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# The prevalence of Corynosoma parasite worms in the great cormorants and the Baltic herring in the northern Baltic Sea, Finland

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ABSTRACT

During 2014–2019, the prevalence of *Corynosoma* spp., a parasite species in great cormorants (*Phalacrocorax carbo* spp.) and in Baltic herring (*Clupea harengus membras*), was studied in the Archipelago and the Bothnian Seas of the northern Baltic Sea. These results suggest that cormorants may act as a definitive host for these acanthocephalan parasites. Adults were more infected with the parasites than juveniles, which could be due to their larger size. A lower prevalence of *Corynosoma* spp. in juveniles may be because smaller cormorants eat smaller fish that have less parasites. We found that the most abundant corynosoma species in both the Baltic herring and cormorants were *Corynosoma semerme*, whereas only a few individuals of *C. strumosum* and only one *C. magdaleni* were found. The prevalence of corynosoma in herring increased from 2014 to 2018, and individuals in the Bothnian Sea were infected less frequently than herring in the Archipelago Sea. Results also showed that infected herring individuals were generally larger than non-infected individuals, which could be explained by their size and their feeding habits. Currently, the changing environment of the Baltic Sea may cause an effect on the herring making them more susceptible to infections. Our results, therefore, emphasize the importance of the regular monitoring of infections and the parasite-host relationships in the Baltic Sea.

## 1. Introduction

Acanthocepahalans or thorny-headed worms are intestinal parasites that occur in vertebrates (Valtonen et al. 2012). Their life cycles include an amphipod as the intermediate host and a fish as a definitive host. Acanthocephalans of the genus *Corynosoma* mature in the intestines of mammals such as seals. They require a fish as the paratenic host to transfer the larvae from the amphipod to the definitive host. As Valtonen et al. (2012) noted, in the Baltic Sea, corynosoma use *Monoporeia affinis* Lindström, a small bottom-dwelling amphipod, as the intermediate host. The cystacanths are capsulated in the body cavity of the fish and can remain there for years waiting for a suitable definitive host to eat the paratenic host. Many fish species eat *M. affinis* and get infected with the corynosoma cystacanths. In the Baltic Sea, the primary hosts are the grey seal (*Halichoerus grypus*), the Baltic ringed seal (*Phoca hispida*) (Sinisalo and Valtonen 2003) and marine birds (e.g. Van Cleave 1945). Corynosoma are also found in the great cormorant (*Phalacrocorax carbo* Linnaeus) in Germany (Oßmann 2008). They mature and mate in the intestines of the host, and new acanthor larvae are released in the feces. Internal parasites may affect the health of the host and are linked with, for example, septicemia and perinatal death (Siebert et al. 2007). However, studies performed on seals suggest that even a heavy corynosoma infection does not harm the host (Valtonen 1983). Humans are infected rarely with corynosoma and this is linked to eating raw fish such as sushi and sashimi (Fujita et al. 2016; Takahashi et al. 2016).

In 2014, a few individuals of helminth parasites were found for the first time in the Baltic herring (*Clupea harengus membras*) during routine sampling conducted annually from May through July as part of a long-term monitoring program of the herring population spawning in the Archipelago Sea, northern Baltic Sea. Based on the external characteristics and location in the body cavity of the fish, the parasites were preliminarily determined to be acanthocephalans of the genus *Corynosoma* (e.g. Leidenberger et al. 2019). Corynosoma parasites have also been previously found in grey seals and the Baltic ringed seals as well as in various fish species including the Baltic herring in the northern Baltic Sea (Helle and Valtonen 1981; Sinisalo and Valtonen 2003).

The sudden emergence of corynosoma infections in the intensively monitored herring population is presumed to be linked to the climate change-induced changes that have occurred in the brackish-water ecosystem of the Baltic Sea in the past decades (e.g. Rajasilta et al.

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2018, 2022).

The aim of this study was to identify the parasites found in the Baltic herring in order to determine if herring can act as a paratenic host for the corynosoma species, before their entry into a higher-order host in the upper-food web. Moreover, we wanted to find out whether the great cormorant, besides seals and fish (e.g., Valtonen 1983; Sinisalo and Valtonen 2003), can also play a role in acting as a host for the corynosoma species found in the area. If this is the case and the home range of infected cormorants and grey seals overlaps with that of the infected herring, the presence of parasites could be a biological tag indicating the home range of the herring populations. For the identification of the parasite species, we used DNA sequencing, which is used in various ecological surveys and, recently, has become a standard method in environmental research and species identification (e.g., Altschul et al. 1990). As a genetic marker, we used the mitochondrial cytochrome *c* oxidase gene (COI) which is widely used in the molecular identification of the species (Herbert et al. 2003), and shown to be species-specific also among the corynosoman parasites (García-Varela et al., 2009; Waindok et al. 2018).

