

ECOLOGY AND DISTRIBUTION OF THE ISOPOD GENUS *IDOTEA* IN THE BALTIC SEA: KEY SPECIES IN A CHANGING ENVIRONMENT

Sonja Leidenberger^{1,*}, Karin Harding², and Per R. Jonsson³

¹ Department of Marine Ecology, University of Gothenburg, Kristineberg (MEK), Kristineberg 566, SE-451 78 Fiskebäckskil, Sweden

² Department of Marine Ecology, Carl Skottsbergs gatan 22B, SE-405 30 Göteborg, Sweden

³ Department of Marine Ecology, University of Gothenburg, Tjärnö Marine Biological Laboratory, SE-452 96 Strömstad, Sweden

ABSTRACT

Marine isopods of the genus *Idotea* [*I. balthica* (Pallas, 1772), *I. chelipes* (Pallas, 1766), and *I. granulosa* Rathke, 1843] are common meso-grazers that enter deep into the Baltic Sea and here appear to live at their physiological limit, determined by salinity and temperature tolerance. We review available data on distribution and community ecology to assess the functional role of *Idotea* in the Baltic Sea and how global change may affect essential ecological interactions. Data from the last 150 years suggest an on-going shift southward for *I. chelipes* and *I. granulosa* that may be caused by a changing climate. Several studies report local extinctions and mass abundances, which may be caused by a changing food web from over-fishing and eutrophication. The three species of *Idotea* have clear habitat segregation in the Baltic Sea, where salinity, temperature and vegetation are the main dimensions. *Idotea* spp. have a central role as grazers and in communities dominated by the perennial macrophytes *Fucus* spp. and *Zostera marina* and attain impressive feeding rates on a range of epiphytes/filamentous algae (top-down effect). *Idotea* can have both a direct negative grazing effect on macrophytes but also an indirect positive effect by removing epiphytes. The relative role of nutritional value and chemical defence for food preference is yet unclear for *Idotea*. Baltic idoteids are also important prey for several fish (bottom-up effect) and fish predation may have increased following over-fishing of piscivorous fish. It is concluded that *Idotea* is a key taxon in the Baltic Sea food web, where guilds often contain few dominant species. Changes in population dynamics of *Idotea*, as a function of human generated global change, may have large-scale consequences for ecosystem functions in a future Baltic Sea, e.g. the extent of vegetation cover in the coastal zone.

KEY WORDS: Baltic Sea, distribution patterns, environmental changes, *Idotea*, key species

DOI: 10.1163/193724012X626485

INTRODUCTION

The Baltic Sea is the youngest regional sea in the Northern Hemisphere (about 13 000 years BP) and the world's second largest brackish environment. The most prominent feature of the Baltic Sea is the salinity gradient with almost freshwater in the northern Gulf of Bothnia to about 25 PSU at the boundary between Kattegat and the almost fully marine Skagerrak towards the North Sea. The reduced salinity makes the Baltic Sea a species-poor ecosystem (Bonsdorff, 2006). Most successful colonizers of the Baltic Sea consist of species with a generally broad salinity tolerance, but it is still unclear to what degree Baltic species have evolved significant local adaptations to a brackish environment. Johannesson and André (2006) showed that Baltic Sea populations have reduced genetic variation compared to Atlantic populations, which may indicate selection for extreme genotypes and/or population bottlenecks during colonization.

The Baltic Sea borders on nine countries and is one of the most environmentally impacted coastal areas in the world with serious effects of habitat loss, eutrophication, pollution and over-fishing (Diaz and Rosenberg, 2008; Halpern et al., 2008; Eriksson et al., 2009). There is

concern that the low biodiversity of the Baltic ecosystem may render it particularly susceptible to environmental deterioration with a low resilience capacity and potential loss of essential ecosystem services (Österblom et al., 2007). It is thus important to improve overall knowledge about the mechanisms controlling the Baltic ecosystem with special emphasis on selected key species.

In the species-poor ecosystem of the Baltic Sea, several species can be regarded as key species since most guilds contain few or sometimes only one dominant species. Important benthic key species are the bladder wrack (*Fucus vesiculosus* and *F. radicans*), the suspension-feeding blue mussel (*Mytilus trossulus/edulis*), deposit-feeding amphipods (*Monoporeia affinis* (Lindström, 1855) and *Pontoporeia femorata* Krøyer, 1842) and meso-grazers of the isopod genus *Idotea*.

In Europe, eight different species of *Idotea* have been described, but only three of these species exist in the Baltic Sea: *Idotea balthica* (Pallas, 1772) (BA), *Idotea chelipes* (Pallas, 1766) (CH) and *Idotea granulosa* Rathke, 1843 (GR), inhabiting the bladder wrack belts (*Fucus* spp.) or eelgrass communities (*Zostera marina*). All three species

* Corresponding author; e-mail: Sonja.Leidenberger@marecol.gu.se

(*Idotea* spp.) are common among the vagile fauna in the vegetation (Kautsky, 2008). Beside snails (*Hydrobia* spp.), amphipods, copepods, and ostracodes, *BA* is the numerically most important taxon of the Baltic eelgrass community (Schaffelke et al., 1995; Boström and Bonsdorff, 2000). In the *Fucus* belt the abundance of *Idotea* spp. may account for up to 28% of crustacean grazers (Korpinen and Jormalainen, 2008). Segerstråle (1932, 1944b) compared exposed and sheltered *Fucus* localities with different salinities in Finland and considered *Idotea* spp. among the most dominant of species, and Råberg and Kautsky (2008) described *BA* as the second most common crustacean. In the 1970's and 1980's together with an observed decline of the bladder wrack in the Baltic Sea, *BA* was described as an important grazer in the *Fucus* belt (Kangas et al., 1982; Haahtela, 1984; Hällfors et al., 1984), and *Idotea* spp. are suggested as dominant benthic herbivores in the western Baltic Sea (Sommer, 1997). Very high abundances of *BA* and *GR* in the bladder wrack belts have been reported (Jansson, 1974) and recently events of mass occurrence have been recorded (Engkvist et al., 2000, 2004; Nilsson et al., 2004; Svensson et al., 2004). However, some recent studies also describe declining distributions of *Idotea* (Jazdzewski et al., 2005; Jephson et al., 2008).

Successful attempts to predict ecosystem responses to environmental hazards, e.g., climate change, will depend on high-quality information on the Baltic ecosystem with emphasis on ecological interactions for key species and their evolutionary potential. We here review and analyse available information of the distribution and community ecology of the three species of *Idotea* and present a synthesis of their ecosystem role in the Baltic Sea and possible effects of ongoing environmental change. We explore the hypothesis that species of *Idotea* have changed their distribution patterns over the past 150 years. The ecological niche of the *Idotea* in the Baltic Sea is then sketched, and we hypothesize that *Idotea* are key species in the Baltic food web. Finally, we present a conceptual model of how environmental impacts may affect Baltic *Idotea* abundance and distribution through demographic and food web changes.

MATERIAL AND METHODS

Study Area

The Baltic Sea is a shallow inland sea located in northern Europe (Fig. 1) and one of the largest brackish water bodies in the world with a surface area of 390 100 km² (Lozan et al., 1996). It is connected to the North Sea via the Skagerrak (about 33 PSU), the Kattegat (20-26 PSU), the Danish straits and the Belt Sea (6-18 PSU, mean cross-section 0.35 km²) (Fig. 1). Hydrographically the natural boundary of the Baltic Sea is formed by the Danish Straits, whereas in a management context, the HELCOM (Helsinki Commission for the Protection of the Baltic Marine Environment) includes the Belt Sea and the Kattegat, motivated by the strong hydrographical influence from the Baltic Sea. The Baltic Sea consists of several sub-basins, separated by sills and other bathymetrical formations and the circulation is largely topographically bound in the sub-basins (Fig. 1). The thermocline ranges between 15-25 m depth during summer, but is deeper and weaker in the cold seasons. The halocline depth is between 40-80 m except in

the Danish straits and in the Kattegat where the thermocline and the halocline coincide at about 15 m in the summer. The Baltic is microtidal (<10 cm) and water exchange is dominated by a surface outflow from the Baltic Sea through the Danish straits with a deeper, more saline counter-current entering into the Baltic Sea. The limited water exchange with the North Sea (residence time in the Baltic around 25-35 years, Lozan et al., 1996) combined with an outflow from around 200 rivers from the Baltic Sea drainage area create a stable salinity gradient from almost freshwater in the northern part to around 18 PSU at the exit. The geographical and hydrographical features largely determine the composition of the Baltic fauna and flora. At the entry more than 500 macrozoobenthic species can be found (the Arkona Basin), but species richness decreases dramatically to around 20 in the Bothnian Bay and Gulf of Finland (Bonsdorff, 2006). A salinity of 5-7 PSU forms a natural barrier for both freshwater and marine species (Khlebovich, 1990). The benthic communities that have colonized the Baltic Sea are the result of tolerance to this extreme environment and the history of a series of geological events influencing the salinity (like the Baltic Ice Lake 14 000-10 300 yrs BP, the freshwater Ancylus Lake 9500-8300 yrs BP and the brackish Littorina Sea 8300-3700 yrs BP), together with anthropogenic interventions mainly during the past century (like eutrophication, climate change, over-fishing and the introduction of invasive species). Established flora and fauna in the Baltic Sea thus have both marine and freshwater origin.

Data Analysis

This study is based on a detailed survey of the literature from 1850-2011 (January), where the largest part is related to the Baltic Sea. This screening resulted in a total of around 300 publications with information about distributions and/or the ecological role of *Idotea* spp. in the Baltic Sea. A subset of 115 articles were used to sketch the distribution patterns, and additionally we investigated the collections of *Idotea* at the Finnish Museum of Natural History (FMNH) in Helsinki, Finland; the Zoological Museum Hamburg (ZMH), Germany; the German Oceanographic Museum (GOM) in Stralsund, Germany; the Zoological Museum in Berlin (ZMB), Germany; the Senckenberg Museum in Frankfurt (SMF), Germany; the Zoological Museum of the Zoological Institute of Russian Academy of Science (ZIN) in St. Petersburg, Russia and the Swedish Museum of Natural History (SMNH) in Stockholm, Sweden, to obtain more historical information about distribution patterns of the species during the 19th century. Geographic data were visualised with a Geographic Information System (GIS software ArcView 9.2, ESRI, Redlands, California, USA).

Analysis of Temporal Change in Distribution of *Idotea* spp.

Based on the geographic positions of all recorded findings of *BA*, *CH*, and *GR* we calculated the mean longitude and latitude and also tested the null-hypothesis that the midpoint of distributions were identical for all species. The hypothesis of a temporal change in geographic distribution for all three species was tested with linear regressions of longitude and latitude against the year of recording.

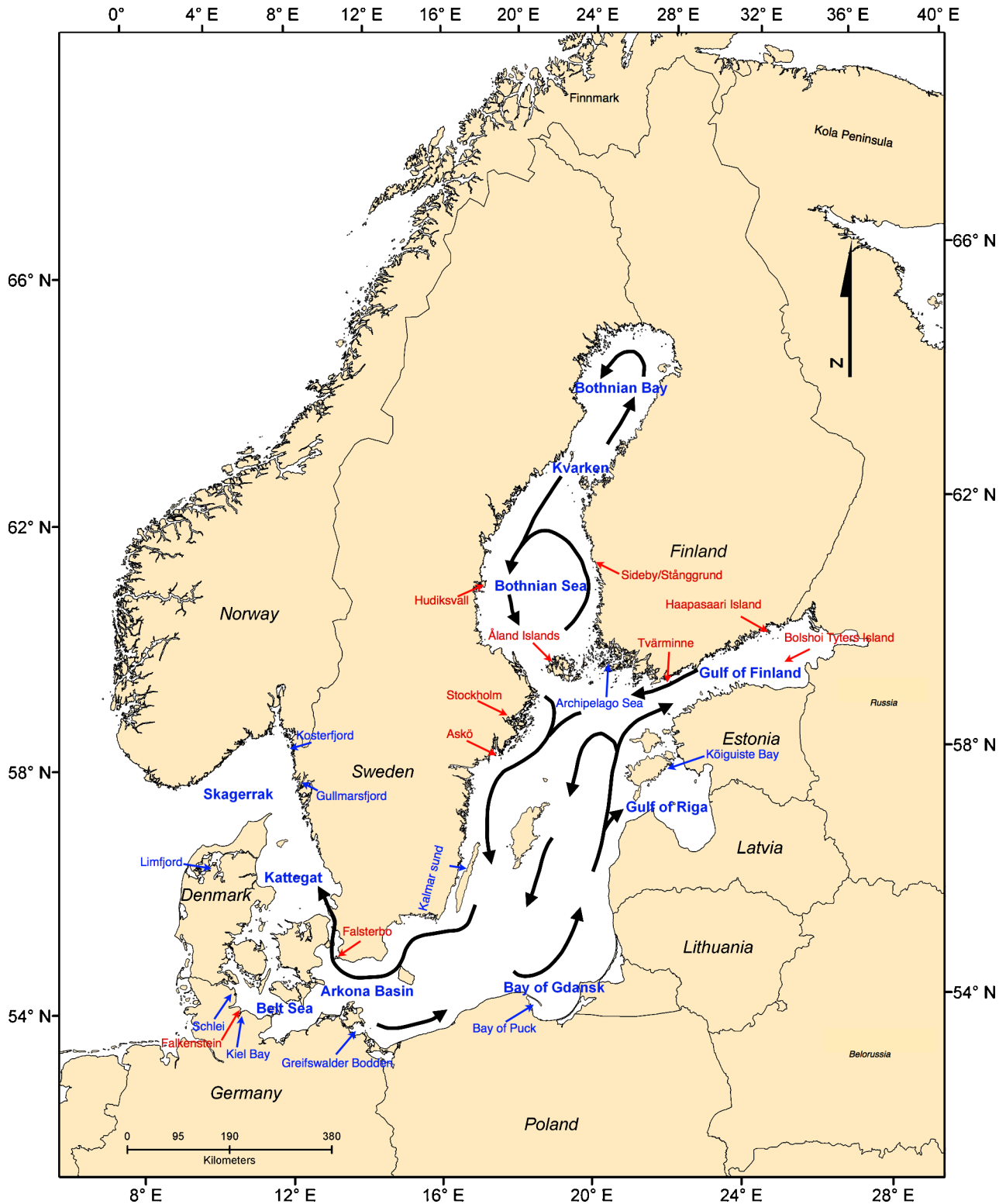


Fig. 1. Detailed map of the Baltic Sea indicating major geographic regions mentioned in the text. The surface water mean circulation is indicated by arrows and based on Elken and Matthäus (2008).

Correlations of Temperature and Salinity with Distribution of *Idotea* spp.

From recorded geographic distributions we estimated the temperature-salinity envelope for all three species. This

was done with a hydrodynamic model (Rossby Centre Oceanographic Model, Meier et al., 2003), which modeled temperature and salinity for the Baltic Sea with a spatial resolution of 3.7 km, a vertical resolution of 3 m and a

temporal resolution of 6 hours. From the position of each record of *Idotea* we extracted modeled temperature and salinity for the months June to August for the years 1995–2004, which well represent the North Atlantic Oscillation cycle (Hurrell and Deser, 2009). We tested differences between the three species of *Idotea* in average temperature and salinity for the recorded locations with a 1-factor Anova for the geographic area defined by 54°N 12°E to 66°N 30°E.

Analysis of Temporal Change in Temperature and Salinity in the Baltic Proper

To explore if potential shifts in the geographic distribution of *Idotea* could be correlated with temporal changes in sea-surface temperature and salinity we extracted empirical data from HELCOM (<http://ocean.ices.dk/Helcom/Default.aspx>) for part of the Baltic Sea (58°N 17°E to 63°N 20°E) from the years 1960–2010. Temporal trends in temperature and salinity were tested with linear regressions. The subset between 58°–63°N was selected since this data set did not show any temporal trend in latitudinal sampling effort that could confound trends in temperature and salinity.

All scientific names used in this study conform to the nomenclature of the World Register of Marine Species (= WoRMS) (Appeltans et al., 2010).

RESULTS

Distribution and Abundance of Baltic of *Idotea* spp.

As noted above, only three species of *Idotea* occur in the species-poor brackish water of the Baltic Sea: *Idotea balthica* (*BA*), *I. chelipes* (*CH*) and *I. granulosa* (*GR*). Maps of their distribution are shown in Figs. 2–4 with all references given in the on-line appendices (A: museum sources and B: literature sources). The European distribution patterns of *Idotea* are described by Naylor (1972) and Hayward and Ryland (1995). More detailed information about distribution patterns in Scandinavia is published by Sars (1899) for Norway, by Segerstråle (1944a) for Finland and by Wahrberg (1930) for Sweden.

Idotea balthica

BA is the most recorded and investigated species in the Baltic Sea (Fig. 2), probably due to its high abundance (Table 1) and the easily distinguished morphological characteristics in adults: the telson shows a tridentate posterior border, where the middle one is the largest (Fig. 2, see also Sars, 1899; Naylor, 1955a; Sywula, 1964a; Gruner, 1965). The telson protrusions are less well developed in the Baltic Sea compared to populations in the North Sea. *BA* occurs in the Limfjord, Skagerrak, Kattegat, and nearly the whole Baltic Sea (Fig. 2). Arndt (1964) and Naylor (1972) mentioned the presence of *BA* for the Gulf of Bothnia without detailed limits, but the northernmost detailed description is from Hudiksvall, Sweden and Sideby/Stånggrund, Finland (Wahrberg, 1930; Segerstråle, 1944a; Gruner, 1965; Forslund, 2009) (Fig. 2). The species does not enter the very low salinity area of the Gulf of Bothnia. *BA* is a dominating species in the Greifswalder Bodden, Germany (Schiewer, 2008), the Stockholm Archipelago (Hill and Wallström, 2008), and the Askö Area and Himmerfjärden (Kautsky,

2008) in Sweden. It is also frequent at some places off the German coast (Mecklenburg Bay: Zettler et al., 2000; Falkenstein: Bobsien, 2006) and in the Gulf of Finland (Segerstråle, 1944a; Tvärminne: Salemaa, 1979). According to Råberg and Kautsky (2008) *BA* is the second most common crustacean meso-grazer beside *Gammarus* spp. on the Swedish east coast. Mean abundance appears to be highest in the *Cladophora glomerata* zone, followed by the eelgrass (*Zostera marina*) community and the bladder wrack (*Fucus vesiculosus/radicans*) belt (Table 1). For the eelgrass beds, *BA* is numerically one of the most dominant taxa (Boström and Bonsdorff, 2000; Boström et al., 2002) with peak abundance in the summer (Bobsien, 2006; Gohse-Reimann, 2007). In contrast, the exposed *Fucus* belt hosts the maximum density of *BA* during winter (Askö Laboratory, Sweden: Haage, 1975) or in the autumn (Finnish Baltic Sea: Salemaa, 1978) (Table 1). Korpinen et al. (2010) observed that the density of *BA* in the *Fucus* belt in Finland varied from a low in June to a peak in August (Table 1). Whereas the abundance of *BA* in the eelgrass beds of the Kiel Bay in Germany has been relatively constant over the last 30 years (Bobsien, 2006), events of mass occurrence in *Fucus* belts have been reported both on the Swedish east coast (Kangas et al., 1982; Hällfors et al., 1984; Engkvist et al., 2000; Svensson et al., 2004) (Table 1) as well as in the Koiguiste Bay in Estonia (Kotta et al., 2000a).

Idotea chelipes

The distribution pattern of *CH* in the Baltic Sea is similar to that of *BA* (Fig. 3). In older literature this species is often called by the junior synonym *I. viridis* Sars, 1899. It occurs in the Limfjord, Skagerrak, and Kattegat, as well as along the Swedish coastline up to the Stockholm Archipelago Sea and south in the Darß-Zingst Boddenkette, Germany. *CH* also extends into the Gulf of Bothnia (Naylor, 1972) and was recorded from Sideby/Stånggrund, Finland (Wahrberg, 1930; Segerstråle, 1944a; Gruner, 1965) (Fig. 3). It does not penetrate as deep into the Gulf of Finland as does *BA* (Fig. 3). Only one report mentioned this species in the Gulf of Riga, Estonia (Kotta and Möller, 2009). Segerstråle (1944a) reported that *CH* in general shows lower density and frequency than *BA* in the Gulf of Finland, but it can vary between different years and occasionally the abundance of *CH* is higher. For the Schlei-Fjord, Germany, the abundance of *CH* was highest between July–August (Betz, 1974; Lotze and Worm, 2000), whereas the peak occurred in the autumn at Tvärminne, Finland (Salemaa, 1979; Kangas et al., 1982). Schiewer (2008) considered *CH* among the dominating species in the Greifswalder Bodden, Germany. Korheina (1981) found that the abundances of *BA* and *CH* were similar at the Falsterbo Peninsula in Sweden. The abundance of *CH* decreases with increasing shore exposure (Korpinen et al., 2010). No mass occurrence has been reported for *CH*.

