Body-snatcher from the deep? The effect of the parasitic copepod, Sarcotretes scopeli (Jungersen, 1911), on its mesopelagic fish host.

Master of Science in Biology – Marine Biology

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June 2022

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Acknowledgments:

First and foremost, I would like to thank my supervisors Anne Gro Vea Salvanes and Henrik Glenner for giving me the opportunity to take my Master thesis in Marine biology, and in the exciting field of marine parasites. I would like to thank you both for all the guidance and encouragement throughout the whole thesis, and especially throughout the last stretch of the process.

Further I would like to thank Richard J. Telford, Francesco Saltalamacchia, Martine R. Solås and Mikko Heino for helping me along the sometimes frustrating and confusing worlds of R and statistics. I would like to further extend my gratitude to Francesco for all the help, interesting talks and encouragement he has given me under the otolith work of the thesis. I would also like to give my gratitude to the rest of the *HypOnFjordFish* group and Frank Midtøy for all the help during the sampling of the material for this thesis under the February cruise of 2021.

A big thanks should also be given to Kamal B.E. Mustafa, Ying Xue and Mohammed A.A.Y. Yassin from the faculty of clinical odontology, University of Bergen; for all the help you gave me before, during and after the Micro-CT methodology used in this thesis.

A special thanks should also be given to Daniel Ottmann, for all the morning talks and coffee breaks during the first semester of the thesis, and to Laura J. Febvre for holding out with the stress case I have been during the last semester of the thesis. You guys have helped me keep some of my sanity throughout this year. The same goes for my friends and fellow students that have survived with my occasionally pessimistic life view during the long days at the lab and at the study hall.

Lastly, but most importantly; I would like to give a huge thanks to my parents for encouraging me throughout not only the higher education, but for believing in me and giving your all, in order to ensure that I would be able to follow me lifelong dream of becoming a Marine biologist. I could not have done it without your help.

Abstract:

Benthosema glaciale (Reinhardt, 1837) is one of the most abundant fish species found globally. The species plays an important role in the food-web of marine ecosystems, as a link between the trophic levels. In west Norwegian fjord systems, *B. glaciale* have been observed to be infected by the parasitic copepod *Sarcotretes scopeli* (Jungersen, 1911), however, there is limited knowledge on how parasitic infections affect the biology of this species. Furthermore, west Norwegian fjords have been experiencing more frequent oxygen loss in the basin water over the last decade and it is not known if such changes could impact the parasite-host relationship between these two species. A cross-sectional study was conducted with infected and uninfected *B. glaciale* from four west Norwegian fjords, which differed in dissolved oxygen. This study was performed in order to investigate how dissolved oxygen affects *S. scopeli* prevalence. In addition, the effect of infection on gonadosomatic, hepatosomatic and heartsomatic indices, Fulton's condition factor and host growth were studied separately for the host sexes. Furthermore, the site-specificity of *S. scopeli* on host exterior and interior, and the relative parasitic volume in relation to the host were investigated. The outcome of the cross-sectional study showed that *S. scopeli* greatly reduces the gonadosomatic index for both host sexes. The hepatosomatic index was similar for infected and uninfected females in all fjords except Sørfjorden, where the hepatosomatic index was higher for infected females. Infected males in all of the fjords had higher hepatosomatic index than uninfected ones. Furthermore, infected fish were found to be in poorer condition than the uninfected ones in all of the investigated fjords. However, infection did not seem to compromise the growth rate. Inconclusive results were presented on the effect of infection on host cardio function. The data presented did not show an effect of dissolved oxygen concentration on the parasitic prevalence but did show that Sørfjorden had a lower prevalence than the other three fjords. Furthermore, the results from the parasitic attachment selectivity showed that *S. scopeli* attach its feeding apparatus randomly both inside and outside of the hosts visceral cavity, while the parasites external part most often located on the hosts dorsal side. Overall, the data suggested that *S. scopeli* acts as a parasitic castrator on the host; areas of reduced oxygen concentration do not affect *S. scopeli* prevalence; and that the parasitic attachment site is randomly distributed in the host internal, while the parasite has a high affinity for dorsal attachment on the host external.

Table of contents:

1. Introduction:

The west Norwegian coastline consists of a network of fjord systems produced during the last ice age. As many of these fjord systems have great depths, the water column can be divided into zones characterized by light intensity; The euphotic zone (0-200 meters) has high light intensity, sustaining phytoplankton production, while in the mesopelagic zone (200-1000 meters) the light intensity rapidly decreases (Aksnes et al., 2004; Webb et al., 2010). The mesopelagic zone of these systems houses vast deep-sea communities with high densities of mesopelagic fish, a species group abundant worldwide (Alvheim et al., 2020; Catul et al., 2011). Many deep-sea species undertake diel vertical migration (DVM), where they reside in the mesopelagic during the day to hide from predators and migrate to the euphotic zone to feed at night (Luo et al., 2000; Staby et al., 2011; Vestheim & Kaartvedt, 2009). The DVM phenomenon is believed to be important in energy transfer from the epipelagic to the deeper water layers (Isla et al., 2015). Fjords provide unique study systems of deep-sea communities as they are semi-enclosed at the fjord entrance by a sill, which is a topographical feature that often has a shallow depth, restricting the water renewal of the basin situated below (Aksnes et al., 2019; Howe et al., 2010). Renewal frequency of the basin water of west Norwegian fjords seems to have reduced over time, with Masfjorden reaching low oxygen levels in recent years, discovered due to repeated visits to the system (Aksnes et al., 2019; Darelius, 2020; Pitcher et al., 2021). As water renewal is restricted in the deep basin, respiration continues to reduce the available dissolved oxygen content in the lower water layers (Diaz, 2001; Kemp et al., 1992). Little is known about how oxygen reduction affects the teleost's residing in the mesopelagic zone. However, as oxygen is a vital component for many species, it can be hypothesized that reduced oxygen content poses challenges for physiological processes. Immune response has, for example, been found to be reduced in mummichogs (*Fundulus heteroclitus,* Linnaeus, 1766) on the west Atlantic coast and channel catfish (*Ictalurus punctatus,* Rafinesque, 1818) found in rivers in the USA when exposed to low oxygen environments (Boleza et al., 2001; Welker et al., 2007). In a fish not adapted to low oxygen, a reduction of immune system function can increase the fish's susceptibility to opportunistic pathogens such as bacteria and viruses (Abdel-Tawwab et al., 2019; Mellergaard & Nielsen, 1995; Varghese et al., 2020). Parasitic response to decreased oxygen conditions on the other hand is poorly understood.

Parasites have adapted to feed on the metabolic resources that otherwise could be used for growth, reproduction, and physiological maintenance by their host (Timi & Poulin, 2020). Parasitic species thus expose the host to a chronic energy loss, which in turn may induce adverse health effects such as anorexia, anemia, and increased cortisol levels (Allan et al., 2020; Chin et al., 2004; Horton & Okamura, 2003). Furthermore, parasite-mediated change to host physiology and the parasite presence itself can change aspects of host behavior such as diet composition, swimming capability, predator avoidance, and foraging effort (Crowden & Broom, 1980; Khan et al., 1993; Loot et al., 2004; Muñoz et al., 2021; Seppälä et al., 2004). The cestode *Schistocephalus solidus* (Müller, 1776) has for instance, been found to change the diel vertical migration of three-spined sticklebacks (*Gasterosteus aculeatus,* Linnaeus, 1758), causing infected individuals to stay shallower during the day, despite increased predator risk (Quinn et al., 2012).

Parasite-mediate effects may also change aspects of host life history, such as; increased mortality rate (Kirk, 2003; Umberger et al., 2013), decreased growth rate (Fjelldal et al., 2020; Fogelman & Grutter, 2008; Khan et al., 1993); or reduced reproduction, by canalization of reproductive resources to growth, through endocrine disruption or gonad tissue destruction (Averbuj & Cremonte, 2010; Geraudie et al., 2010; Grankoto et al., 2001). *Ligula intestinalis* (Linnaeus, 1758), a castrating cestode, for instance, has caused a shift to earlier reproductive age of the lake sardine (*Engraulicypris sardella,* Günther, 1868) population in Lake Nyasa (Gabagambi et al., 2020). While the castrating cestode *Euhaplorchis californiensi* (Martin, 1950), has been shown to decrease the overall population fecundity of California horn snails (*Cerithidea californica*, Haldeman, 1840) due to increased intraspecific competition between infected and uninfected individuals (Lafferty, 1993).

Changes to aspects of host physiology and behavior are believed to be a direct cause of parasitic manipulation of the host (manipulation hypothesis; Poulin et al., 1994) or as an indirect response to chronic drainage of host energy (energy drainage hypothesis; Lafferty & Kuris, 2009). While much is known about the effect of parasites on different teleost species, the host-parasite relationships of the globally abundant *Benthosema glaciale* (Reinhardt, 1873) remain poorly understood.

1.1 Myctophidea and Benthosema glaciale:

The family Myctophidea includes 250 species and is dominating the mesopelagic assemblage of vertically migratory fish species in all parts of the ocean, except in the Arctic Region (Catul et. al, 2011). These small planktivorous fishes have been attributed to consume large parts of the daily zooplankton production in the surface layers during the night (Bagøien et al., 2001; Saunders et al., 2018). Myctophids act as important prey for a variety of different piscivorous species, such as seabirds, marine mammals and commercially important fish species, and thus constitute an important link in the marine food web (Giske et al., 1990; Hedd & Montevecchi, 2006; Pusineri et al., 2007). *B. glaciale* for instance, is the most abundant Myctophid found in the Norwegian fjord systems and acts as an important nutritional source for the commercially important Atlantic mackerel (*Scomber scombrus, Linnaeus, 1758)*, blue whiting (*Micromesistius poutassou*, Risso, 1827) and pollock (*Pollachius virens,* Linnaeus, 1758) (Giske et al., 1990; Priede et al., 1995)

B. glaciale (Fig 1A) is globally one of the most numerous fish species (Klevjer et al. 2020a; 2020b). The species perform diel vertical migration, and its habitat depth range increases with age/size, and tends to aggregate in size stratified layers (Dypvik et al., 2012). Like many deep-sea teleost's, *B. glaciale* have adapted to live in a low light level habitat, expressed as; large eyes, black coloration and bioluminescence producing photophores (Salvanes & Kristoffersen, 2001). Observed maximum age is eight years and the maximum length reported is 100 millimeters, but sizes vary depending on the location (Gjøsæter, 1973, 1981; Halliday, 1970). For example, *B. glaciale* in the North Atlantic reaches larger sizes at slower rate, compared to in the west Norwegian fjords (Kristoffersen & Salvanes, 2009). Females and males can be identified from an external sexual trait, which is the only distinguishable morphological difference between the sexes (Gjøsæter, 1981). Maturation occurs at the age of 2-3 years, and spawning occurs in batches throughout the spawning season; which in west Norwegian fjords takes place between June-July (García-Seoane et al., 2014; Gjøsæter, 1981; Halliday, 1970).

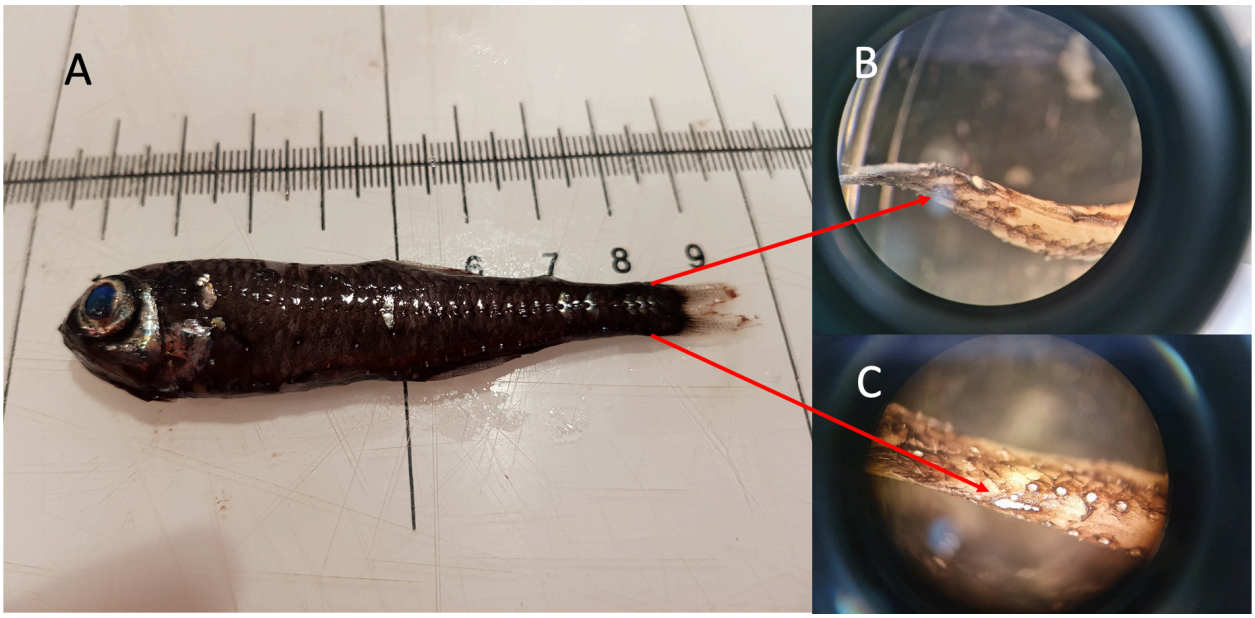

Figure 1: A) Benthosema glaciale with intact scales. Red arrows show the location of the secondary sexual traits. B) supracaudal photophore of a male individual. C) infracaudal photophore of a female individual.

B. glaciale is a visual feeder, and its diet consists mainly of zooplankton (Bagøien et al., 2001; García-Seoane et al., 2013; Pepin, 2013; Sunde, 2018). The species search for prey in a saltatory fashion, where they move, stop and move again (Kaartvedt et al., 2008). *B. glaciale* has a long-term energy reserve consisting of wax esters of similar composition to its prey (Falk-Petersen et al., 1986; 1987) . Feeding primarily takes place in the euphotic zone during the night; however, some daytime feeding at greater depth has been observed (Dypvik et al., 2012; Sameoto, 1988). Furthermore, individual *B. glaciale* from the deeper parts of west Norwegian fjords exhibit an alternative foraging behavior (inverse diel vertical migration; IDVM), where they appear to migrate to the midwater during the day to feed (Dypvik et al., 2012; Kaartvedt et al., 2009).

1.2 Parasitic copepods:

The marine biome houses a diverse and abundant assemblage of parasitic species distributed from the surface to the ocean floor (Palm & Klimpel, 2007; Poulin & Morand, 2000). Parasitic diversity is generally believed to be highest in the epipelagic and decreases with depth until it increases again at the ocean floor due to the higher richness of potential hosts (Campbell et al., 1980; Klimpel et al., 2006; Marcogliese, 2002). Historically, parasitological studies of marine teleost's have been focused on epipelagic and pelagic species with an inherent

economic value (Chugunova & Pronin, 2011; Poulin et al., 2016). In contrast, parasitological studies from deep-sea teleost's consists primarily of natural history studies with a focus on species identification, often neglecting the parasite-mediated effect on the host.

Parasitic copepods are one of the most common taxa found to infect marine teleost's throughout the water column, where they feed on host mucus, skin, and blood (Boxshall, 1998; Fast, 2014). These parasitic crustaceans have a broad range of adult phenotypes, ranging from few morphological changes between larvae and adult stages, to highly modified phenotypes (Williams & Bunkley-Williams, 2019). Few parasitic copepod families have adapted to the deep-sea habitat, with only seven families commonly represented (Boxshall, 1998).

The family Pennelidae is one of the copepod families that have established itself in the mesopelagic and are commonly infecting Myctophids (Boxshall, 1998). All species belonging to this family have a mesoparasitic adult stage, where part of the parasite is embedded in the host internal, and the other part protrude externally (Hogans, 2017). Due to low densities of potential hosts, deep-sea Pennelids are believed to have low host specificity, often including species groups as intermediate and/or final hosts (Boxshall, 1998). Their lifecycles are simple, with either a direct lifecycle often consisting of a single fish host or an indirect lifecycle with only two successive hosts (Boxshall, 2000). *Cardiodectes bellottii* (Richiardi, 1882), for instance, have two successive hosts; a gastropod, where it develops to maturation before the female leaves as a free-swimming larva; and a Myctophid host utilized by the female to complete the life cycle (Perkins, 1983). *Sarcotretes scopeli* (Jungersen, 1911), on the other hand, seemingly has a direct lifecycle, commonly with *B. glaciale* as their only host (Jungersen, 1911).

S. scopeli was first documented and described by Jungersen (1911) a century ago from specimens found on infected *B. glaciale* sampled in the Atlantic Ocean. He noted that the species is usually found dorsally on the host, while the internal holdfast showed low site specificity in the host visceral cavity. After the initial documentation, *S. scopeli* was not present in the scientific literature for 60 years before it was documented in Norway for the first time by Gjøsæter (1971), infecting the *B. glaciale* populations of two west Norwegian fjord systems; Herdlefjorden and Byfjorden, outside of Bergen. Furthermore, Gjøsæter (1971) noted that gonadal development of the infected individuals seemed reduced in comparison to non-infected conspecifics and hypothesized that *S. scopeli* may cause castration of its host. Since

the preliminary observations by Gjøsæter (1971) fifty years ago, the presence of *S.scopeli* have only been sporadically mentioned in the scientific literature (Klimpel et al., 2010; Yves & Geoffrey, 2004). From the initial description of *S. scopeli* until the present, no thorough study has yet been done on the parasite-host interaction between *S. scopeli* and *B. glaciale*

1.3 Aim of the study:

S. scopeli was observed to infect *B. glaciale* when sampling the mesopelagic communities in west Norwegian fjord systems, such as Masfjorden and Fensfjorden, during the annual graduate field course "*Ocean Science*" at the University of Bergen. Preliminary observations indicated that the prevalence of the parasite could be higher in the hypoxic Masfjorden than in the better oxygenated Fensfjorden. Since oxygen contents differ in the deep basin waters of the fjords, data and samples from these fjords can be used to study the effect *S. scopeli* induces on its host, but also if dissolved oxygen concentration influences the prevalence of *S. scopeli*. Moreover, there are two alternative hypotheses on the internal anchoring location of *S. scopeli*; **1.** the holdfast is found randomly anchored in the visceral cavity of the host (Jungersen, 1911); **2.** An anecdotal observation suggesting that the holdfast may be found near the heart of the host (Salvanes, personal communication, 2021).

The aim of this thesis is to investigate the parasite-host relationship between *S. scopeli* and *B. glaciale* and to examine if the susceptibility of *B. glaciale* to *S. scopeli* infection is correlated with oxygen concentrations in the sea. This will be done by comparing prevalence in four fjord systems that differ in dissolved oxygen content. Furthermore, this thesis will aim to document the anchoring point of *S. scopeli* holdfast in the host.

2. Methods:

2.1 Study area:

Main collections of fish and environmental measurements were done as part of the project *HypOnFjordFish* onboard the research vessel "Kristine Bonnevie" in the time period 16.02.2021 - 23.02.2021. Additional samples were provided by the *BIO325 Ocean Science field course* (BIO, UIB) 23.09.2021 - 28.09.2021 onboard the research vessel "Dr. Fridtjof Nansen". Samples were collected from four west Norwegian fjord systems (Fig 2); Fensfjorden, Masfjorden, Osterfjorden and Sørfjorden.

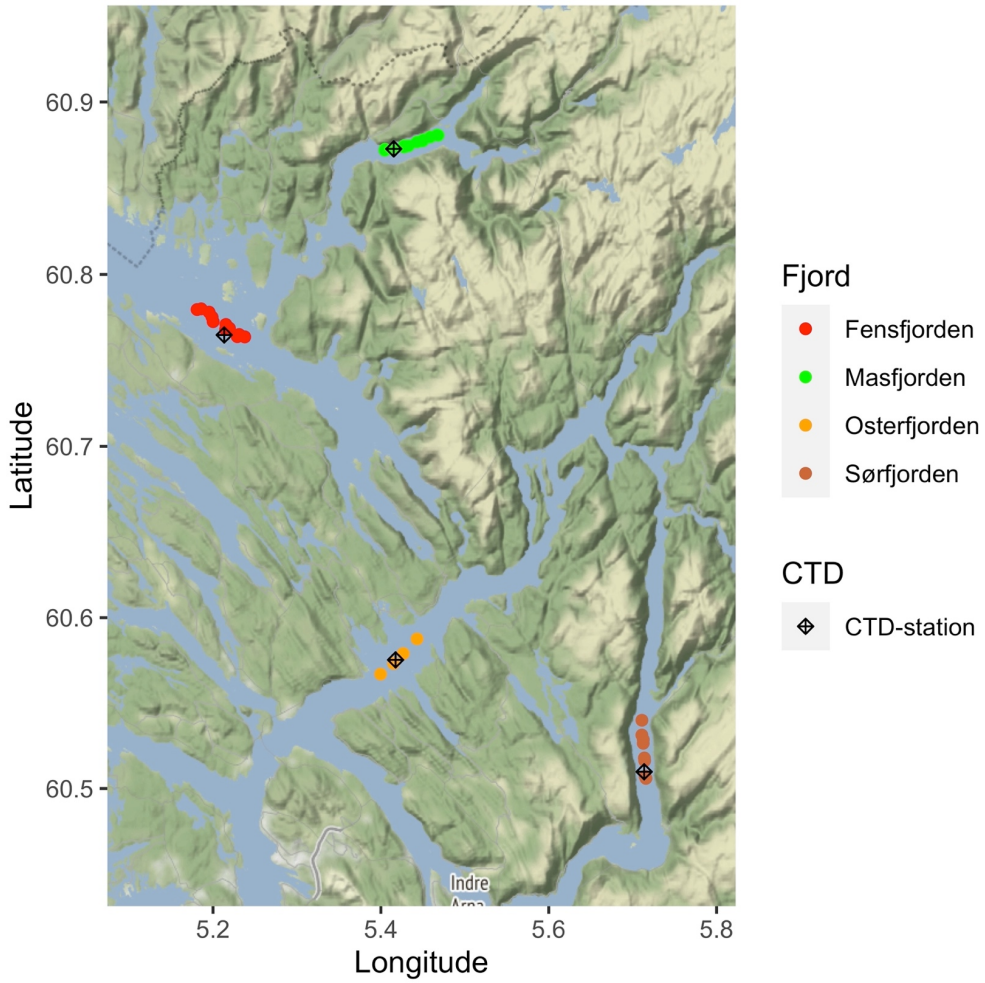

Figure 2: Map over the sampling area containing the location of trawl stations sampled during February 2021. Trawl stations from Fensfjorden are given by red coloration, Masfjorden with green coloration, Osterfjorden with orange coloration and Sørfjorden with brown coloration. CTD stations used in the study are marked as ⌖.

2.2 Sampling methods:

2.2.1 Environmental data:

Environmental data from the four locations were collected using a Sea-Bird SBE 9 CTD unit, fitted with an additional dissolved oxygen sensor. The CTD unit provides continuous measurements of salinity (PSU), temperature (C°) and depth (m) through the water column, while the additional sensor simultaneously provides continuous measurements of the dissolved oxygen content (ml L^{-1}). A total of 13 CTD measurements were taken under the cruise (Tab 1).

Table 1 CTD: Overview of CTD-stations measured during the HypOnFjordFish cruise in February 2021. Max depth shows the deepest sampling depth for the station. CTD-stations used to represent the environmental conditions in Masfjorden, Fensfjorden, Sørfjorden and Osterfjorden under the sampling period for further analysis is given in bold.

Fjord	Date	CTD-station	Latitude	Longitude	Max depth (m)
Sørfjorden	16.02.2021	207	60 31.81 N	005 19.57 E	493
Sørfjorden	16.02.2021	208	60 31.81 N	005 19.57 E	493
Sørfjorden	16.02.2021	209	60 31.81 N	005 19.56 E	491
Sørfjorden	16.02.2021	210	60 28.00 N	005 40.45 E	418
Sørfjorden	17.02.2021	211	60 28.01 N	005 40.42 E	417
Masfjorden	18.02.2021	212	60 52.36 N	005 24.93 E	482
Masfjorden	18.02.2021	213	60 52.36 N	005 24.93 E	481
Masfjorden	**19.02.2021**	**214**	**60 52.37 N**	**005 24.92 E**	**482**
Fensfjorden	19.02.2021	215	60 45.90 N	005 12.80 E	670
Fensfjorden	**20.02.2021**	**216**	**60 45.89 N**	**005 12.80 E**	**669**
Herdlefjord	22.02.2021	217	60 25.80 N	005 15.97 E	332
Osterfjorden	**22.02.2021**	**218**	**60 34.52 N**	**005 25.05 E**	**475**
Sørfjorden	**22.02.2021**	**219**	**60 30.59 N**	**005 42.82 E**	**377**

2.2.2 Biological data:

All biological sampling (Tab 2) was done using a pelagic Harstad-trawl, using two different trawling methods; First, a pelagic trawl with a multisampler fitted, an equipment with three separate cod-ends that can be remotely opened and closed on selected depths (Engås et al., 1997). Fishing time for each 16-millimeter stretched meshed cod-end was approximately 10 minutes before the cod-end was closed and the trawl net in front of the multisampler was washed before the next cod-end was opened. Each of the three cod-ends were given a unique serial number to identify which cod-end had fished at a given depth at each trawl station. Second method was a pelagic trawl with a single 5-millimeter stretched meshed cod-end. The trawl was quickly lowered to a depth 50 meter over the seabed, and it fished for approximately 10 minutes at a depth range between 50-150 meters above the sea floor. As the pelagic trawl was fitted with a single cod-end, some individuals are expected to have been caught throughout the entire water column. Trawling was performed during day light and night but was paused during the twilight (which lasts for one hour before and after sunrise and sunset), in order to avoid the main diel vertical migration activity.

Table 2: Overview over trawl stations and series from the four Fjord systems. Time of day shows if the trawl was performed during day or night. Latitude and Longitude show the coordinates of the sampling station, while haul shows which type of trawling method was used. Fishing depth is the depth where the sampling was performed given in meters. "uninfected (n)" and "infected (n)" show the number of individuals from each series that was examined for parasite infections. NA values show stations where parasitic infection unfortunatly were not recorded. Samples from the two stations sampled in september of 2021, were used for Micro-CT scans of the internal attachment site for S. scopeli.

Fjord	Sampling date	Station	Series	Time of day	Latitude	Longitude	Haul	Fishing depth (m)	Trawl time (min)	uninfected (n)	infected (n)
Osterfjorden	16.02.2021	147	1	night	60.58766	5.44328	oblique	280-200	19	80	11
Masfjorden	18.02.2021	148	2	day	60.87689	5.44340	oblique	280-200	10	92	8
Masfjorden	18.02.2021	148	3	day	60.87393	5.42794	oblique	190-100	10	102	0
Masfjorden	18.02.2021	148	4	day	60.87208	5.40473	oblique	80-0	11	2	0
Masfjorden	18.02.2021	149	5	night	60.87751	5.45010	oblique	290-220	10	97	7
Masfjorden	18.02.2021	149	6	night	60.87465	5.43315	oblique	190-110	10	104	N/A
Masfjorden	18.02.2021	149	7	night	60.87258	5.41478	oblique	90-10	11	98	3
Masfjorden	19.02.2021	150	8	day	60.87813	5.45078	echo.layer	255-190	11	96	4
Masfjorden	19.02.2021	150	9	day	60.87462	5.42780	echo.layer	220-160	10	93	8
Masfjorden	19.02.2021	150	10	day	60.87260	5.40501	echo.layer	120-60	13	97	3
Masfjorden	24.09.2021	190	1	night	60.87660	5.44763	oblique	300-200	9	N/A	N/A
Fensfjorden	19.02.2021	151	11	day	60.77523	5.19880	oblique	310-215	15	101	0
Fensfjorden	19.02.2021	151	12	day	60.76877	5.21953	oblique	190-110	14	5	0
Fensfjorden	19.02.2021	151	13	day	60.76369	5.23781	oblique	110-0	12	5	0
Fensfjorden	19.02.2021	152	14	day	60.77808	5.19530	echo.layer	320-270	12	N/A	N/A
Fensfjorden	19.02.2021	152	15	day	60.77095	5.21531	echo.layer	175-150	12	N/A	N/A
Fensfjorden	19.02.2021	152	16	day	60.76512	5.23114	echo.layer	140-110	11	N/A	N/A
Fensfjorden	19.02.2021	153	17	night	60.77258	5.20011	oblique	300-220	10	95	6
Fensfjorden	19.02.2021	153	18	night	60.76798	5.21489	oblique	190-120	11	101	2
Fensfjorden	19.02.2021	153	19	night	60.76384	5.22896	oblique	90-10	12	103	2
Fensfjorden	20.02.2021	154	21	day	60.78001	5.18588	deep.haul	440-0	101	100	2
Fensfjorden	26.09.2021	203	41	night	60.77514	5.20089	oblique	300-200	11	N/A	N/A
Fensfjorden	20.02.2021	155	22	night	60.77960	5.18102	deep.haul	460-0	101	95	6
Masfjorden	21.02.2021	156	23	day	60.88095	5.46728	deep.haul	330-0	49	105	3
Masfjorden	21.02.2021	157	24	day	60.87970	5.45900	deep.haul	460-0	55	99	3
Masfjorden	21.02.2021	158	25	night	60.88074	5.46845	deep.haul	440-0	59	99	4
Osterfjorden	22.02.2021	159	26	night	60.57909	5.42685	oblique	295-210	11	97	5
Osterfjorden	22.02.2021	159	27	night	60.57328	5.41528	oblique	200-115	10	98	3
Osterfjorden	22.02.2021	159	28	night	60.56703	5.39980	oblique	85-50	11	105	0
Sørfjorden	22.02.2021	160	29	day	60.52871	5.71269	oblique	290-210	11	102	1
Sørfjorden	22.02.2021	160	30	day	60.51793	5.71399	oblique	220-140	13	106	0
Sørfjorden	22.02.2021	160	31	day	60.50728	5.71477	oblique	130-0	12	12	1
Sørfjorden	22.02.2021	161	32	night	60.52653	5.71263	oblique	300-210	12	98	1
Sørfjorden	22.02.2021	161	33	night	60.51633	5.71432	oblique	180-110	10	90	3
Sørfjorden	22.02.2021	161	34	night	60.50597	5.71585	oblique	80-0	18	116	2
Sørfjorden	23.02.2021	162	35	night	60.54001	5.71107	deep.haul	330-0	39	98	4
Sørfjorden	23.02.2021	163	36	day	60.53135	5.71099	deep.haul	330-0	43	103	1

2.3 Processing of trawl catches and preservation:

Trawl catches were processed and sorted in accordance to the description in Chapter 4 of Salvanes et al. (2018). Biological material from the cod-end was transferred to plastic containers and marked with cod-end number to keep samples from different depth ranges separate. Larger fish species and large helmet jellyfish (*Periphylla periphylla,* Péron & Lesueur, 1809) were removed from the total catch and processed separately. The remaining mixed catch consisted primarily of two mesopelagic teleost species, *B. glaciale and Maurolicus muelleri* (Gmelin, 1789); three crustacean, *Sergestes arcticus* (Krøyer, 1855), *Pasiphaea sp.* and *Meganyctiphanes norvegica* (M. Sars, 1857)*;* and small helmet jellyfish*.* Approximately 100 individuals from each species were randomly selected from a sub-sample of the mixed catch and weighted. For *B. glaciale,* standard length, from the snout to the last caudal bone (Fig 3), rounded down to the nearest millimeter; and *S. scopeli* infections were recorded at most trawl stations (Tab 2).

Two preservation methods were used to preserve random sub-samples of *B. glaciale* for later analysis in Fall of 2021*;* **1.** The 100 length measured individuals from each trawl series were frozen in blocks at -20°C in the on-board freezer, and later relocated to an on-site freezer at Biologen, Thormøhlensgate 53A, University of Bergen; **2.** Preservation with 96% ethanol was used for the 300-200 Oblique haul, the deep-hauls and the Echo-layer hauls. 1L Bottles were filled with 1/3 biological material and 2/3 ethanol. Unfortunately, one of the ethanol samples from Osterfjorden (station 159, series 26) had to be excluded from further processing as it had failed to preserve as we unfortunately had forgotten to change the ethanol. It is also possible that higher proportion of *P. perihylla* residue compared to the other samples caused the preservation failure, due to higher water contents. The additional samples provided by the “Ocean science” cruise were preserved on Biosafe-biopsy containers containing 4% formalin buffered in saltwater on board “Dr. Fridtjof Nansen” and were stored at Biologen until later analysis in January 2022.

2.4 Processing of samples:

Ethanol samples of *B. glaciale* were sorted into *S. scopeli* infected and uninfected individuals; except for station 160 and 161 in Sørfjorden, all infected individuals and a random subsample of the uninfected individuals were selected for further analysis. For station 160 and 161 uninfected and infected individuals were length and sex matched. Length and sex for the remaining individuals in all containers were also recorded and used to make statistical weighting factors for further analysis (Tab 3). Prior to biological measurements, each selected fish was given a unique identification, containing; fjord name, sample date, trawl-station, series (cod-end) and fish number.