## 2. Materials and methods

### *2.1. The study area*

The Baltic Sea is a semi-enclosed brackish water sea basin (Nehring and Matthäus 1991) with an overall region of 415 023 km$^2$ and a mean depth of 52 m (Wasmund et al. 1996). There is a clear south-northeast salinity gradient varying from 15 to 20 PSU in the Danish Straits to only 1 to 2 PSU in the Bothnian Bay. Salinity affects particularly the distribution and abundance of species, which are of either marine or freshwater origin (e.g., Leppäkoski et al. 1999). The Archipelago Sea (59°45′–60°45′N and 21°00′–23°00′E) is a mosaic of about 60 000 islands and rocky islets between the Baltic Proper and the Bothnian Sea (Fig. 1). With a mean depth of 24 m, the shallow and sheltered area offers the cormorants a favorable environment with numerous places to build a nest and to establish a colony. Seasonality is a typical feature of the Archipelago Sea, and in winters, the probability of a 1–5-month-long ice cover is 90%, but in summers, the seawater temperature can reach 20 °C (Leppäranta and Myrberg, 2009). The Baltic Sea environment is also affected by various anthropogenic processes and human activities (Leppäkoski et al. 1999). For instance, the seawater salinity has decreased and the surface temperature increased in the study region (Fig. 2) due to increased rainfall and global warming induced by climate change. These changes affect individual species both indirectly and directly causing the abundance and distribution patterns of the species to change both locally and in the whole Baltic Sea (Vuorinen et al. 2015; Reusch et al. 2018).

From the coastline of southwest Finland, we chose three separate sampling locations to collect the materials needed to accomplish the study, but the Archipelago Sea was considered to be the main area of the sampling (Fig. 1). Moreover, a relevant criterion for the selected sites was that cormorants were found commonly in the area and that the cormorants used the locations either as a feeding area and/or as a breeding ground, i.e., permanent cormorant colonies were found nearby. The main site at the Archipelago Sea (Site “A”; Fig. 1) had the widest sampling area, as it extended some 100 km in an east-west direction and consisted of five separate sub-sites. In addition to cormorants, also seals, especially the grey seal, were found commonly in all sampling areas.

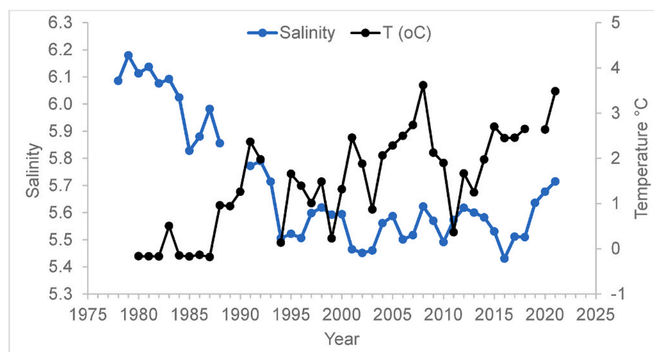


**Fig. 2.** Mean annual salinity (PSU) and temperature (T, °C) of the winter months (January–April) in the Bothnian Sea at 0–50 m depth during 1980–2021. Data from ICES Oceanographic dataset, 2021. ICES, Copenhagen.


**Fig. 1.** Map showing the sampling sites in the northern Baltic Sea: A = Archipelago Sea, B = Uusikaupunki, C = Merikarvia. The sampling locations in region A: 1 = Taivassalo, 2 = Velkua trawl area, 3 = western Rymättylä, 4 = northern Airisto Inlet, 5 = Peimari.

### 2.2. Sampling and treatment of herring

The herring samples were collected from the catches of commercial trawlers operating offshore or from the trap nets, which catch spawning herring on the coast. In the present study, 7002 individual herring were examined (Table 1). During 2014–2017, the herring samples were collected only from the Airisto Inlet and Velkua areas and, in 2018, sampling was extended also to the southern Bothnian Sea in order to get a wider perspective of the distribution of corynosoma in the Baltic herring populations in the northern Baltic Sea. The samples were collected during the spawning season between early May and early July with some additional winter samples in 2019. A random sample of 100–200 fish was taken from the trap net or trawl catch of herring and stored in the freezer at −20 °C until preparation. Before preparation, the samples were thawed at room temperature. Each fish was weighed to an accuracy of 0.1 g, total body length was measured to the nearest 1 mm, and otoliths were collected and stored for age determination following the procedure developed by Peltonen et al. (2002). The abdominal cavities of the fish were dissected, their sex was determined, and the body cavities were inspected visually for the acanthocephalan parasites (Fig. 3). When found, their number was counted, and, from a randomized subset of 20–30 fish per total sample, the parasites were collected and preserved in 70% ethanol for the DNA analysis.

### 2.3. Sampling and treatment of cormorants

In 2018 and 2019, a total of 65 cormorants were hunted for this study under a special license granted by the authorities of the *Southwest Finland Centre for Economic Development, Transport and the Environment* (VARELY/362/2018 and VARELY/3509/2019). The birds were shot by licensed local fishermen following strict prevailing hunting regulations for the protected animals. Altogether, 15 cormorants were randomly harvested from the northern Airisto Inlet area and 50 cormorants in the vicinity of a breeding colony of Tiiraletto, Kustavi (Table 2).

For preservation, the birds were frozen at −20 °C shortly after shooting. Approximately 24 h before dissection, the birds were brought to room temperature to thaw. The birds were weighed to the nearest 1.0 g, and body lengths were measured from the tip of the beak to the tail tip with an accuracy of 1.0 cm. The lengths of the wingspans were measured. During the dissection, the age of the birds was determined according to Baker (1993). The bird heads were removed and preserved at −20 °C for later identification of its subspecies. The abdominal cavities of the birds were dissected, and the pectoralis muscle, liver, and stomach were removed and stored at −20 °C for later analysis. Finally, the intestines were removed, and their sex was determined from the gonads.