Idotea granulosa

The distribution pattern of *GR* differs from those of *BA* and *CH* (Fig. 4). Nierstrasz and Schuhmanns Stekhoven Jr. (1926) and Naylor (1972) mentioned that the distribution of *GR* extends into the Gulf of Bothnia, but the northern-

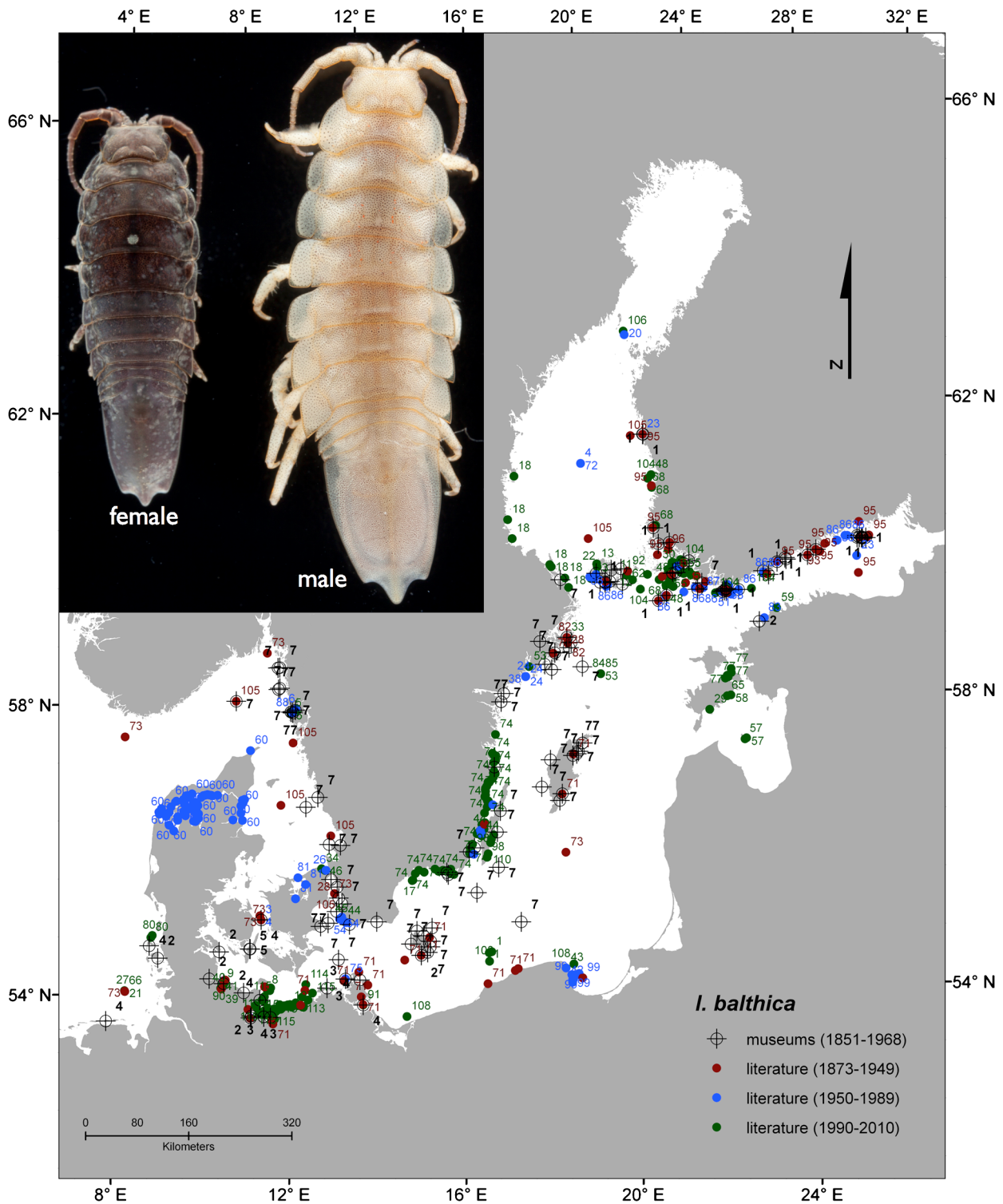


Fig. 2. Female and male of *Idotea balthica* (dorsal view) and the distribution pattern in the Baltic Sea. The number next to the dots gives the reference (see on-line Appendices A and B). Maximum length for males 21.9 mm and for females 14.8 mm (material: SMNH). Telson shape of the posterior border tridentate, the middle one is the largest. The first two coxal pairs do not reach the length of their segments (thorax segments 2 and 3), in contrast to the other (dorsal view).

most confirmed finding is from around the Åland Islands (Fig. 4). *GR* does not seem to enter far into the Gulf of Bothnia, the Gulf of Finland or the Limfjord. Data on dis-

tribution from the Baltic States are very limited (Fig. 4). Moreover, identification of *GR* and *CH* may be uncertain since they are easily confounded in the Baltic Sea due to

Table 1. Average abundances in different habitats of *BA*, *CH* and *GR* in the Baltic Sea (G = Germany, E = Estonia, F = Finland, S = Sweden; ind. = individuals, ww = wet weight). * = This measurement is from 1922 when it was not known that different species of *Idotea* exist in the Baltic Sea. + = Different localities. \wedge = 196 g ww *Fucus*.

		Sampling time	Reference
<i>Eelgrass/Zostera marina</i>			
<i>BA</i>	651 \pm 1072 ind./m ² (2001)	April-October	Bobsien, 2006 (G)
	439 \pm 438 ind./m ² (2002)		
	256 ind./m ²	Early summer	Jaschinski, 2007 (G)
	602 \pm 590 ind./m ²	April-October	Gohse-Reimann, 2007 (G)
	max. 1640 \pm 1783 ind./m ²	August	
<i>CH & GR</i>	2.4 ind./m ²	June-September	Boström and Bonsdorff, 1997 (F)
<i>Bladder wrack/Fucus belt</i>			
<i>Idotea</i> *	6-358 ind./m ²	Summer + autumn	Segestråle, 1944b (F) +
<i>BA</i>	29 ind./1000 cm ³	June	Salemaa, 1979 (F)
	200 ind./1000 cm ³	Autumn	Salemaa, 1978 (F)
	35 ind./1000 cm ³	Winter and spring	Salemaa, 1978 (F)
	1.5 ind./kg ww	August (1968-1970)	Kangas et al., 1982 (F)
	151 ind./kg ww	September 1980	(different localities)
	5 ind./kg ww	November (1968-1970)	
	1681 ind./kg ww	December (1980)	
	1 ind./kg ww	May-June (1969)	
	858 ind./kg ww	June (1981)	
	0.2 \pm 0.2 ind./100 g to	September	Enkvist et al., 2000 (S)
	84 \pm 37 ind./100 g		
	3 \pm 1 ind./100 g to	Min. and max. over 6 years	Enkvist et al., 2004 (S)
	240 \pm 2 ind./100 g		
	77 \pm 11 ind./m ²	November	Svensson et al., 2004 (S)
	3 \pm 2 ind./m ²	Late May	Lauringson and Kotta, 2006 (E)
	300 ind./m ²	April-October	Kotta et al., 2006 (E)
	250-754 ind./m ² (min.-max.)		
	235 \pm 11 ind./m ²	August	Wikström and Kautsky, 2007 (S) +
	450 \pm 242 ind./m ²		
	37.5 ind./m ²	July	Råberg and Kautsky, 2007a (S)
	3 ind. in an average algae	May	Korpinen et al., 2010 (F)
	1.5 ind. in an average algae	June	
	26 ind. in an average algae	August	
<i>CH</i>	9 ind./1000 cm ³	June	Salemaa, 1979 (F)
	240 ind./100 g	Summer	Haage, 1975 (S)
	0.2 ind./kg ww	August (1968-1970)	Kangas et al., 1982 (F) +
	19 ind./kg ww	September 1980	
	5 ind./kg ww	November (1968-1970)	
	112 ind./kg ww	December (1980)	
	8 \pm 3 ind./m ²	Late May	Lauringson and Kotta, 2006 (E)
	28 \pm 19 ind./m ²	August	Wikström and Kautsky, 2007 (S) +
	30 \pm 25 ind./m ²		
	3 \pm 3 ind./m ²	May	Widbom and Westerlund, 2007 (S)
	15 ind. in an average algae	May	Korpinen et al., 2010 (F)
	5 ind. in an average algae	June	
	9 ind. in an average algae	August	
<i>GR</i>	1 \pm 1 ind./100 g to	Min. and max. over 6 years	Engkvist et al., 2004 (S)
	377 \pm 282 ind./100 g		
	15 \pm 23 ind./m ²	August	Wikström and Kautsky, 2007 (S)
	8.3 ind./m ²	July	Råberg and Kautsky, 2007a (S)
<i>Polysiphonia fucoides</i>			
<i>BA</i>	40 \pm 9 ind./m ²	November	Svensson et al., 2004 (S)
<i>Cladophora glomerata</i>			
<i>Idotea</i>	8500 ind./m ²	April-August	Jansson, 1974 (S)
juveniles	max. 28 000 ind./m ²	July	

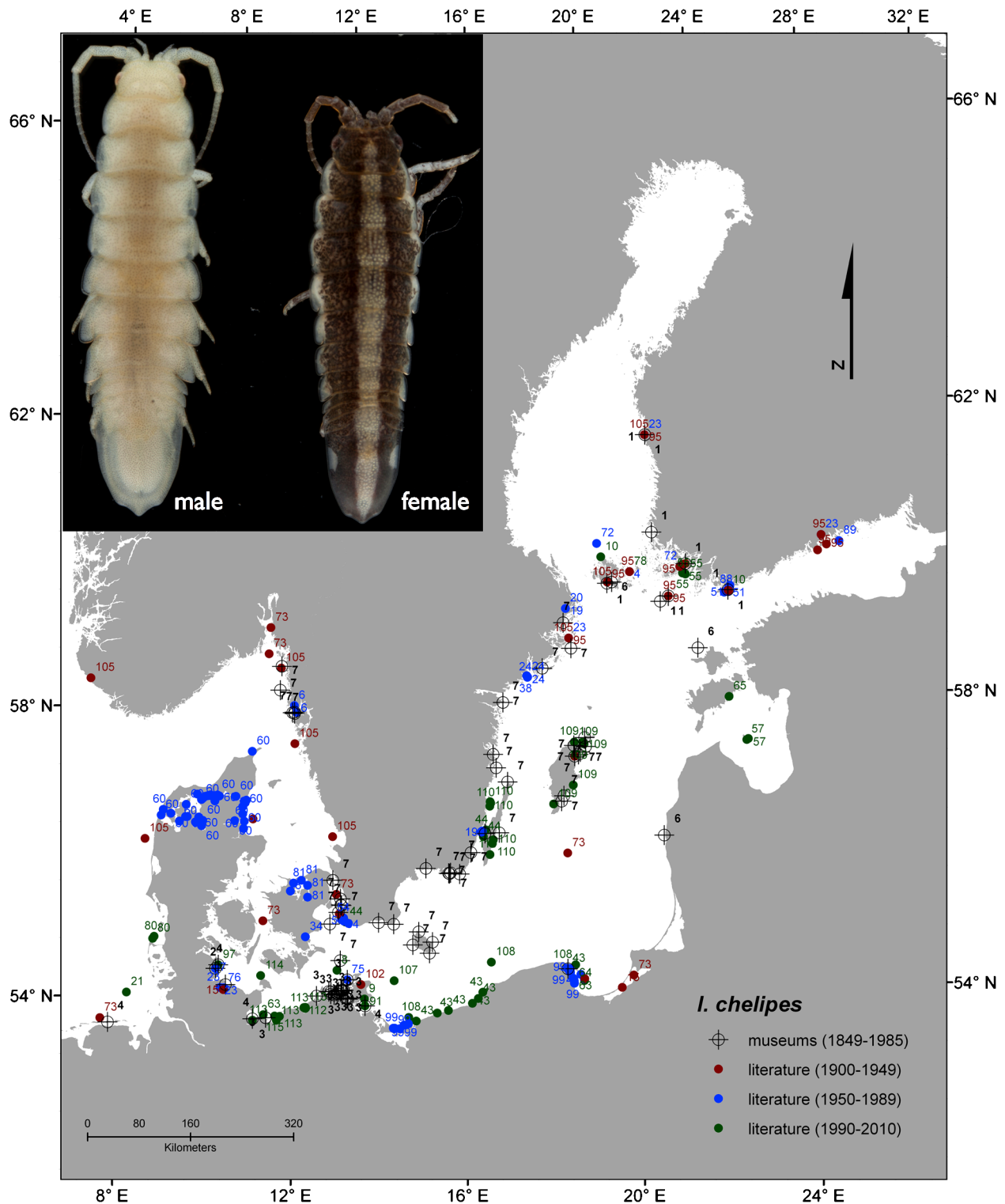


Fig. 3. Female and male of *Idotea chelipes* (dorsal view) and the distribution pattern in the Baltic Sea. The number next to the dots gives the reference (see on-line Appendices A and B). Maximum length for males 17.3 mm and females 13.0 mm (material: SMNH). Slender habitus. Telson shape of the posterior border with a short middle protrusion, as a whole more rounded. Coxal plates of the segments 2, 3, 4 and 5 do not reach the length of their segments (dorsal view).

less distinct differences in the shape of the posterior border of the telson [see legends in Figs. 2-4 and Sywula (1964a)].

Many studies report low abundances of *GR*, typically only few individuals (Hällfors et al., 1984; Zettler et al., 2000), which is in contrast to *BA* and *CH* (Segerstråle, 1944a;

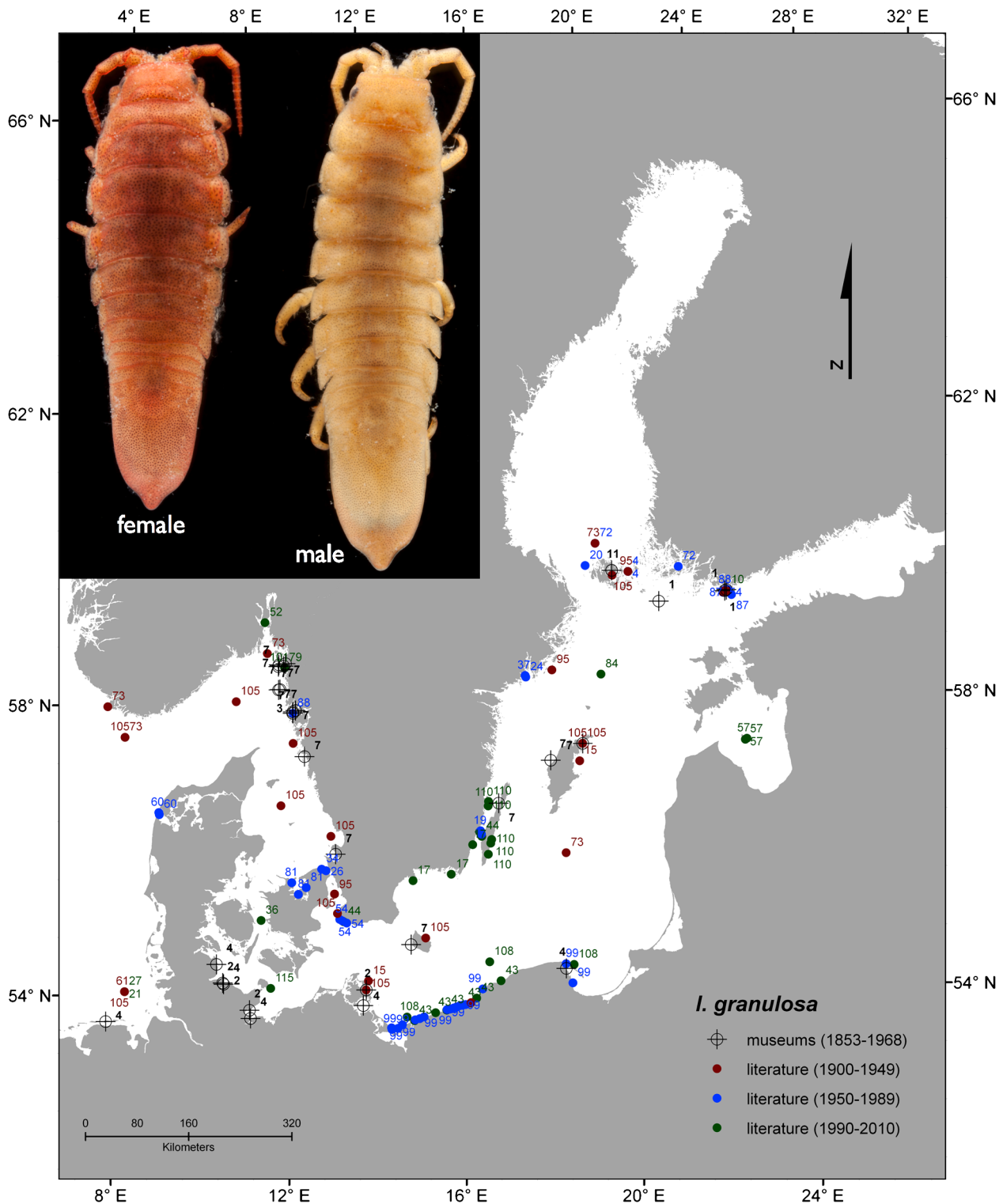


Fig. 4. Female and male of *Idotea granulosa* (dorsal view) and the distribution pattern in the Baltic Sea. The number next to the dots gives the reference (see on-line Appendices A and B). Maximum length for males 16.7 mm and for females 12.6 mm (material: SMNH). Telson shape of the posterior border with a middle protrusion, as a whole more slender. Coxal plates of the segments 2, 3, and 4 do not reach the length of their segments (dorsal view). The posterior edge of the coxal plates of thorax segment 5 outperforms the posterior edge of the segment.

Korheina, 1981; Wikström and Kautsky, 2007). However, on fully exposed shores in the outer archipelago GR can be the dominant species of *Idotea* (Forsman, 1956; Sywula,

1964b; Salemaa, 1979). Maximum densities occur during summer (Falsterbo Peninsula, Sweden: Korheina, 1981) or in the autumn (Askö Laboratory, Sweden: Haage, 1975).

Only Engkvist et al. (2004) have reported mass occurrence of *GR* (Table 1).

Analysis of Temporal Change of the Distribution of *Idotea* spp.

Over the investigated time period (1849-2010) both *CH* and *GR* showed a significant ($p < 0.05$) temporal shift towards the south in the Baltic Sea. The latitudinal shift over the time period was 1.15° and 1.5° for *CH* and *GR*, respectively. No latitudinal trend was detected for *BA*, or any longitudinal trends for any of the three species.

Habitat and Niche Analysis for *Idotea* spp. in the Baltic Sea

Salinity, temperature and wave forcing are known to strongly influence littoral communities. In the microtidal Baltic Sea, the species of *Idotea* are mostly found in the canopy of *Fucus vesiculosus* and in the *Zostera marina* belt (Table 1). Water transparency (Secchi depth) has deteriorated over the past 50 years, probably caused by eutrophication (Sandén and Håkansson, 1996), and has led to an upward shift of many macrophytes in the Baltic Sea. This has most likely also affected the habitat of *Idotea*. Today, *F. vesiculosus* can be found in the Baltic Sea from 0.2 down to 5.5 meters while it occurred down to 10 m 50 years ago (Schories and Wilhelmson, 2006; Torn et al., 2006). The usual depth of *Zostera* in the Baltic Sea is 2-4 m (extremes: 1-10 m), but at some localities (Germany, Poland) the maximum depth of *Z. marina* has been reduced from 6 m (in 1960) to less than 2 m (Boström et al., 2003). During wintertime *Idotea* spp. supposedly take shelter in deeper waters to escape the ice cover (Fig. 5). Kangas et al. (1982) mentioned juveniles over-wintering in the *Fucus* belt, but in general they are rarely found in the littoral zone during the winter months. In spring, Hørlyck (1973b) observed that *BA* migrated earlier

to the littoral than *GR*, but also disappeared before *GR* in autumn. During ice-free winters, downward migration may be less pronounced (Haage, 1975).

The habitat and niche description for Baltic *Idotea* spp. can be found in Table 2 as well as Figs. 5-6. *BA* is a typical inhabitant of the middle zone of the littoral, generally shallow waters with varying wave exposure. It can be dominant at exposed as well as at sheltered sites (Korheina, 1981; Kangas et al., 1982). Orav-Kotta and Kotta (2004) suggested that more exposed habitats allowed *BA* to escape from predation. According to Haage (1975), *BA* occurs in lower numbers at sheltered sites than *CH*. Engkvist et al. (2004) argued that wave exposure determines the choice of microhabitats, based on observations that *BA* in weak water movements grazed both on *F. vesiculosus* and *F. serratus*, whereas in strong water movements *BA* mainly occurred on the more exposure-tolerant *F. vesiculosus*. Outside the Baltic Sea, *Idotea* is often found rafting on floating seaweed (Gutow et al., 2007). For the Baltic Sea rafting idoteids have up to now only been reported on drifting algal mats after mass-blooms of annual algae in the Koinguiste Bay, Estonia (*BA* and *CH*, Lauringson and Kotta, 2006), the open sea north-west of the Åland islands (*Idotea* spp., Bonsdorff, 1992) or on floating *Zostera* blades in the Kiel Bay (M. Thiel, personal communication).

CH occurs more closely to the shore or in lagoons and mainly in the surface layer down to some meters (Zettler, 1999; Lapucki and Normant, 2008) (Fig. 5), but some extreme observations down to 30 m exist (Jazdzewski, 1970; Bobsien, 2006) (Table 2). *CH* does not occur in open coast regions (Sywula, 1964b). The species is characterised by a wide salinity range (Fig. 6). *CH* prefers exposed sites that are fully to moderately exposed (Forsman, 1956; Sywula, 1964b; Lapucki et al., 2005), but *CH* can also be found in

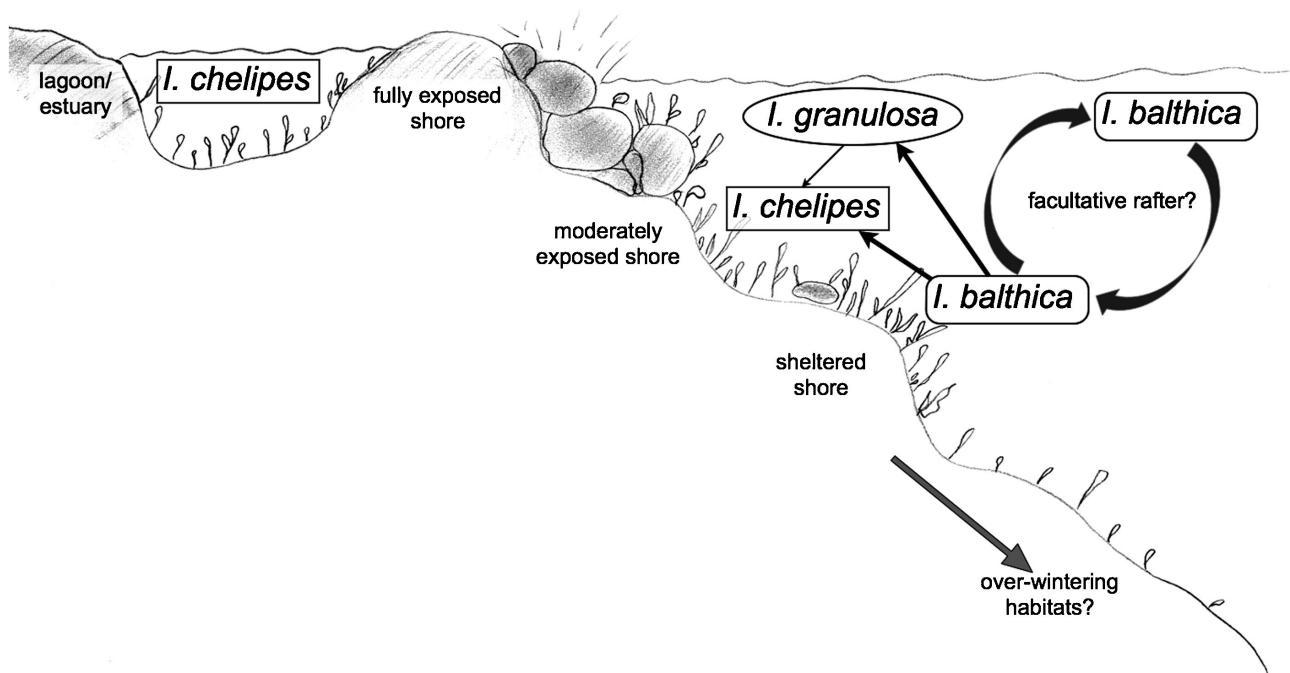


Fig. 5. Possible habitat segregation for *BA*, *CH* and *GR* in the Baltic *Fucus* belt.

