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The parasitic copepod, *Sarcotretes scopeli* Jungersen, 1911 castrate its mesopelagic fish host *Benthosema glaciale*

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Abstract

The mesopelagic fish *Benthosema glaciale* [Actinopterygii: Myctophiformes: Myctophidae], abundant in open ocean and deep fjords, is targeted for future exploitation despite existing knowledge gaps on population vital rates. Among these gaps, the vulnerability to pathogens is poorly understood. Parasites rely on the metabolic energy of their host and infections might compromise host physiology and behaviour, which in turn, may affect growth and survival. Parasitic infections by the copepod *Sarcotretes scopeli* [Crustacea: Copepoda: Pennellidae] have frequently been recorded from the North Atlantic, including west Norwegian fjords. In this paper we present data on how *S. scopeli* infection affect reproductive investment, energetic status, and growth of its host, the mesopelagic fish *B. glaciale*. Our results indicate that (i) *S. scopeli* reduce reproductive investment (measured as gonadosomatic index GSI) of both female and male *B. glaciale*; (ii) that the energy storage (hepatosomatic index HSI) appeared unaffected in female *B. glaciale*, while infected male hosts have higher HSI than uninfected, and (iii) that infected fish are in poorer condition than uninfected. These findings may indicate that *S. scopeli* could have a significant regulatory impact on *B. glaciale* populations.

Keywords Host-parasite system · Parasitic copepod · Parasitic castration · Deep-water fjords · Mesopelagic fish

Introduction

The mesopelagic zone (200–1000 m depth) houses mesopelagic fish, one of the most abundant vertebrate groups on earth that is not yet industrially exploited (Gjøsæter and Kawaguch 1980; Irigoien et al. 2014; St. John et al. 2016; Hidalgo and Browman 2019). Mesopelagic fish have recently gained interest for future exploitation (St. John et al. 2016; Hidalgo and Browman 2019; Fjeld et al. 2023), but there is a huge knowledge gap to fill before sustainable fisheries can be conducted on mesopelagic fish (St. John et al. 2016; Hidalgo and Browman 2019). There is a general lack of population vital rates ("e.g., recruitment, natural mortality and the effects of abiotic and biotic stressors on growth and survival") and which form the basis for stock assessments and sustainable management (St. John et al. 2016; Caiger et al. 2021).

One mesopelagic species, *Benthosema glaciale* [Actinopterygii: Myctophiformes: Myctophidae], is widely distributed in the North Atlantic (Sameoto 1988; Hudson et al. 2014), and in the Mediterranean sea (Goodyear et al. 1972; Contreras et al. 2015), and has particular high densities in deep west Norwegian fjords (Gjøsæter 1973a, b; Giske et al. 1990; Suneetha and Salvanes 2001; Kristoffersen and Salvanes 2009). *B. glaciale* is a common prey for large pelagic predators such as: *Xiphias gladius*, *Delphinus delphis*, and *Mesoplodon bidens* (Chancollon et al. 2006; Spitz et al. 2010; Wenzel et al. 2013) and in gadids in the fjords (own data), but the species also turn out to serve energetic needs for parasites.

The parasitic copepod, *Sarcotretes scopeli* [Crustacea: Copepoda: Pennellidae], is one of commonly reported species to infect fish in the mesopelagic of the North Atlantic (Jungersen 1911; Klimpel et al. 2010), but have also been reported from the south Atlantic (Cherel and Boxshall 2004), the Pacific (Boxshall 1989) and the Indian Ocean (Cherel and Boxshall 2004). Infections has been observed in 14 host species, indicating that the parasite has a low host

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specificity (Boxshall 1998; Cherel and Boxshall 2004). *B. glaciale* is a frequently noted host in the North Atlantic (Jungersen 1911; Klimpel et al. 2010), including west Norwegian Fjords (Gjøsæter 1971). Despite this, it is not yet known if the parasite can influence host reproduction, physiology and growth. In this paper we investigate if *S. scopeli* affects reproductive investment, energetic status and growth of its host.

Bioindicators such as organ somatic indices (relative organ weight to fish body weight), condition factors (weight-length relationship) and somatic growth are frequently utilized metrics to study long-term fish health (Lloret et al. 2012; Khan and Khan 2014; Ragheb 2023). Previous parasitic studies have implemented such indicators in order to determine the effect of infection on host health. For instance, the gonadosomatic index have been used to determine host reproductive investment (Hecker and Karbe 2005; Fogelman et al. 2009; Kaur et al. 2013). The hepatosomatic index have been implemented as proxies for host energetic reserves (Hecker and Karbe 2005; Fogelman et al. 2009),while host growth and condition factors has been utilized as indicators for health and survival probabilities of infected individuals (Gjøsæter 1971; Fogelman et al. 2009; Guidelli et al. 2011).