The processing of individual fish started by removing excess ethanol or residue from other biological material by gently drying it off using paper towels, to avoid bias of individual weights. Prior to dissection, individuals were visually inspected for *S. scopeli* infection. If present, number and infection sites were recorded before removal; However, the parasite often broke and the internal part was extracted later, and its weight was deducted from total weight of *B. glaciale*. Individuals were sexed using the secondary sexual traits expressed as enlarged photophores, located supracaudal in males (Fig 1B) and infracaudal in females (Fig 1C), and by inspecting the gonads. In cases where secondary sexual trait was uninterpretable, only the gonads were used. If, neither gonads or secondary sexual trait were interpretable, as for small uninfected individuals (< 27 mm), sex was noted as unknown (n = 69) and excluded from further analysis. After external examination, standard length rounded down to the nearest mm, and total body weight were noted; A Sartorius Entris II (Appendix A: Fig A1B) was used for all body-weight measurements (total weight, gutted weight and dried gutted weight), which were recorded to the nearest 0.01 g.

Figure 3: Benthosema glaciale infected by a single Sarcotretes scopeli. The red arrow gives the standard length of B. glaciale.

Dissections were conducted under a Leica MZ 95 magnifier (Appendix A: Fig A1C) coupled with a Leica Cls 100x light system. The pericardial and visceral cavity were opened by making a cut from the isthmus back to the anus and on each side of the pectoral gridle (Fig 4A). To standardize the removal of the heart, cuts were made as close to the bulbus arteriosus and sinus venosus as possible (Fig 4C). Visceral content was removed from the carcass by two cuts in the esophagus (Fig 4B) prior to liver and gonad extraction, due to easier handling. Remaining visceral fat was removed to standardize gutted weight. All heart, liver, gonad and *S. scopeli* weights (wet and dry) were measured to the nearest 0,0001 g using a Satorius Micro M3P (Appendix A: Fig A1A) and VWR Aluminum weighing dishes.

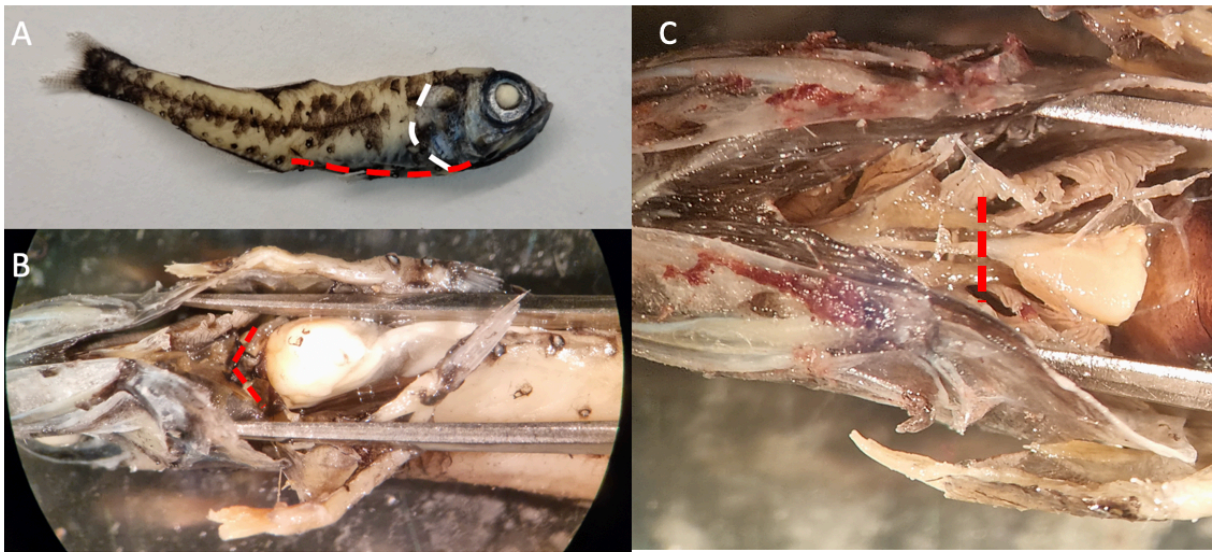

Figure 4: Overview picture of the A) initial cuts made to open the fish, where the red stipulated line shows the cut from the isthmus to the anus, and the white stipulated line shows the cut around the pectoral gridle. B) cuts made to separate the viscera from the esophagus (red stipulated lines). C) location of the cut close to bulbus arteriosus (red stipulated line) used to standardize the extraction of the heart.

Drying of gutted individuals and organs was done in a Fermaks drying oven (Appendix A: Fig A1E) for 48 hours on 60°C, to get the constant weigh. Gutted individuals were placed on a laminated A4 paper separated into quadrants and marked with a place I.D. Organs were placed in nunc wells marked with organ structure and corresponding place I.D. as gutted body (Fig 5).

Figure 5: Depiction of laminated drying sheet marked with placement I.D for each individual fish. Nunc wells were marked with the same placement I.D on the long side of the well, in addition to marks for organ identification (G = gonad, L = liver, H = heart) on the broad side.

Otoliths were taken prior to drying for all infected (n = 93) and size and sex matched uninfected individuals (n = 83) from both the random sub-sample and the remaining ethanol sample. Otoliths were stored in Eppendorf tubes marked with the fish I.D. A Leica M125 dissection microscope (Appendix A: Fig A1D), coupled with a Nikon DSFi2 camera was used to photograph otoliths. Left and right otoliths were photographed both dry and submerged in water. Resolution was standardized by using identical magnification (x32) for all photos and a calibration stick with millimeter measurements was photographed for each session. Otoliths from five individuals were lost before photos could be taken and had to be excluded from further analysis. Additionally, individuals that did not have a matching conspecific (n = 15) were also excluded from further analysis.

Table 3: Overview over the sampling area, sampling date, time of day, type of trawling method and depth of the ethanol preserved Benthosema glaciale used under the study. "sampled uninfected(n)" and "infected (n)" show the number of fish selected from each station for further analysis." Remaining uninfected (n)" shows the number of uninfected fish sexed and length measured to be used for the weighting factor in statistical analysis. Total (n) shows the total number of fish from each preserved sample.

Fjord	Sampling Date	Time of day	Haul	Station	Series	Depth (m)	sampled uninfected (n)	infected (n)	Remaning uninfected (n)	total (n)
Osterfjorden	16.02.2021	Night	Oblique	147	1	300-200	30	11	140	181
Masfjorden	18.02.2021	Day	Oblique	148	2	300-200	15	2	99	116
Masfjorden	18.02.2021	Night	Oblique	149	5	300-200	15	4	87	106
Masfjorden	19.02.2021	Day	echo_layer	150	8	250-190	15	2	94	111
Masfjorden	19.02.2021	Day	echo_layer	150	9	220-160	15	6	166	187
Fensfjorden	19.02.2021	Day	Oblique	151	11	300-200	15	4	96	115
Fensfjorden	19.02.2021	Night	Oblique	153	17	300-200	15	6	55	76
Fensfjorden	20.02.2021	Day	Deep haul	154	21	440-0	15	5	53	73
Fensfjorden	20.02.2021	Night	Deep haul	155	22	460-0	15	8	88	111
Masfjorden	21.02.2021	Day	Deep haul	156	23	330-0	15	4	112	112
Masfjorden	21.02.2021	Day	Deep haul	157	24	470-0	15	7	107	129
Masfjorden	21.02.2021	Night	Deep haul	158	25	440-0	15	6	130	151
Sørfjorden	22.02.2021	Day	Deep haul	160	29	300-200	15	9	107	131
Sørfjorden	22.02.2021	Night	Oblique	161	32	300-200	15	10	91	116
Sørfjorden	23.02.2021	Night	Oblique	162	35	330-0	15	6	83	104
Sørfjorden	23.02.2021	Day	Deep haul	163	36	330-0	15	3	136	154

2.4.1 Micro-Computer tomography:

Micro-Computer tomography (henceforth called Micro-CT) was performed to document the *S. scopeli*'s way through the host. Two formalin preserved *B. glaciale* were selected based on infection site of *S. scopeli*; one dorsal and one ventral. Contrast enhancement of soft tissue was performed in accordance to Metscher (2009). Formalin samples were thoroughly washed for four hours under running water, before they were placed in 1% lugol solution (Appendix A: Fig A2C), diluted in osmosis water to 10%, for approximately 18 hours (Appendix A: Fig A2B). Excess lugol solution was rinsed prior to preservation on 96% ethanol. Samples were stored for a week prior to scans.

Micro-CT scans of samples were taken at the faculty for clinical Odontology, University of Bergen. Scans were performed using a Skyscan 1172 system (Appendix A: Fig A2A), coupled with the NRECON RECONSTUCTIONVR CT software. Source voltage and current were set to 70 kilo volt and 180 micro amperes respectively; while a 0.5 mm aluminum filter was used to optimize images. Oversized scans were used in order to reconstruct the whole visceral cavity. Unfortunately, due to parasite orientation, the internal part of *S. scopeli* was not visible in the reconstruction of the ventral infection.

2.4.2 Volume measurements of *Sarcotretes scopeli*:

15 frozen *B. glaciale,* infected with *S. scopeli* were selected from two stations in Masfjorden (Appendix B: Tab B9) and thawed. Each *B. glaciale* specimen was sexed using the external secondary sex trait, and only females were selected for the statistical analysis (n = 9). *S. scopeli* individuals were carefully removed under a Leica MZ95 stereoscope (Appendix A: Fig A3A); In a few cases the parasite broke, and the internal part had to be retrieved by dissection. Each *B. glaciale* and corresponding *S. scopeli* were given an I.D. that contained the first three letters of the fjord, trawl-station, series, individual number and a letter (A, B, C or D) which stated which part of the parasite had been measured. Volume was measured for *B. glaciale*, whole *S. scopeli*, external part of *S. scopeli* and internal part of *S. scopeli*. The internal part was assumed to start at the narrowest part of the neck (Fig 6).

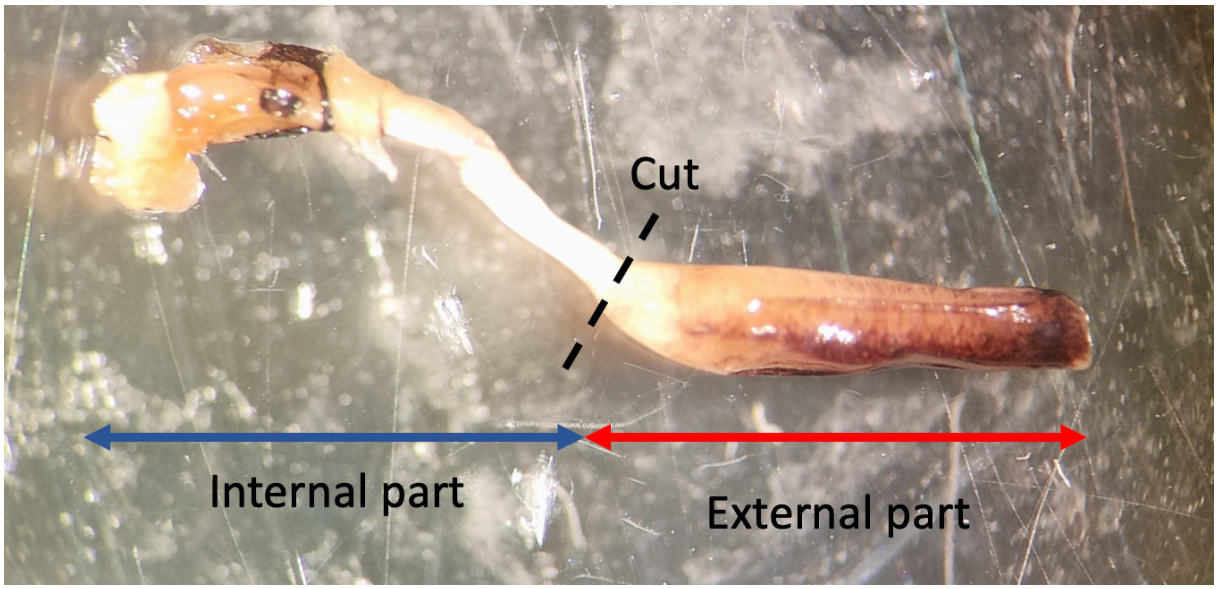

Figure 6: Shows where the internal and external part of Sarcotretes scopeli were assumed to be. The black stipulated line shows where the cut was made. The red arrow shows the external part of S. scopeli, while the blue arrow shows the internal part.

Measuring tubes were designed for *S. scopeli* volume measurements; DNA tubes were filled with exactly 175 μL water, using mechanical pipettes (Appendix A: Fig A3B). Bubbles and displaced water were removed or guided when present. Initial water level was marked with a scalpel as close to the surface layer as possible (Appendix A: Fig A3D). A tube marked at the 150 μL and 160 μL water level was made, in order to calibrate measurements for later analysis. For each measurement a new tube was used to reduce bias due to water loss. Displacement of water was recorded with an Olympus TG-6 camera; picture resolution was standardized by keeping the camera position and magnification constant. Measuring tubes were placed on a holder kept at a fixed distance from the camera (Appendix A: Fig A3C). *B. glaciale* individuals were measured using a storage bottle annotated with 2.5 ml intervals (Appendix A: Fig A3E) and initial water level was set at 40 ml; water loss was replaced between each measurement. All volume measurements were recorded from the initial water level to the lowest point of the displaced water surface.

2.5 Data analysis:

Due to temporal and spatial closeness of CTD measurements in the four fjord systems, one station was selected for further statistical analysis and assumed to be representative for the environmental conditions of each fjord. Dissolved oxygen content was selected for the mean depth from each of the depth ranges. These values were then converted to a categorical dummy variable (Low; oxygen level $\leq$ 3 ml l^{-1}, High; oxygen level > 3 ml l^{-1}), for further analysis. The two categories were divided at 3ml l^{-1}, since Direktoratsgruppen vanndirektivet (2018) categorizes deep-sea dissolved oxygen content $\leq$ 3 ml l^{-1} as moderate-poor, and values > 3 ml l^{-1} as moderate-good.

S. scopeli prevalence was estimated by dividing the total number of infected individuals, by the total number of infected and uninfected individuals measured for each individual fjord system (equation 1):

$$equation\ 1: Prevalence = \frac{N_{inf}}{N_{tot}} * 100$$

Where prevalence = percentage of infected individuals in the population, N_{inf} = number of infected individuals measured, N_{tot} = total number of individuals measured.

Dry organ and dry gutted somatic weight were converted to organosomatic indices; Gonadosomatic index (GSI), hepatosomatic index (HSI) and heartsomatic index (HASI); For further statistical analysis (equation 2). Before conversion, $1*10^{-6}$ were added to the 0 values of the dried gonad weight of males, so the data could be boxcox-transformed for further analysis. Data from five individuals had to be excluded due to errors in the dried gutted weight measurements (n = 3) or in dried gonad weight (n = 2):

$$equation\ 2: OSI = \frac{OW_D}{GTW_D} * 100$$

Where OSI = organosomatic index, refers to GSI, HIS or HASI. OW_D refers to the respective dry organ weights, and GTW_D refers to the dry gutted weight of the fish.

Fresh gutted weight (equation 3.) and fresh standard length (equation 4.) for each individual *B. glaciale* were calculated from the ethanol preserved wet gutted weight and standard length of the fish, using the obtained relationship provided in Kristoffersen and Salvanes (1998):

$$equation\ 3: FW = 0.0074 + (1.430 * WWG)$$

Where FW = fresh gutted weight, and WWG = wet weight gutted

$$equation\ 4: FL = -0.667 + (1.043 * L)$$

Where FL = fresh standard length, and L = preserved standard length.

Fulton's condition factor was calculated using the fresh gutted weight relative to the fresh standard length (equation 5) and was the variable used for further statistical analysis.

$$equation\ 5: CF = \frac{FW}{FL^3}$$

Where CF = Fulton's condition factor, FW = Fresh gutted weight and FL = fresh standard length.

As all individuals from the ethanol samples where sexed and measured for length (see section 2.4), I could use statistical weighting factors when analyzing the data. The use of statistical weighting factors was necessary in order to say something general about the overall fjord populations, as all infected *B. glaciale* were processed, while only a subsample of the uninfected *B. glaciale* was processed (Glen, 2019). In order to adjust for that only a subsample of the uninfected fish was processed, common observations of fish with a given length and sex combination present in both the processed sample and overall population were given a higher weighting factor, thus they got more importance in the statistical analysis (equation 6). This was done in order to balance the processed sample to more accurately represent the overall population. If a given sex and length combination was present in the overall population, but not in the processed sample, the observation was given a weighting factor of zero in order to exclude it from further statistical analysis. Since all infected individuals were processed, these observations were given a weighting factor of one. This way all observations from infected individuals had equal importance in the analysis.

$$equation\ 6: WF = \frac{T}{A}$$

Where WF = weighting factor, T = Total number of unprocessed and processed fish of a given length and sex. A = number of processed fish of a given length and sex.

2.5.1 Otolith measurements and aging:

Photos of dry otoliths were used to trace the otolith-area of the sampled infected and uninfected individuals. Ageing was performed using photos of otoliths submerged in water. All otoliths were aged by following a fixed axis from the otolith core to the highest point of the otolith (Fig 7). Otoliths consist of opaque rings, which are associated with fast growth during summer and translucent rings, which are associated with slow growth during winter (Das, 1994). Thus, in this study a year was defined as one translucent and one opaque ring. Since all fish were sampled in February 2021, the translucent edge of the otoliths was counted as a year. In some instances, there was observed a small translucent band around the otolith core, which was excluded in the year count. The left otolith was selected as the default picture, while in instances where the left otolith consisted of vaterite, missing or unreadable, the right otolith was used instead.

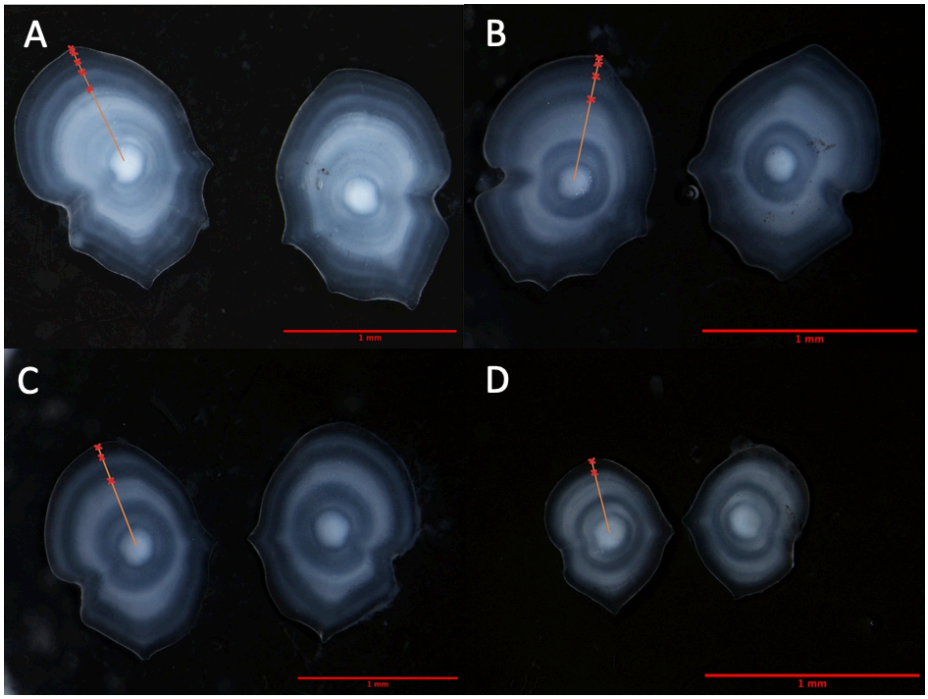

Figure 7: Otoliths from Benthosema glaciale; the orange lines show the axis used to count annuli, while the red marks show the location of each annulus counted. A) Otolith 5 year of age; B) Otolith 4 year of age; C) Otolith 3 years of age; D) Otolith 2 years of age.

2.5.2 Anchoring point of *Sarcotretes scopeli:*

Internal and external parasitic anchoring points were noted to the exact locations on the host (Appendix B: Tab B1) and in later analysis of the anchoring points, they were categorized in pre-made groups. External groups were defined as dorsal, ventral and other, while Internal groups were defined as heart, stomach/pylorus cease, gonads and other.

2.5.3 Volume measurements of *Sarcotretes scopeli:*

Jpeg pictures of *S. scopeli* total, external and internal volume, were further modified in gimp.2.0 (The GIMP Development Team, 2019), by adding digital markers to the middle of the original scalpel marker and to the lowest point of the surface tension. Images were further analyzed in imageJ (Schneider et al. 2012), using the calibration tube to set a global scale for all measurements. To standardize the measurements, volume was defined as the distance between the outer edge of the two digital markers. Due to the small volumes used to measure water displacement, and differences in water tension placement; there was a general trend that the sum of the internal and external parasitic parts was higher than the total parasitic volume measured. As a result, exact internal and external parasitic volume cannot be stated. However, the aim in this thesis is to give a proxy of the parasitic volume relative to the host volume. Parasitic volume in relation to host (V_H) volume was calculated for total parasitic volume (V_{tot}; equation 7), external parasitic volume (V_{ext}; equation 8) and the internal parasitic volume (V_{int}; equation 9).

$$equation\ 7:\ V_{\%tot} = \frac{V_{tot}}{V_H} * 100$$

Where $V_{\%tot}$ = Percentage of total parasitic volume in relation to host volume, V_{tot} = total parasitic volume, V_H = Host volume.

$$equation\ 8: V_{\%ext} = \frac{V_{ext}}{V_H} * 100$$

Where $V_{\%ext}$ = Percentage of external parasitic volume relative to host volume, V_{ext} = external parasitic volume, V_H = Host volume.

$$equation\ 9:\ V_{\%int} = \frac{V_{int}}{V_H} * 100$$

Where $V_{\%int}$ = Percentage of internal parasitic volume in relation to host volume, V_{int} = internal parasitic volume, V_H = Host volume.

2.5.4 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 & Ripley, 2002), ShapeR (Libungan & Pálsson, 2015), vegan (Oksanen et al., 2008), car (Fox & Weisberg, 2019) and emmeans (Russell, 2022). Statistically significance was assumed for α = 0.05.

The effect of dissolved oxygen concentration on parasitic prevalence between fjords was tested using a Generalized linear mixed model (GLMM) (model 1), with a quasibinomial error distribution in order to account for overdispersion. Prevalence was specified as a binary response (0 for uninfected and 1 for infected), while the predictor variable oxygen level (Low; oxygen level $\leq$ 3 ml l^{-1}, High; oxygen level > 3 ml l^{-1}), was categorical. Fjord was used as random factor, due to clustering of observations within this variable. The GLMM was followed by a Chi-square test (model 2). Differences in *S. scopeli* prevalence between fjords was tested using a generalized linear model (GLM) with a quasibinomial error distribution (model 3). Prevalence was specified as a binary response (0 for uninfected, 1 for infected), and fjord was defined as a categorical predictor. Furthermore, differences in length-frequency distribution between the infected and uninfected individuals within each fjord were tested by comparing the distributions of cumulative relative length-frequency's, using a Kolmogorov-Smirnov test (model 4):

$model\ 1$: *glmmPQL(prevalence ~ oxygen, random = ~ 1 |fjord, family = quasibinomial , data = data.df)*

$model\ 2$: *Anova(model1 , type = "III")*

$model\ 3$: *glm (prevalence ~ fjord, family = quasibinomial, data = data.df)*

$model\ 4$: *ks.test(fjord_uninfected_length, fjord_infected_length)*
Where fjord_uninfected_length refers to the length distribution of uninfected *B. glaciale* and fjord_infected_length refers to the length distribution of the infected *B. glaciale*.

For the effect of infection status on host biology (GSI, HIS, HASI and CF) GLM's were also fitted. A quasibinomial error distribution was assumed for all GLM's, due to potential overdispersion in the data. Organosomatic indices (GSI, HSI and HASI) were converted to binomial response variables, using proportions (and not percentage) as response variables. For all GLM's, except for GSI; sex (M for male and F for female) and fjord were specified as categorical variables, and infection status was specified as a binary predictor (0 for uninfected and 1 for infected; model 4). For GSI, a model was fitted for each separate sex, due to inherent differences in gonad size; thus, the model only included fjord and infection status as predictors (model 5). Interactions terms were removed from the model if deemed insignificant. Each GLM was followed up by an Anova, to get the global statistics of the main effects and the interaction terms. Emmeans post-hoc test for pairwise comparison, with a Tuckey adjustment, was used to determine which categories differed significantly from each other (model 6). In addition, the linear relationship between *B. glaciale* dry gutted weight (continuous predictor) and the dry weight of the gonads, liver and heart (continuous response variables) was compared for the infected and uninfected individuals (binary predictor), using a linear model (LM; model 7). Data for dried heart weight of the sexes were pooled, as HASI were similar for males and females. All response variables were box-cox transformed to meet the assumption of normality and homoscedasticity. Dried gonad weight for males from Masfjorden and dried hearts of the pooled sexes from Osterfjorden, were excluded from the analysis due to violation of the assumptions of homoscedasticity and normality both before and after box-cox transformation, determined from visual inspection of diagnostic plots. Interaction terms were removed if found to be insignificant. A weighting factor (wt_factor) was added to all GLM and LM models in order to balance the sample (see section 2.5 above):

$model\ 4$: *glm(GSI_binary ~ Infected * fjord, weights = wt_factor, family = quasibinomial , data = Data.df*

$model\ 5$: *glm(OSI_binary ~ Infected*sex + fjord*infected, weights = wt_factor, family = "quasibinomial", data = Data.df)*

Where OSI = HSI, HASI or CF.

$model\ 6$: *emmeans(Mod, specs = pairwise ~ predictor1*predictor2, type = "response")*

$model\ 7$: *lm(dry_organ_weight ~ dry_weight_gutted * Infected, weights = wt_factor, data = Data.df)*

The effect of infection on host growth was tested by comparing the mean age difference between infected and age/sex matched uninfected *B. glaciale*, using a two-way ANOVA (model 8). This analysis was performed for each fjord separately. Age was defined as a continuous response, while sex was set as a categorical predictor (M for males and F for females) and infection status was defined as a binary predictor (0 for uninfected and 1 for infected). Differences in otolith parameters were tested using a LM (Model 9); otolith length (O_L) and otolith width (O_w) were set as continuous responses, infection status was set as a binary predictor (0 for uninfected, 1 for infected), while fjord and sex were defined as categorical predictors. The interactions between the predictors were removed if found non-significant. The LM was followed by emmeans post-hoc test's (model 6) to test which levels of the categorical predictors differed from each other. Furthermore, the variation in otolith shape between infected and uninfected individuals was tested for each fjord, using a Canonical Analysis of Principal Coordinates (CAP; model 10); followed by an ANOVA-like premutation test with 1000 permutations (model 11) in accordance to Libungan and Pálsson (2015). Mean wavelet coefficients were standardized by adjustments in respect to fjord, fish standard length and infection status. Data on otolith shape were pooled for the sexes as otolith length and width were similar for males and females.

$model\ 8$: *aov(age ~ sex*Infected, data = Data.df)*

$model\ 9$: *lm(otolith_parameter ~ Infected + fjord + sex, data = Data.df)*

$model\ 10$: *cap = capscale(getStdWavelet(shape) ~ getMasterlist(shape)$Infected)*

$model\ 11$: *anova(cap.res1, by = "terms", step = 1000)*

The relationship between parasitic volume (V_{tot}, V_{ext} and V_{int}) and host volume (V_H) was tested with a Pearson correlation test. All volumes were defined as continuous variables. In addition, the relationship between internal (V_{int}) and external (V_{ext}) volume of *S. scopeli* was tested using a Pearson correlation test (model 12).

$model\ 12$: *cor.test(Data.df$volume_fish, Data.df$volume_parasite, method=c("pearson"))*

3. Results:

3.1 Environmental parameters:

Water temperature in the four fjord systems in February 2021 was between 4.7 – 7.7°C, 5.1-8.2 °C, 6.4-7.7°C, and 7.4-7.9°C, for Fensfjorden, Masfjorden, Osterfjorden and Sørfjorden, respectively, and increased from the surface towards the bottom (Fig 8A). Dissolved oxygen content was observed to decrease with depth in all four fjord systems, with values ranging from 6.9-5.4 ml L^{-1}, 6.5-2.3 ml L^{-1}, 7.1-3 ml L^{-1} and 6.4-2.3 ml L^{-1}; for Fensfjorden, Masfjorden, Osterfjorden and Sørfjorden sequentially (Fig 8B). Salinity in the four fjord systems rapidly decreased in the first 100 meters ranging from 31.8-35.1 PSU, 30.6-34.9 PSU, 29.8-34.8 PSU and 27.7-34.8 PSU for Fensfjorden, Masfjorden, Osterfjorden and Sørfjorden respectively (Fig 8C)

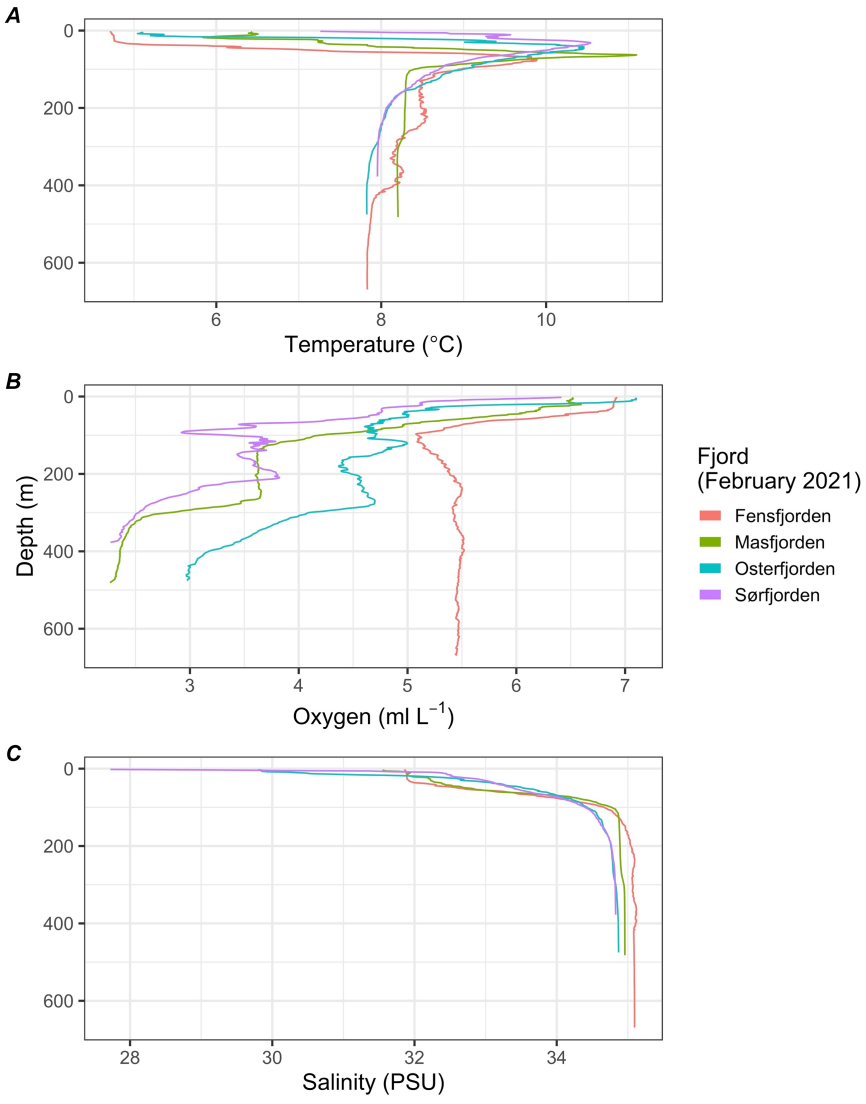

Figure 8: CTD transects from the four fjord systems in February 2021. Values from Fensfjorden are given in red, Masfjorden in green, Osterfjorden in blue and Sørfjorden in purple. All transects are given over depth (y-axis). A) temperature (C°) B) Dissolved oxygen content (ml l^{-1}) C) salinity (PSU).

3.2 Prevalence of Sarcotretes scopeli:

Prevalence of *S. scopeli* in February 2021, was found to be highest in Osterfjorden and Masfjorden (4.76% and 4.33%, respectively; Fig 9), while being lowest in Sørfjorden (1.76%). Fensfjorden, had an intermediate prevalence (2.92%) compared to the other three fjords. Sørfjorden was found to have a lower prevalence compared to Masfjorden and Osterfjorden (GLM; Mas: t = 2.87, p = 0.004; Ost: t = 2.80, p = 0.005), but did not differ from Fensfjorden (GLM; t = 1.45, p = 0.15). Dissolved oxygen level did not affect the prevalence in the four fjord systems (GLMM; X^2 = 2.09, DF_1, p = 0.15).

