Non-indigenous zooplankton – the role of predatory cladocerans and of copepods in trophic dynamics

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Doctoral Thesis in Marine Ecology
ABSTRACT

Human-mediated introductions of non-indigenous species now threaten to homogenize the biota of the Globe, causing huge economic and ecological damage. This thesis studies the ecological role of 3 invasive planktonic crustaceans, the omnivorous copepod *Acartia tonsa* (western Atlantic and Indo-Pacific) and the predatory cladocerans, *Cercopagis pengoi* (Ponto-Caspian) and *Bythotrephes longimanus* (Eurasian). *B. longimanus* invaded the North American Great Lakes in 1982, *C. pengoi* the Baltic in 1992 and the Great Lakes in 1999, while *A. tonsa* has an extensive invasion history that includes the Baltic.

We review current knowledge on feeding biology of the predatory cladocerans. A study of stable C and N isotope ratios indicated mesozooplankton as the main food source of *C. pengoi* in the northern Baltic Sea proper, with young *C. pengoi* also eating microzooplankton, such as rotifers. Young-of-the-year herring did eat *C. pengoi* and herring trophic position shifted from 2.6 before the invasion to 3.4 after, indicating that *C. pengoi* had been “sandwiched” into the modified food web between mesozooplankton and fish.

Salinity tolerance experiments on *Acartia tonsa* and co-occurring *Acartia clausi* showed the formers euryhaline character and high grazing potential. Energy partitioning between ingestion, production and respiration was rather constant over the tested salinity range of 2 to 33, with small differences in gross growth efficiency and cost of growth, but maximum ingestion at 10-20. Egg hatching in *A. tonsa* was only reduced at the lowest salinity. Extreme changes in salinity were needed to cause significant mortality of *A. tonsa* in the field, but its feeding activity could be severely reduced by salinity changes likely to occur in estuaries. A study of a hypertrophic estuary showed that *A. tonsa* can sustain a population despite very high mortality rates, caused by predation, high pH and low oxygen, helping explain the success of *A. tonsa* as an invader of estuaries.

**Keywords:** *Acartia tonsa, Bythotrephes longimanus, Cercopagis pengoi*, egg production, fitness, food web changes, ingestion rates, invasive species, metabolic balance, mortality, non-indigenous zooplankton, predation impact, salinity tolerance, stable isotopes
LIST OF PAPERS

The thesis is based on the following papers, referred to in the text by their Roman numerals.


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INTRODUCTION

Biological invasions

The occurrence of non-indigenous species (NIS, see BOX 1) has been rapidly increasing, due in large part to the escalating amount and speed of trade and transportation, globally as well as locally (Vitousek et al. 1997, Ruiz et al. 2000, Leppäkoski et al. 2002a,b, Galil 2008), and is now often considered as one of the most severe threats to global biodiversity (e.g., Wilcove et al. 1998, Simberloff 2005). One serious concern is that the intense exchange of organisms between previously isolated habitats will lead to a global homogenization of biotas (Olden et al. 2004). Such homogenization may affect all levels of diversity, from genes and species to communities and ecosystems (Olden et al. 2004). Moreover, established NIS may cause huge economic damage. The estimated direct annual costs for damage and control of all NIS (plants, animals and microorganisms) in the USA amounted to 137 billion USD (Pimentel et al. 2000), while for the United Kingdom, Australia, South Africa, India and Brazil together it was around 200 billion USD (Pimentel et al., 2001). In a recent study by Colautti et al. (2006) the projected negative economical impact on Canadian fisheries, agriculture and forestry associated with 16 NIS was estimated to be between 13 and 35 billion CAD per year.

BOX 1. DEFINING AN INVADING SPECIES

An introduced, exotic or non-indigenous species (NIS) can be defined as a species (or subspecies or lower taxon, Hulme 2007) that has been transported deliberately or accidentally by humans, from its native range, across a natural barrier of dispersal, to a new region (Richardson et al. 2000). This definition includes introductions that are mediated by the human removal of barriers, for example when canal constructions allow species to move freely between previously isolated locations. A NIS that manages to establish, spread widely and play a conspicuous role in the recipient region may be termed invasive (Richardson et al. 2000, Falk-Petersen et al. 2006).

Aquatic environments are particularly exposed to NIS introductions (Carlton & Geller 1993, Cohen & Carlton 1998, Padilla & Williams 2004, Gollash 2006) and may be of extra concern, because abiotic conditions are generally more homogeneous and less fluctuating than in terrestrial habitats, meaning that the initial
chances of survival for an aquatic NIS (ANIS) may be higher (Cook 1985, 1990). Considering also that aquatic habitats are difficult to monitor and that species are easily spread with the currents, an ANIS might not be discovered until it has already established over large areas, and is most likely impossible to eradicate. Accordingly, a significant part of the costs estimated by Pimentel et al. (2000) stemmed from ANIS.

Intentional ANIS introductions are carried out for example to improve commercial or recreational fisheries (Northcote 1991, Kaufman 1992) or for ornamental purposes (Cook 1990, Padilla & Williams 2004). The deliberate release of aquarium species into the wild as an ill-advised alternative to destruction is also an important source of ANIS (e.g., Padilla & Williams 2004). Examples of unintended/accidental introductions are escape of organisms from aquaculture facilities (Wallentinus 2002, Minchin 2007) and aquaria (Meinesz & Hesse 1991, Jousson et al., 1998, Padilla & Williams 2004) or even from scientific experiments (e.g., McNaught et al. 2004). The use of live bait for fishing is also important (Moyle 1986, Ludwig & Leitch 1996). On a global scale, the most effective vector for accidental spreading of marine and estuarine organisms is transoceanic shipping, via the release of ballast tank water and sediment, or via hull fouling (Carlton 1989, Carlton & Geller 1993, Ruiz et al. 2000, Minchin & Gollasch 2002). As a result, big international harbours and adjacent coastal areas are among the most exposed to ANIS; a well-known hot-spot for species introductions, the San Francisco Bay and Delta, USA, was by 1998 estimated to host more than 250 ANIS (Cohen & Carlton 1998). Further dispersal is often facilitated via local commercial ship traffic, as well as by transports of small pleasure boats on land to other coastal areas, or to inland waters (Johnson et al. 2001). For the European coastal aquatic region as a whole, an estimated 1000 ANIS have been recorded, 450–600 of which have established permanent populations (Gollash 2006). In estuaries and lagoons, where the relative contribution of non-natives is highest, they now contribute roughly 20% of all plants and animals (Nehring 2006, Reise et al. 2006).

Human removal of natural barriers has often played a crucial role in the spreading of ANIS. Important examples are the constructions of the Suez Canal (connecting the Red- and Mediterranean seas, opened year 1869), the Panama Canal (1914, joining the Atlantic and Pacific Oceans), the St. Lawrence seaway (1959, connecting the
Laurentian Great Lakes with the Atlantic Ocean), and a number of European waterways opened in the period between 1775 to 1952, as well as the most recent Rhine-Danube Canal completed in 1992. These major construction efforts have enabled species migrations, and also greatly enhanced the significance of the shipping traffic vector (e.g., Galil 2008).

Once a NIS is introduced into a new habitat it may be released from one or more factors that control its abundance and distribution in the native area. These can be physical (e.g., salinity, temperature) or biological, for example competitors, predators, diseases, and parasites (“enemy release hypothesis”, Torchin et al. 2003). Furthermore, a NIS may carry with it a new disease that “knocks out” its main potential competitors in the recipient region – leading to a vacant “niche” or resources that may be exploited by the NIS (e.g., signal crayfish, *Pacifastacus leniusculus*, in Europa, Söderhäll & Cerenius 1999). However, probably only a minor fraction of all NIS introductions results in permanent populations in the new habitat (e.g., Williamson 1996, Williamson & Fitter 1996a). Therefore, a much debated issue is if it is possible to identify general characteristics of the species that are most likely to establish in, and invade recipient regions. Among the proposed characteristics are: fast growth and fast (asexual) reproduction, high degree of phenotypic plasticity, broad physiological tolerance (e.g., euryhalinity and eurythermy) and broad diet (Williamson & Fitter 1996b, Reid & Orlova 2002). It is also debated which types of ecosystems are most prone to invasions; one commonly accepted theory being that anthropogenically disturbed/stressed environments are more susceptible (Williamson 1996, Occhipinti-Ambrogi & Savini 2003). Another vigorously discussed issue is if indigenous species diversity plays a predictable role in this respect. The “diversity resistance hypothesis” predicts that less diverse communities are more likely to be invaded (Case 1991), but the existing evidence is contradictory (e.g., Elton 1958, Simberloff 1988, Levine & D’Antonio 1999, Stachowicz et al. 1999, 2002, Levine 2000, Kennedy et al. 2002, Shurin 2000, Stohlgren et al. 2003, Pavola et al. 2005).

Simberloff & Von Holle (1999) found a predominance of positive interactions between marine ANIS, which lead them to formulate the hypothesis of “invasional meltdown”, according to which the risk of new ANIS establishments increases when

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the habitat is already invaded. The observations by, for instance, Ricciardi (2001) in the Laurentian Great Lakes of North America gave strong support to this hypothesis.

Once an ANIS is established the potential effects are multiple and include both economical and ecological damage. Prominent examples of the former are: The clogging of drainage channels and navigation routes by weeds (e.g., *Elodea* spp. and *Eichhornia crassipes*), clogging of power plant water intakes by the zebra mussel, *Dreissena polymorpha*, hull fouling by the barnacle *Balanus improvisus* and destruction of wooden installations in ports and marinas by the ship worm, *Teredo navalis*. Apart from the direct costs related to the invaders and possible costs for controlling measures, significant economical losses might also be caused by reduced recreational values, for instance when inland waters are clogged by vascular submersed plants, and when mass accumulations of macro algae or mollusc shells impair the use of shores and beaches.