Parasites have developed mechanisms that enable them to consume metabolic resources their hosts otherwise could have used for growth, reproduction and physiological maintenance (Timi and Poulin 2020). The adverse effects on the host, following infection may occur as a by-product of excessive parasitic energy drain from the host, often denoted the energy drain hypothesis (Lafferty and Kuris 2009). The chronic energy drain experienced by the host can in some cases result in physiological changes (Chin et al. 2004) and altered behaviour (Quinn et al. 2012). Some parasitic species may, for instance, affect their hosts reproductive capability either by partially or completely inhibiting the growth of gonadal tissues (Lafferty and Kuris 2009) through host manipulation or tissue destruction (Grankoto et al. 2001; Averbuj and Cremonte 2010; Geraudie et al. 2010), thus freeing reproductive energy which can be used to increase the parasites fitness. Parasitic castrators may affect the recruitment, growth and survival rates of the host population, due to resource competition between infected and uninfected hosts, resulting in lower overall fecundity in the host population (Lafferty 1993). Exposure to parasitic castrators may alter host energy allocation in the direction of earlier age of maturation over time, causing spawning to occur prior to potential castration (Gabagambi et al. 2020). For example the parasitic barnacle *Anelasma squalicola* (Lovén, 1844) infecting lantern shark species, and the parasitic copepod *Cardiodectes bellottii* (Richiardi, 1882) from the family Pennellidae infecting the Northern lampfish,

Stenobrachius leucopsarus, (Eigenmann and Eigenmann, 1890) have both been reported to inhibit the maturation of host ova (Moser and Taylor 1978; Yano and Musick 2000).

It is believed that the parasitic lifestyle of copepods has evolved multiple times, through two distinct feeding strategies of free-living ancestral species (Kabata 1979). The first strategy is thought to have developed through predation of free-living copepods on larger fish larvae, where extension of the contact between predator and prey may have developed into a parasite-host system over time (Kabata 1979). The second pathway likely arose from opportunistic bottom-scavenging copepods encountering suitable prey, enabling them to exploit a new food source and transition toward parasitism (Kabata 1979). As a result of the different evolutionary emergence of parasitism in the taxa, a plethora of different morphologies have been adapted by the species (Piasecki and Avenant-Oldewage 2008). Parasitic copepods are well known from the global salmon aquaculture, where their presence is causing substantial economic losses (Johnson et al. 2004). Although parasitic copepods are commonly found on a wide range of non-salmonid fishes, most studies have focused on their morphological traits rather than effects on the host (Johnson et al. 2004; Piasecki and Boxshall 2024). Pennellidae is a copepod family, which can be easily recognized by the relatively large size and greatly modified morphology of the adult stages of the species (Kabata 1979; Boxshall and Halsey 2004). The family displays a complex life cycle, consisting of 5–8 developmental stages depending on species (Perkins 1983; Brooker et al. 2007; Ismail et al. 2013). The life cycle is usually indirect, consisting of an intermediate host where mating occurs, before the female settles on the definitive host (Kabata 1979). These intermediate hosts are often invertebrates or flatfish (Piasecki and Avenant-Oldewage 2008). However, a direct life cycle including only one host has also been described in the family Monacanthidae (Ismail et al. 2013). Adult stages of parasitic species belonging to this family, have a mesoparasitic life style, e.g., the reproductive organ is located externally, while the feeding apparatus is imbedded internally in the host (Kabata 1979). In the mesopelagic water mass the Pennellid genus, *Sarcotretes* Jungersen 1911; has been commonly reported to be parasitizing fish hosts (Gjøsæter 1971; Ho et al. 2007; Uyeno et al. 2012). At present day, the genus contains 5 accepted species: *Sarcotretes eristaliformis* (Brian, 1908), *Sarcotretes gonosomae* (Kensley and Grindley, 1973), *Sarcotretes longirostris* (Ho, Nagasawa & Kim I.H, 2007), *Sarcotretes scopeli* (Jungersen 1911) and *Sarcotretes umiakae* (Uyeno et al. 2012). The species in this genus have a simple morphology and can be differentiated from other pennellids by three main features; A holdfast organ made up of lobes, three pairs of biramous legs, and a constriction on the midsection of the trunk (Kabata 1979).