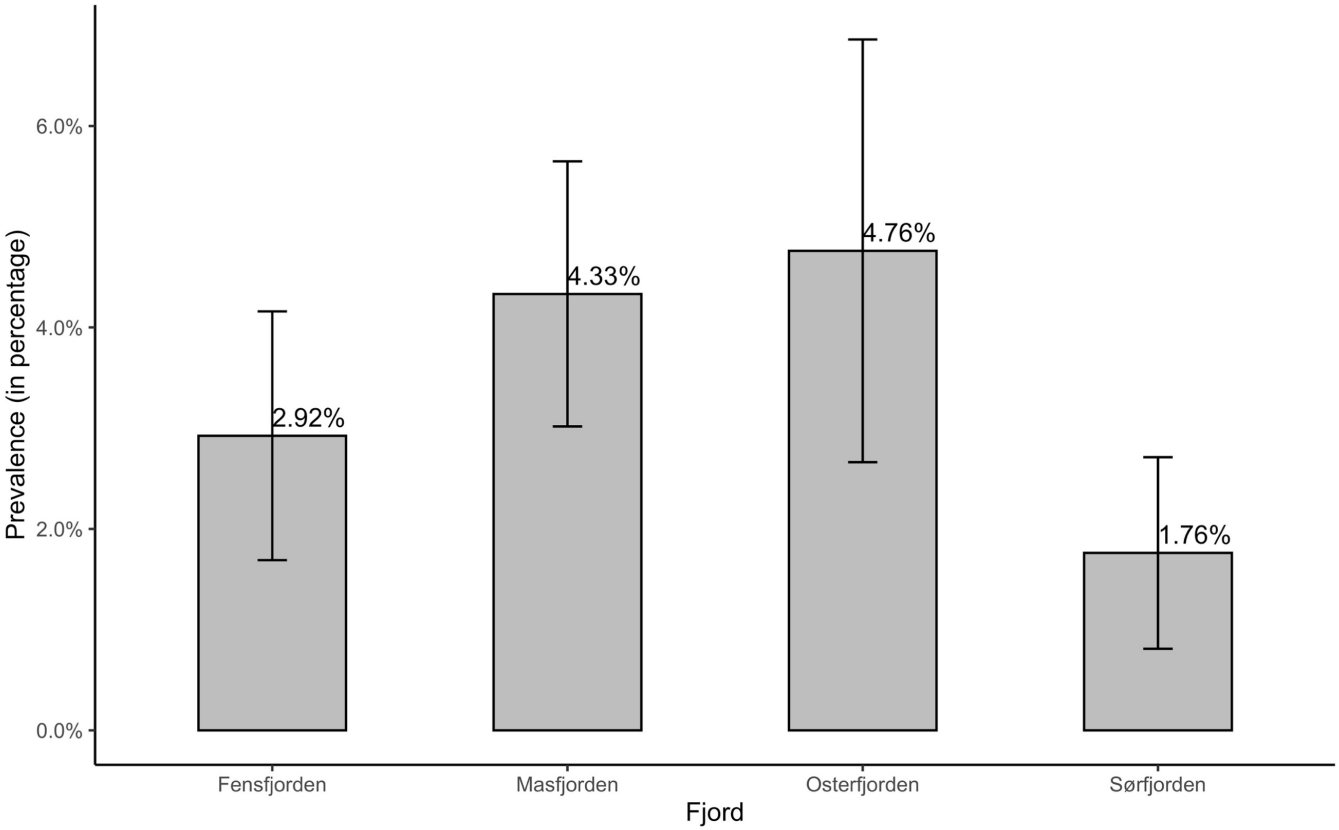

Figure 9: Barplot over Sarcotretes scopeli prevalence (y-axis) from four west Norwegian fjord systems (x-axis), in February 2021.

3.3 Cumulative length frequency:

The length distributions of infected *B. glaciale* were similar as for uninfected individuals in all four fjord systems (Kolmogorov Smirnov test; Mas: D = 0.16, p = 0.29; Fens: D = 0.13, p = 0.87; Sør: D = 0.28, p = 0.25; Ost: D = 0.15, p = 0.81; Fig 10).

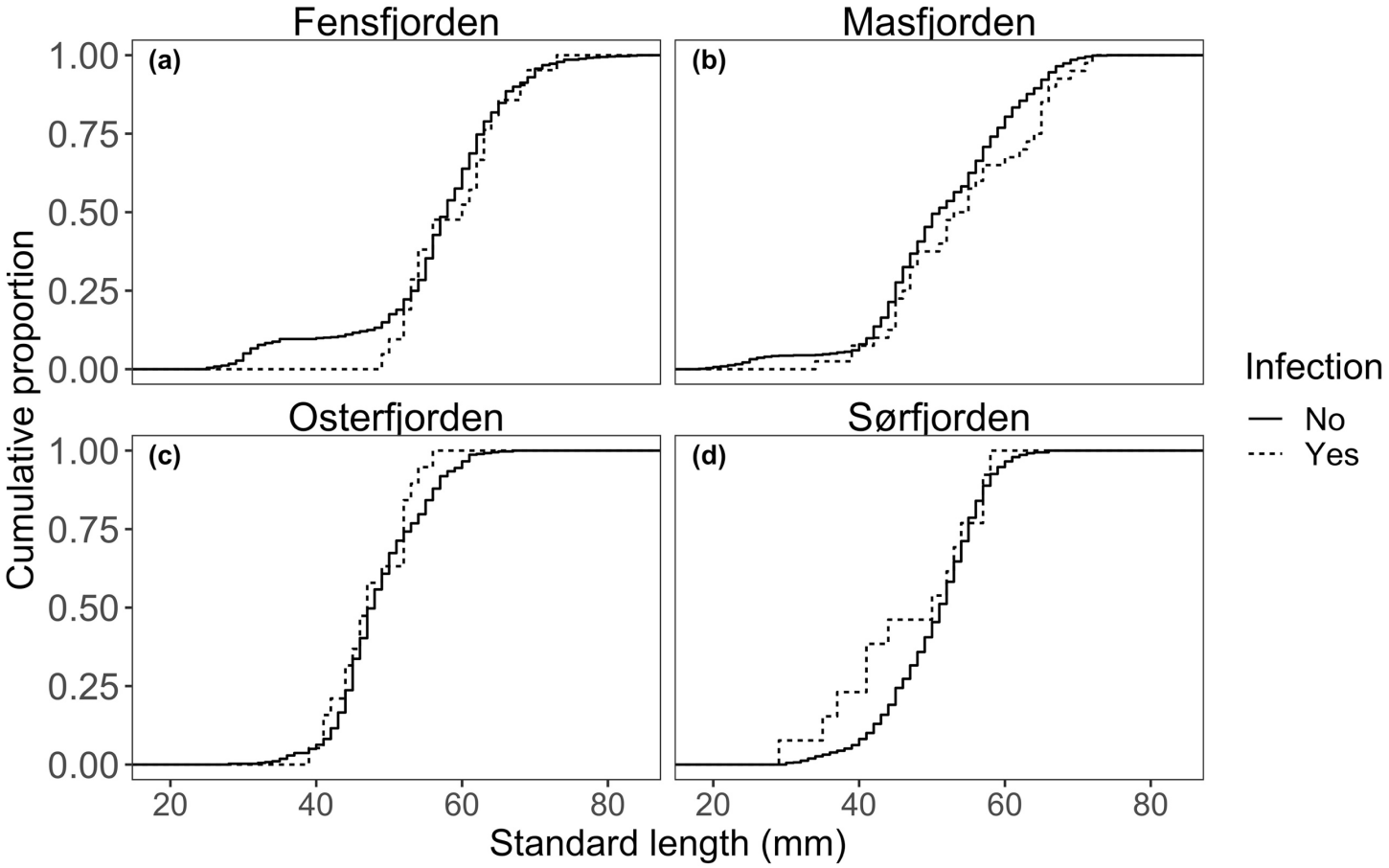

Figure 10: Cummulative relative standard length of Sarcotretes scopeli infected and uninfected Benthosema glaciale from four west Norwegian fjords. A) Infected and uninfected individuals from Fensfjorden. B) Infected and uninfected individuals from Masfjorden. C) Infected and uninfected individuals from Osterfjorden. D) infected and uninfected individual from Sørfjorden.

3.4 Parasitic effect on host gonadosomatic index:

The gonadosomatic index (GSI) was lower for infected individuals than uninfected ones for both females (GLM: Resid. Dev = 5.49, $DF_{1,172}$, p << 0.001; Tab 4, Fig 11A) and males (Resid. Dev = 0.16, $DF_{1,156}$, p << 0.001; Tab 4, Fig 11B).

GSI did not differ for females between fjords (GLM; Resid. dev = 5.38, $DF_{3,169}$, p = 0.35, Tab 4), but did for males (Resid. dev = 0.14, $DF_{3,153}$, p << 0.001, Tab 4), where males from Masfjorden and Fensfjorden had lower GSI than males from Sørfjorden (Emmeans; p < 0.001, Fig 11B, Appendix B, Tab B2).

Table 4: Generalized linear model on the effect of infection (infected and uninfected) and fjord (Masfjorden, Fensfjorden, Sørfjorden and Osterfjorden) on the gonadosomatic index (GSI) of male and female Benthosema glaciale. A quasi-binomial distribution was assumed to account for overdispersion and calculated weighting factors and Chi-square test were used.

Female	D.f	Deviance	Residual. D.f	Residual deviance	*P*
GSI					
Infected	1	4.57	172	5.49	<< 0.001
Fjord	3	0.11	169	5.38	0.35
Infected × fjord	3	< 0.01	166	5.37	0.96

Male	D.f	Deviance	Residual. D.f	Residual deviance	*P*
GSI					
Infected	1	0.02	156	0.16	<< 0.001
Fjord	3	0.03	153	0.14	<< 0.001
Infected × fjord	3	< 0.01	150	0.13	0.66

Since GSI is calculated for an average individual over every length group, the linear relationship of gonad weight as a function of gutted weight of the fish was also tested. Gonad weight increased with gutted weight for both infected and uninfected females and males in all fjords except Masfjorden (LM: p < 0.006, Tab 5, Appendix C: Fig C1a, c & d, Fig C2). In Masfjorden the gonad weight did not increase with gutted weight for infected females (LM; infected x dry gutted weight: $F_{1,70}$ = 8.77, p = 0.004, Tab 5, Appendix C: Fig C1b).

*Table 5: Linear regression (LM) on the box-cox transformed dry gonad weight of **female** Benthosema glaciale as a function of the dry gutted weight and infection (infected and uninfected) on fish from Masfjorden, Fensfjorden, Sørfjorden and Osterfjorden. Weighting factors and a F-test were used. LM on the box-cox transformed dry gonad weight of **male** B. glaciale as a function of the dry gutted weight and infection (infected and uninfected) of fish from Fensfjorden, Sørfjorden and Osterfjorden. Weighting factors and a F-test were used.*

Female	Sum sq.	$F_{(d.f.)}$	*p*	Male	Sum sq.	$F_{(d.f.)}$	*p*
Masfjorden							
Dry gutted weight	1.7	$177.93_{(1,70)}$	<< 0.001		-	-	-
Infected	0.04	$4.75_{(1,70)}$	0.03		-	-	-
Infected × dry gutted weight	0.08	$8.77_{(1,70)}$	0.004		-	-	-
Fensfjorden							
Dry gutted weight	0.26	$8.06_{(1,39)}$	0.007		< 0.01	$22.92_{(1,35)}$	<< 0.001
Infected	2.1	$64.21_{(1,39)}$	<< 0.001		< 0.01	$2.12_{(1,35)}$	0.15
Infected × dry gutted weight	< 0.01	$< 0.01_{(1,38)}$	0.94		< 0.01	$0.07_{(1,34)}$	0.8
Sørfjorden							
Dry gutted weight	15.49	$24.18_{(1,33)}$	<< 0.001		< 0.01	$63.01_{(1,43)}$	<< 0.001
Infected	85.66	$133.67_{(1,33)}$	<< 0.001		< 0.01	$6.33_{(1,43)}$	0.02
Infected × dry gutted weight	0.15	$0.22_{(1,32)}$	0.64		< 0.01	$0.32_{(1,42)}$	0.58
Osterfjorden							
Dry gutted weight	0.74	$7.66_{(1,19)}$	0.01		4.27	$10.42_{(1,15)}$	0.006
Infected	2.27	$23.53_{(1,19)}$	< 0.001		0.75	$1.82_{(1,15)}$	0.2
Infected × dry gutted weight	0.01	$0.12_{(1,18)}$	0.73		0.22	$0.52_{(1,14)}$	0.48

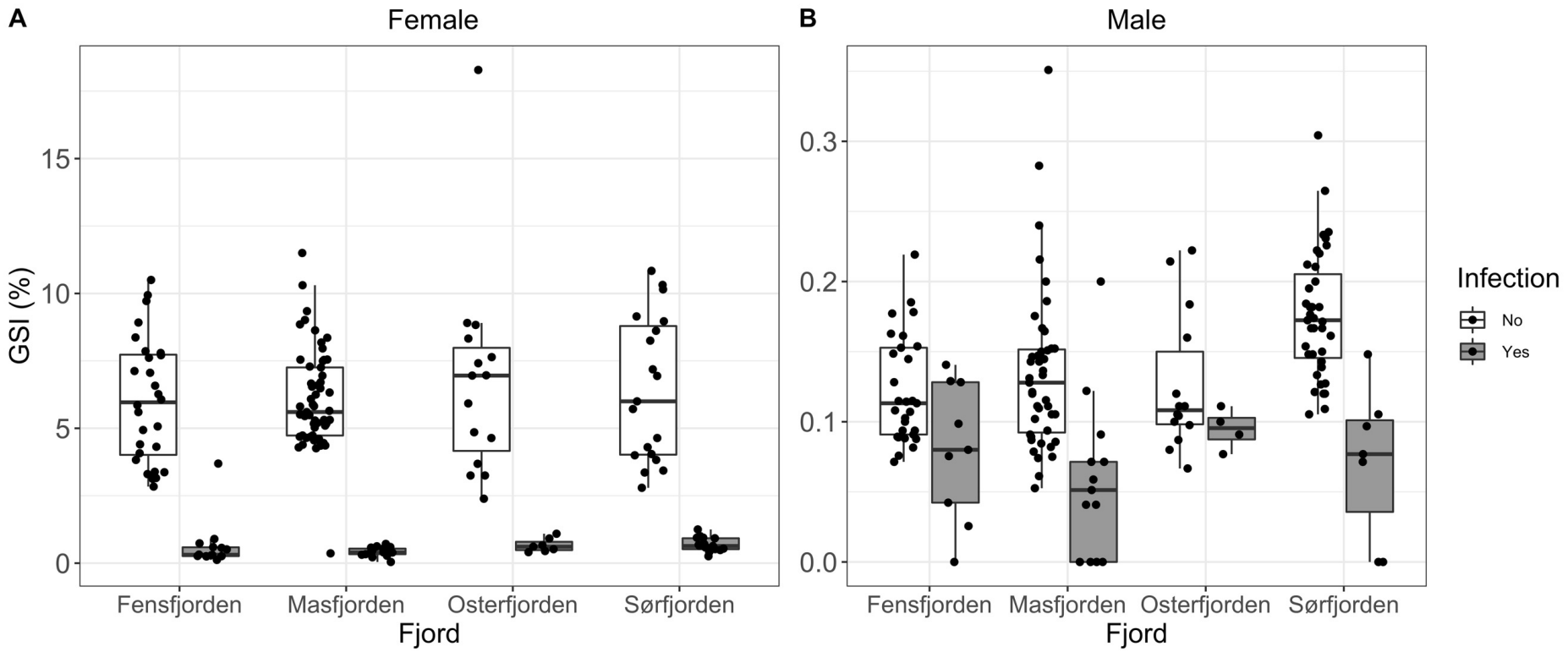

Figure 11: Boxplot of the gonadosomatic index (GSI) in percentage between Sarcotretes scopeli infected and uninfected Benthosema glaciale from four west Norwegian fjords. Uninfected individuals are given in white, while infected individuals are given in gray. Black points indicate individual observations. A) females B) males.

3.5 Parasitic effect on host hepatosomatic index:

The hepatosomatic index (HSI) of *B. glaciale* was affected by infection and the sex of the fish (GLM: infection x sex; Resid. deviance = 1.75, $DF_{1,326}$, p << 0.001, Tab 6, Fig 12); Uninfected males had a lower HSI than uninfected females, while infected males and females had a similar HSI (Emmeans; Uninfected: Z = 21.06, p << 0.001; Infected: Z = 0.34, p = 0.99, Fig 12, Appendix B: Tab B3). Both infected and uninfected females had similar HSI, while infected males had higher HSI than uninfected males (Emmeans: Females: Z = -0.32, p = 0.99; Males: Z = -8.12, p << 0.001, Fig 12, Appendix B: Tab B3).

HSI differed for infected fish between the fjords (GLM; infected x fjord: Resid. deviance = 1.66, $DF_{3,323}$, p < 0.001, Tab 6, Fig 12), where infected fish from Sørfjorden had a higher HSI than infected fish from Masfjorden and Fensfjorden (Emmeans; Mas: Z = -3.94, p = 0.002; Fen: Z = -3.11, p = 0.04, Appendix B: Tab B3).

Table 6: Generalized linear model on the effect of infection (infected and uninfected), sex (male and female) and fjord (Masfjorden, Fensfjorden, Sørfjorden and Osterfjorden) on the hepatosomatic index (HSI) of Benthosema glaciale. 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*
HSI					
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

Since HSI is also calculated for an average individual over every length group, the linear relationship of the liver weight as a function of gutted weight of the fish was estimated. 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, Tab 7, Appendix C: Fig C3 & C4). The increase was similar for infected and uninfected individuals for both sexes and in all four fjords (interaction: infection x dry gutted weight; females > 0.17: males p > 0.39; Tab 7)

*Table 7: Linear regression (LM) on the box-cox transformed dry liver weight of **female** Benthosema glaciale as a function of the dry gutted weight of the fish and infection (infected and uninfected) from Masfjorden, Fensfjorden, Sørfjorden and Osterfjorden. Weighting factors and a F-test were used. LM on the box-cox transformed dry liver weight of **male** Benthosema glaciale as a function of the dry gutted weight of the fish and infection (infected and uninfected) from Masfjorden, Fensfjorden, Sørfjorden and Osterfjorden. Weighting factors and a F-test were used.*

Female	Sum sq.	$F_{(d.f.)}$	*p*	Male	Sum sq.	$F_{(d.f.)}$	*p*
Masfjorden							
Dry gutted weight	0.13	$107.23_{(1,71)}$	<< 0.001		0.09	$70.81_{(1,53)}$	<< 0.001
Infected	< 0.01	$1.57_{(1,71)}$	0.21		< 0.01	$3.52_{(1,53)}$	0.07
Infected × dry gutted weight	< 0.01	$0.82_{(1,70)}$	0.37		< 0.01	$< 0.01_{(1,52)}$	0.99
Fensfjorden							
Dry gutted weight	0.06	$38.62_{(1,39)}$	<< 0.001		0.01	$8.78_{(1,35)}$	0.005
Infected	< 0.01	$2.50_{(1,39)}$	0.12		< 0.01	$3.89_{(1,35)}$	0.06
Infected × dry gutted weight	< 0.01	$1.35_{(1,38)}$	0.25		< 0.01	$0.39_{(1,34)}$	0.53
Sørfjorden							
Dry gutted weight	4.25	$64.62_{(1,33)}$	<< 0.001		7263	$11.75_{(1,43)}$	0.001
Infected	1.14	$17.29_{(1,33)}$	< 0.001		3642	$5.89_{(1,43)}$	0.02
Infected × dry gutted weight	0.12	$1.95_{(1,32)}$	0.17		16	$0.03_{(1,42)}$	0.87
Osterfjorden							
Dry gutted weight	1724.3	$25.06_{(1,19)}$	<< 0.001		0.2	$11.25_{(1,15)}$	0.004
Infected	175	$2.54_{(1,19)}$	0.13		0.19	$10.85_{(1,15)}$	0.005
Infected × dry gutted weight	32	$0.45_{(1,18)}$	0.51		0.01	$0.8_{(1,14)}$	0.39

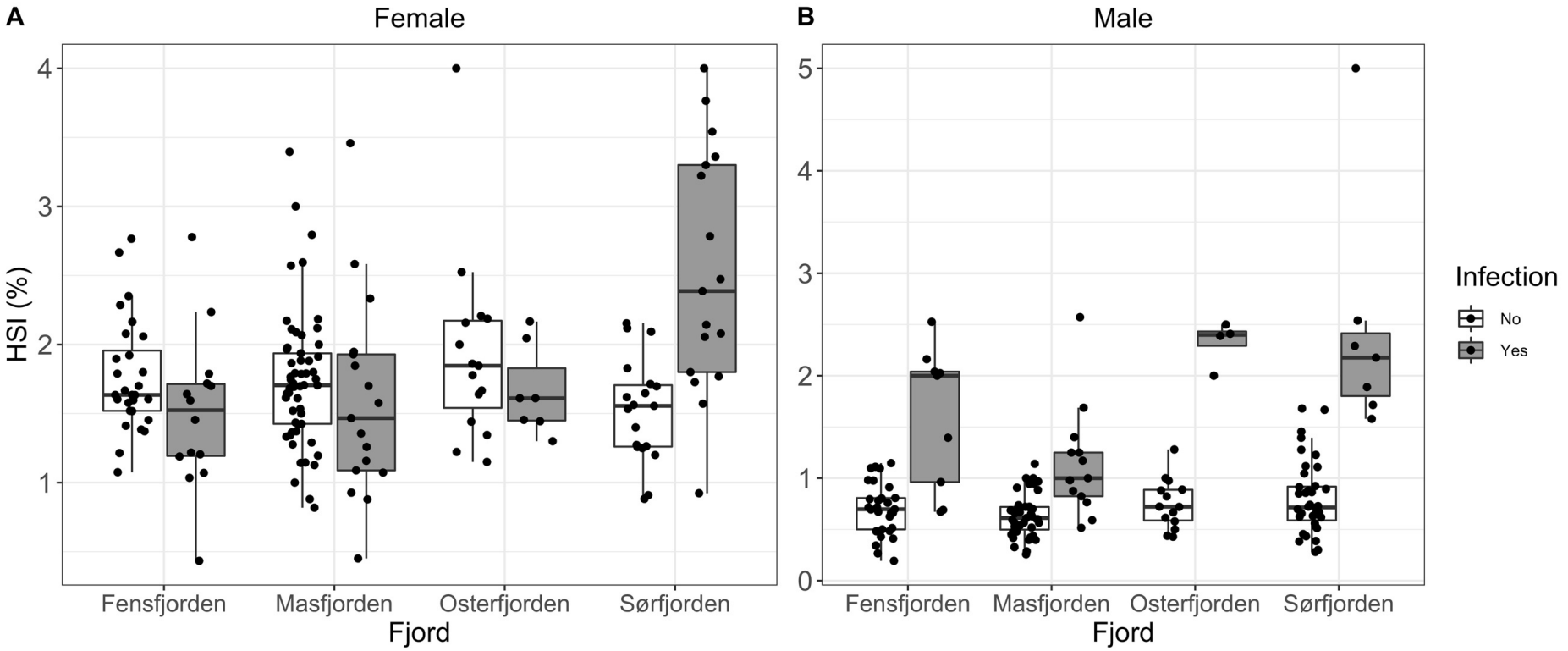

Figure 12: Boxplot of the hepatosomatic index (HSI) in percentage between Sarcotretes scopeli infected and uninfected Benthosema glaciale from four west Norwegian fjords. Uninfected individuals are given in white, while infected individuals are given in gray. Black points indicate individual observations. A) females B) males

3.6 Effect on host cardiac size:

Infected individuals had higher heartsomatic index (HASI) than uninfected individuals (GLM; Resid. dev = 0.87, $DF_{1,331}$, p = 0.033; Fig 13, Tab 8), and was similar for females and males and fjords (Interaction: Infected x Sex; p = 0.57; Infected x fjord: p = 0.58; Tab 8). After removing the interaction effects, a main effect of fjord was detected (GLM; Resid. dev = 0.79, $DF_{3,327}$, p << 0.001, Tab 8), where fish from Sørfjorden had higher HASI than fish from Masfjorden and Fensfjorden (Emmeans; p < 0.002, Fig 13, Appendix B: Tab B4), and fish from Osterfjorden had higher HASI than fish from Masfjorden (Emmeans; Z = -3.09, p = 0.01, Fig 13, Appendix B: Tab B4).

Table 8: Generalized linear model on the effect of infection (infected and uninfected), sex (male and female) and fjord (Masfjorden, Fensfjorden, Sørfjorden and Osterfjorden) on the heartsomatic index (HASI) of Benthosema glaciale. 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*
HASI					
Infected	1	0.01	331	0.87	0.03
Sex	1	< 0.01	330	0.87	0.17
Fjord	3	0.08	327	0.79	<< 0.001
Infected × sex	1	< 0.01	326	0.79	0.57
Infected × fjord	3	< 0.01	323	0.78	0.58

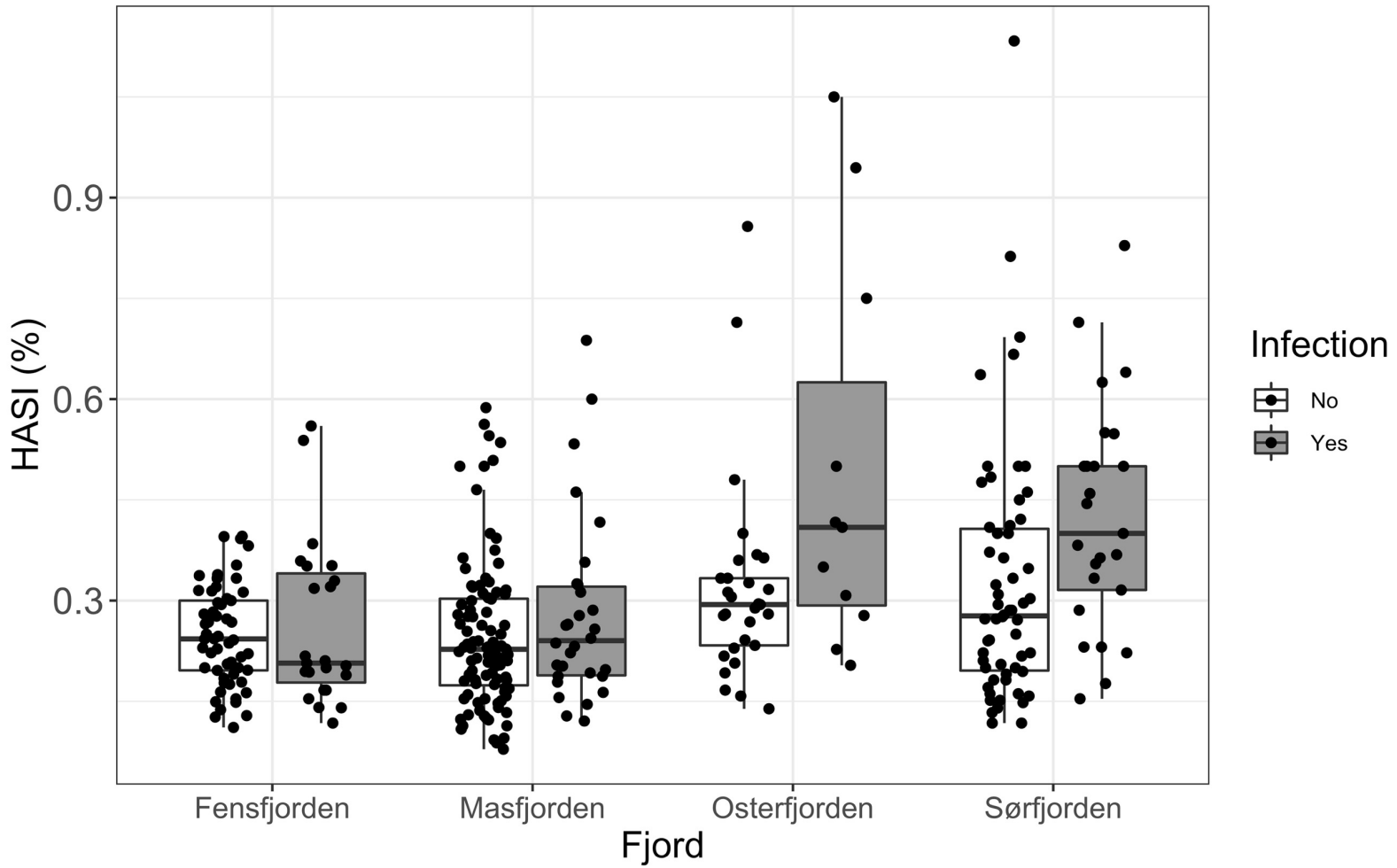

Figure 13: Boxplot of the heartsomatic index (HASI) in percentage between Sarcotretes scopeli infected and uninfected Benthosema glaciale from four west Norwegian fjords. Uninfected individuals are given in white, while infected individuals are given in gray. Black points indicate individual observations.

The heart weight of infected and uninfected individuals increased with gutted weight in all of the fjords (LM: $p < 0.001$, Tab 9, Appendix C: Fig C5). The increase was similar for infected and uninfected fish in all four fjords (Interaction: Infected x dry gutted weight: $p > 0.14$, Tab 9)

Table 9: Linear regression (LM) on the box-cox transformed dry heart weight of Benthosema glaciale as a function of the dry gutted weight and infection (infected and uninfected) of fish from Masfjorden, Fensfjorden and Sørfjorden. Weighting factors and a F-test were used.

	Sum sq.	$F_{(d.f.)}$	*p*
Masfjorden			
Dry gutted weight	46.7	$117.19_{(1,127)}$	<< 0.001
Infected	< 0.01	$0.01_{(1,127)}$	0.93
Infected × dry gutted weight	0.1	$0.29_{(1,126)}$	0.59
Fensfjorden			
Dry gutted weight	< 0.01	$22.82_{(1,77)}$	<< 0.001
Infected	< 0.01	$0.73_{(1,77)}$	0.40
Infected × dry gutted weight	< 0.01	$0.90_{(1,76)}$	0.34
Sørfjorden			
Dry gutted weight	67.3	$15.5_{(1,80)}$	< 0.001
Infected	2.2	$0.5_{(1,80)}$	0.48
Infected × dry gutted weight	9.3	$2.14_{(1,79)}$	0.14

3.7 Fulton's condition factor:

Infected *B. glaciale* had lower condition factors compared to uninfected conspecifics (GLM; Resid. dev = 0.03, $DF_{1,331}$, p << 0.001, Fig 14, Tab 10), and were similar for females and males (GLM; interaction: Infection x Sex; Resid. dev = 0.02, $DF_{1,326}$, p = 0.06; main effect of sex: Resid. dev = 0.03, $DF_{1,330}$, p = 0.57, Tab 10)

Condition factors for infected and uninfected fish were similar between all fjords (GLM; Infection x fjord: Resid. dev = 0.02, $DF_{3,323}$, p = 0.92, Tab 10). When the interaction effect was removed, the condition factors of *B. glaciale* differed between fjords (GLM; Resid. dev = 0.02, $DF_{3,327}$, p << 0.001; Fig 14, Tab 10), with infected and uninfected females and males from Sørfjorden being in the poorest condition of the four fjords (Emmeans; p << 0.001, Fig 14, Appendix B: Tab B5).

Table 10: Generalized linear model on the effect of infection (infected and uninfected), sex (male and female) and fjord (Masfjorden, Fensfjorden, Sørfjorden and Osterfjorden) on Fulton's condition factor (CF) of Benthosema glaciale. 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*
CF					
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
Infected × Sex	1	< 0.01	326	0.02	0.06
Infected × fjord	3	< 0.01	323	0.02	0.92

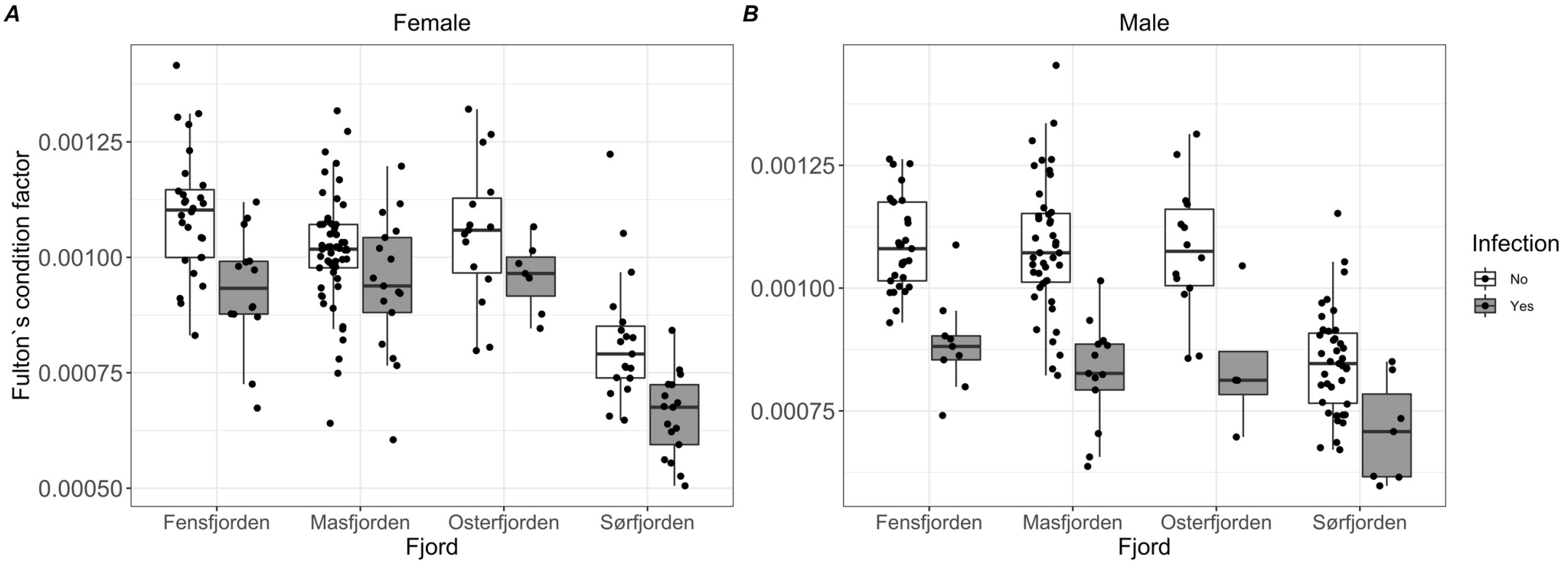

Figure 14: Boxplot of Fulton's condition factor (CF) between Sarcotretes scopeli infected and uninfected Benthosema glaciale from four west Norwegian fjords. Uninfected individuals are given in white, while infected individuals are given in gray. Black points indicate individual observations.A) females B) males.

