	1 (7.7)
8907	Aug. 22 – Sept. 6, 1989	3Ps	917	171 (18.6)	161 (17.6)	**28 (16.4)**
Sum 3Ps	7		3083	855 (27.7)	386 (12.5)	**81 (9.5)**
6208	Oct. 1–13, 1962	3L	384	161 (41.9)	22 (5.7)	11 (6.8)
6210	Nov. 3–25, 1962	3L	1151	417 (36.2)	23 (2.0)	**7 (1.7)**
6414	Oct. 14 – Nov. 2, 1964	3L	1149	465 (40.5)	61 (5.3)	**23 (5.0)**
6416	Nov. 20–25, 1964	3L	768	271 (35.3)	17 (2.2)	9 (3.3)
7905	Oct. 19 – Nov. 5, 1979	3L	437	126 (28.8)	54 (12.4)	21 (16.7)
8006	Oct. 9–19, 1980	3L	766	171 (22.3)	88 (11.5)	**15 (8.8)**
Sum 3L	6		4655	1611 (34.6)	265 (5.7)	**86 (5.3)**
6204	Aug. 11–23, 1962	3K	768	262 (34.1)	10 (1.3)	**2 (0.8)**
6318	Nov. 8–19, 1963	3K	1152	412 (35.8)	26 (2.3)	14 (3.4)
8209	Sept. 20–24, 1982	3K	185	37 (20.0)	17 (9.2)	**2 (5.4)**
8211	Sept. 27–28, 1982	3K	326	63 (19.3)	30 (9.2)	**4 (6.4)**
8305	Sept. 6–15, 1983	3K	634	109 (17.2)	45 (7.1)	**6 (5.5)**
8306	Sept. 24–25, 1983	3K	121	23 (19.0)	8 (6.6)	**0 (0.0)**
8404	Sept. 29 – Oct. 10, 1984	3K	331	72 (21.8)	24 (7.3)	**4 (5.6)**
8405	Oct. 9–15, 1984	3K	318	62 (19.5)	14 (4.4)	**2 (3.2)**
8406	Sept. 30 – Oct. 7, 1984	3K	372	68 (18.3)	32 (8.6)	**4 (5.9)**
Sum 3K	9		4207	1108 (26.3)	206 (4.9)	**38 (3.4)**
6205	Sept.12–21, 1962	2J	1082	232 (21.4)	11 (1.0)	**1 (0.4)**
6308	Aug. 5–9, 1963	2J	768	256 (33.3)	15 (2.0)	7 (2.7)
6309	Aug. 12–14, 1963	2J	1152	240 (20.8)	9 (0.8)	4 (1.7)
8110	Aug. 24, 1981	2J	25	4 (16.0)	0 (0.0)	0 (0.0)
8506	Aug. 2–5, 1985	2J	399	138 (34.6)	14 (3.5)	**2 (1.5)**
Sum 2J	5		3426	870 (25.4)	49 (1.4)	14 (1.6)

Note: The total number of cod inspected for *L. branchialis*, tagged, and released (T), total number reported recaptured (R) and their percentage of the total released (R/T), total number that were infected when tagged (T_i) and their percentage of the total tagged (T_i/T), and total number reported recaptured that were infected when tagged (R_i) and their percentage of the total recaptured (R_i/R) are listed for each study and by each NAFO division (Sum). Total recaptures that were infected when tagged are boldfaced if the proportion is less than that of the proportion infected when tagged.

recapture data into periods of time-free (elapsed time between tagging and recapture). The length-specific analysis of survival required division of the recapture data into length-classes based on the length of cod at tagging. To ensure sufficient sample size in either analysis, we pooled the data by NAFO divisions (as above) which resulted in one sample from each of divisions 2J, 3K, 3L (north of 47.0°N), and 3Ps. This decision was based on three factors: (1) each of the four divisions contained data of similar sample size, representing comparable periods, (2) it was necessary that the combined studies be in geographic proximity, and (3) pooling within divisions maximized the probability that the data came from cod populations sharing similar migration and breeding distributions, at least as a first approximation.

In summary, for these analyses, we limited the second data set of 27 coastal tagging studies conducted in NAFO divisions 2J, 3K, 3L, and 3Ps for which (1) ≥20 cod had been inspected for the parasite, (2) the range in length of the cod among studies was similar (see Taggart et al. 1995), and (3) the cod were tagged and released between August and November. For analyses of temporal- and length-related trends in parasite-induced cod mortality, data within divisions were pooled.

Analyses

Data set 1: Latitudinal variation in parasite prevalence

To test the null hypothesis that *L. branchialis* prevalence in coastal Newfoundland is latitudinally invariant, the 86 inshore studies were pooled according to the latitude of the centroid of the 30′N × 60′W grid cell where tagging occurred. This provided one group for each of the 19 latitudinal categories, resolved to 30 nautical miles. For each study, we calculated the proportion of cod carrying at least one parasite when tagged and then calculated the total proportion infected in each latitudinal category. To assess the relationship between latitude and the probability of infection, we fit the proportional data to a logistic regression model by maximum likelihood estimation (SAS 1988). In addition, we used an arcsine square-root transformation for proportional data (Sokal and Rohlf 1981) from each of the 86 study

subgroups and assessed the relationship between latitude and the transformed proportion infected using least-squares regression.

