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Infection of the planktonic copepod *Calanus finmarchicus* by the parasitic dinoflagellate, *Blastodinium* spp: effects on grazing, respiration, fecundity and fecal pellet production

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Several dinoflagellate species in the genus *Blastodinium* are gut parasites of marine planktonic copepods. However, there is only limited information on the occurrence and infection frequencies of *Blastodinium* spp. in the field and almost no information on the functional impact on their hosts. We report upon the effects of *Blastodinium* sp. infection on *Calanus finmarchicus* from the northeastern Atlantic coast off southern Norway during April 2013 and 2014. Up to 58% of *C. finmarchicus* were infected near the coast, while <5% were infected several kilometers offshore. Ingestion rates of infected females were below detection limits and significantly lower than uninfected females. *Blastodinium* sp.-infected females showed characteristic symptoms of starvation, including lower respiration rates (implying a lower metabolic rate), production of smaller and fewer fecal pellets and significantly fewer eggs than uninfected females. A few females in this study were able to void the infection, however the extended period of starvation is likely to have longer-term repercussions on egg production rates well after the copepod clears the infection. The degree to which the infection affects *C. finmarchicus* recruitment depends on the extent of the spatial distribution of the infection. Monitoring of parasitic infection during routine field surveys will be required in order to clarify this.

KEYWORDS: zooplankton; secondary production; gut parasite; starvation; egg production; sterility; metabolism; ingestion; population dynamics; biogeochemical cycles

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INTRODUCTION

Copepods are the most abundant metazoans in the sea and are a key trophic link in pelagic food webs (Schminke, 2007). As a result of their abundance and key position in the food web, small changes in copepod abundance, productivity and grazing rates have important ramifications for ecosystem function. Numerous parasites are associated with copepods (Theodorides, 1989), causing delays in molting, reduced fecundity and increased mortality (Chatton, 1920; Wickstead, 1963; Sewell, 1951; Kimmerer and Mckinnon, 1990; Albaina and Irigoien, 2006; Skovgaard *et al.*, 2012).

Dinoflagellates are common parasites of copepods (Chatton, 1920; Ho and Perkins, 1985). Several species in the genus *Blastodinium* are endoparasitic gut parasites of marine planktonic copepods (Chatton, 1920; Sewell, 1951; Skovgaard *et al.*, 2012). The life cycle of *Blastodinium* spp. is only partially described. It is speculated that it begins in the naupliar or early copepodite stage of the copepod host. The host appears to ingest the unicellular dinospore of the parasite. Rather than being digested by the copepod, the ingested dinospore enlarges and divides into a trophocyte and a gonocyte. The gonocyte divides repeatedly, producing numerous daughter cells (sporocysts). Contained within a common cuticle, this multicellular arrangement typifies the parasitic stage (trophont) of *Blastodinium* spp. The trophont contains thousands of cells and can grow to reach several 100 μm in length, depending on the parasite species and size of the host organism (Skovgaard *et al.*, 2012). At maturity, numerous zoospores (dinospores) are released through the anus of the host either as free cells or packaged inside a fecal pellet.

Information on the occurrence and infection frequencies of *Blastodinium* spp. in the field is limited, and their functional impact on their hosts is understudied. In warm temperate or tropical waters, large proportions of copepods, most of which were adult females, contained these parasites (Shields, 1994; Coats, 1999; Skovgaard and Saiz, 2006; Coats *et al.*, 2008). While infection with *Blastodinium* spp. is believed to be nonlethal, infected adult females nearly always exhibit reduced or disintegrated gonads and, consequently, are believed to be sterile (Chatton, 1920; Sewell, 1951). Relatively little information is available on the frequency of *Blastodinium* spp. infection, or its implications, in colder water copepods.

Here, we report upon the effects of *Blastodinium* spp. infection on *Calanus finmarchicus* from the northeastern Atlantic, off the coast of southern Norway. During recent sampling, we encountered high numbers of infected *C. finmarchicus*. Opportunistically, we designed experiments to assess the extent and dynamics of the infection, and the impact of *Blastodinium* spp. on fecundity, grazing, fecal pellet production and respiration of infected *C. finmarchicus*.

METHOD

Short-term survey of *C. finmarchicus* infected with *Blastodinium* spp

Calanus finmarchicus were sampled at two locations from 16 April to 2 May 2013, and again from 9 to 30 April 2014, in waters surrounding the Institute of Marine Research's (IMR) Austevoll Research Station (Google Earth coordinates = N60°05′15.36″, E5°15′54″). Water temperature and salinity were measured at five depths (0.5, 5, 10, 20, 165 m). Near-shore copepods were collected using light traps (Bellamare, USA) deployed overnight off the dock of the research station at 35 m depth. Copepods were also collected approximately 3–5 km from shore in Bjørnafjorden (250–300 m deep) using a 333-μm ring net towed obliquely at low speed from 200 m to the surface. Animals were placed into 20 L buckets and transported to a holding room maintained at 13°C where females were sorted and examined under stereo microscopes. Frequencies of *Blastodinium* spp. infection were determined by enumerating hosts with and without parasites. Four infected females were dissected to remove the trophont for morphological characterization.

