Aquaculture 541 (2021) 736774

Contents lists available at ScienceDirect

Aquaculture

journal homepage: www.elsevier.com/locate/aquaculture

Tapeworm (*Eubothrium* sp.) infestation in sea caged Atlantic salmon decreased by lice barrier snorkels during a commercial-scale study

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ARTICLE INFO

Editor: Peter Bossier

Keywords:
Cestode
Mariculture
Pest control
Salmon aquaculture
Salmo salar

ABSTRACT

Reports of infestation by marine parasitic tapeworms (*Eubothrium* sp.) and an associated growth reduction in Norwegian farmed salmon are on the rise. With few acceptable treatment options available, due to drug resistance evolution in tapeworms or negative drug impacts on fish, alternative controls against the parasite are in demand. In a 10-month commercial-scale study involving standard sea cages and lice barrier snorkel sea cages of different depths (4, 8, 12 and 16 m), we examined if this depth-based preventive technology primarily used against salmon lice (*Lepeophtheirus salmonis*) also reduced tapeworm infestation. A submerged net roof opening to a central barrier tube (snorkel) was added to standard cages to move salmon deeper but retain surface access; a cage manipulation that avoids contact with mostly surface-dwelling salmon lice larvae and may also separate fish from calanoid copepods, the intermediate hosts of *Eubothrium* sp. Salmon populations in unmodified standard cages had higher tapeworm prevalence (63–93%) and abundances (4.6–5.7 *Eubothrium* sp. fish^{-1}) than those in snorkel cages (20–36% and 0.2–0.6 *Eubothrium* sp. fish^{-1}). Based on these observations, tapeworm prevention could be another beneficial parasite management outcome of snorkel cage technology or other depth-based prevention techniques against salmon lice.

1. Introduction

Intensive animal farming systems are often associated with a wide range of pathogens, primarily due to abnormally high host densities and host confinement (Hart, 1990; Krkošek, 2010). This is the case in the world's largest finfish mariculture industry sea cage farming of Atlantic salmon *Salmo salar* (FAO, 2020). Norway is the top producer of Atlantic salmon, producing over 64 billion NOK of farmed salmon in 2018 (Norwegian Directorate of Fisheries, 2020). However, in the last few years, industry growth and production volume has stalled partly owing to outbreaks and control of pathogens. The main challenge for salmon farmers in Norway is the ectoparasitic salmon louse (*Lepeophtheirus salmonis*), as Norwegian regulations require low lice intensities on farmed fish to reduce impacts of the parasite on wild salmonids (Stien et al., 2020). Nevertheless, several other parasites also affect Norwegian farmed salmon, including marine tapeworms (cestodes). Tapeworms belonging to the genus *Eubothrium* have been detected in farmed salmonids for several decades (Berland and Bristow, 1990; Engelstad et al., 1990; Bristow and Berland, 1991a) and have become increasingly problematic in recent years. Reports of *Eubothrium* sp. tapeworm infestations are rising in central and western parts of Norway (Hjeltnes et al., 2018, 2019; Sommerset et al., 2020), and now extend beyond historical ranges into regions north of the Trondheim fjord (Hjeltnes et al., 2019).

Eubothrium spp. tapeworms are intestinal parasites commonly found in salmonids of the northern hemisphere (Shulman, 1961; Wardle et al., 1975; Kennedy, 1978). There are two *Eubothrium* species associated with salmonids in Norway; *E. salvelini* (commonly found in Arctic charr) and *E. crassum* (common in brown trout and Atlantic salmon), both associated with freshwater rivers and lakes (Vik, 1963; Kennedy, 1978). There is also a marine variant of *E. crassum*, often referred to as *Eubothrium* sp., found in sea running trout and Atlantic salmon returning from sea (Kennedy, 1978; Fahy, 1980; Berland, 1997). Controversy has surrounded the identity of this marine *Eubothrium* sp., whether it is identical with the freshwater *E. crassum* (Scholz et al., 2003), a marine form of *E. crassum* (Kennedy, 1978) or even a different species (Bristow and

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https://doi.org/10.1016/j.aquaculture.2021.736774
Received 1 October 2020; Received in revised form 9 April 2021; Accepted 12 April 2021
Available online 17 April 2021

Berland, 1989). Here, it will be referred to as *Eubothrium* sp. following past studies (Bristow and Berland, 1989; Bristow and Berland, 1991b, a; Saksvik et al., 2001a; Saksvik et al., 2001b; Sundnes, 2003).