ANIS often negatively affect the native biota and can reduce biodiversity and interfere with ecosystem function through hybridization, competition, predation and ecological cascading effects (e.g., Parker et al. 1999, Olden et al. 2004). Moreover, the ANIS might bring with it new “exotic” parasites and diseases (e.g., Söderhäll & Cerenius 1999, Pimentel et al. 2000). In the worst case the result is loss of endemic species and disruption of ecosystem function, leading to diminishing ecosystem goods and services (Witte et al. 1992, Kideys 1994, Parker et al. 1999, Mack et al. 2000). Thus, evidently also the “ecological damage” caused by ANIS may have severe negative economical consequences. More indirect effects of ANIS may develop, when they interact with native species in complex ways through, for example, shared predators, parasites and pathogens. Also, physical habitat modification, caused by so-called “transformers” or “ecosystem engineering” ANIS (e.g., erosion, formation of dense vegetation, biofouling), may have huge indirect effects and even restructure ecosystems completely (Vitousek et al. 1997, Crooks 2002, Karatayev et al. 2002).

Two well-known examples of invertebrate ANIS with large negative ecological and economical impacts are the comb jelly *Mnemiopsis leidyi*, which was introduced accidentally into the Black Sea (see BOX 2), and the mysid shrimp *Mysis relicta*, introduced deliberately into a large number of lakes (see BOX 3).
It is evident that the effects of ANIS are difficult, if not impossible, to predict - maybe even more so than the effects of other major threats such as eutrophication, pollutants, fisheries and physical habitat destruction - and the ongoing and accelerating worldwide introduction of ANIS has been described by Carlton & Geller (1993) as playing “ecological roulette”.

**BOX 2. CASE STORY: MNEMIOPSIS IN THE BLACK SEA**

The comb jelly *Mnemiopsis leidyi* is native to estuaries of the western Atlantic (Harbison 1978, Travis 1993) and feeds on a large size range of zooplankton, including protozoa, crustacean zooplankton and eggs and larvae of fish (Sullivan & Gifford 2004, Rapoza et al. 2005). It was introduced via ballast water to the Black Sea, where it was first reported in 1982 (Vinogradov et al. 1989). Conditions for *M. leidyi* were probably very favourable due to two decades of increasing eutrophication and overfishing (overexploitation of potential native predators and competitors, Caddy 1993). When the *M. leidyi* population exploded in the late 80s a pronounced decline in zooplankton abundance and a collapse of zooplantivorous fish stocks followed (Shushkina & Musayeva 1990, Shiganova 1998). This resulted in a great reduction in fishery harvest of Black Sea anchovy (*Engraulis encrasicolus*, Kideys 1994). Higher trophic levels, such as piscivorous fish, were also affected (Shiganova & Bulgakova 2000).

**BOX 3. CASE STORY: MYSIS RELICTA IN FLATHEAD LAKE**

The mysid shrimp *Mysis relicta* was introduced by fisheries biologists into a large number of lakes in North America and Scandinavia during the 1960s and early 1970s, with the intent to enhance feeding conditions and growth of salmonids (e.g., Northcote 1991). However, in many lake ecosystems the mysid instead altered and disrupted food webs (Lasenby et al. 1986, Spencer et al. 1991). In Flathead Lake, Montana, US, for instance, where the target fish population, kokanee salmon, *Oncorhynchus nerka*, collapsed because its main food source of cladocerans and copepods had been exhausted by predation from *M. relicta*. The mysid in turn, hid in deep waters near the bottom during daylight hours, and thus could not be effectively preyed upon by the salmon. The kokanee collapse meant a loss of the food source for the bald eagle that consequently moved away from the lake (Spencer et al. 1991).
The Baltic Sea and the North American Great Lakes – invasion hot-spots

Only ca. 7000 years have passed since the last transition of the Baltic from a freshwater to a marine ecosystem, and the present brackish conditions have only existed for the last about 4000 years (Winterhalter et al. 1981, Reid & Orlova 2002). Most species found here are therefore relatively recent immigrants, and the native community is very species-poor. It consists of species of either marine or freshwater origin, some glacial relicts, and a few true brackish water specialists (Remane 1934, Remane & Schlieper 1971). Some authors (e.g., Leppäkoski et al. 2002a) and for instance, the “Baltic Sea Alien Database” (http://www.corpi.ku.lt/nemo/) apply a geographically less restrictive definition of the Baltic Sea, which includes the much more species rich (but still mostly brackish) Danish Straits/Belt Sea and Kattegat.

The North American Great Lakes resemble the Baltic Sea in being geologically young and in that most native species are post-glacial immigrants. The formation of these lakes started 14 000 years ago when the last major glacier called the “Laurentide” began retreating and was completed 4 000 BP when their present form was attained (Flint 1971 cf Mills et al. 1993). The drainage areas of the Baltic Sea and the Great Lakes are both inhabited by large human populations (Baltic Sea: 85 mill. in 14 countries, Great Lakes: 33 mill. in Canada and USA). They also have in common a history of severe anthropogenic stress stemming from eutrophication, pollution with toxic contaminants, overfishing, etc. Today the two systems continue to be very disturbed by human activities. It should be noted however, that the five Great Lakes differ widely in the degree of anthropogenic impact (United States Environmental Protection Agency 2009).

ANIS in the Baltic Sea

The oldest ANIS in the Baltic Sea is probably the sand mussel *Mya arenaria* that died out in Europe before/during the last Ice Age, but was reintroduced sometime before 1245 from North America, possibly by the Vikings (Petersen et al., 1992), and is now a widespread member of the Baltic Sea benthic fauna. Other early ANIS-recordings are the Ponto-Caspian zebra mussel, *Dreissena polymorpha* (early 1800s), and the barnacle *Balanus improvisus*, a North American native first recorded in 1844 (Leppäkoski et al. 2002a and references therein). Both the zebra mussel and, especially, *B. improvisus* are notorious biofoulers and nuisance species causing economical damage to, for instance, shipping and boating in the Baltic Sea (Leppäkoski et al. 2002a).
During the last decades the rate of new introductions has steadily increased, and around 110 ANIS have now been recorded in the Baltic Sea (including the Kattegat). Among these ca. 70 are considered established (Leppäkoski et al. 2002a, Baltic Sea Alien Database 2007). If one includes inland navigational waterways and nearby adjacent inland waters, the numbers increase to 170 recorded and 99 established species (Gollash 2006). Most of them stem from unintended introductions via the most important vectors: ballast water and tank sediment, hull fouling and aquaculture. Most important donor regions during the last 25 years have been brackish water areas of the Indo-Pacific region, North America and the Ponto-Caspian basin (Black, Caspian, and Azov seas), to which the Baltic Sea is connected.
via ship traffic. The Baltic Sea itself constitutes a node in the worldwide web of ANIS transportation, and has in several cases served as a stepping stone, for instance in the transfer of Ponto-Caspian ANIS to the North American Great Lakes (Cristescu et al. 2001, Grigorovich et al. 2003, Cristescu et al. 2004).

The highest numbers of Baltic Sea ANIS are found among benthic- and nectobenthic crustaceans and molluscs, and the most significant ecological effects have generally been found in near-shore areas (e.g., Leppäkoski et al., 2002a). For instance, non-indigenous amphipods and mysids together with zebra mussels now play a key role for the bentho-pelagic coupling in the Curonian Lagoon (Leppäkoski et al. 2002a). Another example of an ecologically important recent NIS establishment in the Baltic Sea is the deep-burrowing polychaete *Marenzelleria* spp. (recorded in 1985, Bick & Burkhardt 1989), that has become a dominant member of soft-bottom communities in many areas (e.g., Zmudzinski 1996, Perus & Bonsdorff 2004).

A large number (25) of non-indigenous fish species have been released deliberately into the Baltic Sea for stocking purposes and an additional 4 species have been accidentally introduced (Baltic Sea Alien Database 2007). However, only 3 species constitute today noteworthy parts of the regional fish communities (*Neogobius melanostomus*, *Carassius gibelio*, and *Oncorhynkus mykiss*), and only the Ponto-Caspian round goby, *N. melanostomus*, and the Asian gibel carp, *C. gibelio*, have established self-reproducing populations (Sapota & Skora 2005, Vetemaa et al. 2005). The round goby was first recorded in 1990 in the Gulf of Gdansk (Skora & Stolarski 1993), and has now become the dominating fish species in shallow coastal areas of the Gulf competing for food with and displacing native species (Sapota & Skora 2005, Almqvist 2008). This aggressive invader is presently colonizing the north-eastern Baltic Sea (Ojaveer 2006) and was recently observed also in the western Baltic Sea (July 2008 in the Karlskrona Archipelago, Sweden, Gustaf Almqvist, pers. comm.).

Among the ANIS affecting the Baltic Sea pelagial are a large number of nectobenthic mysids that were deliberately introduced in the 1960s into freshwater basins of the former USSR, with the intent to enhance the feeding conditions for fish. These include the bloody-red mysid, *Hemimysis anomala*, and *Paramysis lacustris*
(e.g., Salemaa & Hietalahti 1993, Leppäkoski & Olenin 2000, Baltic Sea Alien Species Database 2007). The relatively few truly planktonic NIS recorded include the toxic dinoflagellate *Prorocentrum minimum* (Hajdu et al. 2000), three species of predatory cladocerans and the copepod *Acartia tonsa*.