Data set 2: Influence of infection on survival

As the uniquely tagged cod were recaptured and reported primarily through the commercial fishery, they were not reinspected for the parasite. However, we can assess the effect of the parasite on cod survival through comparisons of the number of cod that were infected and parasite free at the time of tagging and their respective recapture rates. These analyses rest on the hypothesis that if there is no parasite-induced effect on posttagging survival, then cod that were infected and parasite free when tagged should be recaptured at the same rate. We compared recapture rates of infected and parasite-free cod first from an overall perspective, then within studies, and finally at the scale of NAFO divisions as defined above.

For each study, or any group of studies, we can denote the number of tagged fish by T, the number of tagged fish that were infected when tagged by T_i, and the number of tagged fish that were parasite free when tagged by T_f (i.e., $T = T_i + T_f$). We can further denote the total number of recaptured fish by R, the number of recaptured fish that had been infected at the time of tagging by R_i, and the number of recaptured fish that had been parasite free at the time of tagging by R_f (i.e., $R = R_i + R_f$). Our test of the effect of infection on survival (as indicated by differential recovery) centers on the comparison of the proportion of infected individuals at the time of tagging (T_i/T) with the proportion of those recaptured (R_i/R). We used two methods of comparison. In the first method the 27 tagging studies were compared using a sign test on the quantity $(T_i/T) - (R_i/R)$. We then compared the number of recaptured cod that had been infected at tagging (R_i) with the number expected to be recaptured if the parasite had no effect (determined by the proportion infected at tagging (i.e., $(R_i)_{exp} = (T_i/T)\cdot R$) using a chi-square test. Finally, we tested the null hypothesis that studies within one NAFO division exhibited homogeneous variance in T_i/T and R_i/R using heterogeneity chi-square analysis (Zar 1989). If appropriate, we combined the chi-square values of each study (treating each as a sample of a population), applied the Yates correction for continuity, and compared the number of recaptured cod that had been infected at tagging with the expected number for each division.

Data set 2: Temporal trends

We grouped the recapture data (pooled by division) by the number of months that had elapsed between the time of tagging and reported recapture (time-free), resulting in five successive 12-month time-free classes in each of divisions 2J, 3K, and 3L and four successive classes in division 3Ps. Sample size and seasonal variation in commercial fishing (i.e., recapture activity) prevented us from classifying data into shorter time-free periods. We tested for differences in proportions of infected and parasite-free cod recaptured in each year free using paired *t*-tests on transformed proportional data. We then calculated the median number of months-free in each 12-month class. We compared the recapture rates of infected and parasite-free cod over time using least-squares regression on arcsine square-root transformed proportional data and logarithmically transformed median months-free data, as recapture rates in these studies typically show an exponential decay (see Taggart et al. 1995). If *L. branchialis* affects cod survival consistently over time (the null hypothesis), then the reported recapture rate over time (the slope of the relationship) for infected cod should be the same as that for parasite-free cod.

Data set 2: Length-related trends in infection and mortality

For the pooled data in each of the four divisions, we divided the cod into 13 length-classes at 7-cm intervals that roughly approximate ages 2+ to 14+ according to the average age (A, years)-at-length (L, centimetres) relationship, $A = 0.018L^{1.419}$ ($r^2 = 0.969$), calculated for cod in division 3L for the entire 1972–1992 period (Taggart 1994). Within each division, we compared the average length at tagging of infected and parasite-free cod using a *t*-test. To determine the length distribution of infected cod in each region, the number of cod infected with *L. branchialis* at tagging was calculated for each length-class and compared with the number expected if infection was uniformly distributed among all length-classes using a chi-square test. We additionally quantified the relationship between the proportion infected and length using least-squares regression on the arcsine square-root transformed proportional data.

The effect of *L. branchialis* on survival among the various length-classes of cod was determined by comparing T_i/T and R_i/R within each class. Differences between these proportions reflect the relative effect on survival, and the variation among the differences would indicate length-specific (or age-specific) responses to infection. As above, we compared the observed number of recaptured cod that had been infected at tagging with the number expected within each length-class using a chi-square test.

Assumptions

We have adopted several explicit assumptions that are associated with mark–recapture data (e.g., Burnham et al. 1987) and with the tagging database we use: (1) all fish have an equal probability of being captured and of being recaptured, (2) parasites are detected if present, (3) infected and parasite-free fish are equally susceptible to tagging-related mortality (i.e., death resulting from the act of tagging and releasing) and there is no interaction between the state of being tagged and the state of being infected, (4) any infection subsequent to tagging on either infected or parasite-free cod is proportionally constant, (5) reported recapture information is accurate or, if not, any bias is consistent among years, regions, and length-classes, and (6) variation among tagging-study methods (type of tag, etc.) and among recapture methods (gear type, etc.) does not differentially (infected versus parasite free) influence the results.

Results

Latitudinal variation in parasite prevalence

The proportion of cod infected with the gill parasite generally increased from north to south along inshore Labrador and Newfoundland (Fig. 2). Of the 86 independent substudies that constitute the 19 different latitudes, parasite prevalence ranged from 0% of 1150 cod inspected in the most northerly study (Saglek Bay, Labrador; 58.25°N) to 20.1% of the 269 cod at Dantzic Pt., Fortune Bay, some 1200 km further south (46.75°N). The highest prevalence was 20.6% of 1021 cod, at Lance Cove, Conception Bay (division 3L). Logistic regression analysis revealed a negative relationship between the proportion of cod infected and latitude (chi-square = 383.9, $p < 0.0001$; Fig. 2*a*). This relationship was consistent with that described by a least-squares linear regression of infection by latitude ($r^2 = 0.429$, $p < 0.0001$; Fig. 2*b*). However, as the least-squares regression incorporated more of the variance at southern latitudes, it is considered more conservative. The majority (67%) of studies were conducted in the more southern divisions 3L and 3Ps, and the among-study variance in prevalence was greatest there. For example, of the 15 studies conducted at 46.75°N (south coast and southern Avalon Peninsula), infection ranged from 3.3% (n inspected = 2170) to 20.1% (n = 269), while at 53.25°N (southeast Labrador) the range for four studies spanned 0.9% (n = 768) to 3.2% (n = 589).