Adult *Eubothrium* sp. are often found attached with their scolex to the anterior pyloric caeca of a fish host, while their strobila stretches out into the intestine as the parasite grows (Berland, 1997). Adults can grow very large (> 1 m length) and in some cases take up substantial space in a host's gut. In a field study, Bristow and Berland (1991b) found a significant weight difference between farmed Atlantic salmon with and without marine *Eubothrium* sp. infestation. This was further confirmed in a controlled laboratory study where fish infested with *Eubothrium* sp. grew slower than non-infested fish, even at low intensities of one tapeworm per fish (Saksvik et al., 2001a). Significant reductions in salmon farm production and profit loss may be attributed to *Eubothrium* sp., through the direct loss of salmon growth. In one instance, they were estimated to reduce harvest fish size by 10% (Bristow and Berland, 1991b). Increased food consumption by fish due to tapeworm presence (Walkey and Meakins, 1970; Giles, 1987), potentially leading to additional feeding may also lower farm profits, but this is unstudied in salmon. Anthelminthic drugs administered in feed (Fenbendazole and Praziquantel) have been used by salmon farmers to treat against existing tapeworm infestations. Due to negative side-effects in salmon (e.g. anorexia, growth loss) Fenbendazole is rarely used (Sevatdal and Hellberg, 2006; Sevatdal, 2014) and treatment with Praziquantel have dominated. However, widespread resistance to Praziquantel by *Eubothrium* sp. throughout western Norway has meant this treatment is rarely used against tapeworm infestations (Sevatdal et al., 2008; Sevatdal, 2014; Hjeltnes et al., 2019). Therefore, new control methods are required to optimally treat or reduce *Eubothrium* sp. infestations.

Bothriocephalidean tapeworms generally have a copepod first-intermediate host in their life cycle, but transport hosts may also be involved (Akhmerov, 1962; Vik, 1963; Mulcahy and Kennedy, 1970; Scholz and Kuchta, 2017). Experimental infestations have demonstrated that only the copepod first-intermediate host is essential for *Eubothrium* sp. to complete their life cycle (Saksvik et al., 2001b). The final fish host can be infected directly via ingestion of a procercoid infected copepod (Saksvik et al., 2001b). Scolex-formation allows attachment to the caeca and further development into an adult tapeworm in the fish host (Berland, 1997; Saksvik et al., 2001b). It is unknown which copepod(s) are the main intermediate hosts leading to tapeworm infestations in wild or cultured salmon, but four calanoid copepods (*Acartia tonsa*, *Acartia clausi*, *Temora longicornis* and *Pseudocalanus elongatus)* are susceptible to infestation by ingesting *Eubothrium* sp. eggs (Hodneland and Solberg, 1995; Saksvik et al., 2001b). While not fully resolved, there is general consensus that *Eubothrium* sp. infestation intensity increases in summer and autumn months, coinciding with increases in intermediate copepod host abundances in the water column (Gundersen, 1953; Matthews, 1967; Saksvik et al., 2001b; Deschutter et al., 2019). Zooplankton, including copepods susceptible to *Eubothrium* sp. infestation, are often associated with surface waters in summer and autumn as primary production is confined to shallow areas.

Infective free-living salmon lice larvae similarly reside in upper depths of the water column (Bron et al., 1993; Heuch et al., 1995; Hevrøy et al., 2003), and several depth-based parasite prevention technologies combatting this parasite could also reduce tapeworm infestations (Bui et al., 2019). These technologies include barrier cages (skirt or snorkel tarpaulin wrapped around upper depths), submerged cages (repeatedly submerged or submerged with an air dome), semi-enclosed cages (deep water pumped in), and deep lighting and feeding (motivating salmon to swim deeper). They work by either moving salmon deeper or shielding salmon from upper depths while still ensuring air access for salmon swim bladder reinflation, so buoyancy control and optimal welfare are maintained (Fahlén, 1971; Dempster et al., 2009). Several studies show that these depth-based prevention techniques reduce salmon lice infestation with negligible impact on salmon welfare (Stien et al., 2016; Nilsen et al., 2017; Stien et al., 2018; Geitung et al., 2019; Glaropoulos et al., 2019) and that increasing the shielding depth strengthens lice reductions (Oppedal et al., 2017). In addition, there is the potential to control more than one pathogen by using this technology (Wright et al., 2017; Wright et al., 2018).

