Host records and geographical distribution of Corynosoma magdalenii, C. semerme and C. strumosum (Acanthocephala: Polymorphidae)

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Abstract

A literature survey was conducted to investigate the host and geographical distribution patterns of three Corynosoma species (Acanthocephala: Polymorphidae), viz. C. magdalenii, C. semerme and C. strumosum. All three species appear to be restricted to the Northern Hemisphere. Occurrence records of C. magdalenii are limited to the Northern Atlantic coasts, while C. semerme has a circumpolar distribution. The geographical range of Corynosoma strumosum encompasses the distributions of the other two species, but also extends into warmer southern regions. Some Corynosoma populations are living with their definitive hosts in very isolated locations, such as in the brackish Baltic Sea or different freshwater lakes (e.g. Lake Saimaa). All three species have a heteroxenous life cycle, comprising a peracaridan intermediate host, a fish paratenic host and a mammalian definitive host. Occasionally, an acanthocephalan may enter an accidental host, from which it is unable to complete its life cycle. The host records reported here are categorised by type, i.e. intermediate, paratenic, definitive or accidental. While most of the definitive hosts are shared amongst the three Corynosoma species, C. strumosum showed the broadest range of paratenic hosts, which reflects its more extensive geographical distribution. One aim of this study and extensive literature summary is to guide future sampling efforts and
therewith contribute to throw more light on the on-going species and morphotype discussion for this interesting parasite species.

Keywords
Acanthocephala, Corynosoma, host record, life cycle, Northern Hemisphere, seal and zoogeography

Introduction
The genus *Corynosoma* comprises 43 marine species (Amin 2013), that infect mammals and piscivorous birds. Aznar et al. (2006) showed that the original concept of *Corynosoma* was not a monophyletic genus. Phylogenetic analysis revealed that the marine *Corynosoma* species were more closely related to the genus *Andracantha* Schmidt, 1975 than to the species living in freshwater habitats. Aznar et al. (2006) erected the genus *Pseudocorynosoma* Aznar, Pérez-Ponce de León and Raga, 2006 for the freshwater species. Recent phylogenetic analysis based on ribosomal ITS1-5.8S-ITS2 and COI sequences showed that *Corynosoma* spp., hosted by Pinnipedia and marine Mustelidae formed a monophyletic group (Waindok et al. 2018).

The systematics of *Corynosoma* species from seals in northern Europe have recently been investigated using both molecular markers (Waindok et al. 2018) and morphology (Leidenberger et al. 2019). These studies have highlighted the limitations of using traditional morphological characters alone for diagnosing species. To determine the true species diversity in this genus, tandem morphological and molecular studies will be required. To guide future sampling efforts, we have conducted a comprehensive literature survey of the host and geographical distribution of three commonly encountered taxa: *C. magdaleni* Montreuil, 1958, *C. semerme* (Forssell, 1904) Lühe, 1911 and *C. strumosum* (Rudolphi, 1802) Lühe, 1904.

Material and methods
Host and geographical records
Host and geographical records for the three acanthocephalan taxa were collected from literature. Manual searches were conducted using Pubmed, Web of Science and Google Scholar. Additionally, we used the R (R Core Team 2019) package helminthR (Dallas 2016) to extract records from the Host-Parasite Database of The Natural History Museum in London (Gibson et al. 2005). Geographical records for each *Corynosoma* species were summarised by MEOW ecoregions (Spalding et al. 2007) and then plotted as a distribution map using the meow R-package (Byrnes 2016).
Nomenclature

For species names, we followed the nomenclature given by the Catalogue of Life (2019 Annual Checklist: Roskov et al. 2019) and WoRMS (WoRMS Editorial Board 2019).

The term accidental host was used here for a host, where the parasite usually is not found, because the host is not suitable for the parasite's development. This can mean that the accidental host also becomes a dead-end, because the life cycle of the parasite is blocked (e.g., no observed gravid female and/or mature individuals) and the parasite does not reach its definitive host. Since in many literature references, this detailed information was not given, we used the term accidental host as generic term for all of the dead-end/accidental/incidental host records we found.

Results and discussion

Zoogeography

Our literature survey on the zoogeography showed that the three species of Corynosoma (C. magdaleni, C. semerme and C. strumosum) and their definitive hosts are restricted to the Northern Hemisphere (Figs 1, 2, 3). The relatively few records for C. magdaleni suggest that this taxon is restricted to the North Sea, Baltic Sea and northwest Atlantic. By contrast, C. semerme has a circumpolar distribution, having been reported from the Arctic Ocean, north Atlantic and north Pacific (e.g., Popov and Fortunato 1987, Kaimoto et al. 2018, Waindok et al. 2018) (Fig. 2). The geographical range of C. strumosum encompasses the distributions of the other two taxa, but also extends into more southern regions, such as the Mediterranean Sea and coast of California (Fig. 3).

![Figure 1. Geographical distribution of Corynosoma magdaleni.](doi)
In most of the Baltic Sea studies, *C. semerme* was the species most commonly found in seals, followed by *C. magdaleni* and only rare infections were found for *C. strumosum* (Nickol et al. 2002, Sinisalo and Valtonen 2003, Leidenberger and Bäcklin 2008, Waindok et al. 2018). Co-infections have been observed (Nickol et al. 2002, Leidenberger and Bäcklin 2008, Leidenberger et al. 2019), most commonly involving *C. semerme* and *C. magdaleni* (Sinisalo and Valtonen 2003, Leidenberger and Bäcklin 2008, Waindok et al. 2018). Interestingly, land-locked seal species show no mixed infections, but only single infections, for example, *Phoca hispida saimensis* in Lake Saimaa only by *C. magdaleni*.
(Sinisalo and Valtonen 2003) and *Pusa caspica* in the Caspian Sea only by *C. strumosum* (Amin et al. 2011). Garcia-Varela et al. (2005) concluded that the *Corynosoma* species found in the Caspian Sea is *C. caspicum* and not *C. strumosum*. Indeed, *C. strumosum* from the land-locked Caspian seal recorded by Amin et al. 2011 was characterised with proboscis hooks and trunk spines distinct from other Northern European morphological descriptions (Nickol et al. 2002, Waindok et al. 2018, Leidenberger et al. 2019), suggesting that they may not be conspecific. Surprisingly, *Corynosoma caspicum* Golvan and Mokhayer, 1973, described based on immature specimens from sturgeons in Caspian Sea (Golvan and Mokhayer 1973) and often found in three-spined stickleback (*Gasterosteus aculeatus*) (Niksirat et al. 2006), has not yet been reported in *Pusa caspica* or another definitive host. Waindok et al. (2018) described some individuals of *C. strumosum* from the German North and Baltic Seas with different proboscis morphology, similar to those described by Amin et al. (2011) and stated this as *C. magaleni* isolate Pv1NS instead. Additionally, they found a cryptic species refered to as "Candidatus Corynosoma nortmeri sp. nov." Waindok et al. (2018) in the European study area.

The extent of the geographical and host ranges of the three taxa correlates with the year of their description. *Corynosoma strumosum* was the first species of the genus to be described (Rudolphi 1802) and has, by far, the broadest geographical and host distributions. *Corynosoma semerme*, described by Forssell (1904), appears to have a slightly more limited geographical range and far fewer paratenic host records. Relatively few hosts have been reported for *C. magdaleni*, described by Montreuil (1958) and its geographical range appears to be restricted to the northern Atlantic, in contrast to the circumpolar distributions of the other two species. Up until its description in 1958, specimens of *C. magdaleni* were almost certainly assigned to the morphologically similar *C. strumosum*. The potential bias resulting from taxon age should be kept in mind when comparing the reported host and geographical distributions of the three taxa (Fig. 3).

**Overview of the life cycle**

The heteroxenous life cycle of *Corynosoma* species involves a peracaridan intermediate host, a paratenic host (fish) and a mammalian definitive host. While there are numerous studies on *C. semerme* and *C. strumosum* (Tables 3, 4, 5, 6, 7, 8), there have been few studies on *C. magdaleni*, besides its original description by Montreuil 1958 (Tables 1, 2). The intermediate host of *C. magdaleni* is unknown. Lake Saimaa may be a good location to search for the intermediate host of *C. magdaleni*, because the other *Corynosoma* species appear to be absent from this land-locked waterbody (Sinisalo and Valtonen 2003, Sinisalo et al. 2003). A total of five species of paratenic host (all Actinopterygii) have been reported for *C. magdaleni*; three from Canada and two from the Baltic Sea (Table 1). In Canada, only *C. magdaleni* is reported together with *C. wegeneri* Heinze, 1934. In the definitive hosts (Table 2), the species seems to prefer the last part of the small intestine (ileum) and the colon. *Corynosoma semerme* has been reported from the whole intestine, but is typically found at a higher density in the large intestine, especially the cecum and rectum (Nickol et al. 2002, Leidenberger and Bäcklin 2008), where *C. strumosum* and *C. magdaleni* are not generally observed. Microhabitat segregation might facilitate
reproductive isolation of the three species, especially in mixed infections that are often observed in seals from the Baltic Sea (Nickol et al. 2002, Sinisalo and Valtonen 2003, Leidenberger and Bäcklin 2008), but less commonly in the North Sea (Waindok et al. 2018). While the three Corynosoma species share most of their definitive hosts, they show some differences in their paratenic hosts. We found that C. strumosum shares three paratenic hosts with both other species, none with C. magdaleni only, but > 20 paratenic hosts are shared with C. semerme. More than 80 paratenic hosts were described for C. strumosum and these are, up to now, not reported from any of the other two species (Tables 1, 4, 6).

| Host order | Host family | Host species | Host vernacular name | Geographical locality | Reference(s) |
|------------|-------------|--------------|----------------------|-----------------------|--------------|
| Perciformes | Percidae    | Gymnocephalus cernua (Linnaeus, 1758) (as Gymnocephalus cernus) | ruffe | Baltic Sea, North-eastern Bothnian Bay | Valtonen et al. 2001 |
| Pleuronectiformes | Pleuronectidae | Hippoglossus hippoglossus (Linnaeus, 1758) | Atlantic halibut | Atlantic, Canada | Arai 1989 |
| Pleuronectiformes | Pleuronectidae | Hippoglossus hippoglossus (Linnaeus, 1758) | Atlantic halibut | Magdalen Islands region of the Gulf of St. Lawrence | Montreuil 1958 |
| Salmoniformes | Salmonidae | Salvelinus fontinalis (Mitchill, 1814) | brook charr | Tabusintac River, New Brunswick | Frimeth 1987 |
| Scorpaeniformes | Cottidae | Myxocephalus quadricornis (Linnaeus, 1758) | fourhorn sculpin | Baltic Sea, Bothnian Bay | Sinisalo and Valtonen 2003 |
| Scorpaeniformes | Cottidae | Myxocephalus scorpius (Linnaeus, 1758) | shorthorn sculpin | Atlantic, Canada | Arai 1989 |
| Scorpaeniformes | Cottidae | Myxocephalus scorpius (Linnaeus, 1758) | shorthorn sculpin | Magdalen Islands region of the Gulf of St. Lawrence | Montreuil 1958 |

Table 1. Paratenic host records for Corynosoma magdaleni. All Actinopterygii.
## Table 2.
Definitive host records for *Corynosoma magdaleni*. All members of the family Phocidae, order Carnivora.