3.8 Parasitic effect on host growth:

Mean age (Anova: $p > 0.11$, Fig 15,Tab 11), otolith length (LM:$F_{1,150} = 0.48$, $p = 0.49$, Tab 11, Appendix C: Fig C6 & C7), otolith width (LM:$F_{1,150} < 0.01$, $p = 0.99$, Tab 11, Appendix C: Fig C8 & C9) and otolith shape (Anova: $p > 0.05$, Fig 16, Appendix B: Tab B6) were similar between infected and uninfected fish. Females and males had similar mean age (Anova: $p > 0.06$, Tab 11), otolith length (LM: $F_{1,150} < 0.01$, $p = 0.99$) and otolith width ($F_{1,150} < 0.01$, $p = 0.94$, Tab 11).

B. glaciale differed in both otolith length and width between fjords (LM: otolith length: $F_{3,150} = 6.89$, $p < 0.001$; otolith width: $F_{3,150} = 6.81$, $p < 0.001$, Tab 11), where fish from Fensfjorden had larger otolith sizes than fish from the other fjords (Emmeans: otolith length: $p < 0.007$, otolith width: $p < 0.04$, Appendix B: Tab B7 & B8).

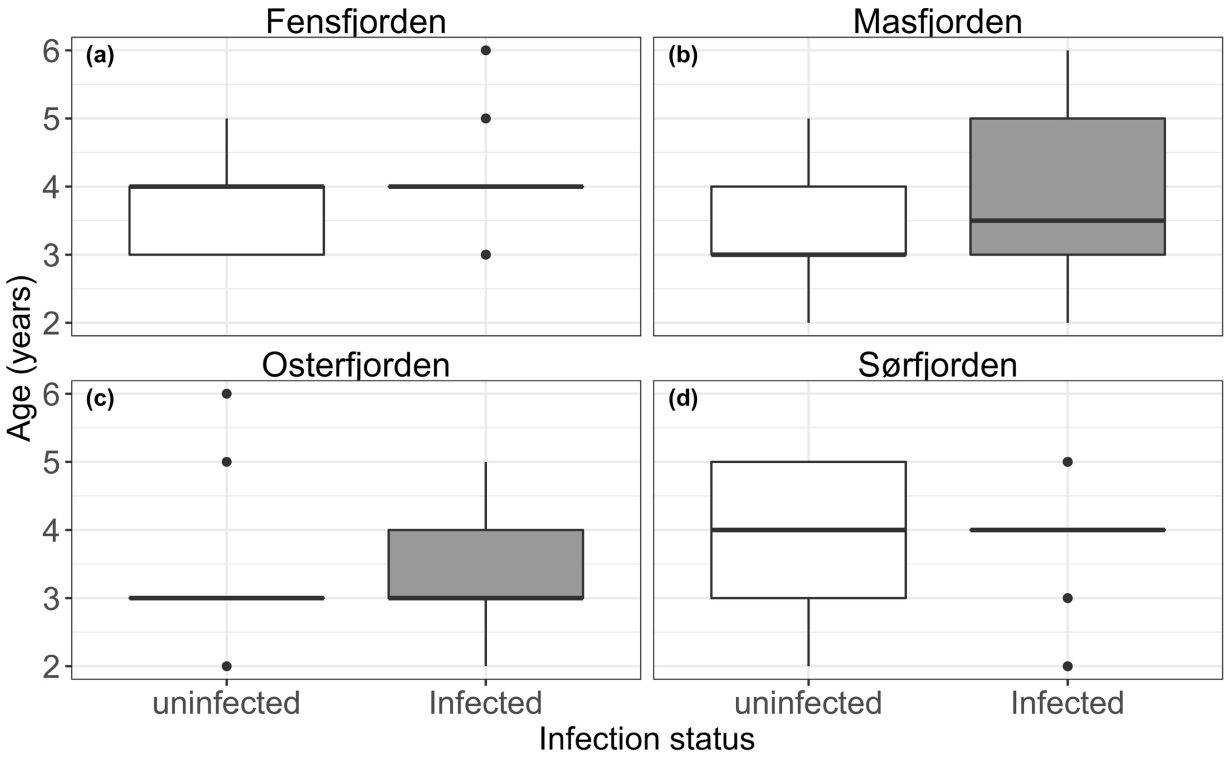

Figure 15: Boxplot of the age (in years) difference between infected and uninfected Benthosema glaciale from four west Norwegian fjords. Uninfected individuals are given in white, while infected individuals are given in gray. a) Fensfjorden. b) Masfjorden. c) Osterfjorden. d) Sørfjorden.

Figure 16: Mean otolith shape based on wavlet reconstuction of Sarcotretes scopeli infected and uninfected Benthosema glaciale, from four west Norwegian fjords. A) Mean otolith shape between infected (n = 24) and uninfected (n = 24) individuals from Sørfjorden. B) Mean otolith shape between infected (n =10) and uninfected (n = 10) individuals from Osterfjorden. A) Mean otolith shape between infected (n = 18) and uninfected (n = 18) individuals from Fensfjorden. A) Mean otolith shape between infected (n = 26) and uninfected (n = 26) individuals from

Table 11: Linear model (LM) on the effect of infection (infected and uninfected), fjord (Masfjorden, Fensfjorden, Sørfjorden and Osterfjorden) and sex (male and female) on the otolith length and width of Benthosema glaciale. A F-test was used. Two-way Anova on the differences in mean age between infection (infected and uninfected) and sex (male and female) of B. glaciale from Masfjorden, Fensfjorden, Sørfjorden and Osterfjorden. A F-test was used.

	Sum sq.	$F_{(d.f.)}$	*p*
Otolith length			
Infected	0.02	$0.48_{(1,150)}$	0.49
Fjord	0.92	$6.89_{(3,150)}$	< 0.001
Sex	< 0.01	$< 0.01_{(1,150)}$	0.99
Infected x Fjord	0.06	$0.42_{(3,146)}$	0.74
Infected x sex	< 0.01	$0.09_{(1,146)}$	0.76
Otolith width			
Infected	< 0.01	$< 0.01_{(1,150)}$	0.99
Fjord	1.72	$6.81_{(3,150)}$	< 0.001
Sex	< 0.01	$< 0.01_{(1,150)}$	0.94
Infected x Fjord	0.02	$0.08_{(3,146)}$	0.97
Infected x sex	< 0.01	$0.03_{(1,146)}$	0.87

	Sum sq.	$F_{(d.f.)}$	*p*
Otolith age Masfjorden			
Sex	3.82	$3.17_{(1,49)}$	0.08
Infected	3.25	$3.25_{(1,49)}$	0.11
Sex × infection	1.6	$1.33_{(1,48)}$	0.25
Otolith age Fensfjorden			
Sex	0.02	$0.04_{(1,33)}$	0.84
Infected	0.44	$0.77_{(1,33)}$	0.39
Sex × infection	0.7	$1.21_{(1,32)}$	0.28
Otolith age Sørfjorden			
Sex	0.37	$0.49_{(1,45)}$	0.49
Infected	0.02	$0.03_{(1,45)}$	0.87
Sex X infection	0.17	$0.21_{(1,44)}$	0.65
Otolith age Osterfjorden			
Sex	4	$4.12_{(1,17)}$	0.06
Infected	0.05	$0.05_{(1,17)}$	0.82
Sex × infection	0.69	$0.70_{(1,16)}$	0.42

3.9 Sarcotretes scopeli anchoring location:

Sarcotretes scopeli was primarily observed attach dorsally on the fish exterior, strictly anterior for the dorsal fin (Fig 17A-C & F, Tab 12). The parasite was also in some cases found to attach to the pelvic fins (Fig 17E, Tab 12), or other places (Tab 12) such as the lateral line (Fig 17F), the head and the gill cover. A few *S. scopeli* were also observed to have attach their feeding apparatus to the hosts gonads (Fig 18B, Tab 12), stomach/pyloric caeca (Fig 18A&D; Fig 19; Tab 12), and heart (Tab 12). While most of the parasites were anchored to other places either in the hosts visceral cavity such as the liver (Fig 18E, n = 5), kidneys (n = 3) and swimbladder (n = 5), or outside of the visceral cavity in the host flesh (Fig 18F, n = 14) and gills (Fig 18G, n = 4).

Table 12: Percentage of external and internal anchoring locations for Sarcotretes scopeli. Anchoring locations show the location categories. Individuals (n) show the number of S. scopeli observed at a given location and percentage is the proportion of S. scopeli found at a given location.

Anchoring location	Individuals (n)	Percentage
External anchoring location:		
dorsal	59	65%
other	9	10%
ventral	23	25%
Internal anchoring location:		
gonads	6	12%
heart	1	2%
other	31	60%
stomach/pyloric caeca	14	27%
Other:		
other	18	58%
viceral	13	42%

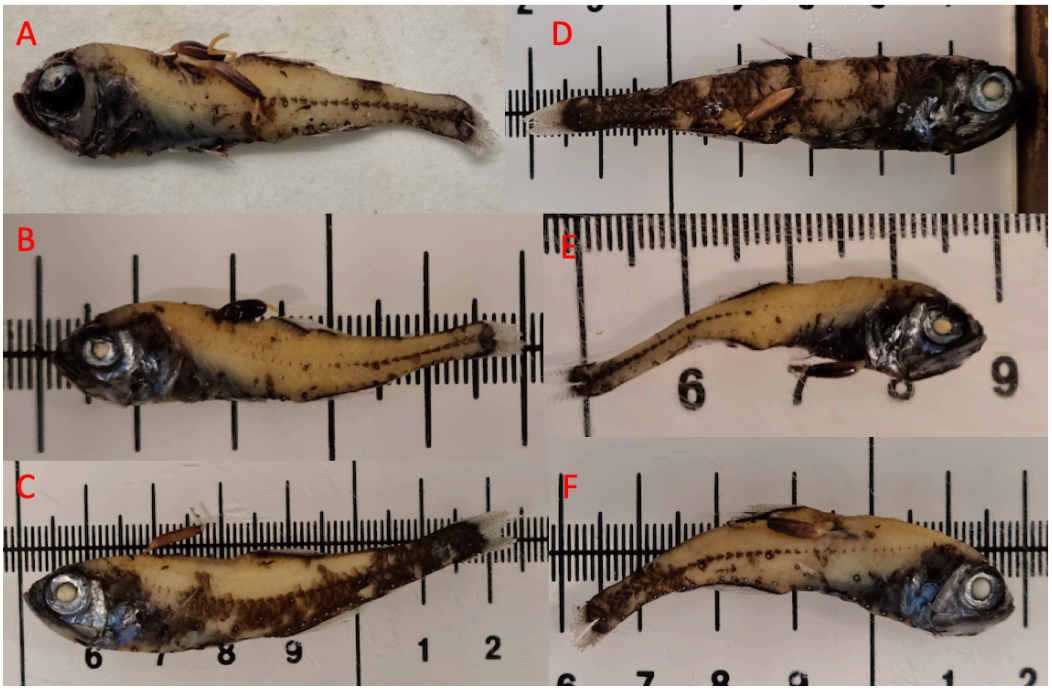

Figure 17: Overview of different Sarcotretes scopeli external anchoring points on Benthosema glaciale. A) B. glaciale infected by two S. scopeli, both dorsally. B) B. glaciale with single S. scopeli infection, dorsally. C) B. glaciale with single infection dorsally close to the head. D) B. glaciale with single lateral infection, left side. E) B. glaciale with single ventral infection. F) B. glaciale with single lateral infection, right side.

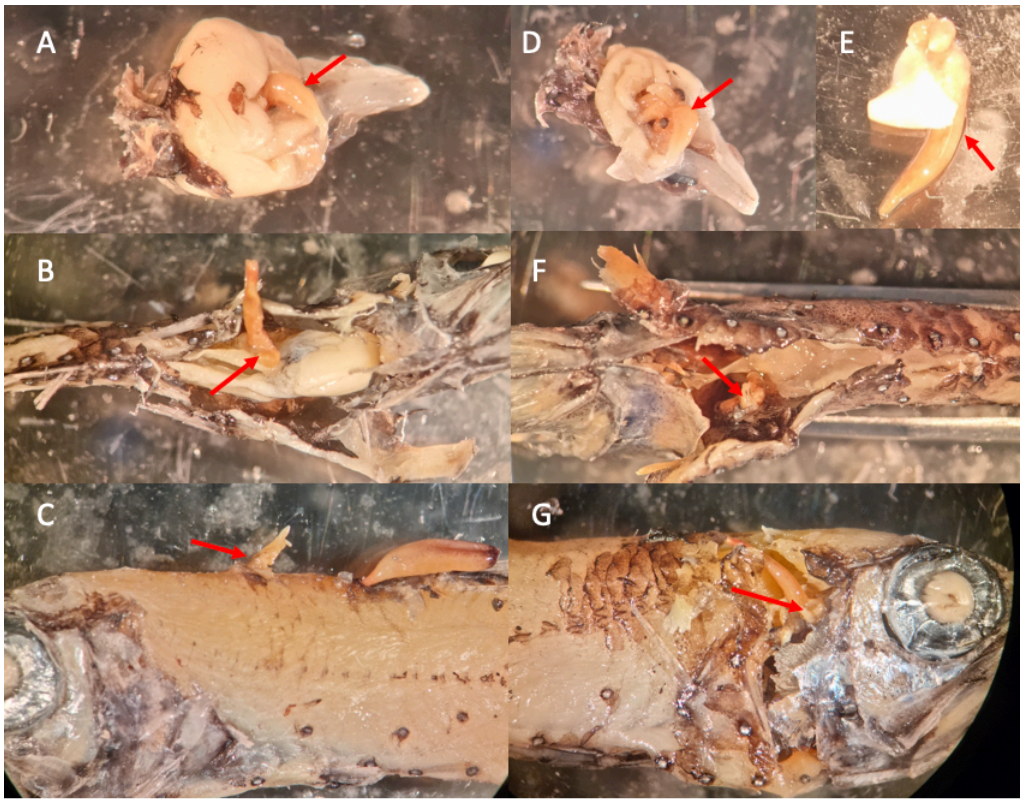

Figure 18:Overview of different Sarcotretes scopeli internal anchoring points in Benthosema glaciale. Red arrows indicates parasitic tissue. A) S. scopeli anchored in host stomach. B) S. scopeli anchored in host gonads. C) S. scopeli anchored in host flesh, penetrating externally on dorsal side of host. D) S. scopeli anchored in pyloric caeca. E) S. scopeli which was anchored in host liver. F) S. scopeli anchored in host flesh. G) S. scopeli anchored in host gills.

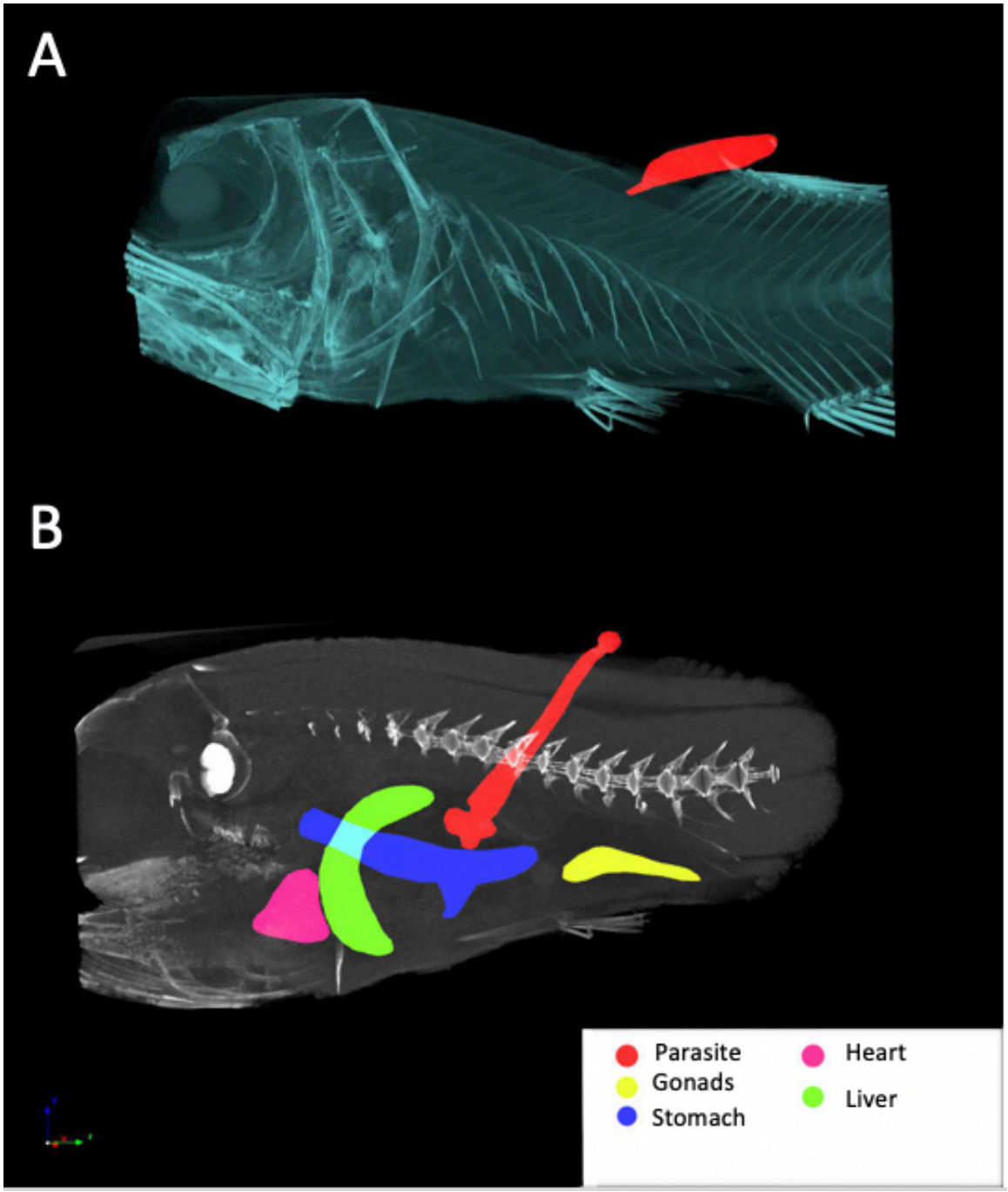

Figure 19: Micro-CT scan of an Sarcotretes scopeli infected Benthosema glaciale. A) External anchoring point of S. scopeli. B) Internal anchoring point of S. scopeli. Parasitic tissue is highlighted in red, host gonadic tissue in yellow, host stomach in blue, host heart in pink and host liver in green.

3.10 Parasitic volume in relation to host volume:

The total parasitic volume showed no significant correlation with the host volume (r = -0.002, N = 9, p = 1 Fig 20A). No significant correlation was found between the external parasitic volume and host volume (r = -0.087, N = 9, p = 0.82; Fig 20B) or between the internal parasitic volume and host volume (r = -0.18, N = 9, p = 0.64; Fig 20C). The internal parasitic volume had a strong positive correlation with the external parasitic volume (r = 0.73, N = 9, p = 0.026; Fig 20D, Tab 13), meaning that the internal part grows proportionally with the external part of the parasite. The parasitic tissue occupied < 1% of the host volume on average (Appendix B: Tab B9).

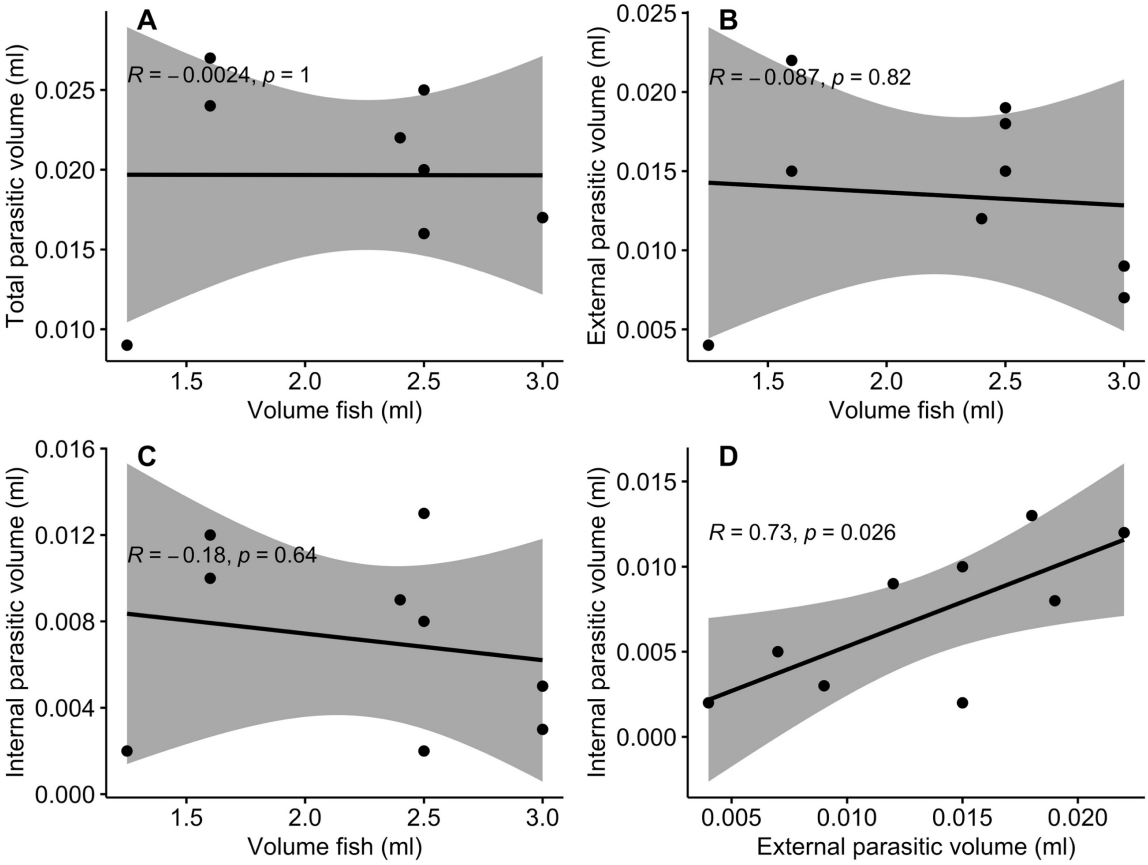

Figure 20: A) The total parasitic volume (ml) in relation to Benthosema glaciale volume (ml). B) The external parasitic volume (ml) in relation to B. glaciale volume (ml). C) Internal parasitic volume in relation to B. glaciale volume (ml). D) Internal parasitic volume (ml) in relation to external parasitic volume (ml).

Table 13: Overview of the proportions of the internal and external parts of Sarcotretes scopeli. Parasite I.D, is the unique identification given to each parasite and corresponding host. V_{int}/V_{tot} is the proportion of the internal parasitic volume in relation to the total volume of the parasite. V_{int}/V_{tot} mean ± s.d, is the mean value and standard deviation of the internal parasitic volume relative to the total parasitic volume. V_{ext}/V_{tot} is the proportion of the external parasitic volume in relation to the total volume of the parasite. V_{ext}/V_{tot} mean ± s.d, is the mean value and standard deviation of the external parasitic volume relative to the total parasitic volume. The volumetric measurements presented are not accurate values, thus the sum of the external and internal parts does not sum up to 100%

Parasite I.D	V_{int}/V_{tot}	V_{int}/V_{tot} Mean ± s.d	V_{ext}/V_{tot}	V_{ext}/V_{tot} Mean ± s.d
Mas149/5.01	29.4%		41.2%	
Mas149/5.04	22.2%		44.4%	
Mas149/5.06	41.7%		62.5%	
Mas149/5.07	17.6%		52.9%	
Mas149/5.08	52.0%	53.2 ± 20.8%	72.0%	66.4 ± 20.3%
Mas149/5.10	40.9%		54.5%	
Mas149/5.11	44.4%		81.5%	
Mas149/5.12	40.0%		95.0%	
Mas149/5.14	12.5%		93.8%	

4. Discussion:

Parasitic species are ubiquitous in the marine ecosystem and are known to cause adverse health effects on their hosts. Nevertheless, the pathology of parasite-host systems in the deep sea remains understudied. In order to bridge some of this knowledge gap, this thesis has investigated the parasite-host relationship between the mesopelagic fish species *B. glaciale* and the parasitic copepod *S. scopeli.* The main focus of this thesis has been on; the pathological effects on the host species, the impact of dissolved oxygen on parasitic prevalence, and the attachment site selectivity of the parasitic infection.

The present study shows that *S. scopeli* reduces the gonadal size of both sexes of *B. glaciale*. Infected males had an increased liver size, whereas no effect was observed for infected females. The infection resulted in poor body condition but remarkably did not compromise host growth. In addition, the data showed inconclusive results for the effect of infection on hosts cardiac size. Despite castrating the host, *S. scopeli* did not seem to follow the expected allometric growth exhibited by parasitic castrators. Furthermore, the parasitic prevalence is seemingly not affected by dissolved oxygen differences, however, Sørfjorden had a statistically lower prevalence than other investigated fjords. It was also found that *S.*

scopeli exhibits low internal anchoring selectivity and a high affinity for external dorsal attachment.

4.1 Parasitic castration:

In this study, the gonadal weight of both infected and uninfected male and female *B. glaciale* was investigated to assess the effect of *S. scopeli* on the reproductive output of its host. The data show that infected females had a remarkable reduction in ovary size compared to uninfected conspecifics. This reduction suggests that the parasitic infection compromises female reproduction. One way parasitic species can affect hosts reproduction is through castration, where the parasite reduce the hosts energy canalization to reproductive organs (Waiho et al., 2020). Castration is believed to only occur in parasite-host interactions where the host species allocates high amounts of energy to reproduction (Lafferty & Kuris, 2009). Inhibition of this energy allocation may allow the parasite to drain large amounts of host energy with negligible effects on the hosts viability, thus potentially increasing its own longevity (Lafferty & Kuris, 2009). Parasitic castration is best known from invertebrate hosts (Calado et al., 2008; Lafferty, 1993; Shields & Wood, 1993) but have been reported from both lantern sharks and a few small fish species (Fogelman et al., 2009; Moser & Taylor, 1978; Yano & Musick, 2000). For instance, the parasitic copepod *C. bellottii* infecting the Northern lampfish (*Stenobrachius leucopsarus*, Eigenmann & Eigenmann, 1890) in the mesopelagic of the Pacific ocean, and the parasitic isopod *Anilocra apogonae* (Bruce, 1987) infecting the five-lined cardinalfish (*Cheilodipterus quinquelineatus*, Cuvier, 1828) in Pacific reefs, has been shown to inhibit the maturation of host eggs (Fogelman et al., 2009; Moser & Taylor, 1978).

Infected males also showed a reduced gonadosomatic index compared to uninfected ones. Although, when differences in body weight of the fish were accounted for, Sørfjorden was the only area where a significant difference between infected and uninfected males could be detected. Nonetheless, infected males from the Fensfjorden and Osterfjorden also showed a reduction in testis weight despite not being significantly lower. This may be due to very small testis in both uninfected and infected males, which may make small differences in weight difficult to detect. It is therefore reasonable to assume that the reproductive output is also compromised for males. The reduction in the gonadosomatic index of the infected males is consistent with findings from other studies of parasitic castrators of fish which have

investigated the pathological effects on male and female hosts separately (Fogelman et al., 2009; Hecker & Karbe, 2005; Trubiroha et al., 2010).

Parasite-induced gonad reduction might be achieved through manipulation of the host energy allocation (manipulation hypothesis; Poulin et al., 1994) or as a by-product of the parasitic drain of the hosts general energy reserves (energy drain hypothesis; Lafferty & Kuris, 2009). In fact, both of these modes have been shown to occur in the parasite-host relationship of fish. For instance, *L. intestinalis* has been shown to cause endocrine disruption in common breams (*Abramis brama,* Linnaeus, 1758), causing negligible effects on the host liver mass (Hecker & Karbe, 2005). The cestode *S. solidus,* on the other hand, has been shown to cause gonadal reduction of the three-spined stickleback in the wild, coupled with severe reduction of the host liver (Arme & Owen, 1967; Heins & Baker, 2008). In contrast, in a laboratory experiment by Barber and Svensson (2003), where experimentally infected three-spined sticklebacks were fed 8% of their body weight each day, it was observed that the cestode infection was associated with increased host ovary weight, indicating that the parasite does not directly target host reproduction. In the data presented here, infected females generally had similar liver weights to uninfected females, suggesting that the infection did not compromise the energetic reserves in the liver. Given that the liver showed no sign of starvation, the parasitic interaction aligns more with the manipulation hypothesis. One factor that might explain this lack of effect is the production of the egg yolk precursor vitellogenin prior to spawning (Moussavi et al., 2009). Production of this precursor is an energetically costly process occurring in the liver and is regulated by sex steroids in the blood plasma (Schneider, 1996) and might thus be readily manipulated by parasitic species. *L. intestinalis* has, for instance, been shown to cause inhibition of the vitellogenin production of roach and common bream by interfering with the pituitary-gonadal-axis, resulting in inhibition of host egg maturation (Hecker & Karbe, 2005; Trubiroha et al., 2010). Considering this, it might be hypothesized that *S. scopeli* also disrupts the hormonal signaling for egg maturation in the female host.

Surprisingly, female hosts from Sørfjorden and male hosts in all fjords showed signs of liver enlargement resulting from the infection. Endocrine disruption of male fish exposed to estrogen compounds has been documented to be able to cause liver enlargement due to vitellogenin accumulation (Barse et al., 2006) due to the fact that male fish inherits the same vitellogenin receptors found in the female liver (Sumpter & Jobling, 1995). While it might be

speculated that the liver enlargement observed for male hosts is due to vitellogenin accumulation, observations from roach infected with *L. intestinalis* have shown that infection causes a reduction of vitellogenin also in males (Trubiroha et al., 2010). Although, since the egg yolk precursor is transported to the gonads through the vascular system (Schneider, 1996), it may be a possibility that *S. scopeli* feeds directly on vitellogenin by filtering it from the host's blood and would thus benefit from increasing the host's production of this protein. If so, infected females in Sørfjorden may overcompensate this production due to low body condition. While the liver enlargement of the host is likely to be of biological importance in the parasite-host relationship, the exact mechanism behind the liver enlargement cannot be explained from the current study and needs further investigation.

Despite the generally negligible effect of the infection on the female liver and the liver enlargement of the males, infected hosts were found to have lower condition than their uninfected conspecifics. Multiple factors might explain this reduction in body condition; One explanation could be that parasitic castrators might not exclusively drain energy from host reproduction but might also have some impact on the overall energy reserves (Ocampo et al., 2021). For *B. glaciale,* this energetic reserve is stored as wax-esters in the liver and adipose tissue and makes up a large part of the species' weight (Falk-Petersen et al., 1986). If so, one may speculate that the parasitic infection reduces the available energy for adipose tissue production. Another explanation could be that the presence of *S. scopeli* on a hosts surface could indirectly affect the swimming cost of *B. glaciale* due to a potential increase in hydrodynamic drag (Östlund-Nilsson et al., 2005). For example, data from a laboratory experiment by Östlund-Nilsson et al. (2005) showed that five-lined cardinalfish infected by the ectoparasitic isopod *A. apogonae* expended more energy on locomotion when infected, resulting in decreasing body condition under low food availability. Since the external part of *S. scopeli* is relatively large and protrudes out of the body surface of *B. glaciale,* the parasite likely causes some disruption of the streamlining when the host swims. Thus, it is likely that the host will experience increased drag while swimming through the water. In contrast, the reduced body condition may not result from the infection but rather be the cause of infection. The cestode *Proteocephalus tetrastomus* (Rudolphi, 1810) is, for example, more prevalent in rainbow smelts (*Osmerus mordax*, Mitchill, 1814) that exhibit reduced early life growth (Blanchet et al., 2009). While one may speculate that this is also the case for *B. glaciale,* the liver and gonad indices indicate that *S. scopeli* mainly targets the reproductive energy of *B.*

glaciale, which is also affected by the body condition of the fish (McBride et al., 2015). Atlantic cod (*Gadus morhua,* Linnaeus, 1758), for instance, has been found to allocate less energy to reproduction when the body condition is poor (Lambert & Dutil, 2000). This may also be applicable for *B. glaciale,* as both species are batch spawners. If so, it is safe to assume that infection of hosts in poor condition would be disadvantageous for parasitic survival and would likely be selected against. Therefore, it is more likely that the infection itself causes the observed reduction in condition factor of the infected fish.