Here, we examined the effects of a depth-based prevention technology on tapeworm infestations in sea caged Atlantic salmon. In a 10-

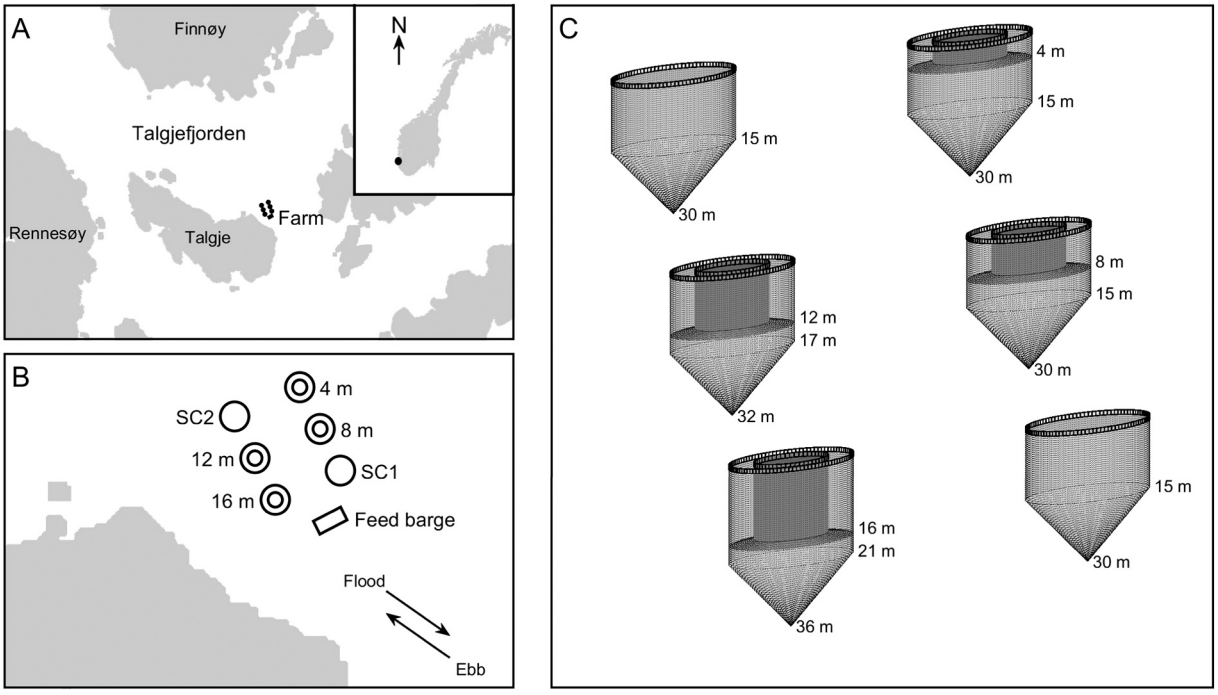

Fig. 1. a) Overview of Norway and area surrounding Prestholmane fish farm, b) Prestholmane fish farm with arrows representing main current and c) cage setup. For b) Prestholmane fish farm, the rectangle represents the feeding barge, the circles represent standard cages (SC) and the double circles represent snorkel cages. All cages were 50 m in diameter and 30–36 m deep, while four cages were also fitted with a 30 m in diameter and 4, 8, 12 or 16 m deep snorkel.

month study, we observed *Eubothrium* sp. infestations in Atlantic salmon kept in commercial-scale standard cages and lice barrier snorkel cages of different depths (4, 8, 12 and 16 m) to determine if a) the technology alters tapeworm infestations and b) whether a relationship exists between snorkel depth and tapeworm infestation, as previously described for salmon lice (Oppedal et al., 2017). Infestation dynamics were followed to detect the onset and peaks in tapeworm infestations in different sea cage types. We hypothesized that snorkel cage technology would reduce and delay *Eubothrium* sp. infestation and that these effects would strengthen with increasing snorkel depth.

2. Materials and method

2.1. Experimental setup

The study was conducted at a commercial fish farm (Prestholmane) in Talgjefjorden, Finnøy commune (59.1° N, 5.8° E). Atlantic salmon (autumn transferred smolts, Salmobreed strain) were stocked at sea in 2 standard sea cages and 4 sea cages fitted with snorkels between 21 November – 6 December 2017 (Fig. 1). The four snorkels were of 4, 8, 12 and 16 m depth, with net roofs placed accordingly, and were installed before fish arrival. At transfer, the number of fish per cage ranged between 142,473–161,651 with an average weight of 108–168 g. Throughout the experimental period the farm was managed according to standard rearing and feeding procedures in salmon aquaculture.

Daily salinity and temperature measurements were performed at the feed barge with a Conductivity, Temperature and Depth (CTD) recorder (SD208, SAIV-AS, Bergen, Norway). Temperature followed normal seasonal variations for the area (Geitung et al., 2019), ranging from 2 °C in March to 18 °C in June and with thermal stratification causing warmer surface waters from mid-May to mid-August (Fig. 2a). Salinity varied slightly throughout the trial, but brackish surface water (< 28 ppt) was generally absent (Fig. 2b). Minor salinity stratification coincided with thermal stratification (Fig. 2).