Studies conducted in autumn (August–November) were clearly responsible for the greatest portion of the overall latitudinal trend (Fig. 3) when using logistic regression

Fig. 2. Relationship between latitude and parasite prevalence for 86 cod-tagging substudies in coastal Newfoundland and Labrador. (*a*) Relationship quantified by logistic regression (chi-square = 383.9, $p < 0.0001$): $(T_i/T) = (1 - e^{(-9.669+0.254 \cdot \text{latitude})})/(1 + e^{(-9.669+0.254 \cdot \text{latitude})})$; (*b*) relationship between latitude and parasite prevalence quantified by least-squares regression ($r^2 = 0.429$, $p < 0.0001$): $\sin^{-1}\sqrt{T_i/T} = -1.47 \cdot \text{latitude} + 85.98$.

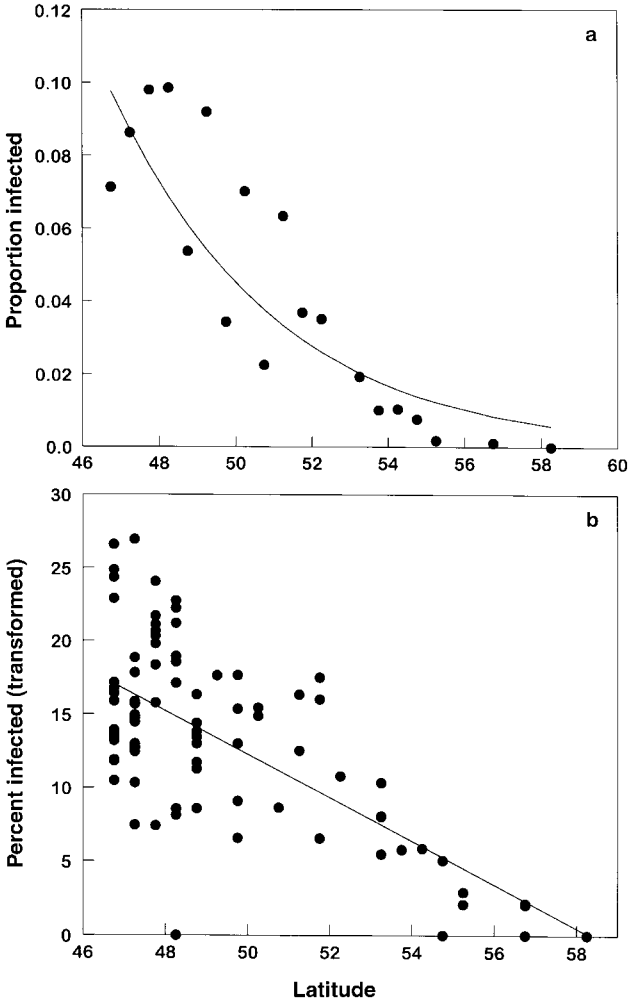
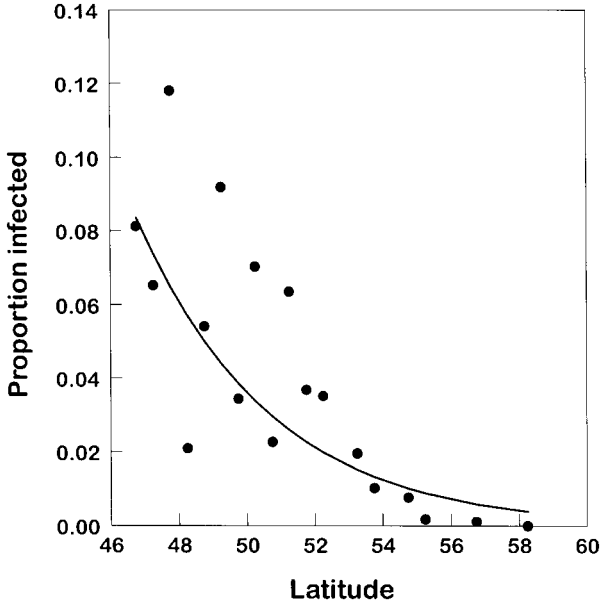


Fig. 3. Relationship between latitude and parasite prevalence for cod tagged between August and November only, quantified by logistic regression (chi-square = 215.6, $p < 0.0001$): $(T_i/T) = (1 - e^{(-10.443+0.275 \cdot \text{latitude})})/(1 + e^{(-10.443+0.275 \cdot \text{latitude})})$.



(chi-square = 215.6, $p < 0.001$). Least-squares regression yielded a higher r^2 value than for all months combined ($r^2 = 0.574$, $p < 0.001$). The studies conducted during spring (May–July) revealed a trend similar to that for autumn, although sample size was smaller ($r^2 = 0.25$, $p < 0.05$). During winter (December–April), there was no relationship ($F = 0.03$, $r^2 = 0.003$, $p = 0.86$). However, there is little to be derived from the latter case, as no studies were conducted north of 48.75°N between December and April. High variance in prevalence in southern latitudes was exhibited in all seasons. The only two examples of 0% infection south of 50°N occurred during winter and spring, and maximum infection was lowest during the winter.