For parasite analysis, the intestines were first thawed at room temperature for 24 h before the preparation. Then, the intestines were dissected starting from the cloaca. The interior of the intestine was thoroughly cleaned by a gentle water jet, and then the intestine was inspected for the parasites (Fig. 3). The acanthocephalans found were counted and removed carefully with tweezers and preserved in 70% ethanol in 1.5 mL or 2 mL Eppendorf tubes for the DNA analysis.

Quantitative descriptors of parasite occurrences were calculated according to Bush et al. (1997). The prevalence was calculated by dividing the number of infected host individuals by the total number of hosts. The intensity of infection was calculated by counting the number of corynosoma individuals per infected host.

**Fig. 3.** Acanthocephala parasites in the body cavity of a herring (left; the red circle indicates the position of worms) and on the inner surface of the intestine of a cormorant (right). The upper photo indicates the size of parasites compared to a match (photos: J. Sahlstén). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

**Table 2**
Number of Great cormorant individuals (n) examined during the study years 2018–2019 and study areas in the northern Baltic Sea.

| Year | Area | n (individuals) | n (females/males) | n (adults/juveniles) |
|---|---|---|---|---|
| 2018 | Airisto | 6 | 2/4 | 3/3 |
| 2019 | Airisto | 9 | 3/6 | 7/2 |
| 2019 | Kustavi | 50 | 27/23 | 2/48 |

### 2.4. DNA extraction

DNA analyses were performed using the QIAGEN Blood N Tissue kit and following the provided protocol with minor adjustments. Instead of 100 μL of Buffer AE, only 50 μL was used to increase the DNA concentration in the final product. Only one corynosoma worm from each fish sample and two from each infected cormorant were used to extract DNA by the PCR method. The worm was split with a surgical scalpel, and a piece of a Parafilm was used for protection on a cutting board to avoid surface contamination. The worm's anterior was stored in 99% ethanol

**Table 1**
Study sites and area for the Baltic herring samples, the mean of individuals in the fish samples, the proportional *Corynosoma* spp. prevalence, and its 95% confidence interval.

| Year | Site | Area | Herring (n) | Parasites (n) | Prevalence (%) | 95% CI |
|---|---|---|---|---|---|---|
| 2014 | A | 4. Northern Airisto Inlet | 750 | 83 | 11.1 | 8.9–13.5 |
| 2015 | A | 4. Northern Airisto Inlet | 1031 | 151 | 14.6 | 12.5–17.0 |
| 2016 | A | 4. Northern Airisto Inlet | 1018 | 38 | 3.7 | 2.6–5.1 |
| 2017 | A | 2. Velkua trawl area | 175 | 6 | 3.4 | 1.3–7.3 |
| 2017 | A | 4. Northern Airisto Inlet | 698 | 134 | 19.2 | 16.3–22.3 |
| 2018 | A | 1. Taivassalo | 570 | 111 | 19.5 | 16.3–23.0 |
| 2018 | B | Uusikaupunki | 542 | 82 | 15.1 | 12.2–18.4 |
| 2018 | C | Merikarvia | 986 | 130 | 13.2 | 11.1–15.5 |
| 2018 | A | 3. Western Rymättylä | 348 | 84 | 24.1 | 19.7–29.0 |
| 2018 | A | 3. Rymättylä trawl area | 635 | 46 | 7.2 | 5.4–9.5 |
| 2018 | A | 5. Peimari open sea | 249 | 55 | 22.1 | 17.1–27.8 |

in a separate Eppendorf tube for possible later morphological identification, and the tail was used for DNA extraction. After DNA extraction, MyTaq RedMix and 15 µl of forward primer (LCO1490GV: AGT TCT AAT CAT AAR GAT ATY GG (Nadler et al. 2006)) and 15 µl of reverse primer (HCO2198: TAA ACT TCA GGG TGA CCA AAA AAT (Folmer et al. 1994)) were used for PCR. After PCR, the final product was purified using 1 µL of Shrimp Alkaline Phosphatase (rSAP) and 1 µL of Exonuclease I (Exo I). The final product was then pipetted into two separate wells in a 96-well microplate (7.5 µL each) and delivered to the Macrogen lab (Amsterdam, Netherlands) for the final sequencing. There, the received sequences were first cleaned, and the forward and reverse sequences were combined using Geneious R6 6.1.8 software. Final sequences were compared to known corynosoma sequences using BLAST Basic Local Alignment Search Tool, which is available at the National Center for Biotechnology Information (Altschul et al. 1990).

### 2.5. Statistical analysis

All statistical analyses were conducted by using *RStudio* statistical software (version 1.3.1073, RStudio Team 2022). To investigate the factors affecting the likelihood of a corynosoma infection in cormorants, a generalized linear model (GLM, function "glm" in package lme4, Bates et al. 2015) was used with the logit link function. Binomial variables, called infected = 1 and non-infected = 0, were used as dependent variables, and by using a stepwise correction protocol (function "stepAIC" from R package MASS, Venables and Ripley, 2002), a best fitting model was constructed. The model fitting in each step was estimated by comparing the changes of the AIC value to reach the best parsimony of the model. Finally, the lowest AIC value proved to be a model with the effect of body length as the only explanatory variable for the corynosoma infection rate of the cormorants. Despite model fitting, the final GLM model was not perfectly fitted due to the skewed data, outliers, small sample size, and multiple variables. Thus, a Fisher's exact test (function "fisher.bintest" from package RVAideMemoire, Hervé, 2021) was also applied to test the differences in the prevalence of corynosoma in the cormorants in the Airisto and Kustavi areas, the sexes, and the age classes. In addition, either a parametric T-test or non-parametric Wilcoxon test was used to test the differences in body characteristics between sexes, sampling areas, age classes, and between infected and non-infected individuals. A Pearson's correlation test was used to test the relationship between the years, and the prevalence of corynosoma in the herring. A chi-squared test, or $\chi^2$-test, was used to the test the differences in prevalence among the locations.