Table 2. Niche description for *BA*, *CH* and *GR* in the Baltic Sea (preferences in bold-type). * Data from circulation model based on monthly averages for the years 1995-2004.

	<i>I. balthica</i>	<i>I. chelipes</i>	<i>I. granulosa</i>
Zone	Middle zone of littoral	Coastal zone, closely to the shore	Sublittoral, open coast region
	Shallow	Shallow	Only shallow
Temperature [°C]*	-0.3-21.8	-0.3-21.9	-0.3-21.7
Depth [m] ∅	Surface water <i>Fucus</i> belt	Surface water down to several meters (3-5)	-
Max.	20-21	7-30	5-11
Wave exposures	Exposed Moderate Shelter	Exposed Moderate Shelter	(Strongly) Exposed - -
Salinity [PSU]*	Euryhaline 2.7-24.3	Euryhaline 3.2-19.7	Euryhaline 4.6-24.7

shallow and sheltered sites (Jazdzewski, 1970; Kangas et al., 1982; Hällfors et al., 1984), like the inner Archipelago Sea (Salemaa, 1979, 1986). Where *CH* is found in sheltered sites it is often the dominant isopod and can constitute up to 77% of all isopods (Jansson and Matthiesen, 1971; Korheina, 1981; Zettler, 1999; Jazdzewski et al., 2005), although Salemaa (1979) reported a shared dominance at sheltered sites for *BA* and *CH* in the Finnish Archipelago Sea. *CH* is numerous on breakwaters (Sywula, 1964b) and often a dominant species in the eelgrass community (Bobsien, 2006).

There are only few studies describing the small-scale distribution for *GR*, which is relatively rare in the Baltic Sea. It prefers strong water movements and is restricted to fully exposed shores and beaches (Forsman, 1956; Sywula, 1964b; Salemaa, 1986; Engkvist et al., 2004) (Fig. 5). In

open Baltic Sea localities *GR* can occur at higher abundances than *CH* (Jazdzewski et al., 2005). *GR* can be found in the surface water down to some meters (Haage, 1975; Korheina, 1981; Salemaa, 1985; Engkvist et al., 2004). Whereas Forsman (1956) maintained that the species never goes deeper than 3 m, Zettler et al. (2000) found *GR* in a sample from 10.5 m (Table 2). *GR* mostly occurs in open coast regions (Fig. 5). The salinity range of *GR* in the Baltic varies between 4.6-24.7 PSU (Table 2).

Based on recorded distributions of *Idotea* and modeled temperature and salinity we found that *CH* on average occurs at higher summer temperatures than *BA* and *GR* (Student-Newman-Keuls, $p < 0.05$), while *BA*, on average, occurs at lower salinities than *CH* and *GR* (Student-Newman-Keuls, $p < 0.05$) (Fig. 6). This coincides with the geographical observations, and salinity ranges described

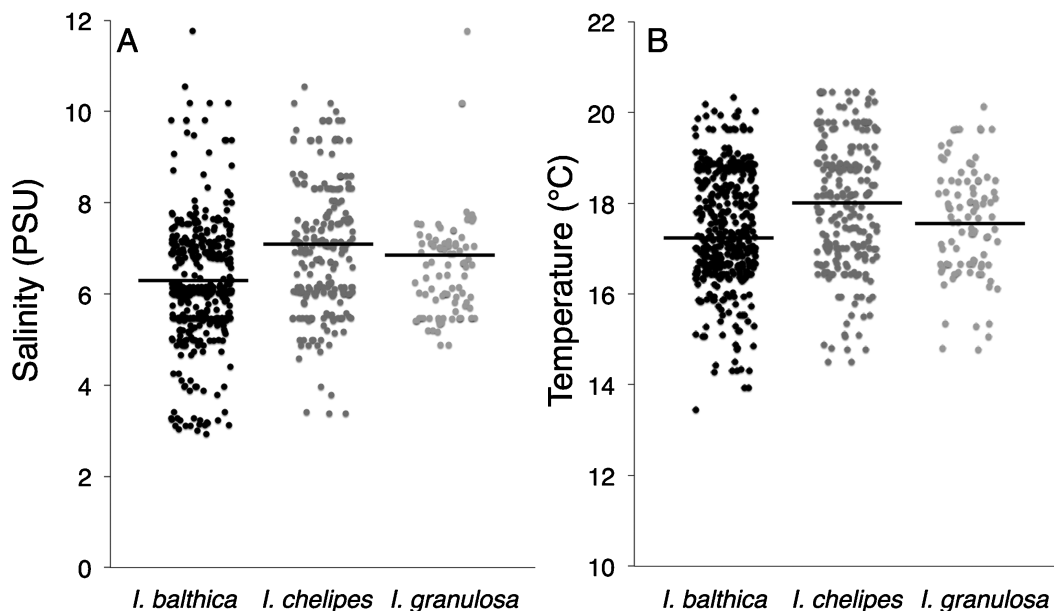


Fig. 6. Salinity and temperature at sites where the three species of *Idotea* have been recorded in the Baltic Sea. Data on salinity and temperature were extracted from the RCO circulation model as averages for the months June-August between 1995-2004. The horizontal bars indicate the means.

above. Whereas *CH* is a typical brackish-water species and can be found in a wide salinity range, it is surprising that *BA* has penetrated deep into the brackish-water of the Baltic Sea. Our analyses also suggest that *BA* and *CH* differ in their temperature preferences (Fig. 6). In the analysis of historical data (HELCOM) on temperature and salinity for the Baltic Sea we detected a significant increase between 1960 and 2010 in surface temperature of 0.06°C per year ($p < 0.0001$) and a declining salinity of 0.014 PSU° per year ($p < 0.0001$). These changes may have caused a shift in the distribution of *Idotea* in the Baltic Sea (see Discussion).

Community Composition and Habitat Segregation

On the rocky shores of the Baltic Sea, *Idotea* spp. are limited to a few habitat types determined by the low species diversity of macroalgae, phanerogams, and their epiphytes. The benthic community serves both as a food source and as shelter against predators. Species of *Idotea* use a range of vegetation types as substratum/shelter, but fewer as a nutritional source. All reported types of vegetation hosting *Idotea* are listed in Table 3. The typical hard-bottom habitat for *Idotea* spp. in the north-eastern Baltic Sea consists of the dominant macroalga *Fucus vesiculosus/radicans* together with some smaller species, e.g., *Pilayella littoralis*, *Cladophora glom-*

Table 3. Reported vegetation and animals used as structural or nutritional host for *BA*, *CH* and *GR* in the Baltic Sea. * Epiphyte; + in the Skagerrak; # *Idotea* in the Baltic Sea.

	<i>I. balthica</i>		<i>I. chelipes</i>		<i>I. granulosa</i>	
	Structural	Nutritional	Structural	Nutritional	Structural	Nutritional
Red algae						
<i>Ceramium</i> sp.	X		X		X	
<i>Ceramium nodulosum</i> *						X ⁺
<i>Ceramium tenuicorne</i>	X	X				
<i>Delesseria</i> sp.					X	
<i>Furcellaria lumbricalis</i>	X		X		X	
Brown algae						
<i>Ascophyllum nodosum</i>	X ⁺		X ⁺		X ⁺	X ⁺
<i>Dictyosiphon foeniculaceus</i> *	X	X	X		X	
<i>Fucus vesiculosus</i>	X	X	X	X	X	
<i>Fucus serratus</i>	X	X			X	X
<i>Fucus evanescens</i>	X	X				
<i>Fucus radicans</i>	X	X				
<i>Ectocarpus</i> sp.	X		X			
<i>Elachista fucicola</i> *	X	X	X			X ⁺
<i>Laminaria</i> sp.	X		X		X	
<i>Pilayella littoralis</i> *	X	X			X	X ⁺
Green algae						
<i>Chara connivens</i>		X				
<i>Chara tomentose</i>		X				
<i>Chorda filum</i>	X	X	X		X	
<i>Cladophora rupestris</i>	X	X	X	X	X	
<i>Cladophora glomerata</i> *	X	X			X	
<i>Spirogyra</i> sp.		X [#]		X [#]		X [#]
<i>Ulothrix implexa</i>				X		
<i>Ulva intestinalis</i>	X	X	X	X	X	
<i>Ulva lactuca</i>	X	X	X		X	
Phanerogams						
<i>Potamogeton pectinatus</i>	X	X				
<i>Ruppia maritima</i>	X	X				
<i>Ruppia spiralis</i>	X	X			X	
<i>Zannichellia palustris</i>	X		X		X	
<i>Zostera marina</i>	X	X	X		X	
Animals						
<i>Chironomus</i> larvae		X				
Dipteran larvae		X				
<i>Einhornia crustulenta</i>	X					
<i>Electra</i>	X					
<i>Balanus improvisus</i>	X					
<i>Mytilus edulis</i>	X		X			
Oligochaetes						
Planktonic animals						
		X				

erata, *Ulva intestinalis*, and *Furcellaria lumbricalis*. Typical soft-bottom habitats are dominated by the eelgrass *Zostera marina* that often co-occurs with other phanerogams like *Potamogeton pectinatus*, *Zannichellia palustris*, and *Ruppia spiralis* (Vesakoski et al., 2008). Other meso-grazers, e.g. amphipods of the genus *Gammarus* are often found together with *Idotea* spp. In mesocosm experiments Gohse-Reimann (2007) demonstrated interspecific competition between *Gammarus salinus* Spooner, 1947 and *BA* where the biomass of *BA* was negatively affected by the amphipod. Betz (1974) observed that the population of *CH* decreased dramatically in August after a mass occurrence of the isopod *Lekanesphaera hookeri* (Leach, 1814) in the *Fucus* belt in the Schlei, Germany, due to competition for food and space.

BA is most abundant on *Fucus vesiculosus* in the Baltic Sea (Salemaa, 1979; Korheina, 1981; Kangas et al., 1982; Jormalainen et al., 2008), which is the preferred microhabitat compared to *Cladomphora glomerata*, *Chorda filum*, *Ulva intestinalis*, and *Ceramium* (Orav-Kotta and Kotta, 2004) and to *Potamogeton pectinatus*, *Zostera marina*, *Z. palustris*, and *C. glomerata* (Vesakoski et al., 2008). In declining *Fucus* belts, *BA* preferentially occurs on *Furcellaria lumbricalis* compared to *Pilayella littoralis* (Kotta et al., 2000a). Vesakoski et al. (2008) found no structural host preferences between the sexes, whereas Merilaita and Jormalainen (1997, 2000) observed that males and females differed in their preferred microhabitat and the host choice (Jormalainen et al., 2001a). Males stayed more on apical than on basal parts of *F. vesiculosus*, while the females stayed equally often on both parts (Jormalainen et al., 2001a). Before females release their brood, however, they switch from *F. vesiculosus* to *C. glomerata* (Jansson and Matthiesen, 1971). Juveniles of *BA* and *CH* are most abundant on *C. glomerata* (up to 100 ind. g⁻¹ dw algae or 28 000 ind. m⁻²) (Jansson and Matthiesen, 1971; Jansson, 1974; Salemaa, 1979). After rapid growth the juveniles switch from filamentous algae (*C. glomerata*) in the upper littoral to the epiphyte *P. littoralis* and then, finally, to the deeper *Fucus* belt (Salemaa, 1978; Kangas et al., 1982), where they reach sexual maturity (Salemaa, 1979). This could be a reason, while the abundance is highest in the *C. glomerata* zone (see Distribution and Abundances) (Table 1). *BA* has been found, e.g., on bryozoans and on hydroids attached to hard substrates (Zettler et al., 2000), on different sediments types (sand, mud, clay, rocks, gravel, pebbles), under stones, and in *Mytilus edulis/trossulus* beds (Anger, 1975; Jormalainen and Tuomi, 1989; material from the SMNH). Jormalainen and Tuomi (1989) found a preference of female *BA* for the underside of stones and *Mytilus* shells, whereas the males often were found on light-green apical parts of *Fucus*. *BA* also occurs in seagrass beds at moderate to high densities (Boström and Bonsdorff, 2000; Boström et al., 2002).

CH occurs on a more narrow range of vegetation types compared to *BA* (Table 3). In Tvärminne, Finland *CH* showed a tendency to prefer the epiphyte *Dictyosiphon* as a microhabitat (Salemaa, 1979). *CH* can also be found on a diversity of bottoms, like clay, sand, detritus, salt marsh or stones and gravel. Korheina (1981) found that *CH* dominated over *BA* and *GR* on sandy clay and soft detrital material at the Falsterbo Peninsula, Sweden.

GR can be found on similar algal species and substrates as *CH* (Table 3). *GR* has been reported only from few sediment types, like sand with scattered rocks, large stones and rocks or pilings covered with vegetation (Sywula, 1964b; Korheina, 1981; material from the SMNH). Zettler et al. (2000) found *GR* on *Delesseria* sp. (Table 3). In an experiment of habitat choice *Idotea* spp. from the Falsterbo Peninsula, Sweden favoured *Ruppia spiralis* (Korheina, 1981). In the presence of *BA*, however, *GR* shifted its preference to *Chorda filum* and in the presence of *CH* to *F. vesiculosus*. Korheina (1981) suggested a lower competitive ability for *GR*, which was supported by the dominance of *BA* and *CH* at exposed localities at the Falsterbo Peninsula, Sweden.

Habitat segregation for *Idotea* in the Baltic Sea seems to depend on the local habitat structure. *BA* and *CH* coexist at different sheltered places in the Baltic Sea (Korheina, 1981; Sommer, 1997; Zettler, 1999; own observations). Moreover, *BA* was observed together with *GR* at fully exposed sites in the outer archipelago or on rocky shores (Salemaa, 1978, 1979; own observations). Coexistence of all three species at exposed sites is possible, but rarely described (Korheina, 1981). Competitive interactions are not well described, but *BA* showed decreased abundance in its preferred microhabitat in the presence of *CH* or *GR* (Salemaa, 1987) (Fig. 5).

Mobility

Baltic specimens of *Idotea* are small crustaceans and show relatively weak mobility (Jansson and Källander, 1968; Salemaa, 1978; Lapucki et al., 2005; own observations). Species of *Idotea* are poor long-distance swimmers (probably few kilometers) and swimming is sporadic including short excursions from alga to alga. According to Jansson and Källander (1968), *BA* and *GR* avoid swimming up into the free water-column. Across substrata, e.g., seaweed surfaces, *Idotea* move by means of crawling. Nevertheless, *Idotea* are more mobile than some other meso-grazers, e.g., some amphipods and gastropods. *BA* swims actively, especially the males, in search for food or for mates (Merilaita and Jormalainen, 1997; Boström and Bonsdorff, 2000; Jaschinski, 2007). *CH* is a less active swimmer than *BA* (Jansson and Matthiesen, 1971). For *GR*, Pavia et al. (1999) suggested a size-dependent mobility: as the body size increases, mobility decreases. However, generally *Idotea* spend most time feeding attached to a host plant. Activity patterns strongly depend on season and light intensity. For *Idotea* the activity is high through the summer and during spring and in the autumn the activity is highest at night (Jansson and Källander, 1968; Hørlyck, 1973a). Jansson and Källander (1968) reported that activity increased for *BA* below 400-800 lux. During the winter season Hørlyck (1973a) could not observe any swimming activity (for *BA*: November- March; for *GR*: September-March).

Food Preferences

The species of *Idotea* are able to use several food types as nutritional source (Table 3). Food preference appears to differ between species, microhabitat and locality. Naylor (1955b) described *Idotea* as mostly omnivorous. Under laboratory conditions both cannibalism and feeding on moulted

exuviae have been observed (Sywula, 1964b; Jansson and Matthiesen, 1971; Sommer, 1997; own observations). Thus *Idotea*, especially *BA*, are considered an omnivore and not only a herbivore in the Baltic Sea (Table 3). In the Baltic Sea, Salemaa (1978) suggested that adults are potentially omnivorous scavengers and Gohse-Reimann (2007) fed *BA* with chironomid larvae. *BA* seems to thrive on plant food as well as on food of purely animal origin (dead conspecifics, dead dipteran larvae, freshwater oligochaetes) (Sywula, 1964b). Fluorescence microscopy of fecal pellets indicated a broad diet for *BA* in the Baltic Sea (Svensson et al., 2004) with a diet including microalgae (including diatom chains), bacteria and planktonic animals (Sommer, 1997; Svensson et al., 2004; Jaschinski and Sommer, 2008). In gut analyses of *BA*, detritus and bacteria also have been found (Möbius, 1873; Jephson et al., 2008). However, *Idotea* are strongly associated with vegetation (Table 3) and among the ecologically most important grazers in the Baltic *Fucus* belt (Engkvist et al., 2000, 2004; Jormalainen et al., 2008; Råberg and Kautsky, 2008) and eelgrass beds (*Zostera marina*) (Boström and Bonsdorff, 1997; Jaschinski and Sommer, 2008). Their grazing activity can have substantial impact on the biomass and community structure, especially on epiphytes of macroalgae or seagrass. Published grazing rates are listed in Table 4 and Salemaa (1987) suggested that feeding rates are proportional to the size of the species. Both males and females prefer *Fucus* not only as food, but also as shelter (Kangas et al., 1982; Salemaa, 1987; Engkvist et al., 2000; Nilsson et al., 2004).

BA is very common on *F. vesiculosus*, and is one of its most important herbivores (Korpinen et al., 2010), but other species like *F. serratus*, *F. evanescens*, and *F. radicans* are also consumed (Schaffelke et al., 1995; Engkvist et al., 2004; Forslund, 2009). Forslund (2009) suggested that selective grazing limited the southern range of *F. radicans*. In general, grazing occurs on all parts of the *Fucus* thallus, younger tissue (Engkvist et al., 2000), as well as older parts (Salemaa, 1987). On the Swedish east coast most grazing activity on *Fucus* spp. was observed in autumn (October–November) (Engkvist et al., 2004) and overlaps with observations from the Finnish Archipelago Sea. While Salemaa (1987) reported more effective grazing by females than by males, Merilaita and Jormalainen (2000) found that males consumed significantly more food than did females. Females preferred the lower, old parts of *F. vesiculosus* and males the younger, apical parts (Jormalainen et al., 1992; Merilaita and Jormalainen, 1997). This difference in feeding behavior coincides with the habitat segregation of the genders, where males occur more on the upper parts of the algae while females seem to prefer the more sheltered, lower parts. Moreover, feeding on decaying parts and dead *Fucus* algae was observed (Sywula, 1964b; Haahtela, 1984). Juveniles of *BA* often feed on the filamentous green alga *Cladophora glomerata*, which is described as a nursing ground (Salemaa, 1978; Haahtela, 1984), or on the brown alga *Pilayella littoralis*. Adults seem not to be well adapted to *Cladophora* where they have been observed to get entangled in the algal filaments and die (Orav-Kotta and Kotta, 2004).

Interestingly, adults from different localities appear to differ in their feeding preference (Goecker and Kåll, 2003), al-

though in most cases *Fucus vesiculosus* was favoured over other species (Korheina, 1981; Haahtela, 1984; Jormalainen et al., 2001b). In a study of *BA* from the Falsterbo Peninsula, Sweden (Korheina, 1981) the green alga *Ulva lactuca* was the least consumed, while *U. lactuca* was the most preferred (together with larvae of *Chironomus* spp.) in a *Zostera marina*-community at Falkenstein, Germany (Gohse-Reimann, 2007). *BA* feeding directly on the eelgrass *Zostera marina* has only been observed during an experimental study in Finland and epiphytic algae appear to form the major food source in eelgrass communities (Boström and Mattila, 1999). Kotta et al. (2004) have also observed seasonal grazing on Charophytes with a peak in October. Nicotri (1980) suggested that *BA* selects host plants more based on its robustness as a microhabitat than its attractiveness as a food source. However, in this trade-off the food choice (= epiphytes) seems to be more important for the grazer than shelter (Boström and Mattila, 1999).

Epiphytes, mainly filamentous algae, are an important food source for *Idotea*. Eelgrass growth appears to be positively affected by grazing from *BA* through removal of epiphytes, which may increase seagrass productivity up to 40% in mesocosm experiments (Jaschinski and Sommer, 2008). Thus, in addition to abiotic factors (temperature, light, nutrients), grazing from *BA* can control the epiphyte growth on seagrass. *BA* significantly preferred filamentous algae, like *Cladophora* spp., *Pilayella littoralis* and *Furcellaria lumbricalis*, after massive increase of filamentous algae or a decline of *Fucus* or when *BA* was exposed to longer starvation periods (Kotta et al., 2000a; Goecker and Kåll, 2003). In Estonia, *BA* showed low long-term grazing rates of 2.2% of the *Furcellaria lumbricalis* and of 4.7% of the *Pilayella littoralis* production (Kotta et al., 2000a; Orav-Kotta and Kotta, 2004). In contrast, based on the dry weight changes of *P. littoralis* in a 48-hour experiment, the short-term grazing rate from *BA* was 400% of the algal production (Orav-Kotta and Kotta, 2004). Despite such high short-term grazing rates, *BA* seems generally unable to control the formation of the enormous mats of filamentous algae frequently observed in the Baltic Sea.