*Cercopagis pengoi* is so far the most important cladoceran NIS, and a focus of the present Thesis (papers I & II). This voracious zooplanktivore has spread rapidly throughout the Baltic Sea since first observed in the early 1990s. It has reached high abundances (Ojaveer & Lumberg 1995, Bielecka 2000, Gorokhova et al. 2000), becoming a local biofouling pest (Leppäkoski et al. 2002a), and has impacted prey population dynamics (I) as well as food web structure (II). Most recently, two additional species of predatory cladocerans, *Evadne anonyx* (first recorded in 2000, Rodionova et al. 2006, Põllupüü et al., 2008) and *Cornigerius maeoticus* (first recorded 2003, Rodionova et al. 2005) have established populations in the Gulfs of Finland (*C. maeoticus*, *E. anonyx*) and Riga (*E. anonyx*). So far, there are no reports of ecological or economical effects of either species. The omnivorous calanoid copepod *Acartia tonsa* was most probably introduced into the Baltic Sea with ballast water in the 1920−1930s (Segerstråle 1957, Jansson 1994) and is now widespread and abundant (Telesh et al. 2008 and references therein). The species has high grazing and reproductive potential as well as impressive physiological tolerance and is a subject of more specific studies in the present Thesis (papers III, IV & V).

The latest ANIS introduction into the Baltic pelagial is the notorious comb jelly *Mnemiopsis leidyi*. It was observed at the Swedish west coast (Hansson 2006) and in the Kiel Bay (Javidpour et al. 2006) in late summer and autumn 2006 and the following winter and spring (2007) it was found in the south and central parts of the Baltic Sea (Kube et al. 2007). By summer 2007 *M. leidyi* had spread further to the Åland Sea, Bothnian Sea and the Gulf of Finland (Lehtiniemi et al. 2007) and incidents of mass occurrence were reported from Danish waters (Tendal et al. 2007, Riisgård et al. 2007). During the winter 2007-2008, which was very mild, the invader was still present in relatively high abundances over large parts of the Baltic Sea (Viitasalo et al. 2008), but it is yet to be seen if it has established permanently. There is currently great concern about potential negative effects similar to those previously documented in the Black and Caspian seas (Haslob et al. 2007).
Human–mediated ANIS introductions to the Great Lakes go back at least 150 years. Important points of reference are the constructions of the Erie (1825) and Welland (1829) canals connecting Lake Ontario to the Atlantic Ocean (via Hudson River) and to Lake Erie (bypassing the Niagara Falls), respectively. The subsequent construction of the lock systems between Lake Ontario and the Saint Lawrence River in 1847, and between Lakes Superior and Huron in 1855, made possible the through passage from the Atlantic Ocean to Lake Superior.Probably as a consequence of these man-made passages the sea lamprey (Petromyzon marinus) and alewife (Alosa pseudoharengus) spread to all of the Great Lakes, where they have had profound impacts on the native fish communities (see Box 5). Otherwise, most ANIS prior to 1900 were either deliberately released plants and fish, or molluscs and Eurasian plants introduced accidentally with solid ballast (e.g., soil, sand or rocks) of trans-oceanic vessels. The deliberate release of non-indigenous salmonines as well as other fish species continued until the 1950s while at the same time the NIS introductions attributable to shipping vectors, range expansion via canals and aquarium release increased (Ricciardi 2006). In 1959 international shipping was further facilitated by the modern St Lawrence Seaway allowing for larger, transatlantic vessels to pass throughout the Great Lakes. This caused a major increase in the rate of ANIS introduced via ballast water and tank sediments (Ricciardi 2006) and many new phyto- and zooplankton NIS became established.

Today there are more than 180 established ANIS in the Great Lakes about half of which have been recorded after the expanded seaway was opened (e.g., Ricciardi 2006). Ballast water is the putative vector for around two-thirds of all invasions recorded since 1959 (Ricciardi 2006), with the most important donor regions being Europe, South-east Asia and the Atlantic coast of North America. At present, a new ANIS is discovered approximately every 28 weeks (Ricciardi 2006). Due to the implementation of regulations requiring mandatory ballast water exchange of transoceanic vessels recent introductions (1994–) are dominated by species with broad salinity tolerance – many of which originate in the Ponto-Caspian basin (Ricciardi 2006). The very large number of ANIS harboured in the Great Lakes today includes 26 fish, 18 mollusc, 11 copepod and 6 cladoceran species, as well as numerous planktonic diatom species. In fact, NIS now dominate both benthic and pelagic food webs. A subset of these species is spreading into inland lakes and
streams of the adjacent regions, with for instance, recreational boats and fishing boats as vectors. The most prominent example is the zebra mussel, which has had profound ecological effects and caused severe economical damage (see Box 6). The species has a long and extensive invasion history in Europe before the introduction to North America.

Non-indigenous cladocerans play an important role in the plankton communities of the Great Lakes. The small herbivorous *Bosmina (Eubosmina) coregoni*, which is indigenous to freshwaters in Europe (Haney & Taylor 2003), was first recorded in Lake Michigan in 1966 and rapidly spread throughout the basin, including many inland waters (Demelo & Hebert 1994a). It is now among the dominant zooplankters during summer (Mills et al. 1993); except in Lake Superior, where its status is uncertain (Barbiero et al. 2001). *B. (E.) coregoni* is a prey item to both native (e.g., bloater, *Coregonus hoyi*) and exotic (e.g., blueback herring, *Alosa aestivalis*, and alewife) fish species of the Great Lakes (Crowder & Crawford 1984, Mills et al. 1995). Another bosminid, *B. (Eubosmina) maritima*, which is native to brackish waters in northern Europe (including the Baltic and Barents seas, De Melo & Hebert 1994b) proved capable of adapting to freshwaters in the Great Lakes, establishing itself in lakes Michigan, Erie and Huron (De Melo & Hebert 1994b) in the late 1980s to early 1990s. Here, in its novel environment *B. (E.) maritima* is usually most abundant during winter (Kipp 2009a). The taxonomic status of the species is somewhat uncertain, and by some authors it is considered merely as a subspecies, *B. (E.) coregoni maritima* of *B. (E.) coregoni* (Haney & Taylor 2003). The Palaeartic *Daphnia galeata galeata* was introduced to Lake Erie around 1980. It frequently hybridizes with native North American *D. g. mendotae* and hybrid clones are now very common (Taylor & Hebert 1993). In addition to the herbivorous cladocerans which are regarded as verified NIS in the Great Lakes, two more species, *D. mendotae* and *D. retrocurva* are considered cryptogenic (i.e., cannot be verified as either indigenous or non-indigenous).

The predatory cladocerans, Eurasian *Bythotrophes longimanus*, and Ponto-Caspian *Cercopagis pengoi* were first recorded in the Great Lakes in 1982 (Johannsson et al., 1991) and 1999, respectively. Interestingly, the sources of both species were populations in the Baltic region (Cristescu et al. 2001, Therriault et al. 2002). The present Thesis includes a comprehensive review of the feeding biology of these two
species and of their ecological effects in invaded ecosystems (paper I). Both *Bythotrephes* and *Cercopagis* have great potential for controlling prey populations directly through predation and may also affect prey morphology, behaviour and phenology (I). Especially *Bythotrephes* have had major effects on the zooplankton communities of the Great Lakes and of inland lakes on the Canadian Shield (I).

Four species of pelagic copepods are currently considered as non-indigenous immigrants to the Great Lakes, but they play a less conspicuous role than their cladoceran counterparts. The most successful species, *Eurytemora affinis*, is a well-known NIS that has invaded many freshwater and brackish ecosystems in the Northern Hemisphere (Lee 1999). It was first recorded from Lake Ontario in 1958 (Faber & Jermolajev 1966), and is considered established in all the Great Lakes (Mills et al. 1993). Apart from being widespread in bays and harbours (Mills et al. 1993), the ecological effects of *E. affinis* in the Great Lakes are unknown (Kipp & Benson 2009a). Another calanoid, *Skistodiaptomus pallidus* (synonymous to *Diaptomus pallidus*), and the cyclopoids *Cyclops strenuus*, and *Megacyclops viridis* (synonymous to *Acanthocyclops viridis*) were reported from the Great Lakes in 1967, 1972 and 1992, respectively, but have not become widespread (Kipp 2009b,c; Kipp & Benson 2009b). There are no recent records of *S. pallidus*, while *C. strenuus* and *M. viridis* are now probably found only in Lake Superior (Kipp 2009b,c; Kipp & Benson 2009b). In the St. Louis River estuary, Lake Superior, the Palaearctic *M. viridis* is an important prey item for the likewise non-indigenous ruffe, *Gymnocephalus cernuus* (Ogle et al. 1995).