## 3. Results

### 3.1. Prevalence of corynosoma in the herring

A total of 13.9% of herring caught from the Archipelago Sea and the Bothnian Sea were infected with corynosoma parasites. Their prevalence in herring varied between the years and study sites ranging from 3.4% to 24.1% (Table 3).

During 2014–2018, the prevalence of corynosoma infections in herring populations in the Archipelago Sea varied remarkably (Fig. 4). Despite the seemingly increasing trend, no statistically significant correlation between the years and prevalence existed (Pearson's correlation: $r = 0.57$, $p = 0.32$, $n = 5$), but when the year 2016, which had a much lower prevalence was omitted, there was a significant and positive correlation ($r = 1.0$, $p < 0.05$, $n = 4$).

**Table 3**
Study years and sites, the total number of great cormorant individuals studied (n), the number of infected individuals, the prevalence (%) and 95% confidence interval of corynosoma infections, and mean parasite intensity ($\bar{x}$).

| Year | Area | n (indiv.) | n (infected) | Preval % | 95% CI | $\bar{x}$ (intensity) |
|---|---|---|---|---|---|---|
| 2019 | Airisto | 9 | 5 | 55.6 | 21.2–86.3 | 29.4 |
| 2019 | Kustavi | 50 | 8 | 16.0 | 7.2–29.1 | 5.4 |
| 2018 | Airisto | 6 | 1 | 16.7 | 0.4–64.1 | 1 |

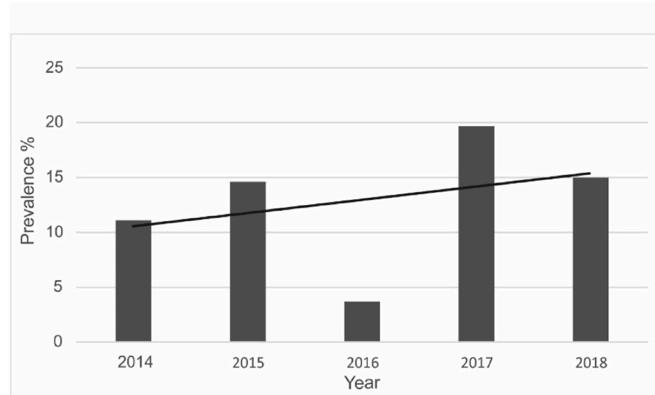


**Fig. 4.** Prevalence (%) of corynosoma infection in the Baltic herring in the "A" area (Archipelago Sea) from 2014 to 2018 (n = 7002). The black solid line expresses a linear trend: $y = 1.29x + 8.95$, $r = 0.34$.

In 2018, when the herring samples were collected from both the Bothnian Sea and the Archipelago Sea, fish in the Archipelago Sea were more likely to be infected with corynosoma ($\chi2$ test: $\chi2 = 26.16$, $n = 2695$, $df = 1$, $p < 0.001$). In the Bothnian Sea, less than 14% of herring were infected, whereas in the Archipelago Sea, more than 20% had these parasites (Fig. 5).

Herring in the Archipelago Sea were significantly larger than those in the Bothnian Sea (*t*-test, $t = 10.30$, $n = 2696$, $p < 0.001$). In the Archipelago Sea, the mean length was 16.1 cm, and, in the Bothnian Sea, it was 15.3 cm. Infected herring were significantly larger than non-infected herring (*t*-test, $t = -28.82$, $df = 1301.2$, $p < 0.05$) with the mean length of infected individuals being 17.5 cm, and in non-infected individuals, it was 15.6 cm (Fig. 6).

### 3.2. Prevalence of corynosoma in the cormorants

In total, 29.4% of cormorants were infected with corynosoma parasites. The data indicated that the prevalence was higher in Airisto than in the Kustavi area, but the difference was not statistically significant (Fisher's exact test, $n = 65$, $p = 0.07$). In the Airisto area, 40% of the cormorants were infected with 17% in 2018 and 56% in 2019, whereas in Kustavi, the respective rate was only 16% (Table 3).

There was no difference in the infection rates between sexes (Fisher's exact test, $n = 65$, $p = 0.37$), and 27.3% of males were infected, whereas

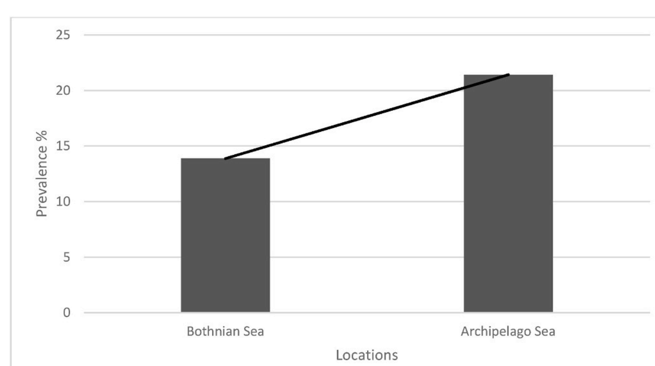


**Fig. 5.** Prevalence (%) of the corynosoma infection in the Baltic herring in the Bothnian Sea (n = 1528) and the Archipelago Sea in 2018 (n = 1167). The black solid line expresses a linear trend: $y = 7.55x + 6.33$, $r = 1.00$.

