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Assessment of population structure in Pacific *Lepeophtheirus salmonis* (Krøyer) using single nucleotide polymorphism and microsatellite genetic markers

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ABSTRACT

The ectoparasitic sea louse, *Lepeophtheirus salmonis* (Krøyer), has caused great concern for both wild salmon fisheries and the salmon aquaculture industry. Identifying the population structure of this parasite is important for better understanding its dispersal capabilities and controlling louse infections. Most of the sea lice population studies carried out to date have been focused on Atlantic Ocean *L. salmonis* where host parasite interactions may be quite different than those in the Pacific Ocean. In this study we examined the genetic population structure of sea lice from 12 Pacific Ocean samples ranging from the Bering Sea to southern Vancouver Island using 27 microsatellite and 87 single nucleotide polymorphisms (SNPs) from 25 loci. Louse samples were analyzed for genetic differentiation among farmed and wild host salmon in addition to temporal differentiation from 2007 to 2009 and spatial differentiation over the entire sampling range. Our analyses failed to resolve significant population structure in *L. salmonis* for any of these three comparisons. Our results therefore support a hypothesis of high migration and panmixis of *L. salmonis* within the studied area of the Pacific Ocean.

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1. Introduction

The sea louse, *Lepeophtheirus salmonis* (Krøyer), is an ectoparasitic copepod of marine salmonids in the northern hemisphere (Kabata, 1979). Sea louse infections are common in adult Pacific salmonids (Nagasawa, 2001; Beamish et al., 2005; Costello, 2006) as well as in farmed Atlantic salmon (*Salmo salar*) in British Columbia. The introduction of salmon farms to the Pacific Ocean may affect infection rates of wild fish through increased *L. salmonis* abundance and exposure of juvenile salmonids to these parasites (Krkošek et al., 2005, 2007). Sea louse infections cause host tissue damage, stress and immune dysregulation, which can lead to secondary infection and increased likelihood of mortality, conditions which may be magnified in juvenile fish (Reviewed in Costello, 2006; Wagner et al., 2008). In addition to negative effects on wild hosts, louse infections on farmed Atlantic salmon are detrimental to the aquaculture industry, resulting in large economic losses (Johnson et al., 2004; Costello, 2009).

An important part of understanding and controlling *L. salmonis* infections is identifying the dispersal capabilities of this species. Dispersal may be possible during all 10 *L. salmonis* life stages; larval stages are planktonic, juvenile through adult stages are mobilized through host migration, and eggs are likewise distributed through maternal release on migrating salmon (Boxaspen, 2006; Johnson and Albright, 1991; Kabata, 1979). This high potential for dispersal, coupled with the significant rate of *L. salmonis* infection in large populations of wild Pacific salmon (Beamish et al., 2005) may result in considerable gene flow and little population structure over the natural range of *L. salmonis* in the Pacific Ocean. The introduction of Atlantic salmon farms to the coast of BC may facilitate rapid, localized increases in louse population density which could affect parasite population dispersal and alter the population structure of this parasite in the areas surrounding farms; if the migration rate into these areas is low, louse populations should remain relatively isolated (Todd et al., 1997). If farm populations are reproductively isolated from lice on wild salmon, then reduced gene flow may be detected through the use of genetic markers that compare louse samples collected from wild and farmed salmon.

Most studies that have examined the population structure of *L. salmonis* have focused on the Atlantic Ocean, particularly the north-eastern Atlantic, where dispersal mechanisms and selective pressures on lice may differ from those experienced by Pacific *L. salmonis*. These Atlantic Ocean studies have produced contradictory conclusions, with results ranging from little to no detectable structure across the Atlantic (Tjensvoll et al., 2006; Todd et al., 2004) to significant structure within a relatively small coastal region (Dixon et al., 2004; Nolan and Powell, 2009). In Ireland, significant temporal structure has been detected between lice collected from the same site sampled multiple times throughout a single year (Nolan and Powell, 2009).

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These conclusions might be affected by small sample sizes and the previously limited availability of molecular markers. This, in addition to the genetic divergence between Atlantic and Pacific *L. salmonis* (Yazawa et al., 2008), warrants further investigation, particularly in the Pacific, where currently only one study by Boulding et al. (2009) has addressed population structure. This study has reported strong population structure in the Pacific, even between samples collected from wild and farmed hosts in the same archipelago; however, only one mitochondrial locus and few louse samples were analyzed, which may have resulted in poor representation of the *L. salmonis* genome.