| Host order | Host family | Host species                  | Host vernacular name | Geographical locality                  | Reference                        |
|------------|------------|-------------------------------|----------------------|----------------------------------------|----------------------------------|
| Carnivora  | Phocidae   | *Halichoerus grypus* (Fabricius, 1791) | grey seal           | Baltic Sea                             | Waindok et al. 2018              |
| Carnivora  | Phocidae   | *Halichoerus grypus* (Fabricius, 1791) | grey seal           | Baltic Sea, Baltic Proper, Bothnian Sea, Bothnian Bay, Sweden | Leidenberger and Bäcklin 2008     |
| Carnivora  | Phocidae   | *Halichoerus grypus* (Fabricius, 1791) | grey seal           | Baltic Sea, Finland, Gulf of Bothnia, Åland Island | Nickol et al. 2002                |
| Carnivora  | Phocidae   | *Halichoerus grypus* (Fabricius, 1791) | grey seal           | Baltic Sea, Sweden                     | Leidenberger et al. 2019         |
| Carnivora  | Phocidae   | *Halichoerus grypus* (Fabricius, 1791) | grey seal           | Eastern Canada                         | Montreuil 1958                   |
| Carnivora  | Phocidae   | *Phoca vitulina* Linnaeus, 1758 | harbour seal         | Eastern Canada                         | Montreuil 1958                   |
| Carnivora  | Phocidae   | *Phoca vitulina* Linnaeus, 1758 (as *Phoca vitulina concolor* De Kay, 1842) | harbour seal         | North Sea, Schleswig-Holstein          | Waindok et al. 2018              |
| Carnivora  | Phocidae   | *Phoca vitulina* Linnaeus, 1758 (as *Phoca vitulina concolor* De Kay, 1842) | harbour seal         | Eastern Canada                         | Montreuil 1958                   |
| Carnivora  | Phocidae   | *Pusa hispida* (Schreber, 1775)    | ringed seal          | Baltic Sea                             | Leidenberger et al. 2019         |
| Carnivora  | Phocidae   | *Pusa hispida* (Schreber, 1775)    | ringed seal          | Baltic Sea, Germany, Schleswig-Holstein | Waindok et al. 2018              |
| Carnivora  | Phocidae   | *Pusa hispida* (Schreber, 1775)    | ringed seal          | Baltic Sea, Bothnian Bay               | Valtonen et al. 2004              |
| Carnivora  | Phocidae   | *Pusa hispida* (Schreber, 1775)    | ringed seal          | Baltic Sea, Gulf of Finland            | Delyamure et al. 1980             |
| Carnivora  | Phocidae   | *Pusa hispida* (Schreber, 1775)    | ringed seal          | European Arctic                        | Treshchev 1982* citet by Raga 1992 |
| Host order | Host family | Host species | Host vernacular name | Geographical locality | Reference |
|------------|-------------|--------------|----------------------|-----------------------|-----------|
| Carnivora  | Phocidae    | *Pusa hispida* *saimensis* Nordquist, 1899 | Saimaa ringed seal | Lake Saimaa, Finland | Sinisalo et al. 2004, Aznar et al. 2006, García-Varela et al. 2011 |
|            |             | *Delphinapterus leucas* (Pallas, 1776) | Beluga, Beluga whale, white whale | Bristol Bay, Alaska, Bering Sea | Neiland 1962, Measures et al. 1995 |
| Carnivora  | Odobenidae  | *Odobenus rosmarus* (Linnaeus, 1758) | walrus | Arctic Ocean, Northern Atlantic | Delyamure 1961, von Sprehn 1966 cited by Raga 1992 |
| Carnivora  | Otaridae    | *Callorhinus ursinus* (Linnaeus, 1758) | Northern fur seal | Alaska, Bering Sea, St. Paul Island | Kuzmina et al. 2012 |
| Carnivora  | Otaridae    | *Callorhinus ursinus* (Linnaeus, 1758) (as *Callorhinus alascanus*) | Northern fur seal | North America | Van Cleave 1953 |
| Carnivora  | Phocidae    | *Cystophora cristata* (Erxleben, 1777) | hooded seal | European Arctic | Delyamure 1961*, Treshchev 1982* cited by Raga 1992 |
| Carnivora  | Phocidae    | *Erignathus barbatus* (Erxleben, 1777) | bearded seal | North America | Van Cleave 1953 |
| Carnivora  | Phocidae    | *Erignathus barbatus* (Erxleben, 1777) | bearded seal | White Sea | Popova et al. 1975* cited by Raga 1992 |
| Carnivora  | Phocidae    | *Halichoerus grypus* (Fabricius, 1791) | grey seal | Arctic Ocean, Northern Atlantic, European Arctic | von Sprehn 1966* cited by Raga 1992 |
| Carnivora  | Phocidae    | *Halichoerus grypus* (Fabricius, 1791) | grey seal | Germany | Lühe 1911 |
| Carnivora  | Phocidae    | *Halichoerus grypus* (Fabricius, 1791) | grey seal | Germany | Aznar et al. 2006 |

Table 3.
Definitive hosts of *Corynosoma semerme*. *Source not viewed, ^Found in Host-Parasite Database NHM London without further reference details.*
| Host order | Host family | Host species | Host vernacular name | Geographical locality | Reference |
|------------|-------------|--------------|----------------------|-----------------------|-----------|
| Carnivora  | Phocidae    | Halichoerus grypus (Fabricius, 1791) | grey seal | Baltic Sea, Finland, Gulf of Bothnia, Åland Island | Nickol et al. 2002 |
| Carnivora  | Phocidae    | Halichoerus grypus (Fabricius, 1791) | grey seal | Baltic Sea, Baltic Proper, Bothnian Sea, Bothnian Bay, Sweden | Leidenberger and Bäcklin 2008 |
| Carnivora  | Phocidae    | Halichoerus grypus (Fabricius, 1791) | grey seal | Baltic Sea, Germany, Schleswig-Holstein | Waindok et al. 2018 |
| Carnivora  | Phocidae    | Histriophoca fasciata (Zimmerman, 1783) (as Phoca fasciata) | ribbon seal | Bering Sea, Alaska | Rausch et al. 1990 |
| Carnivora  | Phocidae    | Histriophoca fasciata (Zimmerman, 1783) (as Phoca fasciata) | ribbon seal | Arctic Ocean, Bering Sea | Shults and Frost 1988 |
| Carnivora  | Phocidae    | Histriophoca fasciata (Zimmerman, 1783) (as Phoca fasciata) | ribbon seal | Sea of Okhotsk | Shults and Frost 1988 |
| Carnivora  | Phocidae    | Pagophilus groenlandicus (Erxleben, 1777) (as Phoca groenlandica) | harp seal, Greenland seal | Arctic Ocean, Northern Atlantic, European Arctic | von Sprehn 1966* cited by Raga 1992 |
| Carnivora  | Phocidae    | Phoca largha Pallas, 1811 | spotted seal, larga seal | Sea of Okhotsk | Sasaki et al. 2019 |
| Carnivora  | Phocidae    | Phoca largha Pallas, 1811 | spotted seal, larga seal | Russia | Aznar et al. 2006 |
| Carnivora  | Phocidae    | Phoca largha Pallas, 1811 | spotted seal, larga seal | Bering Sea, Alaska | Rausch et al. 1990 |
| Carnivora  | Phocidae    | Phoca largha Pallas, 1811 | spotted seal, larga seal | Arctic Ocean, Bering Sea | [On the helminthofauna of largi and harbour seals.]* |
| Carnivora  | Phocidae    | Phoca largha Pallas, 1811 | spotted seal, larga seal | Sea of Okhotsk | [On the helminthofauna of largi and harbour seals.]* |
| Host order | Host family | Host species | Host vernacular name | Geographical locality | Reference |
|------------|-------------|--------------|----------------------|-----------------------|-----------|
| Carnivora  | Phocidae    | *Phoca vitulina* Linnaeus, 1758 | harbour seal | Germany | Lühe 1911 |
| Carnivora  | Phocidae    | *Phoca vitulina* Linnaeus, 1758 | harbour seal | Sweden | Lundström 1942 |
| Carnivora  | Phocidae    | *Phoca vitulina* Linnaeus, 1758 | harbour seal | North Sea, Germany, Schleswig-Holstein | Waindok et al. 2018 |
| Carnivora  | Phocidae    | *Phoca vitulina* Linnaeus, 1758 | harbour seal | Arctic Ocean, Northern Atlantic, European Arctic | von Sprehn 1966* cited by Raga 1992 |
| Carnivora  | Phocidae    | *Phoca vitulina* Linnaeus, 1758 | harbour seal | Alaska, Bering Sea, St. Paul Island | Kuzmina et al. 2012 |
| Carnivora  | Phocidae    | *Pusa hispida* (Schreber, 1775) | ringed seal | Germany | Lühe 1911 |
| Carnivora  | Phocidae    | *Pusa hispida* (Schreber, 1775) | ringed seal | Baltic Sea, Bothnian Bay, Finland | Helle and Valtonen 1981 |
| Carnivora  | Phocidae    | *Pusa hispida* (Schreber, 1775) | ringed seal | Baltic Sea, Bothnian Bay, Finland | Valtonen and Helle 1988 |
| Carnivora  | Phocidae    | *Pusa hispida* (Schreber, 1775) | ringed seal | Baltic Sea, Bothnian Bay, Finland | Valtonen et al. 2004 |
| Carnivora  | Phocidae    | *Pusa hispida* (Schreber, 1775) | ringed seal | North America | Van Cleave 1953 |
| Carnivora  | Phocidae    | *Pusa hispida* (Schreber, 1775) (as *Phoca foetida*) | ringed seal | Baltic Sea, Sweden, Östra Rönnskär | Forssell 1904 |
| Carnivora  | Phocidae    | *Pusa hispida* (Schreber, 1775) (as *Phoca foetida*) | ringed seal | Baltic Sea, Finland, Tvärminne | Forssell 1905 |
Table 4.
Paratenic hosts of *Corynosoma semerme*; all Actinopterygii. *Source not viewed.*