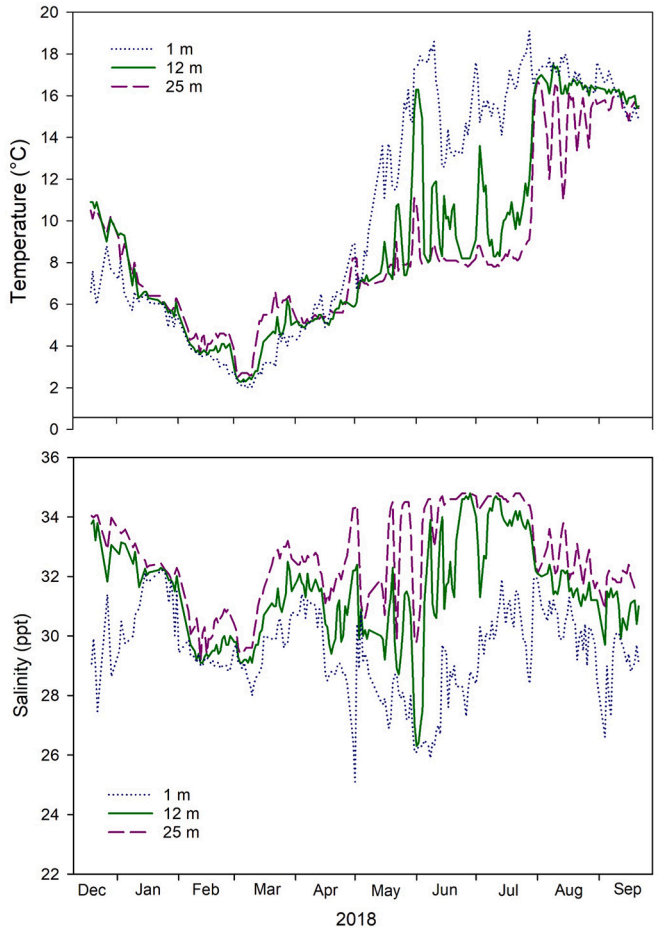

Fig. 2. Daily a) temperature and b) salinity measurements at depths representing surface (1 m), mid cage (12 m) and bottom cage (25 m) from a reference location at the feed barge.

Table 1
Dates for sampling events, number of fish and sampled cages.

Sampling	Date	Time at sea	N fish sampled from each cage	Cages analysed for *Eubothrium* sp.
0	27 Oct 2017	Freshwater	60[a]	
1	31 Jan 2018	2 months	30	Standard cage 1, 2 and 16 m snorkel cage
2	27 Mar 2018	4 months	20	Standard cage 1, 2 and 16 m snorkel cage
3	25 May 2018	6 months	20	Standard cage 1, 2 and 16 m snorkel cage
4	17 Jul 2018	8 months	30	Standard cage 1, 2 and 16 m snorkel cage
5	19 Sep 2018	10 months	30	All cages

[a] Total number of fish sampled.

Tapeworm infestations in salmon were examined over the first 10 months of production, ceasing in September 2018, when the first snorkel was removed and exposed these fish to surface waters which potentially influenced their subsequent tapeworm infestations. To ascertain whether any tapeworms were of freshwater origin, 60 salmon were examined in the freshwater phase before stocking (Trovåg hatchery, Vindafjord commune). In the marine phase, sampling events were performed every second month with the first done two months after stocking (Table 1). At each sampling event, 20–30 fish per cage were randomly netted and lethally dosed with Benzoak vet. (Benzocaine, 200 mg/ml, VESO Vikan, Namsos, Norway). The fish were then weighed (g) and measured (cm), from which Fulton's condition factor ($K = 100 \times W L^{-3}$, *where W* is the weight of the fish and *L* corresponds to the total length) was calculated (Supplementary Table 1), before the gastrointestinal tracts of the fish (i.e. pylorus region and intestine) were dissected out and placed in individually labelled bags. The intestines were stored at −20 °C prior to examination.

2.2. Laboratory analyses

In the laboratory (University of Bergen), the intestines were examined for tapeworm infestation. In order to maximise inferential power from a practical number of examinations, intestines from the most extreme groups (standard cages and 16 m snorkel cage) were examined for worms every second month, while all groups were examined at the final sample (Table 1). Before examination, the pylorus region and the intestine were separated and placed in Petri dishes with physiological saline (1% NaCl). The pylorus region was examined by squeezing it between two Petri dishes and viewing under a stereo microscope, noting the presence of *Eubothrium* sp. as well as the number of individuals per fish based on scolex counts. The intestines were cut open and mucosa scraped off with a scalpel before being squeezed and examined. For smaller fish, the pylorus region and intestine could be squeezed whole, while for larger fish both the pylorus region and intestine were cut into smaller pieces to sufficiently squeeze regions and observe tapeworms. Small (0.4–1.0 mm long) unstrobilated juveniles were referred to as 'plerocercoids', juveniles (<5 mm long) with a few proglottids as 'plerocerciform' and larger immature small worms as 'juveniles'. All worms from each fish were dissected out, washed and either weighed (g) after removing excess moisture on absorbent paper or measured (length mm). The latter was necessary for specimens too small or fragile to be weighed and weight was then estimated from length using a standard