Microalgae used to feed females in experiments was obtained from cultures growing exponentially at 19°C on a 24-h light cycle in Superba growth media Kristalon Indigo (Yara, Inc.) augmented with vitamins. Phytoplankton concentration and cell size were measured using a Beckman Z2-Coulter Counter. The carbon content of the microalgae was estimated using the equations of Menden-Deuer and Lessard (Menden-Deuer and Lessard, 2000).

Ingestion rates of *C. finmarchicus* infected with *Blastodinium* spp

Only copepods that were captured in the light traps were used in grazing experiments. There were two reasons for this. First, copepods collected from light traps are in pristine condition and are, therefore, much more suitable for physiological experimentation than animals collected from zooplankton tows. Further, the collection sites were in such close proximity that there is no reason to expect that animals captured offshore were any different physiologically than those collected near-shore in the light traps. Infected and uninfected *C. finmarchicus* were preconditioned for 24 h in the laboratory on a diet of *Rhodomonas baltica* (ESD 7.7 μm; 38 pg C cell^{-1}) at concentrations of 2×10^4 cells mL^{-1} (760 μg C L^{-1}) in order to provide a

common feeding history for all of the animals prior to the experiments. Algal concentrations in the sea surface above the light traps during this time period were 2.9×10^4 cell mL^{-1} with an average cell size of 12.46 μm (± 3.5 μm). Individual infected and uninfected adult female copepods were handpicked and placed into 2 L flasks at a concentration of four copepods per liter. Algal concentrations at the start of the experiment were 2×10^4 cells mL^{-1} measured in triplicate using a Beckman Z2 Coulter cell counter which requires a total of 3 mL of sample (0.15% of total volume). Removed fluid was replaced with the same quantity of fluid at approximately the same algal concentration, to ensure no bubbles were present in the feeding container. The combination of jar size and the number of copepods used was chosen such that changes in phytoplankton cell numbers due to grazing would be detectable yet would not deplete cell concentrations by >20%. Three control flasks (containing algae but no copepods) and three experimental replicates were used for each treatment. Experiments were run for 24 h in the dark at 13°C. All experimental and control flasks were gently turned on a plankton wheel at 0.5 rpm to maintain algae in suspension.

After 24 h of incubation, each jar was removed from the plankton wheel, gently mixed by inverting it several times, and a 1-mL subsample (in triplicate) was withdrawn with a pipette for immediate cell counts. Initial as well as final cell concentrations were measured in each flask, such that each replicate provided an independent estimate of grazing or phytoplankton growth rate. Contents were then poured through a 100-μm Nitex screen to recover the animals. Copepods were counted and their infection status verified. Ingestion rates were calculated based on the equations provided by Frost (Frost, 1972).

Egg and fecal pellet production rates of *C. finmarchicus* infected with *Blastodinium* spp

Egg and fecal pellet production of uninfected and infected adult female *C. finmarchicus* were compared in replicate jars ($n = 5$). Each replicate contained four animals in a 300-mL chamber with 333-μm Nitex stretched across the bottom to allow the eggs and pellets to pass out of the chamber. The chambers were housed in a larger 400-mL container stocked with a mixture of *Rhodomonas baltica*, *Isochrysis galabana*, *Skeletonema* sp. and *Chaetoceros* sp. at a total concentration of 3.3×10^4 cells mL^{-1}. Chambers were maintained in a climate-controlled room at 13°C. Each day, the 300-mL chambers and animals were transferred to a new 400-mL container with fresh algae. Eggs produced within each chamber were counted daily on all 4 days. Fecal pellet production was not measured on Day 1, but was observed daily starting on Day 2 through Day 4. Egg production rate (EPR) or fecal pellet production rate (FPR) were then calculated as: the number of eggs/the number of live females/duration (d). Data were analyzed using repeated-measures (RM) 2-way ANOVA.

Fecal pellets were imaged at ×40 using a Leica MS5 dissecting scope fitted with a Planapo ×1.0 magnifier and an Olympus DP70 digital camera. The volume of the fecal pellets produced by infected and uninfected *C. finmarchicus* females was calculated as that of a cylinder based on area and width measured using Image J (NIH, USA).