| Host order       | Host family    | Host species           | Host vernacular name | Geographical locality | Reference               |
|------------------|----------------|------------------------|----------------------|------------------------|-------------------------|
| Acipenseriformes | Acipenseridae  | *Acipenser sturio*     | sturgeon             | USSR (CIS)             | Shulman 1954*           |
|                  |                | Linnaeus, 1758          |                      |                        |                         |
| Acipenseriformes | Acipenseridae  | *Acipenser sturio*     | sturgeon             | USSR (CIS)             | Shulman 1954*           |
|                  |                | Linnaeus, 1758          |                      |                        |                         |
| Anguilliformes   | Anguillidae    | *Anguilla anguilla*     | European eel         | Sweden                 | Lundström 1942          |
|                  |                | Linnaeus, 1758          |                      |                        |                         |
| Anguilliformes   | Anguillidae    | *Anguilla anguilla*     | European eel         | Europe                 | Van Cleave 1953         |
|                  |                | (Linnaeus, 1758)        |                      |                        |                         |
| Clupeiformes     | Clupeidae      | *Clupea harengus*      | herring              | Sweden                 | Lundström 1942          |
|                  |                | Linnaeus, 1758          |                      |                        |                         |
| Clupeiformes     | Clupeidae      | *Clupea harengus*      | herring              | Baltic Sea, Finland,   | Forsvell 1904           |
|                  |                | Linnaeus, 1758 (as      |                      | Tvärminne              |                         |
|                  |                | *Clupea harengus*       |                      |                        |                         |
|                  |                | *membras*               |                      |                        |                         |
| Clupeiformes     | Clupeidae      | *Clupea harengus*      | herring              | Baltic Sea, Finland,   | Forsvell 1905           |
|                  |                | Linnaeus, 1758 (as      |                      | Tvärminne              |                         |
|                  |                | *Clupea harengus*       |                      |                        |                         |
|                  |                | *membras*               |                      |                        |                         |
| Clupeiformes     | Clupeidae      | *Clupea harengus*      | herring              | Germany                | Lühe 1911               |
|                  |                | Linnaeus, 1758 (as      |                      |                        |                         |
|                  |                | *Clupea harengus*       |                      |                        |                         |
|                  |                | *membras*               |                      |                        |                         |
| Clupeiformes     | Clupeidae      | *Clupea harengus*      | herring              | Europe                 | Van Cleave 1953         |
|                  |                | Linnaeus, 1758 (as      |                      |                        |                         |
|                  |                | *Clupea harengus*       |                      |                        |                         |
|                  |                | *membras*               |                      |                        |                         |
| Cypriniformes    | Cyprinidae     | *Blicca bjoerkna*       | white bream          | Sweden                 | Lundström 1942          |
|                  |                | Linnaeus, 1758          |                      |                        |                         |
| Cypriniformes    | Cyprinidae     | *Blicca bjoerkna*       | white bream          | Europe                 | Van Cleave 1953         |
|                  |                | Linnaeus, 1758          |                      |                        |                         |
| Cypriniformes    | Cyprinidae     | *Pelecus cultratus*     | ziege                | Finno-Karelian ASSR    | Rumyantsev and Ieshko 1997* |
|                  |                | Linnaeus, 1758          |                      |                        |                         |
| Host order     | Host family     | Host species                      | Host vernacular name | Geographical locality                      | Reference       |
|---------------|-----------------|-----------------------------------|----------------------|--------------------------------------------|-----------------|
| Esociformes   | Esocidae        | *Esox lucius* Linnaeus, 1758       | pike                 | Baltic Sea, Finland, Tvärminne             | Forssell 1905   |
| Gadiformes    | Gadidae         | *Boreogadus saida* (Lepechin, 1774)| polar cod            | Arctic Ocean, USSR zone, Pechora Sea       | Karasev and Mitenev 1993* |
| Gadiformes    | Gadidae         | *Gadus morhua* Linnaeus, 1758     | cod                  | Baltic Sea, Finland, Tvärminne             | Forssell 1905   |
| Gadiformes    | Gadidae         | *Gadus morhua* Linnaeus, 1758 (as *Gadus callarias*) | cod                  | Sweden                                     | Lundström 1942  |
| Gadiformes    | Gadidae         | *Gadus morhua* Linnaeus, 1758 (as *Gadus callarias*) | cod                  | Europe                                     | Van Cleave 1953  |
| Gadiformes    | Lotidae         | *Enchelyopus cimbrius* (Linnaeus, 1766) (as *Onos cimbrius*) | fourbeard rockling   | Europe                                     | Van Cleave 1953  |
| Gadiformes    | Lotidae         | *Lota lota* (Linnaeus, 1758)      | burbot               | Baltic Sea, Bothnian Bay                   | Valtonen and Julkunen 1995 |
| Gadiformes    | Lotidae         | *Lota lota* (Linnaeus, 1758) (as *Lota vulgaris*) | burbot               | Sweden                                     | Lundström 1942  |
| Gadiformes    | Lotidae         | *Lota lota* (Linnaeus, 1758) (as *Lota vulgaris*) | burbot               | Europe                                     | Van Cleave 1953  |
| Gadiformes    | Lotidae         | *Lota lota* (Linnaeus, 1758)      | burbot               | Tuluksak, Bering Sea, Alaska               | Rausch et al. 1990 |
| Gasterosteiformes | Gasterosteidae | *Gasterosteus aculeatus* Linnaeus, 1758 | three-spined stickleback | Sweden                                     | Lundström 1942  |
| Lophiiformes  | Lophidae        | *Lophius piscatorius* Linnaeus, 1758 | angler               | Sweden                                     | Lundström 1942  |
| Osmeriformes  | Osmeridae       | *Osmerus dentex* Steindachner and Kner, 1870 | Pacific rainbow smelt | Japan                                      | Sasaki et al. 2019 |
| Host order       | Host family | Host species                  | Host vernacular name | Geographical locality       | Reference          |
|------------------|-------------|-------------------------------|----------------------|-----------------------------|--------------------|
| Osmeriformes     | Osmeridae   | Osmerus eperlanus             | rainbow smelt        | Baltic Sea, Finland,        | Forssell 1904      |
|                  |             | (Linnaeus, 1758)              |                      | Tvärminne                  |                    |
| Osmeriformes     | Osmeridae   | Osmerus eperlanus             | rainbow smelt        | Baltic Sea, Finland,        | Forssell 1905      |
|                  |             | (Linnaeus, 1758)              |                      | Tvärminne                  |                    |
| Osmeriformes     | Osmeridae   | Osmerus eperlanus             | rainbow smelt        | Germany                     | Lühe 1911          |
|                  |             | (Linnaeus, 1758)              |                      |                             |                    |
| Osmeriformes     | Osmeridae   | Osmerus eperlanus             | rainbow smelt        | Sweden                      | Lundström 1942     |
|                  |             | (Linnaeus, 1758)              |                      |                             |                    |
| Osmeriformes     | Osmeridae   | Osmerus eperlanus             | rainbow smelt        | Europe                      | Van Cleave 1953    |
|                  |             | (Linnaeus, 1758)              |                      |                             |                    |
| Osmeriformes     | Osmeridae   | Osmerus eperlanus             | rainbow smelt        | Baltic Sea, Bothnian Bay    | Valtonen and       |
|                  |             | (Linnaeus, 1758)              |                      |                             | Julkunen 1995      |
| Perciformes      | Labridae    | Ctenolabrus rupestris         | Atlantic herring     | southern Norway, Flødevigen,| Karlsbakk et       |
|                  |             | (Linnaeus, 1758)              |                      |                             | al. 1996           |
| Perciformes      | Percidae    | Gymnocephalus cernua (as Acerina cernua) | ruffe | Baltic Sea, Finland, Tvärminne | Forssell 1905      |
| Perciformes      | Percidae    | Gymnocephalus cernua (as Acerina cernua) | ruffe | Germany                     | Lühe 1911          |
| Perciformes      | Percidae    | Gymnocephalus cernua (as Acerina cernua) | ruffe | Sweden                      | Lundström 1942     |
| Perciformes      | Percidae    | Gymnocephalus cernua (as Acerina cernua) | ruffe | Europe                      | Van Cleave 1953    |
| Perciformes      | Percidae    | Gymnocephalus cernua (as Acerina cernua) | ruffe | Baltic Sea, Bothnian Bay    | Valtonen and       |
|                  |             |                               |                      |                             | Julkunen 1995      |
| Perciformes      | Percidae    | Perca fluviatilis             | perch                | Baltic Sea, Finland,        | Forssell 1905      |
|                  |             | Linnaeus, 1758                |                      | Tvärminne                  |                    |
| Host order       | Host family       | Host species       | Host vernacular name | Geographical locality       | Reference          |
|------------------|-------------------|--------------------|----------------------|-----------------------------|--------------------|
| Perciformes      | Percidae          | *Perca fluviatilis* Linnaeus, 1758 | perch                | Sweden                      | Lundström 1942    |
| Perciformes      | Percidae          | *Perca fluviatilis* Linnaeus, 1758 | perch                | Europe                      | Van Cleave 1953   |
| Perciformes      | Percidae          | *Sander lucioperca* (Linnaeus, 1758) (as *Stizostedion lucioperca*) | zanda, pike-perch     | Finno-Karelian ASSR         | Rumyantsev and Leshko 1997* |
| Perciformes      | Zoarcidae         | *Lycodes raridens* Taranetz & Andriashev, 1937 | marbled eelpout      | Arctic Ocean, Bering Sea    | Shults and Frost 1988 |
| Perciformes      | Zoarcidae         | *Zoarces vivipar*us (Linnaeus, 1758) | eelpout              | Sweden                      | Lundström 1942    |
| Perciformes      | Zoarcidae         | *Zoarces vivipar*us (Linnaeus, 1758) | eelpout              | Europe                      | Van Cleave 1953   |
| Perciformes      | Zoarcidae         | *Zoarces vivipar*us (Linnaeus, 1758) | eelpout              | Baltic Sea, Estonia, Riga Bay | Vismanis et al. 1980* |
| Perciformes      | Zoarcidae         | *Zoarces vivipar*us (Linnaeus, 1758) | eelpout              | Baltic Sea, Germany, Lübecker Bay | Zander 1991 |
| Pleuronectiformes| Pleuronectidae    | *Hippoglossoides platessoides* (Fabricius, 1780) (as *Hippoglossoides platessoides limandoides*) | American plaice       | Arctic Ocean, Greenland/ Icelandic Zone, Icelandic coast | Olafsdottir 1999 |
| Pleuronectiformes| Pleuronectidae    | *Limanda limanda* (Linnaeus, 1758) (as *Pleuronectes limanda*) | common dab           | Sweden                      | Lundström 1942    |
| Pleuronectiformes| Pleuronectidae    | *Limanda limanda* (Linnaeus, 1758) (as *Pleuronectes limanda*) | common dab           | Europe                      | Van Cleave 1953   |
| Pleuronectiformes| Pleuronectidae    | *Platichthys flesus* (Linnaeus, 1758) | flounder             | Baltic Sea, Finland, Tvärminne | Forssell 1905     |
| Pleuronectiformes| Pleuronectidae    | *Platichthys flesus* (Linnaeus, 1758) | flounder             | Germany                      | Lühe 1911         |
| Host order           | Host family     | Host species                          | Host vernacular name | Geographical locality | Reference       |
|----------------------|-----------------|---------------------------------------|----------------------|------------------------|-----------------|
| Pleuronectiformes    | Pleuronectidae  | Platichthys flesus (Linnaeus, 1758)   | flounder Sweden      | Lundström 1942         |                 |
| Pleuronectiformes    | Pleuronectidae  | Platichthys flesus (Linnaeus, 1758)   | flounder Sweden      | Van Cleave 1953        |                 |
| Pleuronectiformes    | Pleuronectidae  | Pleuronectes platessa Linnaeus, 1758  | European plaice      | Van Cleave 1953        |                 |
| Pleuronectiformes    | Pleuronectidae  | Pseudopleuronectes americanus Walbaum, 1792 | winter flounder Atlantic, Canada | Arai 1989 |                 |
| Pleuronectiformes    | Scophthalmidae  | Scophthalmus maximus (Linnaeus, 1758) (as Rhombus maximus) | turbot Baltic Sea, Finland, Tvärminne | Forssell 1904 |                 |
| Pleuronectiformes    | Scophthalmidae  | Scophthalmus maximus (Linnaeus, 1758) (as Rhombus maximus) | turbot Baltic Sea, Finland, Tvärminne | Forssell 1905 |                 |
| Pleuronectiformes    | Scophthalmidae  | Scophthalmus maximus (Linnaeus, 1758) (as Rhombus maximus) | turbot Germany | Lühe 1911 |                 |
| Pleuronectiformes    | Scophthalmidae  | Scophthalmus maximus (Linnaeus, 1758) (as Rhombus maximus) | turbot Sweden | Lundström 1942 |                 |
| Pleuronectiformes    | Scophthalmidae  | Scophthalmus maximus (Linnaeus, 1758) (as Rhombus maximus) | turbot Europe | Van Cleave 1953 |                 |
| Salmoniformes        | Salmonidae      | Coregonus albula (Linnaeus, 1758)      | European cisco Sweden | Lundström 1942 |                 |
| Salmoniformes        | Salmonidae      | Coregonus albula (Linnaeus, 1758)      | European cisco Europe | Van Cleave 1953 |                 |
| Salmoniformes        | Salmonidae      | Coregonus fera Jurine, 1825 true fera | Europe | Van Cleave 1953 |                 |
| Salmoniformes        | Salmonidae      | Salmo salar Linnaeus, 1758 salmon | European USSR (CIS) | Rumyantsev et al. 1998* |                 |
| Salmoniformes        | Salmonidae      | Salmo trutta Linnaeus, 1758 brown trout | European USSR (CIS) | Rumyantsev et al. 1998* |                 |
| Salmoniformes        | Salmonidae      | Thymallus thymallus (Linnaeus, 1758) grayling | Europe | Rumyantsev et al. 1999* |                 |
| Host order     | Host family | Host species                          | Host vernacular name | Geographical locality       | Reference         |
|---------------|-------------|---------------------------------------|----------------------|----------------------------|-------------------|
| Scorpaeniformes | Cottidae    | *Myoxocephalus quadricornis* (Linnaeus, 1758) | fourhorn sculpin     | Baltic Sea, Bothnian Bay    | Sinisalo and Valtonen 2003 |
| Scorpaeniformes | Cottidae    | *Myoxocephalus quadricornis* (Linnaeus, 1758) (as *Cottus quadricornis*) | fourhorn sculpin     | Baltic Sea, Finland, Tvärminne | Forssell 1904    |
| Scorpaeniformes | Cottidae    | *Myoxocephalus quadricornis* (Linnaeus, 1758) (as *Cottus quadricornis*) | fourhorn sculpin     | Baltic Sea, Finland, Tvärminne | Forssell 1905    |
| Scorpaeniformes | Cottidae    | *Myoxocephalus quadricornis* (Linnaeus, 1758) (as *Cottus quadricornis*) | fourhorn sculpin     | Germany                     | Lühe 1911        |
| Scorpaeniformes | Cottidae    | *Myoxocephalus quadricornis* (Linnaeus, 1758) (as *Cottus quadricornis*) | fourhorn sculpin     | Sweden                      | Lundström 1942   |
| Scorpaeniformes | Cottidae    | *Myoxocephalus quadricornis* (Linnaeus, 1758) (as *Cottus quadricornis*) | fourhorn sculpin     | Europe                      | Van Cleave 1953   |
| Scorpaeniformes | Cottidae    | *Myoxocephalus scorpius* (Linnaeus, 1758) | shorthorn sculpin    | Baltic Sea, Bothnian Bay    | Valtonen and Julkunen 1995 |
| Scorpaeniformes | Cottidae    | *Myoxocephalus scorpius* (Linnaeus, 1758) | shorthorn sculpin    | Baltic Sea, North-eastern Bothnian Bay | Valtonen et al. 2001 |
| Scorpaeniformes | Cottidae    | *Myoxocephalus scorpius* (Linnaeus, 1758) (as *Cottus scorpius*) | shorthorn sculpin    | Sweden                      | Lundström 1942   |
| Scorpaeniformes | Cottidae    | *Myoxocephalus scorpius* (Linnaeus, 1758) (as *Cottus scorpius*) | shorthorn sculpin    | Baltic Sea, Finland, Tvärminne | Forssell 1905    |
| Host order       | Host family   | Host species          | Host vernacular name | Geographical locality | Reference                  |
|------------------|---------------|-----------------------|----------------------|------------------------|----------------------------|
| Scorpaeniformes  | Cottidae      | Myxocephalus scorpius | shorthorn sculpin    | Europe                 | Van Cleave 1953            |
| Scorpaeniformes  | Cyclopteridae | Cyclopterus lumpus    | goldsindsay wrasse   | Sweden                 | Lundström 1942             |
| Scorpaeniformes  | Cyclopteridae | Cyclopterus lumpus    | goldsindsay wrasse   | Europe                 | Van Cleave 1953            |
| Scorpaeniformes  | Psychrolutidae| Dasycottus setiger    | spinyhead sculpin    | Arctic Ocean, Bering Sea | Shults and Frost 1988  |
| Artiodactyla     | Monodontidae  | Delphinapterus leucas | Beluga, Beluga whale, white whale | Bristol Bay, Alaska, Barent Sea, Sea of Okhotsk, North Pacific Ocean, Arctic | Krotov and Delyamure 1952*, Delyamure and Kleinenberg 1958*, Neiland 1962, Yablokov et al. 1972* all cited by Measures et al. 1995 |
| Carnivora        | Odobenidae    | Odobenus rosmarus     | walrus                | no area specified      | Dailey 1975, Raga 1992     |
| Carnivora        | Otariidae     | Callorhinus ursinus   | Northern fur seal    | Alaska, Bering Sea, St. Paul Island | Ionita et al. 2008, Kuzmina et al. 2012 |
| Carnivora        | Otariidae     | Zalophus californianus| California sea lion  | California             | Van Cleave 1953            |
| Carnivora        | Phocidae      | Cystophora cristata   | hooded seal          | Europe                 | Van Cleave 1953            |
| Carnivora        | Phocidae      | Erignathus barbatus   | bearded seal         | Alaska, Arctic         | Van Cleave 1953            |