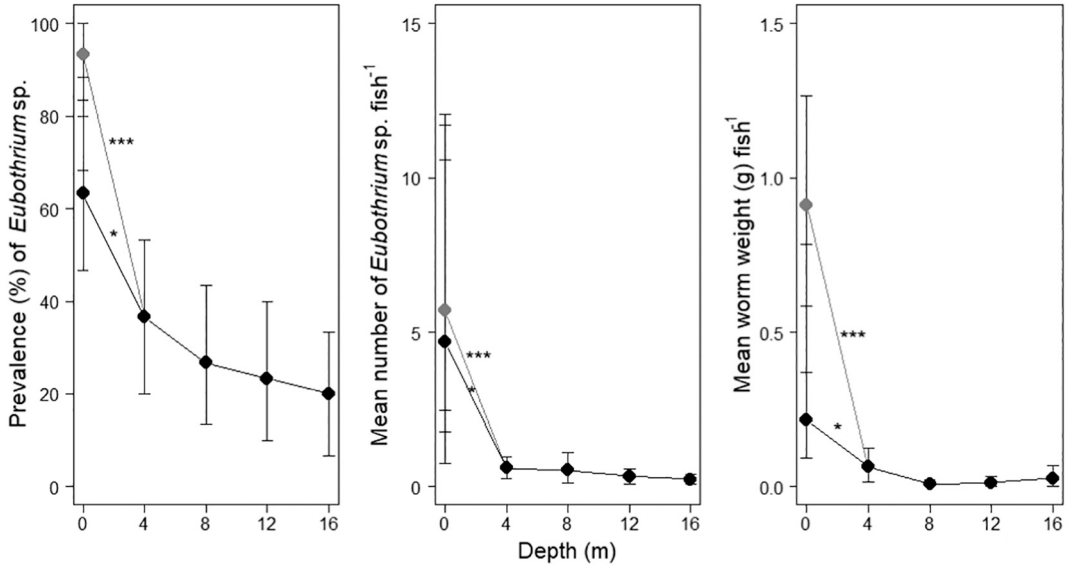

Fig. 3. a) Prevalence of *Eubothrium* sp., b) mean numbers (abundance) and c) mean worm weight (g) of *Eubothrium* sp. fish^{-1} in salmon examined from all cage types in September 2018. Standard cages (SC) are presented at 0 m depth (grey dot = SC1; black dot = SC2) while snorkel cages are presented with a dot at their respective shielding depths (4, 8, 12 and 16 m). The whiskers indicate the respective 95% confidence interval. Stars mark significance level * = $p < 0.05$, *** = $p < 0.001$.

length-weight relationship (Ruud, 2019).

2.3. Data analysis

Data analyses were performed in R software v.3.1.0 (package stats, R Core Team (2019)). The parasitological terms in this study are used as defined by Bush et al. (1997), with prevalence being the proportion of fish that are infected, abundance being the number of individual parasites in a host regardless of whether or not the host is infected and intensity being the number of individual parasites in an infected host. Tapeworm prevalence was compared using one-way Fishers Exact test (FET) (function fisher.test), while tapeworm abundances and total weights were compared using nonparametric Mann-Whitney *U* tests (MW) (function wilcox.test). Differences between standard and snorkel cages were compared for the last sampling point which were representative of tapeworm infestations accumulated over the course of the study. Bootstrapping (function boot, Davison and Hinkley (1997)) was used to obtain 95% confidence intervals and the significance level was set at $P < 0.05$.

