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Quantitative genetic basis for resistance to *Caligus rogercresseyi* sea lice in a breeding population of Atlantic salmon (*Salmo salar*)

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ABSTRACT

A total of 1511 Atlantic salmon smolts representing 75 full-sib and 40 half-sib families from the Antares S.A. breeding program were challenged with *Caligus rogercresseyi* in order to assess the quantitative genetic components of resistance to infection by this parasite. After three weeks of acclimatization in the experimental hatchery conditions, fish were distributed in three 6-m^3 tanks, with an equal number of fish per family per tank. An infection rate of 100 copepods per fish was used for the experiment. Resistance/susceptibility was recorded individually at approximately 5 days (range = 4–7 days) after infestation as the number of sessile lice per fish on all fins (FSL), the estimated total number of sessile lice per fish (TSL), and the total number of sessile lice per fish per unit of body weight (TSL/BW_s). Resistance/susceptibility was also recorded at approximately 25 days (range = 24–26 days) after infestation as the total number of mobile lice per fish (TML) and the total number of mobile lice per fish per unit of body weight (TML/BW_m). The level of infestation on days 5 and 25 post-infestation was 30.7 (SD = 16.3) sessile parasites (TSL) and 13.2 (SD = 6.0) mobile parasites (TML), respectively. A high level of phenotypic variation was observed for parasite load traits when considering fin and total counts as well as counts per unit of body weight (CV = 46–56%). Significant differences between tanks ($P<0.05$) were observed in FSL and TSL. Weight was included as a covariate ($P<0.05$) when performing the genetic analysis on FSL, TSL and TML. Estimated heritabilities for parasite counts in the sessile stage were of low to medium magnitude (0.22–0.34), whereas in the mobile stage heritabilities were very low (0.03–0.06) and not significantly different from zero ($P>0.05$). The genetic correlations between parasite counts in the sessile (FSL, TSL) and the mobile (TML) stages were very high (0.99). Also, body weight shows a high genetic correlation with fish parasite count measured at both the sessile (0.61–0.65) and the mobile stages (0.95). These results show that there is enough additive genetic variation for selection to be applied for improving resistance to sea lice. Measurement of genetic resistance in the sessile stage is a better option than measurement in the mobile stage as a selection criterion in breeding programs of Atlantic salmon aimed at improving resistance to *C. rogercresseyi*.

1. Introduction

Sea lice represent one of the most important health problems in the salmon industry (Costello, 2009). Although fish infestation by sea lice does not usually cause mortality, it does produce stress (Fast et al., 2006; Finstad et al., 2000), loss of appetite, depression of the immune system, and skin damage (Mackinnon, 1998; Tully and Nolan, 2002) and can therefore contribute to a decreased performance and an increased susceptibility to other diseases (Finstad et al., 2000; Pike and Wadsworth, 1999).

In recent years, selection for resistance to pathogens such as *Aeromonas salmonicida* (that causes furunculosis), infectious salmon anemia virus (ISAV) and infectious pancreatic necrosis virus (IPNV) has been performed in Atlantic salmon breeding programs (Gjedrem, 2005) as a key and complementary strategy to improve fish health, productivity and sustainability in salmon farming. However, there are still no breeding programs that include sea lice resistance in their breeding objectives.

Studies of Atlantic salmon infected with sea lice species such as *Lepeophtheirus salmonis* (Gjerde et al., 2010; Glover et al., 2005; Kolstad et al., 2005) and *Caligus elongatus* (Mustafa and MacKinnon, 1999) have shown the existence of sufficient additive genetic variation for increasing resistance to sea lice through selection. These studies have also shown that challenge tests carried out in laboratory conditions are a good option for resistance assessment, as disease

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traits show higher heritabilities than when assessed in field tests, and the genetic correlation between resistance in sea breeding conditions and resistance in laboratory conditions is high (approximately 0.9) (Gjerde et al., 2010; Kolstad et al., 2005).