Recently, as our research group sampled mesopelagic organisms in west Norwegian fjords, we discovered that a proportion of *B. glaciale* were infected by the pennellid copepod parasite *S. scopeli*. Studies on the *S. scopeli–B. glaciale* host-parasite systems are limited in the scientific literature. *S. scopeli* was first reported in the North Atlantic by Jungersen (1911), who described several of its life stages on *B. glaciale*. The next report appeared 60 years later, when Gjøsæter (1971) observed that *B. glaciale* infected with *S. scopeli* showed no signs of maturation. Gjøsæter (1971) also noted a higher prevalence of infection in two-year-old *B. glaciale* compared to older individuals, suggesting that *S. scopeli* infections could contribute to increased host mortality.

In the present study, we conduct a cross-sectional analysis to assess the impact of parasitic infection by *S. scopeli* on *B. glaciale*. This includes evaluating the reproductive investment (measured via the gonadosomatic index), physiological and energetic status (assessed using the hepatosomatic index), and growth (evaluated by comparing otolith size relative to fish body size). Building on Gjøsæter's (1971) findings, which suggest the possibility of host castration induced by the parasite, we elaborate deeper into this aspect of the parasite-host interaction.

Methods

Study area

Fieldwork was conducted in four fjords (Masfjord, Fensfjord, Osterfjord and Sørfjord) in western Norway (Fig. 1). Fish samples of *B. glaciale* in which *S. scopeli* infections (Fig. 2) were noted were collected in October 2019, February 2021, September 2021, May 2022 and September 2022. Fensfjord is closest to the coastal waters and has a 380 m deep sill and maximum depth of 680 m. Masfjord branch off from Fensfjord over a 75 m deep sill, and it has a maximum depth of 490 m (Salvanes et al. 1995). Osterfjord and Sørfjord are both extensions of Salhusfjord and have sill depths of 105 m and 170 m and maximum depths of 640 m and 425 m respectively (Salvanes et al. 1995; Kartverket, https://www.norgeskart.no).

Subsampling trawl catches

The sampling was conducted using a pelagic Harstad-trawl, fitted with and without a multisampler (see Engås et al. 1997; Salvanes et al. 2018). Mesopelagic organisms of the catch were first well mixed, then a subsample of 1000 g was taken and sorted into species. A subsample of ca. 100 *B. glaciale* were next taken, then length measured and scrutinised
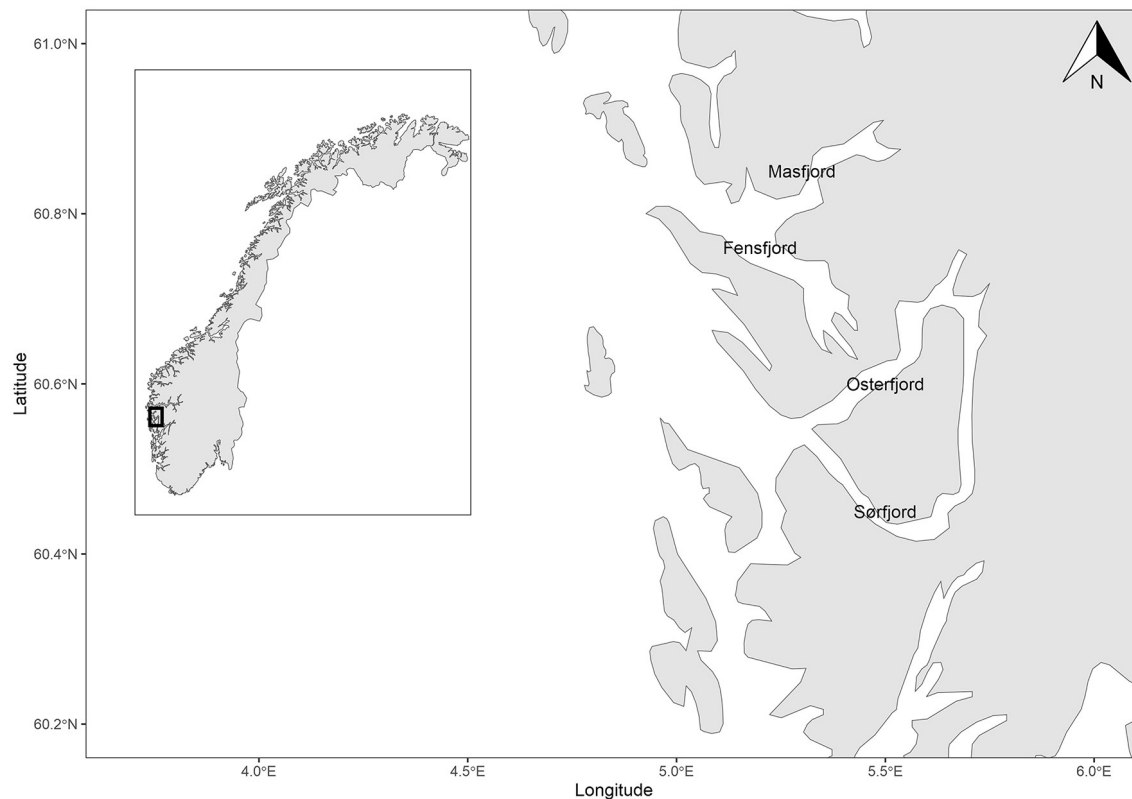

