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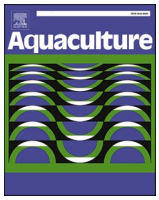

Short communication

Validation of QTL associated with resistance to *Lernanthropus kroyeri* in European seabass

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ABSTRACT

Lernanthropus kroyeri constitutes the most commonly encountered parasitic copepod for European seabass (*Dicentrarchus labrax*). Infection of gills with copepods directly impacts fish survival and growth performance with further economic implications for the aquaculture industry. Earlier studies identified moderate heritability of parasite count and two suggestive candidate QTL that explained 2 % of the total phenotypic variance each. The present study focuses on the two previously identified QTL loci to validate any QTL effect on *L. kroyeri* parasite resistance. In order to facilitate the validation of healthy and infected fish, individuals were selected based on their resistance to parasites, specifically the presence or absence of L. *kroyeri* in fish reared in a standard open sea cage. A subset of samples was genotyped using the 30 k MedFISH SNP array and the putative QTL effects were tested for parasite resistance by fitting an animal model in ASREML-R while the AIC criterion was used to assess model fit. The *p*-values for the two SNP with highest association to parasite resistance AX-373127007 and AX-373218583 were 0.041 (<0.05) and 0.085 (<0.1), respectively. Despite the moderate significance of the second SNP, the lowest AIC score was detected after using both SNPs as fixed effects in the animal model. The findings of the present study, using a different population, validate the important role of the detected QTL loci on parasite resistance, highlighting a possible application of a low-cost Marker Assisted Selection (MAS) breeding program in farmed European seabass populations.

1. Introduction

Copepods are the second largest Crustacean taxa (after Malacostraca) with approximately 12,000 described copepod species (Huys and and, Boxshall, 1991, Humes, 1994, Raisuddin et al., 2007). *Lernanthropus kroyeri* is a parasitic copepod, encountered primarily on the gills of sea bass (*Dicentrarchus*) species (Vagianou et al., 2006; Eissa et al., 2020; Bahri et al., 2002). Parasite infection results primarily in anemia, pale gills, gill lamellar necrosis, and hypoxia while at the same time, the host becomes susceptible to secondary bacterial infections (Abdallah and Hamouda, 2023; Eissa et al., 2020; Tokşen et al., 2010). Ultimately, infection of the host's gills with copepods has a negative impact on fish survival with increased mortality rates resulting in large economic losses for the aquaculture industry (Antonelli et al., 2012).

The L. *kroyeri* infection rate shows seasonal patterns with the most significant differences observed between the winter (cold) and summer (hot) months. In particular, *L. kroyeri* infestation rates increase during spring and/or summer compared to winter (Abdallah and Hamouda,

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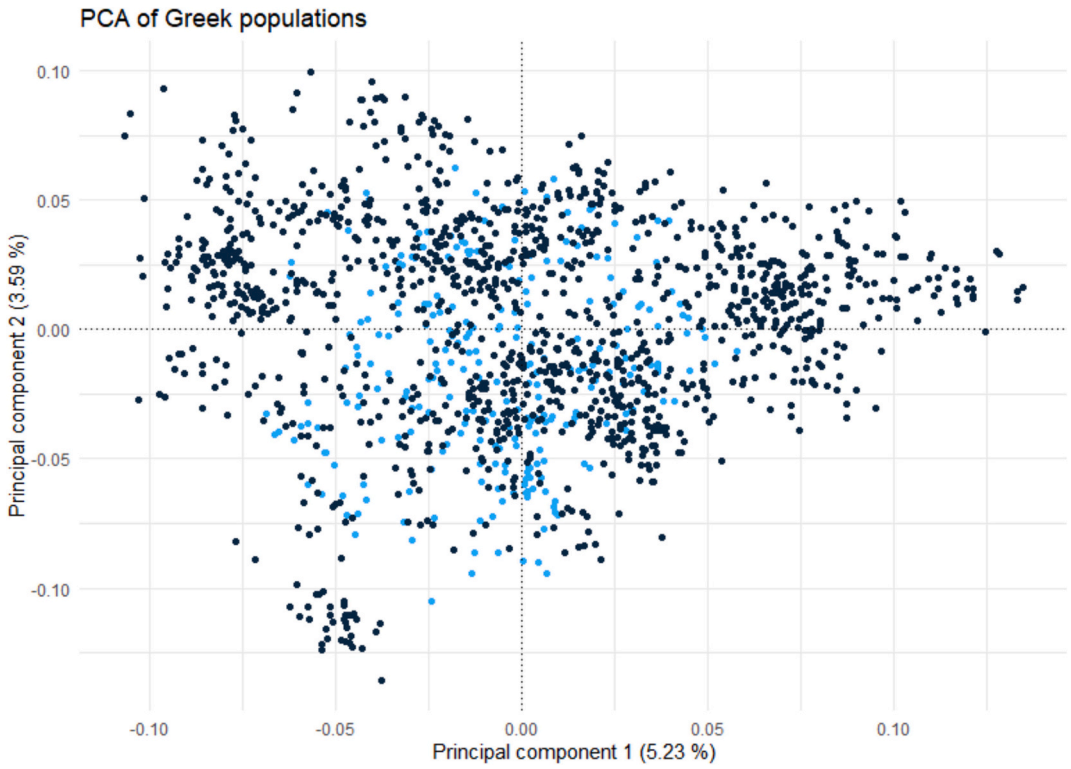