Chemical composition of the diet often plays an important role in food preferences of herbivores (Paul et al., 2001). In general, grazers prefer parts with high nitrogen to carbon content as well as sugar-rich parts of the algae and avoid defensive compounds like phlorotannins (often in high concentrations in basal parts of *F. vesiculosus* [Hemmi et al., 2005]). Some studies have shown that *BA* prefers algae with low levels of phlorotannins or non-grazed parts (Wikström et al., 2006; Yun et al., 2010), while other studies have found no response or even attraction to phlorotannin-rich parts (Jormalainen et al., 2001b, 2005). Further studies are necessary to investigate the relationship between *Idotea* spp. grazing and phlorotannin production in Baltic Sea *Fucus* spp.

Little information is available on the food preference of *CH* (Table 3) and on consumption rates (Table 4). Similar to *BA*, adults of *CH* are often found on *F. vesiculosus*. Salemaa (1987) observed the highest feeding preferences for old stipes of *Fucus vesiculosus* for males of *CH*. *CH* are also reported to consume macroalgae of the genera *Ulva*

Table 4. Daily consumption rates for BA, CH and GR on algae, epiphytes and phanerogams at different localities in the Baltic Sea (E = Estonia, F = Finland, G = Germany, S = Sweden). + = after 24 h of starvation; * = after 48 h of starvation.

Species	Region	<i>I. balthica</i>	<i>I. chelipes</i>	<i>I. granulosa</i>	Reference
<i>Chorda filum</i> [mg ww ind ⁻¹ day ⁻¹]	Falsterbo Peninsula, S	7.1 ⁺			Korheina, 1981
<i>Cladophora rupestris</i> [mg ww ind ⁻¹ day ⁻¹]	Falsterbo Peninsula, S	6.4 ⁺			Korheina, 1981
<i>Cladophora</i> spp. [mg ww ind ⁻¹ day ⁻¹]	Archipelago Sea, F	11.3*			Goecker and Käll, 2003
<i>Fucus evanescens</i> [mg ww ind ⁻¹ day ⁻¹]	Bay of Kiel, G	<1.5			Schaffelke et al., 1995
<i>Fucus vesiculosus</i> [mg ww ind ⁻¹ day ⁻¹]	Archipelago Sea, F	Female: 2.1 Male: 1.2	Female: 0.7 Male: 0.5	Female: 1.6 Male: 1.0	Salemaa, 1987
<i>Ruppia spiralis</i> [mg ww ind ⁻¹ day ⁻¹]	Archipelago Sea, F	Female: 4.33 ± 2.09 Male: 4.8*			Tuomi et al., 1988b
<i>Ulva intestinalis</i> [mg ww ind ⁻¹ day ⁻¹]	Bay of Kiel, G	up to 3.5			Goecker and Käll, 2003
<i>Ulva lactuca</i> [mg ww ind ⁻¹ day ⁻¹]	Falsterbo Peninsula, S	12.5 ⁺			Schaffelke et al., 1995
<i>Fucus vesiculosus</i> [mg ww h ⁻¹]	Falsterbo Peninsula, S	9.0 ⁺			Korheina, 1981
	Falsterbo Peninsula, S	8.3 ⁺			Korheina, 1981
	Archipelago Sea, F	22.6*			Goecker and Käll, 2003
	Falsterbo Peninsula, S	1.6 ⁺			Korheina, 1981
	Archipelago Sea, F	Female day: 0.18 Female night: 0.7 Male day: 0.25 Male night: 1.2			Merilaita and Jormalainen, 2000
Epiphytes [mg dw ind ⁻¹ day ⁻¹]	Åland Islands, F	1.25			Boström and Mattila, 2005
<i>Fucus vesiculosus</i> [mg dw ind ⁻¹ day ⁻¹]	Kukumäe Bay, E	Max. 400.0			Kotta et al., 2006
<i>Pilayella littoralis</i> [mg dw ind ⁻¹ day ⁻¹]	Kukumäe Bay, E	Max. 300.0			Kotta et al., 2006
<i>Potamogeton pectinatus</i> [mg dw ind ⁻¹ day ⁻¹]	Åland Islands, F	1.1			Boström and Mattila, 2005
<i>Ruppia maritima</i> [mg dw ind ⁻¹ day ⁻¹]	Åland Islands, F	0.25			Boström and Mattila, 2005
<i>Zostera marina</i> [mg dw ind ⁻¹ day ⁻¹]	Åland Islands, F	0.21			Boström and Mattila, 2005
<i>Furcellaria lumbicalis</i> [mg dw algae × g dw <i>Idotea</i> ⁻¹ day ⁻¹]	Koiguiste Bay, E	3-20			Kotta et al., 2000
<i>Pilayella littoralis</i> [mg dw algae × g dw <i>Idotea</i> ⁻¹ day ⁻¹]	Koiguiste Bay, E	[= 0.153 mg dw ind ⁻¹ day ⁻¹] 27-49			Kotta et al., 2000
	Koiguiste Bay, E	[= 0.506 mg dw ind ⁻¹ day ⁻¹] 332 ± 77			Orav-Kotta and Kotta, 2004

and *Cladophora* in the Polish Baltic Sea (Lapucki et al., 2005; Lapucki and Normant, 2008). Betz (1974) observed that juveniles of *CH* were not associated with *F. vesiculosus*, but with diatom films and different chlorophytes. Sommer (1997) investigated grazing pressure of adult *CH* on epiphytic diatoms and cyanobacteria, and it was suggested that *CH* has the potential to drive succession in periphyton communities.

Reported diets of *GR* include all sorts of algal material in the Baltic Sea (Salemaa, 1987), but detailed studies are rare (Table 3). In the Skagerrak *GR* is the most abundant crustacean on the knotted wrack *Ascophyllum nodosum* (Pavia et al., 1999). Large *GR* (>10 mm) fed mostly on meristematic apices, while the small conspecifics (3-8 mm) preferred the macroepiphytes on *A. nodosum*. The opposite pattern was reported from Karez et al. (2000), where *GR* preferred older parts instead of meristematic tissues of the brown alga *Fucus vesiculosus*. Both studies noticed a significant preference for the epiphytes on the macroalgae. Neither nutritional values nor effects of chemical defence were investigated, but Toth (2007) observed that different seaweed species from the Skagerrak coast developed induced resistance in response to direct grazing of *GR*.

Predators on *Idotea* spp.

Idotea are important food sources for numerous predators. Some Plathyhelminthes, e.g., *Provortex balticus*, *Promestostoma mamoratum*, *Convoluta* spp., feed on *Idotea*, which can make up to 17% of their total diet (Jansson, 1974). The decapod shrimp (*Palaemon elegans* Rathke, 1837 and *P. adspersus* Rathke, 1837) are known to consume *BA* (Jephson et al., 2008). The goosander duck *Mergus merganser* is reported to feed exclusively on *Gammarus* and *Idotea* during the first half of August in the Finnish Archipelago Sea (Segestråle, 1944b). However, the main predators on *Idotea* are fish (Sywula, 1964b; Salemaa, 1978; Korheina, 1981; Bobsien, 2006). Analyses of stomach contents showed that *BA* and *CH* were eaten by 23 different Baltic marine and freshwater fish species (Salemaa, 1978; Bobsien, 2006) (Table 5). Significant predators feeding on *Idotea* are perch (*Perca fluviatilis*), cod (*Gadus morhua*) and eelpout (*Zoarces viviparus*) (Jansson and Källander, 1968; Haahnela, 1984; Jormalainen and Tuomi, 1989; Engkvist et al., 2000). Around Vilm island/Greifswald Lagoon the straightnose pipefish *Nerophis ophidion* (20% of gut content) and the black goby *Gobius niger* (>60%) were the most important predators on *CH*, whereas at Falkenstein/Kiel Bay *BA* was mainly consumed by sand gobies (*Pomatoschistus minutus*) (>10%), fifteen-spined stickleback (*Spinachia spinachia*) (>60%) and *Zoarces viviparus* (>40%). For the latter two species, Bobsien (2006) described that young isopods were preferred (size: 1.4-3.8 mm), but in some cases individuals up to 15.3 mm were consumed. Korheina (1981) observed that *Z. viviparus* preferred the smaller *CH* over the larger *BA*. When body length reached >16 mm, *BA* seemed to escape predation from *S. spinachia* (Bobsien, 2006).

The *Fucus* belt forms a mosaic of microhabitats of different colours and shades. Evolution of polymorphic cryptic colouration appears to be an adaptation of *Idotea* to reduce predation. Predation experiments with *Z. viviparus* and *Cyclopterus lumpus* by Salemaa (1978) showed that

apostatic selection is involved in maintaining the balance of colour polymorphism of *BA*. Five major phenotypes of *BA* exist (*uniformis*, *albafusca*, *maculata*, *bilineata* and *lineata*), where the *uniformis* type is the most abundant in the Finnish Archipelago Sea followed by *albafusca* (Salemaa, 1978; Merilaita, 2001). The *lineata* type does not exist in the northern Baltic. Phenotypic diversity is lower in fully exposed habitats and may be a consequence of the less diverse *Fucus* communities at fully exposed sites (Salemaa, 1978) or lower predation pressure. Males are often lighter than females and are found more often on brightly coloured and exposed apical algal parts (Jormalainen and Tuomi, 1989). Both sexes also have the ability to adjust their colour intensity according to the background colour. *BA* is more active by night than by day, especially for males in the breeding season (Merilaita and Jormalainen, 2000). The preference for a dark background is stronger at day than at night. The visual protection from predators probably plays a central role in the selection of microhabitats and seems more important for females than for males (Merilaita and Jormalainen, 2000). However, under laboratory conditions Boström and Mattila (1999) observed that habitat choice of *BA* was not affected by the presence of perch (*Perca fluviatilis*). Independently of the presence of the predator, a habitat with low density of *Zostera marina* leaves (but with epiphytes) was still preferred over one with a higher leaf density (= more shelter).

DISCUSSION

Changes in Distribution

The maps for the three species of *Idotea* in the Baltic Sea indicate that the large-scale distribution has remained fairly constant during the last 150 years (Figs. 2-4), but our analyses found a significant shift towards the south for *CH* and *GR*. Although such trends in recorded distributions should be interpreted with caution, there are several examples of distributional changes on the regional scale in the Baltic Sea during the last decades. Whereas Bobsien (2006) mentioned a relatively constant abundance of *BA* in the eelgrass beds of the Kiel Bay over the last 30 years, the survey by Zettler et al. (2000) found only sporadic individuals of *GR* along the German Baltic coastline. Along the Polish coast, all three species of *Idotea* were common during the 20th century, but more recent studies could not find *GR* in the Bay of Puck nor in the Bay of Gdansk, suggesting a long-term change in distribution (Sywula, 1964b; Jazdzewski et al., 2005). Lapucki and Normant (2008) pointed out that *CH* is now most abundant in the Gulf of Gdansk whereas several other benthic species have disappeared through many ecological changes in this region. In contrast, Kotta et al. (2000b) observed that *CH* is now very rare in extensive areas of the Gulf of Riga compared to the 1970s. The authors proposed that the decline of *CH* probably reflects the decreasing cover of benthic vegetation in the area since also other phytophilous species have declined, e.g., *Jaera albifrons* Leach, 1814, *Asellus aquaticus* (Linnaeus, 1758), and *Lymnaea peregra*. Similar patterns were observed by Orav-Kotta et al. (2004) for *BA* in the Väinameri Archipelago Sea, Estonia where *BA* has declined from high abundance in 1960s. There is a rather dramatic decline of *Idotea* spp. along the Swedish West coast

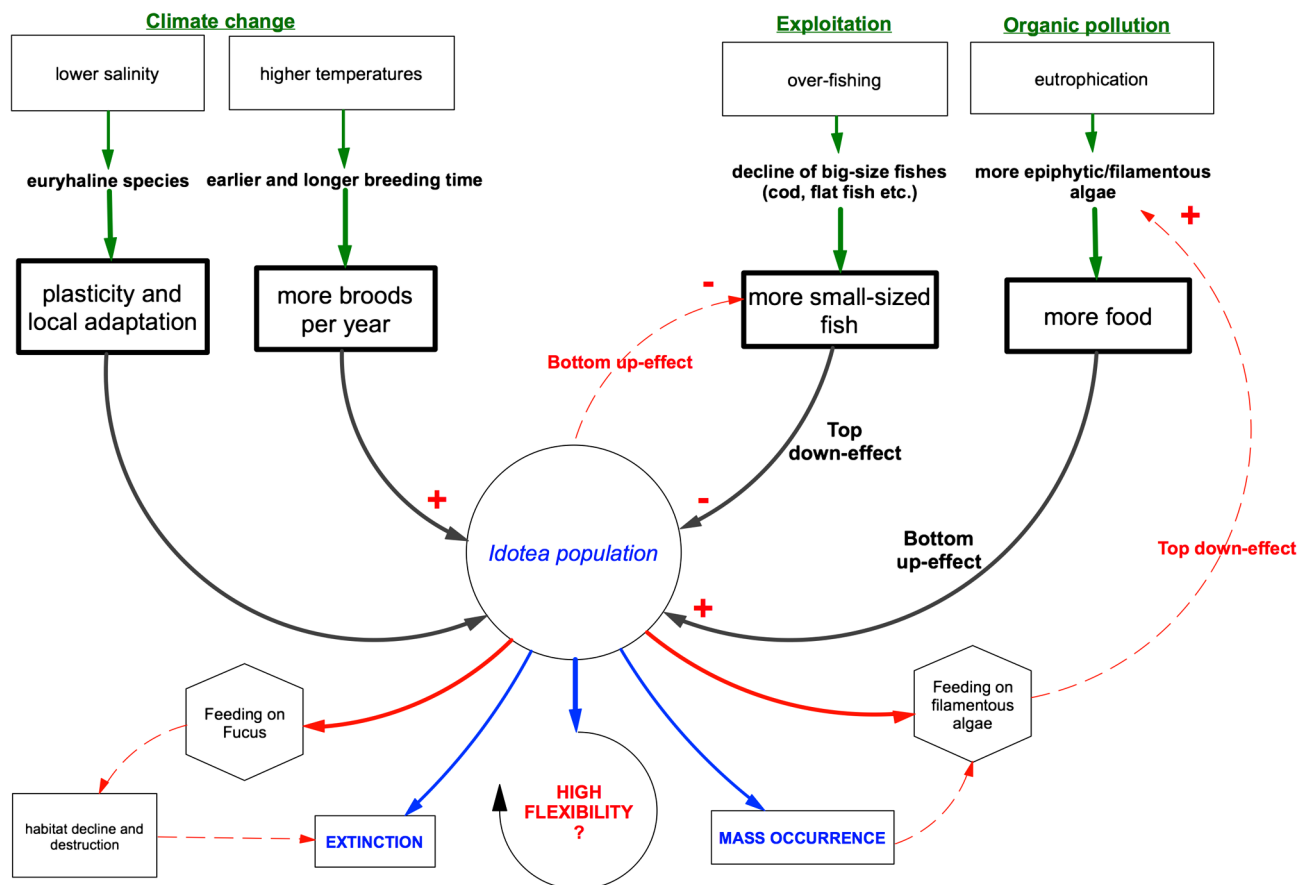


Fig. 7. A conceptual model of community dynamics with focus on *Idotea* spp. The green upper text and the boxes below show on-going environmental and human generated changes. The boxes in bold show possible changes in responses and ecological interactions relevant for *Idotea*. Black arrows indicate direct effects on population dynamics of *Idotea*. Red arrows indicate indirect effects with feedbacks to population dynamics of *Idotea*. Blue arrows suggest how populations of *Idotea* spp. may respond numerically. Hatched arrows indicate weaker effects.

(Skagerrak and Kattegat). Collections at the SMNH (1850-1933) and data from Wahrberg (1930) indicate that *Idotea* used to be numerous at several locations, e.g., in the Gullmar and Koster Fjords. Baden and Pihl (1984) described *Idotea* occurring at high abundances and during the whole season in the Gullmar Fjord, but today especially *BA* and *CH* occur in low densities (personal observations) or may even be difficult to find (Jephson et al., 2008; Moksnes et al., 2008). We might speculate that the decline of *Idotea* in the Kattegat and Skagerrak is caused either by high nutrient loads and the loss of *Zostera* beds (about 58% since the 1980s [Baden et al., 2003]), and/or changes in the food web by overfishing (Baden et al., 2010; Fig. 7). The Skagerrak and Kattegat form an important transition between the Atlantic and the Baltic Sea. If this corridor is disappearing as a habitat for *Idotea*, the Baltic populations will become increasingly isolated from the Atlantic populations. Dispersal from Atlantic populations into the Baltic Sea is further constrained by the water circulation where transport of surface water is mainly out from the Baltic Sea. In addition to possible trends the temporal change in distribution of *Idotea* also seems to be driven by local extinctions and mass occurrences, which are described for some parts of the Baltic Sea (Table 1, Fig. 7). Mass occurrences may appear in cycles although data are still scarce (a first occurrence in the late 1970's and early

1980's: Kangas et al., 1982; Hällfors et al., 1984, and a second around 2000: Engkvist et al., 2004), but were observed to stretch along a 100 km coastline.

The Habitat of *Idotea* spp.

Salinity conditions mainly determine the potential habitat of the species of *Idotea* in the Baltic Sea (Figs. 5-6). *GR* is obviously not able to tolerate low salinity as well as the other two congeners, which is reflected in its distribution pattern coinciding with higher salinities. *CH* may escape competition with the other two species by tolerating periods of very low salinity (Figs. 5-6). *BA*, in contrast, prefers more saline waters (Zettler, 2000, 2001), but in our analyses *BA* is the most abundant idoteid in the northern Gulf of Bothnia and penetrates deeper into the Gulf of Finland than do *CH* and *GR* (Figs. 2-4), where the salinity is lower. In experimental studies *CH* is known to have a better osmoregulatory capability compared to *BA* and *GR* (Hörlyck, 1973b). So why does *CH* not enter deeper into the Gulf of Bothnia and the Gulf of Finland? It may be speculated that the average temperature also plays an important role for the habitat of *CH*. *BA* is known to be better adapted to rapid temperature changes than sudden salinity changes (Bulnheim, 1974), whereas *CH* may prefer warmer temperatures (Fig. 6), which coincides with the

preferred habitat of *CH* in lagoons and estuaries (Zettler, 2000, 2001) and the limit of distribution in the Baltic Sea. Experimental studies of osmoregulatory ability also suggest that salinity and temperature may interact to limit *CH* to higher salinities in high temperatures (Vlasblom et al., 1977). Distribution limits for *Idotea* in Europe outside the Baltic Sea are not well known. Individuals of *Idotea* spp. from Vaideguba/Finnmark, North Norway and the Kola Peninsula, Russia collected during the Sandeberg expedition (1877) are reported in the *Idotea* collection of the SMNH. In addition, Ingolfsson (1992) reported *GR* in Finnmark, Northern Norway. However, the winter-spring water temperatures are generally lower in the Baltic Sea than in many of these subarctic regions. According to Sywula (1964b), *BA* occupies the ecologically most favourable sites (mostly deeper and protected areas) in the Baltic, and may displace *GR* to regions with more water movements and ecologically less favourable areas (open sea, surf zone, man-made structures).

Sywula (1964b) proposed the theory that *CH* entered into the present Baltic Sea between the geological transition from the Ancylus Lake to the Littorina Sea about 7500 yrs BP. He argued that *CH* was the only species of the North Sea *Idotea*, which was able to penetrate early into the newly formed Littorina Sea due to its ability to colonize estuaries and lagoons. Moreover, *CH* is resistant to wave exposure and could supposedly spread widely in the new habitat. With increasing salinity several marine species invaded the Littorina Sea, like *BA* and *GR*. They moved northwards and eastwards along the vegetation belt and pushed *CH* into isolated lagoons again.

Little is known about population structure or the presence of local adaptations of *Idotea* in the Baltic Sea. Individuals of *Idotea* are brooders, which could facilitate evolution of local adaptations. Dispersal of juveniles in the coastal circulation is probably the main mechanism, but all species of *Idotea* are known to disperse through rafting on drifting seaweed (Gutow and Franke, 2003), although this is not yet described for the Baltic Sea. Future studies of population genetics may resolve the question of population structure throughout the Baltic Sea and beyond.

Trophic Interactions and Grazing Effects

Idotea may play an important ecological role in the Baltic Sea through grazing in biotopes formed by the foundation species *F. vesiculosus* and *Zostera marina* (Kangas et al., 1982; Boström and Mattila, 2005). Grazing can affect these macrophytes indirectly by reducing the epiphytes (possible positive effects) or directly by feeding on the macrophyte tissue (negative effect). The effect of *Idotea* thus depends on their food choice and the grazing intensity, which is mainly a function of their abundance (Jaschinski, 2007). However, the numerous studies on grazing by *Idotea* on macrophytes and their epiphytes cannot be easily generalised. *Fucus vesiculosus* seems to be most preferred by *Idotea* spp. both as a nutritional source and as a habitat, but several studies show that *Idotea* are also able to switch to several other food sources and habitats in the Baltic Sea (Table 3). High flexibility in terms of food and habitat characterises *Idotea* in the Baltic Sea (Fig. 7). *Fucus vesiculosus* is the only large, perennial alga in the Baltic Sea forming a complex

habitat structure, which does not disappear during the winter (Jormalainen et al., 2001b). The occasional preference of *BA* for phlorotannin-rich algal species, e.g., *F. vesiculosus*, suggests an adaptation/co-evolution to brown algae, maybe a local adaptation for Baltic Sea populations (Jormalainen et al., 2001b; Hemmi and Jormalainen, 2004). The contrasting results for grazing rates as a function of phlorotannins are interesting and call for further studies.