Among the latest newcomers to the Great Lakes is the Ponto-Caspian mysid *Hemimysis anomala* first reported in 2006 from lakes Ontario, Michigan and Erie (Pothoven et al. 2007, Kipp & Ricciardi 2009). High densities of this opportunistic omnivore have already been recorded (Lake Michigan, Pothoven et al. 2007), and since it is adapted to warmer temperatures than the native *Mysis diluviana*, there is concern that *H. anomala* may colonize many areas in the Great Lakes not harbouring mysids at present.
BOX 5. NIS-DOMINATED FISH COMMUNITIES OF THE GREAT LAKES

The sea lamprey (*Petromyzon marinus*) and alewife (*Alosa pseudoharengus*) were discovered in Lake Ontario in 1835 and 1873, respectively, from where they spread to all of the Great Lakes. Although some authors claim that both species are native to Lake Ontario, there is general consensus on their NIS-status in the other Great Lakes. The sea lamprey parasitizes on other fishes, often killing the host, and has been associated with the decline of several fish species in the Great Lakes. For instance, it was a main factor behind the collapse in important fisheries on native lake trout (*Salvelinus namaycush*) and the extinction of three endemic species of cisco (*Coregonus* spp., Miller et al. 1989). Moreover, by reducing populations of native pelagic top-predators the sea lamprey probably facilitated the later establishment of alewife throughout the lakes. Alewife which is a pelagial zooplanktivore native to the North American Atlantic Coast became very abundant and continues to be a dominating species, especially in Lake Michigan. It is a main prey for the larger lake trout and there are strong indications that reproductive impairments in lake trout due to a deficiency of thiamine (vitamin B1), is linked to a diet of alewives (Fitzsimons et al. 1999). In addition, alewife harms lake trout by preying on its fry. Consequently, the famous sports fishing for lake trout has been seriously damaged, and maintenance of the species now depends on a combination of continuous stocking and very costly measures to control the invaders (Moyle 1986, Mills et al. 2003). Sea lamprey is controlled chemically with the “lampricide” TFM (e.g., MacDonald & Kolar 2007) while large populations of non-indigenous pacific salmon keep up a high predation pressure on alewife. Today the ongoing stockings with coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon as well as with rainbow trout (*O. mykiss*) and European brown trout (*Salmo trutta*) provide the basis for a much valued NIS-based sport fishery in the Great Lakes. Important recent NIS additions to the Great Lakes fish fauna include the Eurasian ruffe (*Gymnocephalus cernuus*, 1986) and the Ponto-Caspian round goby (*Neogobius melanostomus*, 1990).
BOX 6. CASE STORY: THE ZEBRA MUSSEL IN NORTH AMERICA

The Ponto-Caspian zebra mussel, *Dreissena polymorpha*, arrived in the Great Lakes in 1988 (first recorded in Lake St. Clair) and two years later it had been recorded from all of the Great Lakes. *D. polymorpha* has been extremely successful and can now be found in a vast number of inland lakes, rivers and canals in 24 states of the USA (Benson & Raikov 2009). In some areas it forms very dense beds (e.g., Mellina & Rasmussen 1994) and its veliger larvae may at times dominate the zooplankton (Barnard et al., 2003). Zebra mussels may be a serious pest, fouling raw water intakes, pipes and cooling systems of power plants, industrial facilities and municipal water supplies. Moreover, since the shells may cause cuts the presence of zebra mussels negatively affect shoreline recreational activities. Also, pronounced ecological impacts of this very effective filter feeder have been observed. In general, large populations of *D. polymorpha* will tend to shift lake food webs from being pelagically to benthically based. Moreover, bioaccumulation of contaminants may occur (Bruner et al. 1994) and toxic cyanobacteria blooms may be promoted by selective filtration by *D. polymorpha* on non-toxic algae (Vanderploen et al. 2001, Raikov et al. 2004).

Another serious problem is the elimination of native unionid mussels due to epizoic colonization (Baker & Hornbach 1997, Ricciardi et al. 1998). Interestingly, it is also believed that the zebra mussel invasion facilitated the later establishment of other Ponto-Caspian species, e.g., the round goby and the amphipod *Echinogammarus ischnus* both of which co-occur with zebra mussels in their native areas. The round goby is a major predator on zebra mussels and may exploit this new abundant resource much more effectively than native fish species in the Great Lakes (Ricciardi & Maclsaac 2000). The deposit feeding *E. ischnus* has replaced native Great Lakes amphipods in many zebra mussel beds, and is probably an important prey for small round gobies (Ricciardi & Maclsaac 2000).
OBJECTIVE OF THE THESIS

The general objective of this Thesis is to investigate non-indigenous cladocerans and copepods with respect to their predatory and grazing potential and their role in trophic dynamics.

Two target species were chosen for empirical studies: The Ponto-Caspian predatory cladoceran *Cercopagis pengoi* and the omnivorous calanoid copepod *Acartia tonsa* which is native to the Atlantic and Pacific coasts of North and South America as well as the Indian Ocean. Both species have an extensive history of human-mediated spreading and are now well-established components in the pelagic food webs of many habitats outside of their native area. More specific aims were to:

1) Compile published data and review comprehensively the existing literature on the feeding biology of *Cercopagis pengoi* and *Bythotrephes longimanus* - the two most important species of predatory cladocerans with documented invasion histories - and evaluate their impacts on native prey populations (I).

2) Evaluate the ecological effects of invasive *Cercopagis pengoi* in the Baltic Sea by means of stable isotope analyses (II).

3) Investigate the physiological tolerance (III, IV, V) as well as other factors, such as *in situ* reproduction- and mortality rates (V) that may regulate the distribution, population dynamics and grazing potential of *Acartia tonsa* and thus, be decisive for its role in the trophic dynamics of the invaded ecosystems.
CERCOPAGIDID CLADOCERANS
AS NON-INDIGENOUS SPECIES

Within the order of Cladocera two suborders, Haplopoda and Onychopoda are commonly referred to as “predatory water fleas”. These are not all strictly carnivorous but they share a grasping mode of feeding that separates them from other, filter feeding cladocerans. The two species targeted in the present Thesis, *Cercopagis pengoi* and *Bythotrephes longimanus*, both belong to the family Cercopagididae within Onychopoda. Their morphologies and life history characteristics are summarized in paper I. *Bythotrephes* is the larger of the two species, with a body core ca. twice as long and a more stout appearance than the slender *C. pengoi*.

Natural distributions and invasion histories

*Bythotrephes longimanus* is indigenous to Northern Europe (Rivier 1998, MacIsaac et al., 2000) where it inhabits mainly the open waters of large, deep lakes or reservoirs with relatively clear water (Grigorovich et al. 1998, Rivier 1998, Maclsaac et al. 2000) avoiding temperatures >23°C (Garton et al. 1990, Yurista 1999). Populations may also be found in brackish waters (<6‰, Belyaev 1950 cf Aladin & Potts 1995) like for instance, in the Gulf of Finland (Baltic Sea, Orlova et al. 2006).

*Cercopagis pengoi* is of Ponto-Caspian origin, tolerates up to 30°C, and thrives in freshwater as well as brackish water of up to ca. 13-15‰ (Mordukhai-Boltovskoi 1968 cf Aladin & Potts 1995, Rivier 1998). Both species have extended their distributions considerably by the aid of Man, and there are now numerous examples of co-occurrence of the two species in North America (e.g., Lake Michigan: Branstrator 1995, Charlebois et al. 2001) and in the Baltic Sea (Gulf of Finland: Orlova et al. 2006) as well as in many southern East-European reservoirs (Rivier 1998).

*Bythotrephes longimanus* has been introduced across Eurasia (Ketelaars & Gille 1994, Grigorovich et al. 1998), and was recorded in the North American Great Lakes for the first time in 1982 (Johannsson et al. 1991). There are now persistent *Bythotrephes* populations throughout the Great Lakes, except in Lake Ontario and the western basin of Lake Erie (Bur et al. 1986, Garton et al. 1990, Lehman &
The invader has been most successful in Lake Michigan and the central and eastern parts of Lake Erie, and has also spread to >100 inland lakes of North America (e.g., Boudreau & Yan 2003, Branstrator et al. 2006, Strecker & Arnott 2008).

*Cercopagis pengoi* was first recorded in the Baltic Sea 1992, in the gulfs of Riga and Finland (Ojaveer & Lumberg 1995, Panov et al. 1996) and rapidly established permanent populations in many coastal areas, including the upper Neva Estuary (Ojaveer & Lumberg 1995, Uitto et al. 1999). Today, *C. pengoi* is frequently found in the Stockholm Archipelago and the open Baltic Sea proper (Gorokhova et al. 2000) and has expanded its distribution to the Bothnian Bay (Baltic Sea Alien Database 2007, own observations) as well as to several bays and lagoons in the southern Baltic (Bielecka et al. 2000, Olszewska 2006). The highest abundances have been recorded in the epicenters of the invasion, where *Cercopagis* may contribute substantially to the total zooplankton biomass (25%, Gulf of Riga: Ojaveer et al. 1998; 33%, Neva Estuary: Orlova et al. 2006). High abundances have also been reported from the south-eastern Baltic proper (Litvinchuk & Telesh 2006), the Gulf of Gdansk (Bielecka et al. 2000) and the Szczecin Lagoon (Olszewska 2006), while *Cercopagis* is less abundant in the open Baltic proper (Gorokhova et al. 2000, Litvinchuk & Telesh 2006). The seasonal peak abundances have declined during the last years, at least in some locations (Pärnu Bay, Gulf of Riga, Ojaveer et al. 2004, Kotta et al. 2004, 2006; Himmerfjärden, northern Baltic proper, Gorokhova et al. 2000, 2004) but at the same time *Cercopagis* has tended to appear earlier each year, thereby extending its presence in the water column by several weeks.

By 1998, *Cercopagis* had been introduced to the North American Great Lakes, where it is now found in lakes Ontario (Maclsaac et al. 1999), Michigan (Charlebois et al. 2001), and Erie (Kane et al. 2003) but has not yet been recorded from lakes Huron or Superior (Benson et al. 2009). So far, the invader has been most successful in lakes Ontario (Laxson et al. 2003) and Michigan (Witt et al. 2005, Pichlová-Ptáčníková & Vanderploeg in press) and has also spread to a number of inland lakes in New York State and Michigan (Charlebois et al. 2001, Makarewicz et al. 2001, Therriault et al. 2002).
In its native area, sexual reproduction of *Cercopagis* normally begins in late autumn, when the water temperature declines, with low proportion of males and gametogenic females (Mordukhai-Boltovskoi & Rivier 1971, Krylov & Panov 1998, Rivier 1998). In the Baltic (Krylov & Panov 1998, Litvinchuk & Telesh 2006, own unpublished data) and in Lake Ontario (Grigorovich et al. 2000, Makarewicz et al. 2001) large proportions of sexually reproducing females have been found during summer, and their fecundity appears to be higher than in the native area (Krylov et al. 1999, own unpublished data). This intensified sexual reproduction may help establishment of *Cercopagis* in recipient ecosystems (Panov et al. 2004). For instance, the ability to produce resting stages throughout the season may help in large-scale dispersal by currents and animals (Jarnagin et al. 2000, Charalambidou et al. 2003) as well as by humans.