The farming industry employs several strategies to manage *L. salmonis* infestations, including fallowing and spatial separation of farms from wild hosts. In addition to the use of these non-chemical treatment methods, chemical therapeutants remain an important control method (Denholm et al., 2002; Read and Fernandes, 2003; Costello, 2006). As dependence on delousing drugs has increased, the efficacy of these drugs in treating *L. salmonis* infections has declined, particularly in Atlantic Ocean farms (Jones et al., 1992; Fallang et al., 2004; Sevatdal and Horsberg, 2003; Denholm et al., 2002; Lees et al., 2008). Although Pacific and Atlantic forms of *L. salmonis* are genetically distinct (Todd et al., 2004; Tjensvoll et al., 2006; Yazawa et al., 2008), independent development of drug resistance may still be possible in Pacific lice (Denholm et al., 2002). Development of drug resistance has been reported in a closely related species, *Caligus rogercresseyi*, on *S. salar* farms in Chile (Bravo et al., 2008). However, if large wild pacific salmonid populations act as a mechanism for dispersal of *L. salmonis,* resistant louse strains may be less likely to develop due to the homogenizing effects of migration and disparate selective pressures found in wild and farm environments (Sevatdal et al., 2005).

In the present study, we present the most comprehensive population genetic survey of *L. salmonis* to date. We employ the largest set of microsatellite markers and the first reported use of nuclear single nucleotide polymorphisms (SNPs) in population structure analysis of *L. salmonis.* Further, linked SNPs were combined into haplotypes in addition to being treated independently in an effort to increase statistical power (Morin et al., 2009; Haasl and Payseur, 2010). A total of 114 markers from 52 nuclear loci (27 microsatellites and 25 SNP loci) were used in the evaluation of 562 sea lice from 12 sample collections that range from the Bering Sea to southern Vancouver Island. Our analysis was conducted to determine if *L. salmonis* population structure exists in the Pacific Ocean. Understanding the population structure of Pacific *L. salmonis* is important for the successful management of this pest on salmon farms and evaluation of the impact of infections of wild salmonids.

2. Materials and methods

2.1. Sample collection

Lepeophtheirus salmonis were collected from 9 sites in 2009 along the central coast of BC and Vancouver Island (Fig. 1). These collections included 3 *S. salar* farm sites, 2 of which were sampled in 2007 in addition to 2009. Each of these 9 sites was within 675 km of the other sites. One out-group from the Bering Sea was also sampled in 2007; this site was approximately 3160 km from the closest neighboring site. Between 38 and 56 individuals from each site were included in the analysis (see Table 1 for collection details and Fig. 1 for collection locations).

2.2. DNA extractions

DNA was extracted from ethanol-preserved tissue using a Chelex extraction buffer protocol in a 96 well format (adapted from Nelson et al., 1998). Approximately 2 mm^2 of tissue from the anterior of each louse, avoiding mouthparts and reproductive region, was placed in

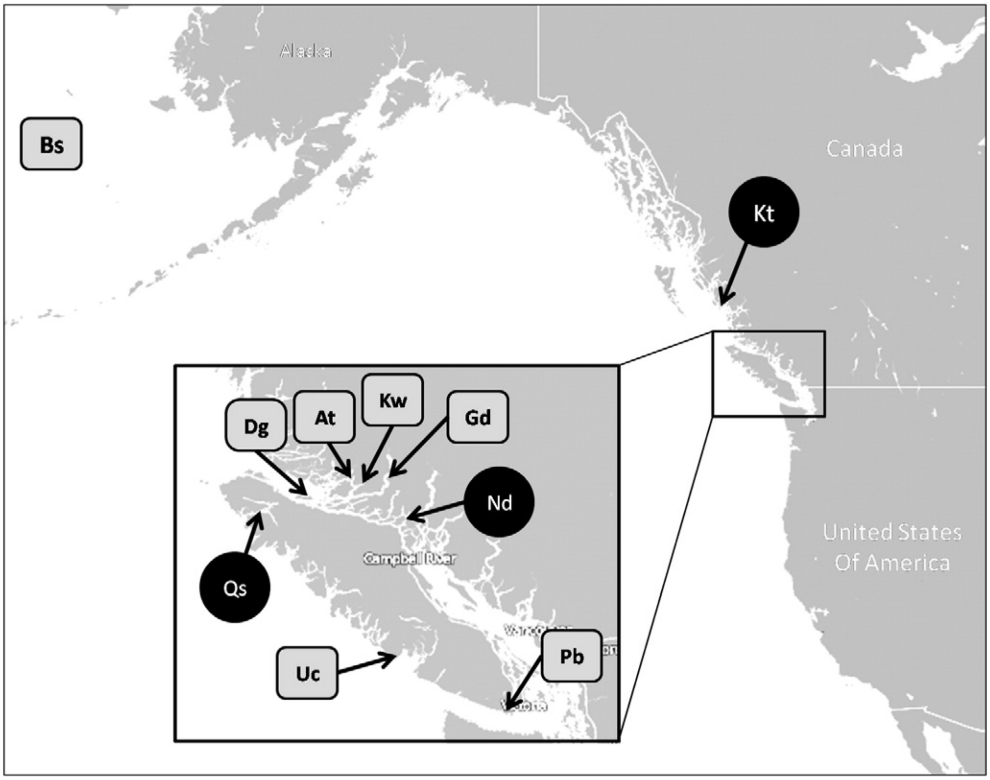

Fig. 1. Map of the collection locations for the *L. salmonis* groups. Maps redrawn from OpenStreetMap; Map data © OpenStreetMap (and) contributors, CC-BY-SA, http://www.openstreetmap.org/.

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