High grazing rates of *Idotea* on epiphytes could reduce ecosystem-wide negative effects from eutrophication by removing epiphytes from foundation species like *F. vesiculosus* and *Z. marina*. Råberg and Kautsky (2007b) showed that a consumer community of *BA* and the gastropod *Theodoxus fluviatilis* significantly reduced the epiphytic biomass. However, experimental studies indicate that *Idotea* spp. cannot always control outbreaks of filamentous epiphytes (Lotze and Worm, 2000; Kotta et al., 2006). Nevertheless, in experimental studies *BA* was able to reduce the epiphytes on *Z. marina* with nearly 50%, which enhanced eelgrass production with up to 63% (Jaschinski, 2007). Boström and Mattila (2005) reported a six-fold higher feeding rate on epiphytes than on *Zostera marina* (Table 4) indicating a net positive effect on the eelgrass. In field experiments in the western Baltic Sea, Worm et al. (2000) found that meso-grazers, including *BA* and *CH*, could partially control epiphytes and buffer against moderate eutrophication. However, under highly eutrophicated conditions *Idotea* do not seem to be able to control the formation of epiphyte blooms in the Baltic Sea. Lotze and Worm (2000) suggested that there might be a critical bloom intensity to escape herbivore control. Other studies from the American Pacific and Atlantic coast found that *Idotea resicata* and *BA* enhanced eelgrass growth and reduced the epiphytic biomass more than other herbivores (Williams and Ruckelshaus, 1993; Duffy et al., 2001). *Idotea* may also graze directly on *F. vesiculosus* and Engkvist et al. (2000) showed that the depth distribution of *F. vesiculosus* was correlated with the density of *BA*. This density-dependent grazing effect can have vast impact on the *Fucus* belt and major declines of the *Fucus* belts along the Swedish southeast coast have been correlated with the mass occurrences of *BA* (Engkvist et al., 2004; Nilsson et al., 2004; Fig. 7). The community effect of *Idotea* grazing apparently varies in time and space in the Baltic Sea and this definitely deserves further attention.

A Changing Food Web

The Baltic Sea is one of the most human impacted coastal areas in the world with eutrophication, over-fishing, and contaminant pollution as the main environmental stressors (Diaz and Rosenberg, 2008; Ducrottoy and Elliott, 2008; Halpern et al., 2008). Intense fishing in the Baltic Sea has dramatically changed the fish community with possible cascading effects through the food web (Baden et al., 2010). A clear decline in cod, herring and flounder is noticed and all stocks have undergone a strong change in abundances (Hammer et al., 2008). In the Kiel Bay, Bobsien (2006) found a disappearance of large species like cod and flatfish in eelgrass meadows that coincided with an increase of the proportion (biomass) of small-sized fish from 1.6% to 36% between 1975-2006. It was suggested that this increase of small-sized fish, e.g., the fifteen-spined

stickleback (*Spinachia spinachia*) and the viviparous blenny (*Zoarces viviparus*), might control *Idotea* spp. populations in eelgrass beds in the southern Baltic Sea (Fig. 7).

Eriksson et al. (2009) found a strong negative correlation between the abundance of piscivorous fishes, e.g., perch (*Perca fluviatilis*) and pike (*Esox lucius*), and the large-scale distribution of bloom-forming macroalgae in the Baltic Sea, where smaller fish preying on invertebrates had significant effects on the meso-grazer community and on the production of ephemeral algae. Thus, excluding larger predatory fish may have top-down cascading effects via an increase of small fish that may control invertebrate grazing on epiphytic algae and macrophytes (Fig. 7). The presence of cascading top-down effects from fish predation on meso-grazers, including *Idotea* spp., was supported in a field experiment by Korpinen et al. (2007) in the Archipelago Sea. At present, it is not clear how strongly predators may control *Idotea* and if this may even lead to local extinction.

An opposite, bottom-up effect is also possible driven by the on-going eutrophication of the Baltic Sea. The Baltic Sea has been eutrophicated since the 1950's (reviewed by Voss et al., 2011) and the high nutrient load has strongly increased the growth of epiphytic and filamentous algae, which form a food resource for *Idotea* spp. (Fig. 7). As a consequence, common meso-grazers like *Idotea* are able to increase in population size, and events of mass occurrence have been observed (Hällfors et al., 1984; Engkvist et al., 2000; Nilsson et al., 2004; Svensson et al., 2004). Hemmi and Jormalainen (2002) found that in nutrient-rich environments *BA* performed significantly better. The food quality affected

consumption rates of females, and their fecundity, mass gain and intermoult duration. Mass occurrences of *Idotea* spp. in some Baltic *Fucus* belts during recent decades along the Swedish and Finnish coasts may serve as food for smaller fish and explain the drastically increased stocks of for example the 3- and 9-spined sticklebacks *Gasterosteus aculeatus* and *Pungitius pungitius* in the Baltic Sea (Bobsien, 2006; Sieben et al., 2011). In conclusion, *Idotea* may act as a key species mediating both top-down and bottom-up effects in the Baltic coastal ecosystem (Fig. 7).

Idotea spp. as Key Species and Future Scenarios

The concept of "keystone species" relates to species that can induce a top-down, trophic cascade at a relatively low biomass, whereas a "key species" drives ecosystem processes or energy flows in general (Paine, 1966, 1969; Piraino and Fanelli, 1999), often caused by high biomass (Ihaksi et al., 2007). Classical key species in the Baltic Sea are the bladder wrack (*Fucus vesiculosus*), the eelgrass (*Zostera marina*), and the blue mussel (*Mytilus edulis/trossulus*) (Kangas et al., 1982; Wikström and Kautsky, 2007), whereas the common eider duck (*Somateria mollissima*) is suggested as a keystone species for the Gulf of Finland (Ihaksi et al., 2007). So, can species of *Idotea* be regarded as key species? Weslawski et al. (2009) termed *BA* and *CH* key species along the Polish coast. They defined key species as a major predator or representing an important food source that is placed centrally in the food web. For *BA* and *CH* we know that they play an important role as grazers (Fig. 7) and serve as food for numerous fish (Table 5). It is uncertain if *GR* can

Table 5. Reported fish predators for *Idotea* (*BA* and *CH*) in the Baltic Sea.

Species	Common name	References
<i>Abramis brama</i>	Bronze/freshwater bream	Salemaa, 1978
<i>Alburnus alburnus</i>	Alver/bleak	Salemaa, 1978
<i>Clupea harengus</i>	Herring	Salemaa, 1978; Jormalainen and Tuomi, 1989; Engkvist et al., 2000
<i>Cottus gobio</i>	Bullhead	Salemaa, 1978
<i>Cyclopterus lumpus</i>	Henfisch/lumpfish	Salemaa, 1978
<i>Gadus morhua</i>	Cod	Jormalainen and Tuomi, 1989; Engkvist et al., 2000
<i>Gasterosteus aculeatus</i>	Three-spined stickleback	Salemaa, 1978; Bobsien, 2006
<i>Gobius niger</i>	Black goby	Salemaa, 1978; Bobsien, 2006
<i>Gobiusculus flavescens</i>	Two-spotted goby	Bobsien, 2006
<i>Gymnocephalus cernuus</i>	Ruffe	Salemaa, 1978
<i>Leuciscus idus</i>	Ide/orfe	Salemaa, 1978
<i>Myoxocephalus scorpius</i>	Sea scorpion/sculpin	Salemaa, 1978
<i>Nerophis ophidion</i>	Straight-nosed pipefish	Bobsien, 2006
<i>Perca fluviatilis</i>	Perch	Salemaa, 1978; Haahtela, 1984; Jormalainen and Tuomi, 1989; Engkvist et al., 2000
<i>Pholis gunnellus</i>	Rock gunnel	Salemaa, 1978
<i>Pomatochistus minutus</i>	Sand goby	Bobsien, 2006
<i>Pungitius pungitius</i>	Nine-spined stickleback	Salemaa, 1978
<i>Rutilus rutilus</i>	Roach	Salemaa, 1978
<i>Scardinius erythrophthalmus</i>	Rudd	Salemaa, 1978
<i>Spinachia spinachia</i>	Fifteen-spined stickleback	Salemaa, 1978; Bobsien, 2006
<i>Syngnathus rostellatus</i>	Lesser pipefish	Bobsien, 2006
<i>Syngnathus typhle</i>	Deep-nosed pipefish	Bobsien, 2006
<i>Zoarces viviparus</i>	Eelpout	Salemaa, 1978; Korheina, 1981; Jormalainen and Tuomi, 1989; Bobsien, 2006

be called a key species due to the limited information about this species for the Baltic Sea, e.g., there is no information available about their role as a food source (Table 5), but mass occurrence has been observed in the Kalmarsund (Engkvist et al., 2004; Table 1). One likely reason why *GR* may not qualify as a key species is their preference for open and exposed habitats (Fig. 5) where they interact less with small-sized fish that feed on benthic invertebrates. Numerous studies report significant top-down effects from *Idotea* grazing on epiphytes (Råberg and Kautsky, 2007b) and *Idotea* spp. may here act as a keystone species by promoting recruitment and growth of perennial macrophytes (Duffy et al., 2001).

The changing climate is expected to affect the Baltic Sea according to recent scenario models (Belkin, 2009; Meier et al., 2011). Analysis of historical data (HELCOM this study) and scenarios up to the year 2100 point to an on-going increase of sea-surface temperature of around 3–5°C and some scenarios predict a dramatic decrease in salinity of around 3–4 PSU. Our review shows that *Idotea* inhabit a wide range of environmental conditions in the Baltic Sea, but are likely limited to areas with an average salinity above 3 PSU for *BA* and *CH* and above 5 PSU for *GR* (Fig. 6). With the present climate change scenarios combined with a possible negative interaction between tolerance to low salinities and an increasing temperature (Vlasblom et al., 1997), the low-salinity limit for *Idotea* may be shifted upwards and, in the absence of evolutionary change, lead to extinction in most of the Baltic Sea. A changing climate may also negatively affect the *Idotea* through declines of the main substratum, *Fucus vesiculosus* (Fig. 7). Higher temperature may reduce the lifespan and Tuomi et al. (1988a) found that a change of only two degrees (from 13°C to 15°C) in the Finnish Archipelago Sea compressed female *BA* lifespan by 10 days. There may also be other effects of temperature like increased susceptibility to pathogens. Under an experimental scenario that mimicked the 2003 European heat wave of 26°C water temperature in the southern Baltic Sea, *BA* responded with a significantly decreased phagocytic activity and a 50% reduction in immuno-competence (Roth et al., 2010). There are also possible positive effects where an increased temperature with milder winters may lead to an earlier and longer breeding period with more broods per year (Fig. 7).

The on-going eutrophication of the Baltic Sea (Voss et al., 2011) causes frequent hypoxic events with mass occurrence of a few generalists often leading to low-diversity communities (Anger, 1975). Our review indicates that *GR* responds with local extinction to increased organic pollution, while *BA* and *CH* seem to be more tolerant. Anger (1975) considered *Gammarus* spp. and *BA* as indicators for local organic pollution. Zettler (2001) agreed with Anger (1975), but replaced *BA* by *CH*. Janas et al. (2004) reported *CH* from sites with permanent hydrogen sulphide and findings of *BA* and *CH* on black sediment with low oxygen content are described (Korheina, 1981). *BA* tolerates short-term (6 hour) exposure to hypoxia (Theede et al., 1969), but as typical inhabitants of the upper benthic *Fucus* belt, *BA* avoids natural hypoxia. *CH* can be expected to survive longer under hypoxia due to habitat preferences in lagoons, shallow waters and estuaries (Fig. 5), where hypoxia occurs naturally

(Diaz and Rosenberg, 2008). Habitat-related differences in the response to oxygen deficiency are known for *BA* and *Idotea emarginata* in the North Sea (Vetter et al., 1999). *BA* is also known for its sensitivity to metal contaminations including zinc, lead and copper (Bat et al., 1999). In summary, species of *Idotea*, particularly *BA* and *CH*, are expected to be even more dominant in a eutrophicated Baltic Sea although this may be tempered by the disappearance of the habitat-forming species *F. vesiculosus* and *Z. marina*.

To conclude, *I. balthica*, *I. chelipes*, and *I. granulosa*, are able to inhabit the Baltic Sea. As euryhaline species they are tolerant to salinity changes, and *BA* and *CH* appear to be more tolerant to low salinities than *GR*. The Baltic species of *Idotea* are all flexible in habitat and food requirements but the three species have different niches (habitat segregation) and seem to differ in their sensitivity to on-going environmental changes in the Baltic Sea. Several macroalgae, filamentous algae, phanerogams as well as animals form not only structural hosts but also nutrition for this omnivorous species. Our review supports a view that *Idotea*, especially *I. balthica* and *I. chelipes*, are key species in the coastal vegetation zone. They serve as food for several Baltic fish (bottom-up effect) and can have impressive grazing rates on filamentous algae (top-down effect). The Baltic Sea is one of the most impacted marine environments and the on-going climate change is expected to strongly affect the Baltic ecosystem. Some climate change scenarios predict extinction of *Idotea* from large areas of the Baltic Sea. Studies are urgently needed to improve our understanding of how new pressures from global change, like overfishing, eutrophication, contaminants and a changing climate, may interact with the *Idotea* ecology in the Baltic Sea.

ACKNOWLEDGEMENTS

The authors are grateful to several people at different museums around the Baltic Sea for some helps with the handling of the collection material: Dr. R. Väinölä (FMNH), Prof. Dr. A. Brandt and K. Philipps-Bussau (ZMH), I. Podszuck (GOM), Dr. C. O. Coleman (ZMB), Prof. Dr. M. Türkay and A. Allspach (SMF), V. Dzhurinskii (ZIN), Dr. S. Boström and Dr. A. Warén (SMNH). The manuscript benefits from constructive suggestions by Dr. M. Thiel, Prof. Dr. O. Vesakoski and one anonymous reviewer. This work was performed within the Linnaeus Centre for Marine Evolutionary Biology at the University of Gothenburg (<http://www.cemeb.science.gu.se/>), and supported by a Linnaeus-grant from the Swedish Research Councils VR and Formas.

REFERENCES

- Anger, K. 1975. On the influence of sewage pollution on inshore benthic communities in the South of Kiel Bay. *Helgoländer wissenschaftliche Meeresuntersuchungen* 27: 408–438.
- Appeltans, W., P. Bouchet, G. A. Boxshall, K. Fauchald, D. P. Gordon, B. W. Hoeksema, G. C. B. Poore, R. W. M. van Soest, S. Stöhr, T. C. Walter, and M. J. Costello (eds.). 2010. *World Register of Marine Species*. Accessed at <http://www.marinespecies.org> (31.01.2011).
- Arndt, E. A. 1964. *Tiere der Ostsee*. Ziemsen Verlag, Lutherstadt Wittenberg. pp. 94–166.
- Baden, S., and L. Pihl. 1984. Abundances, biomass and production of mobile epibenthic fauna in *Zostera marina* (L.) meadows, western Sweden. *Ophelia* 23: 65–90.
- , C. Boström, S. Tobiasson, H. Arponen, and P.-O. Moksnes. 2010. Relative importance of trophic interactions and nutrient enrichment in seagrass ecosystems: a broad-scale field experiment in the Baltic-Skagerrak area. *Limnology and Oceanography* 55: 1435–1448.

- , M. Gullström, B. Lundén, L. Pihl, and R. Rosenberg. 2003. Vanishing seagrass (*Zostera marina*, L.) in Swedish coastal waters. *Ambio* 32: 374-377.
- Bat, L., M. Sezgin, A. Gündođdu, and M. Culha. 1999. Toxicity on zinc, copper and lead to *Idotea baltica* (Crustacea, Isopoda). *Turkish Journal of Biology* 23: 465-472.
- Belkin, I. M. 2009. Rapid warming of large marine Ecosystems. *Progress in Oceanography* 81: 207-213.
- Betz, K.-H. 1974. Phänologie, Reproduktion und Wachstum der valviferen Assel *Idotea chelipes* (Pallas, 1766) in der Schlei. *Kieler Meeresforschung* 30: 65-79.
- Bobsien, I. C. 2006. The role of small fish species in eelgrass food webs of the Baltic Sea. Ph.D. Dissertation, University of Kiel, Germany.
- Bonsdorff, E. 1992. Drifting algae and zoobenthos – effects on settling and community structure. *Netherlands Journal of Sea Research* 30: 57-62.
- . 2006. Zoobenthic diversity-gradient in the Baltic Sea: continuous post-glacial succession in a stressed ecosystem. *Journal of Experimental Marine Biology and Ecology* 330: 383-391.
- Boström, C., and E. Bonsdorff. 1997. Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L.) beds in the northern Baltic Sea. *Journal of Sea Research* 37: 153-166.
- , and ———. 2000. Zoobenthic community establishment and habitat complexity – the importance of seagrass shoot-density, morphology and physical disturbance for faunal recruitment. *Marine Ecology Progress Series* 205: 123-138.
- , and J. Mattila. 1999. The relative importance of food and shelter for seagrass-associated invertebrates: a latitudinal comparison of habitat choice by isopod grazers. *Oecologia* 120: 162-170.
- , and ———. 2005. Effects of Isopod grazing: an experimental comparison in temperate (*Idotea balthica*, Baltic Sea, Finland) and subtropical (*Erichsonella attenuata*, Gulf of Mexico, USA) ecosystems. *Crustaceana* 78: 185-200.
- , S. P. Baden, and D. Krause-Jensen. 2003. The seagrasses of Scandinavia and the Baltic Sea, pp. 27-37. In, E. P. Green and F. T. Short (eds.), *World Atlas of Seagrasses*. UNEP World Conservation Monitoring Centre. University of California Press, Berkeley, USA.
- , E. Bonsdorff, P. Kangas, and A. Norkko. 2002. Long-term changes of a brackish-water eelgrass (*Zostera marina* L.) community indicate effects of coastal eutrophication. *Estuarine, Coastal and Shelf Science* 55: 795-894.
- Bulnheim, H. P. 1974. Respiratory metabolism of *Idotea balthica* (Crustacea, Isopoda) in relation to environmental variables, acclimation processes and moulting. *Helgoländer wissenschaftliche Meeresuntersuchungen* 26: 464-480.
- Diaz, R. J., and R. Rosenberg. 2008. Spreading dead zones and consequences for Marine Ecosystems. *Science* 321: 926-929.
- Ducrot, J.-P., and M. Elliott. 2008. The science and management of the North Sea and the Baltic Sea: natural history, present threats and future challenges. *Marine Pollution Bulletin* 57: 8-21.
- Duffy, J. E., K. S. MacDonald, J. M. Rhode, and J. D. Parker. 2001. Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. *Ecology* 82: 2417-2434.
- Elken, J., and W. Matthäus. 2008. Baltic Sea oceanography, p. 474. In, H. von Storch and A. Omstedt (eds.), *Assessment of Climate Change for the Baltic Sea Basin*. BALTEX Publication. Springer, Berlin.
- Engkvist, R., T. Malm, and J. Nilsson. 2004. Interaction between isopod grazing and wave action: a structuring force in macroalgal communities in the southern Baltic Sea. *Aquatic Ecology* 38: 403-413.
- , ———, and S. Tobiasson. 2000. Density dependent grazing effects of the isopod *Idotea baltica* Pallas on *Fucus vesiculosus* L in the Baltic Sea. *Aquatic Ecology* 34: 253-260.
- Eriksson, B. K., L. Ljunggren, A. Sandström, G. Johansson, J. Mattila, A. Rubach, S. Råberg, and M. Snickars. 2009. Declines in predatory fish promote bloom-forming macroalgae. *Ecological Applications* 19: 1975-1988.
- Forslund, H. 2009. Grazing and the geographical range of seaweeds. Licentiate Thesis, University of Stockholm, Sweden.
- Forsman, B. 1956. Notes on the invertebrate fauna of the Baltic. *Arkiv för Zoologi* (2), Kungliga Svenska Vetenskapsakademien 9: 389-419.
- Goecker, M. E., and S. E. Käll. 2003. Grazing preferences of marine isopods and amphipods on three prominent algal species of the Baltic Sea. *Journal of Sea Research* 50: 309-314.
- Gohse-Reimann, S. S. 2007. Untersuchungen zur Ernährungsökologie benthischer Invertebraten im Makrophytensystem: ein marin-limnischer Ansatz. Ph.D. Dissertation, University of Kiel, Germany.
- Gruner, H.-E. 1965. Krebstiere oder Crustacea. 51. Teil. V. Isopoda. In, M. Dahl and F. Peus (eds.), *Die Tierwelt Deutschlands und der angrenzenden Meeressteile nach ihren Merkmalen und nach ihrer Lebensweise*. VEB Gustav Fischer Verlag, Jena, Germany.
- Gutow, L., and H.-D. Franke. 2003. Metapopulation structure of the marine isopod *Idotea metallica*, a species associated with drifting habitat patches. *Helgoländer Marine Research* 56: 259-264.
- , S. Leidenberger, K. Boos, and H. D. Franke. 2007. Differential life history responses of two *Idotea* species (Crustacea: Isopoda) to food limitation. *Marine Ecology Progress Series* 344: 159-172.
- Haage, P. 1975. Quantitative investigations of the Baltic *Fucus* belt macrofauna. 2. Quantitative seasonal fluctuations. Contributions from the Askö Laboratory, No. 9, University of Stockholm, Sweden.
- Haahetela, I. 1984. A hypothesis of the decline of the Bladder Wrack (*Fucus vesiculosus* L.) in SW Finland in 1975-1981. *Limnologia* 15: 345-350.
- Hällfors, G., P. Kangas, and Å. Niemi. 1984. Recent changes in the phytal at the south coast of Finland. *Ophelia* 3(suppl.): 51-59.
- Halpern, B. S., S. Walbridge, K. A. Selkoe, C. V. Kappel, F. Micheli, C. D'Agrosa, J. F. Bruno, K. S. Casey, C. Ebert, H. E. Fox, R. Fujita, D. Heinemann, H. S. Lenihan, E. M. P. Madin, M. T. Perry, E. R. Selig, M. Spalding, R. Steneck, and R. Watson. 2008. A global map of human impact on marine ecosystems. *Science* 319: 948-952.
- Hammer, C., C. von Dorrien, P. Ernst, T. Gröhsler, F. Köster, B. MacKenzie, C. Möllmann, G. Wegner, and C. Zimmermann. 2008. Fish stock development under hydrographic and hydrochemical aspects, the history of Baltic Sea fisheries and its management. In, R. Feistel, G. Nausch, and N. Wasmund (eds.), *State and Evolution of the Baltic Sea, 1952-2005*. John Wiley and Sons, Inc., New Jersey.
- Hayward, P. J., and J. S. Ryland (eds.). 1995. *Handbook of the Marine Fauna of North-West Europe*. Oxford University Press, Oxford.
- Hemmi, A., and V. Jormalainen. 2002. Nutrient enhancement increases performance of a marine herbivore via quality of its food alga. *Ecology* 83: 1052-1064.
- , and ———. 2004. Geographic covariation of chemical quality of the host alga *Fucus vesiculosus* with fitness of the herbivorous isopod *Idotea baltica*. *Marine Biology* 145: 759-768.
- , A. Mäkinen, V. Jormalainen, and T. Honkanen. 2005. Responses of growth and phlorotannins in *Fucus vesiculosus* to nutrient enrichment and herbivory. *Aquatic Ecology* 39: 201-211.
- Hill, C., and K. Wallström. 2008. Stockholm Archipelago, pp. 309-334. In, U. Schiewer (ed.), *Ecology of Baltic Coastal Waters*. Ecological Studies. Vol. 197. Springer-Verlag, Berlin, Heidelberg.
- Hurrell, J. W., and C. Deser. 2009. North Atlantic climate variability: the role of the North Atlantic Oscillation. *Journal of Marine Systems* 78: 28-41.
- Hørlyck, V. 1973a. Seasonal and diel variation in the rhythmicity of *Idotea baltica* (Pallas) and *Idotea granulosa* Rathke. *Ophelia* 12: 117-127.
- . 1973b. The osmoregulatory ability in three species of the genus *Idotea* (Isopoda, Crustacea). *Ophelia* 12: 129-140.
- Ihaksi, T., I. Helle, T. Lecklin, R. Ryömä, T. Kokkonen, and S. Kuikka. 2007. Using biological knowledge and decisions of society in spatial prioritization of oil combating. *ICES CM 2007/C:02*.
- Ingolfsson, A. 1992. The origin of the rocky shore fauna of Iceland and the Canadian Maritimes. *Journal of Biogeography* 19: 705-712.
- Janas, U., J. Wocial, and A. Szaniawska. 2004. Seasonal and annual changes in the macrozoobenthic populations of the Gulf of Gdansk with respect to hypoxia and hydrogen sulphide. *Oceanologia* 46: 85-102.
- Jansson, A.-M. 1974. Community structure, modelling and stimulation of the *Cladophora* ecosystem in the Baltic Sea. Contributions from the Askö Laboratory, No. 5, University of Stockholm, Sweden.
- , and A.-S. Matthiesen. 1971. On the ecology of young *Idotea* in the Baltic, pp. 71-88. In, *Fourth European Marine Biology Symposium*. Cambridge University Press, Cambridge.
- Jansson, B.-O., and C. Källander. 1968. On the diurnal activity of some littoral peracarid crustaceans in the Baltic Sea. *Journal of Experimental Marine Biology and Ecology* 2: 24-36.
- Jaschinski, S. 2007. The effects of mesograzers in eelgrass communities. Ph.D. Dissertation, University of Kiel, Germany.
- , and U. Sommer. 2008. Top-down and bottom-up control in an eelgrass-epiphyte system. *Oikos* 117: 754-762.

