Thesis for the degree of Doctor of Philosophy

Adaptation to the Baltic Sea -

the case of isopod genus *Idotea*

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Abstract

The three marine isopods of the genus *Idotea*: *I. balthica*, *I. chelipes* and *I. granulosa* have an important functional role as meso-grazers in the Baltic food web. These meso-grazers are key species in the *Fucus* belt and in *Zostera marina* beds and are characterized by top-down effects through impressive feeding rates on filamentous algae as well as through their importance as prey for 23 fish species (bottom-up effects). In the Baltic Sea, the three *Idotea* spp. show clear habitat segregation, but may also coexist and compete for food and space. The habitat differences are also reflected in their different life history strategies. Whereas *I. balthica* is more of a generalist and *K*-selected species, *I. chelipes* shows characteristics of an *r*-selected species. The third species, *I. granulosa*, is displaced by *I. balthica* to less favorable habitats, why the adversity strategy fits best for this species.

A phylogeographic study and reconstruction of demographic history indicated that after the Baltic Sea became a marine habitat, *I. granulosa* first invaded into the young Baltic Sea from the Atlantic followed by *I. balthica* and *I. chelipes*. Small estimated population sizes and the haplotype networks, suggest that *I. balthica* and *I. granulosa* have gone through a bottleneck during colonization, losing genetic diversity in Baltic populations. Although Baltic populations of *I. chelipes* were genetically distinct from populations outside the Baltic Sea, differentiation was ten times lower than in the other two species. Distribution patterns over the past 150 years, showed fairly constant large-scale distributions for the *Idotea* spp., but changes in distribution could be found. *I. chelipes* and *I. granulosa* shifted southwards, probably as a consequence of changes in salinity and temperature reported for the Baltic Sea. In general, the distribution patterns of *Idotea* spp. seem to be more determined by temperature than by salinity as supported by ecological niche modelling. Predicted distributions under a climate change scenario (ECHAM5) demonstrated a northern shift of *Idotea* through increased temperature, deeper into the Bothnian Sea. Such distribution changes may have serious consequences, since the endemic narrow wrack, *Fucus radicans*, today may be protected from intensive grazing pressure through the distribution limit of *Idotea* to the southern parts of the Bothnian Sea.

Demographic analysis demonstrated that all three species live closely to their limits under the Baltic Sea extremes. The obvious change in life history from the North Sea to the Baltic Sea can be a cost of acclimation or adaptation. Whereas *I. balthica* lives close to its carrying capacity, several local extinctions of *I. granulosa* have been reported. As a typical *r*-selected species and with the highest genetic diversity, *I. chelipes* may have the highest capacity to adapt to further predicted climate changes. Today it is not clear if *Idotea* spp. are locally adapted to the Baltic extremes or showing phenotypic plasticity in response to abiotic factors, which calls for further studies.

Keywords: *Idotea* spp., Baltic Sea, life-history strategies, adaptation, phylogeography, ecological niche modelling, climate change

Populärvetenskaplig Sammanfattning

Östersjön är ett relativt ungt innanhav som uppstod efter att den senaste inlandsisen smälte och drog sig tillbaka. För ca 7500 år uppstod de nuvarande förbindelserna med Atlanten som ger Östersjön sitt karakteristiska bräckta vatten från nästan marint vatten i Kattegatt till sötvatten längst upp i Bottenviken och inne i Finska viken. På grund av det bräckta vattnet är det få marina djur och växter som lyckats etablera sig i Östersjön och den låga biologiska mångfalden gör att Östersjön är ett särskilt känsligt ekosystem. Östersjön står idag inför en rad miljöhot, främst utsläpp av gifter och näringsämnen, överfiskning och klimatförändringar. Det är därför viktigt att vi utvecklar kunskap för att förstå vilka djur och växter som riskerar att försvinna på grund av de pågående miljöförändringarna och hur det påverkar viktiga funktioner i Östersjöns ekosystem.

Tre marina gråsuggor av släktet *Idotea*: *I. balthica*, *I. chelipes* och *I. granulosa* har en funktionell roll som växtätare i Östersjöns näringsväv. Dessa kräftdjur är viktiga betare i tångbältet och i sjögräsängar. Vuxna *Idotea* är mellan 7-15 mm långa, kan vara mycket vanliga, och kan beta på både fintrådiga alger och tång. *Idotea* är också en viktig föda för många fiskarter. Det är intressant att i en så pass artfattig miljö som Östersjön har tre närbesläktade *Idotea*-arter lyckats etablera sig. En viktig frågeställning i min doktorsavhandling är att förstå i vilken utsträckning de tre *Idotea*-arterna skiljer sig åt ekologiskt och om de har olika förutsättningar att klara av Östersjöns miljöförändringar.