Fig. 1 Overview map of the sampling areas. The red box represents the sampling areas at a larger scale

Fig. 2 *B. glaciale* infected by *S. scopeli*

for presence/absence of *S. scopeli* infection after length measuring (Fig. 2).

Processing *B. Glaciale*

Subsamples of *B. glaciale* caught in February 2021 at 200 m depth or deeper were preserved in 96% ethanol. All ethanol preserved fish were 7 months later processed. Individual weight was measured to the nearest 0.01-gram, length measured (standard length rounded down to the nearest millimetre) and sexed first using external sexual traits (Gjøsæter 1981) and next by inspecting gonads of dissected individuals. Excess ethanol was removed from the fish prior to weighting. If the fish was infected, the parasite was removed before weighing. The host liver and gonads were dissected out. Organs and the gutted fish where weighted both wet and dry to the nearest 0.0001 gram and 0.01 gram respectively. Liver, gonad and gutted fish were dried at 60 °C for 48 h.

Juvenile fish that was not possible to sex were excluded from further analysis ($n = 69$). All infected fish from the ethanol samples were dissected, while a random subsample of 15 uninfected individuals from each ethanol sample was dissected, except for Osterfjord where we had only one sample and therefore selected 30 individuals for processing. For two stations from Sørfjord, infected and uninfected fish were length and sex matched.

Data analysis

The gonadosomatic index (GSI) was used as an index for reproductive investment and the hepatosomatic index (HSI) was used as an index for energy storage by *B. glaciale*. These organo-somatic indices (HSI and GSI) were calculated as:

$$Organo\ somatic\ index = \frac{Dry\ organ\ weight}{Dry\ gutted\ weight} * 100$$

Fulton`s condition factor was assumed to reflect the well-being of the fish, and was calculated as:

$$Fulton's\ condition\ factor = \frac{Estimated\ fresh\ weight}{Estimated\ fresh\ length^3}$$

where the wet weight and standard length of the fish were converted to estimated fresh weight and length, using the obtained relationship provided in Kristoffersen and Salvanes (1998). In order to establish the effect of *S. scopeli* on host growth, the sagittal otoliths were extracted from all of the infected *B. glaciale* and from a sex and length matched sample of the uninfected individuals. Otoliths were ID-marked. Fish age (years) was determined by counting annuli from the core to the otolith edge using a standard method (Halliday 1970). Since the fish were caught in February of 2021, the translucent otolith edge was counted as an annulus.

Statistical analysis

All statistical analysis were performed in R version 4.0.5 (R Core Team 2021) with the interactive workspace R-studio (RStudio Team 2021), and the additional packages tidyverse (Wickham et al. 2019), MASS (Venables and Ripley 2002), ShapeR (Libungan and Pálsson 2015), vegan (Oksanen et al. 2008), car (Fox and Weisberg 2019) and emmeans (Russell 2022). Statistical significance was assumed for $\alpha = 0.05$.

Generalized linear models (GLM, logit) were used to test if infected and uninfected *B. glaciale* differed in GSI, HSI and Fulton's condition indices, and if these indices differed among fjords (Masfjord, Fensfjord, Sørfjord and Osterfjord). Separate analyses were made for GSI for females and males. The models were run for indices as proportions and by specifying infection as a fixed categorical variable (1 if infected and 0 if uninfected), fjord as a fixed categorical variable (Masfjord, Fensfjord, Sørfjord or Osterfjord), and sex as a fixed categorical variable (female or male). If

Table 1 Overview of the total prevalence recorded for each sampling period in the four fjord-system. Total prevalence is given as the number of infected individuals over the total number of individuals from all the trawl series in a given sampling period

