The use of prevalence as a measure of lice burden: a case study of *Lepeophtheirus salmonis* on Scottish Atlantic salmon, *Salmo salar* L., farms

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Abstract

This study investigates the benefits of using preva lence as a summary measure of sea lice infestation on farmed Atlantic salmon, *Salmo salar* L. Aspects such as sampling effort, the relationship between abundance and prevalence arising from the negative binomial distribution, and how this relationship can be used to indicate the degree of aggregation of lice on a site at a given time point are discussed. As a case study, data were drawn from over 50 com mercial Atlantic salmon farms on the west coast of Scotland between 2002 and 2006. Descriptive sta tistics and formal analysis using a linear modelling technique identified significant variations in sea lice prevalence across year class, region and season. Supporting evidence of a functional relationship between prevalence and abundance of sea lice is provided, which is explained through the negative binomial distribution.

Keywords: abundance, Atlantic salmon, negative binomial distribution, prevalence, sea lice.

Introduction

One of the major challenges faced by the commercial Atlantic salmon, *Salmo salar* L., aquaculture industry is sea lice infection (Johnson, Treasurer, Bravo, Nagasawa & Kabata 2004). Aquatic parasites pose a risk to fish health and consequentially farm produc tion; infection can inhibit growth, cause extensive damage and in extreme cases mortality of stock (Pike & Wadsworth 1999). It has also been hypothesized that sea lice originating from salmon farms present a potential risk to wild salmonid populations (Shaw & Opitz 1996; Butler 2002; McKibben & Hay 2004; Krkosek, Ford, Morton, Lele, Myers & Lewis 2007; Ford & Myers 2008).

Faced with these challenges, monitoring and integrated health management programmes have been developed and implemented in the major salmon producing regions: Canada (Westcott, Hammell & Burka 2004; Saksida, Constantine, Karreman & Donald 2007); Chile (Zagmutt Vergara, Carpenter, Farver & Hedrick 2005); Ireland (O'Donohoe, Kane, Kennedy, Nixon, Power, Naughton & Jackson 2007); Norway (Heuch, Bjorn, Finstad, Holst, Asplin & Nilsen 2005); and Scotland (Treasurer & Pope 2000). These programmes have been largely motivated by investigations into the epidemiology of sea lice (Bron, Sommerville, Wootten & Rae 1993; Sch ram, Knutsen, Heuch & Mo 1998; Revie, Get tinby, Treasurer, Grant & Reid 2002; Revie, Gettinby, Treasurer & Wallace 2003), effective monitoring and treatment strategies (Grant & Treasurer 1993; Rae 2002; Revie, Robbins, Get tinby, Kelly & Treasurer 2005; Revie, Hollinger, Gettinby, Lees & Heuch 2007), and efficacy studies of therapeutants (Stone, Roy, Sutherland, Ferguson, Sommerville & Endris 2002; Gustafson, Ellis, Robinson, Marenghi & Endris 2006; Lees, Baillie, Gettinby & Revie 2008a). A common theme throughout these studies is the use of abundance as the primary measure of sea lice infection; sea lice monitoring, sampling strategies and treatment

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intervention triggers are typically based around abundance as the key measure.

In the context of Scotland, the adoption of abundance over other measures has been motivated by historical results, where a large proportion of sampled farmed fish had at least one louse present (J W Treasurer, personal communication). Therefore, the sea lice prevalence was typically close to 100% and as a consequence prevalence was uninformative in comparison to abundance as a summary measure.

Influenced by a number of recently observed trends in sea lice infection dynamics on Scottish salmon farms, this study assesses the implications of adopting prevalence as a summary measure. For example, the distribution of *Lepeophtheirus salmonis* on farmed Atlantic salmon has been shown to vary both spatially and temporally depending on a range of factors including seasonality, site location and treatment intervention (Revie *et al.* 2003). In addition, a decreasing trend in *L. salmonis* abundance has recently been reported on Scottish farms (Lees, Gettinby & Revie 2008b). Therefore, the sole use of abundance may no longer be sufficient or informative for summarizing sea lice burden with respect to these new trends, where the diversity and dynamics within a parasite population can impact on epidemiological studies such as the accurate determination of infection burden. If a high degree of aggregation exists in the numbers of parasites per host, then a large number of hosts must be sampled to obtain an accurate estimate of abundance.