Caligus rogercresseyi is the only sea louse that affects the Chilean salmon industry in the grow-out stage (Boxshall and Bravo, 2000). The annual losses attributed to this parasite are estimated at over 178 million US dollars (Costello, 2009; FAO, 2008; Rozas and Asencio, 2007). This species is endemic to Chile and has been transmitted to salmon from native fish species such as *Eleginops maclovinus* and *Odonthestes regia* (Carvajal et al., 1998). Its life cycle is described by eight development stages (Gonzalez and Carvajal, 2003): two nauplius, one copepodid, four chalimus and the adult. The nauplius stages (n1-2) and the copepodid stage (the infectious stage) are planktonic stages. The four chalimus stages (chalimus 1–4) are sessile stages and the adult is a mobile stage. Despite the importance of this parasite in the salmon industry, there are no available estimates of genetic parameters for resistance to it.

The objective of this study was to estimate genetic parameters for resistance to *C. rogercresseyi* in Atlantic salmon under a system of controlled infestation. The ultimate goal was to determine the benefit of including resistance to sea lice as a breeding goal in Chilean Atlantic salmon selection programs.

2. Materials and methods

2.1. Fish

Data from a total of 1511 Atlantic salmon representing 75 full-sib families (40 half-sib families) of the Antares S.A. breeding program in Chile were available for the study. These families originated from 75 females that were mated with 40 males under a nested mating system. Eggs from each family were produced during the spawning season of 2008. Fish were individually pit tagged in April 2009 at an average weight of 31 g (SD = 8.0 g) and transferred as smolts in October 2009 to the Aquadvice S.A. experimental station located at Quillaipe, Puerto Montt (Chile). At the experimental station, fish went through a three-week acclimatization period under seawater conditions (salinity of 33‰ and temperature of 12 °C). A health check was performed prior to transfer in order to verify that the fish were free of any viral or bacterial diseases.

2.2. Experimental design and recorded traits

The fish, with an average weight of 130 g, were distributed in equal numbers per family in three tanks of 6 m^3 each and infested with parasite larvae at the copepodid stage. Families were equally represented in the three tanks and each tank contained between 18 and 21 fish of each full-sib family. The number of copepods used per tank was 50,000 (approximately 100 per fish). After infestation, a period of ten hours was managed with a stopped-flow tank at 13 °C and supplied with oxygen to encourage the infestation. During this period, the temperature and oxygen saturation were measured in the three tanks. Two of the tanks (tanks 1 and 2) were used to measure the resistance to caligus in the sessile stage (chalimus 2–3), and one tank (tank 3) was used to measure resistance to caligus in the mobile stage (adult). Different traits were evaluated at each stage as described below.

Parasites in the sessile stage were counted approximately 5 days after infestation (range = 4–7 days). The traits evaluated at this stage were: i) body weight (BW_s); ii) the number of sessile lice per fish on all fins (FSL); iii) the total number of sessile lice per fish (TSL); and iv) the total number of sessile lice per fish per unit of body weight (TSL/BW_s). The total number of sessile lice per fish was estimated via multiple regression using the GLM procedure of SAS (1993), and an initial sample of 80 fish was used to determine the distribution of parasites across the body area and fins. The distribution of sessile lice in the fish showed that 95% of the parasites are found on fins and only 5% on the rest of the body surface. The adjusted multiple regression equation ($R^2 = 0.93$) used to estimate TSL was:

$$TSL = -0.39 + 1.02P + 1.32V + 1.06A + 1.00C + 1.24D$$

where P, V, A, C and D are numbers of parasites on pectoral, ventral, anal, caudal and dorsal fins, respectively.

Given that almost 70% of sessile lice were found among the C and P fins, three additional traits of sessile parasite load were defined and analyzed. These were the number of sessile lice in the caudal fin per fish (CSL), the number of sessile lice in the pectoral fin per fish (PSL), and the number of sessile lice in the caudal plus pectoral fins per fish (CSL + PSL).

Parasites in the mobile stage (adults) were counted approximately 25 days after infestation (range = 24–26 days). The traits evaluated at this stage were: i) fish body weight (BW_m); ii) the total number of mobile lice counted per fish (TML); and iii) the total number of mobile lice per fish per unit of body weight (TML/BW_m). Also, at this time, the sex of the fish was recorded through necropsy.