Fig. 1. Principal component analysis for the two studied populations. The dark blue color illustrates the population in Oikonomou et al. (2022b), and light blue dots depict the fish analyzed in the present study. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Descriptive statistics of the statistically significant SNP.

SNPs		AX-373127007			AX-373218583		
Genotype		CC	CT	TT	CC	CT	TT
Status	Infected fish with L. *kroyeri*	9	107	106	91	93	38
	Healthy	13	44	53	51	49	10
Total number of fish		22	151	159	142	142	48
Physical Position (bp) 30 k MedFish Array		1,594,919			27,519,962		
Linkage Group		7					
p-value		0.041			0.085		

2023; Antonelli et al., 2012; Eissa et al., 2020) with trends indicating that seasonal fluctuations in L. *kroyeri* infestation rates are likely influenced by water temperature fluctuations (Antonelli et al., 2012). Another hypothesis suggests that the water temperature influences the immune response of the fish itself via an increase in the stress response of the host during higher water temperatures (Antonelli et al., 2012; Oikonomou et al., 2022a). From that perspective, the seasonal fluctuation of L. *kroyeri* infestation rates could be explained by a drop in the immunodeficiency of the fish during the spring and summer periods (Antonelli et al., 2012). In addition to seasonality, the high stocking density of farmed fish in rearing cages provides a favorable environment for parasite infection (Antonelli et al., 2012).

Although infestation by L. *kroyeri* has been reported in European seabass in Egypt, Greece, Corsica, Croatia, North Adriatic, and Turkey (Abdallah and Hamouda, 2023; Antonelli et al., 2012; Čolak et al., 2021; Eissa et al., 2020; Manera and Dezfuli, 2003; Papapetrou et al., 2021; Tokşen et al., 2010), only a single Greek population has so far been studied to estimate the heritability and genetic constituent of L. *kroyeri* (Papapetrou et al., 2021; Oikonomou et al., 2022b). Papapetrou et al. (2021) studied the genetic heritability of parasite count in 1576 European seabass fish reared in an aquaculture facility in Sagiada (a cohabitation experiment in W. Greece with high infestation rates), showing a moderate heritability of the trait (0.28 ± 0.03), and a moderate positive genetic correlation between parasite count and body weight of the host (0.34 ± 0.05). These findings prompted a study on European seabass resistance to L. *kroyeri* to further explore the genetic architecture and its correlation with growth and body weight using a commercial SNP array. A GWAS analysis using L. *kroyeri* parasite count revealed two putative QTL in LG7 which explained approximately 2 % of the phenotypic variance each (Oikonomou et al., 2022b). Furthermore, a high genomic heritability was estimated (0.75 ± 0.04) for parasite count and a moderate genomic correlation with body weight (0.24 ± 0.1) using a selected subset of the Sagiada population (Oikonomou et al., 2022b). However, the two QTL are currently considered only as putative, due to their small effect on the parasite count of this cohabitation experiment and further analysis is required in order to validate the effect of the two candidate QTL regions.