- Jazdzewski, K. 1970. Biology of Crustacea Malacostraca in the Bay of Puck, Polish Baltic Sea. *Zoologica Poloniae* 20: 423-480.
- , A. Konopacka, and M. Grabowski. 2005. Native and alien Malacostracan Crustacea along the Polish Baltic Sea coast in the twentieth century. *Oceanological and Hydrobiological Studies* 24(1)(suppl.): 175-193.
- Jephson, T., P. Nyström, P.-O. Moksnes, and S. P. Baden. 2008. Trophic interactions in *Zostera marina* beds along the Swedish coast. *Marine Ecology Progress Series* 369: 63-76.
- Johannesson, K., and C. André. 2006. Life on the margin: genetic isolation and diversity loss in a peripheral marine ecosystem, the Baltic Sea. *Molecular Ecology* 15: 2013-2029.
- Jormalainen, V., and J. Tuomi. 1989. Sexual differences in habitat selection and activity of the colour polymorphic isopod *Idotea baltica*. *Animal Behaviour* 38: 576-585.
- , T. Honkanen, and N. Heikkilä. 2001b. Feeding preferences and performance of a marine isopod on seaweed hosts: cost of habitat specialization. *Marine Ecology Progress Series* 220: 219-230.
- , ———, and O. Vesakoski. 2008. Geographical divergence in host use ability of a marine herbivore in alga-grazer interaction. *Evolutionary Ecology* 22: 545-559.
- , J. Tuomi, and S. Merilaita. 1992. Mate choice for male and female size in aquatic isopod *Idotea balthica*. *Annales Zoologici Fennici* 29: 161-167.
- , T. Honkanen, O. Vesakoski, and R. Koivikko. 2005. Polar extracts of the brown alga *Fucus vesiculosus* (L.) reduce assimilation efficiency but do not deter the herbivorous isopod *Idotea baltica* (Pallas). *Journal of Experimental Marine Biology and Ecology* 317: 143-157.
- , ———, A. Mäkinen, A. Hemmi, and O. Vesakoski. 2001a. Why does herbivore sex matter? Sexual differences in utilization of *Fucus vesiculosus* by the isopod *Idotea baltica*. *Oikos* 93: 77-86.
- Kangas, P., H. Autio, G. Hällfors, H. Luther, Å. Niemi, and H. Salemaa. 1982. A general model of the decline of *Fucus vesiculosus* at Tvärminne, south coast of Finland in 1977-81. *Acta Botanica Fennica* 118: 1-27.
- Karez, R., S. Engelbert, and U. Sommer. 2000. Co-consumption and protective coating: two new proposed effects of epiphytes on their macroalgal hosts in mesograzer-epiphyte interactions. *Marine Ecology Progress Series* 205: 85-93.
- Kautsky, H. 2008. Askö area and Himmerfjärden, pp. 335-360. In U. Schiewer (ed.), *Ecology of Baltic Coastal Waters*. Ecological Studies. Vol. 197. Springer-Verlag, Berlin, Heidelberg.
- Khlebovich, V. V. 1990. Some physico-chemical and biological phenomena in the salinity gradient. *Limnologica* 20: 5-8.
- Korheina, A. K. 1981. Environment and co-existence of *Idotea* species in the southern Baltic. Ph.D. Dissertation, University of Lund, Sweden.
- Korpinen, S., and V. Jormalainen. 2008. Grazing effects in macroalgal communities depend on timing of patch colonization. *Journal of Experimental Marine Biology and Ecology* 360: 39-46.
- , ———, and T. Honkanen. 2007. Bottom-up and cascading top-down control of macroalgae along a depth gradient. *Journal of Experimental Marine Biology and Ecology* 343: 52-63.
- , ———, and E. Pettay. 2010. Nutrient availability modifies species abundance and community structure of *Fucus*-associated littoral benthic fauna. *Marine Environmental Research* 70: 283-292.
- Kotta, J., and T. Möller. 2009. Important scales of distribution patterns of benthic species in the Gretagrund area, the central Gulf of Riga. *Estonian Journal of Ecology* 58: 259-269.
- , T. Paalme, G. Martin, and A. Mäkinen. 2000a. Major changes in macroalgae community composition affect the food and habitat preference of *Idotea baltica*. *International Review of Hydrobiology* 85: 697-705.
- , H. Orav-Kotta, T. Paalme, I. Kotta, and H. Kukk. 2006. Seasonal changes *in situ* grazing of the mesoherbivores *Idotea baltica* and *Gammarus oceanicus* on the brown algae *Fucus vesiculosus* and *Pylaiella littoralis* in the central Gulf of Finland, Baltic Sea. *Hydrobiologia* 554: 117-125.
- , K. Torn, G. Martin, H. Orav-Kotta, and T. Paalme. 2004. Seasonal variation in invertebrate grazing on *Chara connivens* and *C. tomentosa* in Koiguste Bay, NE Baltic Sea. *Helgoländer Marine Research* 58: 71-76.
- , V. Lauringson, G. Martin, M. Simm, I. Kotta, K. Herkül, and H. Ojaveer. 2000b. Gulf of Riga and Pärnu Bay, pp. 217-244. In U. Schiewer (ed.), *Ecology of Baltic Coastal Waters*. Ecological Studies. Vol. 197. Springer-Verlag, Berlin, Heidelberg.
- Krøyer, H. 1842. Nye nordiske slægter og arter af Amphipodernes orden, hørende til familien Gammarina. *Naturhistorisk Tidsskrift*. Copenhagen 1(4): 153.
- Lapucki, T., and M. Normant. 2008. Physiological responses to salinity changes of the isopod *Idotea chelipes* from the Baltic brackish waters. *Comparative Biochemistry and Physiology, Part A* 149: 299-305.
- , ———, M. Feike, G. Graf, and A. Szaniawska. 2005. Comparative studies on the metabolic rate of the isopod *Idotea chelipes* (Pallas) inhabiting different regions of the Baltic Sea. *Thermochimica acta* 435: 6-10.
- Lauringson, V., and J. Kotta. 2006. Influence of the thin drift algal mats on the distribution of macrozoobenthos in Koiguste Bay, NE Baltic Sea. *Hydrobiologia* 554: 97-105.
- Leach, W. E. 1813-1814. Crustaceology. In, D. Brewster (ed.), *The Edinburgh Encyclopedia*. Vol. 7. Edinburgh.
- Lindström, G. 1855. Bidrag till kännedom om Östersjöns invertebratfauna. Öfversättning af Kongliga Vetenskap Akademien förhandlingar. 12. Stockholm.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. Edit. decima, reformata. Laurentii Salvius, Stockholm: i-iii, 1-828.
- Lotze, H. K., and B. Worm. 2000. Variable and complementary effects of herbivores on different life stages of bloom-forming macroalgae. *Marine Ecology Progress Series* 200: 167-175.
- Lozan, J. L., R. Lampe, W. Matthäus, E. Rachor, H. Rumohr, and H. von Westerhagen (eds.). 1996. *Warnsignale aus der Ostsee*. Parey Buchverlag, Berlin.
- Meier, H. E. M., R. Döscher, and T. Faxén. 2003. A multi processor coupled ice-ocean model for the Baltic Sea: application to salt inflow. *Journal of Geophysical Research* 108(C8): 327.
- , K. Eilola, and E. Almroth. 2011. Climate-related changes in marine ecosystems simulated with a three-dimensional coupled biogeochemical-physical model of the Baltic Sea. *Climate Research* 48: 31-55.
- Merilaita, S. 2001. Habitat heterogeneity, predation and gene flow: colour polymorphism in the isopod, *Idotea baltica*. *Evolutionary Ecology* 15: 103-116.
- , and V. Jormalainen. 1997. Evolution of sex differences in microhabitat choice and colour polymorphism in *Idotea baltica*. *Animal Behaviour* 54: 769-778.
- , and ———. 2000. Different roles of feeding and protection in diel microhabitat choice of sexes in *Idotea baltica*. *Oecologia* 122: 445-451.
- Möbius, K. 1873. Die Expedition zur physikalisch-chemischen und biologischen Untersuchung der Ostsee im Sommer 1871 auf S.M. Avisodampfer Pommerania. IV. Die faunistischen Untersuchungen. A. Die wirbellosen Thiere der Ostsee, pp. 97-144. In, H. A. Meyer, K. Möbius, G. Karsten, and V. Hensen (eds.), *Jahresbericht der Commission zur wissenschaftlichen Untersuchung der deutschen Meere in Kiel für das Jahr 1871*. Verlag von Wiegandt & Hempel, Berlin.
- Moksnes, P., M. Gullström, K. Tryman, and S. Baden. 2008. Trophic cascades in a temperate seagrass community. *Oikos* 117: 763-777.
- Naylor, E. 1955a. The comparative external morphology and revised taxonomy of the British species of *Idotea*. *Journal of the Marine Biological Association of the United Kingdom* 34: 467-493.
- . 1955b. The diet and feeding mechanism of *Idotea*. *Journal of the Marine Biological Association of the United Kingdom* 34: 347-355.
- . 1972. *British Marine Isopods*. Academic Press, London, New York.
- Nicotri, M. E. 1980. Factors involved in herbivore food preference. *Journal of Experimental Marine Biology and Ecology* 42: 13-26.
- Nierstrasz, H. F., and J. H. Schuurmanns Steckhoven Jr. 1926. *Isopoda genuina*, pp. 57-133. In, *Tierwelt der Nord- und Ostsee*. Grimpe and Wagler, Leipzig.
- Nilsson, J., R. Engkvist, and L.-E. Persson. 2004. Long-term decline and recent recovery of *Fucus* populations along the rocky shores of southeast Sweden, Baltic Sea. *Aquatic Ecology* 38: 587-598.
- Orav-Kotta, H., and J. Kotta. 2004. Food and habitat choice of the isopod *Idotea baltica* in the northeastern Baltic Sea. *Hydrobiologia* 514: 79-85.
- , ———, and I. Kotta. 2004. Comparison of macrozoobenthic communities between the 1960s and the 1990-2000s in the Väinameri, NE Baltic Sea. *Proceedings of the Estonian Academy of Sciences Biology Ecology* 53: 283-291.

- Österblom, H., S. Hansson, O. Hjerne, U. Larsson, F. Wulff, R. Elmgren, and C. Folke. 2007. Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. *Ecosystems* 10: 877-889.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100: 65-75.
- . 1969. A note on trophic complexity and community stability. *American Naturalist* 103: 91-93.
- Pallas, P. S. 1766. *Miscellanea zoologica. Quibus novae imprimis atque obscurae animalium species describuntur et observationibus iconibusque illustrantur.* xii, 224 pp. 14 pls. Hague Comitum.
- . 1772. *Spicilegia zoologica. Quibus novae imprimis et obscurae animalium species iconibus, descriptionibus atque commentariis illustrantur.* 9, pp. 66-68. Berolini.
- Paul, V. J., E. Cruz-Rivera, and R. W. Thacker. 2001. Chemical mediation of macroalgal-herbivore interactions: ecological and evolutionary perspectives, pp. 227-265. In, J. B. McClintock and B. J. Baker (eds.), *Marine Chemical Ecology*. CRC Press, Boca Raton.
- Pavia, H., H. Carr, and P. Åberg. 1999. Habitat and feeding preferences of crustacean mesoherbivores inhabiting the brown seaweed *Ascophyllum nodosum* (L.) Le Jol. and its epiphytic macroalgae. *Journal of Experimental Marine Biology and Ecology* 236: 15-32.
- Piraino, S., and G. Fanelli. 1999. Keystone species: what are we talking about? *Conservation Ecology* 3(1): r4 [online]. URL: <http://www.consecol.org/vol3/iss1/resp4/>.
- Råberg, S., and L. Kautsky. 2007a. A comparative biodiversity study of the associated fauna of perennial fucoids and filamentous aglae. *Estuarine, Coastal and Shelf Science* 73: 249-258.
- , and ———. 2007b. Consumers affect prey biomass and diversity through resource partitioning. *Ecology* 88: 2468-2473.
- , and ———. 2008. Grazer identity is crucial for facilitating growth of the perennial brown alga *Fucus vesiculosus*. *Marine Ecology Progress Series* 361: 111-118.
- Rathke, H. 1837. *Zur Fauna der Krym. Mémoires de l'Académie Impériale des Sciences de Saint Pétersbourg. Sciences Mathématiques, Physiques et Naturelles 2. Partie, Sciences Naturelles 3: 368-370.*
- . 1843. *Beiträge zur Fauna Norwegens. Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum 20. Breslau et Bonn.*
- Roth, O., J. Kurtz, and T. B. H. Reusch. 2010. A summer heat wave decreases the immunocompetence of the mesograzer, *Idotea baltica*. *Marine Biology* 157: 1605-1611.
- Salemaa, H. 1978. Geographical variability in the colour polymorphism of *Idotea baltica* (Isopoda) in the northern Baltic. *Hereditas* 88: 165-182.
- . 1979. Ecology of *Idotea* spp. in the North Baltic. *Ophelia* 18: 133-150.
- . 1985. Kryptological studies in *Idotea* spp. (Isopoda, Valvifera). *Crustaceana* 48: 74-87.
- . 1986. Ecological and genetic adaptations of *Idotea* spp. (Isopoda, Crustacea). Ph.D. Dissertation, University of Helsinki, Finland.
- . 1987. Herbivory and microhabitat preferences of *Idotea* spp. (Isopoda) in the northern Baltic Sea. *Ophelia* 27: 1-15.
- Sandén, P., and B. Håkansson. 1996. Long-term trends in Secchi depth in the Baltic Sea. *Limnology and Oceanography* 41: 346-351.
- Sars, S. O. 1899. Isopoda, pp. 78-86, pls. 32-35. In, *An Account of the Crustacea of Norway. Vol. 2.* Bergen.
- Schaffelke, B., D. Evers, and A. Walhorn. 1995. Selective grazing of the isopod *Idothea baltica* between *F. evanescens* and *F. vesiculosus* from Kiel Fjord (western Baltic). *Marine Biology* 124: 215-218.
- Schiewer, U. 2008. Greifswalder Bodden, Wismar-Bucht, Salzhaff, pp. 87-114. In, U. Schiewer (ed.), *Ecology of Baltic Coastal Waters. Ecological Studies. Vol. 197.* Springer-Verlag, Berlin, Heidelberg.
- Schories, D., and U. Wilhelmson. 2006. Die Ostsee, p. 58. In, *Tiere und Pflanzen. Kosmosnaturführer. Franckh-Kosmos-Verlags-GmbH and Co. KG, Stuttgart.*
- Segerstråle, S. G. 1932. Quantitative Studien über den Tierbestand der Fucus-Vegetation in den Schären von Pellinge (an der Südküste Finnlands). *Societas Scientiarum Fennica. Commentationes Biologicae* 3: 1-14.
- . 1944a. Über die Verbreitung der *Idotea*-Arten im baltischen Meeresgebiet Finnlands. *Societas Scientiarum Fennica. Commentationes Biologicae* 9: 1-6.
- . 1944b. Weitere Studien über die Tierwelt der *Fucus*-Vegetation an der Südküste Finnlands. *Societas Scientiarum Fennica. Commentationes Biologicae* 9: 1-30.
- Sieben, K., L. Ljunggren, U. Bergström, and B. K. Eriksson. 2011. A mesopredator release of stickleback promotes recruitment of macroalgae in the Baltic Sea. *Journal of Experimental Marine Biology and Ecology* 397: 79-84.
- Sommer, U. 1997. Selectivity of *Idothea chelipes* (Crustacea: Isopoda) grazing on benthic microalgae. *Limnology and Oceanography* 42: 1622-1628.
- Spooner, G. M. 1947. The distribution of *Gammarus* species in estuaries. Part 1. *Journal of the Marine Biological Association of the United Kingdom* 27: 1-52.
- Svensson, P. A., T. Malm, and R. Engkvist. 2004. Distribution and host plant preference of *Idotea baltica* (Pallas) (Crustacea: Isopoda) on shallow rocky shores in the central Baltic Sea. *Sarsia* 89: 1-7.
- Sywula, T. 1964a. A study on the taxonomy, ecology and the geographical distribution of species of genus *Idotea* Fabricius (Isopoda, Crustacea) in Polish Baltic. I. Taxonomical part. *Bulletin de la société des amis des sciences et des lettres de Poznan D 4: 141-172.*
- . 1964b. A study on the taxonomy, ecology and the geographical distribution of species of genus *Idotea* Fabricius (Isopoda, Crustacea) in Polish Baltic. II. Ecological and zoogeographical part. *Bulletin de la société des amis des sciences et des lettres de Poznan D 4: 173-199.*
- Theede, H., A. Ponat, K. Hiroki, and C. Schlieper. 1969. Studies on the resistance of marine bottom invertebrates to oxygen-deficiency and hydrogen sulphide. *Marine Biology* 2: 325-337.
- Torn, K., D. Krause-Jensen, and G. Martin. 2006. Present and past depth distribution of bladderwrack (*Fucus vesiculosus*) in the Baltic Sea. *Aquatic Botany* 84: 53-62.
- Toth, G. 2007. Screening for induced herbivore resistance in Swedish intertidal seaweeds. *Marine Biology* 151: 1597-1604.
- Tuomi, J., V. Jormalainen, and H. Ilvessalo. 1988a. Does the aquatic isopod *Idotea baltica* minimize the survival costs of reproduction? *Oikos* 52: 245-249.
- , ———, and ———. 1988b. Growth, food consumption and reproductive tactics of the aquatic isopod *Idotea baltica*. *Annales Zoologici Fennici* 25: 145-155.
- Vesakoski, O., C. Boström, T. Ramsay, and V. Jormalainen. 2008. Sexual and local divergence in host exploitation in the marine herbivore *Idotea baltica* (Isopoda). *Journal of Experimental Marine Biology and Ecology* 367: 118-126.
- Vetter, R.-A. H., H.-D. Franke, and F. Buchholz. 1999. Habitat-related differences in the responses to oxygen deficiencies in *Idotea baltica* and *Idotea emarginata* (Isopoda, Crustacea). *Journal of Experimental Marine Biology and Ecology* 239: 259-272.
- Vlasblom, A. G., S. J. Graafsma, and J. T. A. Verhoeven. 1977. Survival, osmoregulatory ability, and respiration of *Idotea chelipes* (Crustacea, Isopod) from lake Veere in different salinities and temperatures. *Hydrobiologia* 52: 33-38.
- Voss, M., J. W. Dippner, C. Humborg, J. Hürdler, F. Korth, T. Neumann, G. Schernewski, and M. Venohr. 2011. History and scenarios of future development of Baltic Sea eutrophication. *Estuarine, Coastal and Shelf Science* 92: 307-322.
- Wahrberg, R. 1930. *Sveriges marina och Lacustra Isopoder*, pp. 32-40. In, *Göteborgs Kungliga Vetenskaps- och Vitterhets-Samhälles Handlingar 5. Ser. B Matematiska och Naturvetenskapliga skrifter, Band 1, Nr. 9.* Wettergren and Kerber, Göteborg.
- Weslawski, J. M., J. Warzocha, J. Wiktor, J. Urbanski, K. Bradtke, L. Kyla, A. Tatrek, L. Kotwicki, and J. Piwowarczyk. 2009. Biological valorisation of the southern Baltic Sea (Polish Exclusive Economic Zone). *Oceanologia* 51: 415-435.
- Widbom, B., and E. Westerlund. 2007. *Bedömning av miljö kvaliteten i Gotlands kustvatten med utgångspunkt från mjukbottenfaunans sammansättning. Länsstyrelsen Gotlands Län. Rapporter om natur och miljö nr 2007: 12.*
- Wikström, S. A., and L. Kautsky. 2007. Structure and diversity of invertebrate communities in the presence and absence of canopy-forming *Fucus vesiculosus* in the Baltic Sea. *Estuarine, Coastal and Shelf Science* 72: 168-176.
- , M. B. Steinarsdóttir, L. Kautsky, and H. Pavia. 2006. Increased chemical resistance explains low herbivore colonization of introduced seaweed. *Oecologia* 148: 593-601.
- Williams, S. L., and M. H. Ruckelshaus. 1993. Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. *Ecology* 74: 904-918.