2.3. Statistical analysis

Basic statistics for the different traits analyzed were first obtained using SAS (1993). Traits related with caligus counts (FSL, TSL, CSL, PSL, CSL + PSL, TML, TSL/BW_s and TML/BW_m) were not normally distributed (Shapiro–Wilk test, $P<0.05$) and were therefore transformed for subsequent analyses. Traits FSL, TSL, CSL, PSL, CSL + PSL and TSL/BW_s were normalized using the transformation $\sqrt[3]{x}$, and TML and TML/BW_m were normalized using the transformation $\sqrt{x}$, using the box–cox transformation (Peltier et al., 1998).

Estimation of variance and covariance components was carried out using the restricted maximum likelihood (REML) method (Johnson and Thompson, 1995) with the ASREML software (Gilmour et al., 1999). Univariate and bivariate models were fitted for obtaining variance and covariance components, respectively, for all traits evaluated. The linear mixed model equation for each trait was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e}$$

where **y** is the vector of observations, **b** is the vector of fixed effects (the tank for traits measured at the sessile stage, and the tank and sex for traits measured at the mobile stage), **a** is the vector of random breeding values, **e** is the vector of random residual errors and **X** and **Z** are design matrices relating, respectively, fixed and random effects to observations. An extra set of univariate analyses were performed including weight as a covariate given that the linear regression of TSL, CSL, PSL, CSL + PSL and TML on weight was significant ($P<0.01$). In bivariate analyses, body weight was always included as a covariate because the sessile and mobile stages of sea louse load were measured at significantly different fish sizes ($P<0.05$).

3. Results

3.1. Parasite load, tank and sex effects

Descriptive statistics of body weight and parasite load measured at the sessile and mobile stages are shown in Table 1. Average fish body weight was 132.7 g and 165.2 g at parasite evaluation in the sessile and mobile stages, respectively. The coefficient of variation of weight was close to 30% in both evaluation times. The parasite load in the sessile stages (FSL, TSL) measured in tanks 1 and 2 reached 30 chalimus parasites per fish, which is 30% of the infestation rate used in the experiment. The average parasite loads CSL and PSL were equal (9.4 and 9.5, respectively), and CSL + PSL reached 19

Table 1
Mean, standard deviation and CV for body weight, parasite load and ratio of parasite load to body weight in the sessile and mobile states of the parasites.

Trait[a]	*n*	Mean	SD	CV (%)
Data recorded in the sessile state (Ch2-3), tanks 1–2				
BW_s	970	132.7	41.0	31
FSL	960	28.6	14.9	52
TSL	960	30.7	16.3	53
CSL	969	9.5	5.4	57
PSL	969	9.4	6.7	71
CSL + PSL	969	18.9	10.1	54
TSL/BW_s	960	0.24	0.13	53
Data recorded in the mobile state (adults), tank 3				
BW_m	507	165.2	59.0	36
TML	507	13.2	6.0	46
TML/BW_m	507	0.09	0.05	56

[a] BW_s and BW_m = fish body weight evaluated, respectively, at the parasite sessile and mobile stage, FSL = the number of sessile lice on all fins per fish, CSL and PSL = the number of sessile lice per fish in, respectively, the caudal and pectoral fin, TSL = the estimated total number of sessile lice per fish, TML = the total number of mobile lice per fish, and TSL/BW_s and TML/BW_m = the total numbers of lice per fish per unit of body weight.

sessile parasites per fish. In the adult state, the parasite load (TML) measured in tank 3 was much lower, with 13.2 adult parasites per fish. The variation observed in total caligus count per fish was high in both the sessile and mobile stages (CV = 46–71%). Variation was even higher for parasite load per unit of fish weight in both stages of parasite development (CV = 53–56%).

No significant differences ($P > 0.05$) were observed between tanks for weight measured 4 days post-infestation (Table 2). However, there were significant differences between tanks ($P < 0.01$, Table 2) for parasite load measured in the sessile stage, although no significant differences concerning temperature and oxygen saturation variables were observed between tanks during the infestation period ($P > 0.05$). For parasite load and weight recorded in the adult state, no significant differences were observed between sexes ($P > 0.05$).