Respiration rates of *C. finmarchicus* infected with *Blastodinium* spp

Dissolved oxygen concentrations were measured with a Clark-type oxygen microelectrode (Unisense; Aarhus, Denmark). The linear response of each electrode was calibrated with 0.2-μm filtered seawater bubbled for a minimum of 1 h to set the 100% dissolved oxygen calibration point. The anoxic calibration point was determined by placing seawater into a silicone tube that was immersed in a solution of 0.1 M sodium ascorbate and 0.1 M sodium hydroxide for over 4 h. The 95% response time of the sensor was below 1 s. All respiration measurements were made in a 4.8 mL chamber at 12°C (± 0.01°C) using a ThermoScientific water bath (Model A10B with thermostat SC100). Three replicate measurements were made for each treatment and each replicate consisted of three adult females. Respiration chambers were gently stirred using a glass-encased magnetic stir bar. Measurements were made for up to 1.25 h at a frequency of 0.5 Hz. At these animal concentrations and experiment durations, the oxygen concentrations within the chambers never decreased by >20% below saturation.

RESULTS

During 15 April–2 May 2013, the upper water column was well mixed with temperatures ranging from 5.5 to 6.5°C down to a depth of 20 m. The upper water column was considerably cooler than at 165 m where temperatures remained consistent at 7.7°C (Fig. 1A). Salinity ranged from 29 to 31 PSU with the lowest values recorded in the surface samples (0.5 m; Fig. 1C). The following year from 15 April to 30 April 2014, surface water temperatures were considerably warmer and less saline (Fig. 1B and D) reaching temperatures of 12.5°C and salinity of 27 PSU.

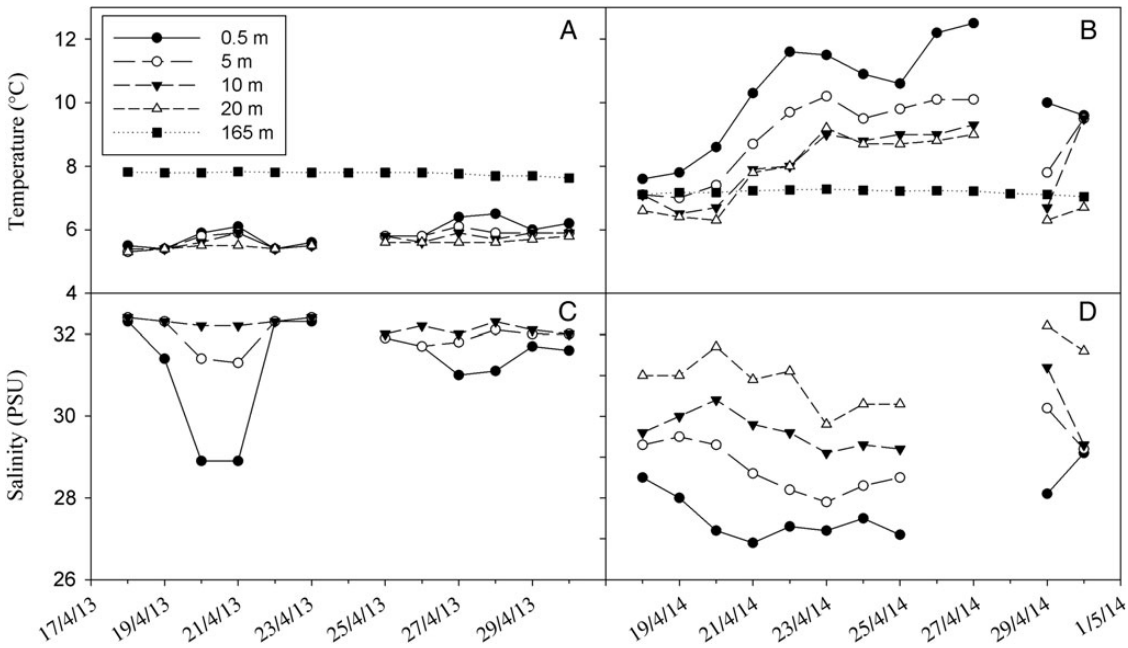

Fig. 1. Temperature and salinity profiles at the near-shore sampling sites during the 2013 (**A**,**C**) and 2014 (**B**,**D**) sampling periods in waters surrounding the Institute of Marine Research's (IMR) Austevoll Research Station (60°05′15.36″N, 5°15′54″E).

Short-term survey of *C. finmarchicus* infected with *Blastodinium* spp

From 16 April to 2 May 2013 the frequency of infection was assessed for 1153 female *C. finmarchicus* collected from both the near-shore site and in the fjord. During the first 8 days, infection levels at the near-shore site ranged between 43 and 58% of the adult female population. During the same period in the fjord, infections ranged between 0 and 5%. It is unclear when the infection began or reached maximum levels, however, by 2 May 2013, the infection levels in the near-shore samples had decreased to <2% of the female population. During the following year between 9 April and 2 May 2014, there was no outbreak of infection at the near-shore site except on 14 and 16 April, when the infection percentage was 4 and 2%, respectively (Table I).