In comparison to analysis of farmed salmonid populations, prevalence has been more widely used to measure sea lice infection on wild populations (Todd, Walker, Hoyle, Northcott, Walker & Ritchie 2000; Costello 2006; Todd, Whyte, MacLean & Walker 2006; Urquhart, Pert, Kilburn, Fryer & Bricknell 2008). This investigation into the merits of prevalence thus has a wider relevance to studies of wild salmonid populations. The advantages of using prevalence as an additional measure of lice burden are highlighted. Aspects such as sampling effort, the relationship between abundance and prevalence arising from the negative binomial distribution, and how these relationships can be used to indicate the degree of aggregation of lice found on a site are discussed. As a case study, the implications of adopting prevalence are illustrated through the analysis of the population structure and epidemiology of *L. salmonis* on data gathered from Atlantic salmon farms in Scotland.

Materials and methods

Data

Sea lice data were made available from 50 commercial Atlantic salmon farms located along the west coast of Scotland during the period 2002 06. Each farm site operated a 2 year production cycle, stocked with a single year class of fish. Farms were typically stocked between January and June of the first production year and harvested between August and December of the second. On occasions fish were introduced into some sites as early as October and others were not harvested until spring of the third year of production.

In accordance with previous studies (Revie *et al.* 2003; Lees *et al.* 2008b), sites were grouped together based on geographic location. Sites on the west coast of the Scottish mainland were divided above and below the 57°N line of latitude and referred to as the 'North' (20 sites) and 'South' (12 sites) regions, respectively. Those sites classified as 'Western Isles' (18 sites) included farms on the east coast of South Uist and on both the east and west coasts of the isles of Harris and Lewis.

All sites were managed by a single industrial partner who adopted a uniform sea lice monitoring regime integrated into a health management programme. As part of this programme, sea lice levels were regularly monitored over the entire production cycle. During a single inspection between two and six pens were randomly selected dependent on the number of pens stocked (Treasurer & Pope 2000), with approximately 10 30 fish sampled randomly overall. Fish were removed from the pen by dip net, anaesthetized and examined for the presence of lice. Each fish sampled was examined according to five gender/life stages of *L. salmonis*: chalimus, pre adult, adult male, non gravid female and gravid female. In this case study, only the *L. salmonis* chalimus and mobile stages were analysed, the latter being the aggregation of the pre adult, adult male, non gravid female and gravid female stages.

Measurements

The main focus of this study was to investigate the relationship between abundance (Bush, Lafferty, Lotz & Shostak 1997), the mean lice per fish, and prevalence, the proportion of fish sampled with at least one observed louse. The relationship between prevalence and other measures such as intensity, the abundance of infected sampled fish, could also be investigated. However, this study limits its scope to abundance for a number of reasons: (i) at present abundance is the most commonly adopted measure of lice burden; (ii) as prevalence tends to 100%, intensity tends to abundance; and (iii) as prevalence tends to 0%, the number of sampled infected fish also decreases thereby providing a potentially more skew estimate of infection in comparison to prevalence and abundance.

Sea lice burden was measured and analysed at different levels of granularity, both spatially and temporally. Sample statistics were derived for each sample recorded across the production cycle of each site. For analysis of trends, the data from each site were pooled at various levels of granularity such as region (North, South and Western Isles), year, year class, and season. When lice burden was analysed on a yearly basis, sites were labelled as being in the first or second year of production to take account of the age of the stocked fish. When sites were analysed over the full production cycle, the grouping of sites was by year class. During the period under consideration data from four full year classes were available, i.e. 2002 03, 2003 04, 2004 05 and 2005 06.

Lice counts were also grouped seasonally. The definition of season followed the official UK MET office definition (UK MET Office 2008); Winter included December, January and February; Spring, March, April and May; Summer, June, July and August; and Autumn, September, October and November.

Statistical tests

Statistical comparison of mean prevalence between geographic regions, year class and season was under taken using a general linear model (GLM) approach with follow up pair wise comparisons using Tukey's test. As the variances of the prevalence measurements were not always equal, an arc sine square root transformation was applied to the prevalence of each sample before statistical analysis (Zar 1998). All summarized results presented in this paper were transformed back into the original prevalence scale.