3. Results

3.1. Snorkel versus standard cages

Tapeworm infestations were low in all examined cages until May and were lower in snorkel compared to standard cages at the end of the study (Fig. 3). At the final sampling time (September 2018), sample prevalence appeared to decrease with increasing snorkel depth (Fig. 3a), but the only significant step was between standard cages (or 0 m depth) and the first snorkel depth (Fig. 3a, FET, $p < 0.001$ and $p = 0.024$ respectively). Similarly, mean abundance of *Eubothrium* sp. (Fig. 3b, MW, w = 1562, p < 0.001 and w = 1158, $p = 0.019$) and mean worm weight fish^{-1} was highest in standard cages (Fig. 3c, MW, w = 1577, p < 0.001 and w = 1173, $p = 0.014$). Final mean numbers of *Eubothrium* sp. fish^{-1} were 5.7 [2.4–11.6] and 4.6 [0.8–12.3] (standard cage), 0.6 [0.3–1.0] (4 m snorkel), 0.5 [0.1–1.2] (8 m snorkel), 0.3 [0.1–0.6] (12 m snorkel) and 0.2 [0.1–0.4] (16 m snorkel) *Eubothrium* sp. fish^{-1} (details in Supplementary Table 2). This equated to salmon in standard cages having 10–20 times more tapeworms than those in snorkel cages at the end of the experiment. The effect of cage type or tapeworm biomass on fish growth and condition was not examined. Variable degrees of pancreas disease (PD) outbreaks affected fish during summer, resulting in poor salmon growth (Supplementary Table 1).

3.2. Infestation dynamics

No tapeworms were found in fish sampled in the freshwater phase. Tapeworm growth is variable and cannot be used to accurately back-calculate the duration of infestation (Saksvik et al., 2001b). Therefore, in the present study, significant increases in tapeworm prevalence and abundances between sampling times were taken as evidence that infestation had been recently acquired. In standard cage 1, in the cage row most distant from shore (Fig. 1), no tapeworm infestations were registered until May, when a 2 mm plerocerciform worm was found. Prevalence then markedly increased to 83% in July and 93% in September (Fig. 4a), while abundances increased to a mean of 2.5 *Eubothrium* sp. fish^{-1} in July and 5.7 *Eubothrium* sp. fish^{-1} in September (Fig. 4b). At the last sampling time in September both plerocerciform juveniles and larger adult worms (max. 75 cm) occurred. In standard cage 2, closest to shore (Fig. 1), the first tapeworm, a 14 mm juvenile, was found in January (70 days post sea transfer). The prevalence thereafter increased gradually, reaching 25% in May and 63% in September (Fig. 4a). Abundances also gradually increased, reaching a mean of 0.5 *Eubothrium* sp. fish^{-1} in May and 4.7 *Eubothrium* sp. fish^{-1} in September (Fig. 4b). In the 16 m snorkel cage, the first evidence for infestation was seen in July (13%) with a mean abundance of 0.63 *Eubothrium* sp. fish^{-1}, where both plerocercoids and juvenile worms were found (0.5–14 mm long) (Fig. 4). In September, mean abundance (0.23 *Eubothrium* sp. fish^{-1}) and prevalence (20%) remained similar, but both plerciform and larger subgravid worms (≤37 cm) were present (Fig. 4).

4. Discussion

In this study we demonstrated the potential for depth-based technologies, currently used to prevent salmon lice, to also reduce *Eubothrium* sp. tapeworm infestations in Atlantic salmon kept in commercial-scale sea cages. Over the 10-month trial from winter to autumn, standard cages had 3–5 times as many fish infected with 10–20 times more worms than lice barrier snorkel cages. All snorkel cages, even those with