Table 5.
Definitive hosts of *Corynosoma strumosum*. *Source not viewed. *Found in Host-Parasite Database NHM London without further reference details.
| Host order | Host family | Host species | Host vernacular name | Geographical locality | Reference |
|------------|-------------|--------------|----------------------|-----------------------|-----------|
| Carnivora  | Phocidae    | *Erignathus barbatus* (Erxleben, 1777) | bearded seal | Barent Sea, Sea of Okhotsk, Chukchi seas, Eastern Siberian Sea | Popov and Fortunato 1987 |
| Carnivora  | Phocidae    | *Halichoerus grypus* (Fabricius, 1791) | grey seal | Germany | Lühe 1911 |
| Carnivora  | Phocidae    | *Halichoerus grypus* (Fabricius, 1791) | grey seal | Holland, Germany | Aznar et al. 2006 |
| Carnivora  | Phocidae    | *Halichoerus grypus* (Fabricius, 1791) | grey seal | Atlantic coast, Ireland | O’Neill and Whelan 2002 |
| Carnivora  | Phocidae    | *Halichoerus grypus* (Fabricius, 1791) | grey seal | Baltic Sea, Finland, Gulf of Bothnia, Åland Island | Nickol et al. 2002 |
| Carnivora  | Phocidae    | *Halichoerus grypus* (Fabricius, 1791) | grey seal | Baltic Sea, Baltic Proper, Bothnian Sea, Bothnian Bay, Sweden | Leidenberger and Bäcklin 2008 |
| Carnivora  | Phocidae    | *Halichoerus grypus* (Fabricius, 1791) | grey seal | North Sea, Germany, Schleswig-Holstein | Waindok et al. 2018 |
| Carnivora  | Phocidae    | *Halichoerus grypus* (Fabricius, 1791) | grey seal | Arctic Ocean, Northern Atlantic, European Arctic | Delyamure 1961*, von Sprehn 1966* cited by Raga 1992 |
| Carnivora  | Phocidae    | *Halichoerus grypus* (Fabricius, 1791) | grey seal | Alaska, Arctic | Van Cleave 1953 |
| Carnivora  | Phocidae    | *Histriophoca fasciata* (Zimmermann, 1783) | ribbon seal | Barent Sea, Sea of Okhotsk, Chukchi seas, Eastern Siberian Sea | Popov and Fortunato 1987 |
| Host order | Host family | Host species | Host vernacular name | Geographical locality | Reference |
|------------|-------------|--------------|----------------------|-----------------------|-----------|
| Carnivora  | Phocidae    | *Histriophoca fasciata* (Zimmermann, 1783) (as *Phoca fasciata*) | ribbon seal | Bering Sea, Alaska | Rausch et al. 1990 |
| Carnivora  | Phocidae    | *Histriophoca fasciata* (Zimmermann, 1783) (as *Phoca fasciata*) | ribbon seal | Bering Sea | Shults and Frost 1988 |
| Carnivora  | Phocidae    | *Pagophilus groenlandicus* (Erxleben, 1777) | harp seal | Greenland | Van Cleave 1953 |
| Carnivora  | Phocidae    | *Pagophilus groenlandicus* (Erxleben, 1777) (as *Phoca groenlandica*) | harp seal | Germany | Lühe 1911 |
| Carnivora  | Phocidae    | *Phoca largha* Pallas, 1811 | spotted seal | Sea of Okhotsk, Japan Sea | Sasaki et al. 2019 |
| Carnivora  | Phocidae    | *Phoca largha* Pallas, 1811 | spotted seal | Bering Sea, Alaska | Rausch et al. 1990 |
| Carnivora  | Phocidae    | *Phoca largha* Pallas, 1811 | spotted seal | Bering Sea | [On the helminthofauna of largi and harbour seals.]* |
| Carnivora  | Phocidae    | *Phoca largha* Pallas, 1811 | Larga seal, spotted seal | Barent Sea, Sea of Okhotsk, Chukchi seas, Eastern Siberian Sea | Popov and Fortunato 1987 |
| Carnivora  | Phocidae    | *Phoca largha* Pallas, 1811 | Larga seal, spotted seal | Russia: Anadyr Gulf | Aznar et al. 2006 |
| Carnivora  | Phocidae    | *Phoca largha* Pallas, 1811 | spotted seal | no area specified | [On the helminthofauna of largi and harbour seals.]* |
| Host order | Host family | Host species | Host vernacular name | Geographical locality | Reference |
|------------|-------------|--------------|----------------------|-----------------------|-----------|
| Carnivora  | Phocidae    | *Phoca largha* Pallas, 1811 | spotted seal | Japan, Hokkaido, Nemuro Peninsula | Nakaoka et al. 1986* |
| Carnivora  | Phocidae    | *Phoca vitulina* Linnaeus, 1758 | harbour seal | Baltic Sea | Mühling 1989 |
| Carnivora  | Phocidae    | *Phoca vitulina* Linnaeus, 1758 | harbour seal | Germany | Rudolphi 1802 |
| Carnivora  | Phocidae    | *Phoca vitulina* Linnaeus, 1758 | harbour seal | Germany | Lühe 1911 |
| Carnivora  | Phocidae    | *Phoca vitulina* Linnaeus, 1758 | harbour seal | Sweden | Lundström 1942 |
| Carnivora  | Phocidae    | *Phoca vitulina* Linnaeus, 1758 | harbour seal | Baltic Sea and North Sea, Germany, Schleswig-Holstein | Waindok et al. 2018 |
| Carnivora  | Phocidae    | *Phoca vitulina* Linnaeus, 1758 | harbour seal | Alaska, Bering Sea, St. Paul Island | Kuzmina et al. 2012 |
| Carnivora  | Phocidae    | *Phoca vitulina* Linnaeus, 1758 | harbour seal | Alaska, Arctic | Van Cleave 1953 |
| Carnivora  | Phocidae    | *Phoca vitulina* Linnaeus, 1758 | harbour seal | USA, California, Monterey Bay | García-Varela et al. 2011 |
| Carnivora  | Phocidae    | *Phoca vitulina* Linnaeus, 1758 | harbour seal | Pacific | Sasaki et al. 2019 |
| Carnivora  | Phocidae    | *Phoca vitulina* Linnaeus, 1758 (as *Phoca vitulina stejnegeri* J.A.Allen, 1902) | Kuril harbour seal | Japan, Hokkaido, Erimo Cape | Kaimoto et al. 2018 |
| Carnivora  | Phocidae    | *Phoca vitulina* Linnaeus, 1758 (as *Phoca vitulina stejnegeri* J.A.Allen, 1902) | Kuril harbour seal | Japan, Hokkaido, Nemuro Peninsula | Nakaoka et al. 1986* |
| Host order | Host family | Host species | Host vernacular name | Geographical locality | Reference |
|------------|-------------|--------------|----------------------|-----------------------|-----------|
| Carnivora  | Phocidae    | *Phoca vitulina richardii* (Gray, 1864) | Californian harbour seal | California | Van Cleave 1953 |
| Carnivora  | Phocidae    | *Phoca vitulina richardii* (Gray, 1864) | Pacific harbor seal | Washington, Northern Pacific | Dailey and Fallace 1989 |
| Carnivora  | Phocidae    | *Pusa caspica* (Gmelin, 1788) | Caspian seal | Iran, Mazandaran Province, Ramsar City | Amin et al. 2011 |
| Carnivora  | Phocidae    | *Pusa caspica* (Gmelin, 1788) (as *Phoca caspica* Gmelin, 1788) | Caspian seal | Caspian Sea | Kurochkin 1975* cited by Raga 1992 |
| Carnivora  | Phocidae    | *Pusa hispida saimensis* (Nordquist, 1899) | Saimaa ringed seal | Lake Saimaa, Finland | Valtonen and Helle 1988 |
| Carnivora  | Phocidae    | *Pusa hispida* (Schreber, 1775) | ringed seal | Germany | Lühe 1911 |
| Carnivora  | Phocidae    | *Pusa hispida* (Schreber, 1775) | ringed seal | Sweden | Lundström 1942 |
| Carnivora  | Phocidae    | *Pusa hispida* (Schreber, 1775) | ringed seal | Baltic Sea, Bothnian Bay, Finland | Helle and Valtonen 1981 |
| Carnivora  | Phocidae    | *Pusa hispida* (Schreber, 1775) | ringed seal | Baltic Sea, Bothnian Bay, Finland | Valtonen and Helle 1988 |
| Carnivora  | Phocidae    | *Pusa hispida* (Schreber, 1775) | ringed seal | Baltic Sea, Bothnian Bay, Finland | Valtonen et al. 2004 |
| Carnivora  | Phocidae    | *Pusa hispida* (Schreber, 1775) | ringed seal | Baltic Sea, Sweden | Leidenberger et al. 2019 |
| Carnivora  | Phocidae    | *Pusa hispida* (Schreber, 1775) | ringed seal | Alaska, Arctic | Van Cleave 1953 |
| Carnivora  | Phocidae    | *Pusa hispida* (Schreber, 1775) | ringed seal | Barent Sea, Sea of Okhotsk, Chukchi seas, Eastern Siberian Sea | Popov and Fortunato 1987 |
| Host order           | Host family | Host species                                      | Host vernacular name | Geographical locality                  | Reference          |
|----------------------|-------------|---------------------------------------------------|----------------------|----------------------------------------|---------------------|
| Carnivora            | Phocidae    | *Pusa hispida* (Schreber, 1775)                   | ringed seal          | Baltic Sea, Finland, Tvärminne         | Forssell 1904       |
|                       |             | (as *Phoca foetida*)                               |                      |                                        |                     |
| Carnivora            | Phocidae    | *Pusa hispida* (Schreber, 1775)                   | ringed seal          | Baltic Sea, Finland, Tvärminne         | Forssell 1905       |
|                       |             | (as *Phoca foetida*)                               |                      |                                        |                     |
| Cetartiodactyla      | Phocoeridae | *Phocoena phocoena* (Linnaeus, 1758)              | harbour porpoise     | Pacific                                | Sasaki et al. 2019  |
| Cetartiodactyla      | Phocoeridae | *Neophocaena phocaenoides* (G. Cuvier, 1829)      | finless porpoise     | Pacific                                | Sasaki et al. 2019  |

Table 6.
Paratenic host records for *Corynosoma strumosum*. *Source not viewed, NA: not available, ^Found in Host-Parasite Database NHM London without further reference details.*