Results

Overview of sea lice prevalence between 2002 and 2006

Figures 1 and 2 display the mean prevalence observed in sites pooled by year for *L. salmonis* chalimus and mobiles, respectively. For each year sites were further grouped by production stage (i.e. first or second year). The trend in *L. salmonis* chalimus (Fig. 1) was relatively consistent in the first year of production, with mean prevalence ranging from 0.20 to 0.26. In comparison, there was a decreasing trend observed from 2002 to 2006 for sites in the second year of production. Analysing sites on a yearly basis, the prevalence of *L. salmonis* chalimus was lower in sites in the first year of production between 2002 and 2004. However, this pattern reversed in 2005 and 2006, with those sites in the second year of production reporting lower prevalence of chalimus on average; this was partic ularly notable in 2006.

In contrast, mobile prevalence was consistently higher in the second year of production when compared to the first (Fig. 2). Mobile prevalence was relatively consistent across all years analysed for sites in the first year of production, with 2005 recording the lowest prevalence on average. This trend was mirrored for those sites in the second year of production, with 2005 again recording the lowest mean prevalence.

The regional variation in sea lice prevalence was also analysed; Figs 3 & 4 display the prevalence of chalimus and mobiles with sites grouped into the North, South and Western Isles regions. The overall profile of chalimus and mobiles indicated that prevalence varied regionally, as well as among years and across the production stage on a site. While those sites in the North and South broadly followed the national trend, sites from the Western Isles were found to have a higher prevalence of chalimus (Fig. 3). A similar pattern of infection was observed

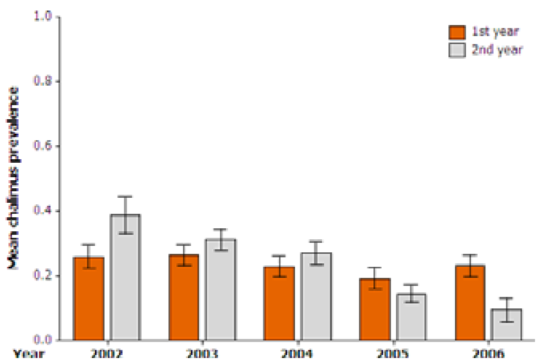

Figure 1 A comparison of mean *Lepeophtheirus salmonis* chalimus prevalence by year, with farm sites further grouped into the first or second year of production. The associated 95% confidence interval for mean prevalence is also given.

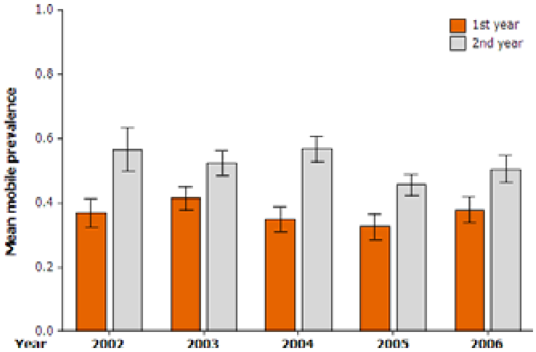

Figure 2 A comparison of mean *Lepeophtheirus salmonis* mobile prevalence by year, with farm sites further grouped into the first or second year of production. The associated 95% confidence interval for mean prevalence is also given.

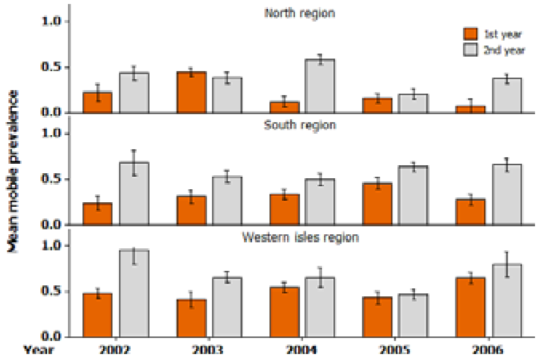

Figure 4 A comparison of mean prevalence and associated 95% confidence interval of *Lepeophtheirus salmonis* mobiles by year and region. Farm sites were further grouped by production stage (i.e. first or second year).

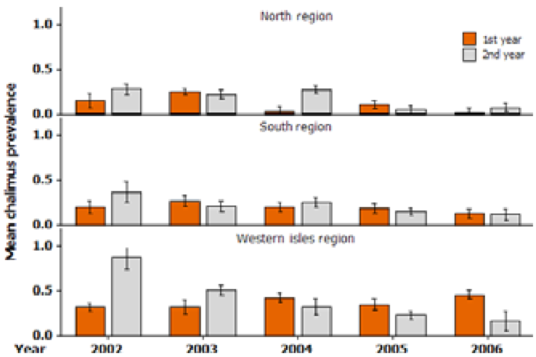

Figure 3 A comparison of mean prevalence and associated 95% conference interval of *Lepeophtheirus salmonis* chalimus by year and region. Farm sites were further grouped by production stage (i.e. first or second year).

for mobile sea lice across the three regions (see Fig. 4). In general, these observations were in agreement with previous studies of lice burden which adopted abundance as a descriptive measure (Lees *et al.* 2008b).