The species of *Blastodinium* underlying the infection was not determined definitively. However, according to Chatton (Chatton, 1920), size and shape of the trophont can be used to identify *Blastodinium* species. In our samples, the trophonts within the infected copepods were relatively large (1.5–2.5 mm), encompassing the entire midgut and foregut of the infected animals. The trophont was never observed to extend past the midgut–hindgut sphincter (see video in the Supplementary data). The trophonts were often light olive green in color and cylindrical to fusiform in shape (Fig. 2A and B). In the 172 infected copepods that were examined, the vast majority were infected by only one parasite while in a few cases copepods had two distinct trophonts. When the trophont was removed from the copepod, the *Blastodinium* spp.

Table I: Number and proportion of infected and uninfected Calanus finmarchicus *females collected using light traps off the Austevoll Research Station dock (40 m depth) and from offshore in the fjord at 250–300 m 60°05′15.36″N, 5°15′54″E.*

Date	Location	Number clean	Number infected	Total	Percentage infected
16/4/2013	Dock	31	43	74	58
18/4/2013	Fjord	96	4	100	4
19/4/2013	Dock	24	19	43	44
20/4/2013	Dock	55	57	112	51
22/4/2013	Fjord	17	0	17	0
24/4/2013	Dock	23	17	40	43
27/4/2013	Dock	99	4	103	4
29/4/2013	Fjord	117	6	123	5
30/4/2013	Dock	75	3	78	4
2/5/2013	Dock	334	6	340	2
Total	Dock	758	155	913	17
Total	Fjord	230	10	240	4
9/4/2014	Dock	158	0	158	0
14/4/2014	Dock	136	5	141	4
16/4/2014	Dock	100	2	102	2
21/4/2014	Dock	105	0	105	0
30/4/2014	Dock	42	0	42	0
Total	Dock	541	7	548	1

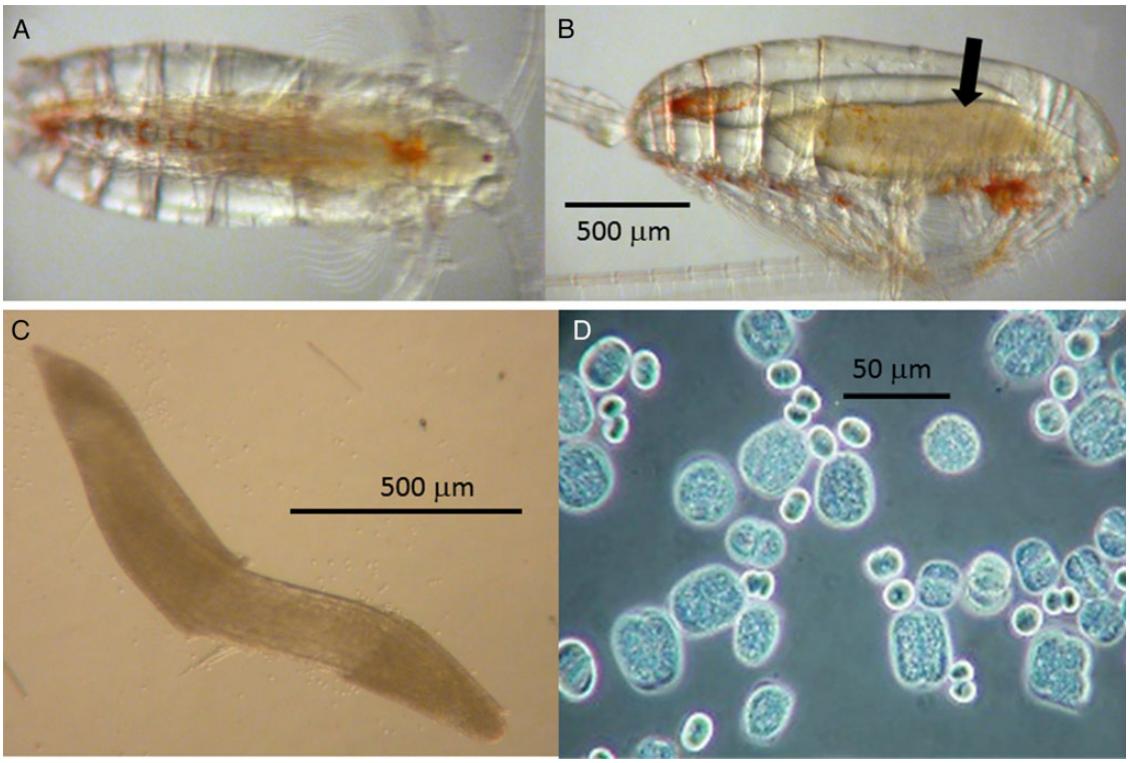

Fig. 2. *Blastodinium sp.* in *Calanus finmarchicus* females from a Norwegian fjord in waters surrounding the Institute of Marine Research's (IMR) Austevoll Research Station (60°05′15.36″N, 5°15′54″E). (**A**,**B**) Dorsal and lateral view of infected copepods illustrating the infection. Arrow indicates trophont. (**C**) An individual *Blastodinium* sp. trophont removed from its host. (**D**) Cells extruded from a *Blastodinium* sp. trophont .

maintained its shape as a result of the robust exterior cuticle encasing the multicellular parasite (Fig. 2C). When the exterior cuticle was ruptured, several different cell types were released (Fig. 2D).