Fjord	Days	Month	Year	Prevalence
Masfjord	2, 3, 4	October	2019	12.1%
Masfjord	18,19,21	February	2021	4.3%
Masfjord	24, 25, 27, 28	September	2021	6.8%
Masfjord	23, 24, 25, 26	May	2022	6.1%
Masfjord	24, 25, 26, 28, 29, 30	September	2022	8.3%
Fensfjord	19, 20	February	2021	2.9%
Fensfjord	25, 26, 27	September	2021	3.3%
Fensfjord	24, 25, 26	May	2022	3.1%
Fensfjord	24, 26, 27, 28, 29	September	2022	5.7%
Osterfjord	16, 22	February	2021	4.8%
Osterfjord	27	May	2022	1%
Sørfjord	22, 23	February	2021	1.8%
Sørfjord	27	May	2022	2%

interaction terms were not significant, they were removed. Emmeans post-hoc test for pairwise comparison, with a Tukey adjustment, was used to determine which categories differed significantly from each other.

A two-way ANOVA was used to test the effects of the categorical predictors: Infection (1 for infected and 0 for uninfected) and sex (male or female) separately for the response variables: age, otolith length and otolith width. Age was defined as a discrete response, while otolith length and otolith width were defined as continuous responses. All two-way ANOVA were followed by an emmeans post hoc test for pairwise comparison, with a Tukey adjustment, to determine which categories were significantly different.

Results

Variation in prevalence of *S. Scopeli*

Masfjord had the highest prevalence of the four fjords when compared within sampling periods, except for in February of 2021, when the prevalence was slightly higher in Osterfjord (Table 1).

Gonadosomatic indices in infected and uninfected *B. glaciale*

The gonadosomatic index (GSI) was lower in infected individuals than in uninfected for both females (Table 2; Fig. 3A) and males (Table 2; Fig. 3B). The GSI of females were similar between all fjords, but GSI differed between the fjords for males (Table 2). Males from Masfjord and Fensfjord had a lower GSI than those from Sørfjord (Emmeans; $p < 0.001$). Gonad weight increased with gutted weight for both infected and uninfected females and males in all fjords except for Masfjord (LM: $p < 0.006$). In Masfjord the gonad weight did not increase with gutted weight for infected females (LM; Interaction infected x dry gutted weight: $F_{1,70} = 8.77, p = 0.004$).

Hepatosomatic indices of infected and uninfected *B. glaciale*

The hepatosomatic index (HSI) differed between infected and uninfected *B. glaciale* depending on the sex of the fish (Table 2). Infected females had similar HSI to the uninfected females in all fjords, except Sørfjord where the infected females had a higher HSI (Fig. 3C). For the males the infected individuals had a higher HSI than the uninfected inn all four fjords (Fig. 3D). Uninfected males had a lower HSI than uninfected females (Emmeans: Uninfected: $p \ll 0.001$), while infected males and females had similar

Table 2. Results of Generalised linear models of gonadosomatic index, hepatosomatic index and fulton`s condition factor. A quasi-binomial distribution was assumed to account for overdispersion and calculated weighting factors and Chi-square test were used

	D.f	Deviance	Residual D.f	Residual deviance	p
Gonadosomatic index for Female					
Infected	1	4.57	172	5.49	<< 0.001
Fjord	3	0.11	169	5.38	0.35
Gonadosomatic index for Male					
Infected	1	0.02	156	0.16	<< 0.001
Fjord	3	0.03	153	0.14	<< 0.001
Hepatosomatic index					
Infected	1	0.25	331	4.55	<< 0.001
Sex	1	2.56	330	2	<< 0.001
Fjord	3	0.05	327	1.95	0.02
Infected × Sex	1	0.2	326	1.75	<< 0.001
Infected × Fjord	3	0.09	323	1.66	< 0.001
Condition factor					
Infected	1	< 0.01	331	0.03	<< 0.001
Sex	1	< 0.01	330	0.03	0.57
Fjord	3	0.01	327	0.02	<< 0.001

HSI (Emmeans: Infected: $p = 0.99$). The HSI of infected fish differed among the fjords (Table 2; Fig. 3C & D). Infected fish from Sørfjord had a higher HSI than infected fish from Masfjord and Fensfjord (Emmeans: $p = 0.002$; Fen: $p = 0.04$). Liver weight increased with the gutted weight for both females and males and for both infected and uninfected fish in all fjords (LM: $p < 0.005$). The increase was similar for infected and uninfected individuals for both sexes and in all four fjords (Interaction: infection x dry gutted weight, Females $p > 0.17$; Males $p > 0.39$).