To further analyse the prevalence of sea lice across the production cycle, as well as to investigate the relationship between prevalence and abundance, lice burden was plotted across the entire production cycle. Figures 5 & 6 illustrate the seasonal variation in sea lice prevalence and abundance over the 2 year production period for all sites, averaged over the years 2002 to 2006. Abundance and prevalence are displayed on the same plot with the left hand axis indicating abundance and the right hand axis prevalence.

There was evidence of seasonal variation in the signature for chalimus prevalence (Fig. 5), with an increase during the winter and spring period of the second year followed by a drop in the summer season. This was again followed by an increase in prevalence for autumn and winter before harvesting commenced. The seasonal trend in abundance followed that of prevalence. A relative increase in prevalence was accompanied by an increase in abundance and vice versa, suggesting an approximately linear relationship between the measures.

In contrast, the prevalence signature for mobiles exhibited a strong seasonal trend (Fig. 6). The initial spring and summer seasons in the first production year had a low prevalence of approximately 30%, before an increase in infection over the following autumn through to spring of the second production year. Again, summer of the second production year marked a drop in prevalence subsequent to the wide administration of treatments (Lees *et al.* 2008b) followed by a similar increase over autumn and winter of the second year. During this period, mobile prevalence was between 55% and 75% on average. Mobile abundance also followed a similar pattern to prevalence, with abundance increasing during the autumn and winter periods before decreasing during the summer of the second year of the production cycle. Abundance then increased towards the end of the production cycle until harvesting commenced.

These observations provide supporting evidence of a functional relationship between sea lice abundance and prevalence. This relationship can be explained through a number of models all of which depend on the underlying assumption applied to the count data; He, Gaston & Wu (2002) provide a detailed overview of the relationship between

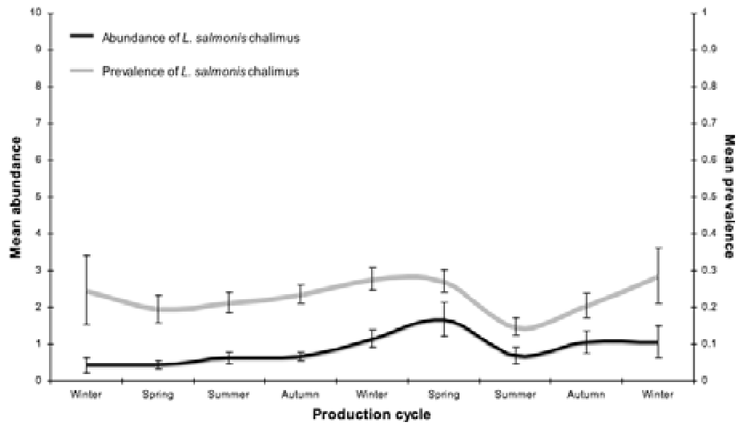

Figure 5 The prevalence and abundance profile with associated 95% confidence interval of *Lepeophtheirus salmonis* chalimus sea lice over the 2-year production cycle between 2002 and 2006. Note that there are nine time-points in this plot as production often commenced during the middle of the winter season with the start of harvesting beginning during autumn-winter of the second year of production.

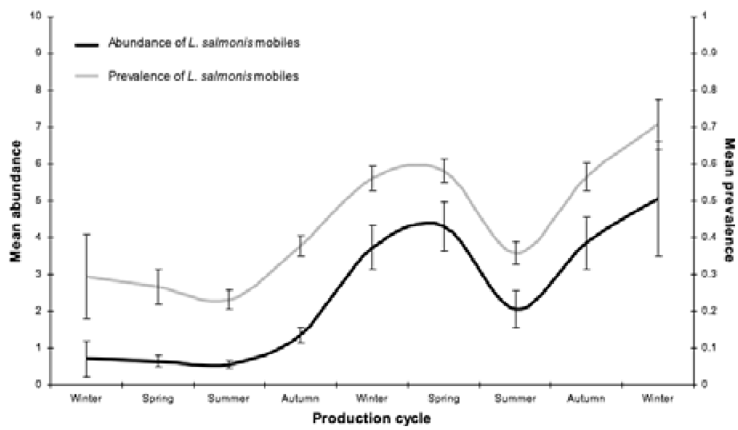

Figure 6 The prevalence and abundance profile with associated 95% confidence interval of *Lepeophtheirus salmonis* mobile sea lice over the 2-year production cycle between 2002 and 2006.