Influence of infection on survival

Parasite prevalence for studies conducted in autumn varied greatly, not only as a function of latitude as determined above, but also among studies (years) within locations and among locations in close proximity at the same latitude, particularly on the south and southeast coasts of Newfoundland (Table 1).

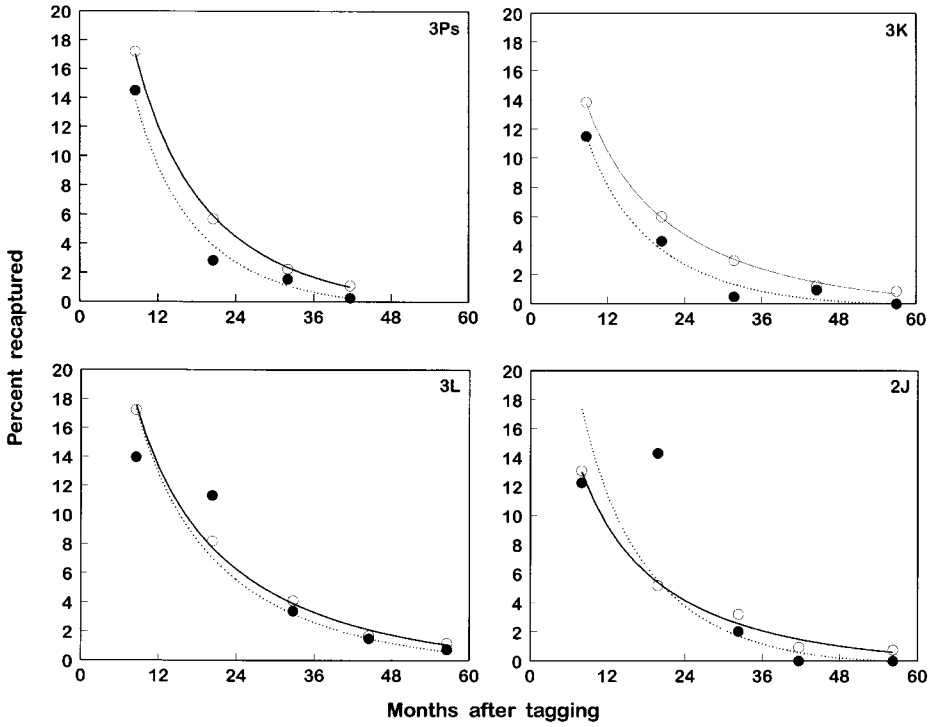
In 18 of the 27 studies (i.e., 70%), proportionally fewer of the parasitized cod than parasite-free cod (at tagging) were recaptured (sign test: $p_{N\geq 18} = 0.038$). This discrepancy was most pronounced in division 3K (see Table 1) where cod that were infected at tagging were underrepresented in the reported recaptures in eight of nine studies (sign test: $p_{N\geq 9} = 0.020$). Similar differences were observed in division 3Ps where in five of seven studies (70%), infected cod were underrepresented in recaptures, although the difference was not significant. Division 3L was less remarkable, with only three of five studies (60%) being underrepresented, and in division 2J, one half of the studies were underrepresented and one half were overrepresented, with 0% infected at tagging in one case. In no individual tagging study was the difference significant between the observed number of recaptured cod that had been infected at tagging and the number expected (chi-square tests: $p > 0.05$).

The heterogeneity chi-square analyses performed on studies conducted within each division indicated that studies from each of 3K (northeast Newfoundland) and 2J (Labrador coast) were homogeneous, exhibiting statistically similar differences between R_i/R and T_i/T, and so data within each of these regions were pooled. In 3K, fewer fish infected at tagging were recaptured than was expected if the parasite did not influence survival (pooled chi-square, corrected for continuity: 4.81, $p = 0.028$; Table 2). In this division, 4.97% (206 of 4207) of the tagged fish were infected, and only 38 of 1108 (3.43%) recaptured fish had been infected at tagging relative to the 54 expected based on the proportion T_i/T. Thus, the infected fish were recaptured at a rate 8.3% lower (38 of 206 = 18.4%) than that of parasite-free fish (1070 of 4001 = 26.7%). For cod tagged in 3Ps and 3L, 7.7 and 2.3% fewer infected than

Table 2. Summary of heterogeneity and pooled chi-square tests on observed and expected recaptures of infected (R_i) and parasite-free (R_f) cod in NAFO divisions 3Ps, 3L, 3K, and 2J.

NAFO division	Expected R_i	Observed R_i	Expected R_f	Observed R_f	Heterogeneity		Pooled	
					Chi-square	p	Chi-square	p
3Ps	107	81	748	774	18.734	0.005	—	—
3L	92	86	1519	1525	47.133	<0.0001	—	—
3K	54	38	1054	1070	8.635	0.374	4.810	0.028
2J	12	14	858	856	4.629	0.201	0.091	0.763

Fig. 4. Reported recapture rates of parasite-free (solid lines, open circles) and infected (dotted lines, solid circles) cod as a function of the months elapsed between tagging and recapture for each NAFO division using cod tagged between August and November (inclusive). Intercepts (at time = 8 months after tagging) are significantly lower for infected cod in divisions 3Ps and 3K (t-tests: $p < 0.05$) but not in divisions 3L and 2J. There are no differences in the slopes of parasite-free and infected cod return rates over time within divisions.



parasite-free cod were recaptured, respectively (Table 2). However, in these divisions, heterogeneity was too great to allow pooled chi-square tests (Table 2). In 2J, the number of recaptures that had been infected at tagging was not significantly different from that expected if the parasite had no effect on survival (pooled chi-square, corrected for continuity: 0.091, $p = 0.763$).