Ingestion rates of *C. finmarchicus* infected with *Blastodinium* spp

Uninfected *C. finmarchicus* females ingested significantly more *R. baltica* than infected females (Fig. 3; t-test df = 2; t = 24.91; $P = 0.002$). Healthy uninfected females consumed on average 2.93×10^4 cells copepod^{-1} d^{-1} (11.1 µg C d^{-1}) with average clearance rates of ~1.5 mL copepod^{-1} d^{-1} at cell concentrations of 2.0×10^4 cells mL^{-1}. In contrast, infected animals showed no measureable ingestion rate over the 24-h period.

Egg and fecal pellet production rates of *C. finmarchicus* infected with *Blastodinium* spp

FPRs in both infected and uninfected females increased significantly over the course of the experiment (RM 2-way ANOVA; $F_{2,16} = 25.78$, $P = 0.001$; Fig. 4). By the

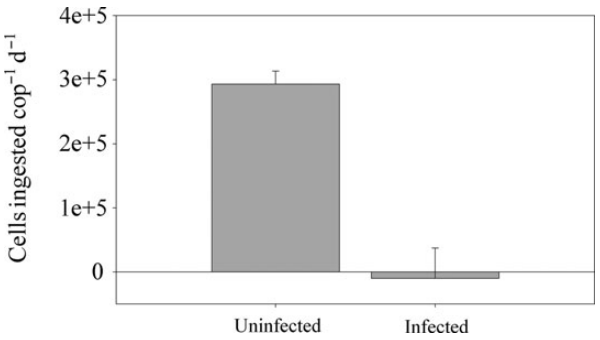

Fig. 3. Ingestion rates of uninfected and *Blastodinium* sp. infected *Calanus finmarchicus* females fed on *Rhodomonas baltica.* Values are averages (± SD) of three replicate flasks.

fourth day of feeding, the mean FPR was 63 FP female (f)$^{-1}$ d^{-1} among the uninfected females and 25 FP f^{-1} d^{-1} for the infected. Over the 4-day experiment, the average FPR differed significantly between treatments (RM 2-way ANOVA; $F_{1,16} = 6.073$; $P = 0.039$) with an average of 46.3 (± 11.1; SE) fecal pellets produced each day by uninfected females and 16.4 (± 6.1; SE) produced by infected females. Not only did infected females produce fewer pellets, but the pellets were significantly smaller (*t*-test, df = 137, $t = 12.1$, $P \ll 0.001$). Based on

image analysis, the mean volume of the fecal pellets produced by uninfected copepods ($n = 61$) was 417% larger than those produced by infected copepods ($n = 78$; Fig. 5). The fecal pellet volume produced per day by infected copepods was nearly eight times lower than that produced by healthy females. In addition, fecal pellets produced by the infected copepods were much lighter in color and appeared to have *Blastodinium* spp. dinospores encased within the peritrophic membrane.

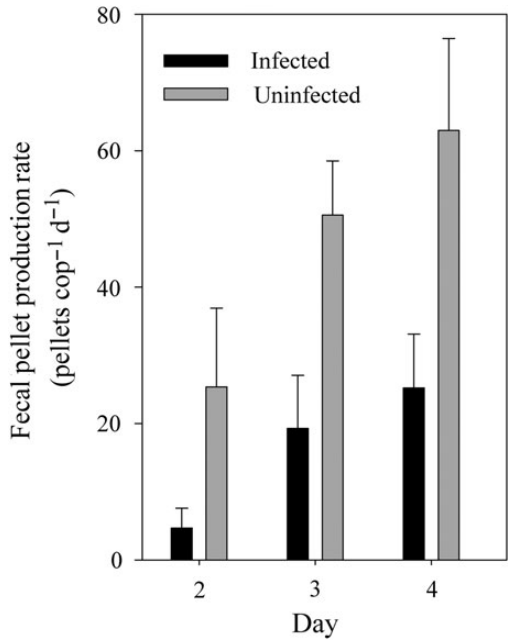

Fig. 4. Fecal pellet production rates of uninfected and *Blastodinium* sp. infected *Calanus finmarchicus* females fed on a diet of *Rhodomonas baltica*. Values are averages (± SE) of five replicate flasks. Note that fecal pellet production was not measured on Day 1.