**Feeding biology and ecological impacts of invasive Cercopagidids**

*Summary of Paper I: Review on the feeding biology of Bythotrephes and Cercopagis*

*Bythotrephes longimanus* and *Cercopagis pengoi* are the fastest swimmers among cladocerans, and possess a number of distinct morphological adaptations to their predatory mode of life. They search actively for prey swimming continuously by oarlike strokes with the very strongly developed second antennae that bear plumose swimming setae. A large compound eye provides a good vision and an effective mechano-reception enables also feeding in the dark, although at lower rates than under light conditions. The rod-like thoracic limbs without filtering structures are mobile and can perform complex grasping movements, and the carapace valves are strongly reduced which frees up the thoracic limbs to handle prey. Moreover the mandibles of cercopagidids are equipped with strong, pointed, chitinized denticles and strongly developed muscles.

The visual prey encounter field in *Bythotrephes* appears to be hemispheric with most reactions orientated directly in front of the predator and reaction distances ranging from 3 to 15 mm, depending on light intensity. Some data indicate that *Cercopagis* may be less dependent on light than *Bythotrephes* is for maintaining high predation
rates. However, the importance of light for prey detection in cercopagidids needs further investigation as does the possible role of chemical cues.

In *Bythotrephes* the prey is subdued, shredded and the soft parts ingested while hard parts (e.g., the chitinous exoskeleton of crustaceans) are discarded. Prey handling time is relatively long and ingestion efficiency is low, but this is compensated for by a very rapid and efficient assimilation of ingested prey material, and a fast gut turnover rate. As detailed studies on the feeding mode and energy acquisition of *Cercopagis* are lacking, the species is assumed to resemble *Bythotrephes*. However, some observations suggest that *Cercopagis* may puncture and suck out larger copepod prey. To what extent cercopagidids are capable of ingesting solid prey parts is unclear.

The diets of *Cercopagis* and *Bythotrephes* are broad with crustacean zooplankton appearing to be the most important prey. Cladocerans are preferred over copepods, which could be related to the poorer swimming and escaping capacity of cladocerans as well as their stoichiometric suitability. The realized *in situ* diet is, however, flexible and copepods may indeed constitute a large proportion of the biomass consumed. Regarding cyclopoid copepods probably only the smaller species and the young stages of larger species are susceptible to predation from cercopagidids.

The smallest prey consumed by *Bythotrephes* in experiments are small cladocerans and copepod nauplii with a body length of ca. 0.25 mm. Large prey seem to be preferred over small, but the upper size limit has not been established experimentally. Results from correlative field studies suggest that *Bythotrephes* do not prey effectively on cladocerans larger than 2.5 mm. On the other hand, large indigenous *Leptodora kindtii* as well as *Cercopagis* may readily be killed and eaten, and stable isotope analyses suggested that *Bythotrephes* occupies a somewhat higher trophic level than *Leptodora*.

*Cercopagis* may feed on rotifers and mussel veligers as small as ca. 0.10 mm and stable isotope analysis indicated zooplankton <0.2 mm as substantial diet contributor. Thus, *Cercopagis* probably has a larger diet overlap with indigenous *Leptodora* and predatory copepods than does *Bythotrephes*. *Cercopagis* is capable of preying on copepods two thirds of its own body core length, but the upper size limit
for copepods and other prey taxa is still to be explored. Predation experiments showed that *Cercopagis* preferred easily caught prey over more rapidly swimming (rotifers to copepod nauplii and copepod nauplii to copepodites), but so far no clear pattern in prey size preference has emerged.

Predation rates for *Bythotrephes* in single-prey experiments were 0.8–30 prey *Bythotrephes*⁻¹ d⁻¹ (17 prey l⁻¹ to *ad lib* conc.). For larger cladocerans, such as *Daphnia pulicaria* and *D. g. mendotae* and for “natural zooplankton assemblages” rates were generally 6–9 prey *Bythotrephes*⁻¹ d⁻¹. *Cercopagis* consumed 0.1–22 prey *Cercopagis*⁻¹ d⁻¹ in single prey experiments (10–300 prey l⁻¹). The highest rate obtained, 40 prey *Cercopagis*⁻¹ d⁻¹ was with a mixture of the rotifer *Synchaeta balthica* and copepod nauplii as prey (80 prey l⁻¹). Estimated weight specific predation rates of both species ranged up to ca. 1.0 d⁻¹.

Weight specific predation rates (WSR) of *Bythotrephes* estimated from bioenergetic modelling ranged from 0.5 to 1.7 d⁻¹ (16–20°C). Predation rates calculated from WSRs indicate that the predator could in many cases sharply reduce prey populations. This is in line with the results of a number of correlative studies of cercopagid invaders and their potential prey. Moreover, the number of small prey required to satisfy the daily energetic demand of *Bythotrephes* is most likely so high that it excludes rotifers, and probably also copepod nauplii from being energetically important prey. This finding is supported by results from predation experiments.

Negative impacts of invasive cercopagidids on native zooplankton populations are widely reported from the Baltic Sea, the North American Great Lakes and North American inland lakes. Prey populations may be affected, not only through direct predation, but also indirectly by induction of behavioural responses (e.g., migration to deeper, colder waters), investment in (apparently inefficient) morphological defence structures or changes in phenology. The negative effects of such prey responses may equal or even exceed the effects from direct predation.

Due to the patchy distributions and short-lived peak densities of invasive cercopagidids their impacts on prey populations are expected to be highly variable both in time and space. Moreover, concurrent invasions by other NIS as well as human impacts for instance, from eutrophication and overfishing, may render the
effects of cercopagidids in recipient ecosystems hard to deduce. However, as shown from analyses of stable isotopes in the northern Baltic proper, cercopagidids do indeed have the potential to change food webs and trophic dynamics on an ecosystem scale.

Background paper II: Cercopagidids as novel prey for fish and invertebrates

_Bythotrephes_ is preyed upon by a number of fish species in Lake Michigan, including alewife, rainbow smelt (_Osmerus mordax_), and yellow perch (_Perca flavescens_) (Bur & Klarer 1991, Hartman et al. 1992, Mills et al. 1992, Coulas et al 1998, Parker Stetter 2005) and fish >10 cm have in many cases been shown to prey on the newcomer selectively, due to its large size and conspicuousness (Coulas et al. 1998, Parker et al. 2001). However, the long caudal spine offers some protection from smaller fish, _Bythotrephes_ is not easily ingested by fish <10 cm (Barnhisel 1991a, b), and is rarely found in the stomachs of those smaller than 5–6 cm (Barnhisel & Harvey 1995). Small fish struggle to ingest _Bythotrephes_ (Barnhisel 1991a, b) and prey handling time may be increased around an order of magnitude due to the spine (Compton & Kerfoot 2004). This is both energetically costly and increases the risk of falling prey and, as a response, some fish species develop aversion against _Bythotrephes_ (Barnhisel 1991a, b, Compton & Kerfoot 2004). The caudal spine is indigestible and may be differentially retained in the fish stomachs (Coulas et al. 1999). In Lake Erie, _Bythotrephes_ is suspected to have lead to a more than two-fold reduction in the growth of rainbow smelt (Parker et al. 2001, Parker Stetter et al. 2005), because they occupy a substantial part of the stomach space during summer and fall, thereby reducing the “realized” daily ration of the fish (Parker Stetter et al. 2005). In addition, there are reports of internal damage caused by spines that puncture the stomach or lower intestine in small fish (Compton & Kerfoot 2004). North American _Cercopagis_ has been found in the stomachs of alewife and rainbow smelt (Charlebois et al. 2001, Bushnoe et al. 2003, Thompson et al. 2005). In Lake Ontario alewife appears to be a major predator on _Cercopagis_ as 70–90% of adults contained _Cercopagis_ spines during summer (Bushnoe et al. 2003). Individuals <66 mm did not contain spines, probably due to gape limitation.
The native mysid, *Mysis diluviana* (formerly *Mysis relicta*, Audzijonyte & Väinölä 2005) is an abundant invertebrate predator potentially preying on cercopagidids in the Great Lakes (Johannsson et al. 1994, 2001). In smaller *Bythotrephes*-invaded lakes in central Ontario 13–100% of *M. diluviana* (adults ≥13 mm) contained *Bythotrephes* in their guts (Nordin et al. 2008). However, in contrast to fish predators, *M. diluviana* does not ingest the caudal spine of *Bythotrephes* (Nordin et al. 2008), and handling time is probably long. Differences in gut contents and fatty acid profiles of *M. diluviana* between *Bythotrephes*-invaded and non-invaded lakes suggested competition for cladocera between the two predators (Nordin et al. 2008). Depending on its future success in the Great Lakes the non-indigenous *Hemimysis anomala* could also play a role as predator on cercopagids.

Baltic Sea *Cercopagis* is potentially an important prey in late summer, when fish zooplanktivory in coastal areas reaches its maximum (Rudstam et al. 1992, Axenrot & Hansson 2004) and the zooplankton stocks are declining rapidly (Johannsson 1992). Some species, such as, herring (*Clupea harengus membras*) and sprat (*Sprattus sprattus*) may exhibit strong selective predation on *Cercopagis* (Ojaveer & Lumberg 1995, Antsulevich & Välipakka 2000) and gametogenic females carrying resting eggs seem to be preferred (Antsulevich & Välipakka 2000). In the Gulf of Riga, *Cercopagis* constituted 25–85% of the fish stomach contents during June–September (Ojaveer & Lumberg 1995, Ojaveer et al. 2004, Lankov 2006, Kotta et al. 2006) and in the Gulf of Finland it may comprise 40–50% of the food in herring stomachs (Antsulevich & Välipakka 2000). In the northern Baltic proper even benthic sand gobies (*Pomatoschistus minutus*) may at times contain significant amounts of *Cercopagis* (Ehrenberg 2008).