Sørfjorden deviated from the other fjords, as both infected and uninfected *B. glaciale* from this fjord were found to be in the poorest condition. One potential explanation for this may be that there is less available prey in this system as it is located furthest from the Norwegian coast. This is supported by a study from Salvanes et al. (1995), who showed through ecological modeling that the productivity in the fjords declined with distance from the coastline. They also found that the copepod *Calanus finmarchicus* (Gunnerus, 1770), an important prey species for *B. glaciale,* also became scarcer further from the coast.

Due to the decreased body weight of the infected individuals, it was expected that infection would cause a reduction in host growth. Surprisingly, both the mean age and otolith parameters were similar between infected and uninfected fish, indicating that the infection does not compromise the otolith growth of the host. These findings are in contrast to Gjøsæter (1971) findings, who reported an average 2.8% length reduction for age groups 1 to 4. His and mine results might not be strictly comparable since we used somewhat different measures. I used length and sex-matched *B. glaciale* to investigate the growth, while Gjøsæter (1971) combined data from both sexes and reported differences in the mean size of each age class. Considering that otoliths grow independently of the somatic growth (Folkvord et al., 2004), one would expect to detect larger otolith sizes of infected fish compared to uninfected fish at the same size, assuming that somatic growth was compromised. Nevertheless, a 2.8% size reduction might not be severe enough to cause detectable differences in otolith size. Though, Gjøsæter (1971) also reported a decline in the infection rate of older individuals, suggesting that it might be due to mortality increasing with age. The data presented here show that the length distributions of infected and uninfected fish were similar in all four investigated fjords, and this suggests that infection is not selective on host size. Despite the parasite not being selective on the host size, it is a possibility that increased mortality of the infected individuals could be a factor that explains the similarities in growth between the

infected and uninfected hosts. The condition factor and the lack of effect on growth may indicate that *S. scopeli* drains large amounts of the overall host energy. Perhaps the parasite has a fast-growing adult stage with a short lifespan, where it drains large amounts of the overall nutrient reserves of the host over a relative short time period. If so, it is likely that the parasite induces mortality of the host before detectable effects on the hosts somatic growth can manifest.

4.2 Effect of infection on host cardiac function:

Parasitic species which are in part or totally embedded in the host interior can adversely affect the hosts cardiovascular functions (Behrens et al., 2014; Coleman, 1993). Attachment to the heart or veins of the host can, for instance, reduce the blood flow past the attachment location (Smith et al., 2007). Blood-feeding species might also reduce the red blood cell count of the host, resulting in anemia (Horton & Okamura, 2003). Pathological interference of the hosts vascular system can in some cases result in a heart enlargement to compensate for the increased strain on the cardiac musculature (Powell & Yousaf, 2017). For instance, the parasitic copepod *Lernaeocera branchialis* (Linnaeus, 1767) is known to attach its feeding apparatus to both the gills and heart of the Atlantic cod; and is believed to cause host heart enlargement through the elevation of blood pressure (Behrens et al., 2014; Smith et al., 2007).

In this study, the heart weight of both infected and uninfected *B. glaciale* was measured to investigate the effect of *S. scopeli* infection on the cardiac function of the host. From the data presented here, it was found that infected fish had a higher heartsomatic index (HASI) compared to uninfected conspecifics. While this may suggest that infection increases the workload of the hosts' cardiac function, the model on the heart weight as a function of fish weight did not detect a difference in heart weight between infected and uninfected fish. These contrasting results may be due to differences in the sample size of the two models. The generalized linear model used the whole dataset to estimate the HASI of an average infected and uninfected fish over every length group. In contrast, the linear regression for heart weight as a function of fish weight for the two groups was performed for each fjord separately. Due to this difference, the linear regression may not have the statistical power needed to detect a difference in heart weight between the infected and uninfected fish. Therefore, it is safe to assume that larger sample sizes from each fjord are needed to reach a firm conclusion on the effect of infection on the hosts' cardiac function.

4.3 Volume of Sarcotretes scopeli:

Parasitic species are often small compared to their host and usually make up for less than 1% of the host volume (Lafferty & Kuris, 2002). Species that castrates their host, on the other hand, tend to deviate from the usual pattern observed from non-castrators, as they usually have a volume close to the gonadic tissue of uninfected hosts but might range from 3% up to 50 % relative to the host volume (Lafferty & Kuris, 2002, 2009). The parasitic isopod *A. apogonae* infecting the five-lined cardinalfish has, for example, been reported to reach a size representing 3.8% of the host volume (Fogelman et al., 2009). In the current study, *S. scopeli* was found to have a mean total volume of 0.87 ± 0.37% relative to the host volume, while the largest individual had a relative volume of 1.69%. This result indicates that *S. scopeli* does not reach the relative size expected from parasitic castrators. One may speculate that *S. scopeli* invests more energy into reproduction rather than growth, which could explain why the parasite does not exhibit the large size expected for parasitic castrators.

In addition to having a large volume relative to the host, parasitic castrators are suggested to grow allometrically relative to the host size (Kuris & Lafferty, 2000). This is since the reproductive effort of fish increases with body size (Roff, 1983); thus, it would be expected that parasitic castrators should also increase with host size (Hechinger et al., 2008). However, the data presented here showed no correlation between the parasite volume and the host volume, for neither the internal, external, or total volume of the parasite. It should be noted that the sample size in this study was small (n = 9) and may thus not have the statistical power to detect potential correlations. This small sample size and the roughness of the volume measurements make it difficult to provide a firm conclusion from this study. Further investigations on these aspects would require larger sample sizes and more accurate volumetric measurements. One method which may be useful and gives more accurate measurements is Micro-CT. Despite being a labor demanding method, it can provide good resolution of both the host and parasitic volume.

4.4 Effect of oxygen on parasitic prevalence:

In the present study, the prevalence of *S. scopeli* on *B. glaciale* from four west Norwegian fjord systems, differing in dissolved oxygen content, was examined to investigate if decreasing oxygen affects *S. scopeli* infection. Due to earlier preliminary observations of infections of fish from Masfjorden and Fensfjorden, it was hypothesized that decreased oxygen could be a potential explanation for an increase in infection cases. Surprisingly, the data presented here show that oxygen did not seem to affect the prevalence of *S. scopeli* in the four fjord systems investigated. This result differs from at least two studies of other parasitic copepods, which reported decreased prevalence at low oxygen concentrations (Morales-Serna et al., 2011; Raymond et al., 2006). However, both of the aforementioned studies regard shallow water fish hosts, which usually experience well-oxygenated environments. The mesopelagic zone of shallow silled west Norwegian fjords, on the other hand, has periodic low oxygen events due to the cyclic renewal of the basin water (Aksnes et al., 2019). Repeated exposure could have caused *B. glaciale* to become acclimatized to reduced oxygen conditions (Gilmore et al., 2019), thus reducing the adverse effects on their physiology (Guillen et al., 2019). If so, *B. glaciale* might not experience a higher susceptibility to parasitic infections during periods of low oxygen. By the fact that *S. scopeli* is partly exposed to the exterior environment of the host, it is safe to assume that changes in the environment would also affect this species. While parasites are usually more sensitive to changes in the water chemistry than their hosts (Gérard et al., 2003; Majumder et al., 2015), this does not seem to be the case for *S. scopeli* regarding dissolved oxygen. One may speculate that the parasite may also have adapted to the reduced oxygen environment, as was suggested for the host.

An alternative but not mutually exclusive explanation might be given by the vertical migratory behavior of *B. glaciale*. Fish residing in low oxygen environments might experience reduced metabolic function during the exposure time (Van Ginneken et al., 2001; Van Waversveld et al., 1989). The bearded goby (*Sufflogobius bibarbatus*, Von Bonde, 1923) can, for example, survive in hypoxic environments by decreasing its metabolic function, resulting in the accumulation of lactic acid (Salvanes et al., 2011; Utne-Palm et al., 2010). In order to rid itself of the metabolic waste, this species undergoes diel vertical migration to normoxic layers during the night to breathe (Utne-Palm et al., 2010). Since *B. glaciale* have been shown to perform some migration throughout the diel cycle (Dypvik et al., 2012; Kaartvedt et al., 2009), it might be speculated that the species does not reside in the low oxygen layers of the water

column for prolonged periods of time, but rather migrates to the normoxic layers frequently to breathe. If so, it could be that *S. scopeli* is also able to cope with restricted oxygen for short periods but is not able to survive chronic exposure. In a laboratory experiment by Krishnaswamy (1960) for instance, it was shown that the parasitic copepod *Caligus diaphanous* (Nordmann, 1832) could survive up to 14 hours of anoxic water exposure with no adverse effects after a half-hour recuperation period in normoxic water. Perhaps, *S. scopeli* exhibits a similar behavior of metabolic reduction during low oxygen exposure as was suggested for the host, where it needs to catch up on metabolic rent during the time the host resides in the oxygenated layers.

Despite the observation that the prevalence of *S. scopeli* did not differ with decreasing dissolved oxygen, it was found to be relatively high in three of the fjord systems (Masfjorden, Fensfjorden, and Osterfjorden) compared to the 1.8% recorded from the North Atlantic by Jungersen (1911). The findings from these three fjords are however in correspondence with records from other west Norwegian fjords (3.6%) made by Gjøsæter (1971). Sørfjorden, on the other hand, had a prevalence (1.76%) resembling that of the North Atlantic. The lower prevalence in the latter fjord might be explained by both biological and environmental differences compared to the other fjords. As mentioned earlier, uninfected hosts from Sørfjorden are in a poorer condition than the other fjords. Perhaps, there are less suitable hosts for parasitic survival due to this fact. Sørfjorden is also less saline in the upper part of the water column compared to the other fjords. From other parasitic copepods, reduced salinity has been shown to cause decreased infection and hatching success (Brazenor & Hutson, 2013; Bricknell et al., 2006), thus decreasing the parasitic prevalence. Although, due to likely under sampling of juvenile stages of *B. glaciale*, and considering that juvenile stages of *S. scopeli* have a translucent coloration making them hard to spot (Jungersen, 1911), it is safe to assume that the prevalence is in reality higher than what has been recorded in this study. Nevertheless, the sampling methods were standardized between sampling areas and should therefore not severely bias the results. In addition, it should be kept in mind that the current study was a cross-sectional study and that environmental factors in each fjord were based on one ctd-station each. This timeframe might not be sufficiently long to detect variations in parasitic prevalence due to oxygen fluctuations.

4.5 Parasitic site selection:

In the present study *S. scopeli* showed low site specificity in the internal anchoring point of the feeding apparatus, where individuals had a random distribution both within and outside of the host visceral cavity. This result corresponds to the findings of the original description of *S. scopeli* by Jungersen (1911). From earlier studies, it has been shown that blood feeding might be a common way of nutritional acquisition for species in the family Pennelidea (Lovy et al., 2020; Poltev, 2010). Additionally, some pennellid species have been found to attach their feeding apparatus to major blood-filled organs (Moser & Taylor, 1978) and blood veins (Aneesh et al., 2021). Due to the ethanol preservation used in this study, it could not be determined if the feeding apparatus of *S. scopeli* was attached to the veins of the host. Although, it is not unlikely that the species feeds on host blood, and thus it might be hypothesized that the feeding apparatus is attached to major blood veins; which could explain the low attachment site specificity observed in this study. Interestingly, parts of the holdfast of one *S. scopeli* observed in this study, penetrated the host exterior on the dorsal side; where the parasite had managed to undergo metamorphosis. It should be noted that the internal part of the holdfast was close to the location of the caudal vein, which could explain how the specimen might have survived in this location.

Furthermore, one of the *S. scopeli* observed in this study was anchored near to the heart of the host. Despite this, no evidence was found to support the hypothesis that *S. scopeli* have a high affinity for anchoring in the heart of the host and thus it is rejected. One potential explanation for the observations made by Salvanes might be that she was investigating *C. bellottii,* a closely related species to *S. scopeli,* which is known to anchor in the bulbous arteriosus of both the Northern lampfish and *B. glaciale* (Hogans, 2017; Moser & Taylor, 1978). *C. bellottii* shares an almost identical morphology to *S. scopeli*, except for processes protruding from the hold fast of the prior species (Hogans, 2017), and could thus easily be mistaken for *S. scopeli*.

In contrast to the internal anchoring point, *S. scopeli* showed a high site selectivity of the external anchoring point with an affinity for the dorsal side (65%) of the host, which is in alignment with the previous documentation of both Jungersen (1911) and Gjøsæter (1971). The high site selectivity observed in this and previous studies might be explained by multiple factors; Perhaps the innate immune system is less efficient near the fins of *B. glaciale* and thus a higher number of *S. scopeli* is successfully retained at these locations. This has been shown

to affect the attachment success of another parasitic copepod; *Lepeophtheirus salmonis* (Krøyer, 1837), where most parasites were able to retain attachment at the dorsal side of the host compared to other attachment locations, mainly the gills (Johnson, 1992). While this may be a contributing factor, it would not by itself explain why fewer infections were observed near the other fins compared to the dorsal one. Perhaps the dorsal fin provides a more optimal attachment substratum during the initial attachment (Loot et al., 2004). Since *S. scopeli* have specialized cheliform antenna likely used for attachment to the host during the pre-metamorphosis stages (Jungersen, 1911), it is not unlikely that fins act as important attachment substratum, such as for other parasitic copepods (Loot et al., 2004; Tucker et al., 2002). If so, it might be that the paired fins are more susceptible to erosion caused by parasitic presence, resulting in fewer individuals to be successfully retained, thus making them unsuitable attachment points for the free-living infective stages of the parasite. Such a mechanism could explain why only 25% of the infections were observed ventrally and 10% in other places on the host body. It could also be argued that the parasite may be provided with a higher fitness benefit depending on its anchoring position on the host (Timi et al., 2010). For example, under the assumption that *S. scopeli* attaches the feeding apparatus to host veins, it is a possibility that dorsal attachment gives a higher success rate of finding a suitable internal anchoring location, as most major veins of fish are located dorsally. Rohde (1979) proposed a hypothesis that high site selectivity might also arise due to increased chances of mate encounters at specific locations of the host. Perhaps dorsal attachment gives a higher encounter rate with males of the species. Considering that the life cycle *S. scopeli* consists of only one host and the infective stages are all females (Jungersen, 1911), this might be a plausible explanation. Despite this, the mechanisms behind both internal and external site selectivity remain poorly known for both *S. scopeli* and parasitic copepods in general. Further studies can unravel more of the host-parasite system and how their relationship affect the population dynamics of both the parasite and the host.

5. Future aspects:

Despite being one of the most common fish globally, little is known about how *Benthosema glaicale* interacts with parasitic species such as *Sarcotretes scopeli*. In fact, our knowledge is limited regarding parasite-host systems of deep-sea teleost's in general, as it is difficult to obtain sufficient samples from the deep sea. However, since west Norwegian fjords house extensive deep-sea communities, they can provide easily accessible natural infrastructures for such studies and grant further knowledge about the deep-sea ecosystem as a whole.

As the first comprehensive study to investigate the *S. scopeli – B. glaciale* interaction in 50 years, this dataset includes observation from one winter season in four fjords systems. The data demonstrate clearly that *S. scopeli* acts as a parasitic castrator on *B. glaciale,* and as the host liver does not decrease following infection, it indicates that the parasite somehow inhibits the energy transportation from the liver to the gonads. While parasitic castration is known from other fish hosts (Fogelman et al., 2009; Moser & Taylor, 1978), the underlying mechanisms of this pathological effect remain poorly understood.

In order to gain more knowledge on the interaction between *S. scopeli* and *B. glaciale*, further studies should be done on the mechanism behind the castration. This could, for example, be done by measuring hormone expression linked to reproduction from the blood and liver of *B. glaciale*, as has been done for some fish hosts of *L. intestinalis* (Hecker & Karbe, 2005; Trubiroha et al., 2010).

As shown by the data presented here, *S. scopeli* attaches its feeding apparatus randomly in the host internal. Despite this, nothing is known about how this species acquires nutrition from its host. Histological studies on the parasite-host assemblage at the location of the feeding apparatus could be one possible way to gain a better understanding of whether host veins are essential for feeding or not.

Almost nothing is also known about the life history of *S. scopeli*, as Jungersen (1911) only described a few life stages of the species. To describe the species early life stages, one could collect eggs of the species and rear them in the laboratory. Since *S. scopeli* produces egg strings from its external part, these eggs could easily be obtained by trawling. If the parasite survives in a laboratory setting, it is also a possibility to do experiments on dead or living *B. glaciale.* This, in order gain an understanding on which life stage the parasite infects the host, and how infection occurs.

Additionally, in a time of ocean warming and loss of oxygen in the seawater, the habitats in the marine ecosystem will change. No one knows how the steady decrease of dissolved oxygen in the ocean will impact parasite-host interactions in this system. While the Investigated fjords presented in this study differed slightly in dissolved oxygen in the basin water, the oxygen categories used in this study may be too rough to detect an effect on *S. scopeli* prevalence. Therefore, the *HypOnfjordfish* group has started a time series analysis, where they will register parasitic infection from random samples collected on future cruises in west Norwegian fjords. Such a time series will give more accurate insight into how environmental fluctuations influence the prevalence of *S. scopeli*.

6. Conclusion:

In this study, the relationship between the parasitic copepod *Sarcotretes scopeli* and the globally dominating *Benthosema glaciale* was investigated by comparing data of one winter season from four west Norwegian fjords. The prevalence of *S. scopeli* most likely fluctuates with seasons. Thus, this study only provides a snapshot of the parasite-host interaction, however, a thorough and well documented one. The data presented here show that difference in dissolved oxygen in the basin water did not seem to affect *S. scopeli* prevalence. Despite this, the parasite was significantly less prevalent in one of the four fjords, suggesting that other factors might regulate the population. Infection was most often a dorsal attachment on the host exterior, while internal attachment was not found to be associated with a specific location. Infected female and male *B. glaciale* showed evidence of castration, as they exhibited a significant reduction of gonad size. This reduction was especially apparent for females as ovaries were small regardless of fish size. Infection was found to be associated with liver enlargement in males but did not affect the liver mass of females. This suggests that *S. scopeli* inhibits host energy allocation from the liver to reproduction. Contrastingly, *S. scopeli* was found to reduce host body condition, indicating that parts of the overall energy reserve were compromised. Despite this, host growth was not affected, as otolith sizes were found to be similar between infected and uninfected fish. The overall data provides evidence that *S. scopeli* castrates its host, however, no categorical conclusion can be drawn in favor of either the manipulation hypothesis or the energy drain hypothesis. The literature shows that the castratory effect of parasites can alter the host population dynamics. Since *B. glaciale* is a

key species in the fjord ecosystem, further studies on the parasite-host system could increase our understanding of the role of parasites at an ecosystem level.

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Appendix A:

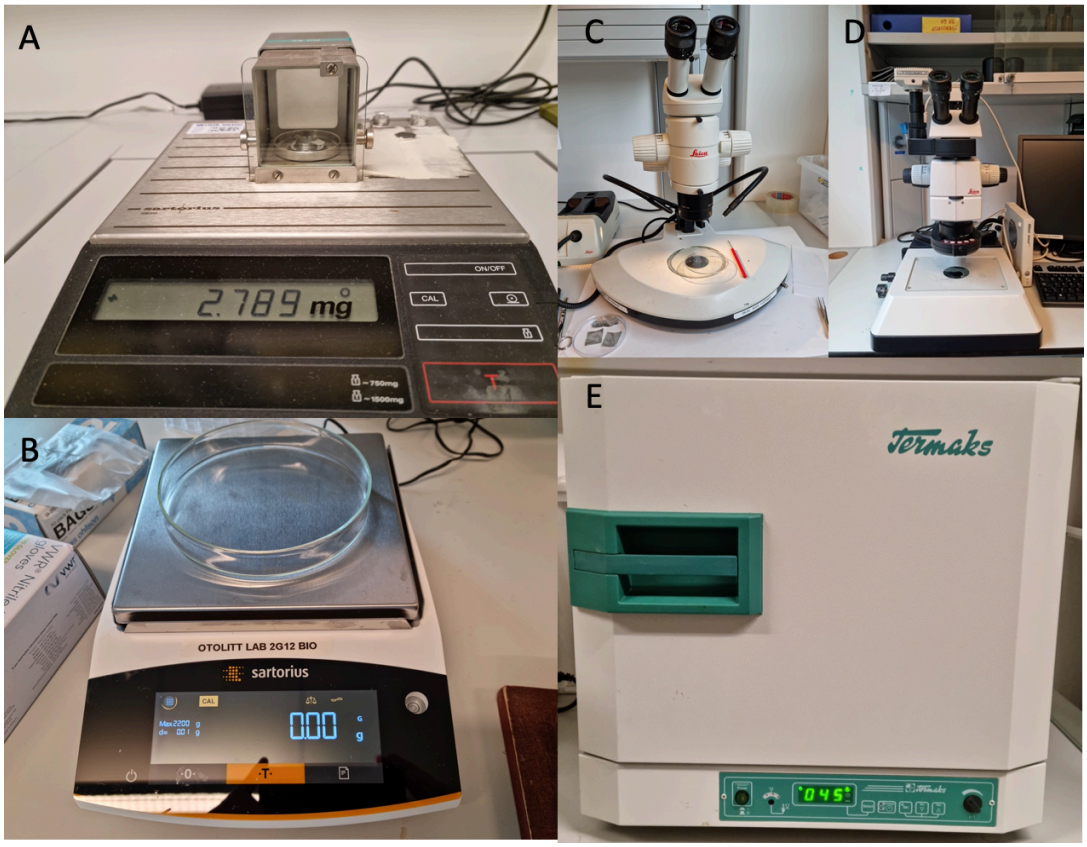

Figure A1: Overview figure of scales and dissection microscopes used for biological measurements. A) Satorius micro M3P. B) Satorius Entris II. C) Leica MZ95 dissection microscope. D) Leica M125 dissection microscope. E) Fermaks drying oven.

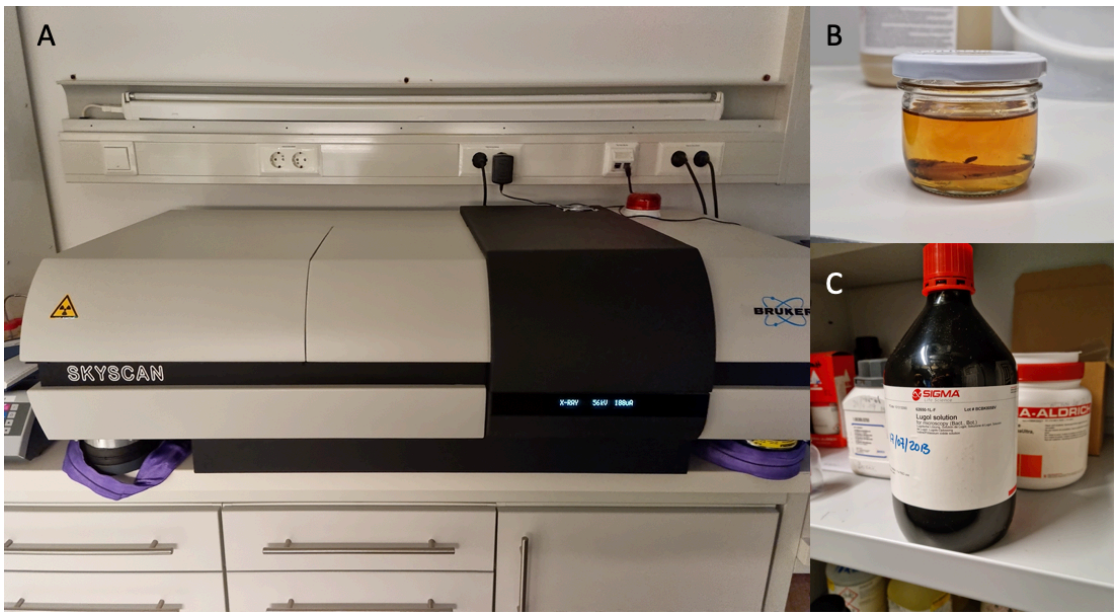

Figure A2: Overview figure of equipment and methodology used for micro-CT experiment: A) Skyscan 1172. B) Benthosema glaciale submerged in a 10% Lugol solution. C) The Lugol solution used to make the 10% dilution to contrast fish before micro-CT scanning.

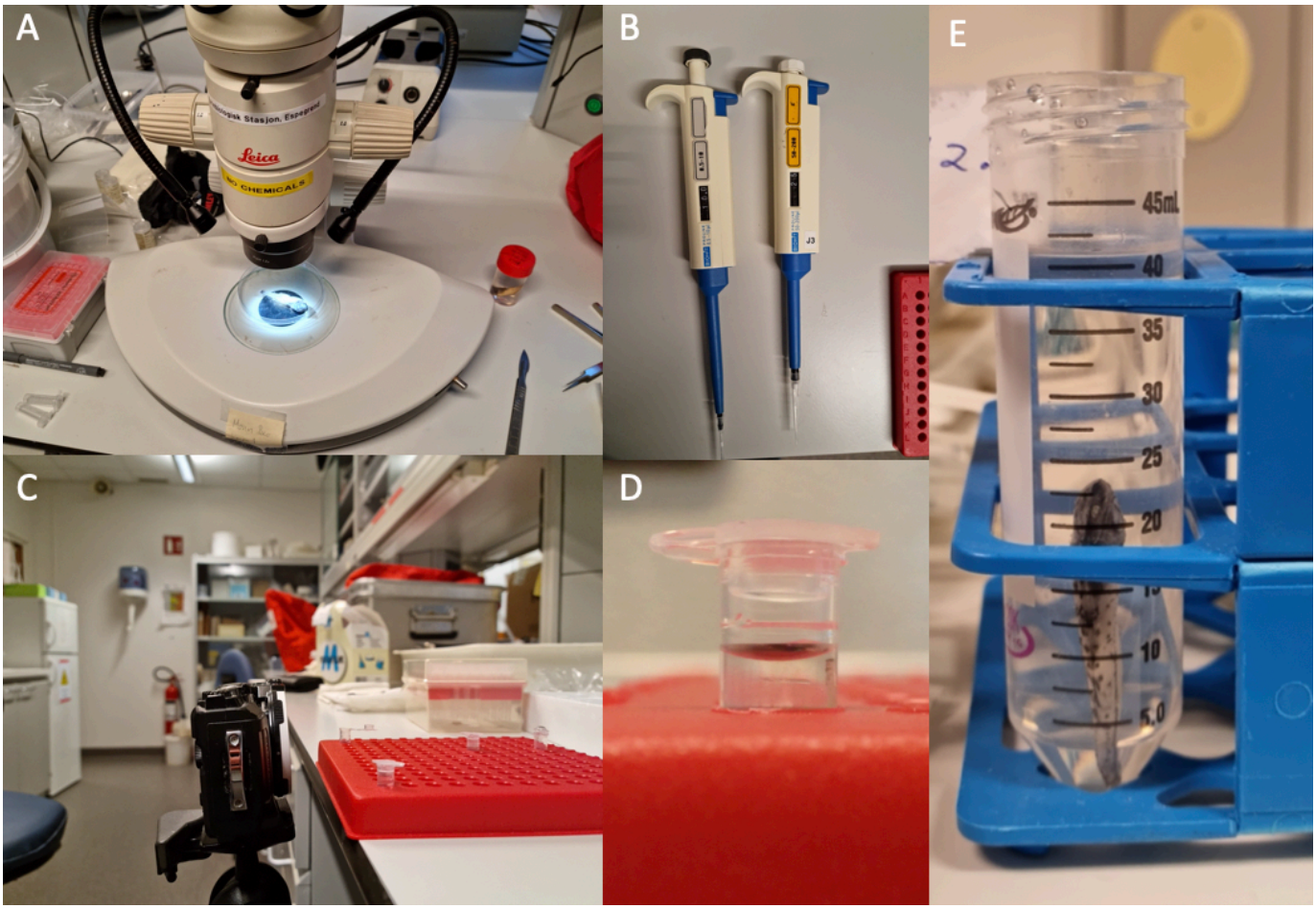

Figure A3: Overview picture of equipment and methodology used for parasitic volume measurements: A) Leica MZ95 dissection microscope. B) two mechanical pipettes; 0.5-10 µL on the left and 50-200 µL on the right. C) the setup of the Olympus TG-6 and the measuring tubes for parasitic volume, used to standardized pictures. D) DNA tube used for volume measurement, with initial water level marked off with a scalpel. E) measuring container used to record the volume of Benthosema glaciale.

Appendix B:

Table B1: Overview of external and internal Sarcotretes scopeli anchoring locations. Fish ID is the unique I.D given to each host. Parasite (n) shows the number of parasites on each host (1 for one and 2 for two parasites). External anchoring point gives the external location of S. scopeli. Side external shows which side the external anchoring point was located. Internal anchoring point shows the exact location of the holdfast. NA values indicated values that unfortunatly were not recored.