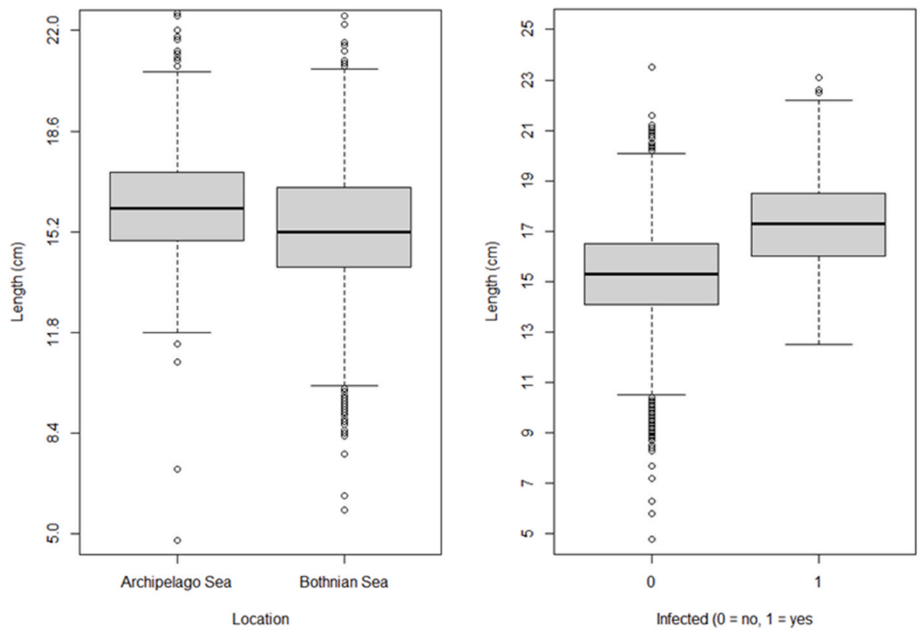


**Fig. 6.** Left: Body length of herring in the Archipelago Sea (n = 1167) and the Bothnian Sea (n = 1528) in 2018 and in the infected and non-infected herring (n = 7002). The black line represents the median length, and the grey box is the middle 50% of the data.

only 15.6% of females had an infection. Results also indicated that adult cormorants were more likely to be infected than juveniles, but the result was not statistically significant (Fisher's exact test, n = 65, $p = 0.10$). Some 41.7% of adult cormorants had corynosoma, whereas only 17.0% of juveniles had them.

The cormorants in the Airisto area were significantly larger in terms of body length (*t*-test, t = 2.19, df = 63, $p < 0.05$) as well as in terms of body weight (Wilcoxon test, W = 589, df = 63, $p < 0.05$) (Fig. 6). Male cormorants were larger than females, and adults were larger than juveniles (Fig. 7). Males were significantly larger in terms of wing length (Wilcoxon test, W = 116, n = 65, $p < 0.05$), body length (t = −7.66, df = 62.73, $p < 0.05$), and weight (Wilcoxon test, W = 168, n = 65, $p < 0.05$). Adults were significantly larger than juveniles in terms of wing length (Wilcoxon test, W = 504, n = 65, $p < 0.05$), body length (Wilcoxon test, W = 445, n = 65, $p < 0.05$), and weight (Wilcoxon test, W = 531, n = 65, $p < 0.05$) (Fig. 8).

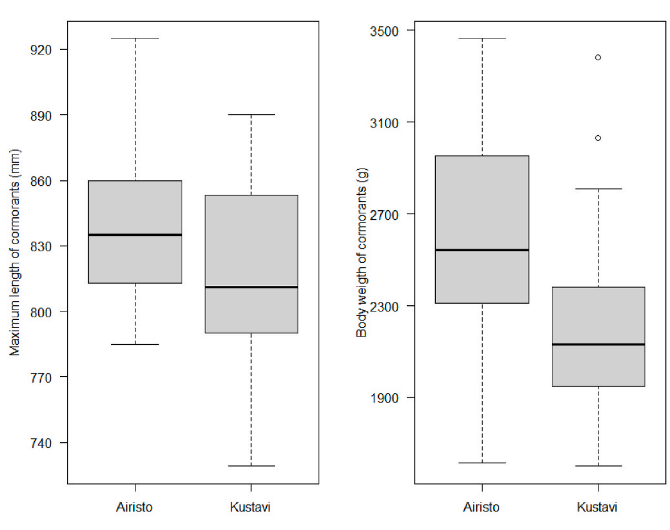


**Fig. 7.** Size differences of cormorants between Kustavi and Airisto in terms of body length and body weight (n = 65). The black line represents the median length and weight. The grey box represents the middle 50% of the data (n = 65).

No statistically significant differences between infected and non-infected cormorants in terms of wing length (t = 0.90, df = 18.37, $p = 0.38$), body length (t = 1.79, df = 22.05, $p = 0.09$), or weight (Wilcoxon test, W = 464, $p = 0.09$) existed, but the results indicated that infected individuals were generally larger (Fig. 9). The generalized linear model (GLM) indicated that female cormorants were less likely to get infected by corynosoma than males (Table 4).