Apparently, the selectivity for *Cercopagis* increases with fish size in herring and smelt (Gorokhova et al. 2004, Ojaveer et al 2004, Kotta et al. 2006), while this is not the case for sticklebacks (Ojaveer et al 2004, Kotta et al. 2006) and sprat (Gorokhova et al. 2004). The smallest fish able to consume *Cercopagis* in the Gulf of Riga were from 3.4 to 7.3 cm, depending on species (Ojaveer et al 2004). However, *Cercopagis* may be consumed by sand gobies as small as 1.4 cm (Ehrenberg 2008). In contrast to *Bythotrephes*, the spines of *Cercopagis* appear not to damage the fish stomachs or intestines (Antsulevich & Välipakka 2000, Ehrenberg 2008).
In a recent study on *Cercopagis* population dynamics in the Askö Bay (north-western Baltic Proper), we found indications that fish predation may strongly affect *Cercopagis* abundance and population structure (own unpublished data), the latter probably due to selective predation on larger individuals by non-gape limited fish. During the study period (August–September), there was also a significant increase in allocating resources to the *Cercopagis* defence structure – the long caudal spine (own unpublished data).

A number of invertebrate species in the Baltic Sea are potentially able to prey on *Cercopagis*. These include mysids, decapods, jellyfish, and native *Bythotrephes longimanus*. Both *Mysis mixta* and *M. relicta* consumed *Cercopagis* in predation experiments, although the caudal spine was often not ingested (Gorokhova & Lehtiniemi 2007) and *Cercopagis* DNA was found in the stomachs of wild-caught individuals of the two species (Gorokhova & Lehtiniemi 2007) as well as in *Neomysis integer* (Gorokhova 2006). Depending on the strength of these trophic interactions, mysids might mediate the strength of the juvenile fish–*Cercopagis* competition for zooplankton prey. These interactions may also be affected by *Bythotrephes* that co-occurs with *Cercopagis* in the Neva estuary (Krylov et al 1999, Panov et al. 2004).

Thus, *Cercopagis* seems to be fully incorporated into the pelagic food web of the Baltic Sea. There is evidence that *Cercopagis* is affecting the zooplankton communities by selective predation (see I), and also evidence that it has become a considerable prey item for, at least, certain species and size groups of fish (e.g., Antsulevich & Välipakka 2000, Lankov 2006). Moreover, *Cercopagis* is prey for mysids (Gorokhova 2006, Gorokhova & Lehtiniemi 2007) and probably also for *Bythotrephes* (Witt & Cáceres 2004, Orlova et al. 2006). However, at this point, it is difficult, to assess the strength of the interactions between *Cercopagis* and its prey, competitors and predators, respectively. A method that may yield integrated information on food web interactions, and has been effectively applied to gain knowledge on effects of invading species on native food webs, is stable isotope analyses (Fry & Sherr 1984, Vander Zander & Rasmussen 1999, Post 2002). In brief, the N isotope signatures (δ¹⁵N) indicate the trophic level of species, because a
consumer is enriched ∼3.4‰ relative to its diet (Post 2002), while $\delta^{13}C$ can be used to trace sources of organic C.

**Summary paper II: Cercopagis and food web changes in the Baltic Sea**

The main purpose of the study was to determine relative trophic positions of *Cercopagis pengoi* and its importance to fish diets in a coastal area in the northern Baltic proper using stable isotope analyses (SIA). Moreover, we attempted to quantify differences in the trophic position of zooplanktivorous fish (young-of-the-year, YOY, herring) before and after the invasion.

Sampling of *Cercopagis pengoi* and zooplankton was conducted in Himmerfjärden Bay which is a spawning and nursery area for many fish species including herring (Axenrot & Hansson 2004), and has had a permanent population of *Cercopagis* since at least 1997 (Gorokhova et al. 2000, 2004). Two size groups of herring (5−10 cm: YOY fish and 10−15 cm: mainly >2-year-old fish) and sprat (9−11 cm: mainly >2-year-old) were collected on five occasions. For *Cercopagis*-SIA different developmental stages were analysed separately. Zooplankton was divided into two size fractions prior to SIA, namely microzooplankton (90−200 µm), consisting mainly of rotifers and nauplii and early calanoid copepodites, and mesozooplankton (>200 µm) which was mainly older copepodites, adult copepods, and cladocerans.

We determined the relative importance of food sources of *Cercopagis* and YOY−herring with an N isotope two-source mixing model using micro− and mesozooplankton as potential prey for *Cercopagis* and mesozooplankton and *Cercopagis* as prey for YOY−herring.

Results showed a general trend of enrichment in both $^{13}C$ and $^{15}N$ with trophic level: $\delta^{15}N$ in sprat, herring and *Cercopagis* (ca. 13.1 to 13.6) were much higher than in micro- (~9.0) and mesozooplankton (~10.4). Moreover, YOY herring (~14.5) known to be sedentary in the study area were significantly more enriched than *Cercopagis*, which suggests a trophic linkage between the species. Young stages of *Cercopagis* had slightly lower (but not statistically significant) $\delta^{15}N$ values than the older stages. The mixing model suggested that mesozooplankton was the main food source for *Cercopagis*. However, there was some evidence that rotifers and copepod nauplii

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might be a significant food source for young stages. For YOY herring, the model suggests diet proportions of mesozooplankton and *Cercopagis* from 50:50 to 80:20, for assumed trophic fractionations of 2.4‰ and 3.4‰, respectively. These values are in accordance with gut content analyses of fish from the study site (Gorokhova et al. 2004).

Data published by Hansson et al. (1997) on stable isotopes in fish Himmerfjärden in 1988, enabled a comparison of the relative trophic position of YOY herring, before and after the invasion. These analyses showed a trophic shift in YOY herring, from 2.6 to 3.4, indicating considerable changes in the food web structure. In conclusion, the study suggests that *Cercopagis* has been “sandwiched” into the food web, between mesozooplankton and fish, resulting in a modified food web structure in this part of the northern Baltic proper.

**NON-INDIGENOUS COPEPODS**

**Invasion histories and reported impacts**

There are numerous reports of copepod NIS established in both freshwater, estuarine and marine water (e.g., Reid & Pinto-Coelho 1994, Lee 1999, Mauchline 1998, Bollens et al. 2002, Cordell et al. 2008). For instance, the Mediterranean has received eight copepod NIS from the Red Sea (*Acartia centura*, *A. fossae*, *Calanopia* spp., *Labidocera* spp.) - probably facilitated by the establishment of the Suez Canal – and has itself been a donor region for 3 species (*Calocalanus pavo*, *Clausocalanus aruicornis* and *Acartia tonsa*) now found in the Black Sea (Mauchline 1998 and references therein). In fjords of southern Chile; *Centropages abdominalis*, *Oithona davisae* and *Acartia omorii* have been recorded as NIS (Hirakawa 1986, 1988). The latter species, which is indigenous to Japan waters, was lately also found in the southern North Sea (Seuront 2005).

Estuaries along the west coast of USA are highly invaded, and harbour at present a total of nine established planktonic copepod NIS (e.g., Orsi & Ohtsuka 1999, Bollens et al. 2002, Cordell et al 2008), apparently brought in by the discharge of ships ballast water (Choi et al. 2005, Cordell et al 2008). The copepod assemblages in the San Francisco Bay–Sacramento/San Joaquin Delta area at many localities
now resemble an East Asian fauna. This dramatic change in the zooplankton communities is reported to have had detrimental effects on native striped bass, *Morone saxatilis*. The bass larvae fed less efficiently on the non-indigenous copepods (e.g., *Sinocalanus doerii* and *Pseudodiaptomus forbesi*) compared to native, displaced species (*Eurytemora affinis*, *Cyclops* sp.) and the result was recruitment failure (Meng & Orsi 1991). Today, NIS like *Oithona davisae*, first recorded in 1963, *Pseudodiaptomus marinus* (1986) and *Tortanus dextrilobatus* (1992) dominate the more saline parts of the area, and *Limnoithona doerri* (1993) make up around 95% of the copepod abundance in the low-salinity region (Bouley & Kimmerer 2006).

An important example of invasion from saline waters into freshwater is *Eurytemora affinis* (Lee 1999, 2000). It is a strongly euryhaline and eurythermal calanoid that tolerates high turbidity, and is widely distributed in estuaries, brackish seas and salt marshes in the Northern Hemisphere (Andersen & Nielsen 1997 and references therein). On numerous occasions the species has invaded freshwater habitats in North America, Europe and Asia – primarily within the last 60–70 years (Lee 1999). For instance, *E. affinis* originating from saline populations in the St. Lawrence River drainage is now established in all of the North American Great Lakes, where it is a dominating species in bays and harbour (Mills et al. 1993, Lee 1999, 2000). While a lack of genetic overlap in *E. affinis* among continents imply that recent transoceanic transport has not taken place, the discontinuous distributions of the species within river systems suggests that human vectors play a key role for the local dispersal (Lee 1999). So far, no in-depth study of the ecological effects of invading *E. affinis* has been published. A congener species, *E. americana* invaded the inner parts of the Bahia Blanca estuary, Argentina, in the 1980s (Hoffmeyer 2004) and has become the numerically dominating copepod during winter-spring season. *E. americana* is probably the major reason for the large decrease in indigenous *Acartia tonsa* observed during this time of year compared with pre-invasion abundances (Hoffmeyer 2004).