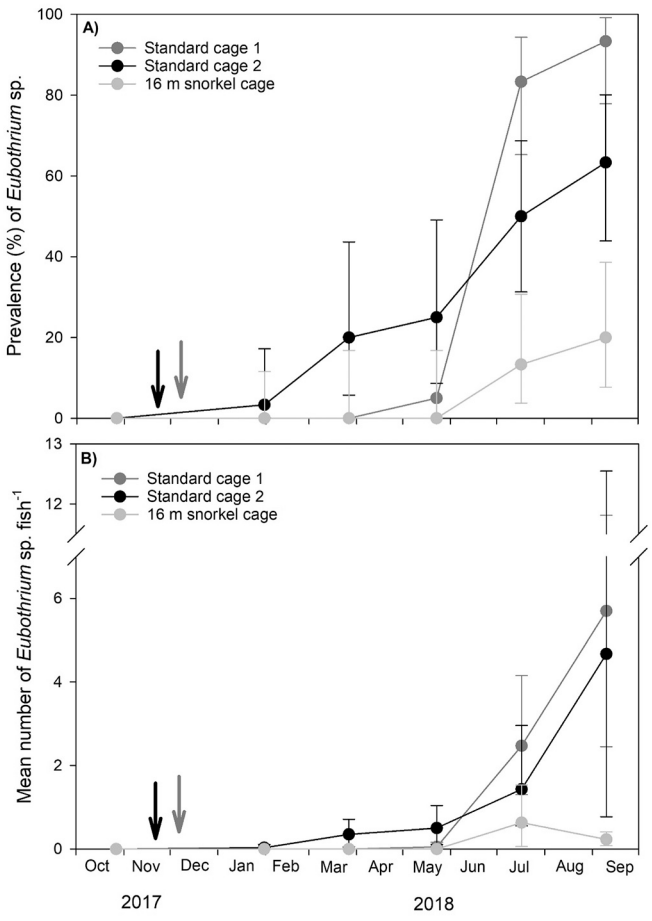

Fig. 4. a) Prevalence of *Eubothrium* sp. and b) mean numbers (abundance) of *Eubothrium* sp. fish^{-1} in salmon examined in two standard cages (SC) and one 16 m snorkel cage every second months from October 2017 until September 2018. Arrows indicate stocking time with the black arrow (21.11.2017) representing stocking time for SC2 and the grey arrow (06.12.2018) stocking time for SC1 and 16 m snorkel. The whiskers indicate the respective 95% confidence interval.

barriers of 4 m depth, decreased tapeworm prevalence and abundance. This suggests that prevention of *Eubothrium* sp. could be an additional benefit when using snorkel sea cages or other depth-based prevention techniques against salmon lice, as these are generally of 10 m depth when used in commercial-scale sea cages (Wright et al., 2017; Stien et al., 2018; Geitung et al., 2019). To address additional aspects of the effects of depth-based prevention technologies further studies using alternate designs (e.g. cage replication, longer duration) are needed.

Tapeworm prevalence appeared to decrease with increasing snorkel depth, however there was no clear relationship between tapeworm infestation and snorkel depth as previously observed for salmon lice (Oppedal et al., 2017). Effectiveness of a depth-based technology in this study suggests that *Eubothrium* sp. transmission events are more likely in surface waters. Transmission of *Eubothrium* sp. involves salmon ingesting infected copepods (Hodneland and Solberg, 1995; Saksvik et al., 2001b). Atlantic salmon are usually fed from the surface in commercial sea cages and typically spend extensive periods in surface waters due to a combination of abiotic and biotic factors (Oppedal et al., 2011). Calanoid copepods in the upper water masses may be voluntary or accidentally ingested by salmon in upper cage depths and forcing fish into deeper water in snorkel cages likely minimises exposure to them.

Eubothrium sp. can affect salmon growth at both high and low intensities, even at one tapeworm fish^{-1} (Saksvik et al., 2001a). One reason for this is the 'crowding effect' causing worms at high intensities in a single host to remain small (Read, 1951; Roberts, 2000), while a single worm in a host can grow to >1 m in length and 5.9 g in weight and weigh more than hundreds of smaller individuals (Berland and Bristow, 1994; Ruud, 2019). Hence worm biomass may be a better predictor of any effects on salmon growth than worm intensities. If the effects on host growth relates to parasite mass, it is vital that a prevention technique not only reduces the number of worms in each fish but also the proportion of fish infected, as observed in this study. However, contrary to the expectation from crowding (Saksvik et al., 2001b), worm weight per fish was lower for the lighter infestations occurring in snorkel cages compared to the higher intensity infestations occurring in standard cages. One reason is that infestations were delayed in snorkel compared to standard cages and more time may be needed before worm weight per fish in cages with lighter infestations exceed those in cages with higher intensity infestations. In addition, slower worm development may have occurred in snorkel fish exposed to lower temperatures below or within snorkels (filled with water at the snorkel depth) during thermal stratification over summer. As salmon and tapeworms are ectotherms, their growth rates are influenced by external temperatures with cooler water slowing growth (Chubb, 1982; Handeland et al., 2008). While depth-based manipulations like snorkel sea cages can alter the temperatures experienced by salmon and their parasites, previous research has found no difference in salmon growth between snorkel and standard sea cages (Stien et al., 2016; Oppedal et al., 2017; Wright et al., 2018; Oppedal et al., 2019). Our results, from this long-term 10-month study suggest that snorkels of 4–16 m depth lower tapeworm prevalence, abundance and worm weight which should minimise growth losses normally experienced due to worm presence. However, studies of even longer duration, at different locations (e.g. with strong vertical salinity gradients (Oppedal et al., 2019)), with designs adding cage replication and using different depth-based technologies should be conducted to ascertain the consistency of these effects on tapeworm infestations in salmon aquaculture.