| Host order           | Host family | Host species                                      | Host vernacular name | Geographical locality                  | Reference          |
|----------------------|-------------|---------------------------------------------------|----------------------|----------------------------------------|---------------------|
| Acipenseriformes     | Acipenseridae | *Acipenser gueldenstaedti* Brandt & Ratzeburg, 1833 | Danube sturgeon      | Caspian Sea, southern part, Sefid-Rud River | Sattari and Mokhayer 2005 |
| Acipenseriformes     | Acipenseridae | *Acipenser persicus* Borodin, 1897 (as *Acipenser gueldenstaedti persicus natio kurensis*) | Persian sturgeon     | Georgia, River Kura                    | Kurashvili et al. 1980* |
| Acipenseriformes     | Acipenseridae | *Acipenser stellatus* Pallas, 1771                | starry sturgeon      | Caspian Sea, southern part, Sefid-Rud River | Sattari and Mokhayer 2005 |
| Acipenseriformes     | Acipenseridae | *Acipenser transmontanus* Richardson, 1836        | white sturgeon       | British Columbia, Canada                | Arai 1989           |
| Acipenseriformes     | Acipenseridae | *Huso huso* (Linnaeus, 1758)                      | beluga               | Caspian Sea, southern part, Sefid-Rud River | Sattari and Mokhayer 2005 |
| Host order     | Host family | Host species                      | Host vernacular name | Geographical locality | Reference       |
|---------------|-------------|-----------------------------------|----------------------|------------------------|-----------------|
| Anguilliformes| Anguillidae | *Anguilla anguilla* (Linnaeus, 1758) | European eel         | Germany                | Lühe 1911       |
| Anguilliformes| Congridae   | *Conger conger* (Linnaeus, 1758)   | European conger      | Sweden                 | Lundström 1942  |
| Anguilliformes| Congridae   | *Conger conger* (Linnaeus, 1758)   | European conger      | Europe                 | Van Cleave 1953 |
| Clupeiformes  | Clupeidae   | *Alosa braschnikowi* (Borodin, 1904) (as *Alosa braschnikovi grimmi*) | Caspian marine shad  | Caspian Sea            | Ibragimov and Vetchanin 1988* |
| Clupeiformes  | Clupeidae   | *Alosa braschnikowi* (Borodin, 1904) (as *Alosa braschnikovi kisselewitschi*) | Caspian marine shad  | Caspian Sea            | Ibragimov and Vetchanin 1988* |
| Clupeiformes  | Clupeidae   | *Alosa kessleri* (Grimm, 1887) (as *Alosa kessleri volgensis*) | Caspian anadromous shad | Caspian Sea           | Izyumova 1977*   |
| Clupeiformes  | Clupeidae   | *Alosa kessleri* (Grimm, 1887) (as *Alosa kessleri volgensis*) | Caspian anadromous shad | USSR (CIS)             | Izyumova 1977*   |
| Clupeiformes  | Clupeidae   | *Clupea harengus* Linnaeus, 1758   | herring               | Sweden                 | Lundström 1942  |
| Clupeiformes  | Clupeidae   | *Clupea harengus* Linnaeus, 1758   | herring               | Europe                 | Van Cleave 1953 |
| Clupeiformes  | Clupeidae   | *Clupea harengus* Linnaeus, 1758 (as *Clupea harengus membras*) | herring               | Baltic Sea, Finland, Tvärminne | Forssell 1905 |
| Clupeiformes  | Clupeidae   | *Clupea pallasi* Valenciennes, 1847 | Pacific herring       | Pacific ocean, Sea of Okhotsk | Sasaki et al. 2019 |
| Host order | Host family | Host species | Host vernacular name | Geographical locality | Reference |
|------------|-------------|--------------|----------------------|-----------------------|-----------|
| Clupeiformes | Clupeidae | Clupea pallasii | Pacific herring | Pacific ocean, Canada | Arai 1989 |
| | | (Valenciennes, 1847) | | | |
| | | (as Clupea harengus pallasii) | | | |
| Clupeiformes | Clupeidae | Clupeonella caspia | Caspian tyulka | Caspian Sea | Ibragimov 1988* |
| | | Svetovidov, 1941 (as Clupeonella delicatula caspia) | | | |
| Clupeiformes | Clupeidae | Clupeonella cultriventris | Black Sea sprat | Caspian Sea | Shamsi et al. 1998* |
| | | (Nordmann, 1840) | | | |
| | | (as Clupea cultriventris) | | | |
| Clupeiformes | Clupeidae | Clupeonella grimmi | Caspian sprat, big-eyed kilka | Capian Sea, southern part | Habibi and Shamsi 2018 |
| | | Kessler, 1877 | | | |
| Cypriniformes | Cyprinidae | Abramis brama | freshwater bream | Georgia, River Kura | Kurashvili et al. 1980* |
| | | (Linnaeus, 1758) | | | |
| Cypriniformes | Cyprinidae | Alburnus chalcoides | shemaya | Georgia, River Kura (USSR) | Kurashvili et al. 1980* |
| | | (Güldenstädt, 1772) | | | |
| | | (as Chalcalburnus chalcoides) | | | |
| Cypriniformes | Cyprinidae | Alburnus chalcoides | shemaya | USSR (CIS) | Izyumova 1977* |
| | | (Güldenstädt, 1772) | | | |
| | | (as Chalcalburnus chalcoides) | | | |
| Cypriniformes | Cyprinidae | Barbus barbus | barbel | USSR (CIS) | Izyumova 1977* |
| | | (Linnaeus, 1758) | | | |
| Cypriniformes | Cyprinidae | Barbus brachycephalus | Caspian barbel | River Kura (USSR) | Kurashvili et al. 1980* |
| | | caspius Berg, 1914 | | | |
| Cypriniformes | Cyprinidae | Carassius carassius | Crucian carp | Azerbaijan | Leidenberger S et al. |
| Host order      | Host family    | Host species                      | Host vernacular name            | Geographical locality                  | Reference           |
|-----------------|----------------|-----------------------------------|---------------------------------|----------------------------------------|---------------------|
| Cypriniformes   | Cyprinidae     | *Cyprinus carpio* Linnaeus, 1758  | common carp                     | Georgia, River Kura (USSR)             | Kurashvili et al. 1980* |
|                 |                | *Leuciscus idus* (Linnaeus, 1758) | orfe, ide                       | Finno-Karelian ASSR                    | Rumyantsev and Ieshko 1997* |
|                 |                | *Pelecus cultratus* (Linnaeus, 1758) | sabrefish, razorfish, knife     | Finno-Karelian ASSR                    | Rumyantsev and Ieshko 1997* |
|                 |                | *Rutilus frisii* (Nordmann, 1840) | Black Sea roach                 | Georgia, River Kura (USSR)             | Kurashvili et al. 1980* |
|                 |                | *Rutilus rutilus* (Linnaeus, 1758) | roach                           | Caspian Sea                            | Ibragimov 1989*     |
|                 |                | *Vimba vimba* (Linnaeus, 1758)    | vimba bream                     | Lithuania                               | Rauckis 1988*       |
| Esociformes     | Esocidae       | *Esox lucius* Linnaeus, 1758      | pike                            | Baltic Sea, Finland, Tvärminne         | Forssell 1905       |
| Gadiformes      | Gadidae        | *Boreogadus saida* (Lepechin, 1774) | Polar cod                       | Arctic Ocean: USSR zone                | Karasev and Mitenev 1993* |
|                 |                | *Eleginus gracilis* (Tilesius, 1810) | saffron cod                     | Gertner Bay, Cape of Nyukliya near Magadan | Skorobrechova and Nikishin 2014 |
|                 |                | *Eleginus nawaga* (Walbaum, 1792) (as *Eleginus navaga*) | saffron cod                     | Japan, Shikotan Island                 | Zhukov 1960*        |
|                 |                |                                   | Arctic cod                      | Arctic Ocean: USSR zone                | Karasev and Mitenev 1993* |
| Host order | Host family | Host species                  | Host vernacular name | Geographical locality | Reference          |
|------------|-------------|-------------------------------|----------------------|-----------------------|--------------------|
| Gadiformes | Gadidae     | *Gadus chalcogrammus*         | Alaska pollock       | Bering Sea            | Shults and Frost 1988 |
|            |             | Pallas, 1814 (as *Theragra*   |                      |                       |                    |
|            |             | chalcogramma)                 |                      |                       |                    |
| Gadiformes | Gadidae     | *Gadus chalcogrammus*         | Alaska pollock       | Bering Sea            | Avdeev and Avdeev 1998* |
|            |             | Pallas, 1814 (as *Theragra*   |                      |                       |                    |
|            |             | chalcogramma)                 |                      |                       |                    |
| Gadiformes | Gadidae     | *Gadus chalcogrammus*         | Alaska pollock       | Pacific ocean,        | Arai 1989          |
|            |             | Pallas, 1814 (as *Theragra*   |                      | Canada                |                    |
|            |             | chalcogramma)                 |                      |                       |                    |
| Gadiformes | Gadidae     | *Gadus macrocephalus*         | Pacific cod          | Pacific coast,        | Van Cleave 1953    |
|            |             | Tilesius, 1810                |                      | USA and Canada        |                    |
| Gadiformes | Gadidae     | *Gadus morhua* Linnaeus, 1758 | cod                  | Sweden                | Lundström 1942     |
|            |             | (as *Gadus callarias*)        |                      |                       |                    |
| Gadiformes | Gadidae     | *Gadus morhua* Linnaeus, 1758 | cod                  | Europe                | Van Cleave 1953    |
|            |             | (as *Gadus callarias*)        |                      |                       |                    |
| Gadiformes | Gadidae     | *Melanogrammus aeglefinus*    | haddock              | Atlantic, Canada      | Arai 1989          |
|            |             | (Linnaeus, 1758)              |                      |                       |                    |
| Gadiformes | Lotidae     | *Lota lota* (Linnaeus, 1758)  | burbot               | Baltic Sea,           | Valttonen and      |
|            |             |                               |                      | Bothnian Bay          | Julkunen 1995      |
| Gadiformes | Lotidae     | *Lota lota* (Linnaeus, 1758)  | burbot               | Baltic Sea,           | Forssell 1905      |
|            |             | (as *Lota vulgaris*)          |                      | Finland,              |                    |
|            |             |                               |                      | Tvärminne             |                    |
| Gadiformes | Lotidae     | *Lota lota* (Linnaeus, 1758)  | burbot               | Germany               | Lühe 1911          |
|            |             | (as *Lota vulgaris*)          |                      |                       |                    |
| Gadiformes | Lotidae     | *Lota lota* (Linnaeus, 1758)  | burbot               | Sweden                | Lundström 1942     |
|            |             | (as *Lota vulgaris*)          |                      |                       |                    |
| Host order     | Host family | Host species                          | Host vernacular name                                      | Geographical locality          | Reference                |
|----------------|-------------|---------------------------------------|------------------------------------------------------------|-------------------------------|--------------------------|
| Gadiformes     | Lotidae     | *Lota lota* (Linnaeus, 1758) (as *Lota vulgaris*) | burbot                                                      | Europe                        | Van Cleave 1953          |
| Gadiformes     | Merlucciidae| *Macruronus novaezelandiae* (Hector, 1871) | whiptail, tailed hake, Patagonian whiphake, New Zealand whiptail, blue hake, blue grenadier | New Zealand coast             | Klimpel et al. 2001*    |
| Gadiformes     | Merlucciidae| *Merluccius capensis* Castelnau, 1861 | whiting, stockfish, South African whiting, shallow-water Cape hake, shallow water hake, hake, Cape hake | no area specified             | Parukhin 1989*           |
| Gasterosteiformes | Gasteroideae | *Gasterosteus aculeatus* Linnaeus, 1758 | three-spined stickleback                                   | Sweden                        | Lundström 1942           |
| Gasterosteiformes | Gasteroideae | *Gasterosteus aculeatus* Linnaeus, 1758 | three-spined stickleback                                   | Europe                        | Van Cleave 1953          |
| Gasterosteiformes | Gasteroideae | *Gasterosteus aculeatus* Linnaeus, 1758 | three-spined stickleback                                   | Caspian Sea, southeast part, Gomishan Lagoon | Niksirat et al. 2006 |
| Lophiiformes   | Lophiidae   | *Lophius piscatorius* Linnaeus, 1758   | angler                                                      | Baltic Sea                    | Mühling 1989             |
| Lophiiformes   | Lophiidae   | *Lophius piscatorius* Linnaeus, 1758   | angler                                                      | Sweden                        | Lundström 1942           |
| Lophiiformes   | Lophiidae   | *Lophius piscatorius* Linnaeus, 1758   | angler                                                      | Europe                        | Van Cleave 1953          |
| Lophiiformes   | Lophiidae   | *Lophius piscatorius* Linnaeus, 1758   | monkfish, angler-fish                                       | no area specified             | Parukhin 1989*           |
| Ophidiiformes  | Ophidiidae  | *Hoplobrotula gnathopus* (Regan, 1921) | false kinglip                                               | no area specified             | Parukhin 1989*           |
| Host order | Host family | Host species | Host vernacular name | Geographical locality | Reference |
|------------|-------------|--------------|----------------------|-----------------------|-----------|
| Osmeriformes | Osmeridae | *Hypomesus japonicus* (Brevoort, 1856) | Japanese smelt | Pacific ocean | Sasaki et al. 2019 |
| Osmeriformes | Osmeridae | *Hypomesus japonicus* (Brevoort, 1856) | Japanese smelt | Japan, Shikotan Island | Zhukov 1960* |
| Osmeriformes | Osmeridae | *Hypomesus japonicus* (Brevoort, 1856) | Japanese smelt | Japan, Hokkaido, Erimo Cape | Araki and Machida 1987* |
| Osmeriformes | Osmeridae | *Hypomesus japonicus* (Brevoort, 1856) (as *Hypomesus preiosus japonicus*) | Japanese smelt | Japan, Hokkaido | Nagasawa et al. 1989* |
| Osmeriformes | Osmeridae | *Hypomesus olidus* (Pallas, 1814) | pond smelt | Nagaev and Gertner Bay, Magadan, Russia, Sea of Okhotsk | Skorobrechova and Nikishin 2011 |
| Osmeriformes | Osmeridae | *Hypomesus olidus* (Pallas, 1814) | pond smelt | Japan, Shikotan Island | Zhukov 1960* |
| Osmeriformes | Osmeridae | *Osmerus dentex* Steindachner and Kner, 1870 | Pacific rainbow smelt | Japan, Sea of Okhotsk, Pacific ocean | Sasaki et al. 2019 |
| Osmeriformes | Osmeridae | *Osmerus eperlanus* (Linnaeus, 1758) | rainbow smelt | Sweden | Lundström 1942 |
| Osmeriformes | Osmeridae | *Osmerus eperlanus* (Linnaeus, 1758) | rainbow smelt | Europe | Van Cleave 1953 |
| Osmeriformes | Osmeridae | *Osmerus eperlanus* (Linnaeus, 1758) | rainbow smelt | Baltic Sea, Bothnian Bay | Valtonen and Julkunen 1995 |
| Osmeriformes | Osmeridae | *Osmerus mordax dentex* Steindachner & Kner, 1870 | rainbow smelt | Nagaev and Gertner Bay, Magadan, Russia, Sea of Okhotsk | Skorobrechova and Nikishin 2011 |
| Host order       | Host family    | Host species                      | Host vernacular name             | Geographical locality            | Reference       |
|------------------|----------------|-----------------------------------|----------------------------------|----------------------------------|-----------------|
| Osmeriformes     | Osmeridae      | *Spirinchus lanceolatus* (Hikita, 1913) | Sishamo smelt | Japan Hokkaido, Mukawa River | Fujita 1921*     |
| Osmeriformes     | Osmeridae      | *Spirinchus lanceolatus* (Hikita, 1913) (as *Osmerus lanceolatus*) | Shishamo, willow leaf fish | Japan | Van Cleave 1953 |
| Perciformes      | Gobiidae       | *Benthophilus stellatus* (Sauvage, 1874) | Stellate tadpole-goby | Caspian Sea | Ibragimov 1988* |
| Perciformes      | Gobiidae       | *Gobius Linnaeus*, 1758 | goby | Caspian Sea | Ibragimov 1988* |
| Perciformes      | Gobiidae       | *Neogobius fluviatilis* (Pallas, 1814) (as *Gobius fluviatilis*) | monkey goby | Caspian Sea | Ibragimov 1988* |
| Perciformes      | Gobiidae       | *Neogobius fluviatilis* (Pallas, 1814) (as *Neogobius fluviatilis pallasi* (Pallas, 1814) | monkey goby | Caspian Sea, south-eastern part | Pazooki et al. 2011 |
| Perciformes      | Gobiidae       | *Neogobius melanostomus* (Pallas, 1814) | round goby | Caspian Sea | Ibragimov 1988* |
| Perciformes      | Gobiidae       | *Ponticola bathybius* (Kessler, 1877) (as *Neogobius bathybius*) | NA | Caspian Sea, south-eastern part | Pazooki et al. 2011 |
| Perciformes      | Gobiidae       | *Ponticola gorlap* (Iljim, 1949) (as *Neogobius kessleri gorlap*) | Caspian bighead goby | Caspian Sea, south-eastern part | Pazooki et al. 2011 |
| Perciformes      | Gobiidae       | *Ponticola kessleri* (Günther, 1861) (as *Neogobius kessleri*) | bighead goby | Caspian Sea | Ibragimov 1988* |
| Perciformes      | Hexagrammidae  | *Hexagrammos octogrammus* (Pallas, 1814) | masked greenling | Sea of Okhotsk | Skorobrechova 2009* cited in Skorobrechova et al. 2011 |
| Host order       | Host family | Host species                                                                 | Host vernacular name           | Geographical locality                  | Reference         |
|------------------|-------------|-------------------------------------------------------------------------------|--------------------------------|-----------------------------------------|-------------------|
| Perciformes      | Mugilidae   | *Chelon auratus* (Risso, 1810) (as *Mugil auratus*)                           | golden grey mullet             | Caspian Sea                             | Ibragimov 1988*   |
| Perciformes      | Mugilidae   | *Chelon auratus* (Risso, 1810) (as *Mugil auratus*)                           | leaping mullet                 | Caspian Sea                             | Ibragimov 1988*   |
| Perciformes      | Percidae    | *Gymnocephalus cernua* (Linnaeus, 1758) (as *Gymnocephalus cernuus*)          | ruffe                          | Baltic Sea, Bothnian Bay                | Valtonen and Julkunen 1995 |
| Perciformes      | Percidae    | *Perca fluviatilis* Linnaeus, 1758                                            | perch                          | Baltic Sea, Finland, Tvärminne          | Forssell 1905     |
| Perciformes      | Percidae    | *Perca fluviatilis* Linnaeus, 1758                                            | perch                          | Germany                                 | Lühe 1911         |
| Perciformes      | Percidae    | *Perca fluviatilis* Linnaeus, 1758                                            | perch                          | Europe                                  | Van Cleave 1953   |
| Perciformes      | Percidae    | *Sander lucioperca* (Linnaeus, 1758) (as *Lucioperca lucioperca*)             | zander, pike-perch             | Georgia, River Kura (USSR)              | Kurashvili et al. 1980*|
| Perciformes      | Percidae    | *Sander lucioperca* (Linnaeus, 1758) (as *Lucioperca lucioperca*)             | zander, pike-perch             | USSR (CIS)                              | Izyumova 1977*    |
| Perciformes      | Percidae    | *Sander lucioperca* (Linnaeus, 1758) (as *Stizostedion lucioperca*)            | zander, pike-perch             | Finno-Karelian ASSR                     | Rumyantsev and Ieshko 1997* |
| Perciformes      | Sciaenidae  | *Umbrina roncador* Jordan & Gilbert, 1882                                     | yellowfin croaker              | Catalina Island, California             | Van Cleave 1953   |