- Worm, B., H. K. Lotze, and U. Sommer. 2000. Coastal food web structure, carbon storage, and nitrogen retention regulated by consumer pressure and nutrient loading. *Limnology and Oceanography* 45: 339-349.
- Yun, H. Y., S. Rohde, K. Linnane, M. Wahl, and M. Molis. 2010. Seaweed-mediated indirect interaction between two species of meso-herbivores. *Marine Ecology Progress Series* 408: 47-53.
- Zettler, M. L. 1999. Untersuchungen zum Makrozoobenthos des Breitlings (südliche Ostsee) unter besonderer Berücksichtigung der Crustacea. Rostock. Meeresbiologische Beiträge 7: 79-90.
- . 2000. Biologische Artenvielfalt in Küstengewässern der Ostsee am Beispiel der Krebse (Malacostraca). Deutsche Gesellschaft für Limnologie (DGL) Tagungsbericht 1999 (Rostock) Bd. 1: 414-418.
- . 2001. Some malacostracan crustacean assemblages in the southern and western Baltic Sea. *Rostocker Meeresbiologische Beiträge* 9: 127-143.
- , R. Bönsch, and F. Gosselck. 2000. Verbreitung des Makrozoobenthos in der Mecklenburger Bucht (südliche Ostsee) – rezent und im historischen Vergleich, pp. 1-144. In, *Meereswissenschaftliche Berichte*. Marine Science Reports. Institut für Ostseeforschung, Warnemünde.

RECEIVED: 1 June 2011.

ACCEPTED: 31 October 2011.

Appendix A. References from the museum material used for the distribution patterns of *BA*, *CH* and *GR* in the Baltic Sea, Kattegat and Skagerrak.

Nr.	Species	Museum	ID-nr.	Year
1	<i>I. balthica</i>	Helsinki	989	1864
1	<i>I. balthica</i>	Helsinki	990	1867
1	<i>I. balthica</i>	Helsinki	992	1887
1	<i>I. balthica</i>	Helsinki	997	1887
1	<i>I. balthica</i>	Helsinki	2663	1887
1	<i>I. balthica</i>	Helsinki	2664	1888
1	<i>I. balthica</i>	Helsinki	2665	1888
1	<i>I. balthica</i>	Helsinki	2666	1889
1	<i>I. balthica</i>	Helsinki	991	1892
1	<i>I. balthica</i>	Helsinki	2667	1893
1	<i>I. balthica</i>	Helsinki	993	1895
1	<i>I. balthica</i>	Helsinki	2668	1902
1	<i>I. balthica</i>	Helsinki	2669	1903
1	<i>I. balthica</i>	Helsinki	2670	1904
1	<i>I. balthica</i>	Helsinki	2671	1904
1	<i>I. balthica</i>	Helsinki	2672	1904
1	<i>I. balthica</i>	Helsinki	994	1905
1	<i>I. balthica</i>	Helsinki	995	1905
1	<i>I. balthica</i>	Helsinki	996	1905
1	<i>I. balthica</i>	Helsinki	998	1905
1	<i>I. balthica</i>	Helsinki	2673	1905
1	<i>I. balthica</i>	Helsinki	2675	1907
1	<i>I. balthica</i>	Helsinki	999	1908
1	<i>I. balthica</i>	Helsinki	2676	1910
1	<i>I. balthica</i>	Helsinki	1000	1915
1	<i>I. balthica</i>	Helsinki	1001	1922
1	<i>I. balthica</i>	Helsinki	1002	1926
1	<i>I. balthica</i>	Helsinki	1003	1928
1	<i>I. balthica</i>	Helsinki	1004	1928
1	<i>I. balthica</i>	Helsinki	1005	1928
1	<i>I. balthica</i>	Helsinki	1006	1928
1	<i>I. balthica</i>	Helsinki	2687	1929
1	<i>I. balthica</i>	Helsinki	1007	1932
1	<i>I. balthica</i>	Helsinki	1008	1934
1	<i>I. balthica</i>	Helsinki	1009	1934
1	<i>I. balthica</i>	Helsinki	1010	1936
1	<i>I. balthica</i>	Helsinki	2678	1936
1	<i>I. balthica</i>	Helsinki	2679	1936
1	<i>I. balthica</i>	Helsinki	2680	1936
1	<i>I. balthica</i>	Helsinki	2681	1936

Appendix A. (Continued.)

Nr.	Species	Museum	ID-nr.	Year
1	<i>I. balthica</i>	Helsinki	2682	1936
1	<i>I. balthica</i>	Helsinki	2683	1936
1	<i>I. balthica</i>	Helsinki	2684	1936
1	<i>I. balthica</i>	Helsinki	2685	1936
1	<i>I. balthica</i>	Helsinki	2686	1936
1	<i>I. balthica</i>	Helsinki	1011	1937
1	<i>I. balthica</i>	Helsinki	2688	1939
1	<i>I. balthica</i>	Helsinki	1012	1943
1	<i>I. balthica</i>	Helsinki	2689	1943
1	<i>I. balthica</i>	Helsinki	2690	1951
1	<i>I. balthica</i>	Helsinki	2691	1956
1	<i>I. balthica</i>	Helsinki	2692	1961
1	<i>I. balthica</i>	Helsinki	1013	1968
2	<i>I. balthica</i>	Hamburg	19420	1894
2	<i>I. balthica</i>	Hamburg	23492	1895
2	<i>I. balthica</i>	Hamburg	19439	1895
2	<i>I. balthica</i>	Hamburg	22219	1901
2	<i>I. balthica</i>	Hamburg	23528	1911
2	<i>I. balthica</i>	Hamburg	19444	1913
2	<i>I. balthica</i>	Hamburg	11296	1924
2	<i>I. balthica</i>	Hamburg	20804	1930
2	<i>I. balthica</i>	Hamburg	25274	1937
2	<i>I. balthica</i>	Hamburg	28802	1968
3	<i>I. balthica</i>	Stralsund	IIG-739	1966
3	<i>I. balthica</i>	Stralsund	IIG-731	1966
3	<i>I. balthica</i>	Stralsund	II-G/1655	1967
3	<i>I. balthica</i>	Stralsund	II-G/2335	1968
3	<i>I. balthica</i>	Stralsund	II-G/2336	1968
3	<i>I. balthica</i>	Stralsund	IIG-906	1968
4	<i>I. balthica</i>	Berlin	22101	1917
4	<i>I. balthica</i>	Berlin	26700	1985
4	<i>I. balthica</i>	Berlin	26700	1985
4	<i>I. balthica</i>	Berlin	10571	1915
4	<i>I. balthica</i>	Berlin	22038	1907
4	<i>I. balthica</i>	Berlin	22100	1914
4	<i>I. balthica</i>	Berlin	22015	1929
5	<i>I. balthica</i>	Frankfurt	522	1911
5	<i>I. balthica</i>	Frankfurt	829	1911
6	<i>I. balthica</i>	St. Petersburg	ID 2/50088	1908
6	<i>I. balthica</i>	St. Petersburg	ID 6/50092	1908
7	<i>I. balthica</i>	Stockholm	2913	1851
7	<i>I. balthica</i>	Stockholm	2975	1854
7	<i>I. balthica</i>	Stockholm	2874	1855
7	<i>I. balthica</i>	Stockholm	2916	1862
7	<i>I. balthica</i>	Stockholm	2931	1862
7	<i>I. balthica</i>	Stockholm	2946	1862
7	<i>I. balthica</i>	Stockholm	2942	1863
7	<i>I. balthica</i>	Stockholm	2923	1864
7	<i>I. balthica</i>	Stockholm	2933	1864
7	<i>I. balthica</i>	Stockholm	2934	1864
7	<i>I. balthica</i>	Stockholm	2936	1864
7	<i>I. balthica</i>	Stockholm	2912	1865
7	<i>I. balthica</i>	Stockholm	2943	1865
7	<i>I. balthica</i>	Stockholm	2921	1870
7	<i>I. balthica</i>	Stockholm	2922	1870
7	<i>I. balthica</i>	Stockholm	2924	1870
7	<i>I. balthica</i>	Stockholm	2930	1870
7	<i>I. balthica</i>	Stockholm	2937	1870
7	<i>I. balthica</i>	Stockholm	2968	1870
7	<i>I. balthica</i>	Stockholm	2938	1871
7	<i>I. balthica</i>	Stockholm	2939	1871

Appendix A. (Continued.)

Nr.	Species	Museum	ID-nr.	Year
7	<i>I. balthica</i>	Stockholm	2872	1875
7	<i>I. balthica</i>	Stockholm	2893	1875
7	<i>I. balthica</i>	Stockholm	2873	1875
7	<i>I. balthica</i>	Stockholm	2940	1877
7	<i>I. balthica</i>	Stockholm	2949	1877
7	<i>I. balthica</i>	Stockholm	2836	1878
7	<i>I. balthica</i>	Stockholm	2837	1878
7	<i>I. balthica</i>	Stockholm	2839	1878
7	<i>I. balthica</i>	Stockholm	2840	1878
7	<i>I. balthica</i>	Stockholm	2841	1878
7	<i>I. balthica</i>	Stockholm	2842	1878
7	<i>I. balthica</i>	Stockholm	2843	1878
7	<i>I. balthica</i>	Stockholm	2844	1878
7	<i>I. balthica</i>	Stockholm	2848	1878
7	<i>I. balthica</i>	Stockholm	2950	1878
7	<i>I. balthica</i>	Stockholm	2850	1879
7	<i>I. balthica</i>	Stockholm	2851	1879
7	<i>I. balthica</i>	Stockholm	2953	1880
7	<i>I. balthica</i>	Stockholm	8778	1880
7	<i>I. balthica</i>	Stockholm	2854	1881
7	<i>I. balthica</i>	Stockholm	2855	1881
7	<i>I. balthica</i>	Stockholm	2856	1881
7	<i>I. balthica</i>	Stockholm	2857	1882
7	<i>I. balthica</i>	Stockholm	2858	1882
7	<i>I. balthica</i>	Stockholm	2859	1882
7	<i>I. balthica</i>	Stockholm	2860	1882
7	<i>I. balthica</i>	Stockholm	2861	1882
7	<i>I. balthica</i>	Stockholm	2863	1882
7	<i>I. balthica</i>	Stockholm	2864	1882
7	<i>I. balthica</i>	Stockholm	2867	1882
7	<i>I. balthica</i>	Stockholm	2951	1882
7	<i>I. balthica</i>	Stockholm	2954	1882
7	<i>I. balthica</i>	Stockholm	2955	1882
7	<i>I. balthica</i>	Stockholm	2957	1882
7	<i>I. balthica</i>	Stockholm	2959	1882
7	<i>I. balthica</i>	Stockholm	2869	1883
7	<i>I. balthica</i>	Stockholm	2891	1883
7	<i>I. balthica</i>	Stockholm	2875	1884
7	<i>I. balthica</i>	Stockholm	2876	1884
7	<i>I. balthica</i>	Stockholm	2948	1884
7	<i>I. balthica</i>	Stockholm	2952	1890
7	<i>I. balthica</i>	Stockholm	2882	1895
7	<i>I. balthica</i>	Stockholm	2885	1902
7	<i>I. balthica</i>	Stockholm	2886	1902
7	<i>I. balthica</i>	Stockholm	2964	1903
7	<i>I. balthica</i>	Stockholm	2944	1907
7	<i>I. balthica</i>	Stockholm	2941	1908
7	<i>I. balthica</i>	Stockholm	6826	1933
1	<i>I. chelipes</i>	Helsinki	2693	1864
1	<i>I. chelipes</i>	Helsinki	1017	1887
1	<i>I. chelipes</i>	Helsinki	2694	1887
1	<i>I. chelipes</i>	Helsinki	1019	1907
1	<i>I. chelipes</i>	Helsinki	1020	1928
1	<i>I. chelipes</i>	Helsinki	1021	1929
1	<i>I. chelipes</i>	Helsinki	1023	1943
1	<i>I. chelipes</i>	Helsinki	1024	1943
1	<i>I. chelipes</i>	Helsinki	1025	1968
2	<i>I. chelipes</i>	Hamburg	32995	1973
3	<i>I. chelipes</i>	Stralsund	IIG-782	1965
3	<i>I. chelipes</i>	Stralsund	IIG-788	1965
3	<i>I. chelipes</i>	Stralsund	II-G/1572	1965

Appendix A. (Continued.)

Nr.	Species	Museum	ID-nr.	Year
3	<i>I. chelipes</i>	Stralsund	IIG/1408	1965
3	<i>I. chelipes</i>	Stralsund	IIG/1413	1965
3	<i>I. chelipes</i>	Stralsund	II-G/1410	1965
3	<i>I. chelipes</i>	Stralsund	II-G/1573	1965
3	<i>I. chelipes</i>	Stralsund	IIG-940	1965
3	<i>I. chelipes</i>	Stralsund	II-G/1589	1965
3	<i>I. chelipes</i>	Stralsund	IIG-898	1965
3	<i>I. chelipes</i>	Stralsund	IIG-738	1966
3	<i>I. chelipes</i>	Stralsund	IIG/1407	1966
3	<i>I. chelipes</i>	Stralsund	IIG-732	1966
3	<i>I. chelipes</i>	Stralsund	IIG-939	1966
3	<i>I. chelipes</i>	Stralsund	IIG-941	1966
3	<i>I. chelipes</i>	Stralsund	IIG-744	1967
3	<i>I. chelipes</i>	Stralsund	IIG-774	1967
3	<i>I. chelipes</i>	Stralsund	II-G/1656	1967
3	<i>I. chelipes</i>	Stralsund	II-G/1588	1967
3	<i>I. chelipes</i>	Stralsund	II-G/1570	1967
3	<i>I. chelipes</i>	Stralsund	IIG/1411	1967
3	<i>I. chelipes</i>	Stralsund	II-G/1465	1967
3	<i>I. chelipes</i>	Stralsund	IIG-719	1967
3	<i>I. chelipes</i>	Stralsund	IIG/1409	1968
3	<i>I. chelipes</i>	Stralsund	II-G/1406	1968
3	<i>I. chelipes</i>	Stralsund	II-G/1403	1968
3	<i>I. chelipes</i>	Stralsund	II-G/1404	1968
3	<i>I. chelipes</i>	Stralsund	IIG-960	1968
3	<i>I. chelipes</i>	Stralsund	IIG-1119	1968
3	<i>I. chelipes</i>	Stralsund	IIG/1412	1968
3	<i>I. chelipes</i>	Stralsund	IIG-905	1968
3	<i>I. chelipes</i>	Stralsund	II-G/1587	1968
3	<i>I. chelipes</i>	Stralsund	IIG-848	1968
3	<i>I. chelipes</i>	Stralsund	II-G/1405	1969
3	<i>I. chelipes</i>	Stralsund	II-G/1586	1971
3	<i>I. chelipes</i>	Stralsund	II-G/1725	1972
3	<i>I. chelipes</i>	Stralsund	II-G/1746	1973
3	<i>I. chelipes</i>	Stralsund	II-G/1741	1973
3	<i>I. chelipes</i>	Stralsund	II-G/1773	1973
4	<i>I. chelipes</i>	Berlin	22017	1929
4	<i>I. chelipes</i>	Berlin	23292	1931
4	<i>I. chelipes</i>	Berlin	18429	1904
4	<i>I. chelipes</i>	Berlin	25286	1942
4	<i>I. chelipes</i>	Berlin	26701	1985
4	<i>I. chelipes</i>	Berlin	26701	1985
5	<i>I. chelipes</i>	St. Petersburg	ID 6/50052	1908
5	<i>I. chelipes</i>	St. Petersburg	ID 5/50052	1908
5	<i>I. chelipes</i>	St. Petersburg	ID 4/50051	1908
7	<i>I. chelipes</i>	Stockholm	3064	1849
7	<i>I. chelipes</i>	Stockholm	3213	1862
7	<i>I. chelipes</i>	Stockholm	3247	1862
7	<i>I. chelipes</i>	Stockholm	3249	1863
7	<i>I. chelipes</i>	Stockholm	3226	1864
7	<i>I. chelipes</i>	Stockholm	3227	1864
7	<i>I. chelipes</i>	Stockholm	3229	1864
7	<i>I. chelipes</i>	Stockholm	3232	1864
7	<i>I. chelipes</i>	Stockholm	3233	1864
7	<i>I. chelipes</i>	Stockholm	3235	1864
7	<i>I. chelipes</i>	Stockholm	3243	1864
7	<i>I. chelipes</i>	Stockholm	3215	1870
7	<i>I. chelipes</i>	Stockholm	3221	1870
7	<i>I. chelipes</i>	Stockholm	3242	1871
7	<i>I. chelipes</i>	Stockholm	3198	1875
7	<i>I. chelipes</i>	Stockholm	3195	1876

Appendix A. (Continued.)

Nr.	Species	Museum	ID-nr.	Year
7	<i>I. chelipes</i>	Stockholm	3244	1877
7	<i>I. chelipes</i>	Stockholm	3174	1878
7	<i>I. chelipes</i>	Stockholm	3175	1878
7	<i>I. chelipes</i>	Stockholm	3256	1878
7	<i>I. chelipes</i>	Stockholm	3257	1878
7	<i>I. chelipes</i>	Stockholm	3264	1878
7	<i>I. chelipes</i>	Stockholm	3176	1881
7	<i>I. chelipes</i>	Stockholm	3177	1881
7	<i>I. chelipes</i>	Stockholm	3182	1881
7	<i>I. chelipes</i>	Stockholm	3251	1881
7	<i>I. chelipes</i>	Stockholm	3261	1881
7	<i>I. chelipes</i>	Stockholm	3183	1882
7	<i>I. chelipes</i>	Stockholm	3184	1882
7	<i>I. chelipes</i>	Stockholm	3185	1882
7	<i>I. chelipes</i>	Stockholm	3186	1882
7	<i>I. chelipes</i>	Stockholm	3188	1882
7	<i>I. chelipes</i>	Stockholm	3189	1882
7	<i>I. chelipes</i>	Stockholm	3190	1882
7	<i>I. chelipes</i>	Stockholm	3191	1882
7	<i>I. chelipes</i>	Stockholm	3255	1882
7	<i>I. chelipes</i>	Stockholm	3259	1882
7	<i>I. chelipes</i>	Stockholm	3253	1885
7	<i>I. chelipes</i>	Stockholm	3192	1888
7	<i>I. chelipes</i>	Stockholm	3199	1894
7	<i>I. chelipes</i>	Stockholm	3200	1895
7	<i>I. chelipes</i>	Stockholm	3250	1907
7	<i>I. chelipes</i>	Stockholm	3234	1964
1	<i>I. granulosa</i>	Helsinki	1026	1867
1	<i>I. granulosa</i>	Helsinki	1030	1867
1	<i>I. granulosa</i>	Helsinki	1028	1907
1	<i>I. granulosa</i>	Helsinki	1027	1932
1	<i>I. granulosa</i>	Helsinki	1029	1943
2	<i>I. granulosa</i>	Hamburg	23472	1893
2	<i>I. granulosa</i>	Hamburg	23509	1902
2	<i>I. granulosa</i>	Hamburg	26940	1924
2	<i>I. granulosa</i>	Hamburg	26941	1893
3	<i>I. granulosa</i>	Stralsund	IIG-897	1968
7	<i>I. granulosa</i>	Stockholm	3066	1853
7	<i>I. granulosa</i>	Stockholm	3078	1863
7	<i>I. granulosa</i>	Stockholm	3049	1864
7	<i>I. granulosa</i>	Stockholm	3080	1865
7	<i>I. granulosa</i>	Stockholm	3053	1870
7	<i>I. granulosa</i>	Stockholm	3061	1874
7	<i>I. granulosa</i>	Stockholm	3056	1877
7	<i>I. granulosa</i>	Stockholm	3060	1880
7	<i>I. granulosa</i>	Stockholm	2866	1882
7	<i>I. granulosa</i>	Stockholm	3058	1882
7	<i>I. granulosa</i>	Stockholm	3069	1884
7	<i>I. granulosa</i>	Stockholm	3070	1886
7	<i>I. granulosa</i>	Stockholm	3070	1886
7	<i>I. granulosa</i>	Stockholm	3067	1890
7	<i>I. granulosa</i>	Stockholm	3057	1895
7	<i>I. granulosa</i>	Stockholm	3075	1902

Appendix B. References from the literature used for the distribution patterns of *BA*, *CH* and *GR* in the Baltic Sea, Kattegat and Skagerrak.