3.2. Heritabilities

Heritability estimates for the traits considered in this study are shown in Table 3. Estimates for body weight were of medium to high magnitude and very similar at the initial (parasites in sessile stage) and final (parasites in mobile stage) phases of the experiment (0.58 and 0.54, respectively). Including weight as a covariate led to a significant reduction ($P < 0.01$) in the magnitude of the heritability of traits associated with parasite count per fish. The largest decrease was for TML, for which heritability decreased by a factor of three (Table 3).

The heritability estimates of parasite load traits measured at the sessile stage (FSL, TSL, CSL, PSL, CSL + PSL and TSL/BW_s) were low to medium in magnitude (0.12–0.34) and significantly different from zero ($P < 0.05$) when traits were adjusted for weight. The heritability

Table 2
Least squares means (±SE) for body weight, parasite load and ratio of parasite load to body weight in the sessile state in tanks challenged with parasites at this stage.

Trait[a]	Tank 1	Tank 2	[Tk1 − Tk2]/Tk2 (%)
BW_s	131.6 ± 1.81^a	133.9 ± 1.92^a	−1.7
FSL	29.9 ± 0.66^a	27.2 ± 0.69^b	9.9
TSL	31.9 ± 0.72^a	29.2 ± 0.76^b	9.2
CSL	9.9 ± 0.24^a	8.9 ± 0.25^b	11.2
PSL	10.3 ± 0.29^a	8.5 ± 0.31^b	21.2
CSL + PSL	20.1 ± 0.44^a	17.5 ± 0.47^b	14.8
TSL/BW_s	0.25 ± 0.01^a	0.23 ± 0.01^b	8.7

[a] BW_s = fish body weight, FSL = the number of sessile lice on all fins per fish, CSL and PSL = the number of sessile lice per fish in, respectively, the caudal and pectoral fin, TSL = the estimated total number of sessile lice per fish, TML = the total number of mobile lice per fish, and TSL/BWs = the total number of lice per fish per unit of body weight. Different superscript letters indicate significant differences ($P < 0.05$).

Table 3
Estimated heritability (±SE) for body weight, parasite load and number of parasites per unit of weight, including or excluding weight as a covariate in the model.

Trait[a]	Including weight as a covariate	Excluding weight as a covariate
Data recorded in the sessile state (Ch2-3), tanks 1–2		
BW_s	NA[b]	0.58 ± 0.08*
FSL	0.34 ± 0.07*	0.42 ± 0.08
TSL	0.34 ± 0.07*	0.42 ± 0.08
CSL	0.12 ± 0.07	0.23 ± 0.07*
PSL	0.26 ± 0.09*	0.26 ± 0.07*
CSL + PSL	0.32 ± 0.07*	0.36 ± 0.07*
TSL/BW_s	NA	0.22 ± 0.06*
Data recorded in the mobile state (adults), tank 3		
BW_m	NA	0.54 ± 0.11*
TML	0.06 ± 0.06	0.19 ± 0.08
TML/BW_m	NA	0.03 ± 0.05

[a] BW_s and BW_m = fish body weight evaluated, respectively, at the parasite sessile and mobile stage, FSL = the number of sessile lice on all fins per fish, CSL and PSL = the number of sessile lice per fish in, respectively, the caudal and pectoral fin, TSL = the estimated total number of sessile lice per fish, TML = the total number of mobile lice per fish, and TSL/BW_s and TML/BW_m = the total numbers of lice per fish per unit of body weight.
[b] NA = not applicable.
* Significantly different from zero ($P < 0.05$).

estimates for FSL and TSL had equal value (0.34), and this value was similar to that for CSL + PSL (0.32). However, the heritabilities for CSL and PSL were of lower magnitude (0.12 and 0.26, respectively). Parasite load measured in the mobile stage (TML) showed a very low heritability (0.06) that was not significantly different from zero ($P > 0.05$).

3.3. Genetic correlations

Estimated genetic correlations between the different measurements of parasite load taken at different stages and between these measurements and body weights are shown in Table 4. High genetic correlations between body weight and parasite counts in both the sessile (0.55–0.89) and the mobile stage (0.95) were obtained.