The present study uses a second population from a different Greek fish stock farm site to validate the significance of the two putative QTL effects on parasite resistance and assess their potential utilization on a genomic/MAS breeding program.

2. Materials and methods

2.1. Genotyped population and studied trait

European seabass samples were collected from a common sea cage in Astakos, Greece, during a natural infestation outbreak with *Lernanthropus kroyeri*. The fish used in this experiment originated from the AVRAMAR company's breeding program. At 580 days post-hatching (dph), fish average weight was 415.76 g (SD = 78.37 g). During this weighing, all fish were monitored for infestation from L. *kroyeri* (presence/absence of parasites on the gills). Fin-clips were collected from 222 fish that had at least one parasite attached on them, and 110 parasite-free fish from the same site in Astakos, Greece (June 2022). Collected

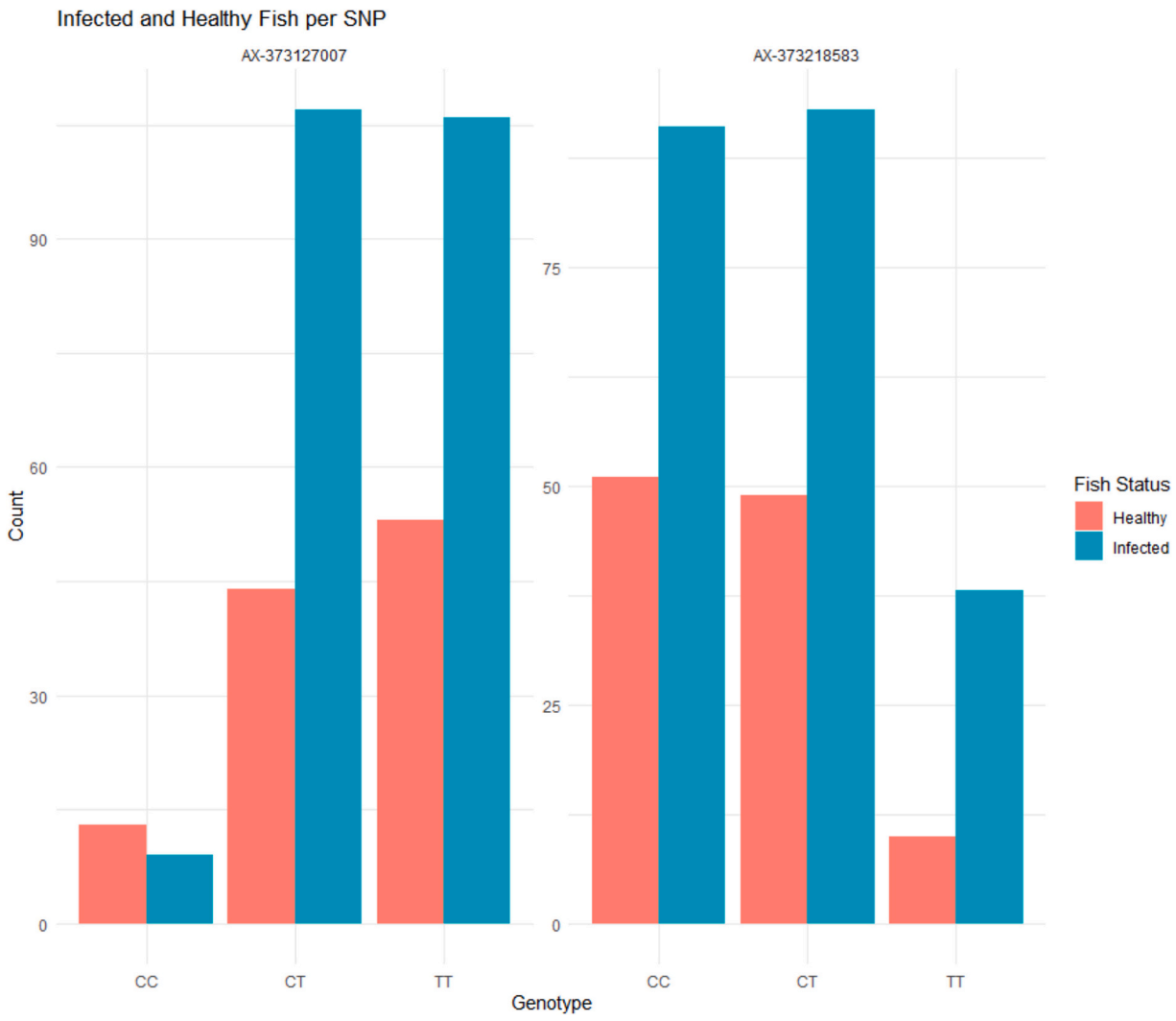

Fig. 2. Number of fish per SNP (AX-373127007, and AX-373218583) and SNP genotype (CC, CT and TT) based on their status (healthy or infested).

samples were genotyped using the 30 K MedFISH array (Peñaloza et al., 2021). Then, a PCA analysis was performed in R between the two studied populations, i.e., the one included in the present study from Astakos and the former one from Sagiada which was used for the GWAS analysis in Oikonomou et al. (2022b). Fig. 1 illustrates the PCA plot using the first two principal components per population, revealing no clustering between the population now studied and the former population in Oikonomou et al. (2022b). The absence of genetic differentiation between these populations provides a solid foundation for testing the QTL across both groups, and for possible future utilization of MAS.