### 3.3. DNA sequencing

We sequenced a total of 124 acanthocephalans collected from fish of the Archipelago Sea and the Bothnian Sea (88 and 36 herring, respectively). The results revealed that sequences matched with *C. semerme* (accession number MK11925) (Lisitsyna et al., 2019), *C. magdaleni* (accession number EF4678729) (García-Varela & Perez-Ponce de Leon 2008), and *C. strumosum* (accession number EF467871) (García-Varela & Perez-Ponce de Leon 2008) with more than 98.6% accuracy. In most cases they matched with 100% accuracy. The majority of parasites, 121 individuals, represented *C. semerme*, and only two specimens of *C. strumosum* and one specimen of *C. magdaleni* were found. Similarly, a total of 23 acanthocephalans from 14 cormorant individuals were sequenced, and based on these analyses, all acanthocephalans from cormorants represented specimens of *C. semerme*.

## 4. Discussion

Our main result showed that the great cormorant, besides seals, does act as a definitive host for the corynosoma thorny-headed worm species in the northern Baltic Sea. The herring's main predator, the cod (*Gadus morhua*), has almost disappeared from the northern sea areas (e.g., Heikinheimo 2008; Lindegren et al. 2011), while the populations of the two other predators, the grey seal and the great cormorant, have increased rapidly since the mid-20th century (Harding and Härkönen 1999; Lehikoinen 2003; HELCOM 2019). Cormorants nested on the Finnish coast for the first time in 1996, and by 2015, the nesting population was about 24 000 individuals (Ministry of the Environment, 2016). An increase in the host populations has probably led to the rise of corynosoma in the food webs as well. In addition, the quality of the

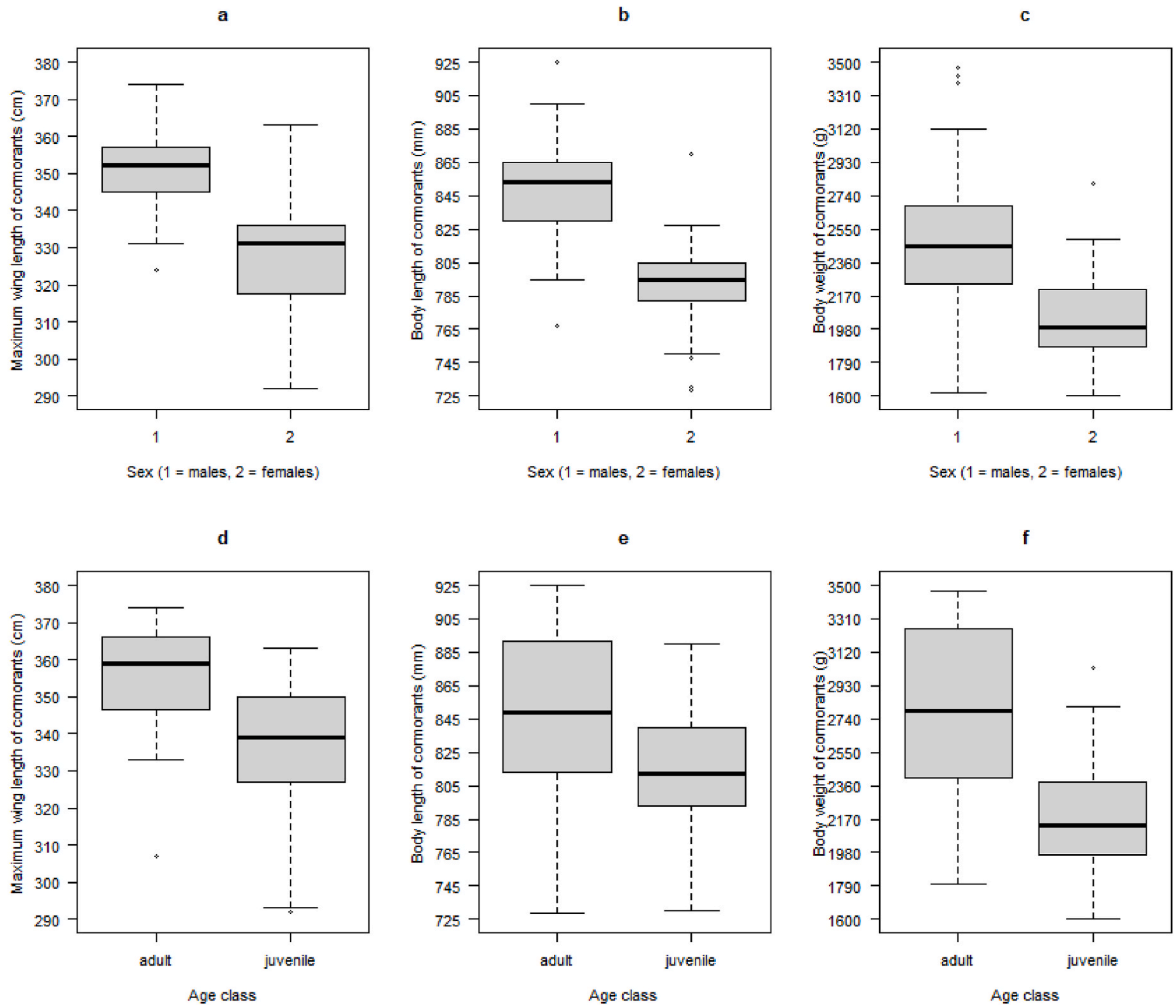


**Fig. 8.** Size differences of cormorants between sexes (a, b, and c) and adults and juveniles (d, e, and f). The black line represents the median length (a, b, d, and e) and median weight (c and f). The grey box represents the middle 50% of the data (n = 65).

seawater, specifically salinity and temperature, has changed with the studied effects of it on the size, energy content, and condition of the herring, especially in the northern Baltic Sea (e.g., Rajasilta et al. 2018, 2022). Thus, one contributing reason for the emergence of corynosoma infections could be the general decrease in the fish's condition, as it can make organisms more susceptible to infections (Lafferty and Kurtis 1999).