Temporal trends

For cod tagged in coastal regions of 3Ps and 3K, the proportion of infected cod recaptured in each year after tagging was consistently lower than the proportion of uninfected cod (3Ps: $t = -4.71$, $p = 0.009$; 3K: $t = 3.22$, $p = 0.016$). For cod tagged in 2J and 3L, the proportions recaptured did not differ. The least-squares regressions of the proportion recaptured as a function of the time-free quantified exponential declines in tag return rate in all divisions for both infected and parasite-free cod (Fig. 4). There was no significant difference between the slopes of the regressions for infected and parasite-free cod in any division (t-tests: $p > 0.05$). However, the intercept (proportions of infected and uninfected cod recaptured) at time = 8 months was significantly lower for infected cod.

Length trends

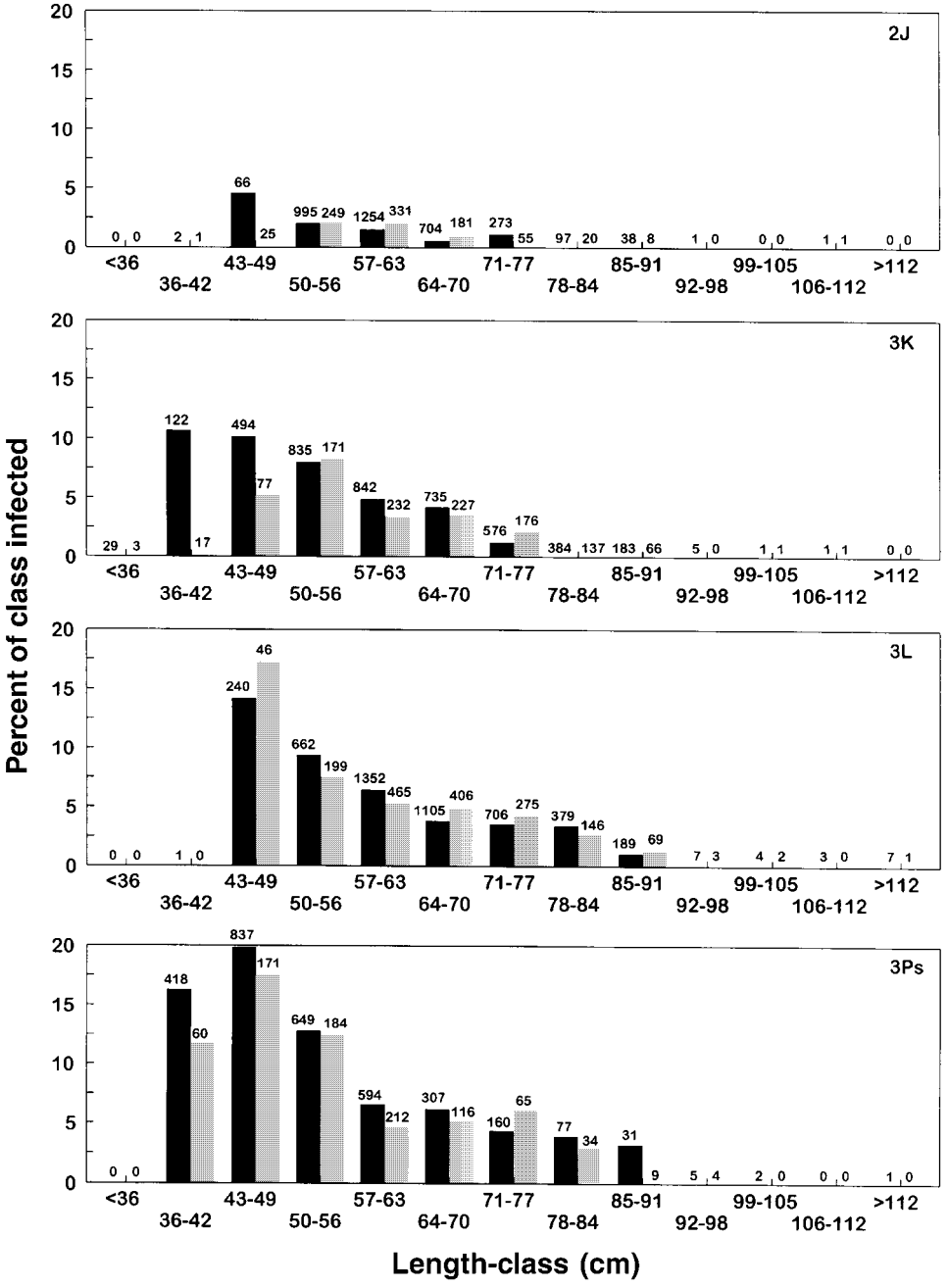
The length distributions of tagged cod in the Newfoundland tagging database are generally skewed right, and averages and ranges differ among divisions (Taggart et al. 1995). Overall, the length of cod tagged in the studies we analyzed ranged from 28 to 129 cm. The average length (±1 SE) of all inspected and tagged cod in 3Ps was 54.2 ± 0.20 cm, conspicuously lower than that for cod in 3L (65.2 ± 0.15 cm), 3K (62.5 ± 0.19 cm), and 2J (61.1 ± 0.13 cm). The modal length-class was 43–49 cm in 3Ps and 57–63 cm in all other regions. At the time of tagging, parasitized cod were shorter than parasite-free cod in all four divisions (t-tests: $p < 0.005$; Table 3). The difference in average length was greatest in 3K and lowest in 2J (Table 3).