EPRs were higher for uninfected females [792 total eggs; mean of 20.8 eggs f^{-1} d^{-1} (± 1.2; SE); $n = 11$ females] than for infected females [total 22 eggs; mean of 0.6 eggs f^{-1} d^{-1} (± 0.3; SE); $n = 12$ females] (Fig. 6). EPR did not change significantly over time (RM 2-way ANOVA; $F_{3,24} = 0.05$, $P = 0.99$) but differed significantly between treatments ($F_{1,24} = 12.604$; $P = 0.008$). Eggs were found in two of the five chambers that contained infected females. In one chamber, two of the infected females had cleared the *Blastodinium* spp. from their guts at some point during the 4 days. While we did not record the state of the gonads in the infected females used in this experiment, in a separate study immediately after the egg production experiments, we examined 10 infected females fed high food concentrations in separate petri dishes. All of those infected females had undeveloped gonads [GS1, using criteria in Niehoff and Runge (Niehoff and Runge, 2003)] initially and showed no development of gonads after 3 days. Therefore, it is likely that the eggs found in the infected chambers were produced by females that had successfully voided the trophont during the course of incubation.

Respiration rates of *C. finmarchicus* infected with *Blastodinium* spp

Blastodinium-infected female *C. finmarchicus* respired at approximately half the rate of uninfected females (Fig. 7). Average respiration rates for uninfected adult females was 40.7 nmol O_2 f^{-1} h^{-1} while infected females respired at

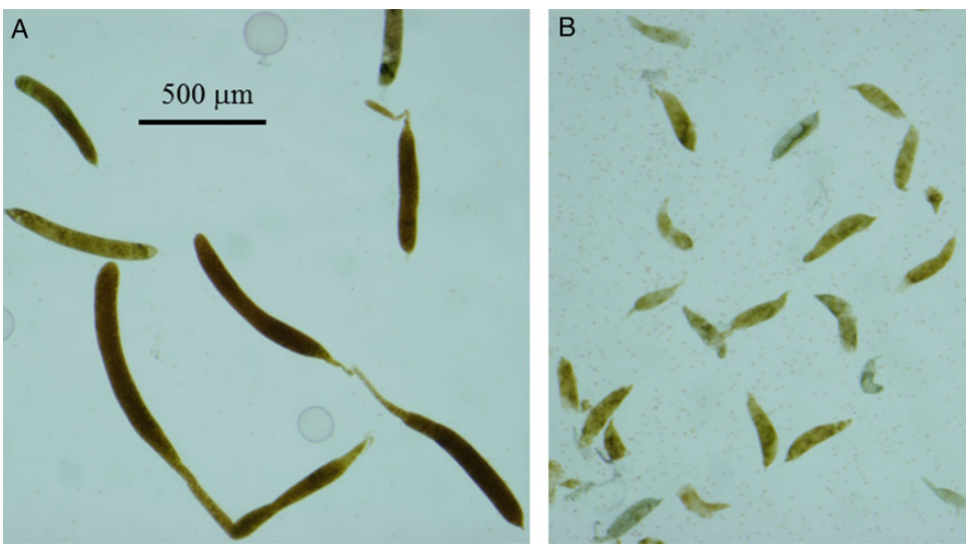

Fig. 5. Fecal pellets produced by (**A**) uninfected and (**B**) *Blastodinium* sp. infected *Calanus finmarchicus* females.

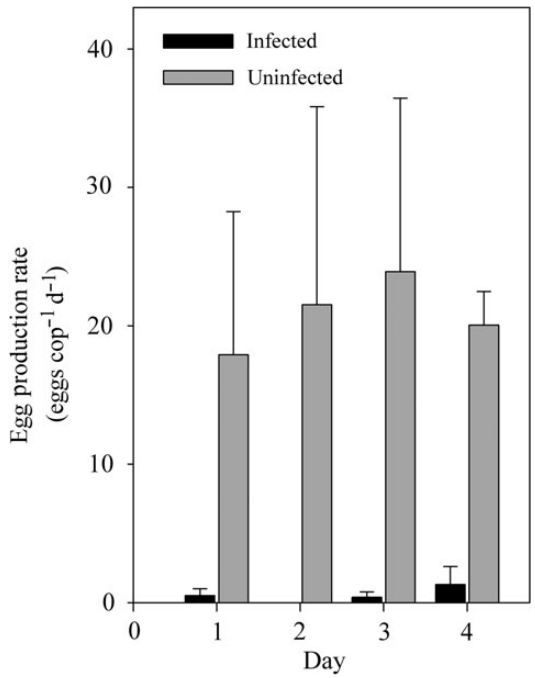

Fig. 6. Egg production rates of uninfected and *Blastodinium* sp. infected *Calanus finmarchicus* females fed on a diet of *Rhodomonas baltica*. Values are averages (± SE) of five replicate flasks.