As the great cormorant is a protected species, a special permit is required to hunt it and also to collect samples for the research. For this reason, only 65 cormorant individuals could be obtained for the current study. Nevertheless, several differences between the individuals and study sites were found. The observation that male cormorants were larger than females, and adults were bigger than juveniles is corroborated by Koffijberg and Van Eerden (1995). Previous studies also show that male cormorants eat larger fish than females (Liordos and Goutner, 2009), which could explain why male birds were more prone to corynosoma infections. In most fish species, large fish tend to have corynosoma parasites more often than the small ones (Valtonen 1983).

Cormorants in the Airisto area were infected more frequently than in the neighboring Kustavi region, but this result could be skewed by the size and age of the birds. The cormorants, which were hunted in Kustavi, were smaller, and there were more juveniles among the samples, because they were shot at a fish farm situated close to a breeding colony. By contrast, in the Airisto area, cormorants were hunted farther from the breeding colony, and adults were, therefore, overrepresented. This makes it hard to reliably compare the results obtained from these two areas. However, different ages of the studied cormorants might explain the lower corynosoma prevalence in the Kustavi samples, as the juveniles in this area have had less time to get infected. Smaller cormorants also eat smaller fish, which generally have less parasites. Cormorants are also migratory birds that overwinter in southern, central, and western Europe (Lehikoinen 2003). Adult cormorants have already migrated during the previous winter, whereas juveniles born just some months prior to being shot have not. Previous studies (Oßmann 2008) show that cormorants in Germany have corynosoma parasites as well. Therefore, adult cormorants of our study area could be infected during their migration to the southern Baltic Sea, where the overwintering areas of different populations overlap. However, since juveniles had corynosoma infections as well, the results suggest that the infections were likely not linked to long-distance migrations but are of local origin.

In 2014, corynosoma was for the first time found in the samples of spawning herring in the Airisto area. Their prevalence in herring showed an increase from 2014 to 2018, except for 2016, when herring research was mainly focused on morphological abnormalities of gonads, which was also found recently (Rajasilta et al. 2016). Possibly, in that year, the parasites were not detected due to their small size and the research focus was on other characteristics of the fish besides the gonads. The infected herring were generally larger in size than the non-infected ones, which could be explained by the feeding habits of herring. In general, herring feed on zooplankton and macroscopic prey, such as small crustaceans

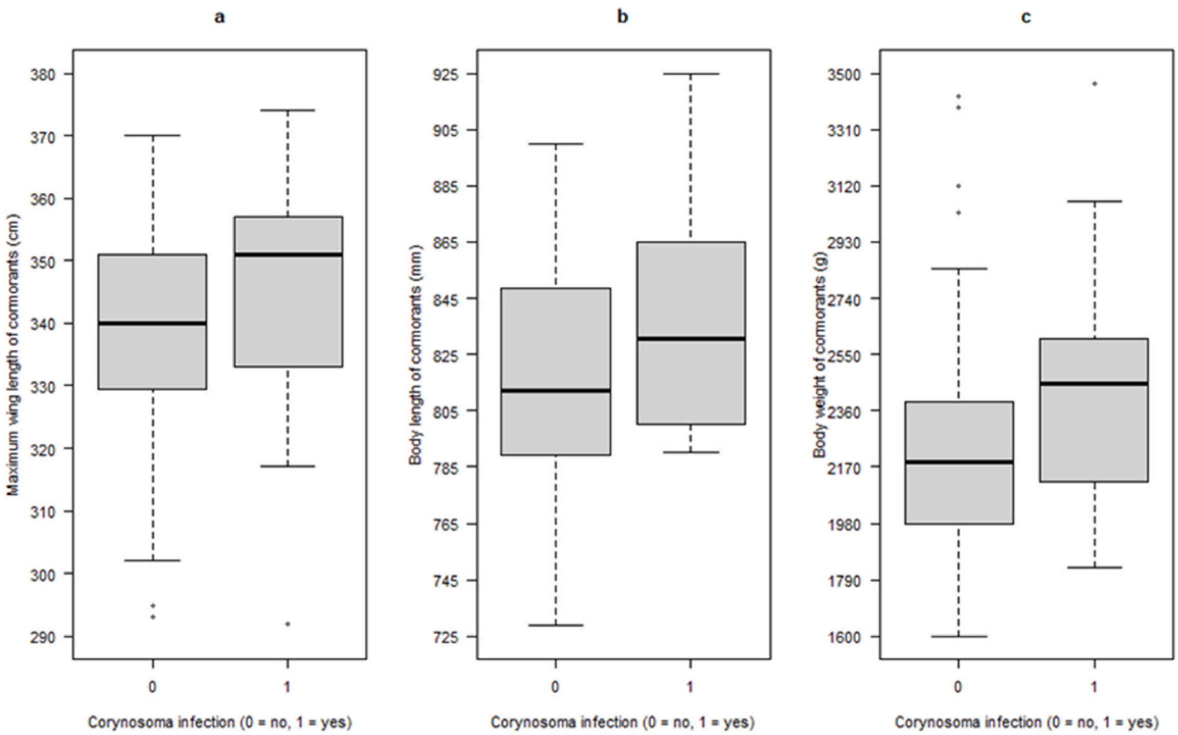


**Fig. 9.** Size differences between infected and non-infected cormorants. The black line represents the median length (a and b) and median weight (c). The grey box represents the middle 50% of the data (n = 65).