2.2. Statistical analysis

In order to evaluate the significance of the QTL, the following animal model was used in ASReml-R v4.2 (Butler et al., 2023, R Core Team, 2021)

$$y = \mu + Xb + Z\,u + e \qquad \text{(Model 1)}$$

where the y is the vector of the status (healthy or infected fish with the L. *kroyeri)*, the X is the incidence matrix related to the fixed effects, and b is the vector of the fixed effects of SNP genotypes (including the genotype of the best SNP *AX-373127007*, based on -log(p-value), with 3 levels (CC, CT, TT), and the genotype of the second SNP *AX-373218583* with 3 levels (CC, TC, TT), respectively). Z is the incidence matrix related to the random effect, and u is the additive genetic effect using the Genomic Relationship Matrix (GRM) estimated using the 30 K MedFISH array, and it is illustrated *as* $\sim N(0, G\sigma_a^2)$, where the G is the GRM and σ_a^2 is the polygenic additive variance arising from the GRM and the e is the residual. The proportion of phenotypic variance (PVE) explained by a given SNP was estimated as described in Oikonomou et al., (2022 a and b), using the following formula

$$\mathrm{PVE} = \left(2\,\mathrm{b}^2\,\mathrm{MAF}\,(1-\mathrm{MAF})\right) \Big/ \left[2\,\mathrm{b}^2\,\mathrm{MAF}\,(1-\mathrm{MAF}) + (\mathrm{se}\,(\mathrm{b}))^2\,2\,\mathrm{N}\,\mathrm{MAF}\,(1-\mathrm{MAF})\right]$$

where *MAF* is the Minor Allele Frequency of the SNP, b is the effect size estimated, and N is the sample size.