prevalence and abundance across a number of these assumptions. The most common explanation is to assume the underlying distribution of sea lice follows a negative binomial distribution, a discrete probability distribution often used to describe biological count data (Bliss & Fisher 1953), including parasite counts on host species (Shaw, Grenfell & Dobson 1998). The negative binomial distribution can be defined as the probability of observing a specific value x (in case discussed here, the number of lice on a sampled fish):

$$\Pr(X = x) = \binom{\kappa + x - 1}{\kappa - 1}\left(\frac{\mu}{\kappa}\right)^{x}\left(1 + \frac{\mu}{\kappa}\right)^{(\kappa + x)}$$

where $x = 0,1,2,\ldots$

The parameter μ is the arithmetic mean or expected value of x, which is equivalent to the mean abundance of the sampled population. The κ parameter measures the dispersion of the distribu tion and enables the modelling of different popu lation characteristics, in this case changes in mean abundance and the degree of parasite aggregation.

Assuming the underlying distribution of sea lice follows a negative binomial distribution, the rela tionship between abundance and prevalence is given by

$$p = 1 - \Pr(X = 0) = 1 - \left(1 + \frac{\mu}{\kappa}\right)^{\kappa}$$

where prevalence p is the proportion of non zero lice counts, μ is the corresponding abundance and κ is the dispersion parameter of the population. For small values of μ, this approximates to a linear relationship between prevalence and abundance, taking into consideration the variance in dispersion observed in the lice population. Through this relationship, prevalence can provide an approximation of abun dance and vice versa, thus explaining the approxi mately linear relationship indicated in Figs 5 & 6 between these measures of sea lice burden.

Analysis

The variation in mean *L. salmonis* chalimus and mobile prevalence across region, year class, and season was formally tested. Tables 1 and 2 present the statistical analysis of these factors for chalimus and mobile prevalence, respectively.

Chalimus

Table 1 shows the results of the GLM analysis for mean chalimus prevalence. All factors were found to be statistically significant ($P < 0.05$) and are listed along with least squares estimates of chalimus prevalence and their associated 95% confidence intervals. Significant interaction factors are also listed and further illustrated in Fig. 7.

Chalimus were found to be more prevalent in sites located in the Western Isles region (0.34, CI [0.30, 0.38]), with approximately one in three fish infected. In comparison, one in seven fish were found with chalimus on sites in the North (0.13, CI [0.10, 0.16]), and one in four fish in the South (0.23, CI [0.20, 0.27]). Chalimus was less prevalent on sites that began production in 2004 and 2005, compared to the earlier year classes.

Significant interactions were indicated between both region and year class ($P < 0.05$), and region and season ($P < 0.05$) (Table 1). Figure 7a high lights this interaction across region over the 4 year classes under investigation. The Western Isles reported a downward trend across year classes, while for both the North and South regions there was an increase in chalimus prevalence in 2003 in comparison to 2002, followed by a drop in 2004. The North region differed from the South in 2005, where an increase in prevalence was shown in comparison to 2004.

Chalimus were more prevalent during the winter. This trend can be explained by the interaction between region and season; Fig. 7b illustrates the seasonal signatures for the prevalence of chalimus over the production cycle across the three regions. The South region observed a more cyclical trend than the other two regions, with clear peaks in the winter and troughs during spring and summer. The Western Isles indicated a constant infection, while the North region observed a gradual increase in chalimus

Table 1 Results of the general linear model analysis of the mean *Lepeophtheirus salmonis* chalimus prevalence across region, year class and season