Fulton's condition factor of infected and uninfected *B. glaciale*

The condition factor was lower in infected than in uninfected *B. glaciale* (Table 2; Fig. 3E & F), and were similar for females and males (Table 2.). Condition factors for both infected and uninfected fish were similar for all fjords (GLM: interaction Infection x fjord, Resid. dev = 0.02, $DF_{3,323}$, $p = 0.92$, Table 2). After removing the interaction effect from the model, the condition factors differed between fjords (GLM: Resid. dev = 0.02, $DF_{3,327}$, $p << 0.001$, Table 2; Fig. 3E & D), with fish from Sørfjord being in the poorest condition (Emmeans; $p << 0.001$).

Parasitic effect on host growth

Mean age (ANOVA: $p > 0.11$), otolith length (LM: $F_{1,150} = 0.48$, $p = 0.49$), otolith width (LM: $F_{1,150} < 0.01$, $p = 0.99$) and otolith shape (ANOVA: $p > 0.05$) were similar between infected and uninfected fish. Females and males had similar mean age (ANOVA: $p > 0.06$), otolith length (LM: $F_{1,150} < 0.01$, $p = 0.99$) and otolith width ($F_{1,150} < 0.01$, $p = 0.94$).

Discussion

In a comparison between *B. glaciale* specimens with and without *S. scopeli* infections, we observed a substantial reduction in the gonadosomatic index among the infected fish. This reduction aligns with what Gjøsæter (1971) reported, indicating a substantial impact of the infection on the reproductive output of the host. The infection's effects varied between male and female hosts; it led to liver enlargement in males, whereas the energy reserves in females' livers remained unaffected. Across all four studied fjords, infected fish generally had a lower condition factor than uninfected ones. However, the infection did not impact the otolith growth rate in the hosts. Overall, our findings were consistent with our initial hypotheses that *S. scopeli* affects host condition and causes castration, except for the unexpected lack of effect on host growth and the notable increase in Hepatosomatic Index (HSI) in infected male fish.

The fact that our data show that *S. scopeli* infection completely halted the maturation of the female ovary, suggests that the infection likely has huge impact on the fitness and reproductive capacity of the female host. Such a castration effect has previously been reported from another
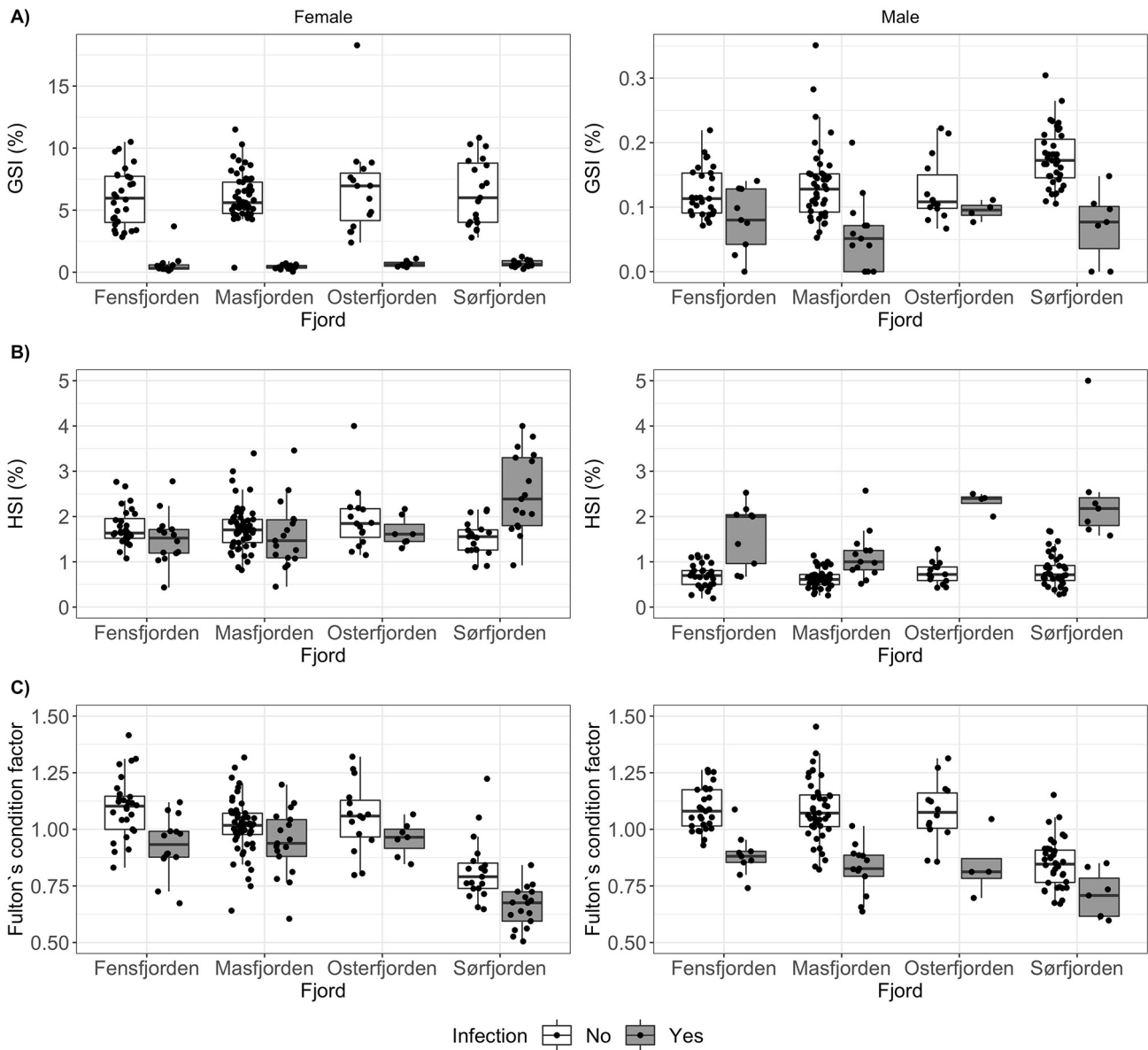
Fig. 3 Gonadosomatic index (GSI) of infected and uninfected (**A**) females, (**B**) males. Hepatosomatic index (HSI) of infected and uninfected (**C**) females, (**D**) males. Fulton`s condition factor of infected and uninfected (**E**) females, (**F**) males