As expected, FSL and TSL behaved almost exactly as the same trait. Not only did they show the same heritability, but the genetic correlation between them was very close to one (0.99). TSL showed the same high genetic correlations as FSL with TSL/BW (0.77), TML (0.99) and CSL + PSL (0.97), and almost exactly the same high genetic correlation with CSL (0.92) and PSL (0.85). These figures were omitted from Table 4 for simplicity. TML showed a higher genetic correlation with CSL (0.99) than with PSL (0.65). In general, genetic correlations involving TML/BW at the mobile stage were not significantly different from zero ($P > 0.05$).

Table 4
Estimated genetic correlations (±SE) between measurements of parasite load in the sessile and mobile stages and between parasite load and body weight.

Trait[a]	BW	FSL	TML
FSL	0.61 ± 0.10*	–	–
TSL	0.61 ± 0.10*	0.99 ± 0.01*	–
CSL	0.89 ± 0.08*	0.90 ± 0.05*	0.99 ± 0.01*
PSL	NI	0.86 ± 0.05*	0.64 ± 0.05*
CSL + PSL	0.55 ± 0.11*	0.97 ± 0.01*	0.99 ± 0.47*
TSL/BW	–	0.77 ± 0.07*	0.59 ± 0.23
TML	0.95 ± 0.16*	0.99 ± 0.02*	–

[a] BW = body weight, FSL = the number of sessile lice on all fins per fish, CSL and PSL = the number of sessile lice per fish in, respectively, the caudal and pectoral fin, TSL = the estimated total number of sessile lice per fish, TML = the total number of mobile lice per fish, and TSL/BW and TML/BW = the total number of lice per fish per unit of body weight. Genetic correlations involving TML/BW are not given because their SE were too large for the estimate to have any predictive value.
* Significantly different from zero ($P < 0.05$).

4. Discussion

The results presented here provide very useful information on genetic parameters for resistance to *C. rogercresseyi* in Atlantic salmon which were obtained from a controlled infestation challenge of breeding populations managed in Chile.

The distribution of sessile parasites on the body of fish observed in this study agrees with that observed by Araya et al. (2011) who shown that 94% of the same ectoparasite in the chalimus stage is found on the fins in 120 g Atlantic salmon. In line with this finding, a high coefficient of determination was obtained for the adjusted multiple regression ($R^2 = 0.93$) of TSL on different fins. Other studies on infestation with *L. salmonis* have also reported a preference of sessile stage (chalimus) for the fins in salmonids (Dawson et al., 1997; Tucker et al., 2000, 2002). Accordingly, a very high and positive genetic correlation was obtained between FSL and TSL (0.99), indicating that the parasite count on all the fins is a very good estimate of the total parasite load in the sessile stage for the purposes of selection. From an operational point of view, in a challenge test for genetic resistance to sea lice, a high number of fish must be measured for parasite load and processed in a short period of time to manage reasonable costs. FSL is easier and more feasible to measure than TSL which must be measured *in situ*, implying a slow and error-prone process.

With the exception of PSL, the levels of phenotypic variation (CV) in parasite load in the sessile (FSL, TSL, CSL, CSL + PSL) and adult stages (TML) estimated in this study (CV = 46–57%) were lower in magnitude than those reported from other experiments in Atlantic salmon where infestation was carried out with *L. salmonis* (CV = 68–78%, Gjerde et al., 2010; CV > 100% Kolstad et al., 2005). However, the magnitude of CV obtained here still indicates a good potential for improvement of resistance to *C. rogercresseyi* in this species.

Males and females showed no significant differences in resistance to *C. rogercresseyi* when total parasite count in the mobile stage was measured. Also, there were no significant differences between sexes in final body weight. Glover et al. (2005) presented similar results for total parasite load for infestations with *L. salmonis* and *C. elongatus* in Atlantic salmon of 250 g. Despite this finding, due to the positive correlation obtained between weight and caligus count and to the fact that sexual dimorphism is more significant in larger than in smaller fish (Gjerde et al., 1994; Myers et al., 2001), the effect of sex on parasite level should be reviewed for fish of a larger size.