Variable	*P* value	Class	Prevalence of chalimus: Least squares mean	Prevalence of chalimus: 95% CI
Region	< 0.01	North	0.13	[0.10, 0.16]
		South	0.23	[0.20, 0.27]
		Western Isles	0.34	[0.30, 0.38]
Year class	< 0.01	2002	0.27	[0.24, 0.30]
		2003	0.29	[0.26, 0.32]
		2004	0.18	[0.16, 0.21]
		2005	0.19	[0.16, 0.22]
Season	< 0.01	Winter (Year 1)	0.26	[0.11, 0.40]
		Spring (Year 1)	0.17	[0.12, 0.21]
		Summer (Year 1)	0.23	[0.20, 0.26]
		Autumn (Year 1)	0.23	[0.21, 0.26]
		Winter (Year 1 2)	0.29	[0.26, 0.32]
		Spring (Year 2)	0.25	[0.23, 0.28]
		Summer (Year 2)	0.16	[0.13, 0.19]
		Autumn (Year 2)	0.24	[0.20, 0.27]
		Winter (Year 2)	0.29	[0.23, 0.36]
Region * Year class	< 0.01	See Figure 7a		
Region * Season	< 0.01	See Figure 7b		

The table indicates those variables found to be statistically significant ($P < 0.05$). Mean *L. salmonis* chalimus prevalence and their 95% confidence intervals are also provided.

Table 2 Results of the general linear model analysis of mean *Lepeophtheirus salmonis* mobile prevalence across region, year class and season

Variable	*P* value	Class	Prevalence of mobiles: Least squares mean	Prevalence of mobiles: 95% CI
Region	< 0.01	North	0.32	[0.28, 0.35]
		South	0.46	[0.42, 0.50]
		Western Isles	0.51	[0.47, 0.56]
Year class	< 0.01	2002	0.42	[0.39, 0.45]
		2003	0.47	[0.44, 0.51]
		2004	0.38	[0.35, 0.41]
		2005	0.45	[0.41, 0.48]
Season	< 0.01	Winter (Year 1)	0.25	[0.09, 0.42]
		Spring (Year 1)	0.21	[0.16, 0.26]
		Summer (Year 1)	0.22	[0.18, 0.25]
		Autumn (Year 1)	0.37	[0.34, 0.40]
		Winter (Year 1 2)	0.54	[0.51, 0.57]
		Spring (Year 2)	0.57	[0.54, 0.60]
		Summer (Year 2)	0.37	[0.34, 0.40]
		Autumn (Year 2)	0.59	[0.56, 0.63]
		Winter (Year 2)	0.75	[0.68, 0.82]
Region * Year class	< 0.01	See Figure 8a		
Region * Season	< 0.01	See Figure 8b		

The table indicates those variables found to be statistically significant ($P < 0.05$). Mean *L. salmonis* mobile prevalence and their 95% confidence intervals are also provided.

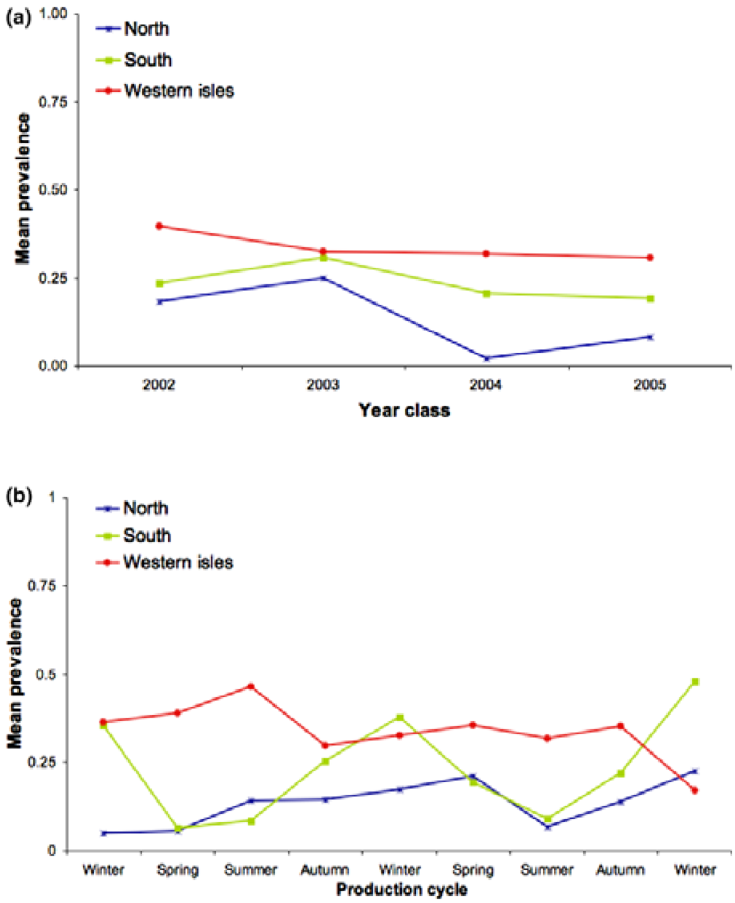

Figure 7 Profile plots reporting the least squares *Lepeophtheirus salmonis* chalimus mean prevalence associated with significant ($P < 0.05$) interaction factors between (a) region and year, and (b) region and season.

prevalence across the production cycle with a drop in the spring of the second year of production.