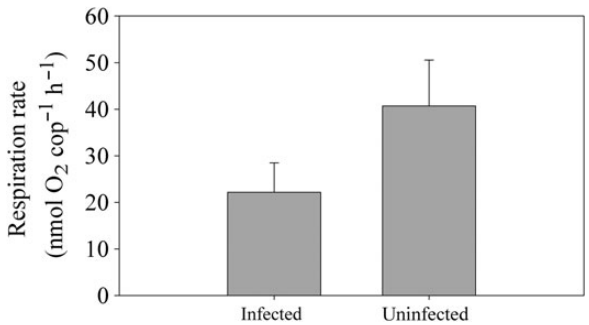

Fig. 7. Respiration rates of uninfected and *Blastodinium* sp. infected *Calanus finmarchicus* females. Values are averages (± SD) of three replicate flasks.

a rate of 22.2 nmol O_2 f^{-1} h^{-1}. These differences were statistically discernible (*t*-test, df = 6, $t = 3.16$, $P = 0.01$).

DISCUSSION

The life cycle of *Blastodinium* is atypical for a dinoflagellate, having a multicellular stage that grows parasitically in the gut of marine planktonic copepods. While it has been hypothesized that the infection occurs when the copepod ingests the *Blastodinium* dinospore (Skovgaard *et al.*, 2012), this has yet to be demonstrated. Attempts to transmit *Blastodinium* from infected adult copepods to uninfected adults have been unsuccessful (Chatton, 1920; Skovgaard, 2005), leading to speculation that the infection may occur during the naupliar or early copepodite stage (Chatton, 1920; Alves-De-Souza *et al.*, 2011).

Based on morphological features of the trophont, Chatton (Chatton, 1920) arranged *Blastodinium* spp. into three characteristic groups based on size, shape and number of trophonts observed in a single animal. The trophonts within the infected copepods in our samples were relatively large (lengths up to 2.5 mm), particularly compared with Mediterranean or tropical species which appear to range in size from 100 to 500 μm depending on the host species. Similar length trophonts have been reported previously. Øresland (Øresland, 1991) found large *Blastodinium* trophonts between 2.5 and 3.5 mm in *Euchaeta antarctica* from Antarctic waters. In addition, the trophonts were olive green in color and cylindrical to fusiform shape. Thus, based upon the large size, fusiform shape and the color, we suspect that the infections that we observed were *Blastodinium hyalinum*. This is supported by the early observations that *B. hyalinum* is the only species of *Blastodinium* found in cold environments (Apstein, 1911; Chatton, 1920; Lebour, 1925; Jepps, 1937; Vane, 1952).

The ingestion rates of uninfected adult female *C. finmarchicus* on monoalgal diets are similar to other reported values for this species at this temperature (Bamstedt *et al.*, 1999; Harris *et al.*, 2000). Assuming a carbon content of ~200 μg C f^{-1} (Harris *et al.*, 2000), daily ingestion rates of laboratory-fed copepods reached values of 5.5% of total body carbon content. This is ~20% greater than natural samples from the North Atlantic, in which *C. finmarchicus* have typically been observed to ingest between 1.1 and 4.5% of total body carbon per day (Ohman and Runge, 1994; Irigoien *et al.*, 1998; Meyer-Harms *et al.*, 1999). *Blastodinim* spp.-infected females showed no measureable ingestion within the 24-h observation period. The combination of low ingestion rates and the high infection frequency found in this study suggest a significant decrease in the grazing impact of *C. finmarchicus* on local phytoplankton populations during periods of high *Blastodinium* spp. infection.

Infected females retained the trophonts for well over a week—that is, they were starving during this period despite being cultured at saturated food levels. It is unclear how long the copepods in our study were infected and, thus, not eating. However, the infected copepods were active and maintained their position in the water column, which suggests that the animals were not moribund. Besides the lack of feeding, other symptoms of starvation in the infected *C. finmarchicus* included lower respiration rates, FPRs and EPRs compared with uninfected females.

Egg production rates in the uninfected females remained relatively high during the 4-day incubation experiments (~20 eggs f^{-1} d^{-1}) but well below the maximum EPRs at this temperature (60 eggs f^{-1} d^{-1}; Harris *et al.*, 2000). Food availability and egg production in *Calanus* spp. are coupled with a response time of one or a few days in fluctuating food environments (Runge, 1984, 1985; Hirche *et al.*, 1997). However, after extended periods of starvation, copepods will revert to an undeveloped reproductive state and then require many days of high food concentrations to begin producing eggs again (Runge, 1984). *Calanus finmarchicus* had significantly lower EPRs (between 4 and 35% of the control) when exposed to 12 days of starvation followed by 9 days of feeding (Hirche *et al.*, 1997). Thus, in the short term, egg production will reflect recent feeding conditions. However, after prolonged starvation followed by high food concentration, egg production can take days to weeks to reach prestarvation levels and much of the ingested food is used in the restoration of internal structures, including the gonads.