**Table 4**
Generalized linear model (GLM) output of the fixed effects on infection. Estimates and standard error (SE) values with z- and p-values are shown.

| Parameter | Estimate ±SE | z-value | p-value |
|---|---|---|---|
| **Intercept** | 56.18 ± 27.80 | 2.02 | <0.04 |
| **length:sex (female)** | 0.11 ± 0.05 | 2.49 | <0.05 |
| **sex (female)** | −72.74 ± 32.10 | −2.27 | <0.05 |
| **wing length** | −0.16 ± 0.09 | −1.90 | 0.06 |
| **age class (juvenile)** | −56.08 ± 30.11 | −1.86 | 0.06 |
| **Length** | 0.00 ± 0.02 | 0.21 | 0.83 |
| **sex (female): wing length** | −0.20 ± 0.15 | −1.36 | 0.17 |
| **age class (juvenile): wing length** | 0.15 ± 0.08 | 1.80 | 0.07 |

(Aneer 1975), but younger and smaller herring primarily feed on zooplankton (Arrhenius and Hansson 1993). As fish grow larger, they start to feed on larger prey, especially amphipods, such as *Monoporeia affinis*, (e.g., Rajasilta et al. 2014), which are intermediate hosts for corynosoma. By eating this prey, fish become susceptible to infection. *M. affinis* is more abundant in the open sea areas (e.g., Kangas 1976; Laine 2003), where also the seals, the primary host of corynosoma, are abundant. Therefore, as Valtonen (1983a,b) suggests, *M. affinis* has a high probability to get a corynosoma infection in the open sea areas, where also herring have their feeding grounds. Most likely then, fish get infected in this environment and not in the coastal waters where they reproduce.

The Baltic herring reproduce for the first time at the age of 2–3 years, and they may live even 15–20 years in our study area (Peltonen et al. 2002). Thus, the older, larger herring caught in the spawning locations have migrated to the feeding grounds repeatedly over several years. The prevalence of corynosoma could therefore indicate the migratory routes and the feeding areas visited by the herring to some extent. The taggings of spawning herring carried out in the 1990s in the Archipelago Sea (Kääriä et al., 2001) showed that after spawning, fish either stayed within the Archipelago Sea or migrated north to the Bothnian Sea to their feeding grounds (Kääriä et al., 2001). Here, herring were less frequently infected with corynosoma than in the Archipelago Sea. This, however, was probably due to a smaller fish size, as the probability of infection increased with fish size. In any case, the ranges of all three species, herring, cormorants, and seals, overlap, at least partly, which is undoubtedly advantageous for the parasite.

Our results suggest that *C. semerme* is the most abundant acanthocephalan species found in the herring and cormorants both in the Archipelago Sea and the Bothnian Sea. Farther north in the Bothnian Bay, *C. semerme* was also the most common (98.3%) of all corynosoma species found in the fourhorn sculpin (*Myoxocephalus quadricornis*; Sinisalo and Valtonen 2003). As the cormorants' diet consists of a variety of fish (Finnish Environmental Institute 2022; Koffijberg and Van Eerden 1995), it is logical that this dominant corynosoma species that exists in the cormorants' prey would also be dominant in them. This dominance occurs in seals as well (Valtonen 1983). In the Archipelago Sea, *C. strumosum* and *C. magdaleni* were also found in the herring, but the prevalence of both species was low. As they are also found in the Gulf of Bothnia (Nickol et al. 2002), it is likely that their low prevalence in the current study was due to the small sample size. A more extensive sampling from different areas could therefore reveal the differences in the species composition, as there is evidence that the distributions of corynosoma species are different at least on a large geographical scale (e.g. Reimer 2002; Leidenberger et al. 2020). For instance, *C. magdaleni* is limited to the Northern Atlantic coasts, *C. semerme* has a circumpolar distribution, and *C. strumosum* has the broadest distributional range extending further south.

In the Baltic Sea, the Baltic herring is the most important commercial fish species (Natural Resources Institute Finland 2022). In Finland alone, approximately 90 million kg of herring are caught annually. Even though corynosoma parasites are not harmful to humans, a high number of parasites may affect public opinion about the safety of herring for human consumption and decrease the consumer's perceived value of fish. Corynosoma parasites do not mature in fish but rather stay in their body cavities as cystacanths. According to Valtonen et al. (2012), they can remain in fish for years, which suggests that their higher prevalence in larger and older herring found in the current study was a consequence of a gradual accumulation in fish over the years. In that case, corynosoma do not increase the mortality of the infected fish, and, hence, the parasite remains permanently in the population. Since corynosoma can also occur in other commercially important fish species, regular monitoring of the infections and investigations of the parasite-host relationships are recommended in the whole Baltic Sea.

## Declaration of competing interest

I declare that there are no conflicts of interest regarding the publication of this manuscript.

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