Parasite prevalence (Fig. 5) was greatest in the 43–49 cm class in 2J (4.5% of class infected), 3L (14.2%), and 3Ps (19.8%) and decreased with increasing length. In division 3K, the highest prevalence occurred in the 36–42 cm class

Table 3. Average lengths and standard error (SE) of infected (T_i) and parasite-free (T_f) cod at the time of tagging in NAFO divisions 3Ps, 3L, 3K, and 2J and the results of *t*-tests for length differences.

	Infected (T_i)			Parasite-free (T_f)			Length		
NAFO division	Number tagged	Average length (cm)	SE	Number tagged	Average length (cm)	SE	difference (cm)	*t*	*p*
3Ps	386	49.6	0.43	2697	54.9	0.22	5.3	10.97	<0.001
3L	265	60.3	0.58	4390	65.5	0.16	5.2	08.73	<0.001
3K	206	54.6	0.58	4001	62.9	0.20	8.3	13.53	<0.001
2J	049	57.2	0.94	3377	61.2	0.13	4.0	04.22	<0.001

Fig. 5. Histogram of comparison between the percentage of each length-class (L) of cod infected at tagging, $(T_i/T)_L$ (black bars), and the percentage of reported recaptures that were infected when tagged, $(R_i/R)_L$ (grey bars), within each of the sequential 7-cm length-classes of tagged cod in each NAFO division. Numbers shown for each length-class represent the total number of cod tagged (T) or recaptured (R) in each class. Differences between $(T_i/T)_L$ and $(R_i/R)_L$ are not significant within length-classes.



(10.7%), although it was only marginally higher than in the 43–49 cm class (10.1%). In all cases the number of infected cod in each length-class was different from that expected if infection was uniformly distributed among all length-classes (chi-square: $p < 0.001$). This result was consistent with least-squares regression analyses that quantified negative relationships between prevalence and length for cod tagged in each of divisions 3Ps ($r^2 = 0.87$, $p < 0.001$), 3L ($r^2 = 0.92$, $p < 0.001$), and 2J ($r^2 = 0.89$, $p < 0.005$). The one exception to this pattern occurred on the northeast coast of Newfoundland in division 3K where the slope of the relationship was not significantly different from zero ($p = 0.18$). However, division 3K was also the only region where sample size (≥20 per length-class) permitted the inclusion of the 29–36 cm length-class, and surprisingly, none of these cod in division 3K were infected at tagging. The few tagged cod in this size-class in division 3Ps ($n = 5$) were also parasite free, although the small sample size precluded their use in the analysis.

Analysis within length-classes (L) did not indicate significant differences between the proportions infected at tagging, $(T_i/T)_L$, and the proportions of recaptures that had been infected when tagged, $(R_i/R)_L$, in any division. Thus, we could not reject the null hypothesis that survival of infected fish was equal among length-classes.

Discussion

Latitude and infection

The proportion of cod infected with *L. branchialis* increases from north to south along inshore Labrador and Newfoundland. This latitudinal trend in parasite prevalence may be a function of temperature and (or) the distribution of the parasite's intermediate host (lumpfish). The average annual sea surface temperature (1971–1990 normal) increases from 2.1°C in the north along the Labrador coast to 5.1°C along southeastern Newfoundland (inner Labrador current) and to 6.1°C further offshore on the St. Pierre Bank (Drinkwater et al. 1994) and, therefore, parallels the latitudinal trend in parasite prevalence. Templeman and Fleming (1963) noted that the highest gill parasite prevalence in inshore areas occurred in warmer, rather than colder, parts of Newfoundland. The physiological effects of *L. branchialis* on cod vary with water temperature as does the parasite's egg sac development rate (Khan 1988). As cod growth rates are generally a function of temperature (Brander 1994), high growth rates at warmer latitudes may mitigate the deleterious effects of *L. branchialis*, allowing southern Newfoundland cod populations to support a higher level of infection.

The distribution of the parasite's intermediate host undoubtedly influences cod infection rates, especially given the parasite's brief free-swimming period for transfer between the intermediate and definitive host (Sproston and Hartley 1941; Templeman and Fleming 1963). The latitudinal trend in prevalence also parallels the distribution of lumpfish in the Newfoundland region. Reported lumpfish landings are negligible along the southern Labrador coast (Stevenson and Baird 1988), and the species' highest biomass estimates are for the south coast of Newfoundland (Stansbury et al. 1995).

Although the negative relationship we have quantified between infection and latitude is consistent with other qualitative studies (Templeman and Fleming 1963; Templeman et al. 1976), positive relationships are not unknown (e.g., from the northern Bay of Fundy to Rhode Island, Sherman and Wise 1961; along the Norwegian coast, Sundnes 1970). Thus, at the ocean basin scale, there may be a dome-shaped relationship between infection and latitude, with the highest reported prevalence occurring in the Bay of Fundy (Sherman and Wise 1961; Appy 1978). This implies that factors determining gill parasite distribution in cod may reach optimal levels in the Bay of Fundy region.