Determining tapeworm induced effects on fish in a field study can be difficult. Competition for limited food resources between parasite and host explains the reduced condition often observed in fish hosts with internal tapeworms (Smith, 1973; Hoffmann et al., 1986). However, sufficient food supply for the host is thought to diminish these effects (Rees, 1967). A normal feeding regime in salmon aquaculture may therefore reduce or eliminate growth differences caused by tapeworms compared with situations where fish are not fed to excess (Boyce, 1979; Saksvik et al., 2001a). In field studies co-infection of other parasites and diseases affecting salmon growth also occur. In the present study, pancreas disease (PD), known to affect the weight gain of salmon (Taksdal et al., 2007, 2015), was diagnosed on the farm. In addition, as tapeworm growth is highly variable and size cannot be used to estimate the age of an infestation (Saksvik et al., 2001a), it is difficult to control for the time of infestation and potential concurrent infestations in field studies. Due to this, growth effects of cage type or tapeworm density were not examined here. Nonetheless, the potential for tapeworm presence to reduce growth rates (Boyce, 1979; Bristow and Berland, 1991b; Saksvik et al., 2001a), increase food consumption (Walkey and Meakins, 1970; Giles, 1987), or potentially cause immunodepression in fishes (Boyce and Yamada, 1977; Bristow and Berland, 1991b; Saksvik et al., 2001a) should be of concern to salmon farmers from both economic and fish welfare perspectives. Further controlled laboratory studies of tapeworm impacts on salmon are required to properly gauge the extent of these problems.

Eubothrium sp. infestations observed in this study varied seasonally, with the first evidence of parasite acquisition in winter-spring and increasing prevalence and abundance from late May to September. Elevated infestation pressure during summer and autumn is in line with previous studies (Berland and Bristow, 1991; Ruud, 2019). Several cestodes show seasonal fluctuations in infestation pressure (Chubb, 1982; Kennedy, 1996; Scholz and Moravec, 1996; Hanzelová and Gerdeaux, 2003), often associated with the availability of infectious stages

and changes in host behaviour throughout the seasons (Chubb, 1982; Williams and Jones, 1994). Information on the seasonality of *Eubothrium* sp. infestation is scarce but appears to be linked to the presence of possible intermediate hosts. The relevant calanoid copepods in Norwegian fjords peak in abundance from May–September (Gundersen, 1953; Matthews, 1967) covering the period when the highest infestation pressure of *Eubothrium* sp. are observed in farmed salmon. An alternative infestation route is through smaller fish acting as paratenic hosts (Rosen, 1919; Vik, 1963). However, this is unlikely since few possible paratenic hosts enter salmon sea cages holding large fish. Larger salmon may have a lower chance of infestation, as their coarser gill rakers make it more difficult to filter copepods (adult size range: 1.1–2.5 mm) (Enckell, 1980; Ruud, 2019). Based on these infestation dynamics, depth-based technologies such as snorkel cages should ideally be deployed from May–September (possibly longer) for optimal tapeworm prevention and preferably in the first part of the seawater production cycle while fish are small.

The use of depth-based prevention techniques to reduce or limit salmon lice infestations are increasing in salmon aquaculture (Bui et al., 2019), yet commercial-scale testing and effects on co-occurring parasites are seldom documented (Geitung et al., 2019). Here we show that snorkel lice barrier cages, which reduce salmon lice (Stien et al., 2016; Oppedal et al., 2017; Wright et al., 2017; Geitung et al., 2019; Oppedal et al., 2019), also have the potential to limit *Eubothrium* sp. infestations in commercial-scale salmon sea cages. This adds to previous research on controlling co-occurring parasites in snorkel sea cages where freshwater-filling of snorkels has been tested as a prophylactic control method for Amoebic Gill Disease (AGD) outbreaks (Wright et al., 2017; Wright et al., 2018), which appear to worsen in snorkel sea cages (Wright et al., 2017). This work underlines the importance and potential advantages of considering multiple parasites when developing new parasite control strategies (Groner et al., 2016) and testing these strategies at commercial-scale (Geitung et al., 2019).

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2021.736774.

CRediT authorship contribution statement

Lena Geitung: Conceptualization, methodology, formal analysis, investigation, data curation, writing – original draft, writing – review and editing, visualization. **Daniel William Wright**: Conceptualization, methodology, formal analysis, investigation, writing – review and editing, supervision. **Lars Helge Stien**: Conceptualization, formal analysis, writing – review and editing, visualization, supervision. **Frode Oppedal**: Conceptualization, investigation, resources, writing – review and editing, supervision, project administration, funding acquisition. **Egil Karlsbakk**: Conceptualization, methodology, formal analysis, investigation, resources, writing – review and editing, supervision.

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.

Acknowledgements

We wish to thank Bremnes Seashore AS, Norway, for commercial salmon farm operations and access, especially Geir Magne Knudsen, Hanne Grytdal and Prestholmane farm staff. We also want to thank Velimir Nola for his valuable assistance with practical work. Funding was provided by Bremnes Seashore, through time-restricted research licenses and SkatteFUNN 279226, as well as from the Institute of Marine Research and University of Bergen, Norway. The work was conducted in accordance with the laws and regulations controlling experiments and procedures on live animals in Norway, following the Norwegian Regulations on Animal Experimentation 1996.

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