Earlier studies on the fecundity of *Blastodinium* spp.-infected copepods are contradictory. Infected copepod females were believed to be sterile since they do not produce eggs (Skovgaard, 2005) and they have poorly developed ovaries (Chatton, 1920; Sewell, 1951). However, more recent studies report that *Blastodinium* spp.-infected females can have normally developed gonads (Ianora *et al.*, 1990) and may be capable of producing eggs. In the present study, *Blastodinium* spp.-infected females may have produced some eggs, although at a fraction of the rate for uninfected females. Therefore, it appears that infected females were not rendered permanently sterile. In a few of the culture chambers, some females successfully voided the infection and were found (by visual inspection) to be parasite free. The chambers containing these females produced a marginally higher number of eggs than chambers containing females that retained the infection throughout the experiment.

Fecal pellet production rates in the uninfected females were high during the 4-day incubation experiments, reaching maximum production rates under saturated food conditions (Campbell *et al.*, 2001). While infected copepods showed no measureable grazing in the 24-h feeding experiments, over the 4-day incubation experiments they produced some fecal material, albeit low volumes. Fecal pellets produced by infected copepods were significantly smaller and had very different color than those of healthy copepods (Figs 4 and 5). Video observations (see Supplementary data) show the large trophont in the mid- and foregut of the copepods, with cells resembling *Blastodinium* spp. dinospores in the hindgut being incorporated into fecal pellets. Since many larger crustaceans selectively feed on larger particle sizes (Kleppel, 1993), ingestion of dinospores within fecal pellets may provide a mechanism for larger crustaceans to become infected.

Poorly developed or disintegrated ovaries are associated with extended periods of starvation (Niehoff, 2000). Therefore, given the low grazing rates that were observed in infected females, starvation rather than permanent sterility is likely the cause of their low EPRs. This conclusion is supported by the lower respiration rates, FPRs and EPRs of infected *C. finmarchicus* compared with uninfected females. Extended periods of starvation lowers respiration rates in copepods (Kiørboe *et al.*, 1985; Thor, 2003) and other marine crustaceans (Herrera *et al.*, 2011). In *Acartia tonsa*, extended starvation led to a 75% decrease in respiration rates (Kiørboe *et al.*, 1985; Thor, 2003). In this study, respiration rates of the infected females were nearly half that of healthy feeding *C. finmarchicus* and are consistent with differences in the respiration rates found for other starved versus fed *Calanus* species (Ikeda, 1977).

CONCLUSIONS

Calanus finmarchicus is the biomass dominant copepod species in North Atlantic pelagic ecosystems. In Norwegian coastal waters, they have a life cycle with one or more generations per year with the main reproductive activity coincident with the phytoplankton bloom in spring (Melle *et al.*, 2014). *Calanus finmarchicus* is an important consumer of primary production (and some secondary) and is one of the main conduits for organic carbon up the food web. What is not assimilated by the copepods is packaged into fecal pellets that sink into deeper waters. The impact of *Blastodinium* spp. infections on ecosystem processes depends on the impact of the infection on grazing rates, FPRs and EPRs of the copepods that it infects. The extended starvation periods associated with *Blastodinium* spp. infections decrease EPRs, and likely have longer-term repercussions on EPRs well after the copepod clears the infection. After extended starvation, egg production resumes in about 3–15 days of feeding (Hirche *et al.*, 1997; Niehoff, 2000). However, maximum EPRs took an additional 15–20 days of feeding even when placed in saturated food conditions (Niehoff, 2000). The high infection rates recorded in spring in this study (58% at peak infection) suggest that *Blastodinium* spp. infections could have considerable impact on the species' population dynamics and the transport of organic carbon to deeper waters (via fecal pellets). The degree to which this impact is manifested depends on the extent of the spatial distribution of the infection. Our observation that high infection rates are confined to near-shore areas

suggest that dinospores accumulate as a result of the restrictive advection. However, Vane (Vane, 1952) reported observations of high infection rates for *C. finmarchicus* in the central North Sea and Skovgaard and Salomonsen (Skovgaard and Salomonsen, 2009) and Alves-de-Souza *et al.* (Alves-de-Souza *et al.* 2011) found high rates of infection for other copepod species in the central Atlantic and Mediterranean Sea, respectively. Therefore, the alternative, that high infestation rates over a duration of one to several weeks also occur in populations of *C. finmarchicus* in the deeper ocean may have gone largely unnoticed, with potentially greater ecosystem impacts. To evaluate these alternatives, we suggest that the extent of *Blastodinium* infections be reported routinely in field surveys.

SUPPLEMENTARY DATA

Supplementary data can be found online at http://plankt.oxfordjournals.org.

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