Fish ID	Parasite (n)	External anchoring point	Side external	Internal anchoring point
Ost.16.02.21.147.1.01	1	ventral	NA	NA
Ost.16.02.21.147.1.02	1	ventral	NA	NA
Ost.16.02.21.147.1.03	1	dorsal	NA	NA
Ost.16.02.21.147.1.04	1	dorsal	NA	NA
Ost.16.02.21.147.1.05	1	dorsal	NA	NA
Ost.16.02.21.147.1.06	1	dorsal	NA	NA
Ost.16.02.21.147.1.07	1	dorsal	NA	NA
Ost.16.02.21.147.1.08	1	dorsal	NA	NA
Ost.16.02.21.147.1.09	1	dorsal	right	NA
Ost.16.02.21.147.1.10	1	dorsal	left	NA
Ost.16.02.21.147.1.11	1	dorsal	NA	NA
Mas.18.02.21.148.2.01	1	dorsal-head	NA	kidney
Mas.18.02.21.148.2.02	1	dorsal	left	flesh-close to gills
Mas.18.02.21.149.5.01	1	dorsal	NA	flesh
Mas.18.02.21.149.5.02	1	ventral	left	pyloric_caeca
Mas.18.02.21.149.5.03	1	dorsal	NA	swimbladder
Mas.18.02.21.149.5.04	1	dorsal	NA	flesh
Mas.19.02.21.150.8.01	1	lateral	right	pyloric_caeca
Mas.19.02.21.150.8.02	1	dorsal	NA	NA
Mas.19.02.21.150.9.01	2	dorsal	right	stomach
Mas.19.02.21.150.9.01	2	dorsal	left	stomach
Mas.19.02.21.150.9.02	1	dorsal	NA	gonads
Mas.19.02.21.150.9.03	1	ventral	right	NA
Mas.19.02.21.150.9.04	1	dorsal	right	stomach
Mas.19.02.21.150.9.05	1	dorsal	right	gonads
Mas.19.02.21.150.9.06	1	dorsal	NA	NA
Mas.21.02.21.156.23.01	1	dorsal-head	NA	gills
Mas.21.02.21.156.23.02	1	dorsal	NA	flesh
Mas.21.02.21.156.23.03	1	dorsal	right	pyloric_caeca
Mas.21.02.21.156.23.04	1	dorsal	left	flesh
Mas.21.02.21.157.24.01	1	lateral	right	gonads
Mas.21.02.21.157.24.02	1	dorsal	right	liver
Mas.21.02.21.157.24.03	1	dorsal	NA	kidney
Mas.21.02.21.157.24.04	1	dorsal	right	liver
Mas.21.02.21.157.24.05	1	dorsal	NA	flesh
Mas.21.02.21.157.24.06	1	dorsal	NA	flesh
Mas.21.02.21.157.24.07	1	ventral	NA	NA
Mas.21.02.21.158.25.01	1	ventral	left	NA
Mas.21.02.21.158.25.02	1	dorsal-head	left	flesh
Mas.21.02.21.158.25.03	1	dorsal	NA	stomach
Mas.21.02.21.158.25.04	1	dorsal	right	liver
Mas.21.02.21.158.25.05	1	ventral	right	NA
Mas.21.02.21.158.25.06	1	dorsal	NA	flesh

Table continous

Fish ID	Parasite (n)	External anchoring point	Side external	Internal anchoring point
Fen.19.02.21.151.11.01	1	dorsal	NA	swimbladder
Fen.19.02.21.151.11.02	1	ventral-gillcover	NA	near eye
Fen.19.02.21.151.11.03	1	dorsal-gillcover	left	in gills
Fen.19.02.21.151.11.04	1	dorsal	NA	near heart
Fen.19.02.21.153.17.01	1	lateral	right	swimbladder
Fen.19.02.21.153.17.02	1	dorsal	left	swimbladder
Fen.19.02.21.153.17.03	1	dorsal	NA	kidney
Fen.19.02.21.153.17.04	1	dorsal	NA	swimbladder
Fen.19.02.21.153.17.05	1	dorsal	right	flesh
Fen.19.02.21.153.17.06	2	dorsal	NA	stomach
Fen.19.02.21.153.17.06	2	dorsal	left	gills
Fen.20.02.21.154.21.01	1	dorsal	left	flesh
Fen.20.02.21.154.21.02	1	dorsal	NA	flesh
Fen.20.02.21.154.21.03	1	dorsal	right	stomach
Fen.20.02.21.154.21.04	1	dorsal	NA	NA
Fen.20.02.21.154.21.08	1	dorsal	NA	NA
Fen.20.02.21.155.22.01	1	ventral	left	pyloric_caeca
Fen.20.02.21.155.22.02	1	dorsal	left	NA
Fen.20.02.21.155.22.03	1	ventral	right	gonads
Fen.20.02.21.155.22.04	1	dorsal	right	NA
Fen.20.02.21.155.22.05	1	ventral	right	NA
Fen.20.02.21.155.22.06	1	ventral	left	liver
Fen.20.02.21.155.22.07	1	dorsal	left	flesh
Fen.20.02.21.155.22.08	1	ventral	left	liver
Sør.22.02.21.160.29.01	1	NA	NA	NA
Sør.22.02.21.160.29.02	1	ventral	NA	NA
Sør.22.02.21.160.29.03	1	dorsal	NA	NA
Sør.22.02.21.160.29.04	1	ventral	NA	NA
Sør.22.02.21.160.29.05	1	NA	NA	NA
Sør.22.02.21.160.29.11	1	dorsal	NA	NA
Sør.22.02.21.160.29.13	1	ventral	NA	NA
Sør.22.02.21.160.29.15	1	ventral	NA	NA
Sør.22.02.21.161.32.01	1	ventral	NA	NA
Sør.22.02.21.161.32.02	1	ventral	NA	NA
Sør.22.02.21.161.32.03	1	dorsal	right	NA
Sør.22.02.21.161.32.04	1	dorsal	left	NA
Sør.22.02.21.161.32.05	1	ventral	left	NA
Sør.22.02.21.161.32.06	1	ventral	left	NA
Sør.22.02.21.161.32.10	1	ventral	left	NA
Sør.22.02.21.161.32.13	1	dorsal	NA	NA
Sør.22.02.21.161.32.37	1	dorsal	NA	NA
Sør.22.02.21.161.32.68	1	NA	NA	NA
Sør.23.02.21.162.35.01	1	ventral	right	gonads
Sør.23.02.21.162.35.02	1	dorsal	NA	stomach
Sør.23.02.21.162.35.03	1	ventral	NA	gonads
Sør.23.02.21.162.35.04	1	dorsal	NA	NA
Sør.23.02.21.162.35.05	1	dorsal	NA	pyloric_caeca
Sør.23.02.21.162.35.06	1	dorsal	NA	gills
Sør.23.02.21.163.36.01	1	ventral-gillcover	left	pyloric_caeca
Sør.23.02.21.163.36.02	1	dorsal	right	stomach
Sør.23.02.21.163.36.03	1	dorsal	NA	NA

Table B2: Emmeans post-hoc test for pairwise comparison of the gonadosomatic index (GSI) of male Benthosema glaciale between fjords. A Tuckey adjustment was used.

contrast	odds.ratio	SE	z.ratio	*P*
Pairwise comparison of GSI of males between fjords				
Fensfjorden / Masfjorden	0.92	0.08	-0.94	0.78
Fensfjorden / Osterfjorden	0.99	0.14	-0.1	1
Fensfjorden/ Sørfjorden	0.70	0.06	-4.34	< 0.001
Masfjorden / Osterfjorden	1.07	0.15	0.48	0.96
Masfjorden / Sørfjorden	0.76	0.05	-4.14	< 0.001
Osterfjorden / Sørfjorden	0.71	0.10	-2.51	0.06

Table B3: Emmeans post-hoc test for pairwise comparison of the hepatosomatic index (HSI) of male Benthosema glaciale for the interaction effect of Infected x Sex. Infection was coded as 0 for uninfected and 1 for infected and Sex was coded as F for female and M for male. A tuckey adjustment was used. Emmeans post-hoc test for pairwise comparison for the interaction effect of Infected x fjord. Infection was coded as 0 for uninfected and 1 for infected and fjord was coded as Masfjorden, Fensfjorden, Osterfjorden and Sørfjorden. A tuckey adjustment was used.

contrast	odds.ratio	SE	z.ratio	*P*
Interaction effect of Infected x Sex on hepatosomatic index				
0 F / 1 F	0.97	0.08	-0.32	0.99
0 F / 0 M	2.39	0.10	21.06	<< 0.001
1 F / 1 M	1.04	0.13	0.34	0.99
0 M / 1 M	0.42	0.04	-8.12	<< 0.001
Interaction effect of Infected x Fjord on the hepatosomatic index				
0 Fensfjorden / 1 Fensfjorden	0.74	0.10	-2.25	0.32
0 Fensfjorden / 0 Masfjorden	1.06	0.06	1.16	0.94
0 Fensfjorden / 0 Osterfjorden	0.87	0.07	-1.78	0.64
0 Fensfjorden / 0 Sørfjorden	1.04	0.06	0.73	1
1 Fensfjorden / 1 Masfjorden	1.10	0.19	0.59	1
1 Fensfjorden / 1 Osterfjorden	0.81	0.16	-1.03	0.97
1 Fensfjorden / 1 Sørfjorden	0.61	0.10	-3.11	0.04
0 Masfjorden/ 1 Masfjorden	0.77	0.09	-2.21	0.34
0 Masfjorden / 0 Osterfjorden	0.82	0.05	-2.99	0.06
0 Masfjorden / 0 Sørfjorden	0.98	0.05	-0.35	1
1 Masfjorden / 1 Osterfjorden	0.73	0.15	-1.56	0.77
1 Masfjorden / 1 Sørfjorden	0.56	0.08	-3.94	0.002
0 Osterfjorden / 1 Osterfjorden	0.69	0.12	-2.16	0.37
0 Osterfjorden / 0 Sørfjorden	1.19	0.09	2.44	0.22
1 Osterfjorden / 1 Sørfjorden	0.76	0.14	-1.47	0.82
0 Sørfjorden / 1 Sørfjorden	0.44	0.05	-7.92	<< 0.001

Table B4: Emmeans post-hoc test for pairwise comparison of the heartsomatic index of Benthosema glaciale between Masfjorden, Fensfjorden, Sørfjorden and Osterfjorden. A tuckey adjustment was used.

contrast	odds.ratio	SE	z.ratio	*P*
Pairwise comparison of HASI between fjords				
Fensfjorden / Masfjorden	1.03	0.08	0.34	0.99
Fensfjorden / Osterfjorden	0.76	0.08	-2.51	0.06
Fensfjorden / Sørfjorden	0.76	0.06	-3.54	0.002
Masfjorden / Osterfjorden	0.74	0.07	-3.09	0.01
Masfjorden / Sørfjorden	0.74	0.05	-4.76	<< 0.001
Osterfjorden / Sørfjorden	0.99	0.10	-0.09	1

Table B5: Emmeans post-hoc test for pairwise comparison of Fulton's condition factor of Benthosema glaciale between Masfjorden, Fensfjorden, Sørfjorden and Osterfjorden. A tuckey adjustment was used.

contrast	odds.ratio	SE	z.ratio	*P*
Pairwise comparison of CF between fjords				
Fensfjorden / Masfjorden	1.03	0.02	1.82	0.26
Fensfjorden / Osterfjorden	0.10	0.03	-0.08	1
Fensfjorden / Sørfjorden	1.30	0.03	13.31	<< 0.001
Masfjorden / Osterfjorden	0.97	0.02	-1.40	0.5
Masfjorden / Sørfjorden	1.26	0.02	13.71	<< 0.001
Osterfjorden / Sørfjorden	1.31	0.03	10.11	<< 0.001

Table B6: Canonical Analysis of Principal coordinates (CAP) on the variation in otolith shape between infected and uninfected Benthosema glaciale from Masfjorden, Fensfjorden, Sørfjorden and Osterfjorden. An Anova-like premutation test (1000 permutations) was used.

Fjord	Sum sq.	$F_{(d.f)}$	*p*
Mean otolith shape between infected and uninfected *B. glaciale*			
Masfjorden	0.67	$1.05_{(1,50)}$	0.39
Fensfjorden	0.65	$1.09_{(1,34)}$	0.33
Sørfjorden	1.21	$2.06_{(1,46)}$	0.053
Osterfjorden	0.52	$1.28_{(1,18)}$	0.23

Table B7: Mean and standard deviation (mean ± s.d) of the otolith length and width of Benthosema glaciale from Masfjorden, Fensfjorden, Sørfjorden and Osterfjorden. n gives the number of individuals measured in each fjord.

Fjord	n	otolith length (mean ± s.d)	otolith width (mean ± s.d)
Fensfjorden	36	1.54 ± 0.158 mm	1.96 ± 0.253 mm
Masfjorden	52	1.43 ± 0.271 mm	1.79 ± 0.347 mm
Osterfjorden	20	1.29 ± 0.213 mm	1.60 ± 0.286 mm
Sørfjorden	48	1.38 ± 0.161 mm	1.79 ± 0.240 mm

Table B8: Emmeans post-hoc test for pairwise comparison of the otolith length of Benthosema glaciale between Masfjorden, Fensfjorden, Sørfjorden and Osterfjorden. A tuckey adjustment was used. Emmeans post-hoc test for pairwise comparison of the otolith width of B. glaciale between Masfjorden, Fensfjorden, Sørfjorden and Osterfjorden. A tuckey adjustment was used.

contrast	estimate	SE	df	t.ratio	*P*
Pairwise comparison of otolith length between fjords					
Fensfjorden / Masfjorden	0.11	0.06	150	2.33	0.96
Fensfjorden / Osterfjorden	0.25	0.06	150	4.28	< 0.001
Fensfjorden / Sørfjorden	0.15	0.05	150	3.28	0.007
Masfjorden / Osterfjorden	0.15	0.06	150	2.61	0.049
Masfjorden / Sørfjorden	0.05	0.04	150	1.09	0.70
Osterfjorden / Sørfjorden	-0.10	0.06	150	-1.76	0.30

contrast	estimate	SE	df	t.ratio	*P*
Pairwise comparison of otolith width between fjords					
Fensfjorden / Masfjorden	0.17	0.06	150	2.69	0.04
Fensfjorden / Osterfjorden	0.36	0.08	150	4.43	< 0.01
Fensfjorden / Sørfjorden	0.17	0.06	150	2.64	0.04
Masfjorden / Osterfjorden	0.19	0.08	150	2.48	0.07
Masfjorden / Sørfjorden	< 0.01	0.06	150	< 0.01	1
Osterfjorden / Sørfjorden	-0.19	0.08	150	-2.45	0.07

Table B9: Overview table of Sarcotretes scopeli and Benthosema glaciale volume measurments and relative proportions of parasitic volume. Fish ID is the uniqe I.D given to each fish and corresponding parasite. Volume fish is the volume of B. glaciale (ml). Total parasite volume is the volume of the whole parasite (ml). V_{tot}/V_H shows the volume of the whole parasite volume relative to host volume for each individual sample. V_{tot}/V_H Mean±S.d shows the mean value with standard deviation for the total parasitic volume relative to host volume. External parasite volume is the volume of the external part of the parasite (ml). V_{ext}/V_H shows the volume of the external parasitic volume relative to host volume for each individual sample. V_{ext}/V_H Mean±S.d shows the mean value with standard deviation for the external parasitic part relative to host volume. Internal parasite volume is the volume of the internall part of the parasite (ml). V_{int}/V_H shows the volume of the internal parasitic part relative to host volume for each individual sample. V_{int}/V_H Mean±S.d shows the mean value with standard deviation for the internal parasitic volume relative to host volume.

Fish I.D	Volume Fish (ml)	Total parasite volume (ml)	V_{tot}/V_H	V_{tot}/V_H Mean ± S.d	External parasite volume (ml)	V_{ext}/V_H	V_{ext}/V_H Mean ± S.d	Internal parasite volume (ml)	V_{int}/V_H	V_{int}/V_H Mean ± S.d
Mas 149/5.01	3.00	0.017	0.57%		0.007	0.23%		0.005	0.17%	
Mas 149/5.04	1.25	0.009	0.72%		0.004	0.32%		0.002	0.16%	
Mas 149/5.06	1.60	0.024	1.5%		0.015	0.94%		0.010	0.62%	
Mas 149/5.07	3.00	0.017	0.57%		0.009	0.3%		0.003	0.1%	
Mas 149/5.08	2.50	0.025	1%	0.933 ± 0.405%	0.018	0.72%	0.638 ± 0.405%	0.013	0.52%	0.344 ± 0.243%
Mas 149/5.10	2.40	0.022	0.92%		0.012	0.5%		0.009	0.38%	
Mas 149/5.11	1.60	0.027	1.69%		0.022	1.37%		0.012	0.75%	
Mas 149/5.12	2.50	0.020	0.8%		0.019	0.76%		0.008	0.32%	
Mas 149/5.14	2.50	0.016	0.64%		0.015	0.6%		0.002	0.08%	

Appendix C:

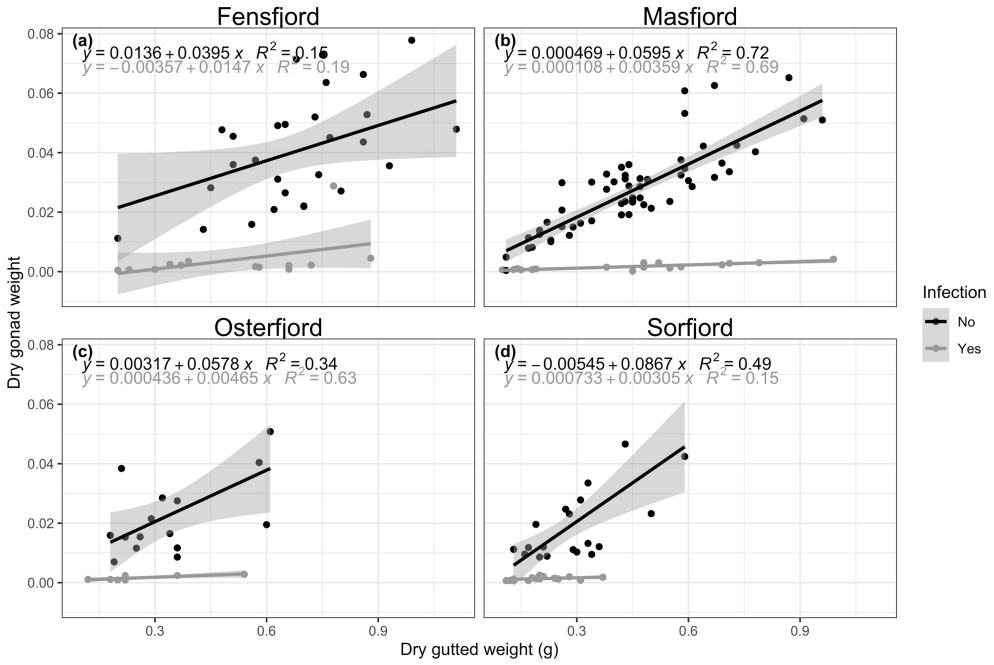

*Figure C1: Relationship between dry gutted weight and dry gonad weight for Sarcotretes scopeli infected and uninfected **female** Benthosema glaciale. Plots have been produced with untransformed data. Infected individuals are given in gray and uninfected indiviuals are given in black. A) infected and uninfected females from Fensfjorden. B) infected and uninfected females from Masfjorden. C) infected and uninfected females from Osterfjorden. D) infected and uninfected females from Sørfjorden.*

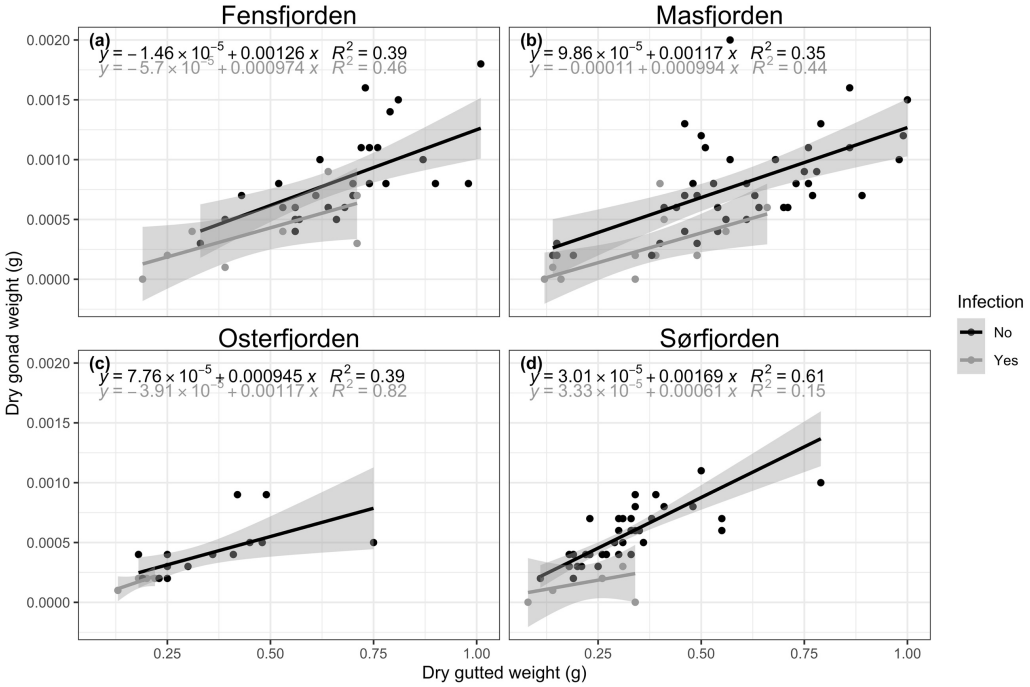

*Figure C2: Relationship between dry gutted weight and dry gonad weight for Sarcotretes scopeli infected and uninfected **male** Benthosema glaciale. Plots have been produced with untransformed data. Infected individuals are given in gray and uninfected indiviuals are given in black. A) infected and uninfected males from Fensfjorden. B) infected and uninfected males from Masfjorden. C) infected and uninfected males from Osterfjorden. D) infected and uninfected males from Sørfjorden.*

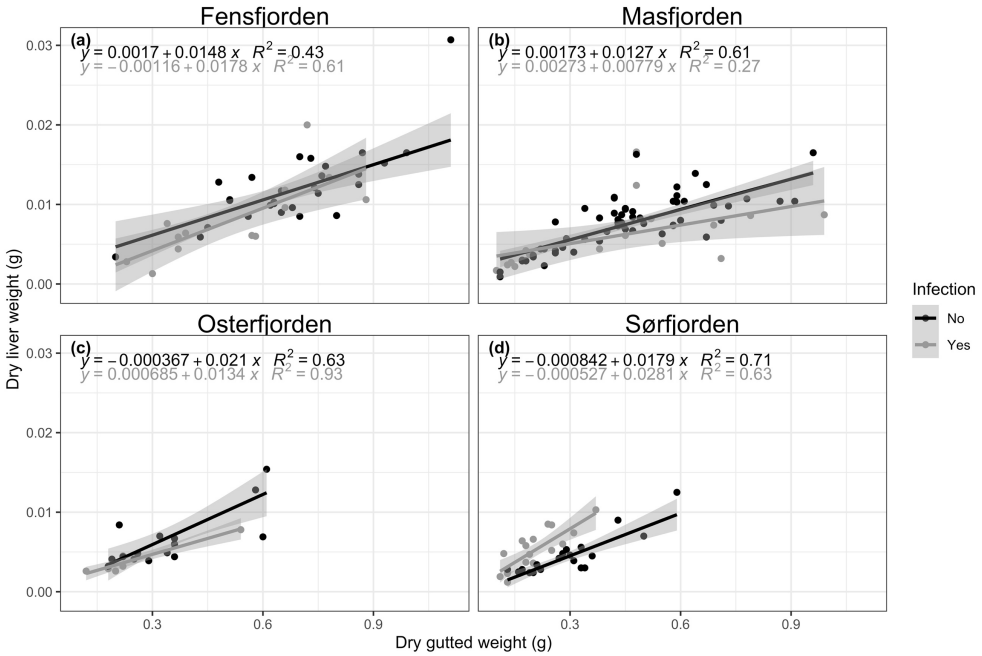

*Figure C3: Relationship between dry gutted weight (g) and dry liver weight (g) for Sarcotretes scopeli infected and uninfected **female** Benthosema glaciale. Plots have been produced with untransformed data. Infected individuals are given in gray and uninfected indiviuals are given in black. A) infected and uninfected individuals from Fensfjorden. B) infected and uninfected individuals from Masfjorden. C) infected and uninfected individuals from Osterfjorden. D) infected and uninfected individuals from Sørfjorden.*

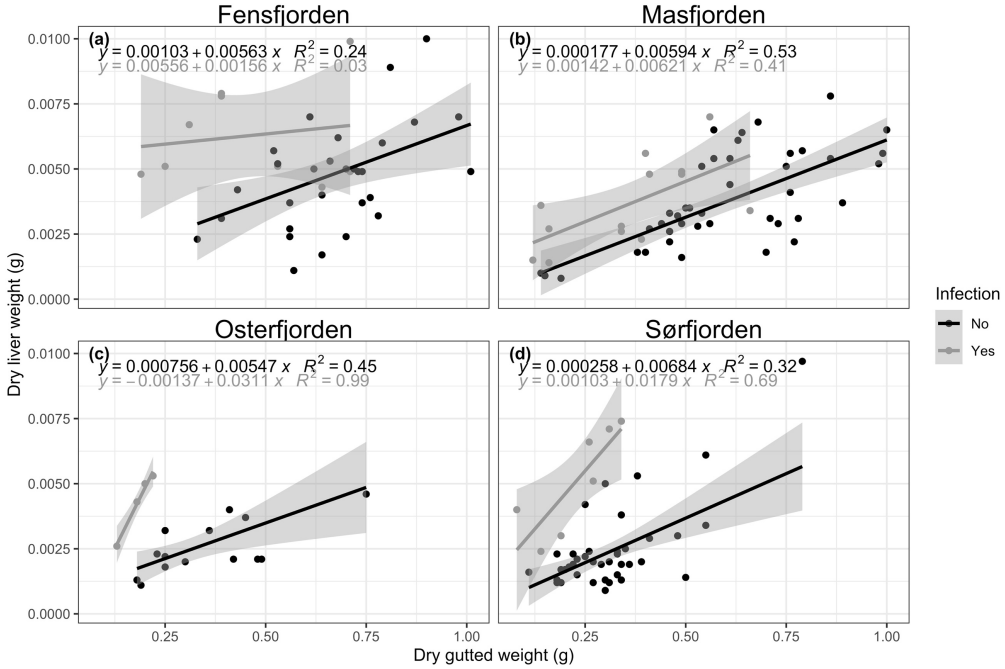

*Figure C4: Relationship between dry gutted weight (g) and dry liver weight (g) for Sarcotretes scopeli infected and uninfected **male** Benthosema glaciale. Plots have been produced with untransformed data. Infected individuals are given in gray and uninfected indiviuals are given in black. A) infected and uninfected individuals from Fensfjorden. B) infected and uninfected individuals from Masfjorden. C) infected and uninfected individuals from Osterfjorden. D) infected and uninfected individuals from Sørfjorden.*

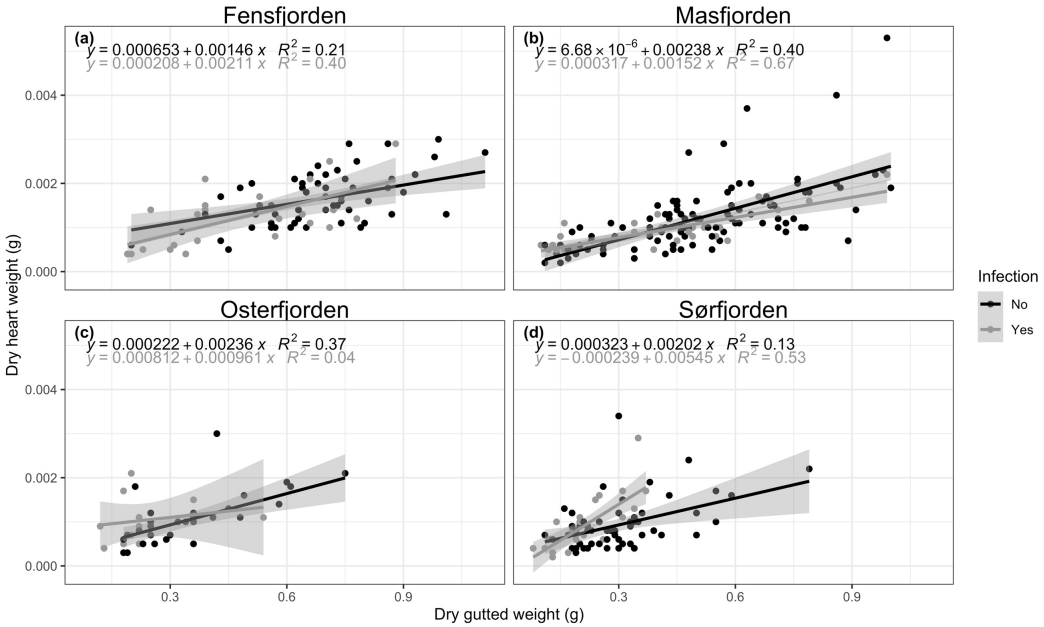

Figure C5: Relationship between dry gutted weight (g) and dry heart weight for Sarcotretes scopeli infected and uninfected Benthosema glaciale. Plots have been produced with untransformed data. Infected individuals are given in gray and uninfected indiviuals are given in black. A) infected and uninfected individuals from Fensfjorden. B) infected and uninfected individuals from Masfjorden. C) infected and uninfected individuals from Osterfjorden. D) infected and uninfected individuals from Sørfjorden.

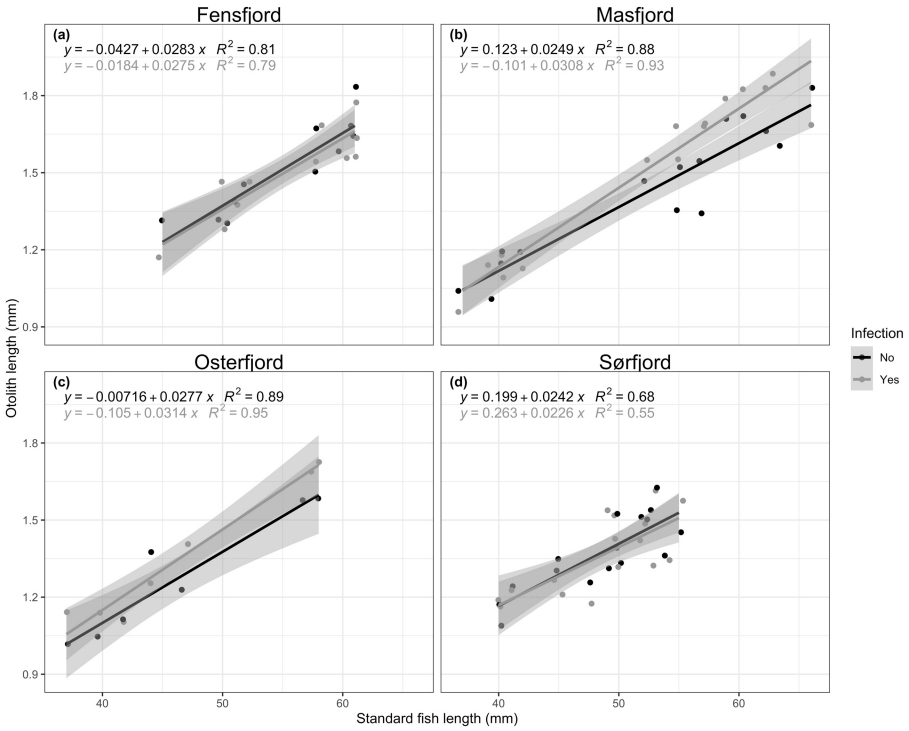

*Figure C6: Relationship between standard fish length (mm) and otolith length (mm) for Sarcotretes infected and uninfected **female** Benthosema glaciale, from four west Norwegian fjords. Infected individuals are given in gray and uninfected individuals are given in black. a) Fensfjorden. b) Masfjorden. c) Osterfjorden. D) Sørfjorden.*

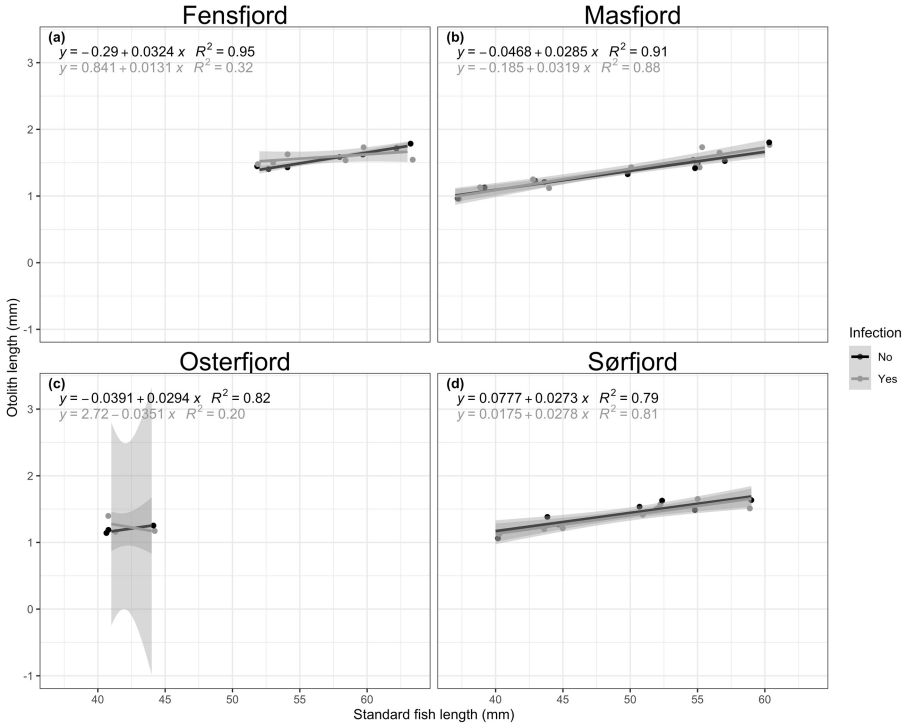

*Figure C7: Relationship between standard fish length (mm) and otolith length (mm) for Sarcotretes infected and uninfected **male** Benthosema glaciale from four west Norwegian fjords. Infected individuals are given in gray and uninfected individuals are given in black. a) Fensfjorden. b) Masfjorden. c) Osterfjorden. D) Sørfjorden.*

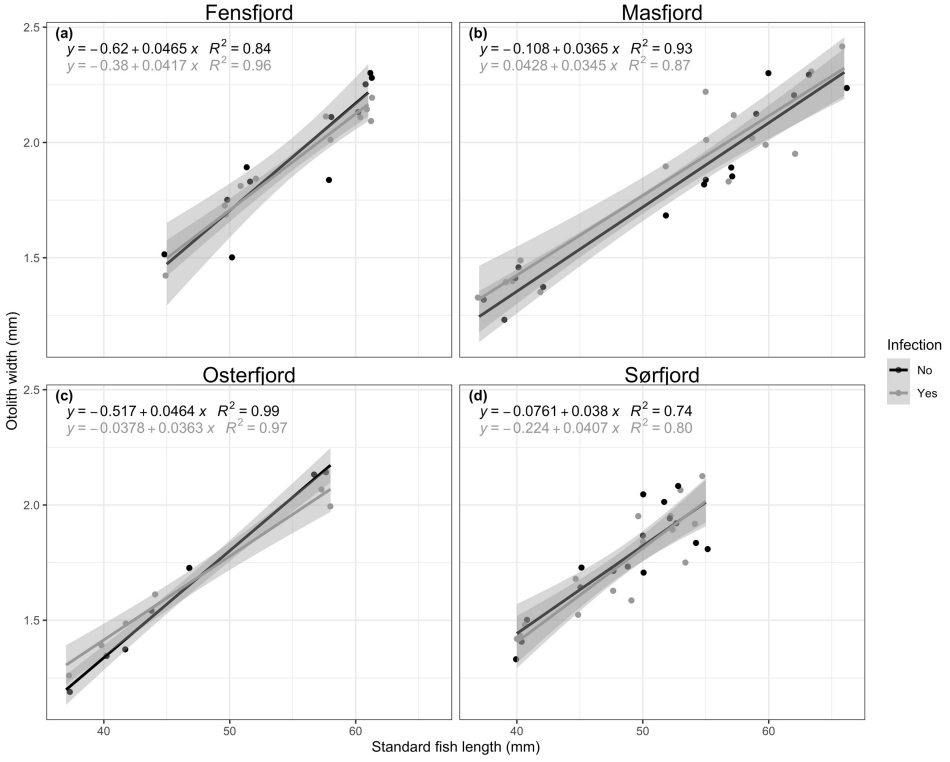

*Figure C8: Relationship between standard fish width (mm) and otolith width (mm) for Sarcotretes infected and uninfected **female** Benthosema glaciale from four west Norwegian fjords. Infected individuals are given in gray and uninfected individuals are given in black. a) Fensfjorden. b) Masfjorden. c) Osterfjorden. D) Sørfjorden.*