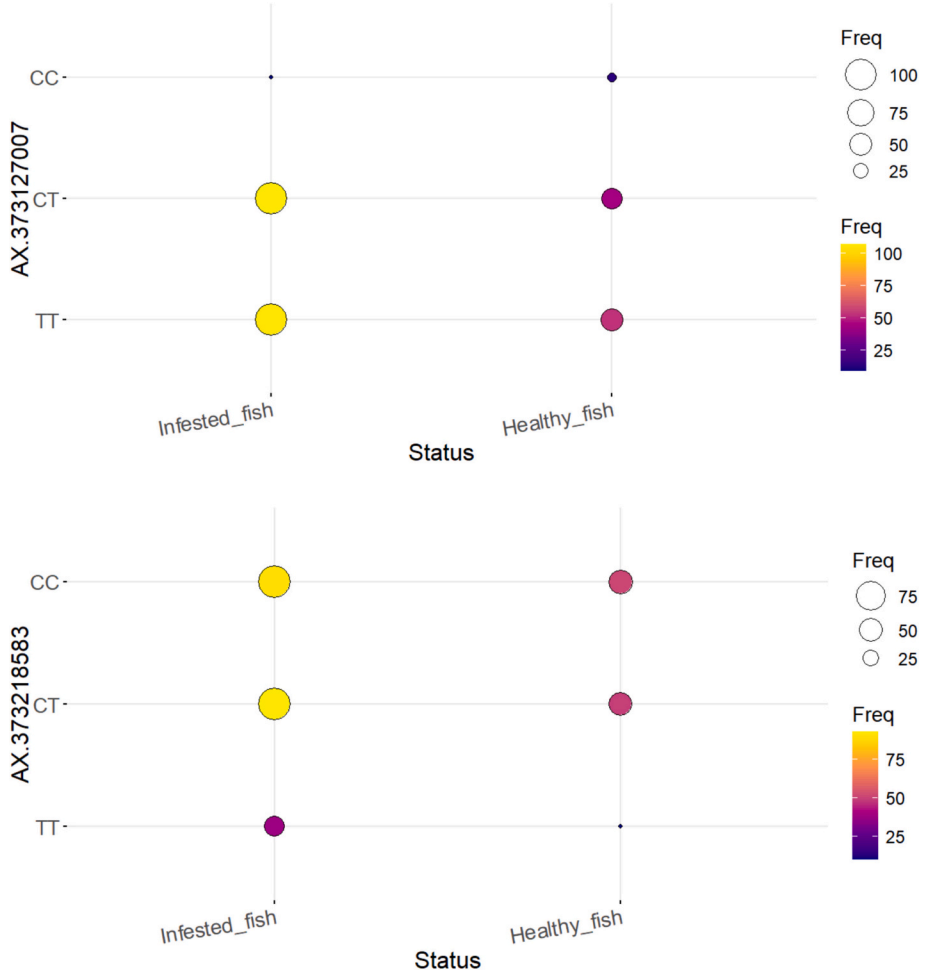

Fig. 3. The frequency of the fish status (infested versus healthy) per genotype for a) AX-373127007, and b) AX-373218583.

Table 2
Akaike Information Criterion (AIC) per model.

	Model	AIC
Reduced models	Model 1	– 156.30
	Removing the AX-373218583 and AX.373127007 (Model 2)	– 166.05
	Removing the AX-373218583 (Model 3)	– 162.10

To assess the effect of the two SNPs on the genetic selection model, the Akaike Information Criterion (AIC) was used to select the most appropriate model based on the goodness-of-fit. In order to do that, two separate reduced models were fitted in ASReml-R v4.2 (Butler et al., 2023, R Core Team, 2021); in the first model, no SNP was included (Model 2) while in the second model, the AX-373218583 SNP was removed (Model 3). In both reduced models, the additive polygenic variance was also fitted using the GRM. Each of the fitted reduced models was compared against Model 1.

2.3. Linkage disequilibrium

In addition to statistical significance, the presence of Linkage disequilibrium (LD) between the two studied SNP was investigated using plink1.9 (Purcell et al., 2007). To estimate LD, the r^2 metric was used, which is the square of the correlation coefficient between two loci (Wall and Pritchard, 2003).

2.4. Alignment to the European sea bass reference genome and identification of gene candidates

The physical position of the two SNP with highest association to L. *kroyeri* resistance was examined to identify potential overlap between the SNP and functional elements in the European seabass genome. In

Table 3
Probe sequence information of the two best SNP for L. *kroyeri* parasite count using the older and most recent versions of the European seabass genome reference (dicLab v1.0c and dlabrax2021, respectively). *E*-value and percentage of sequence identity represent the accuracy metrics for sequence match between the two genome reference versions whereas the overlap between each probe and functional elements is indicated on the last column, based on the latest version of the European seabass functional annotation (dlabrax2021, Ensembl release 105).