| Perciformes      | Sparidae    | *Pomatoscion eleginoides* (Linnaeus, 1758)                                    | red porgy, Couch's seabream, common seabream | no area specified                      | Parukhin 1966*    |
| Host order   | Host family   | Host species                      | Host vernacular name | Geographical locality | Reference                  |
|--------------|---------------|-----------------------------------|----------------------|------------------------|----------------------------|
| Perciformes  | Sparidae      | *Sparus heterodus* Peters, 1877   | NA                   | no area specified      | Parukhin 1966*             |
| Perciformes  | Sphyraenidae  | *Sphyraena barracuda* (Edwards, 1771) | great *barracuda*    | no area specified      | Parukhin 1966*             |
| Perciformes  | Stichaeidae   | *Pholidapus dybowskii* (Steindachner, 1880) | stichaeid fish      | Japan, Shikotan Island | Zhukov 1960*               |
| Perciformes  | Trachinidae   | *Trachinus draco* Linnaeus, 1758  | weever               | Baltic Sea             | Mühlung 1989               |
| Perciformes  | Trachinidae   | *Trachinus draco* Linnaeus, 1758  | weever               | Sweden                 | Lundström 1942             |
| Perciformes  | Trachinidae   | *Trachinus draco* Linnaeus, 1758  | weever               | Germany                | Lühe 1911                  |
| Perciformes  | Trachinidae   | *Trachinus draco* Linnaeus, 1758  | weever               | Europe                 | Van Cleave 1953            |
| Perciformes  | Trichodontidae| *Arctoscopus japonicus* (Steindachner, 1881) | Japanese sandfish    | Japan, Shikotan Island | Zhukov 1960*               |
| Perciformes  | Zoarcidae     | *Lycodes raridens* Taranetz & Andriashev, 1937 | marbled eelpout     | Bering Sea             | Shultz and Frost 1988      |
| Perciformes  | Zoarcidae     | *Hadropareia middendorffii* Schmidt, 1904 | NA                   | Sea of Okhosk          | Skorobrechova 2010* cited in Skorobrechova et al. 2011 |
| Perciformes  | Zoarcidae     | *Zoarces viviparus* (Linnaeus, 1758) | eelpout              | Baltic Sea, Polen, Gdansk Bight | Markowski 1938 |
| Perciformes  | Zoarcidae     | *Zoarces viviparus* (Linnaeus, 1758) | eelpout              | Sweden                 | Lundström 1942             |
| Perciformes  | Zoarcidae     | *Zoarces viviparus* (Linnaeus, 1758) | eelpout              | Europe                 | Van Cleave 1953            |
| Perciformes  | Zoarcidae     | *Zoarces viviparus* (Linnaeus, 1758) | eelpout              | Baltic Sea, Germany, Salzhaff | Reimer and Walter 1998   |
| Host order | Host family | Host species | Host vernacular name | Geographical locality | Reference |
|------------|-------------|--------------|----------------------|-----------------------|-----------|
| Pleuronectiformes | Pleuronectidae | *Atheresthes stomias* (Jordan & Gilbert, 1880) | arrow-tooth flounder | British Columbia | Wierzbicka and Piasecki 1998* |
| Pleuronectiformes | Pleuronectidae | *Eopsetta jordani* (Lockingston, 1879) | petraie sole | Canada | Arai 1989 |
| Pleuronectiformes | Pleuronectidae | *Hippoglossoides platessoides* (Fabricius, 1780) (as *Hippoglossoides platessoides limandoides*) | sand-dab, long rough dab, Canadian plaice, American plaice | Arctic Ocean, Greenland/ Icelandic zone | Olafsdottir 1999 |
| Pleuronectiformes | Pleuronectidae | *Hippoglossus stenolepis* (Schmidt, 1904) | Pacific halibut | Northern Pacific | Blaylock et al. 1998* |
| Pleuronectiformes | Pleuronectidae | *Lepidopsetta bilineata* (Ayres, 1855) | rock sole | Pacific coast, USA and Canada | Van Cleave 1953 |
| Pleuronectiformes | Pleuronectidae | *Lepidopsetta bilineata* (Ayres, 1855) | rock sole | Pacific ocean, Canada | Arai 1989 |
| Pleuronectiformes | Pleuronectidae | *Limanda aspera* (Pallas, 1814) | yellowfin sole | Nagaev and Gertner Bay, Magadan, Russia, Sea of Okhotsk | Skorobrechova and Nikishin 2011 |
| Pleuronectiformes | Pleuronectidae | *Limanda limanda* (Linnaeus, 1758) (as *Pleuronectes limanda*) | common dab | Europe | Van Cleave 1953 |
| Pleuronectiformes | Pleuronectidae | *Platichthys flesus* (Linnaeus, 1758) | flounder | Baltic Sea, Finland, Tvärminne | Forssell 1905 |
| Pleuronectiformes | Pleuronectidae | *Platichthys flesus* (Linnaeus, 1758) | flounder | Germany | Lühe 1911 |
| Pleuronectiformes | Pleuronectidae | *Platichthys flesus* (Linnaeus, 1758) | flounder | Sweden | Lundström 1942 |
| Host order       | Host family     | Host species                      | Host vernacular name | Geographical locality | Reference       |
|------------------|-----------------|-----------------------------------|----------------------|------------------------|-----------------|
| Pleuronectiformes| Pleuronectidae  | *Platichthys flesus* (Linnaeus, 1758) | perch                | Sweden                 | Lundström 1942 |
| Pleuronectiformes| Pleuronectidae  | *Platichthys flesus* (Linnaeus, 1758) (as *Platessa flesus*) | flounder             | Baltic Sea             | Mühling 1989   |
| Pleuronectiformes| Pleuronectidae  | *Platichthys flesus* (Linnaeus, 1758) (as *Pleuronectes flesus*) | flounder             | Baltic Sea, Finland, Tvärminne | Forssell 1905 |
| Pleuronectiformes| Pleuronectidae  | *Platichthys flesus* (Linnaeus, 1758) (as *Pleuronectes flesus*) | flounder             | Europe                 | Van Cleave 1953 |
| Pleuronectiformes| Pleuronectidae  | *Platichthys stellatus* (Pallas, 1787) | starry flounder      | Japan, Shikotan Island | Zhukov 1960*   |
| Pleuronectiformes| Pleuronectidae  | *Platichthys stellatus* (Pallas, 1787) | starry flounder      | Pacific coast, USA and Canada | Van Cleave 1953 |
| Pleuronectiformes| Pleuronectidae  | *Platichthys stellatus* (Pallas, 1787) | starry flounder      | Pacific ocean, Canada | Arai 1989      |
| Pleuronectiformes| Pleuronectidae  | *Pleuronectes obscurus* Herzenstein, 1890 | black plaice         | Japan, Shikotan Island | Zhukov 1960*   |
| Pleuronectiformes| Pleuronectidae  | *Reinhardtius hippoglossoides* (Walbaum, 1792) | turbot               | Atlantic, Canada       | Arai 1989      |
| Pleuronectiformes| Pleuronectidae  | *Verasper moseri* Jordan & Gilbert, 1898 | barfin flounder      | Japan, Hokkaido, Erimo Cape | Araki and Machida 1987* |
| Pleuronectiformes| Scophthalmidae  | *Scophthalmus maximus* (Linnaeus, 1758) (as *Rhombus maximus*) | trubot               | Baltic Sea, Finland, Tvärminne | Forssell 1904 |
| Pleuronectiformes| Scophthalmidae  | *Scophthalmus maximus* (Linnaeus, 1758) (as *Rhombus maximus*) | trubot               | Baltic Sea, Finland, Tvärminne | Forssell 1905 |
| Host order     | Host family         | Host species                                    | Host vernacular name | Geographical locality | Reference          |
|----------------|---------------------|------------------------------------------------|----------------------|------------------------|--------------------|
| Pleuronectiformes | Scophthalmidae     | *Scophthalmus maximus* (Linnaeus, 1758) (as *Rhombus maximus*) | trubot               | Germany                | Lühe 1911          |
| Pleuronectiformes | Scophthalmidae     | *Scophthalmus maximus* (Linnaeus, 1758) (as *Rhombus maximus*) | trubot               | Sweden                 | Lundström 1942     |
| Pleuronectiformes | Scophthalmidae     | *Scophthalmus maximus* (Linnaeus, 1758) (as *Rhombus maximus*) | trubot               | Europe                 | Van Cleave 1953    |
| Salmoniformes   | Hemitripteridae    | *Hemitripterus villosus* (Pallas, 1814)         | shaggy sea raven     | Japan, Hokkaido, Nemuro Peninsula | Nakaoka et al. 1986* |
| Salmoniformes   | Salmonidae         | *Coregonus fera* Jurine, 1825                   | true fera            | Europe                 | Van Cleave 1953    |
| Salmoniformes   | Salmonidae         | *Coregonus lavaretus* (Linnaeus, 1758)          | lavaret              | Europe                 | Van Cleave 1953    |
| Salmoniformes   | Salmonidae         | *Oncorhynchus gorbuscha* (Walbaum, 1792)        | pink salmon          | Pacific ocean, Canada  | Arai 1989          |
| Salmoniformes   | Salmonidae         | *Oncorhynchus gorbuscha* (Walbaum, 1792)        | pink salmon          | Sakhalin Island        | Vyalova 2003*      |
| Salmoniformes   | Salmonidae         | *Oncorhynchus keta* (Walbaum, 1792)             | chum salmon          | Sakhalin Island        | Vyalova 2003*      |
| Salmoniformes   | Salmonidae         | *Oncorhynchus masou* (Brevoort, 1856) (as *Oncorhynchus masu*) | masu salmon          | Russia                 | Ermolenko et al. 1989* |
| Salmoniformes   | Salmonidae         | *Oncorhynchus nerka* (Walbaum, 1792)            | sockeye salmon       | Pacific ocean, Canada  | Arai 1989          |
| Salmoniformes   | Salmonidae         | *Salmo salar* Linnaeus, 1758                    | salmon               | European USSR (CIS)    | Rumyantsev et al. 1988* |
| Host order    | Host family | Host species | Host vernacular name | Geographical locality | Reference                          |
|--------------|-------------|--------------|----------------------|-----------------------|------------------------------------|
| Salmoniformes | Salmonidae  | *Salmo trutta* Linnaeus, 1758 | trout | European USSR (CIS) | Rumyantsev et al. 1998* |
| Salmoniformes | Salmonidae  | *Salvelinus alpinus alpinus* (Linnaeus, 1758) | Arctic charr | Canada, Quebec, Ungava Bay | Desjardins et al. 1998* |
| Salmoniformes | Salmonidae  | *Salvelinus alpinus alpinus* (Linnaeus, 1758) (as *Salvelinus alpinus*) | Arctic charr | River Chaun | [On the helminthofauna of fish of the River Chaun.]* |
| Salmoniformes | Salmonidae  | *Salvelinus leucomaenis leucomaenis* (Pallas, 1814) | white-spotted charr | Japan, Shikotan Island | Zhukov 1960* |
| Salmoniformes | Salmonidae  | *Salvelinus leucomaenis leucomaenis* (Pallas, 1814) (as *Salvelinus leucomaenis*) | white-spotted charr | Japan, Hokkaido | Nagasawa et al. 1989* |
| Salmoniformes | Salmonidae  | *Salvelinus malma* (Walbaum, 1792) | dolly varden | Russia | Ermolenko 1994* |
| Salmoniformes | Salmonidae  | *Salvelinus malma* (Walbaum, 1792) | dolly varden | Russia | Ermolenko et al. 1989* |
| Salmoniformes | Salmonidae  | *Thymallus thymallus* (Linnaeus, 1758) | grayling | European waters of NE Atlantic and Mediterranean | Rumyantsev et al. 1999* |
| Scorpaeniformes | Cottidae   | *Gymnocanthus galeatus* Bean, 1881 | armoured sculpin | Bering Sea | Shults and Frost 1988 |
| Scorpaeniformes | Cottidae   | *Gymnocanthus herzensteini* Jordan & Starks, 1904 | staghorn sculpin | Japan, Hokkaido, Erimo Cape | Araki and Machida 1987* |
| Scorpaeniformes | Cottidae   | *Leptocottus armatus* Girard, 1854 | Pacific staghorn sculpin | Pacific coast, USA and Canada | Van Cleave 1953 |
| Scorpaeniformes | Cottidae   | *Myoxocephalus brandti* (Steindachner, 1867) | snowy sculpin | Japan, Shikotan Island | Zhukov 1960* |
| Host order       | Host family | Host species                       | Host vernacular name | Geographical locality | Reference                  |
|------------------|-------------|-----------------------------------|----------------------|------------------------|---------------------------|
| Scorpaeniformes  | Cottidae    | Myoxocephalus polyacanthocephalus  | great sculpin        | Japan, Hokkaido, Erimo Cape | Araki and Machida 1987*   |
|                  |             | (Pallas, 1814) (as Ainocottus ensiger) |                      |                        |                           |
| Scorpaeniformes  | Cottidae    | Myoxocephalus quadricornis        | fourhorn sculpin     | Baltic Sea, Bothnian Bay | Sinisalo and Valtonen 2003 |
|                  |             | (Linnaeus, 1758) (as Cottus quadricornis) |                      |                        |                           |
| Scorpaeniformes  | Cottidae    | Myoxocephalus quadricornis        | fourhorn sculpin     | Sweden                 | Lundström 1942            |
|                  |             | (Linnaeus, 1758) (as Cottus quadricornis) |                      |                        |                           |
| Scorpaeniformes  | Cottidae    | Myoxocephalus quadricornis        | fourhorn sculpin     | Baltic Sea, Finland, Tvärminne | Forsell 1904       |
|                  |             | (Linnaeus, 1758) (as Cottus quadricornis) |                      |                        |                           |
| Scorpaeniformes  | Cottidae    | Myoxocephalus quadricornis        | fourhorn sculpin     | Baltic Sea, Finland, Tvärminne | Forsell 1905       |
|                  |             | (Linnaeus, 1758) (as Cottus quadricornis) |                      |                        |                           |
| Scorpaeniformes  | Cottidae    | Myoxocephalus quadricornis        | fourhorn sculpin     | Germany                | Lühe 1911                  |
|                  |             | (Linnaeus, 1758) (as Cottus quadricornis) |                      |                        |                           |
| Scorpaeniformes  | Cottidae    | Myoxocephalus quadricornis        | fourhorn sculpin     | Sweden                 | Lundström 1942            |
|                  |             | (Linnaeus, 1758) (as Cottus quadricornis) |                      |                        |                           |
| Scorpaeniformes  | Cottidae    | Myoxocephalus quadricornis        | fourhorn sculpin     | Europe                 | Van Cleave 1953            |
|                  |             | (Linnaeus, 1758) (as Cottus quadricornis) |                      |                        |                           |
| Scorpaeniformes  | Cottidae    | Myoxocephalus scorpius (Linnaeus, 1758) | fourhorn sculpin     | Baltic Sea, Bothnian Bay | Valtonen and Julkunen 1995 |
| Scorpaeniformes  | Cottidae    | Myoxocephalus scorpius (Linnaeus, 1758) | fourhorn sculpin     | Baltic Sea, North-eastern Bothnian Bay | Valtonen et al. 2001 |
| Host order        | Host family | Host species                        | Host vernacular name          | Geographical locality | Reference       |
|-------------------|-------------|-------------------------------------|-------------------------------|------------------------|-----------------|
| Scorpaeniformes   | Cottidae    | *Myoxocephalus scorpius* (Linnaeus, 1758) (as *Cottus scorpius*) | shorthorn sculpin             | Germany                | Lühe 1911       |
|                   |             |                                     |                               |                        |                 |
| Scorpaeniformes   | Cottidae    | *Myoxocephalus scorpius* (Linnaeus, 1758) (as *Cottus scorpius*) | shorthorn sculpin             | Sweden                 | Lundström 1942  |
|                   |             |                                     |                               |                        |                 |
| Scorpaeniformes   | Cottidae    | *Myoxocephalus stelleri* (Tilesius, 1811) | fourhorn sculpin              | Europe                 | Van Cleave 1953 |
|                   |             |                                     |                               |                        |                 |
| Scorpaeniformes   | Cottidae    | *Myoxocephalus stelleri* (Tilesius, 1811) | Steller's sculpin             | Gertner Bay, Cape of Nyuklia near Magadan | Skorobrechova and Nikishin 2014 |
| Scorpaeniformes   | Cottidae    | *Taurulus bubalis* (Euphrasen, 1786) | sea scorpion                  | Germany                | Lühe 1911       |
| Scorpaeniformes   | Cyclopteridae | *Cyclopterus lumpus* (Linnaeus, 1758) | lumpfish                      | Baltic Sea             | Mühling 1989    |
| Scorpaeniformes   | Cyclopteridae | *Cyclopterus lumpus* (Linnaeus, 1758) | lumpfish                      | Germany                | Lühe 1911       |
| Scorpaeniformes   | Cyclopteridae | *Cyclopterus lumpus* (Linnaeus, 1758) | lumpfish                      | Sweden                 | Lundström 1942  |
| Scorpaeniformes   | Cyclopteridae | *Cyclopterus lumpus* (Linnaeus, 1758) | lumpfish                      | Europe                 | Van Cleave 1953 |
| Scorpaeniformes   | Hemitripteridae | *Hemitripterus villosus* (Pallas, 1814) | shaggy sea raven              | Japan, Shikotan Island | Zhukov 1960*    |
| Scorpaeniformes   | Hexagrammidae | *Hexagrammos lagocephalus* (Pallas, 1810) | rock greenling                | Japan, Shikotan Island | Zhukov 1960*    |
| Host order      | Host family       | Host species               | Host vernacular name      | Geographical locality                  | Reference         |
|-----------------|-------------------|----------------------------|---------------------------|----------------------------------------|-------------------|
| Scorpaeniformes | Hexagrammidae     | *Hexagrammos lagoscephalus* (Pallas, 1810) | rock greenling            | Japan, Hokkaido, Nemuro Peninsula      | Nakaoka et al. 1986* |
| Scorpaeniformes | Hexagrammidae     | *Hexagrammos octogrammuses* (Pallas, 1814) | masked greenling          | Japan, Shikotan Island                 | Zhukov 1960*      |
| Scorpaeniformes | Hexagrammidae     | *Hexagrammos stelleri* Tilesius, 1810 | whitespotted greenling    | Gertner Bay, Cape of Nyuklya near Magadan | Skorobrechova and Nikishin 2014 |
| Scorpaeniformes | Hexagrammidae     | *Pleurogrammus azonus* Jordan and Metz, 1913 | Okhotsk atka mackerel     | Sea of Okhotsk                        | Sasaki et al. 2019 |
| Scorpaeniformes | Sebastidae        | *Sebastes mentella* Travin, 1951 | deepwater redfish, beaked redfish | NW Atlantic: Norwegian Sea and Barents Sea | Bakay 2001       |
| Scorpaeniformes | Sebastidae        | *Sebastes paucispinis* Ayres, 1854 | bocaccio                  | Pacific coast of USA                  | Love et al. 2002* |
| Scorpaeniformes | Sebastidae        | *Sebastes trivittatus* Hilgendorf, 1880 | threestripe rockfish      | Japan, Shikotan Island                 | Zhukov 1960*      |
| Scorpaeniformes | Sebastidae        | *Sebastes trivittatus* Hilgendorf, 1880 | threestripe rockfish      | Pacific ocean                          | Sasaki et al. 2019 |
| Scorpaeniformes | Triglidae         | *Chelidonichthys capensis* (Cuvier, 1829) (as *Trigla capensis*) | Cape gurnard              | no area specified                     | Parukhin 1966*    |
| Sygnathiformes  | Sygnathidae       | *Sygnathus sp.* Linnaeus, 1758 | seaweed pipifishes        | Caspian Sea                            | Ibragimov 1988*   |
| Pleuronectiformes| Pleuronectidae    | *Pseudopleuronectes herzensteini* (Jordan and Snyder, 1901) (as *Pleuronectes herzensteini*) | yellow striped flounder    | Pacific ocean                          | Sasaki et al. 2019 |
| Host order       | Host family   | Host species                     | Host vernacular name       | Geographical locality | Reference           |
|------------------|---------------|----------------------------------|----------------------------|-----------------------|---------------------|
| Pleuronectiformes| Pleuronectidae| Pseudopleuronectes obscurus      | darkflounder               | Pacific ocean         | Sasaki et al. 2019  |
|                  |               | Herzenstein, 1890 (as Pleuronectes obscurus) |                            |                       |                     |
| Petromyzontiformes| Petromyzontidae| Caspiomyzon wagneri (Kessler, 1870) (as Caspiomyzon wagneri caspius) | Caspian lamprey      | Georgia, River Kura (USSR) | Kurashvili et al. 1980* |
| Petromyzontiformes| Petromyzontidae| Lampetra fluviatilis (Linnaeus, 1758) | river lamprey           | Germany               | Lühe 1911           |
| Petromyzontiformes| Petromyzontidae| Lampetra fluviatilis (Linnaeus, 1758) (as Petromyzon fluviatilis) | river lamprey           | Baltic Sea            | Mühling 1989        |