Mobiles

Table 2 shows the results of the GLM analysis of mean mobile prevalence. All factors were found to be statistically significant ($P < 0.01$). Significant interaction factors are also listed and further illustrated in Fig. 8.

Mobiles were also found to be more prevalent in sites in the Western Isles (0.51, CI [0.47, 0.56]), where approximately one in two fish were infected with mobiles. In the North (0.32, CI [0.28, 0.35]) one in three fish had at least one mobile louse, however, the difference between the Western Isles and the South (0.46, CI [0.42, 0.50]) was not significant. A significant interaction between region and year class ($P < 0.05$), and region and season ($P < 0.05$) was indicated. Figure 8a highlights this interaction across region over the 4 year classes under investigation. Sites in the Western Isles reported a downward trend across year classes, while the North region followed a similar pattern to that observed with chalimus, with an increase in 2003 and 2005, in comparison to the subsequent year classes. However, the South region reported a gradual upward trend from 2002 to 2005.

Figure 8b illustrates the regional mobile prevalence signatures across a production cycle. All regions show a relatively similar trend with a gradual increase in mobile prevalence across the production cycle and a sharp rise in the period prior to harvesting. The South region provided evidence of a sharper increase in mobile prevalence during the first year of production, although all regions observed a drop in mobile prevalence during the summer months of the second year of production.

Discussion

As this case study of data drawn from salmon farms in Scotland serves to illustrate, prevalence is an informative measure for sea lice epidemiology and

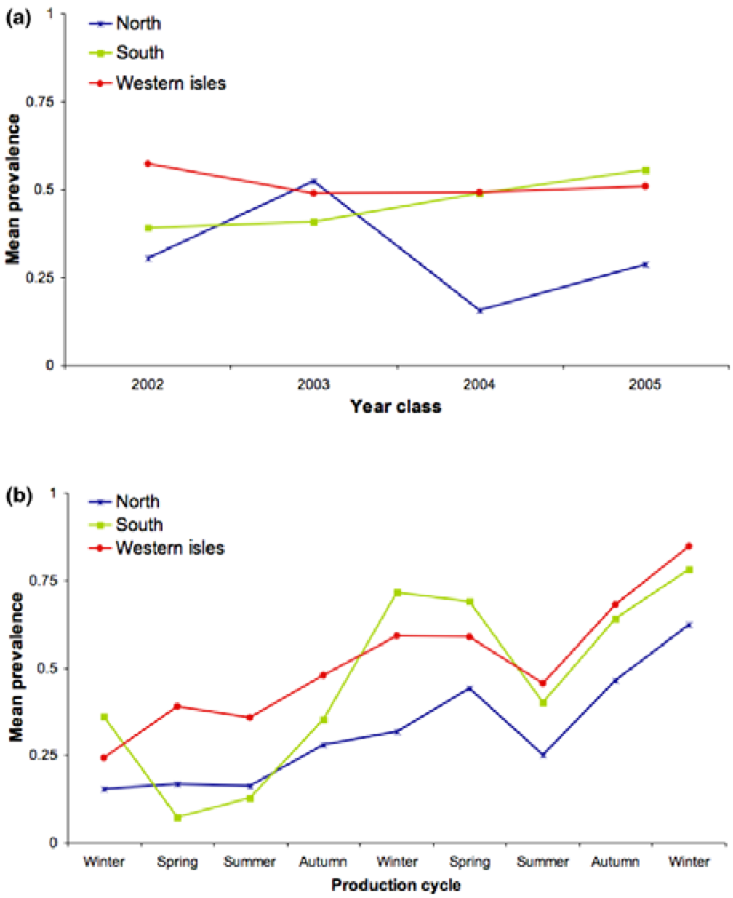

Figure 8 Profile plots reporting the least squares *Lepeophtheirus salmonis* mobile mean prevalence associated with significant ($P < 0.05$) interaction factors between (a) region and year, and (b) region and season.