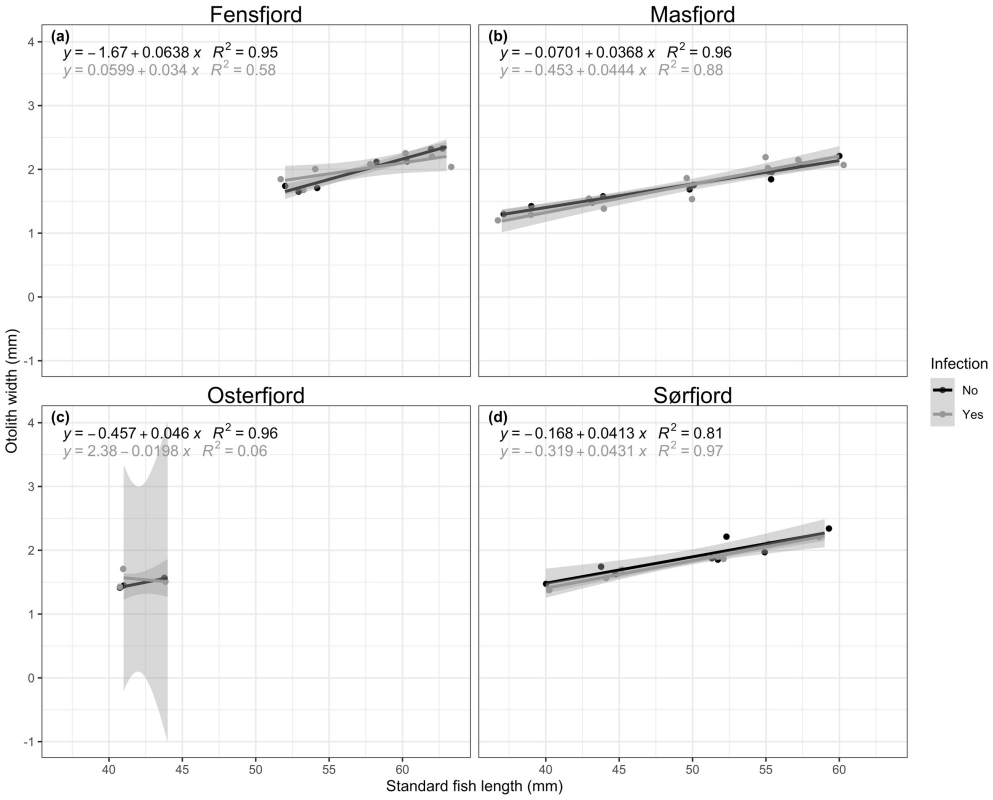

*Figure C9: Relationship between standard fish width (mm) and otolith width (mm) for Sarcotretes infected and uninfected **male** Benthosema glaciale from four west Norwegian fjords. Infected individuals are given in gray and uninfected individuals are given in black. a) Fensfjorden. b) Masfjorden. c) Osterfjorden. D) Sørfjorden.*

Appendix D:

Prevalence and effect of oxygen analysis:

```
> prev.mod1 <- glmmPQL(parasitized ~ foxy_cat,
+                      random = ~ 1 |farea, family = quasibinomial, data = fjordprev4.df)
iteration 1
iteration 2
iteration 3
> summary(prev.mod1)
Linear mixed-effects model fit by maximum likelihood
  Data: fjordprev4.df
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | farea
        (Intercept)  Residual
StdDev:   0.2631148 0.9880164

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects:  parasitized ~ foxy_cat
                Value Std.Error   DF    t-value p-value
(Intercept)  -3.702826 0.2895317 2773 -12.789018   0.000
foxy_catHigh  0.412122 0.2855073 2773   1.443474   0.149
 Correlation:
             (Intr)
foxy_catHigh -0.809

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-0.2190626 -0.2115806 -0.1833277 -0.1712023  7.3636647

Number of Observations: 2778
Number of Groups: 4
```

```
> Anova(prev.mod1, type= 3)
Analysis of Deviance Table (Type III tests)

Response: zz
               Chisq Df Pr(>Chisq)
(Intercept) 163.6768  1     <2e-16 ***
foxy_cat      2.0851  1     0.1487
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Prevalence between fjords:

```
> prev.mod2 <- glm(parasitized ~ farea, family = quasibinomial, data = fjordprev4.df)
> summary(prev.mod2)

Call:
glm(formula = parasitized ~ farea, family = quasibinomial, data = fjordprev4.df)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-0.3124  -0.2977  -0.2437  -0.1885   2.8422

Coefficients:
                Estimate Std. Error t value Pr(>|t|)
(Intercept)      -4.0212     0.2800 -14.362  < 2e-16 ***
fareaFensfjord    0.5190     0.3571   1.453  0.14627
fareaMasfjord     0.9268     0.3234   2.866  0.00419 **
fareaOsterfjord   1.0255     0.3657   2.804  0.00508 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for quasibinomial family taken to be 1.001521)

    Null deviance: 814.67  on 2777  degrees of freedom
Residual deviance: 802.62  on 2774  degrees of freedom
AIC: NA

Number of Fisher Scoring iterations: 6
```

```
> anova(prev.mod2, test = "Chisq")
Analysis of Deviance Table

Model: quasibinomial, link: logit

Response: parasitized

Terms added sequentially (first to last)


      Df Deviance Resid. Df Resid. Dev Pr(>Chi)
NULL                  2777     814.67
farea  3   12.054      2774     802.62 0.007262 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Cumulative length distribution Sørfjorden:

```
> ks.test(sør_c$length_mm, sør_p$length_mm)

        Two-sample Kolmogorov-Smirnov test

data:  sør_c$length_mm and sør_p$length_mm
D = 0.28393, p-value = 0.2546
alternative hypothesis: two-sided

Warning message:
In ks.test(sør_c$length_mm, sør_p$length_mm) :
  cannot compute exact p-value with ties
```

Cumulative length distribution Osterfjorden:

```
> ks.test(ost_c$length_mm, ost_p$length_mm)

        Two-sample Kolmogorov-Smirnov test

data:  ost_c$length_mm and ost_p$length_mm
D = 0.15, p-value = 0.8102
alternative hypothesis: two-sided

Warning message:
In ks.test(ost_c$length_mm, ost_p$length_mm) :
  cannot compute exact p-value with ties
```

Cumulative length distribution Masfjorden:

```
>  ks.test(mas_c$length_mm, mas_p$length_mm)

        Two-sample Kolmogorov-Smirnov test

data:  mas_c$length_mm and mas_p$length_mm
D = 0.15852, p-value = 0.2914
alternative hypothesis: two-sided

Warning message:
In ks.test(mas_c$length_mm, mas_p$length_mm) :
  p-value will be approximate in the presence of ties
```

Cumulative length distribution Fensfjorden:

```
>  ks.test(fens_c$length_mm, fens_p$length_mm)

        Two-sample Kolmogorov-Smirnov test

data:  fens_c$length_mm and fens_p$length_mm
D = 0.13199, p-value = 0.8696
alternative hypothesis: two-sided

Warning message:
In ks.test(fens_c$length_mm, fens_p$length_mm) :
  p-value will be approximate in the presence of ties
```

Analysis of GSI for males with interaction term:

```
> GSISM <- glm(gsi_bin  ~ fparasitized * farea  , weights = sample_wt, family = quasibinomial
 , data = effect_male.df )
> summary(GSISM)

Call:
glm(formula = gsi_bin ~ fparasitized * farea, family = quasibinomial,
    data = effect_male.df, weights = sample_wt)

Deviance Residuals:
      Min         1Q     Median         3Q        Max
-0.116412  -0.019394  -0.004472   0.012787   0.137366

Coefficients:
                             Estimate Std. Error t value Pr(>|t|)
(Intercept)                -6.6961694  0.0713193 -93.890  < 2e-16 ***
fparasitized1              -0.4201246  0.3660820  -1.148    0.253
fareaMasfjord               0.0932616  0.0876916   1.064    0.289
fareaOsterfjord            -0.0006312  0.1525245  -0.004    0.997
fareaSorfjord               0.3688986  0.0843213   4.375 2.26e-05 ***
fparasitized1:fareaMasfjord -0.4476228  0.5135903  -0.872    0.385
fparasitized1:fareaOsterfjord  0.1588272  0.6323830   0.251    0.802
fparasitized1:fareaSorfjord -0.4763006  0.5661895  -0.841    0.402
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for quasibinomial family taken to be 0.0009404227)

    Null deviance: 0.17725  on 157  degrees of freedom
Residual deviance: 0.13436  on 150  degrees of freedom
AIC: NA

Number of Fisher Scoring iterations: 10
```

```
> anova(GSISM, test = "Chisq")
Analysis of Deviance Table

Model: quasibinomial, link: logit

Response: gsi_bin

Terms added sequentially (first to last)


                  Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                157    0.17725
fparasitized       1 0.015527       156    0.16172 4.839e-05 ***
farea              3 0.025842       153    0.13588 4.670e-06 ***
fparasitized:farea 3 0.001513       150    0.13436    0.6574
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Analysis of GSI males without interaction term:

```
> GSISM2 <- glm(gsi_bin  ~ fparasitized + farea, family = quasibinomial, weights = sample_wt ,
 data = effect_male.df)
> summary(GSISM2)

Call:
glm(formula = gsi_bin ~ fparasitized + farea, family = quasibinomial,
    data = effect_male.df, weights = sample_wt)

Deviance Residuals:
      Min         1Q     Median         3Q        Max
-0.115813  -0.019246  -0.004551   0.013330   0.137902

Coefficients:
               Estimate Std. Error t value Pr(>|t|)
(Intercept)    -6.68764    0.06969 -95.966  < 2e-16 ***
fparasitized1  -0.67326    0.20074  -3.354    0.001 **
fareaMasfjord   0.08044    0.08565   0.939    0.349
fareaOsterfjord 0.01420    0.14668   0.097    0.923
fareaSorfjord   0.35766    0.08248   4.336 2.62e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for quasibinomial family taken to be 0.0009264584)

    Null deviance: 0.17725  on 157  degrees of freedom
Residual deviance: 0.13588  on 153  degrees of freedom
AIC: NA

Number of Fisher Scoring iterations: 10
```

```
> anova(GSISM2, test = "Chisq")
Analysis of Deviance Table

Model: quasibinomial, link: logit

Response: gsi_bin

Terms added sequentially (first to last)


             Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                           157    0.17725
fparasitized  1 0.015527       156    0.16172 4.244e-05 ***
farea         3 0.025842       153    0.13588 3.823e-06 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Post-hoc test:

```
> emmeans(GSISM2, specs = pairwise ~ farea, type = "response")
$emmeans
 farea          prob       SE  df asymp.LCL asymp.UCL
 Fensfjord  0.000889 0.000104 Inf  0.000707   0.00112
 Masfjord   0.000964 0.000104 Inf  0.000780   0.00119
 Osterfjord 0.000902 0.000142 Inf  0.000662   0.00123
 Sorfjord   0.001271 0.000136 Inf  0.001030   0.00157

Results are averaged over the levels of: fparasitized
Confidence level used: 0.95
Intervals are back-transformed from the logit scale

$contrasts
 contrast               odds.ratio     SE  df null z.ratio p.value
 Fensfjord / Masfjord        0.923 0.0790 Inf    1  -0.939  0.7837
 Fensfjord / Osterfjord      0.986 0.1446 Inf    1  -0.097  0.9997
 Fensfjord / Sorfjord        0.699 0.0577 Inf    1  -4.336  0.0001
 Masfjord / Osterfjord       1.068 0.1481 Inf    1   0.478  0.9640
 Masfjord / Sorfjord         0.758 0.0508 Inf    1  -4.137  0.0002
 Osterfjord / Sorfjord       0.709 0.0970 Inf    1  -2.512  0.0581

Results are averaged over the levels of: fparasitized
P value adjustment: tukey method for comparing a family of 4 estimates
Tests are performed on the log odds ratio scale
```

Analysis of GSI for females with interaction term:

```
> GSISF <- glm(gsi_bin  ~ fparasitized * farea  , weights = sample_wt, family = quasibinomial
 , data = effect_female.df )
> summary(GSISF)

Call:
glm(formula = gsi_bin ~ fparasitized * farea, family = quasibinomial,
    data = effect_female.df, weights = sample_wt)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-0.69238  -0.08662  -0.01203   0.04951   0.90726

Coefficients:
                            Estimate Std. Error t value Pr(>|t|)
(Intercept)                -2.71726    0.07995 -33.989  < 2e-16 ***
fparasitized1              -2.31328    0.61569  -3.757 0.000238 ***
fareaMasfjord              -0.03414    0.09034  -0.378 0.706019
fareaOsterfjord             0.14230    0.12305   1.157 0.249133
fareaSorfjord               0.03729    0.11115   0.336 0.737664
fparasitized1:fareaMasfjord -0.41226    0.92639  -0.445 0.656886
fparasitized1:fareaOsterfjord -0.11499    1.05515  -0.109 0.913348
fparasitized1:fareaSorfjord  0.01618    0.82229   0.020 0.984323
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for quasibinomial family taken to be 0.03365639)

    Null deviance: 10.0525  on 173  degrees of freedom
Residual deviance:  5.3671  on 166  degrees of freedom
AIC: NA

Number of Fisher Scoring iterations: 8
```

```
> anova(GSISF, test = "Chisq")
Analysis of Deviance Table

Model: quasibinomial, link: logit

Response: gsi_bin

Terms added sequentially (first to last)


                  Df Deviance Resid. Df Resid. Dev Pr(>Chi)
NULL                                173    10.0525
fparasitized       1   4.5669       172     5.4856   <2e-16 ***
farea              3   0.1087       169     5.3769   0.3577
fparasitized:farea 3   0.0099       166     5.3671   0.9613
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Analysis of GSI for females without interaction term:

```
> GSISF2 <- glm(gsi_bin  ~ fparasitized + farea  , weights = sample_wt, family = quasibinomial
  , data = effect_female.df )
> summary(GSISF2)

Call:
glm(formula = gsi_bin ~ fparasitized + farea, family = quasibinomial,
    data = effect_female.df, weights = sample_wt)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-0.69186  -0.08998  -0.01635   0.04997   0.90725

Coefficients:
                Estimate Std. Error t value Pr(>|t|)
(Intercept)     -2.71540    0.07891 -34.412  < 2e-16 ***
fparasitized1   -2.43018    0.32276  -7.529 2.92e-12 ***
fareaMasfjord   -0.03727    0.08919  -0.418    0.677
fareaOsterfjord  0.14046    0.12139   1.157    0.249
fareaSorfjord    0.03793    0.10942   0.347    0.729
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for quasibinomial family taken to be 0.03321698)

    Null deviance: 10.0525  on 173  degrees of freedom
Residual deviance:  5.3769  on 169  degrees of freedom
AIC: NA

Number of Fisher Scoring iterations: 8
```

```
> anova(GSISF2, test = "Chisq")
Analysis of Deviance Table

Model: quasibinomial, link: logit

Response: gsi_bin

Terms added sequentially (first to last)


             Df Deviance Resid. Df Resid. Dev Pr(>Chi)
NULL                           173    10.0525
fparasitized  1   4.5669       172     5.4856   <2e-16 ***
farea         3   0.1087       169     5.3769   0.3517
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Analysis of HSI:

```
> HSIS <- glm(hsi_bin ~ fparasitized * fsex + farea*fparasitized, weights = sample_wt ,family
 = "quasibinomial", data = effect.df)
> summary(HSIS)

Call:
glm(formula = hsi_bin ~ fparasitized * fsex + farea * fparasitized,
    family = "quasibinomial", data = effect.df, weights = sample_wt)

Deviance Residuals:
      Min         1Q     Median         3Q        Max
-0.174159  -0.043441  -0.009678   0.037081   0.307482

Coefficients:
                            Estimate Std. Error t value Pr(>|t|)
(Intercept)                -4.02314    0.04817 -83.528  < 2e-16 ***
fparasitized1              -0.11594    0.14130  -0.821  0.41252
fsexM                      -0.87314    0.04147 -21.056  < 2e-16 ***
fareaMasfjord              -0.06151    0.05298  -1.161  0.24654
fareaOsterfjord             0.13396    0.07536   1.777  0.07643 .
fareaSorfjord              -0.04425    0.06038  -0.733  0.46415
fparasitized1:fsexM         0.83195    0.12923   6.438 4.38e-10 ***
fparasitized1:fareaMasfjord -0.03805    0.17712  -0.215  0.83003
fparasitized1:fareaOsterfjord  0.07724    0.21791   0.354  0.72322
fparasitized1:fareaSorfjord    0.53097    0.16754   3.169  0.00167 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for quasibinomial family taken to be 0.005406991)

    Null deviance: 4.8096  on 332  degrees of freedom
Residual deviance: 1.6604  on 323  degrees of freedom
AIC: NA

Number of Fisher Scoring iterations: 7



> anova(HSIS, test = "Chisq")
Analysis of Deviance Table

Model: quasibinomial, link: logit

Response: hsi_bin

Terms added sequentially (first to last)


                  Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                332     4.8096
fparasitized       1  0.25468       331     4.5550 6.737e-12 ***
fsex               1  2.55808       330     1.9969 < 2.2e-16 ***
farea              3  0.05087       327     1.9460 0.0243355 *
fparasitized:fsex  1  0.19573       326     1.7503 1.781e-09 ***
fparasitized:farea 3  0.08986       323     1.6604 0.0008461 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Post-hoc test Parasiteized * area:

```
> emmeans(HSIS, specs = pairwise ~ fparasitized:farea, type = "response")
$emmeans
 fparasitized farea        prob       SE  df asymp.LCL asymp.UCL
 0            Fensfjord  0.0114 0.000510 Inf    0.0105    0.0125
 1            Fensfjord  0.0154 0.001895 Inf    0.0121    0.0196
 0            Masfjord   0.0108 0.000309 Inf    0.0102    0.0114
 1            Masfjord   0.0139 0.001577 Inf    0.0112    0.0174
 0            Osterfjord 0.0131 0.000786 Inf    0.0116    0.0147
 1            Osterfjord 0.0189 0.003030 Inf    0.0138    0.0259
 0            Sorfjord   0.0109 0.000432 Inf    0.0101    0.0118
 1            Sorfjord   0.0248 0.002345 Inf    0.0206    0.0298

Results are averaged over the levels of: fsex
Confidence level used: 0.95
Intervals are back-transformed from the logit scale


$contrasts
 contrast                   odds.ratio     SE  df null z.ratio p.value
 0 Fensfjord / 1 Fensfjord       0.741 0.0986 Inf    1  -2.255  0.3191
 0 Fensfjord / 0 Masfjord        1.063 0.0563 Inf    1   1.161  0.9428
 0 Fensfjord / 1 Masfjord        0.818 0.1009 Inf    1  -1.626  0.7347
 0 Fensfjord / 0 Osterfjord      0.875 0.0659 Inf    1  -1.777  0.6355
 0 Fensfjord / 1 Osterfjord      0.600 0.1016 Inf    1  -3.018  0.0519
 0 Fensfjord / 0 Sorfjord        1.045 0.0631 Inf    1   0.733  0.9960
 0 Fensfjord / 1 Sorfjord        0.455 0.0487 Inf    1  -7.350  <.0001
 1 Fensfjord / 0 Masfjord        1.436 0.1845 Inf    1   2.814  0.0916
 1 Fensfjord / 1 Masfjord        1.105 0.1867 Inf    1   0.589  0.9990
 1 Fensfjord / 0 Osterfjord      1.181 0.1644 Inf    1   1.193  0.9343
 1 Fensfjord / 1 Osterfjord      0.810 0.1655 Inf    1  -1.033  0.9695
 1 Fensfjord / 0 Sorfjord        1.411 0.1854 Inf    1   2.620  0.1485
 1 Fensfjord / 1 Sorfjord        0.615 0.0961 Inf    1  -3.114  0.0390
 0 Masfjord / 1 Masfjord         0.770 0.0911 Inf    1  -2.214  0.3434
 0 Masfjord / 0 Osterfjord       0.822 0.0542 Inf    1  -2.968  0.0599
 0 Masfjord / 1 Osterfjord       0.564 0.0935 Inf    1  -3.454  0.0129
 0 Masfjord / 0 Sorfjord         0.983 0.0489 Inf    1  -0.347  1.0000
 0 Masfjord / 1 Sorfjord         0.428 0.0434 Inf    1  -8.373  <.0001
 1 Masfjord / 0 Osterfjord       1.069 0.1389 Inf    1   0.512  0.9996
 1 Masfjord / 1 Osterfjord       0.733 0.1456 Inf    1  -1.564  0.7720
 1 Masfjord / 0 Sorfjord         1.277 0.1552 Inf    1   2.014  0.4720
 1 Masfjord / 1 Sorfjord         0.556 0.0828 Inf    1  -3.939  0.0021
 0 Osterfjord / 1 Osterfjord     0.686 0.1195 Inf    1  -2.165  0.3733
 0 Osterfjord / 0 Sorfjord       1.195 0.0874 Inf    1   2.436  0.2240
 0 Osterfjord / 1 Sorfjord       0.521 0.0597 Inf    1  -5.695  <.0001
 1 Osterfjord / 0 Sorfjord       1.743 0.2929 Inf    1   3.305  0.0213
 1 Osterfjord / 1 Sorfjord       0.759 0.1425 Inf    1  -1.467  0.8249
 0 Sorfjord / 1 Sorfjord         0.436 0.0457 Inf    1  -7.918  <.0001

Results are averaged over the levels of: fsex
P value adjustment: tukey method for comparing a family of 8 estimates
Tests are performed on the log odds ratio scale
```

Post-hoc test parasitized*sex:

```
> emmeans(HSIS, specs = pairwise ~ fparasitized:fsex, type = "response")
$emmeans
 fparasitized fsex    prob       SE  df asymp.LCL asymp.UCL
 0            F    0.01770 0.000467 Inf   0.01681   0.01864
 1            F    0.01817 0.001383 Inf   0.01565   0.02109
 0            M    0.00747 0.000257 Inf   0.00698   0.00799
 1            M    0.01745 0.001712 Inf   0.01439   0.02115

Results are averaged over the levels of: farea
Confidence level used: 0.95
Intervals are back-transformed from the logit scale

$contrasts
 contrast  odds.ratio     SE  df null z.ratio p.value
 0 F / 1 F      0.974 0.0799 Inf    1  -0.324  0.9882
 0 F / 0 M      2.394 0.0993 Inf    1  21.056  <.0001
 0 F / 1 M      1.015 0.1049 Inf    1   0.141  0.9990
 1 F / 0 M      2.459 0.2088 Inf    1  10.595  <.0001
 1 F / 1 M      1.042 0.1275 Inf    1   0.337  0.9869
 0 M / 1 M      0.424 0.0448 Inf    1  -8.123  <.0001

Results are averaged over the levels of: farea
P value adjustment: tukey method for comparing a family of 4 estimates
Tests are performed on the log odds ratio scale
```

Analysis of HASI with interaction term:

```
> HASIS <- glm(hasi_bin ~ fparasitized * fsex + farea * fparasitized,
+              weights = sample_wt, family = "quasibinomial", data = effect.df)
> summary(HASIS)

Call:
glm(formula = hasi_bin ~ fparasitized * fsex + farea * fparasitized,
    family = "quasibinomial", data = effect.df, weights = sample_wt)

Deviance Residuals:
      Min         1Q     Median         3Q        Max
-0.146568  -0.028439  -0.007922   0.017697   0.280140

Coefficients:
                            Estimate Std. Error t value Pr(>|t|)
(Intercept)                -5.98045    0.07628 -78.398  < 2e-16 ***
fparasitized1              -0.02451    0.24180  -0.101  0.91933
fsexM                       0.01782    0.05822   0.306  0.75978
fareaMasfjord              -0.04053    0.08038  -0.504  0.61442
fareaOsterfjord             0.21885    0.11530   1.898  0.05858 .
fareaSorfjord               0.25902    0.08289   3.125  0.00194 **
fparasitized1:fsexM         0.12971    0.20297   0.639  0.52323
fparasitized1:fareaMasfjord 0.09997    0.29182   0.343  0.73215
fparasitized1:fareaOsterfjord 0.42561  0.33132   1.285  0.19986
fparasitized1:fareaSorfjord 0.23929    0.28069   0.852  0.39457
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for quasibinomial family taken to be 0.002743706)

    Null deviance: 0.88780  on 332  degrees of freedom
Residual deviance: 0.78458  on 323  degrees of freedom
AIC: NA

Number of Fisher Scoring iterations: 8
```

```
> anova(HASIS, test = "Chisq")
Analysis of Deviance Table

Model: quasibinomial, link: logit

Response: hasi_bin

Terms added sequentially (first to last)


                   Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                 332    0.88780
fparasitized        1 0.012472       331    0.87533    0.0330 *
fsex                1 0.005159       330    0.87017    0.1703
farea               3 0.079374       327    0.79079 2.317e-06 ***
fparasitized:fsex   1 0.000886       326    0.78991    0.5699
fparasitized:farea  3 0.005325       323    0.78458    0.5848
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Analysis of HASI without interaction term:

```
> HASIS2 <- glm(hasi_bin ~ fparasitized + fsex + farea,
+               weights = sample_wt, family = "quasibinomial", data = effect.df)
> summary(HASIS2)

Call:
glm(formula = hasi_bin ~ fparasitized + fsex + farea, family = "quasibinomial",
    data = effect.df, weights = sample_wt)

Deviance Residuals:
      Min         1Q     Median         3Q        Max
-0.145085  -0.028748  -0.007994   0.017780   0.278752

Coefficients:
               Estimate Std. Error t value Pr(>|t|)
(Intercept)    -6.00356    0.07335 -81.851  < 2e-16 ***
fparasitized1   0.20487    0.09976   2.054 0.040801 *
fsexM           0.02789    0.05546   0.503 0.615467
fareaMasfjord  -0.02584    0.07700  -0.336 0.737355
fareaOsterfjord 0.27014    0.10741   2.515 0.012385 *
fareaSorfjord   0.27936    0.07900   3.536 0.000464 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for quasibinomial family taken to be 0.002730709)

    Null deviance: 0.88780  on 332  degrees of freedom
Residual deviance: 0.79079  on 327  degrees of freedom
AIC: NA

Number of Fisher Scoring iterations: 8
```

```
> anova(HASIS2, test = "Chisq")
Analysis of Deviance Table

Model: quasibinomial, link: logit

Response: hasi_bin

Terms added sequentially (first to last)


             Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                          332    0.88780
fparasitized  1 0.012472       331    0.87533   0.03259 *
fsex          1 0.005159       330    0.87017   0.16927
farea         3 0.079374       327    0.79079 2.168e-06 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Post-hoc test for area:

```
> emmeans(HASIS2, specs = pairwise ~ farea, type = "response")
$emmeans
 farea         prob       SE  df asymp.LCL asymp.UCL
 Fensfjord  0.00277 0.000207 Inf   0.00239   0.00320
 Masfjord   0.00270 0.000165 Inf   0.00239   0.00304
 Osterfjord 0.00362 0.000340 Inf   0.00301   0.00435
 Sorfjord   0.00366 0.000228 Inf   0.00323   0.00413

Results are averaged over the levels of: fparasitized, fsex
Confidence level used: 0.95
Intervals are back-transformed from the logit scale

$contrasts
 contrast               odds.ratio     SE  df null z.ratio p.value
 Fensfjord / Masfjord        1.026 0.0790 Inf    1   0.336  0.9870
 Fensfjord / Osterfjord      0.763 0.0820 Inf    1  -2.515  0.0576
 Fensfjord / Sorfjord        0.756 0.0597 Inf    1  -3.536  0.0023
 Masfjord / Osterfjord       0.744 0.0712 Inf    1  -3.092  0.0107
 Masfjord / Sorfjord         0.737 0.0473 Inf    1  -4.757  <.0001
 Osterfjord / Sorfjord       0.991 0.0979 Inf    1  -0.093  0.9997

Results are averaged over the levels of: fparasitized, fsex
P value adjustment: tukey method for comparing a family of 4 estimates
Tests are performed on the log odds ratio scale
```

Analysis of Condition factor with interaction term:

```
> KS <- glm(K ~ fparasitized * fsex + farea*fparasitized,
+           weights = sample_wt, family = "quasibinomial", data = effect.df)
> summary(KS)

Call:
glm(formula = K ~ fparasitized * fsex + farea * fparasitized,
    family = "quasibinomial", data = effect.df, weights = sample_wt)

Deviance Residuals:
       Min          1Q      Median          3Q         Max
-0.0279999  -0.0037575   0.0002445   0.0039948   0.0210715

Coefficients:
                             Estimate Std. Error  t value Pr(>|t|)
(Intercept)                -6.864410   0.017430 -393.819  < 2e-16 ***
fparasitized1              -0.109334   0.059652   -1.833 0.067741 .
fsexM                       0.053783   0.013991    3.844 0.000146 ***
fareaMasfjord              -0.030742   0.018006   -1.707 0.088714 .
fareaOsterfjord             0.003095   0.027838    0.111 0.911542
fareaSorfjord              -0.263610   0.020589  -12.804  < 2e-16 ***
fparasitized1:fsexM        -0.116570   0.059702   -1.953 0.051738 .
fparasitized1:fareaMasfjord 0.009585   0.072714    0.132 0.895215
fparasitized1:fareaOsterfjord -0.001387   0.096650   -0.014 0.988556
fparasitized1:fareaSorfjord   -0.043992   0.081703   -0.538 0.590647
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for quasibinomial family taken to be 5.826253e-05)

    Null deviance: 0.035990  on 332  degrees of freedom
Residual deviance: 0.018786  on 323  degrees of freedom
AIC: NA

Number of Fisher Scoring iterations: 10
```

```
> anova(KS, test = "Chisq")
Analysis of Deviance Table

Model: quasibinomial, link: logit

Response: K

Terms added sequentially (first to last)


                   Df  Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                                  332   0.035990
fparasitized        1 0.0020727       331   0.033917 2.455e-09 ***
fsex                1 0.0000189       330   0.033898   0.56948
farea               3 0.0148684       327   0.019030 < 2.2e-16 ***
fparasitized:fsex   1 0.0002144       326   0.018816   0.05509 .
fparasitized:farea  3 0.0000300       323   0.018786   0.91547
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Analysis of condition factor without interaction:

```
> KS2 <- glm(K ~fparasitized + fsex + farea ,
+            weights = sample_wt, family = "quasibinomial", data = effect.df)
> summary(KS2)

Call:
glm(formula = K ~ fparasitized + fsex + farea, family = "quasibinomial",
    data = effect.df, weights = sample_wt)

Deviance Residuals:
       Min          1Q      Median          3Q         Max
-0.0282108  -0.0041482   0.0000401   0.0039764   0.0215285

Coefficients:
                Estimate Std. Error  t value Pr(>|t|)
(Intercept)     -6.860202   0.016898 -405.978  < 2e-16 ***
fparasitized1   -0.162110   0.028916   -5.606  4.4e-08 ***
fsexM            0.047851   0.013555    3.530 0.000475 ***
fareaMasfjord   -0.031769   0.017426   -1.823 0.069208 .
fareaOsterfjord  0.002188   0.026662    0.082 0.934635
fareaSorfjord   -0.265088   0.019915  -13.311  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for quasibinomial family taken to be 5.831059e-05)

    Null deviance: 0.03599  on 332  degrees of freedom
Residual deviance: 0.01903  on 327  degrees of freedom
AIC: NA

Number of Fisher Scoring iterations: 10
```

```
> anova(KS2, test = "Chisq")
Analysis of Deviance Table

Model: quasibinomial, link: logit

Response: K

Terms added sequentially (first to last)


             Df  Deviance Resid. Df Resid. Dev  Pr(>Chi)
NULL                           332   0.035990
fparasitized  1 0.0020727       331   0.033917 2.492e-09 ***
fsex          1 0.0000189       330   0.033898    0.5696
farea         3 0.0148684       327   0.019030 < 2.2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Post-hoc for area:

```
> emmeans(KS2, specs = pairwise ~ farea, type = "response")
$emmeans
 farea          prob       SE  df asymp.LCL asymp.UCL
 Fensfjord  0.000989 1.87e-05 Inf  0.000953  0.001027
 Masfjord   0.000959 1.57e-05 Inf  0.000928  0.000990
 Osterfjord 0.000992 2.51e-05 Inf  0.000944  0.001042
 Sorfjord   0.000759 1.43e-05 Inf  0.000732  0.000788

Results are averaged over the levels of: fparasitized, fsex
Confidence level used: 0.95
Intervals are back-transformed from the logit scale

$contrasts
 contrast               odds.ratio     SE  df null z.ratio p.value
 Fensfjord / Masfjord        1.032 0.0180 Inf    1   1.823  0.2624
 Fensfjord / Osterfjord      0.998 0.0266 Inf    1  -0.082  0.9998
 Fensfjord / Sorfjord        1.304 0.0260 Inf    1  13.311  <.0001
 Masfjord / Osterfjord       0.967 0.0234 Inf    1  -1.401  0.4985
 Masfjord / Sorfjord         1.263 0.0215 Inf    1  13.713  <.0001
 Osterfjord / Sorfjord       1.306 0.0345 Inf    1  10.110  <.0001

Results are averaged over the levels of: fparasitized, fsex
P value adjustment: tukey method for comparing a family of 4 estimates
Tests are performed on the log odds ratio scale
```

Linear relationship of gonad weight and dried gutted weight of males:

Sørfjorden with interaction:

```
> sør_gonadM <- lm(trans_gonad ~  dry_weight_gutted * parasitized,
+                  weights = sample_wt, data = effect_sor_M.df)
> Anova(sør_gonadM, type = "III")
Anova Table (Type III tests)