Table 7.
Accidental hosts of Corynosoma semerme. *Source not viewed, ^Found in Host-Parasite Database NHM London without further reference details.

| Host order       | Host family | Host species                     | Host vernacular name       | Geographical locality | Reference           |
|------------------|-------------|----------------------------------|----------------------------|-----------------------|---------------------|
| Anseriformes     | Anatidae    | Clangula hyemalis (Linnaeus, 1758) (as Nyroca hyemalis) | long-tailed duck           | Germany               | Lühe 1911           |
| Charadriiformes  | Laridae     | Larus fuscus Linnaeus, 1758       | black-backed gull          | Baltic Sea, Finland   | Forssell 1905       |
| Suliformes       | Phalacrocoracidae | Phalacrocorax carbo (Linnaeus, 1758) | great cormorant           | Baltic Sea, Finland   | Forssell 1905       |
| Suliformes       | Phalacrocoracidae | Phalacrocorax carbo (Linnaeus, 1758) | great cormorant           | Germany               | Lühe 1911           |
| Suliformes       | Phalacrocoracidae | Phalacrocorax pelagicus Pallas, 1811 (as Phalacrocorax pelagicus pelagicus) | pelagic cormorant         | North America         | Van Cleave 1953     |
| Host order       | Host family | Host species                      | Host vernacular name | Geographical locality | Reference       |
|------------------|-------------|-----------------------------------|----------------------|------------------------|-----------------|
| Carnivora        | Canidae     | *Canis lupus familiaris* Linnaeus, 1758 (as *Canis familiaris*) | Husky dog           | North America          | Van Cleave 1953 |
| Carnivora        | Canidae     | *Vulpes lagopus* Linnaeus, 1758 (as *Alopex lagopus*) | Arctic fox, polar fox | European USSR (CIS)    | Yushkov 1995*   |
| Carnivora        | Canidae     | *Vulpes lagopus* Linnaeus, 1758 (as *Alopex lagopus*) | Arctic fox, polar fox | St. Lawrence Island, Bering Sea, Alaska | Rausch et al. 1990 |
| Carnivora        | Mustelidae  | *Mustela erminea* Linnaeus, 1758 | stoat                | Sweden                 | Lundström 1942  |
| Carnivora        | Mustelidae  | *Mustela putorius* Linnaeus, 1758 (as *Putorius foetorius*) | European polecat     | Germany                | Lühe 1911       |
| Carnivora        | Mustelidae  | *Neovison vison* (Schreber, 1777) (as *Mustela vison*) | mink                 | Finland                | Nuorteva 1966   |
| Carnivora        | Mustelidae  | *Neovison vison* (Schreber, 1777) (as *Mustela vison*) | American Mink        | Iceland                | Skirmisson 1995 |
| Cetartiodactyla  | Eschrichtiidae | *Eschrichtius robustus* (Liljeborg, 1861) (as *Eschrichtius gibbosus*) | gray/grey whale     | Arctic Ocean, Pacific Ocean | [Whales and dolphins. Monographic outline.]* |
| Cetartiodactyla  | Phocoenidae | *Phocoena phocoena* Linnaeus, 1758 | harbour porpoise    | Germany                | Lühe 1911       |
| Cetartiodactyla  | Phocoenidae | *Phocoena phocoena* Linnaeus, 1758 | harbour porpoise    | Northern Atlantic      | [Whales and dolphins. Monographic outline.]* |
| Cetartiodactyla  | Phocoenidae | *Phocoena phocoena* Linnaeus, 1758 | harbour porpoise    | Arctic Ocean, Northern Pacific Ocean | [Whales and dolphins. Monographic outline.]* |
| Cetartiodactyla  | Phocoenidae | *Phocoena phocoena* Linnaeus, 1758 (as *Phocoena communis*) | harbour porpoise    | Finland, Tvärminne      | Forssell 1904   |
| Host order     | Host family   | Host species        | Host vernacular name          | Geographical locality | Reference        |
|----------------|---------------|---------------------|-------------------------------|------------------------|------------------|
| Cetartiodactyla| Phocoenidae   | Phocoena phocoena   | harbour porpoise              | Baltic Sea, Finland    | Forssell 1905    |
|                |               | (Linnaeus, 1758)    |                               |                        |                  |
|                |               | (as Phocoena communis) |                             |                        |                  |
| Accipitriformes| Accipitridae  | Haliaeetus leucocephalus | Bald eagle                  | North America, Alaska | Van Cleave 1953  |
|                |               | (Linnaeus, 1766)    |                               |                        |                  |
| Anseriformes   | Anatidae      | Clangula hyemalis   | oldsquaw                      | Europe                 | Mühling 1989     |
|                |               | (Linnaeus, 1758)    |                               |                        |                  |
| Anseriformes   | Anatidae      | Mergus merganser    | common merganser              | Germany                | Lühe 1911        |
|                |               | (Linnaeus, 1758)    |                               |                        |                  |
| Anseriformes   | Anatidae      | Mergus serrator     | red-breasted merganser        | Germany                | Lühe 1911        |
|                |               | Linnaeus, 1758      |                               |                        |                  |
| Anseriformes   | Anatidae      | Somateria mollissima| eider duck                    | Iceland                | Skirnisson and Jonsson 1996 |
|                |               | (Linnaeus, 1758)    |                               |                        |                  |
| Charadriiformes| Alcidae       | Uria lomvia         | thick-billed murre            | Point Barrow, Alaska   | Rausch et al. 1990|
|                |               | (Linnaeus, 1758)    |                               |                        |                  |
| Charadriiformes| Laridae       | Larus argentatus    | herring gull                  | Finland                | Forssell 1905    |
|                |               | Pontoppidan, 1763   |                               |                        |                  |
| Charadriiformes| Laridae       | Larus glaucescens   | glaucous-winged gull          | Napaskiak, Alaska      | Rausch et al. 1990|
|                |               | Naumann, 1840       |                               |                        |                  |
| Charadriiformes| Laridae       | Larus hyperboreus   | glaucous gull                 | Bear Island, Barents Sea | Sagerup et al. 2000 |
|                |               | Gunnerus, 1767      |                               |                        |                  |
| Charadriiformes| Laridae       | Sterna hirundo      | common tern                   | Sweden                 | Lundström 1942   |
|                |               | Linnaeus, 1758      |                               |                        |                  |