Infection and survival

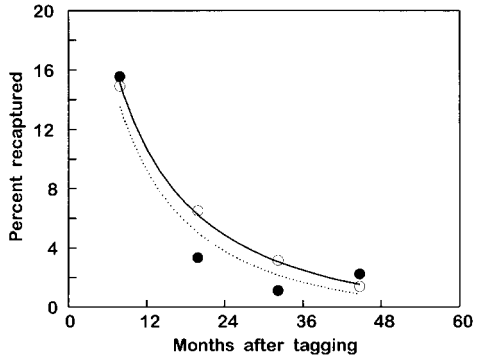
Using the combined studies conducted on the northeast coast of Newfoundland, we have shown that cod infected with *L. branchialis* when tagged and released were recaptured at a lower rate than were uninfected cod. As recapture rates are an index of survival, and as fishing rates are assumed to have been equal on infected and parasite-free fish within studies, the difference between the two led us to reject the null hypothesis that the parasite has no effect on survival for cod tagged in autumn in NAFO division 3K. This result from field studies is entirely consistent with laboratory studies, although the magnitude of natural parasite-induced mortality appears lower than in experimentally infected cod. Under experimental conditions, cod death resulted from hemorrhage, anemia, and aorta blockage (Kabata 1970; Khan and Lacey 1986; Khan 1988; Khan et al. 1990), and Khan (1988) found a mortality rate of 30% in laboratory-infected cod. Of cod tagged in autumn on the northeast coast of Newfoundland, 8.3% fewer infected than parasite-free fish were recaptured. As a first approximation, this suggests that the total mortality for infected cod is of the order 8% higher than that experienced by parasite-free fish in division 3K over the period between tagging and recapture (nominal maximum of 5 years). This estimate is entirely consistent with similar tagging-related studies on infected Norwegian coastal cod in the Borgenfjord population where the mortality rate is 6% higher than that of uninfected cod (Sundnes 1970).

We were not able to reject the null hypothesis that parasitized cod tagged in coastal Labrador (division 2J) in autumn have the same survival probability as parasite-free cod. Given the extremely low parasite prevalence along the Labrador coast (0.0–3.5%), this result may not be surprising. Parasite-induced mortality at such low parasite levels would, at best, be very difficult to detect using the tagging studies we used.

An alternative explanation for the underrepresentation of infected fish in recaptures in 3K, 3L, and 3Ps is that parasitism reduces the probability of a fish being caught in commercial fishing gear. We have explicitly assumed that there is no effect of infection on catchability. However, S.P. Reidy, J.A. Nelson, and S.R. Kerr (unpublished)[2] found that infection with *L. branchialis* decreases aerobic swimming performance in cod. Other authors have also suggested the possibility of detrimental effects of the parasite on swimming behaviour (Sproston and Hartley 1941; Khan 1988). With mobile fishing gear (specifically, otter trawlers), catchability is a function of maximum sustainable swimming speed and time to exhaustion (Fernö 1993; He 1993). Catchability with fixed gear (e.g., cod

[2] The effect of a parasitic copepod (*Lernaeocera branchialis*) on the swimming performance and metabolism of Atlantic cod (*Gadus morhua*).

Fig. 6. Reported recapture rates of parasite-free (solid line, open circles) and infected (dotted line, solid circles) cod as a function of the months elapsed between tagging and recapture in NAFO division 3K using only cod tagged in October and November. Neither the slopes nor the intercepts are significantly different when August and September data are excluded (see Fig. 4).



trap, longline, gill net) is generally related to activity rates and satiation levels (Fernö 1993). It is clear that cod catchability in the Newfoundland region varies among gear types and among years when assessed using the same database used here (Myers and Hoenig 1997). It is therefore possible that infected fish may be overrepresented in recaptures from otter trawlers, and thus, our assessment of parasite-induced mortality in 3K may be a conservative underestimate. The representation of infected cod in fixed gear recaptures is less predictable, as feeding and satiation levels appear to vary erratically in infected cod (Khan and Lee 1989). Using 13 studies from the tagging database, we compared the estimated prevalence of *L. branchialis* in cod captured with fixed and mobile gear in inshore areas (Conception Bay and Trinity Bay) and found no significant difference (M.E.B. Jones and C.T. Taggart, unpublished data). This suggests that among-region differences in fishing gear did not bias either our survival estimates of infected cod or our estimates of parasite prevalence.

The temporal trends in the recapture rates of infected and parasite-free fish suggest that the parasite-induced mortality occurs primarily, or perhaps almost exclusively, within the first year after tagging, if not within the first year after infection. The suggestion concurs with the work of Khan (1988) who reported that 50% of the mortality in laboratory-infected cod occurred within 2 months of parasite attachment and 75% within the first 4 months. Although the maximum duration of a living adult female's parasitic state on cod is not known, the majority of parasites reportedly die when egg release is completed, some dropping off postmortem and leaving embedded holdfasts in the host (Kabata 1970). Our results are consistent with a parasite life cycle lasting approximately 1 year or less.

We acknowledge that the high among-study variance in recapture rates of infected cod statistically precludes the pooling of data from the south and southeast coasts of Newfoundland. Nevertheless, the similarity of trends among divisions 3K, 3L, and 3Ps is noteworthy, and the close proximity of the study sites provides an exploratory basis for pooling data within divisions. In all three regions, fewer infected than parasite-free cod were recaptured, and the difference in 3Ps is very close to that in 3K (8.6 and 7.7%, respectively). In division 3L (north of 47.0°N), infected cod were underrepresented by only 2.3% in recaptures. The relatively small difference in recapture rates on the southeast coast (3L) may result from the timing of parasite-induced mortality relative to that of the tagging studies. The seasonal and geographic constraints we imposed on the analyses, and the timing of all studies conducted in division 3L, resulted in only October and November studies being used in the analyses. Data from the other divisions spanned the entire August–November period. As the probability of death is highest within the first few months following infection (Khan 1988; this study), and as infection in the wild occurs mainly in early autumn (Templeman et al. 1976), the mortality estimated for divisions 3Ps and 3K may have already occurred prior to the inspection, tagging, and release of cod in the October and November studies in division 3L.