While *Acartia tonsa* may suffer negative impacts from copepod NIS established in its native area, the species is itself a well-known NIS with a long history of successful introductions into neritic and estuarine water, including the Baltic Sea.
The role of salinity tolerance

The distribution of copepods, and hence, their interaction in trophodynamics, is dependent on both physical and biological factors. A number of field studies point at salinity as a determining factor for the species composition in copepod communities, and have also shown that individual species are often distributed in space and time according to horizontal and vertical salinity gradients (Jeffries 1962, Collins & Williams 1981, Soetaert & Rijsvik 1993, Cervetto et al. 1999, Andersen & Nielsen 2002, Renz & Hirche 2006). Organisms living in estuaries and coastal seas – where most copepod NIS have been recorded – are likely to experience strong salinity gradients and are inherently subjected to reduced and often very fluctuating salinities. Thus, salinity tolerance is likely to play a decisive role for the initial survival of a copepod NIS as well as for the outcome of competitive interactions with native copepod species and the possible niche segregation. Despite this, our knowledge about the physiological and ecological responses of copepods exposed to different salinities and to salinity changes is relatively limited.

The Baltic Sea including the entire Baltic Sea–Kattegat corridor constitutes a transition zone with very pronounced gradients in salinity, harbouring a variety of copepod species (Ackefors 1969, Kiørboe & Nielsen 1994). The hydrography in the region is dynamic, implying that each copepod species is exposed to a broad range of ambient salinities, and may also be subjected to abrupt changes. Both high and low ambient salinities, as well as quick salinity changes may cause physiological stress in copepods, and set limits for survival, growth and reproduction, according to the adaptation and physiological capacity of the individual species. Abrupt changes in the ambient salinity may occur, for instance, when the freshwater inflow into an estuary/fjord creates a halocline, and a circulation pattern with an outgoing surface current and a deeper compensating inflow of more saline water from outside the estuary. Copepods may be entrained in the compensation current, transported to the mixing zone at the head of the fjord, and exposed to abrupt salinity changes. It is therefore possible that fjords and stratified estuaries constitute veritable “graveyards” for coastal copepods (Kaartvedt & Aksnes 1992, Soetaert & Herman 1994, Hubareva et al. 2008). Likewise, tidal mixing, storms and strong precipitation may also impose osmotic stress on marine copepods.
The ubiquitous *Acartia tonsa*

The calanoid copepod *Acartia tonsa* has a wide distribution in temperate and subtropical estuarine, and neritic waters of the western Atlantic Ocean and the Indo-Pacific (e.g., Maucline 1998, Razouls et al. 2005-2009). It is omnivorous and capable of feeding on both phytoplankton and protozoan prey (e.g., Jonsson and Tiselius 1990). *Acartia tonsa* is considered as an opportunistic species and is more or less confined to coastal waters with high food concentrations and relatively high temperatures (Conover 1956, Paffenhöfer & Stearns 1988, Lawrence et al. 2004). The species may respond to adverse conditions by producing diapause eggs (Castro-Longoria 2001). Also, subitaneous eggs may enter into quiescense as a response to a hostile environment (Holmstrup et al. 2006).

The exact invasion history of *Acartia tonsa* is somewhat confused, partly because different *Acartia* species resemble each other. It was recorded for the first time in the North Sea in 1916, and has then spread to estuaries throughout Europe (e.g., Rémy 1927, Redeke 1934, Brylinski 1981, David 2007). *A. tonsa* reached the Baltic Sea Proper in 1925 (Segerstråle 1957), the Gulf of Finland in 1939 and is now considered established in the entire Baltic Sea (Pienimäki & Leppäkoski 2004, Telesh et al. 2008). Later it was reported from the Black (in 1976, Gubanova 2000) and Caspian (1981, Kurashova & Abdullaeva 1984) seas as well as in the Mediterranean (1982, Gaudi & Viñas 1985). Recent genetic studies point at the East coast USA as being the donor region for European *A. tonsa* (Drillet et al. 2008).

In the Baltic Sea *Acartia tonsa* is most abundant in the southern and western coastal areas (Ackefors 1969, 1981, Telesh et al 2008); for instance, in the Darss-Zingst estuary, Gulf of Gdansk and Vistula lagoon, where it dominates the copepod community together with *A. bifilosa* and *Eurytemora affinis* (Arndt & Schnese 1986; Schiever 2008 and references therein). *A. tonsa* is also a significant species in the Belt Sea, Kattegat and in Danish estuaries (e.g, Kiørboe & Nielsen 1994). Other common *Acartia* species in the Baltic Region are *A. longiremis*, *A. clausi* and *A. discudata* (Ackefors 1969, 1981, Kiørboe & Nielsen 1994, Schiever 2008, Telesh et al 2008). In warmer regions in Europe *A. tonsa* primarily co-occurs with *A. clausi* (Sei et al. 2006, Marques et al. 2008). The impacts of the *A. tonsa* invasion into the Baltic Sea are, so far, unknown, but the species is likely to act as a food competitor.
with co-occurring congeners. *Acartia* spp. (including *A. tonsa*) constitute significant prey for fish in the Baltic (Möllmann et al. 2004, 2005).

**Summary paper III: Salinity effects on energy balance and reproductive success**

The objective of this study was to assess salinity effects on metabolic energy partitioning and egg hatching success (EHS) of the two co-occurring copepod species: *Acartia tonsa* and *A. clausi*.

Rates of ingestion (I), respiration (R) egestion (E) and egg production (EPR) were measured in adult females at 5 different salinities: 33, 20, 10, 5 and 2 PSU for *A. tonsa* and 33, 28, 24, 20 and 16 PSU for *A. clausi*. Experimental animals were acclimated to experimental conditions of salinity, temperature (18°C) and food (100 µgC L⁻¹, *Thalassiosira weissflogii*) and incubated in bottles under the natural light:dark cycle. After 24 h, eggs and faecal pellets were counted and measured, and EHS determined. Respiration was measured in separate experiments in small glass chambers, using flow-through technique. All measured rates were converted into carbon units and relevant metabolic ratios were calculated.

For *A. tonsa*, ingestion showed a dome-shape response with maximum values between 10 and 20 PSU. EPR and R largely reflected ingestion rate and, thus, differences in gross growth efficiency (GGE = EPR/I) and cost of growth (CG = R/P) were small. EHS was generally high in *A. tonsa* (≥75%) except at 2 PSU where it dropped to 55%. This was reflected in the realized fecundity (RF = EPR * EHS), being 15–19 nauplii female⁻¹ d⁻¹ in the range 5–33 PSU, but decreasing to 11 nauplii female⁻¹ d⁻¹ at 2 PSU. Our results confirm the euryhaline character of *A. tonsa*, and suggest no higher energetic cost of osmoregulation at low salinities for this species.

*A. clausi* exhibited significantly reduced ingestion and GGE and dramatically elevated CG at salinities ≤20, likely reflecting the effects of osmotic stress. At 16 PSU, EHS was only 20% (compared with 65–97% at higher salinities) and RF was only 2 nauplii female⁻¹ d⁻¹. These results were unexpected considering the previously reported tolerance for *A. clausi* in the range 2–65 PSU. A physiological optimum of
A. clausi around 24 PSU was suggested by maximum EPR, GGE and RF combined with minimum CG observed at this salinity.

Our results may help explaining the distribution patterns of the two species along salinity gradients. The observed responses would allow the dominance of A. tonsa at low salinities, although its higher energetic requirement and feeding activity would subject it to stronger predation pressure than the competing A. clausi.

Summary paper IV: Effects of sudden salinity changes on feeding and survival

The aim of this study was to assess the effects of various degrees of instantaneous salinity decrease on short-term mortality and feeding response in the copepod congener species Acartia tonsa and A. clausi.

Adult females were transferred directly from 32 PSU to bottles filled with water of lower salinity, for Acartia tonsa 26, 20, 14, 8 and 4 PSU, for A. clausi 26, 20 and 14 PSU. The bottles (containing 150 µgC L⁻¹ Thalassiosira weisflogii as food) were incubated in the dark (19°C) and after 1, 2, 4, 8 and 12 h a water sample was taken, and the food concentration determined. Clearance rate, F (mL ind⁻¹ h⁻¹), was calculated as a time-integrated F response from the beginning of the experiment until the corresponding sampling time. Responses in ingestion rate, I (µgC ind⁻¹ h⁻¹), were calculated by multiplying F by the average food concentration (µgC mL⁻¹) during the corresponding time period. Clearance and ingestion rates were corrected for mortality and calculated as rates per surviving animal. Total clearance rate (Fₜₒᵗₜ, mL h⁻¹) and total ingestion rate (Iₜₒᵗₜ, µgC h⁻¹) within each bottle were estimated as the product of individual rate times the number of surviving animals.

Mortality after 12 h of Acartia tonsa was low, 0–3%, except for the 32/4 PSU treatment where it was 31%. A. clausi mortality was 0% for the 32/26 and 32/20 PSU treatments, but 22%, for the 32/14 PSU treatment. Thus, both species could withstand a significant osmotic change, although A. tonsa tolerated a salinity decrease of at least 10 PSU larger than A. clausi. For both species F and I in controls were higher than (or similar to) rates in the salinity shock treatments. The differences tended to decrease with increase of observation period, showing the
potential for recovery on a time scale of hours in shocked animals, although this was not the case for the extreme shock treatments. $F$ and $I$ decreased significantly at extreme treatments; for $A.\ tonsa$ $F_{tot}$ was reduced by 62% (32/8 PSU change) and 95% (32/4 PSU change) compared with non-shocked controls. Corresponding $I_{tot}$ for $A.\ tonsa$ were reduced by 54% and 90%. The 32/14, 32/20 and 32/26 PSU treatments did not affect either clearance or ingestion rates. For $A.\ clausi$ 32/20 and 32/14 PSU treatments reduced $F_{tot}$ by 40% and 80%, while the corresponding $I_{tot}$ were reduced by 12% and 76%, respectively. There was no effect of the 32/26 PSU treatment on either feeding parameter in $A.\ clausi$.