Nr.	Author	Year	Title	Source
1	Andrulewicz et al.	2004	Phytobenthos and macrozoobenthos of the Slupsk Bank stony reefs, Baltic Sea.	Hydrobiologia 514: 163-170.
2	Anger	1975	On the influence of sewage pollution on inshore benthic communities in the South of Kiel Bay.	Helgoländer wissenschaftliche Meeresuntersuchungen 27: 408-438.
3	Anger et al.	1977	In-situ investigations on the echinoderm <i>Asterias rubens</i> as a predator of the soft-bottom communities in the western Baltic Sea.	Helgoländer wissenschaftliche Meeresuntersuchungen 29: 439-459.
4	Arndt	1964	Tiere der Ostsee.	A. Ziemsen Verlag, Wittenberg Lutherstadt.
5	Baden	1990	The ecology and physiology of epibenthic crustaceans used as biomarkers of oil pollution and hypoxia.	Ph.D. Dissertation, University of Gothenburg, Sweden.
6	Baden and Pihl	1984	Abundance, biomass and production of mobile epibenthic fauna in <i>Zostera marina</i> (L.) meadows, western Sweden.	Ophelia 23: 65-90.
7	Betz	1974	Phänologie, Reproduktion und Wachstum der valviferen Assel <i>Idotea chelipes</i> (Pallas, 1766) in der Schlei.	Kieler Meeresforschung 30: 65-79.
8	Bleich	2006	Messung der beta-Diversität entlang eines Salzgehaltgradienten anhand von Makrozoobenthoszönosen der Ostsee.	Diploma Thesis, University of Rostock, Germany.
9	Bobsien	2006	The role of small fish species in the eelgrass food webs of the Baltic Sea.	Ph.D. Dissertation, Christian-Albrechts-Universität, Kiel, Germany.
10	Boström and Bonsdorff	1997	Community structure and spatial variation of benthic invertebrates associated with <i>Zostera marina</i> (L.) beds in the northern Baltic Sea.	Journal of Sea Research 37: 153-166.
11	Boström and Bonsdorff	2000	Zoobenthic community establishment and habitat complexity – the importance of seagrass disturbance for faunal recruitment.	Marine Ecology Progress Series 205: 123-138.
12	Boström and Mattila	1999	The relative importance of food and shelter for seagrass-associated invertebrates: latitudinal comparison of habitat choice by isopod grazers.	Oecologia 120: 162-170.
13	Boström and Mattila	2005	Effects of Isopod grazing: an experimental comparison in temperate (<i>Idotea balthica</i> , Baltic Sea, Finland) and subtropical (<i>Erichsonella attenuata</i> , Gulf of Mexico, USA) ecosystems.	Crustaceana 78: 185-200.
14	Bulnheim	1974	Respiratory metabolism of <i>Idotea balthica</i> (Crustacea, Isopoda) in relation to environmental variables, acclimation processes and moulting.	Helgoländer wissenschaftliche Meeresuntersuchungen 26: 464-480.
15	Dahl	1916	Die Asseln oder Isopoden Deutschlands, pp. 22-27.	Jena.
16	Engkvist et al.	2000	Density dependent grazing effects of the isopod <i>Idotea baltica</i> Pallas on <i>Fucus vesiculosus</i> L in the Baltic Sea.	Aquatic Ecology 34: 253-260.
17	Engkvist et al.	2004	Interaction between isopod grazing and wave action: a structuring force in macroalgal communities in the southern Baltic Sea.	Aquatic Ecology 38: 403-413.
18	Forslund	2009	Grazing and the geographical range of seaweeds.	Plant and Ecology, Licentiate Thesis, University of Stockholm, Sweden.
19	Forsman	1956	Notes on the invertebrate fauna of the Baltic.	Arkiv för Zoologi Serie 2, Bd. 9(17): 389-419.
20	Forsman	1972	Evertebrater vid svenska östersjökusten.	In, J. Ladin, Djur och växer i Östersjön. Zoologisk Revy 34: 6-31.
21	Franke et al.	1999	The recent arrival of the oceanic isopod <i>Idotea metallica</i> Bosc off Helgoland (German Bight, North Sea): an indication of a warming trend in the North Sea?	Helgoländer wissenschaftliche Meeresuntersuchungen 52: 347-357.
22	Goecker and Kåll	2003	Grazing preferences of marine isopods and amphipods on three prominent algal species of the Baltic Sea.	Journal of Sea Research 50: 309-314.

Appendix B. (Continued.)

Nr.	Author	Year	Title	Source
23	Gruner	1965	Krebstiere oder Crustacea. V. Isopoda, pp. 27-88.	In, M. Dahl and F. Peus (eds.), Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise, 51. Teil. VEB Gustav Fischer Verlag, Jena, Germany.
24	Haage	1975	Quantitative investigations of the Baltic <i>Fucus</i> belt Macrofauna. 2. Quantitative seasonal fluctuations.	Askö Laboratory, University Stockholm, Sweden. 9.
25	Haavisto et al.	2010	Induced resistance in a brown alga: phlorotannins, genotypic variation and fitness costs for the crustacean herbivore.	Oecologia 162: 685-695.
26	Hagerman	1966	The Macro- and Microfauna associated with <i>Fucus serratus</i> L. with some ecological remarks.	Ophelia 4: 1-43.
27	Hammrich	2003	Vergleichende Untersuchungen zur ökologischen Diversifikation der Helgoländer <i>Idotea</i> -Arten.	Diploma Thesis, Universität Hamburg/Alfred-Wegener-Institut für Polar- und Meeresforschung, Germany.
28	Hansen	1916	Crustacea Malacostraca, III. V. The order Isopoda. Sub-Order Valvifera, pp. 187-190.	In, The Danish Ingolf-Expedition 3(5): 185-190.
29	HELCOM	2009	Biodiversity in the Baltic Sea – An integrated thematic assessment on biodiversity and nature conservation in the Baltic Sea.	Baltic Sea Environment Proceedings, No. 116B.
30	Hemmi et al.	2010	Genetic and environmental variation in performance of a marine isopod: effect of eutrophication.	Oecologia 140: 302-311.
31	Hemmi and Jormalainen	2002	Nutrient enhancement increases performance of a marine herbivore via quality of its food alga.	Ecology 83: 1052-1064.
32	Hemmi and Jormalainen	2004	Geographic covariation of chemical quality of the host alga <i>Fucus vesiculosus</i> with fitness of the herbivorous isopod <i>Idotea baltica</i> .	Marine Biology 145: 759-768.
33	Hill and Wallström	2008	The Stockholm Archipelago, pp. 309-334.	In, U. Schiewer (ed.), Ecology of Baltic Coastal Waters. Springer-Verlag, Heidelberg.
34	Hørlyck	1973	The osmoregulatory ability in three species of the genus <i>Idotea</i> (Isopoda, Crustacea).	Ophelia 12: 129-140.
35	Janas et al.	2004	Seasonal and annual changes in the macrozoobenthic populations of the Gulf of Gdąnsk with respect to hypoxia and hydrogen sulphide.	Oceanologia 46: 85-102.
36	Janke and Kremer	1999	Düne, Strand und Wattenmeer. – Tiere und Pflanzen unserer Küsten, p. 223.	Kosmos Naturführer. Franckh-Kosmos-Verlags GmbH and Co., Stuttgart.
37	Jansson and Källander	1968	On the diurnal activity of some littoral peracarid crustaceans in the Baltic Sea.	Journal of Experimental Marine Biology and Ecology 2: 24-36.
38	Jansson and Matthiesen	1971	On the ecology of young <i>Idotea</i> in the Baltic, pp. 71-88.	Fourth European Marine Biology Symposium. Cambridge University Press.
39	Jaschinski	2007	The effects of mesograzers in eelgrass communities.	Ph.D. Dissertation, Christian-Albrechts-Universität, Kiel, Germany.
40	Jaschinski et al.	2008	Carbon sources and trophic structure in an eelgrass <i>Zostera marina</i> bed, based on stable isotope and fatty acid analyses.	Marine Ecology Progress Series 358: 103-114.
41	Jaschinski and Sommer	2008	Top-down and bottom-up control in an eelgrass-epiphyte system.	Oikos 117: 754-762.
42	Jazdzewski	1970	Biology of Crustacea Malacostraca in the Bay of Puck, Polish Baltic Sea.	Zoologica Poloniae 20: 423-480.
43	Jazdzewski et al.	2005	Native and alien Malacostracan Crustacea along the Polish Baltic Sea coast in the twentieth century.	Oceanological and Hydrobiological Studies 34(1)(suppl.): 175-193.
44	Jephson et al.	2008	Trophic interactions in <i>Zostera marina</i> beds along the Swedish coast.	Marine Ecology Progress Series 369: 63-76.
45	Jormalainen et al.	1992	Mate choice for male and female size in aquatic isopod <i>Idotea balthica</i> .	Annales Zoologici Fennici 29: 161-167.

Appendix B. (Continued.)

Nr.	Author	Year	Title	Source
46	Jormalainen et al.	2000	Dynamics of intersexual conflict over precopulatory mate guarding in two populations of the isopod <i>Idotea baltica</i> .	Animal Behaviour 60: 85-93.
47	Jormalainen et al.	2001	Why does herbivore sex matter? Sexual differences in utilization of <i>Fucus vesiculosus</i> by the isopod <i>Idotea baltica</i> .	Oikos 93: 77-86.
48	Jormalainen et al.	2008	Geographical divergence in host use ability of the marine herbivore in alga-grazer interaction.	Evolutionary Ecology 22: 545-559.
49	Jormalainen and Tuomi	1989a	Reproductive ecology of the isopod <i>Idotea baltica</i> (Pallas) in the northern Baltic.	Ophelia 30: 213-223.
50	Jormalainen and Tuomi	1989b	Sexual differences in the habitat selection and activity of the colour polymorphic isopod <i>Idotea baltica</i> .	Animal Behaviour 38: 576-585.
51	Kangas et al.	1982	A general model of the decline of <i>Fucus vesiculosus</i> at Tvärminne, south coast of Finland in 1977-81.	Acta Botanica Fennica 118: 1-27.
52	Karez et al.	2000	Co-consumption and protective coating: two new proposed effects of epiphytes on their macroalgal hosts in mesograzer-epiphyte interactions.	Marine Ecology Progress Series 205: 85-93.
53	Kautsky	2008	Askö and Himmerfjärden, pp. 335-360.	In, U. Schiewer (ed.), Ecology of Baltic Coastal Waters. Springer-Verlag, Heidelberg.
54	Korheina	1981	Environments and co-existence of <i>Idotea</i> species in the southern Baltic.	Ph.D. Dissertation, Department of Animal Ecology, University of Lund, Sweden.
55	Korpinen et al.	2010	Nutrient availability modifies species abundance and community structure of <i>Fucus</i> -associated littoral benthic fauna.	Marine Environment Research 70: 283-292.
56	Korpinen and Jormalainen	2008	Grazing effects in macroalgal communities depend on timing of patch colonization.	Journal of Experimental Marine Biology and Ecology 360: 39-46.
57	Kotta and Möller	2009	Important scales of distribution patterns of benthic species in the Gretagrund area, the central Gulf of Riga.	Estonian Journal of Ecology 58: 259-269.
58	Kotta et al.	2000	Major changes in macroalgae community composition affect the food and habitat preference of <i>Idotea baltica</i> .	International Review of Hydrobiology 85: 697-705.
59	Kotta et al.	2006	Seasonal changes in situ grazing of the mesoherbivores <i>Idotea baltica</i> and <i>Gammarus oceanicus</i> on the brown algae <i>Fucus-vesiculosus</i> and <i>Pylaiella littoralis</i> in the central Gulf of Finland, Baltic Sea.	Hydrobiologia 554: 117-125.
60	Kroer	1986	Distribution and habitat segregation of four species of <i>Idotea</i> (Isopoda) in a Danish Fjord.	Ophelia 25: 199-207.
61	Kunze	1923	Helgoländer Meeresalgen und die Assel <i>Idothea</i> . Ein Beitrag zur Frage nach den Schutzmitteln der Pflanzen gegen Tierfrass.	Wissenschaftliche Meeresuntersuchungen Abteilung Helgoland Bd. 14: 189-195.
62	Køie and Svedberg	2004	Havets Djur, p. 143.	Bokförlaget Prisma, Stockholm.
63	Lapucki et al.	2005	Comparative studies on the metabolic rate of the isopod <i>Idotea chelipes</i> (Pallas) inhabiting different regions of the Baltic Sea.	Thermochimica Acta 435: 6-10.
64	Lapucki and Normant	2008	Physiological responses to salinity changes of the isopod <i>Idotea chelipes</i> from the Baltic brackish waters.	Comparative Biochemistry and Physiology, Part A 149: 299-305.
65	Lauringson and Kotta	2006	Influence of the thin drift algal mats on the distribution of macrozoobenthos in Koiguste Bay, NE Baltic Sea.	Hydrobiologia 554: 97-105.
66	Leidenberger	2004	Konkurrenzfähigkeit und Habitatwahl bei marinen Isopoden: <i>Idotea baltica</i> und <i>Idotea metallica</i> .	Diploma Thesis, Justus-Liebig-Universität Gießen/Alfred-Wegener-Institut für Polar- und Meeresforschung, Germany.
67	Merilaita	1998	Crypsis through disruptive coloration in an isopod.	Proceedings of the Royal Society of London, Series B, Biological Sciences 265: 1059-1064.
68	Merilaita	2001	Habitat heterogeneity, predation and gene flow: colour polymorphism in the isopod, <i>Idotea baltica</i> .	Evolutionary Ecology 15: 103-116.

Appendix B. (Continued.)

Nr.	Author	Year	Title	Source
69	Merilaita and Jormalainen	1997	Evolution of sex differences in microhabitat choice and colour polymorphism in <i>Idotea baltica</i> .	Animal Behaviour 54: 769-778.
70	Merilaita and Jormalainen	2000	Different roles of feeding and protection in diel microhabitat choice of sexes in <i>Idotea baltica</i> .	Oecologia 122: 445-451.
71	Möbius	1873	Die Expedition zur physikalisch-chemischen und biologischen Untersuchung der Ostsee im Sommer 1871 auf S.M. Avisodamper Pommerania. IV. Die faunistischen Untersuchungen. A. Die wirbellosen Thiere der Ostsee, pp. 97-144.	In, H. A. Meyer, K. Möbius, G. Karsten, and V. Hensen (eds.), Jahresbericht der Commission zur wissenschaftlichen Untersuchung der deutschen Meere in Kiel für das Jahr 1871. Verlag von Wiegandt & Hempel, Berlin.
72	Naylor	1972	British Marine Isopods.	Synopses of the British Fauna. No. 3. Academic Press, London, New York.
73	Nierstrasz and Schuurmans Stekhoven	1926	Isopoda genuina, pp. 57-133.	Tierwelt Nord- und Ostsee. Grimpe and Wagler, Leipzig.
74	Nilsson et al.	2004	Long-term decline and recent recovery of <i>Fucus</i> populations along the rocky shores of southeast Sweden, Baltic Sea.	Aquatic Ecology 38: 587-589.
75	Oertzen von	1965	Stoffwechselaktivitätsmessungen (Sauerstoffverbrauch) an Invertebraten der <i>Fucus</i> coenose aus der mittleren Ostsee.	Zoologischer Anzeiger 175: 166-173.
76	Ohm (1964) in Hagerman	1966	The Macro- and Microfauna associated with <i>Fucus serratus</i> L. with some ecological remarks.	Ophelia 4: 1-43.
77	Orav-Kotta et al.	2004	Comparison of macrozoobenthic communities between the 1960s and the 1990s-2000s in the Väinameri, NE Baltic Sea.	Estonian Academy of Sciences Biology Ecology 53: 283-291.
78	Orav-Kotta and Kotta	2004	Food and habitat choice of the isopod <i>Idotea baltica</i> in the northeastern Baltic Sea.	Hydrobiologia 514: 79-85.
79	Pavia et al.	1999	Habitat and feeding preferences of crustacean mesoherbivores inhabiting the brown seaweed <i>Ascophyllum nosodum</i> (L.) Le Jol. and its epiphytic marcolgae.	Journal of Experimental Marine Biology and Ecology 236: 15-32.
80	Polet et al.	2005	The contribution of seagrass beds (<i>Zostera noltii</i>) to the function of tidal flats as a juvenile habitat for dominant, mobile epibenthos in the Wadden Sea.	Marine Biology 147: 813-822.
81	Rasmussen	1973	Systematics and ecology of the Isefjord marine fauna (Denmark).	Ophelia 11: 1-495.
82	Richardson	1905	A monograph on the Isopods of North America.	Bulletin of the United States National Museum 54: 356-367.
83	Romanova	1974	Size-weight ratios and fecundity of <i>Idotea baltica</i> from the Baltic Sea.	Hydrobiological Journal 10: 74-77.
84	Råberg and Kautsky	2007	A comparative biodiversity study of the associated fauna of perennial fucoids and filamentous algae.	Estuarine, Coastal and Shelf Science 73: 249-258.
85	Råberg and Kautsky	2008	Grazer identity is crucial for facilitating growth of the perennial brown alga <i>Fucus vesiculosus</i> .	Marine Ecology Progress Series 361: 111-118.
86	Salemaa	1978	Geographical variability in the colour polymorphism of <i>Idotea baltica</i> (Isopoda) in the northern Baltic.	Hereditas 88: 165-182.
87	Salemaa	1979	Ecology of <i>Idotea</i> spp. (Isopoda) in the northern Baltic.	Ophelia 18: 133-150.
88	Salemaa	1985	Kryptological studies in <i>Idotea</i> spp. (Isopoda, Valvifera).	Crustaceana 48: 74-87.
89	Salemaa	1986	Ecological and genetic adaptations of <i>Idotea</i> spp. (Isopoda, Crustacea).	Ph.D. Dissertation, University of Helsinki, Finland.
90	Schaffelke et al.	1995	Selective grazing of the isopod <i>Idothea baltica</i> between <i>F. evanescens</i> and <i>F. vesiculosus</i> from Kiel Fjord (Western Baltic).	Marine Biology 124: 215-218.
91	Schiewer	2008	Greifswalder Bodden, Wismar-Bucht and Salzhaff, pp. 87-114.	In, U. Schiewer (ed.), Ecology of Baltic Coastal Waters. Springer-Verlag, Heidelberg.

Appendix B. (Continued.)

Nr.	Author	Year	Title	Source
92	Schories and Wilhelmsen	2006	Die Ostsee. Tiere und Pflanzen, p. 58.	Kosmos Naturführer. Franckh-Kosmos-Verlags GmbH and Co., Stuttgart.
93	Segerstråle	1932	Quantitative Studien über den Tierbestand der Fucus-Vegetation in den Schären von Pellinge (an der Südküste Finnlands).	Societas Scientiarum Fennica. Commentationes Biologicae 3: 1-14.
94	Segerstråle	1933	Studien über die Bodentierwelt in südfinnländischen Küstengewässern. II. Übersicht über die Bodentierwelt, mit besonderer Berücksichtigung der Produktionsverhältnisse.	Societas Scientiarum Fennica. Commentationes Biologicae 4: 1-79.
95	Segerstråle	1944a	Über die Verbreitung der <i>Idotea</i> -Arten im baltischen Meeresgebiet Finnlands.	Societas Scientiarum Fennica. Commentationes Biologicae 9: 1-6.
96	Segerstråle	1944b	Weitere Studien über die Tierwelt der Fucus-Vegetation an der Südküste Finnlands.	Societas Scientiarum Fennica. Commentationes Biologicae 9: 1-30.
97	Sommer	1997	Selectivity of <i>Idothea chelipes</i> (Crustacea: Isopoda) grazing on benthic microalgae.	Limnology and Oceanography 42: 1622-1628.
98	Svensson et al.	2004	Distribution and host plant preference of <i>Idotea baltica</i> (Pallas) (Crustacea: Isopoda) on shallow rocky shores in the central Baltic Sea.	Sarsia 89: 1-7.
99	Sywula	1964	A study on the taxonomy, ecology and the geographical distribution of species of genus <i>Idotea</i> Fabricius (Isopoda, Crustacea) in Polish Baltic. II. Ecological and zoogeographical part.	Bulletin de la societe des amis des sciences et des lettres de Poznan D 4: 173-199.
100	Tattersall	1905	The marine fauna of the coast of Ireland. Part V Isopoda.	Fisheries, Ireland, Sci. Invest. 1904, II. Dublin.
101	Tooth	2007	Screening for induced herbivore resistance in Swedish intertidal seaweeds.	Marine Biology 151: 1597-1604.
102	Trahms	1939	Beiträge zur Ökologie kustennaher Gewässer. 1. Das Plankton des Grossen Jasmunder Bodden.	Archiv für Hydrobiologie 32: 75-90.
103	Tuomi et al.	1988a	Growth, food consumption and reproductive tactics of the aquatic isopod <i>Idotea baltica</i> .	Annales Zoologici Fennici 25: 145-151.
104	Vesakoski et al.	2008	Sexual and local divergence in host exploitation in the marine herbivore <i>Idotea baltica</i> (Isopoda).	Journal of Experimental Marine Biology and Ecology 367: 118-126.
105	Wahrberg	1930	Sveriges marina och Lacustra Isopoder, pp. 32-40.	Göteborgs Kungliga Vetenskaps- och Vitterhets-Samhälles Handlingar 5, Serie B, Band 1. Elanders Boktryckeri Aktiebolag, Göteborg.
106	Wallentinus	1991	The Baltic Sea gradient, pp. 83-108.	In: A. C. Mathison and P. H. Nienhuis (eds.), Ecosystems of the World 24. Intertidal and Littoral Ecosystems. Elsevier, Amsterdam, London, New York, Tokyo.
107	Wasmund et al.	2005	Biologische Zustandseinschätzung der Ostsee im Jahre 2004.	Institut für Ostseeforschung Warnemünde an der Universität Rostock im Auftrag des Bundesamtes für Seeschifffahrt und Hydrographie Hamburg und Rostock. Oceanologia 51: 415-435.
108	Weslawski et al.	2009	Biological valorisation of the southern Baltic Sea (Polish Exclusive Economic Zone).	
109	Widbom and Westerlund	2007	Bedömning av miljö kvalitet i Gotlands kustvatten med utgångspunkt från mjukbottenfaunans sammansättning.	Rapporter om natur och miljö. Nr. 2007: 12 Länsstyrelsen Gotlands Län.
110	Wikström and Kautsky	2006	Structure and diversity of invertebrate community in the presence and absence of canopy-forming <i>Fucus vesiculosus</i> in the Baltic Sea.	Estuarine, Coastal and Shelf Science 72: 168-176.
111	Yun et al.	2010	Seaweed-mediated indirect interaction between two species of meso-herbivores.	Marine Ecology Progress Series 408: 47-53.
112	Zettler	1999	Untersuchungen zum Makrozoobenthos des Breitlings (südliche Ostsee) unter besonderer Berücksichtigung der Crustacea.	Rostocker Meeresbiologische Beiträge 7: 79-90.

Appendix B. (Continued.)

Nr.	Author	Year	Title	Source
113	Zettler	2001	Some malacostracan crustacean assemblages in the southern and western Baltic Sea.	Rostocker Meeresbiologische Beiträge 9: 127-143.
114	Zettler and Gosselck	2006	Benthic assessment of marine areas of particular ecological importance within the German Baltic Sea EEZ, pp. 141-156.	In, H. von Nordheim, D. Boedeker, and J. C. Krause (eds.), Progress in Marine Conservation in Europe – NATURA 2000 sites in German Offshore Waters. Springer, Berlin.
115	Zettler et al.	2000	Verbreitung des Makrozoobenthos in der Mecklenburger Bucht (südliche Ostsee) – rezent und im historischen Vergleich.	Meereswissenschaftliche Berichte – Marine Sciences Report. Institut für Ostseeforschung. Warnemünde.