We assessed the effects of tagging month on our estimates of mortality through a reanalysis of the 3K data excluding all cod tagged in August and September (Fig. 6). Of the remaining 1963 parasite-free cod, 29% (574) were recaptured. Of the 90 infected cod, 24% (23) were recaptured and the difference was not statistically significant (chi-square test: $p > 0.05$). Although the sample size was smaller than that used in division 3L, the lack of significant differences in October–November 3K data is consistent with the timing of inspection and tagging being crucial to these kinds of analyses and the interpretation of the results. We cautiously conclude that the lack of evidence for parasite-induced mortality in division 3L is related to the timing of the studies conducted there as well as to the among-study variance in recapture rates.

Size and infection

Infected cod were significantly shorter than parasite-free cod in all regions we examined, and our data revealed a negative relationship between cod length and infection. This concurs with results of previous field and laboratory studies on cod and other gadoids (Templeman et al. 1976; van den Broek 1979; Khan and Lacey 1986; Khan 1988; Alsuth and Ebeling 1989; Lang 1989; Khan et al. 1990). Templeman et al. (1976) attributed the infection-at-length relationship to age-related differences in migration behaviour; juvenile fish tend to remain inshore for longer periods and, thus, have a higher probability of exposure to the intermediate host (Blackwood 1983). An equally simple explanation is that the parasite decreases growth rate in infected cod, an effect that has been shown in laboratory studies (Khan and Lee 1989). In using a general age-at-length relationship to determine approximate ages, we implicitly assumed that the relationship was applicable to infected and parasite-free fish. Shorter, infected cod may actually be of the same ages as the larger, parasite-free cod. However, as age data were not collected, we were unable to determine whether this is the case.

Despite the increased infection in small cod, we found no statistically significant length-specific differences in the effects of parasitism on mortality. Sundnes (1970) and Khan (1988) reported higher *Lernaeocera*-induced mortality rates in juvenile cod relative to mature cod. Our results suggest that smaller cod, which have relatively high growth rates, may be more resilient towards infection and, thus, are more likely to be observed harbouring one or more parasites. The trend may also indicate an immune response that increases with fish age and the number of previous infections. Although van Damme and Hamerlynck (1992) found that immunological effects

probably influenced the seasonal infection pattern of *L. branchialis* in whiting, Khan (1988) found no evidence of an immunological response in laboratory-infected cod.

Implications

Our results reveal a great deal of variation in the prevalence of *L. branchialis* among studies. This variation suggests that parasite–host relationships are influenced by factors acting at small geographic (tens of kilometres) and time (weeks to months) scales, in addition to the larger scale latitudinal and seasonal variation. Natural variation among studies is difficult to explain with the data available, yet it may have significantly affected our results despite our attempts to constrain the data using sound biological criteria.

In general, we conclude that the use of *L. branchialis* as a natural population tag requires caution. Our results show that infected cod can be subject to parasite-induced mortality, the magnitude of which varies geographically; this violates an important criterion for assessing the suitability of this as a biological tag (MacKenzie 1983). In addition, if used as a marker, the parasite's higher prevalence in small length-classes of cod may lead to a biased discrimination of stocks with different length distributions. Separate breeding populations of cod are most easily distinguished when they are aggregated for spawning (Templeman 1979). However, as infection occurs mainly inshore in the autumn, the use of *L. branchialis* as a population marker may be more appropriate for identifying populations that overwinter inshore (e.g., Ruzzante et al. 1996*a*, 1997). Our study suggests that *L. branchialis* is most useful as a population tag under the following conditions: (1) timing should be seasonally consistent among samples to avoid bias introduced by seasonal differences in spatial infection patterns, (2) due to small-scale variation in parasite prevalence, a large spatial area for sampling should be used to distinguish among populations at the scale of bays or submarine banks, and (3) length distributions should be consistent among samples or any differences should be factored into any analyses. Furthermore, it was not within the scope of this study to assess the possibility of long-term variation in the parasite's abundance or distribution. Temporal changes, such as the reduction of geographic variation in parasite prevalence, could render a useful population tag useless. Thus, any changes in cod stock distributions instigated by the collapse of the fishery could affect the usefulness of *L. branchialis* as a population marker.

Any negative influence on cod survival has the potential to affect the recovery of the Northwest Atlantic cod stocks from their currently depleted status. Infection rates of cod with *L. branchialis* may normally be in equilibrium and may fluctuate at levels that can be, and have been historically, supported by the cod population (van Damme et al. 1994). However, fishing-induced changes in cod stock abundance, biomass, and age structure could have the potential to disrupt this equilibrium and change the pattern of the parasite–host relationship. The relatively intense prosecution of the intermediate host through the lumpfish fishery may further complicate the parasite–host interaction.

Knowledge of the influence of *L. branchialis* on cod survival facilitates a more precise definition of natural mortality. Our data suggest that mortality was of the order 8% greater for infected fish on the northeast coast of Newfoundland. This is a first approximation of mortality due to *Lernaeocera* in at least one region of inshore Newfoundland, relative to other causes of mortality, but it is entirely consistent with the findings of Sundnes (1970) for Norwegian coastal cod. However, in many fish stock assessments, natural mortality is assumed to be constant. On an interannual basis, this is not realistic, as it does not account for natural population dynamics and environmental variation. Through studies similar to that reported here, it is possible to begin to estimate each of the components of natural mortality and their variation in time and space, such that natural mortality may be more realistically incorporated into population assessments and predictions of cod stock recovery.

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