SNP	SNP probe position (dicLab v1.0c)	SNP probe position (dlabrax2021)	E-value	Sequence identity (%)	Functional overlap (dlabrax2021)
AX-373127007	LG7:1594904–1,594,934	CAJNNU010000021: 2455556–2,455,586	2.28e-09	100.000	capn9 (ENSDLAG00005018075)
AX-373218583	LG7:27519947–27,519,977	CAJNNU010000021: 33266525–33,266,555	2.28e-09	100.000	cacna1lb (ENSDLAG00005003623)

Table 4
Original and reverse-complement sequences for the two QTL SNP probes. The original location of SNPs was extracted from the MedFISH SNP array. In addition, 15 base pairs (bp) upstream and downstream of the SNP were extracted from the older version of the European seabass genome reference (dicLab v1.0c). Highlighted nucleotides in the probe sequence indicate the alleles for each SNP using the original and complement-reverse sequence.

SNP	Sequence (dicLab v1.0c)	Sequence probe
AX-373127007	Original sequence	TTGGTATTTGTACTTGGACTTGGCCCCACGG
	Reverse complement	CCGTGGGGCCAAGTCCAAGTACAAATACCAA
AX-373218583	Original sequence	CACCTGGTTCAGAGCGCCTATTATGGCCATC
	Reverse complement	GATGGCCATAATAGGCGCTCTGAACCAGGTG

order to improve the genomic resolution and accuracy of the functional scan, the latest versions of the reference genome and transcriptome for European seabass were used, featuring a chromosome-level genome assembly with improved contiguity and an additionally improved gene annotation (dlabrax2021, accession number GCA_905237075.1). For this purpose, the physical position of each SNP was retrieved from the MedFISH SNP-array (Peñaloza et al., 2021), which was designed based on the first European seabass reference genome (dicLab v1.0c, accession GCA_000689215.1) (Tine et al., 2014). For each of the two SNPs, a lift-over mapping approach was performed: the nucleotide sequence of the SNP itself together with 15 base pairs (bp) upstream and downstream from the polymorphism was extracted from the earlier version of the European seabass reference genome (dicLab v1.0c, accession GCA_000689215.1) using the software bedtools (Quinlan and Hall, 2010). A BLASTn search (Zhang et al., 2000) was then performed using the extracted 31 bp sequences for the two SNP probes as well as their respective reverse-complements (Table 4) against the latest version of the genome reference for European seabass (dlabrax2021, accession GCA_905237075.1). The best match of the two SNP probe sequences was finally identified on the latest genome reference based on statistical significance (e-value) and percentage of sequence identity metrics whereas the overlap of each SNP probe with genes was investigated using the publicly available gene annotation for European seabass in Ensembl (dlabrax2021, release 105).

3. Results and discussion

It was previously reported (Oikonomou et al., 2022b) that the difference between the genotype TT and CC for the AX-373127007 was 6.09 parasites, and for the AX-373218583 it was 11.9 parasites. Those findings indicate that genotypes CC in both SNP are associated with lower numbers of parasites in the European seabass. The number of fish per genotype per SNP is illustrated based on their status (healthy/infested) in Table 1 and Fig. 2, and their frequency in Fig. 3. Examining Model 1 in ASReml-R v4.2 (Butler et al., 2023, R Core Team, 2021), the *p*-values for AX-373127007 and AX_373218583 were 0.041 (<0.05) and 0.085 (<0.1), respectively. Thus, the AX-373127007 SNP was statistically significant for parasite resistance and can therefore be considered as a QTL locus associated with resistance to L. *kroyeri*. On the other hand, the AX-373218583 SNP was only significant at a 10 % level of significance and could therefore continue to be considered as a putative QTL and not a false positive detection given the results by Oikonomou et al. (2022b). Furthermore, any future SNP saturation of the genomic region may reveal haplotype blocks suitable for MAS. Nevertheless, in order to detect the most efficient prediction model for parasite resistance, both the reduced and Model 1 were examined using the AIC metric. Under the AIC criterion, lower scores indicate a better fit and consequently a better parasite resistance prediction. Model 1 had the lowest AIC which means that this model showed the highest goodness-of-fit compared to the reduced models irrespective of the borderline significance of AX-373218583. Table 2 illustrates the AIC per model, showing the superiority of Model 1. Furthermore, in the present study, the PVE was estimated to be 13.3 % for AX-373127007 and 4 % for AX-373218583.