population structure. It was observed in this analysis that sea lice prevalence varied significantly across region, temporally over seasons, and also production years. For example, farms located in the Western Isles region exhibited a higher prevalence of *L. salmonis* chalimus and mobile sea lice in comparison to farms in the North and South of the Scottish mainland. Also, during the production cycle, the prevalence of *L. salmonis* mobiles was higher during winter in comparison to the summer months of the second year of production. This variation was a consequence of a range of underlying factors such as infection pressure and treatment intervention amongst others. Overall, these general observations were in agreement with the trends reported using abundance as a summary measure (Lees *et al.* 2008b).

As highlighted in this study, the relationship between prevalence and abundance can be explained through the negative binomial distribution. This approximately linear relationship indicates that given the sample prevalence, an estimate for abundance can be derived without the need of detailed lice counts. This relationship raises a number of implications and potential benefits in the context of simplified monitoring and sampling protocols. For example, the current monitoring protocol in Scotland advises that fish be removed from pens and anaesthetized, with lice counted by species and stage. An advantage of prevalence over abundance is that sampling effort is reduced because only the presence or absence of a louse type need be recorded rather than a count. Recording the presence or absence will decrease the time fish are out of the pens, reducing stress, as well as minimizing the effort in counting by stage and species.

Adopting prevalence may also provide a more stable measure than abundance for monitoring chalimus stages. Accurate chalimus counts in practice are often difficult to achieve, with counts doubled in some cases to avoid the problem of underestimation (Treasurer & Pope 2000). However, under the prevalence model, only the presence or absence of chalimus is required. Given the relationship between prevalence and abundance through the negative binomial distribution, better estimates of chalimus infection may be achieved.

Reporting prevalence together with abundance may help indicate estimate problems for abundance because of atypical samples. For example, as parasite abundance decrease, the likelihood of sampling an infected host also decreases. Therefore, through traditional means [i.e. in Scotland, randomly sampling 10 30 fish from between two and six cages at each farm (Revie *et al.* 2007)] the accuracy of estimating abundance at low prevalence also decreases because of the increased variability and uncertainty in the measure. However, the use of prevalence alongside abundance can help identify cases of under or overestimation of infection, such as when highly infected fish skew the sample estimate.

The use of prevalence has further implications in the light of the potential of new passive monitoring technologies (Tillett, Bull & Lines 2000). Accurate counts of lice may not be achievable with current technology, but the identification of the presence or absence of adult lice stages can be realized (J A Lines, personal communication). This should allow for larger numbers of fish to be sampled automatically without stress to fish or the human effort of removing fish from the pen. Large sample sizes would provide accurate estimates of lice burden in terms of prevalence and the subsequent estimation of abundance through the negative binomial distribution.

The potential for large sample sizes using passive monitoring may also address one of the current limitations of prevalence as a summary measure, which is a coarse measure given small sample sizes. For example, the current sampling practice in Scotland is to remove five fish from a number of pens. Therefore, analysing differences in prevalence at a pen level under this protocol is problematic; with a sample size of 5, only 6 values of prevalence are possible, i.e.$\{0/5, 1/5, \ldots, 5/5\}$. As a consequence, a change from one fish out of five infected to two out of five is a shift in prevalence from 20% to 40%. However, as the sample size increases, this uncertainty in prevalence accuracy decreases rapidly, with a sample size of 15 assumed to be a reasonable trade off between sampling effort and estimate accuracy (Jovani & Tella 2006).

Treatment intervention or 'trigger' levels are conventionally set according to the average number of lice per fish (Heuch *et al.* 2005; Revie *et al.* 2007; Saksida *et al.* 2007). A breach of the trigger level will typically result in treatment intervention or harvesting. Setting a trigger level in terms of prevalence would require a move from an average number of lice per fish estimate to using a proportion of fish within a sample that are infected. A number of strategies exist for evaluation using multi stage sampling that assess whether a population is infection free (Ziller, Selhorst, Teuffert, Kramer & Schluter 2002). The adoption of prevalence in studies of aquatic parasites would similarly require multi stage sampling approaches. To summarize, the relationship between prevalence and abundance, the potential for new passive monitoring technology, and the resulting minimization of sampling effort, are all motivating factors for continued research related to these issues.

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