Table 8.
Accidental hosts of Corynosoma strumosum. * Source not viewed.
| Host order       | Host family       | Host species                  | Host vernacular name               | Graphical locality          | Reference                  |
|------------------|-------------------|-------------------------------|------------------------------------|-----------------------------|----------------------------|
| Podicipediformes | Podicipedidae      | Podiceps grisegena (Boddaert, 1783) | red-necked grebe                   | Germany                      | Lühe 1911                  |
| Suliformes       | Phalacrocoridae    | Phalacrocorax auritus (Lesson, 1831) | double-crested cormorant           | Germany                      | Lühe 1911                  |
| Suliformes       | Phalacrocoridae    | Phalacrocorax carbo (Linnaeus, 1758) | great cormorant                    | France: Bretagne, Baltic Sea: Finland and Germany | Forssell 1905, Lühe 1911, Reimer 2002* |
| Suliformes       | Phalacrocoridae    | Phalacrocorax pelagicus Pallas, 1811 | pelagic cormorant                  | Barents Sea, Alaska          | Rausch et al. 1990         |
| Carnivora        | Canidae           | Canis familiaris Linnaeus, 1758 | domestic dog                       | Alaska                       | Van Cleave 1953            |
| Carnivora        | Canidae           | Canis familiaris Linnaeus, 1758 | domestic dog (as sledge dog)       | Tununak, Alaska              | Rausch et al. 1990         |
| Carnivora        | Canidae           | Vulpes lagopus (Linnaeus, 1758) (as Alopex lagopus) | Arctic fox, polar fox             | St. Lawrence Island, Bering Sea, Alaska | Rausch et al. 1990         |
| Carnivora        | Canidae           | Vulpes vulpes (Linnaeus, 1758) | red fox                            | Hopper Bay, Cold Bay, Alaska | Rausch et al. 1990         |
| Carnivora        | Felidae           | Felis catus Linnaeus, 1758     | domestic cat                       | Germany                      | Lühe 1911                  |
| Carnivora        | Mustelidae        | Enhydra lutris (Linnaeus, 1758) | sea otter                          | Alaska                       | Van Cleave 1953            |
| Carnivora        | Mustelidae        | Lutra lutra (Linnaeus, 1758)   | European otter                     | Eire, Northern Ireland, England, Wales, Isle of Man, Orkneys, Shetlands, Scotland | McCarthy and Hassett 1993*, Jefferies et al. 1990, Weber 1991 |
| Carnivora        | Mustelidae        | Mustela putorius Linnaeus, 1758 | European polecat                   | Germany                      | Lühe 1911                  |
| Carnivora        | Mustelidae        | Neovison vison (Schreber, 1777) | mink                               | Oregon, North America        | Van Cleave 1953            |
Carnivora Mustelidae

Neovison vison (Schreber, 1777)
mink
Finland
Nuorteva 1966

Cetacea Phocoenidae

Phocoena phocoena (Linnaeus, 1758)
harbour porpoise
Tvärminne, Finland
Forssell 1904, Forssell 1905, Lühe 1911

Primates Hominidae

Homo sapiens Linnaeus, 1758
human
Chevak, Alaska
Rausch et al. 1990

While for *C. magdaleni*, all definitive host records belong to the family Phocidae (order Carnivora), the definitive hosts for *C. semerme* include, besides numerous Phocidae, also Otariidae and Odobenidae from the same order and Monodontidae (belonging to the order Artiodactyla) (Table 3). For this reason, more paratenic hosts of *Corynosoma semerme* in Europe and North America are reported (Table 4), but which all are also Actinopterygii. *Monoporeia affinis* (Amphipoda) is the only known intermediate host of *Corynosoma semerme* (Nybelin 1924). Some further intermediate hosts are suggested for the Baltic Sea area, mainly isopods (*Saduria entomon, Asellus aquaticus*), amphipods (*Gammarus* spp.) ostracods and Mysidae, because such invertebrate species were found in the intestines of infected paratenic fish (e.g. Valtonen and Julkunen 1995). From North America, the intermediate host is still unknown.

For *C. strumosum*, an arthropod (probably an amphipod) is suggested as an intermediate host in North America (Van Cleave 1953), which is similar to the suggested intermediate hosts in Europe. Recently, Skorobrechova and Nikishin (2019) found corynosome cystacanths in *Spinulogammarus ochotensis* (Brandt, 1851), which further confirmed amphipods as potential intermediate hosts. *Corynosoma strumosum* seems to have fewer definitive hosts than *C. semerme* (Table 5), but the species shows also numerous reported paratenic hosts in Europe, North America, the Caspian Sea, Sea of Okhotsk and Northwest Pacific (Table 6), belonging to the classes Actinopterygii and Petromyzonti. Even if the *Corynosoma* spp. are observed in many fish species, they are not able to become sexually mature in fish (Forssell 1905, Lundström 1942). This is the reason why fish may only play an important role as paratenic host.

The definitive host of *Corynosoma* has fish as prey, but numerous fish-eating species become accidentally infected and become dead-end hosts (see Tables 7, 8 *C. semerme* and *C. strumosum*, respectively). While it is not known how long a life cycle of *Corynosoma* spp. takes, the development of the cystacanths to become mature helminths in seals is suggested to take 2-3 weeks (Helle and Valtonen 1981) and the season and/or temperature might have a strong effect on the sex-age structure of *Corynosoma* spp. (Helle and Valtonen 1981, Popov and Fortunato 1987).
Aznar et al. (2006) characterised the marine Corynosoma clade as cosmopolitan and, in the past, the marine genus was able to adapt their complex life cycle to extreme environments like the brackish Baltic Sea, Lake Saimaa and the Caspian Sea. It is also postulated that the right intermediate and paratenic host is available and serves as a reservoir for the cystacanth. Marine glacial relict species serve or are supposed to serve as intermediate hosts for Corynosoma species in the Baltic Sea (e.g. the amphipod Monoporeia affinis (Lindström, 1855) and the isopod Saduria entomon (Linnaeus, 1758)). Lundström (1942) discussed the idea that the Corynosoma spp., like Echinorhynchus salmonis Müller, 1784, may be a marine glacial relict species, because these species are also found in the Arctic Sea, White Sea and numerous freshwater and relict lakes (e.g. Lake Saimaa, Lake Ladoga, Lake Onega).

Sinisalo and Valtonen (2003) mentioned, that the C. semerme cystacanths, observed in Baltic fish, differed clearly in the morphological characters (trunk length), while C. magdaleni and C. strumosum cystacanths were hard to separate (C. strumosum only slightly larger than C. magdaleni). This is interesting, especially since also Waindok et al. (2018) mentioned some difficulties with the identification of C. strumosum. Acanthocephalans from harbour seals of the North Sea were initially diagnosed as C. strumosum, based on morphological characters; however, molecular markers (COI and ITS) indicated that they should have been assigned to C. magdaleni.

Another study, Hernández-Orts et al. (2017), based on partial sequences of the mitochondrial cytochrome c oxidase 1 gene (cox1), clearly segregated the Northern Hemisphere species (C. magdaleni and C. strumosum) and Southern Hemisphere species (C. hannae and C. australe Johnston, 1937). Corynosoma hannae from the Southern Hemisphere is most similar to C. semerme from the Northern Hemisphere, having no genital spines in females. It could be possible that parallel evolution may have evolved two similar complex parasitic Corynosoma systems in pinnipeds. It is still unresolved, whether the only report of C. semerme from the Southern Hemisphere by Johnston and Edmonds (1953) is C. hannae or not (discussed by Hernández-Orts et al. 2017).

Another possible assumption could be that the marine genus, Corynosoma, entered the Baltic Sea at the same time as their definitive hosts and this reflects their population history. The Baltic grey seal population is suggested to have diverged from the Eastern Atlantic/North Sea ones between 4,200 and 10,000 years ago (Fietz et al. 2016, Klimova et al. 2014), when the breeding habitats were shifted more easterly during the Baltic Sea formation. For the ringed seal, the allele frequency differentiation between the Baltic and Arctic populations were weak (Palo et al. 2001), while a northern invasion from continental seals during the Plio-Pleistocene to the basins was suggested to be most likely (Palo and Väinölä 2006). The ringed seal is the exclusive seal species in the land-locked Lake Saimaa, Finland. It also formed isolated populations in the Arctic and North-western Pacific (Popov and Fortunato 1987). The Caspian seal is another very isolated population and is supposed to be a relict species as well. Today, the ringed seal is very isolated in the Baltic Sea, as well as a small population of harbour seals (Härkönen et al. 2005).
Conclusion

Obviously, with the geographical isolation, *Corynosoma* species show plastic morphological characters and possible morphotypes (e.g. Popov and Fortunato 1987, Amin et al. 2011). Which role the intermediate and paratenic host play in the isolation is not known today. Sinisalo and Valtonen (1998) found an indication of segregation of *C. magdaleni* and *C. strumosum* in their paratenic hosts in the Gulf of Bothnia, Baltic Sea, Finland. In general, there is too little information available on the ecology and distribution of each of the *Corynosoma* spp. Future studies should try to combine genetic and new morphological tools (like SEM and the proboscis profiler) to throw more light on the ongoing species and morphotype discussion for *Corynosoma* spp. We see the greatest challenge is the access to good and sufficient material for further analyses. Our reported geographical distribution patterns (Suppl. material 1) and summary of definitive and paratenic hosts may contribute to and motivate further investigations on this interesting parasite group.

*Corynosoma semerme* and *C. strumosum* have extensive host and geographical ranges, providing opportunities for reproductive isolation of lineages. Speciation in acanthocephalans is often cryptic and Waindok et al. (2018) have already demonstrated the presence of a cryptic species, "Candidatus *Corynosoma nortmeri," in the North Sea. Further work to investigate the species diversity in *Corynosoma* will require a tandem morphological and molecular study of acanthocephalans collected from all known hosts, throughout their geographical ranges. The present study should prove to be a useful guide for future sampling efforts.

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Grant title

Swedish thorny-headed worms (Acanthocephala: *Corynosoma* spp.) in grey (*Halichoerus grypus*) and ringed seals (*Pusa hispida*).

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Supplementary material

Suppl. material 1: R script for generating geographical distribution maps. doi

Authors: Leidenberger S., Boström S. & Wayland M.
Data type: R script
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