Furthermore, LD testing between the two SNP showed an r^2 value of 0.079, indicating that the two SNP are not in linkage disequilibrium, and therefore not co-inherited. This could likely explain the independent effect of each SNP on the phenotype along with the estimated *p*-value in Model 1. These results support any future inclusion of SNP AX-373218583 in a genetic evaluation model, also showing reduced statistical significance ($P = 0.085$) in the current analysis.

Looking at the physical position of the two polymorphisms on the latest version of the European seabass genome reference, both SNPs overlapped functional elements, namely the genes *calpain-9* and *calcium voltage-gated channel subunit alpha1 Ib* (cacna1Ib) for SNPs for AX-373127007 and AX-373218583, respectively (Table 3 and 4). The two genes are related to Ca^{2+} influx with earlier studies suggesting the presence of a link between parasite attachment and upregulation of the Ca^{2+} signaling pathway (Bagnall et al., 2009). In addition, *calpain* genes are involved in immune response, working as a mediator of oxidative stress, a state likely explained during L. *kroyeri* infection (Hwang et al., 2020). Furthermore, *cacna1b* controls neurotransmitter release from neurons and is directly involved in pain signaling (Uniprot). Despite the suggested roles of the two genes, little is known about their importance and involvement in response to parasite infestation; further studies are required in order to accurately address the role of these genes on L. *kroyeri* resistance as well as investigate whether the overlapping genes represent gene candidates or if the QTL SNPs are indicative of nearby causal variation that was omitted due to low SNP density in the MedFISH genotyping array.

Taken together, the present study's findings indicate that both SNPs may be important in the prediction of the likelihood of L. *kroyeri* parasite resistance. The absence of sufficient SNP association significance trailing observed in Oikonomou et al. (2022b), could indicate that these SNPs could likely be spuriously associated. However, based on the present study, those SNPs could not be considered anymore as putative QTL loci or false positive results but rather as QTL loci most likely linked to the parasite resistance.

The identification of QTL linked to L. *kroyeri* parasite resistance is vital for the Greek as well as for the Mediterranean aquaculture industry. Until now, conventional pedigree-based selection approaches have been applied in European seabass breeding populations. Such approaches included resistance to L. *kroyeri* as a breeding goal by using sib or progeny testing in fish sampled from sites with high infestation rates (such as the Sagiada site) to evaluate healthy and infested broodstock candidates. However, such selection (sib or progeny testing) and recording (parasite count using a stereoscope) methods are costly both in terms of human labor as well as the speed of genetic gain (i.e., increased generation interval). Nevertheless, numerous studies have been conducted to date, demonstrating the superiority of fitting the genomic relationship matrix (GRM) over the traditional pedigree approach. Comparison of pedigree-based against GRM-based approaches in European seabass has thus far shown lower predicted ability or accuracy of prediction of breeding values for body weight, stress indicators (Oikonomou et al., 2022a) and resistance to L. *kroyeri* (Oikonomou et al., 2022c). However, the utilization of a GRM from an SNP array can also increase rapidly the cost associated with genotyping. One way to reduce the cost of including such a breeding goal (i.e.,

resistance to *L. kroyeri*) can be the use of a combination of Marker Assisted Selection (MAS) and the traditional pedigree approach. The identified QTL can be utilized via MAS in the industry, improving the selection accuracy of the candidates, and consequently offering higher resistance to fish infestation from L. *kroyeri*.

CRediT authorship contribution statement

Stavroula Oikonomou: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis. **Domniki Manousi:** Writing – review & editing, Writing – original draft, Visualization, Software, Formal analysis. **Arkadios Dimitroglou:** Investigation. **Zoi Kazlari:** Writing – original draft, Resources, Data curation. **Dimitrios Loukovitis:** Resources, Data curation. **Kantham Papanna:** Supervision, Resources, Investigation, Data curation, Conceptualization. **Konstantinos Tzokas:** Resources, Data curation. **Nikos Katribouzas:** Resources, Data curation. **Leonidas Papaharisis:** Writing – review & editing, Validation, Supervision, Resources, Investigation, Data curation, Conceptualization. **Costas S. Tsigenopoulos:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Dimitrios Chatziplis:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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