myctophid-pennellid system, the northern lampfish that was infected by *Cardiodectes bellottii* (Moser and Taylor 1978). Parasitic species that castrate their host are often believed to do so in an intensity-independent manner, e.g. host castration is achieved by a single parasitic infection (Kuris and Lafferty 2000; Lafferty and Kuris 2002). In our study the majority of the infected fish harboured one specimen of *S. scopeli*, which could indicate that the castration of the host is indeed intensity-independent. Infected males did not exhibit the same pronounced gonadal reduction as observed for the females. This was not unexpected since male gonads are considerably smaller than female gonads in healthy

fishes, and males allocate much less energy to reproduction compared than female fishes (Roff 1983).

Previous studies on other parasitic castrators have shown mixed results concerning liver reducing effects of parasitism. For five-lined cardinalfish, *Cheilodipterus quinquelineatus*, (Cuvier, 1828), results show decrease in energy reserves in the liver of the host fish infected with cymothoid isopods (Fogelman et al. 2009), but for common breams, *Abramis brama* (Linnaeus, 1758), there was no difference in liver size between infected and uninfected hosts (Hecker and Karbe 2005). In our study, infection on male and female *B. glaciale* had different effects on the liver mass. We found little difference in liver sizes between infected and

uninfected females, while infected males had liver enlargements. The underlying mechanism causing the difference in liver size between infected and uninfected males is yet known, but it may be caused by the production of the egg yolk precursor, vitellogenin (VTG), that normally takes place in females (Moussavi et al. 2009). Production of VTG is an energetically demanding process, that takes place in the fish liver, where it is regulated by sex steroids in the blood plasma (Schneider 1996). These sex steroids may be readily manipulated through endocrine disruption, resulting in alterations to the VTG production (Hecker and Karbe 2005; Trubiroha et al. 2010). The same endocrine receptors responsible for VTG production in females, is also present in males (Sumpter and Jobling 1995), and exposure to estrogen compounds can facilitate its production causing accumulation in the liver (Barse et al. 2006). Because VTG is transported through the vascular system (Schneider 1996), it can be speculated that *S. scopeli* could directly feed on this precursor. Thus, the parasite would benefit from facilitating the production also in males. However, parasitic induced liver enlargement in fish has only been reported a few times (Tierney et al. 1996; Seppänen et al. 2009) and the mechanism behind the phenomenon remains poorly understood.