Response: trans_gonad
                             Sum Sq Df    F value    Pr(>F)
(Intercept)                  50.208  1 5.4203e+06 < 2.2e-16 ***
dry_weight_gutted             0.001  1 6.1968e+01 8.452e-10 ***
parasitized                   0.000  1 1.3680e-01    0.7133
dry_weight_gutted:parasitized 0.000  1 3.1730e-01    0.5763
Residuals                     0.000 42
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Sørfjorden without interaction:

```
> sør_gonadM2 <- lm(trans_gonad ~ dry_weight_gutted + parasitized,
+                   weights = sample_wt, data = effect_sor_M.df)
> Anova(sør_gonadM2, type = "III")
Anova Table (Type III tests)

Response: trans_gonad
                  Sum Sq Df    F value    Pr(>F)
(Intercept)       51.196  1 5.6161e+06 < 2.2e-16 ***
dry_weight_gutted  0.001  1 6.3006e+01 5.811e-10 ***
parasitized        0.000  1 6.3293e+00   0.01569 *
Residuals          0.000 43
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Osterfjorden with interaction:

```
> ost_gonadM <- lm(trans_gonad ~ dry_weight_gutted * parasitized,
+                  weights = sample_wt, data = effect_ost_M.df)
> Anova(ost_gonadM, type = "III")
Anova Table (Type III tests)

Response: trans_gonad
                             Sum Sq Df   F value    Pr(>F)
(Intercept)                 476.19  1 1123.5593 9.007e-15 ***
dry_weight_gutted             4.07  1    9.6052  0.007845 **
parasitized                   0.40  1    0.9330  0.350482
dry_weight_gutted:parasitized 0.22  1    0.5190  0.483136
Residuals                     5.93 14
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Osterfjorden without interaction:

```
> ost_gonadM2 <- lm(trans_gonad ~ dry_weight_gutted + parasitized,
+                   weights = sample_wt, data = effect_ost_M.df)
> Anova(ost_gonadM2, type = "III")
Anova Table (Type III tests)

Response: trans_gonad
                  Sum Sq Df   F value    Pr(>F)
(Intercept)       481.21  1 1173.0148 1.171e-15 ***
dry_weight_gutted   4.27  1   10.4192  0.005633 **
parasitized         0.75  1    1.8224  0.197050
Residuals           6.15 15
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Fensfjorden with interaction:

```
> fen_gonadM <- lm(trans_gonad ~ dry_weight_gutted * parasitized,
+                  weights = sample_wt, data = effect_fens_M.df)
> Anova(fen_gonadM, type = "III")
Anova Table (Type III tests)

Response: trans_gonad
                              Sum Sq Df    F value    Pr(>F)
(Intercept)                  23.8803  1 3.9027e+05 < 2.2e-16 ***
dry_weight_gutted             0.0012  1 2.0147e+01 7.826e-05 ***
parasitized                   0.0000  1 6.0670e-01    0.4414
dry_weight_gutted:parasitized 0.0000  1 6.6600e-02    0.7979
Residuals                     0.0021 34
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Fensfjorden without interaction:

```
> fen_gonadM2 <- lm(trans_gonad ~ dry_weight_gutted + parasitized,
+                   weights = sample_wt, data = effect_fens_M.df)
> Anova(fen_gonadM2, type =  "III")
Anova Table (Type III tests)

Response: trans_gonad
                   Sum Sq Df    F value    Pr(>F)
(Intercept)       25.5496  1 4.2900e+05 < 2.2e-16 ***
dry_weight_gutted  0.0014  1 2.2925e+01 3.038e-05 ***
parasitized        0.0001  1 2.1226e+00    0.1541
Residuals          0.0021 35
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Linear relationship of gonads weight and dried gutted weight of females:

Sørfjorden with interaction:

```
> sør_gonadF <- lm(trans_gonad ~ dry_weight_gutted * parasitized,
+                   weights = sample_wt, data = effect_sor_F.df)
> Anova(sør_gonadF, type = "III")
Anova Table (Type III tests)

Response: trans_gonad
                              Sum Sq Df  F value    Pr(>F)
(Intercept)                  308.052  1 469.3620 < 2.2e-16 ***
dry_weight_gutted             14.915  1  22.7254 3.906e-05 ***
parasitized                    6.903  1  10.5171  0.002766 **
dry_weight_gutted:parasitized  0.146  1   0.2218  0.640860
Residuals                     21.002 32
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Sørfjorden without interaction:

```
> sør_gonadF2 <- lm(trans_gonad ~ dry_weight_gutted + parasitized,
+                   weights = sample_wt, data = effect_sor_F.df)
> Anova(sør_gonadF2, type = "III")
Anova Table (Type III tests)

Response: trans_gonad
                  Sum Sq Df F value    Pr(>F)
(Intercept)       332.42  1 518.728 < 2.2e-16 ***
dry_weight_gutted  15.49  1  24.176 2.356e-05 ***
parasitized        85.66  1 133.673 3.793e-13 ***
Residuals          21.15 33
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Osterfjorden with interaction:

```
> ost_gonadF <- lm(trans_gonad ~  dry_weight_gutted * parasitized,
+                  weights = sample_wt, data = effect_ost_F.df)
> Anova(ost_gonadF, type = "III")
Anova Table (Type III tests)

Response: trans_gonad
                             Sum Sq Df  F value    Pr(>F)
(Intercept)                  58.214  1 576.2138 4.039e-15 ***
dry_weight_gutted             0.721  1   7.1322   0.01559 *
parasitized                   0.322  1   3.1827   0.09129 .
dry_weight_gutted:parasitized 0.012  1   0.1221   0.73080
Residuals                     1.819 18
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Osterfjorden without interaction:

```
> ost_gonadF2 <- lm(trans_gonad  ~ dry_weight_gutted + parasitized,
+                   weights = sample_wt, data = effect_ost_F.df)
> Anova(ost_gonadF2, type = "III")
Anova Table (Type III tests)

Response: trans_gonad
                  Sum Sq Df  F value    Pr(>F)
(Intercept)       63.478  1 658.7527 3.277e-16 ***
dry_weight_gutted  0.738  1   7.6617 0.0122477 *
parasitized        2.267  1  23.5282 0.0001111 ***
Residuals          1.831 19
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Masfjorden with interaction:

```
> mas_gonadF <- lm(trans_gonad ~ dry_weight_gutted * parasitized,
+                  weights = sample_wt, data = effect_mas_F.df)
> Anova(mas_gonadF, type = "III")
Anova Table (Type III tests)

Response: trans_gonad
                              Sum Sq Df    F value  Pr(>F)
(Intercept)                  185.894  1 19495.2647 < 2e-16 ***
dry_weight_gutted              1.697  1   177.9326 < 2e-16 ***
parasitized                    0.045  1     4.7541 0.03259 *
dry_weight_gutted:parasitized  0.084  1     8.7694 0.00418 **
Residuals                      0.667 70
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Fensfjorden with interaction:

```
> fen_gonadF <- lm(trans_gonad ~dry_weight_gutted * parasitized,
+                  weights = sample_wt, data = effect_fens_F.df)
> Anova(fen_gonadF, type = "III")
Anova Table (Type III tests)

Response: trans_gonad
                              Sum Sq Df  F value    Pr(>F)
(Intercept)                  21.2989  1 633.9169 < 2.2e-16 ***
dry_weight_gutted             0.2005  1   5.9675  0.019331 *
parasitized                   0.2877  1   8.5615  0.005766 **
dry_weight_gutted:parasitized 0.0002  1   0.0064  0.936652
Residuals                     1.2768 38
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Fensfjorden without interaction:

```
> fen_gonadF2 <- lm(trans_gonad ~ dry_weight_gutted + parasitized,
+                   weights = sample_wt, data = effect_fens_F.df)
> Anova(fen_gonadF2, type = "III")
Anova Table (Type III tests)

Response: trans_gonad
                  Sum Sq Df F value    Pr(>F)
(Intercept)       26.8752  1 820.797 < 2.2e-16 ***
dry_weight_gutted  0.2640  1   8.063  0.007141 **
parasitized        2.1023  1  64.207 9.097e-10 ***
Residuals          1.2770 39
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Linear relationship of liver weight and dried gutted weight of males:

Sørfjorden with interaction:

```
> Sør_liver_M <- lm(trans_liver  ~ dry_weight_gutted * parasitized,
+                   weights = sample_wt, data = effect_sor_M.df)
> Anova(Sør_liver_M, type = "III")
Anova Table (Type III tests)

Response: trans_liver
                             Sum Sq Df  F value    Pr(>F)
(Intercept)                  118489  1 187.4133 < 2.2e-16 ***
dry_weight_gutted              7008  1  11.0853  0.001819 **
parasitized                     320  1   0.5061  0.480773
dry_weight_gutted:parasitized    16  1   0.0258  0.873109
Residuals                     26554 42
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Sørfjorden without interaction:

```
> Sør_liver_M2 <- lm(trans_liver  ~ dry_weight_gutted + parasitized,
+                    weights = sample_wt, data = effect_sor_M.df)
> Anova(Sør_liver_M2, type = "III")
Anova Table (Type III tests)

Response: trans_liver
                  Sum Sq Df  F value    Pr(>F)
(Intercept)       121223  1 196.1826 < 2.2e-16 ***
dry_weight_gutted   7263  1  11.7549  0.001349 **
parasitized         3642  1   5.8946  0.019447 *
Residuals          26570 43
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Osterfjorden with interaction:

```
> Ost_liver_M <- lm(trans_liver  ~ dry_weight_gutted * parasitized,
+                   weights = sample_wt, data = effect_ost_M.df)
> Anova(Ost_liver_M, type = "III")
Anova Table (Type III tests)

Response: trans_liver
                             Sum Sq Df   F value    Pr(>F)
(Intercept)                  64.920  1 3613.2599 < 2.2e-16 ***
dry_weight_gutted             0.189  1   10.4921  0.005939 **
parasitized                   0.001  1    0.0566  0.815408
dry_weight_gutted:parasitized 0.014  1    0.7991  0.386475
Residuals                     0.252 14
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Osterfjorden without interaction:

```
> Ost_liver_M2 <- lm(trans_liver  ~ dry_weight_gutted + parasitized,
+                    weights = sample_wt, data = effect_ost_M.df)
> Anova(Ost_liver_M2, type = "III")
Anova Table (Type III tests)

Response: trans_liver
                 Sum Sq Df  F value    Pr(>F)
(Intercept)      65.532  1 3696.841 < 2.2e-16 ***
dry_weight_gutted  0.199  1   11.251  0.004348 **
parasitized        0.192  1   10.845  0.004928 **
Residuals          0.266 15
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Masfjorden with interaction:

```
> Mas_liver_M <- lm(trans_liver  ~  dry_weight_gutted * parasitized,
+                    weights = sample_wt, data = effect_mas_M.df)
> Anova(Mas_liver_M, type = "III")
Anova Table (Type III tests)

Response: trans_liver
                              Sum Sq Df    F value    Pr(>F)
(Intercept)                  110.697  1 85425.8957 < 2.2e-16 ***
dry_weight_gutted              0.088  1    67.6199 5.661e-11 ***
parasitized                    0.001  1     0.6406    0.4271
dry_weight_gutted:parasitized  0.000  1     0.0002    0.9890
Residuals                      0.067 52
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Masfjorden without interaction:

```
> Mas_liver_M2 <- lm(trans_liver  ~ dry_weight_gutted + parasitized,
+                     weights = sample_wt, data = effect_mas_M.df)
> Anova(Mas_liver_M2, type = "III")
Anova Table (Type III tests)

Response: trans_liver
                  Sum Sq Df    F value    Pr(>F)
(Intercept)       113.387  1 89184.2145 < 2.2e-16 ***
dry_weight_gutted   0.090  1    70.8097 2.447e-11 ***
parasitized         0.004  1     3.5185    0.0662 .
Residuals           0.067 53
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Fensfjorden with interaction:

```
> fen_liver_M <- lm(trans_liver  ~ dry_weight_gutted * parasitized,
+                   weights = sample_wt, data = effect_fens_M.df)
> Anova(fen_liver_M, type = "III")
Anova Table (Type III tests)

Response: trans_liver
                              Sum Sq Df    F value    Pr(>F)
(Intercept)                  26.2560  1 22806.2389 < 2.2e-16 ***
dry_weight_gutted             0.0104  1     8.9944  0.005037 **
parasitized                   0.0020  1     1.7324  0.196907
dry_weight_gutted:parasitized 0.0005  1     0.3937  0.534531
Residuals                     0.0391 34
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Fensfjorden without interaction:

```
> fen_liver_M2 <- lm(trans_liver  ~  dry_weight_gutted + parasitized,
+                    weights = sample_wt, data = effect_fens_M.df)
> Anova(fen_liver_M2, type = "III")
Anova Table (Type III tests)

Response: trans_liver
                  Sum Sq Df    F value    Pr(>F)
(Intercept)       28.0259  1 24772.6683 < 2.2e-16 ***
dry_weight_gutted  0.0099  1     8.7814  0.005443 **
parasitized        0.0044  1     3.8949  0.056370 .
Residuals          0.0396 35
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Linear relationship of liver weight and dried gutted weight of females:

Sørfjorden with interaction:

```
> Sør_liver_F <- lm(trans_liver ~ dry_weight_gutted * parasitized,
+                   weights = sample_wt, data = effect_sor_F.df)
> Anova(Sør_liver_F, type = "III")
Anova Table (Type III tests)

Response: trans_liver
                              Sum Sq Df   F value    Pr(>F)
(Intercept)                  233.818  1 3657.4860 < 2.2e-16 ***
dry_weight_gutted              3.431  1   53.6692 2.497e-08 ***
parasitized                    0.000  1    0.0017    0.9672
dry_weight_gutted:parasitized  0.124  1    1.9456    0.1727
Residuals                      2.046 32
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Sørfjorden without interaction:

```
> Sør_liver_F2 <- lm(trans_liver  ~ dry_weight_gutted + parasitized,
+                    weights = sample_wt, data = effect_sor_F.df)
> Anova(Sør_liver_F2, type = "III")
Anova Table (Type III tests)

Response: trans_liver
                  Sum Sq Df  F value    Pr(>F)
(Intercept)       258.995  1 3938.453 < 2.2e-16 ***
dry_weight_gutted   4.249  1   64.620 2.825e-09 ***
parasitized         1.137  1   17.288 0.0002144 ***
Residuals           2.170 33
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Osterfjorden with interaction:

```
> Ost_liver_F <- lm(trans_liver  ~ dry_weight_gutted * parasitized,
+                   weights = sample_wt, data = effect_ost_F.df)
> Anova(Ost_liver_F, type = "III")
Anova Table (Type III tests)

Response: trans_liver
                              Sum Sq Df  F value    Pr(>F)
(Intercept)                  13309.3  1 187.8574 5.774e-11 ***
dry_weight_gutted             1402.6  1  19.7975 0.0003097 ***
parasitized                    119.4  1   1.6848 0.2106758
dry_weight_gutted:parasitized   32.0  1   0.4512 0.5103186
Residuals                     1275.3 18
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Osterfjorden without interaction:

```
> Ost_liver_F2 <- lm(trans_liver  ~ dry_weight_gutted + parasitized,
+                    weights = sample_wt, data = effect_ost_F.df)
> Anova(Ost_liver_F2, type = "III")
Anova Table (Type III tests)

Response: trans_liver
                  Sum Sq Df  F value    Pr(>F)
(Intercept)       15077.0  1 219.1383 6.941e-12 ***
dry_weight_gutted  1724.3  1  25.0623 7.840e-05 ***
parasitized         175.0  1   2.5429    0.1273
Residuals          1307.2 19
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Masfjorden with interaction:

```
> Mas_liver_F <- lm(trans_liver  ~ dry_weight_gutted * parasitized,
+                   weights = sample_wt, data = effect_mas_F.df)
> Anova(Mas_liver_F, type = "III")
Anova Table (Type III tests)

Response: trans_liver
                              Sum Sq Df    F value    Pr(>F)
(Intercept)                  151.616  1 1.2349e+05 < 2.2e-16 ***
dry_weight_gutted              0.127  1 1.0339e+02 1.988e-15 ***
parasitized                    0.000  1 2.7500e-02    0.8689
dry_weight_gutted:parasitized  0.001  1 8.2000e-01    0.3683
Residuals                      0.086 70
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Masfjorden without interaction:

```
> Mas_liver_F2 <- lm(trans_liver  ~ dry_weight_gutted + parasitized,
+                    weights = sample_wt, data = effect_mas_F.df)
> Anova(Mas_liver_F2, type = "III")
Anova Table (Type III tests)

Response: trans_liver
                  Sum Sq Df    F value    Pr(>F)
(Intercept)       162.552  1 1.3273e+05 < 2.2e-16 ***
dry_weight_gutted   0.131  1 1.0723e+02 7.788e-16 ***
parasitized         0.002  1 1.5679e+00    0.2146
Residuals           0.087 71
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Fensfjorden with interaction:

```
> fen_liver_F <- lm(trans_liver  ~ dry_weight_gutted * parasitized,
+                   weights = sample_wt, data = effect_fens_F.df)
> Anova(fen_liver_F, type = "III")
Anova Table (Type III tests)

Response: trans_liver
                              Sum Sq Df    F value    Pr(>F)
(Intercept)                  17.3443  1 10891.8918 < 2.2e-16 ***
dry_weight_gutted             0.0395  1    24.8133 1.407e-05 ***
parasitized                   0.0044  1     2.7432    0.1059
dry_weight_gutted:parasitized 0.0022  1     1.3506    0.2524
Residuals                     0.0605 38
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Fensfjorden without interaction:

```
> fen_liver_F2 <- lm(trans_liver  ~ dry_weight_gutted + parasitized,
+                    weights = sample_wt, data = effect_fens_F.df)
> Anova(fen_liver_F2, type = "III")
Anova Table (Type III tests)

Response: trans_liver
                  Sum Sq Df    F value    Pr(>F)
(Intercept)       22.0431  1 13719.3519 < 2.2e-16 ***
dry_weight_gutted  0.0620  1    38.6172  2.61e-07 ***
parasitized        0.0040  1     2.4978    0.1221
Residuals          0.0627 39
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Linear relationship of heart weight and dried gutted weight:

Sørfjorden with interaction:

```
> sør_heart <- lm(trans_heart ~ dry_weight_gutted * parasitized,
+                 weights = sample_wt, data = effect_sor.df)
> Anova(sør_heart, type = "III")
Anova Table (Type III tests)

Response: trans_heart
                             Sum Sq Df   F value    Pr(>F)
(Intercept)                  4878.9  1 1139.3351 < 2.2e-16 ***
dry_weight_gutted              54.4  1   12.7047 0.0006225 ***
parasitized                     5.6  1    1.3055 0.2566542
dry_weight_gutted:parasitized   9.3  1    2.1706 0.1446455
Residuals                     338.3 79
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Sørfjorden without interaction:

```
> sør_heart2 <- lm(trans_heart  ~ dry_weight_gutted + parasitized,
+                  weights = sample_wt, data = effect_sor.df)
> Anova(sør_heart2, type = "III")
Anova Table (Type III tests)

Response: trans_heart
                  Sum Sq Df   F value    Pr(>F)
(Intercept)       5172.5  1 1190.4582 < 2.2e-16 ***
dry_weight_gutted   67.3  1   15.4974 0.0001753 ***
parasitized          2.2  1    0.4999 0.4816018
Residuals          347.6 80
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Masfjorden with interaction:

```
> mas_heart <- lm(trans_heart ~ dry_weight_gutted * parasitized,
+                 weights = sample_wt, data = effect_mas.df)
> Anova(mas_heart, type = "III")
Anova Table (Type III tests)

Response: trans_heart
                              Sum Sq  Df   F value Pr(>F)
(Intercept)                   3772.6   1 9412.4638 <2e-16 ***
dry_weight_gutted               45.3   1  113.0738 <2e-16 ***
parasitized                      0.1   1    0.2656 0.6072
dry_weight_gutted:parasitized    0.1   1    0.2894 0.5916
Residuals                       50.5 126
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Masfjorden without interaction:

```
> mas_heart2 <- lm(trans_heart ~ dry_weight_gutted + parasitized,
+                  weights = sample_wt, data = effect_mas.df)
> Anova(mas_heart2, type = "III")
Anova Table (Type III tests)

Response: trans_heart
                  Sum Sq  Df   F value Pr(>F)
(Intercept)       3935.9   1 9875.0600 <2e-16 ***
dry_weight_gutted   46.7   1  117.1898 <2e-16 ***
parasitized          0.0   1    0.0084  0.927
Residuals           50.6 127
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Fensfjorden with interaction:

```
> fen_heart <- lm(trans_heart ~ dry_weight_gutted * parasitized,
+                 weights = sample_wt, data = effect_fens.df)
> Anova(fen_heart, type = "III")
Anova Table (Type III tests)

Response: trans_heart
                              Sum Sq Df    F value    Pr(>F)
(Intercept)                   36.020  1 3.7658e+05 < 2.2e-16 ***
dry_weight_gutted              0.002  1 1.6971e+01 9.571e-05 ***
parasitized                    0.000  1 1.4372e+00    0.2343
dry_weight_gutted:parasitized  0.000  1 9.0180e-01    0.3453
Residuals                      0.007 76
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Fensfjorden without interaction:

```
> fen_heart2 <- lm(trans_heart ~ dry_weight_gutted + parasitized,
+                  weights = sample_wt, data = effect_fens.df)
> Anova(fen_heart2, type = "III")
Anova Table (Type III tests)

Response: trans_heart
                  Sum Sq Df    F value    Pr(>F)
(Intercept)       40.976  1 4.2893e+05 < 2.2e-16 ***
dry_weight_gutted  0.002  1 2.2820e+01 8.332e-06 ***
parasitized        0.000  1 7.2560e-01    0.3969
Residuals          0.007 77
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Mean Otolith shape analysis:

Sørfjorden:

```
> sør.mod <- anova(cap.res1, by = "terms", step = 1000)
> sør.mod
Permutation test for capscale under reduced model
Terms added sequentially (first to last)
Permutation: free
Number of permutations: 999

Model: capscale(formula = getStdWavelet(shape) ~ getMasterlist(shape)$parasitized)
                                Df SumOfSqs      F Pr(>F)
getMasterlist(shape)$parasitized  1   1.2102 2.0571  0.053 .
Residual                         46  27.0625
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Osterfjorden:

```
> ost.mod <- anova(cap.res2, by = "terms", step = 1000)
> ost.mod
Permutation test for capscale under reduced model
Terms added sequentially (first to last)
Permutation: free
Number of permutations: 999

Model: capscale(formula = getStdWavelet(shape) ~ getMasterlist(shape)$parasitized)
                                Df SumOfSqs      F Pr(>F)
getMasterlist(shape)$parasitized  1   0.5171 1.2837  0.228
Residual                         18   7.2511
```

Masfjorden:

```
> mas.mod
Permutation test for capscale under reduced model
Terms added sequentially (first to last)
Permutation: free
Number of permutations: 999

Model: capscale(formula = getStdWavelet(shape) ~ getMasterlist(shape)$parasitized)
                                Df SumOfSqs    F Pr(>F)
getMasterlist(shape)$parasitized  1    0.665 1.05   0.39
Residual                         50   31.678
```

Fensfjorden:

```
> fens.mod <- anova(cap.res4, by = "terms", step = 1000)
> fens.mod
Permutation test for capscale under reduced model
Terms added sequentially (first to last)
Permutation: free
Number of permutations: 999

Model: capscale(formula = getStdWavelet(shape) ~ getMasterlist(shape)$parasitized)
                                Df SumOfSqs      F Pr(>F)
getMasterlist(shape)$parasitized  1   0.6512 1.0949  0.331
Residual                         34  20.2219
```

Analysis of otolith length with interaction:

```
> otolith_lenght_lm <- lm(otolith.length ~ parasitized * area + parasitized*sex, data = Data2)
> anova(otolith_lenght_lm)
Analysis of Variance Table

Response: otolith.length
                  Df Sum Sq  Mean Sq F value    Pr(>F)
parasitized        1 0.0213 0.021322  0.4692 0.4944348
area               3 0.9187 0.306246  6.7393 0.0002735 ***
sex                1 0.0037 0.003714  0.0817 0.7753728
parasitized:area   3 0.0574 0.019123  0.4208 0.7383380
parasitized:sex    1 0.0043 0.004303  0.0947 0.7587412
Residuals        146 6.6345 0.045442
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Analysis of otolith length without interaction:

```
> otolith_lenght_lm2 <- lm(otolith.length ~ parasitized  + sex + area, data = Data2)
> anova(otolith_lenght_lm2)
Analysis of Variance Table

Response: otolith.length
             Df Sum Sq  Mean Sq F value    Pr(>F)
parasitized   1 0.0213 0.021322  0.4776 0.4905660
sex           1 0.0000 0.000002  0.0001 0.9940773
area          3 0.9224 0.307483  6.8879 0.0002236 ***
Residuals   150 6.6962 0.044641
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Post-hoc for otolith length:

```
> emmeans(otolith_lenght_lm2, specs =  pairwise ~ area, type = "response")
$emmeans
 area       emmean     SE  df lower.CL upper.CL
 Fensfjord    1.54 0.0354 150     1.47     1.61
 Masfjord     1.43 0.0294 150     1.37     1.49
 Osterfjord   1.28 0.0478 150     1.19     1.38
 Sørfjord     1.38 0.0311 150     1.32     1.44

Results are averaged over the levels of: parasitized, sex
Confidence level used: 0.95

$contrasts
 contrast               estimate     SE  df t.ratio p.value
 Fensfjord - Masfjord     0.1068 0.0458 150   2.331  0.0956
 Fensfjord - Osterfjord   0.2522 0.0590 150   4.275  0.0002
 Fensfjord - Sørfjord     0.1531 0.0466 150   3.284  0.0069
 Masfjord - Osterfjord    0.1454 0.0558 150   2.608  0.0488
 Masfjord - Sørfjord      0.0463 0.0424 150   1.092  0.6951
 Osterfjord - Sørfjord   -0.0991 0.0562 150  -1.762  0.2957

Results are averaged over the levels of: parasitized, sex
P value adjustment: tukey method for comparing a family of 4 estimates
```

Analysis of otolith width with interaction:

```
> otolith_width_lm <- lm(otolith.width ~ parasitized * area + parasitized * sex, data = Data2)
> anova(otolith_width_lm)
Analysis of Variance Table

Response: otolith.width
                 Df  Sum Sq Mean Sq F value    Pr(>F)
parasitized       1  0.0000 0.00003  0.0003 0.9862695
area              3  1.7193 0.57310  6.6391 0.0003103 ***
sex               1  0.0005 0.00048  0.0055 0.9409255
parasitized:area  3  0.0220 0.00734  0.0850 0.9681499
parasitized:sex   1  0.0025 0.00246  0.0285 0.8660820
Residuals       146 12.6029 0.08632
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Analysis of otolith length without interaction:

```
> otolith_width_lm2 <- lm(otolith.width ~ parasitized + area + sex, data = Data2)
> anova(otolith_width_lm2)
Analysis of Variance Table

Response: otolith.width
             Df  Sum Sq Mean Sq F value    Pr(>F)
parasitized   1  0.0000 0.00003  0.0003 0.9860956
area          3  1.7193 0.57310  6.8078 0.0002473 ***
sex           1  0.0005 0.00048  0.0057 0.9401784
Residuals   150 12.6274 0.08418
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Post-hoc for otolith width:

```
> emmeans(otolith_width_lm2, specs = pairwise ~  area, type = "response")
$emmeans
 area       emmean     SE  df lower.CL upper.CL
 Fensfjord    1.96 0.0487 150     1.87     2.06
 Masfjord     1.79 0.0404 150     1.71     1.87
 Osterfjord   1.60 0.0656 150     1.47     1.73
 Sørfjord     1.79 0.0426 150     1.71     1.88

Results are averaged over the levels of: parasitized, sex
Confidence level used: 0.95

$contrasts
 contrast               estimate     SE  df t.ratio p.value
 Fensfjord - Masfjord    1.69e-01 0.0629 150   2.691  0.0393
 Fensfjord - Osterfjord  3.59e-01 0.0810 150   4.429  0.0001
 Fensfjord - Sørfjord    1.69e-01 0.0640 150   2.644  0.0444
 Masfjord - Osterfjord   1.90e-01 0.0766 150   2.475  0.0679
 Masfjord - Sørfjord     6.00e-07 0.0582 150   0.000  1.0000
 Osterfjord - Sørfjord  -1.90e-01 0.0772 150  -2.454  0.0716

Results are averaged over the levels of: parasitized, sex
P value adjustment: tukey method for comparing a family of 4 estimates
```

Analysis of otolith age:

Sørfjorden with interaction:

```
> aov_sør <- aov(age ~ sex * parasitized, data = growth_sør.df)
> summary(aov_sør)
                Df Sum Sq Mean Sq F value Pr(>F)
sex              1   0.37  0.3750   0.482  0.491
parasitized      1   0.02  0.0208   0.027  0.871
sex:parasitized  1   0.17  0.1667   0.214  0.646
Residuals       44  34.25  0.7784
```

Sørfjorden without interaction:

```
> aov_sør <- aov(age ~ sex + parasitized, data = growth_sør.df)
> summary(aov_sør)
            Df Sum Sq Mean Sq F value Pr(>F)
sex          1   0.37  0.3750   0.490  0.487
parasitized  1   0.02  0.0208   0.027  0.870
Residuals   45  34.42  0.7648
```

Osterfjorden with interaction:

```
> aov_ost <- aov(age ~ sex * parasitized, data = growth_ost.df)
> summary(aov_ost)
                Df Sum Sq Mean Sq F value Pr(>F)
sex              1  4.002   4.002   4.051 0.0613 .
parasitized      1  0.050   0.050   0.051 0.8249
sex:parasitized  1  0.688   0.688   0.696 0.4163
Residuals       16 15.810   0.988
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Osterfjorden without interaction:

```
> aov_ost <- aov(age ~ sex + parasitized, data = growth_ost.df)
> summary(aov_ost)
            Df Sum Sq Mean Sq F value Pr(>F)
sex          1  4.002   4.002   4.124 0.0582 .
parasitized  1  0.050   0.050   0.052 0.8231
Residuals   17 16.498   0.970
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Masfjorden with interaction:

```
> aov_mas <- aov(age ~ sex * parasitized, data = growth_mas.df)
> summary(aov_mas)
                Df Sum Sq Mean Sq F value Pr(>F)
sex              1   3.82   3.818   3.193 0.0803 .
parasitized      1   3.25   3.250   2.718 0.1057
sex:parasitized  1   1.60   1.595   1.334 0.2538
Residuals       48  57.39   1.196
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Masfjorden without interaction:

```
> aov_mas <- aov(age ~ sex + parasitized, data = growth_mas.df)
> summary(aov_mas)
            Df Sum Sq Mean Sq F value Pr(>F)
sex          1   3.82   3.818   3.172 0.0811 .
parasitized  1   3.25   3.250   2.700 0.1068
Residuals   49  58.99   1.204
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Fensfjorden with interaction:

```
> aov_fens <- aov(age ~ sex * parasitized, data = growth_fens.df)
> summary(aov_fens)
                Df Sum Sq Mean Sq F value Pr(>F)
sex              1  0.023  0.0231   0.040  0.842
parasitized      1  0.444  0.4444   0.773  0.386
sex:parasitized  1  0.698  0.6984   1.215  0.279
Residuals       32 18.390  0.5747
```

Fensfjorden without interaction:

```
> aov_fens <- aov(age ~ sex + parasitized, data = growth_fens.df)
> summary(aov_fens)
            Df Sum Sq Mean Sq F value Pr(>F)
sex          1  0.023  0.0231   0.040  0.843
parasitized  1  0.444  0.4444   0.768  0.387
Residuals   33 19.088  0.5784
```

Analysis of parasite volume relative to host:

Correlation of total parasite volume:

```
> cor_tot_vol <- cor.test(volume.df$volume_fish,
+                         volume.df$par_tot_ml, method=c("pearson"))
> cor_tot_vol

        Pearson's product-moment correlation

data:  volume.df$volume_fish and volume.df$par_tot_ml
t = -0.006282, df = 7, p-value = 0.9952
alternative hypothesis: true correlation is not equal to 0
95 percent confidence interval:
 -0.6654467  0.6627925
sample estimates:
         cor
-0.002374353
```

Correlation of the external parasite volume:

```
> cor_ext_vol <- cor.test(volume.df$volume_fish,
+                         volume.df$par_extern_ml, method=c("pearson"))
> cor_ext_vol

        Pearson's product-moment correlation

data:  volume.df$volume_fish and volume.df$par_extern_ml
t = -0.23004, df = 7, p-value = 0.8246
alternative hypothesis: true correlation is not equal to 0
95 percent confidence interval:
 -0.7099029  0.6127518
sample estimates:
        cor
-0.08661859
```

Correlation of the internal parasite volume:

```
> cor_int_vol <- cor.test(volume.df$volume_fish,
+                         volume.df$par_intern_ml, method=c("pearson"))
> cor_int_vol

        Pearson's product-moment correlation

data:  volume.df$volume_fish and volume.df$par_intern_ml
t = -0.49037, df = 7, p-value = 0.6389
alternative hypothesis: true correlation is not equal to 0
95 percent confidence interval:
 -0.7549863  0.5482339
sample estimates:
       cor
-0.1822405
```

Correlation of the internal and external parasite volume:

```
> cor_par_vol <- cor.test(volume.df$par_extern_ml,
+                         volume.df$par_intern_ml, method=c("pearson"))
> cor_par_vol

        Pearson's product-moment correlation

data:  volume.df$par_extern_ml and volume.df$par_intern_ml
t = 2.8235, df = 7, p-value = 0.02565
alternative hypothesis: true correlation is not equal to 0
95 percent confidence interval:
 0.1272332 0.9388465
sample estimates:
      cor
0.7296968
```