The heritability estimates obtained for parasite load of *C. rogercresseyi* in the sessile stage, measured as the parasite count of total fish (TSL), total fins (FSL) or CSL plus PSL fins, were very similar (0.32–0.34). Slightly lower values were obtained by Kolstad et al. (2005) in Atlantic salmon for a load of *L. salmonis* at the same stage of development (0.15–0.26). The estimates obtained by results Kolstad et al. (2005) agree with the estimates obtained here for CSL (0.12) and PSL (0.26) in our study. The magnitude of the heritability obtained for the total number of lice in the sessile stage per fish per unit of body weight (0.22) was consistent with the results published by Gjerde et al. (2010) for Atlantic salmon (0.26) infested with *L. salmonis*. In contrast, in our study of resistance to *C. rogercresseyi*, parasite count measured at the mobile stage showed very low heritabilities (0.03 for TML/BW and 0.06 for TML). Although the estimates for TML/BW and TML heritabilities must be taken with caution given the high magnitude of their standard errors, these low values agree with those obtained by Glover et al. (2005) for total parasite load (sessile and mobile) of *L. salmonis* in Atlantic salmon (0.07). The loss of parasites due to on-site manipulation when measuring the trait and the fact that the parasites in the mobile stage can migrate (Kolstad et al., 2005; Ritchie, 1997) could partly explain these results. Thus, load measurements involving mobile adult stages are not the best option for evaluating resistance through parasite counting. Gjerde et al. (2010) obtained a higher level of heritability for resistance (0.31) when the count of mobile adults *L. salmonis* was considered. However, they used two successive infestations prior to parasite measurement and therefore, their estimate is not comparable to the estimates obtained in our study.

The positive relationship between weight and parasite count in the sessile (FSL, TSL, CSL and CSL + PSL) and mobile (TML) stages shown here has been observed by other authors (Tucker et al., 2002; Glover et al., 2003; Glover et al., 2004a,b). The decrease in the level of heritability for the caligus count in both stages when including weight as a covariate ratifies the need to adjust parasite load data to fish weight when performing genetic analyses. Validating this relationship, high and positive genetic correlations were obtained between weight and caligus count in the sessile (0.55–0.89) and mobile (0.95) stages, which agree with previously reported genetic correlations between weight and parasite load of *L. salmonis* in 200 g Atlantic salmon (0.44, Kolstad et al., 2005; 0.47, Gjerde et al., 2010).

Selection for improving resistance to specific diseases could make possible that the host eliminates the pathogen or modulates its life cycle (Bishop and Mackenzie, 2003). The high and positive genetic correlation obtained between parasite count measured in the sessile and mobile (adult) stages (0.65–0.99) is a strong indication that for the purposes of selection in post-smolt Atlantic salmon, selecting for the sessile stage for resistance to *C. rogercresseyi* actually modulates the reproductive cycle of the parasite. Genetic correlations between the sessile and mobile stages reported by Gjerde et al. (2010) and Kolstad et al. (2005), where parasite load was measured as such (0.98) or as the ratio between load and fish size (0.87), confirm our results. In addition, both studies evaluated the genetic correlation of resistance to *L. salmonis* in Atlantic salmon following a first infestation and resistance to the parasite following a second infestation. They obtained a positive genetic correlation (0.26–0.31, Gjerde et al., 2010; 0.50–0.80, Kolstad et al., 2005), which shows that selecting for resistance to sea lice in smolt fish between 100 and 200 g exposed to a first infestation improves the resistance response to subsequent infestations.

Looking for alternative selection criteria for parasite load, the sessile parasite count of CSL, PSL and CSL + PSL fins were considered in our study. The trait CSL + PSL showed a heritability similar to that for FSL (Table 3) and a genetic correlation with FSL similar to that for TSL and TML (Table 4). From a selection point of view, in order to improve resistance to *C. rogercresseyi* in Atlantic salmon, CSL + PSL could be considered as an alternative to FSL since it is easier and cheaper to measure.

5. Conclusions

This study demonstrates that there is sufficient additive genetic variation in resistance to the sea louse *C. rogercresseyi*, as evaluated by parasite load in the sessile stage, for it to be included as a breeding goal in selection programs of Atlantic salmon. Results indicate that selecting against parasite load at the sessile stage makes possible to reduce the parasite load at the adult stage by modulating the reproductive cycle of the parasite. Measurements of parasite load at the sessile stage based on the total count of parasites on the fins (FSL) or on the sum of parasites on the pectoral and caudal fins (CSL + PSL) are good options for selection criteria, with the latter being a more practical option.

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