Infected individuals were found to exhibit a lower condition factor compared to the uninfected conspecifics. There may be multiple factors which are not mutually exclusive that could explain the reduced condition of the infected fish. One explanation may be that the infection is more energetically costly than the host`s reproductive energy allocation, thus also drawing energy from the somatic body tissue of the host. A model study on parasitic energy budget suggests that parasitic castrators should evolve towards exhibiting a similar level of energetic drain as the host allocates to reproduction (O'Keefe and Antonovics 2002; Bonds 2006). However, in some cases, the energetic drain posed by the infection exceeds the host`s reproductive energy, resulting in a decrease of host condition (Ebert et al. 2004).

Another explanation could be that parasitic presence on the host exterior generate an increased hydrodynamic drag experienced by the host. Östlund-Nilsson et al. (2005) found that five-lined cardinalfish, *Cheilodipterus quinquelineatus*, (Cuvier, 1828) experienced reduced swimming capability and increased fatigue when parasitized by the ectoparasitic isopod *Anilocra apogonae* (Bruce, 1987), suggesting that the presence of external parasitic structures also can disrupt the weight balance and streamlining of the host. This could be the case for *B. glaciale*, as the species undergoes pronounced vertical migrations during the diel cycle, in order to feed in shallower water during night (Dypvik et al. 2012). Since the external part of *S. scopeli* constitute a large structure (Andersen 2022), it is possible that the fish experience reduction in swimming capability.

The decrease in body condition observed in the infected individuals might not be solely caused by the infection itself. Instead, it could also be that individuals with a reduced body condition are more susceptible to becoming infected. Malnourished fish have less energy to allocate to physiological mechanisms such as the immune system, which role is to prevent and fight infections. Both the innate and the adaptive immune system are energetically costly to maintain (Lochmiller 1996; Sheldon and Verhulst 1996) and often become reduced under periods of nutritional stress (Blazer 1992). While a decrease in immune system function may increase the susceptibility to infection, parasitic fitness may also be reduced if the host is malnourished, (Seppälä et al. 2008), as it have less consumable energy available.

Since the condition factor was reduced of the infected *B. glaciale*, a reduction in the growth rate of these fish was expected. Interestingly, such a decrease could not be detected when investigating if otolith ring bands/size correlated in relation to body size in infected and uninfected male and female fishes. These findings are in contradiction to the findings of Gjøsæter (1971), who compared the average size per year class of a combined male/female data set. Nevertheless, the lack of parasitic effect on host growth, interpreted together with the reduction in host condition, may indicate that *S. scopeli* drains large energetic reserves of its host in a dramatically short period of time. If so, it is likely that *B. glaciale* experience an elevated mortality rate following infection, thus dying before an effect on growth can be detected.

While our study provide data on the parasitic effects of *S. scopeli* infection on *B. glaciale*, other aspects of the parasite-host relationship remains poorly understood. For instance, most species belonging to the family Pennellidae, have been described to have an indirect life cycle (Kabata 1979), often with an intermediate invertebrate host (Piasecki and Avenant-Oldewage 2008). However, a direct life cycle has been proposed for the species *Peniculus minuticaudae*, with the thread-sail filefish, *Stephanolepis cirrhifer*, (Temminck & Schlegel, 1850) as its only host (Ismail et al. 2013). In the original description of *S. scopeli* by Jungersen (1911), some of the life stages was described, and it was concluded that the parasite had a direct life cycle on *B. glaciale*. However, as Jungersen (1911) does not provide a complete description of the life cycle of *S. scopeli*, it is not yet known if *B. glaciale* acts as the only host during the life cycle or if it is a definite host, with a yet to be discovered intermediate host.

Conclusion

The overall data provide evidence for *S. scopeli* having a castratory effect on its host, while the underlying mechanism behind the host castration is yet not fully known. The increased liver size of infected fish may indicate direct manipulation, while the reduced host condition and lack of response in growth strongly indicates excessive parasitic energy drain.

Parasitic castration is likely to affect vital rates of *B. glaciale* populations. The reduced number of spawning females will reduce recruitment into the *B. glaciale* population and reduce population sizes in the fjord system. In addition, *S. scopeli* is presumed to increase the mortality of infected fish, which likely may reduce life span which also will have negative effect on the population size of the host. Higher risk of castration may cause affected *B. glaciale* populations to evolve earlier reproduction over time, similar to what has been found for the freshwater fish *Engraulicypris sardella* infected by the tapeworm *Ligula intestinalis* (Gabagambi et al. 2020). Earlier spawning usually means that the females are less fecund (Roff 1983), which would further affect host recruitment. As a parasitic castrator, *S. scopeli* may have a larger regulatory effect on the *B. glaciale* fjord populations than first anticipated.

Declarations

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