Our results may help explaining the outstanding ability of $A.\ tonsa$ to colonize and dominate the estuarine plankton communities over ample regions of the world. They suggest that $A.\ tonsa$ is unlikely to suffer significant mortalities due to sudden salinity reductions in the surrounding medium – except under extreme circumstances – while $A.\ clausi$ cannot tolerate changes >18 PSU. However, in both species the feeding activity could be severely compromised by sublethal salinity reductions. Also, the abnormal swimming patterns and impaired escape responses observed during the initial phase of salinity shock may render copepods more vulnerable to predators.

**A case study of non-indigenous *Acartia tonsa* population dynamics**

Estuaries are characterised by strong gradients, for instance, in salinity and by fluctuations in the physical/chemical environment. In general, survival in the estuarine environment requires not only wide salinity tolerance but also the ability to cope with, for instance, fluctuating and extreme temperatures, fluctuating and often very high pH (due to high primary production), anoxia/sulphide, high turbidity, strong turbulence, and high predation pressure from fish and invertebrates such as jellyfish (e.g., Roman et al 1993, Macedo et al. 2001). In addition, there is often a tight benthic-pelagic coupling with, for instance, high biomasses of suspension feeding bivalves which may be significant zooplankton consumers (Davenport et al. 2000, Nielsen & Maar 2007). Also, large densities of sediment deposit feeders and epibenthic foragers (e.g., mysids) may impose high mortality on eggs in aerated bottoms (Viitasalo & Viitasalo 2004, Viitasalo et al. 2007).
An example of an estuary with such adverse physical conditions is Mariager Fjord, Denmark. It is a 30 m deep, silled, hyper-eutrophic estuary characterised by high phytoplankton production, high pH in surface waters, permanent stratification and oxygen-depleted bottom waters (Fenchel et al. 1995, Olesen 2001). Moreover, dense beds of blue mussels, *Mytilus edulis*, cover the oxygenated bottoms at 1–10 m depth (Møller 2005). Initially, we wanted to study the copepod community in the fjord to assess the relative importance of non-indigenous *Acartia tonsa*, but it turned out that *A. tonsa* was practically the only copepod species living in the fjord.

**Summary paper V: *A. tonsa* in the hyper-eutrophic Mariager Fjord**

The objective of this study was to explore population dynamics of the copepod *Acartia tonsa* in Mariager Fjord. During summer we monitored water column structure, as well as the abundance, depth distribution and a range of life-history parameters for *A. tonsa* at a permanent station in the deepest, central part of the Fjord.

Plankton samples collected at discrete depths were analysed for mesozooplankton, and copepods were determined to stage. Mortality rates of *A. tonsa* were calculated from vertical life table analyses, expressed for each developmental stage, and also calculated as a function of water depth. Egg production rate (EPR) of *A. tonsa* was determined from bottle incubations, and the egg hatching success subsequently recorded. Copepod survival was investigated by incubating caged adult females *in situ* at different depths. To explore the sedimentation of copepod eggs we deployed sediment traps in the water column, and collected sediment cores at different depths.

During the study the mixed upper layer was warm (17–20°C) with a salinity of 15–16 PSU while water below the pycnocline was cold (<5°C) and more saline (ca. 20 PSU). An intense bloom of *Skeletonema costatum* resulted in exceedingly high chlorophyll concentrations and pH in the surface water was up to 9.8. The mesozooplankton community was very sparse and dominated by *Acartia tonsa*. Nauplii resided mainly in the upper 5 m of the water column. Copepodites tended to stay increasingly deeper with age and C5 copepodites and adults were concentrated in the deepest part of the mixed layer. EPR was high: 30–65 eggs female$^{-1}$ d$^{-1}$, and
the egg hatching success was >90%. Yet, A. tonsa abundance remained low (≤3 nauplii l⁻¹, ≤1.5 copepodites l⁻¹). Accordingly, calculated daily mortality was high: 18% for nauplii, 16% for C1, 70% for C2 and C3, 43% for C4 and 53% for C5. The life table analysis showed a peak in A. tonsa mortality at 6–8 m coinciding both with the depth distribution of C2/C3 copepodites and with the optimal depth (5–10 m) of suspension feeding Mytilus edulis in the fjord. Thus, the very high mortality rates of C2 and C3 could have been due to predation from M. edulis which is probably the main zooplanktivore in the Fjord. Yet, the fact that older copepodite stages migrated to deeper areas of the fjord suggested that predation by fish may also be important. Results from the cage experiments demonstrated that such deep migration is hazardous due to the proximity to toxic sulphide-containing deep water. Decreased survivorship of older life stages swimming or sinking below 20 m depth, would contribute further to the low copepod abundance.

Most copepod eggs produced in Mariager Fjord sink into anoxic bottom water before hatching. This most likely results in very high egg mortality. Eggs that sink to the sediment where the water is oxygenated are more likely to hatch, but such bottoms are to a large extent covered with beds of Mytilus edulis, and mussel filtration will also be a significant sink for copepod eggs. This leaves the bottom at approximately 10–15 m (covering only 22% of the estuary) as the main potential area for successful egg hatching, survival and recruitment to the copepod population. Such a restricted area from which copepod eggs may hatch is rather unique to Mariager Fjord. In other coastal areas with anoxia at greater depths, most eggs will hatch before reaching the anoxic layer.

Intrusions of water from the Kattegat would occasionally introduce a variety of copepod species to Mariager Fjord, among them several Acartia species. However, only Acartia tonsa appears capable of maintaining a population under the adverse conditions in the Fjord.
CONCLUDING REMARKS

The three pelagic crustaceans, *Bythotrephes longimanus*, *Cercopagis pengoi* and *Acartia tonsa* are all highly successful invaders, which have become well integrated and even dominant parts of the pelagic food webs in the recipient ecosystems, acting both as predators/grazers and as prey. They have in common a high reproductive potential and the ability to produce resting eggs – both features which may favour their spread to and establishment in new areas. *A. tonsa* also has an impressive physiological tolerance which enables it to sustain populations in estuaries under conditions that most other pelagic copepod species cannot tolerate. The ability of this species to survive abrupt changes in salinity may also be an important feature for helping it survive in ballasts tanks after ballast water exchange and after being released into a new environment. Unfortunately, only little is known about physiological tolerance in the cercopagidids.

Evidently, both *B. longimanus* and *C. pengoi* have strong potential to suppress populations of crustacean (and rotifer, *C. pengoi*) prey and cause food web changes on an ecosystem scale. The effects of *Acartia tonsa* invasions are less obvious, and not fully understood. This may partly be ascribed to the omnivorous nature of the species and the fact that it quite closely resembles other, native, *Acartia* species. However, as shown for instance in the present thesis, close congener species can indeed show important differences in physiology, feeding biology, behavior etc. All the three species investigated are likely to continue to expand their distributions and invade new ecosystems. Being temperate/sub-tropical species *C. pengoi* and *A. tonsa* may be expected to benefit from the ongoing global climate change. In northern Europe this could be at the expense of species tending to prefer colder water, such as *Acartia bifilosa* and *Acartia longiremis*.

Neither the invading species nor the invaded ecosystems should be seen as static entities and it is important to incorporate evolutionary considerations in invasional biology. Studies of e.g., *Eurytemora affinis*, have shown that key physiological traits may undergo very rapid evolution during an invasion process (Lee 1999). Genetic studies of populations from a wide geographical range may allow the reconstruction of invasion history, reveal possible vectors of transportation and help in distinguishing evolutionarily isolated populations. Recent studies have revealed a
number of genetically diverging clades within the nominal species *Acartia tonsa*, and it has been argued that the taxon may include one or more cryptospecies (Chen & Hare 2008). Likewise, *E. affinis* is now regarded as a species complex (Lee 2000). Although the invasion of *C. pengoi* into the Baltic is very recent in an evolutionary context *C. pengoi* populations differ somewhat from source area populations in reproductive strategy and behavior. It will be interesting to observe whether *C. pengoi* continues to adapt to its new environment, which is also likely to change as future non-indigenous species establish themselves in the Baltic Sea.

**LITERATURE CITED**


Pichlová-Páčniková R, Vanderpløeg HA (in press) The invasive cladoceran *Cercopagis pengoi* is a generalist predator capable of feeding on a variety of prey species of different sizes and escape abilities. Fundam Appl Limnol.


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**MY CONTRIBUTION TO THE PAPERS**

**Paper I:** CMAB was the responsible author, planning, compiling available information (including all tables), and doing most of the writing.

**Paper II:** CMA did sample preparation of fish tissues for stable isotope analysis, with minor contributions to data processing and paper writing.

**Paper III:** CMA planned and carried out the experiments together with DC and PT and did the RNA/DNA - analyses together with EG. In all, CMA did about 50% of the practical work. Data processing was done by DC and CMA together. CMA contributed substantially to the writing, providing input to several versions of the draft and to the final revisions according to the referee reports.

**Paper IV:** CMAB planned and carried out the experiments in collaboration with PT and DC. CMAB did the major part of the practical work and of data processing and contributed substantially to the writing, providing input to several versions of the draft and to the final revisions according to the referee reports.

**Paper V:** CMAB conducted the field work together with PT, BWH, PJH, TGN and BV. CMAB was responsible for the biological and physical/chemical sampling programme and conducted copepod experiments together with PT and BWH. CMAB contributed significantly to data processing and to the writing.