Den vanliga tånggråsuggan *I. balthica* har en generalistisk livsstil och finns på de flesta platser där blåstången *Fucus vesiculosus* finns. De två andra arterna av *Idotea* är däremot mer specifika i sitt habitatval. *Idotea chelipes* föredrar strandkanten, där vattnet är lugnare och varmare, medan *I. granulosa* gärna vill ha det mer turbulent i mer öppna kustavsnitt. Ofta hittar man *I. balthica* tillsammans med en av de andra arterna, men på vissa platser finns även alla tre arterna tillsammans då de sannolikt konkurrerar om mat och plats.

I en fylogeografisk analys baserad på genetisk information (mitokondriellt DNA) jämfördes genetiska skillnader mellan populationer inom och utanför Östersjön. Syftet med den fylogeografiska studien var att försöka rekonstruera den tidiga historien när de olika *Idotea*-arterna koloniserade Östersjön. I motsats till tidigare antaganden tyder mina resultat på att *I. granulosa* först invaderade den unga Östersjön från Atlanten och sen följdes av *I. balthica* och *I. chelipes*. *Idotea balthica* och *I. granulosa* tycks båda ha gått igenom en flaskhals med små populationer under kolonisationen av Östersjön varvid betydande genetisk mångfald gått förlorad. Även populationer av *I. chelipes* är genetiskt annorlunda i Östersjön jämfört med utanför, men *I. chelipes* har behållit tio gånger högre genetisk mångfald jämfört med de två andra arterna. Det betyder att *I. chelipes* förmodligen har bättre möjligheter att

anpassa sig till olika förändringar i framtiden, eftersom en högre genetisk variation ger större potential för anpassningar till förändringarna i miljön.
I min avhandling studerade jag också spridningsmönster av *Idotea*-arterna under de senaste 150 åren. Det visade sig att den storskaliga utbredning för *Idotea* arterna var relativt konstant i Östersjön, men små förändringar i utbredningen kunde hittas. *Idotea chelipes* och *I. granulosa* har flyttat sin utbredning mer söderut, förmodligen som en följd av förändringar i salthalt och temperatur som är rapporterade för Östersjön. I allmänhet verkar spridningsmönstret av *Idotea*-arterna mer bestämt av temperatur än av salthalt.

Flera olika modeller och emissionsscenarier för det framtida klimatet förutsäger betydande förändringar av Östersjöns miljö. En av de senaste modellerna (ECHAM5) förutsäger ett mycket varmare ytvatten i egentliga Östersjön och att även salthalten kommer att sjunka. I en så kallad ekologisk niche-modellering visar jag att en klimatförändring kan innebära att utbredningen hos *Idotea* förskjuts norrut högre upp i Bottenhavet. Sådana förändringar i utbredningen hos *Idotea* kan få allvarliga konsekvenser för den endemiska (unik i Östersjön) smaltången *Fucus radicans*. Idag är smaltången sannolikt skyddad från alltför intensiv betning genom att utbredningsgränsen för *Idotea* slutar ungefär där smaltången börjar i Bottenhavet.

En demografisk analys av de tre *Idotea*-arterna, där jag mätte dödligheten, antal födda djur per kull och tid till könsmognad, visade att alla tre arterna lever nära sin gräns för överlevnad i Östersjön, och antyder en kostnad för acklimatisering och anpassning till det bräckta vattnet för *Idotea* som ursprungligen kommer från en marin miljö. Idag lever *I. balthica* nära sin maximala abundans i Östersjön, medan det för *I. granulosa* rapporterats om lokala utdöenden på flera platser. I min avhandling föreslår jag att *I. chelipes* förmodligen har den högsta kapaciteten för att anpassa sig till de ytterligare klimatförändringar som förväntas i Östersjön, eftersom den arten har en snabb populationstillväxt i en redan varierande miljö och dessutom visar den högsta genetiska mångfalden.

Idag är det inte klart om *Idotea* arterna är lokalt anpassade till den baltiska miljön i Östersjön eller om arterna visar en så kallade fenotypisk plasticitet, som betyder att individerna har stor tolerans för miljöförändringar. Därför behövs ytterligare studier av graden av lokal anpassning och eventuell genetisk bakgrund.

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List of Papers

My thesis is a summary of the following publications, which will be referred to in the text by their Roman numbers:

Paper I: **Leidenberger S**, Harding K, Jonsson PR (2012) Ecology and distribution of the isopod genus *Idotea* in the Baltic Sea: key species in a changing environment. *Journal of Crustacean Biology* 32(3): 359-381. *

Paper II: **Leidenberger S**, Jonsson PR (Manuscript submitted)
Closely related meso-grazers (Crustacea: Isopoda) in the Baltic Sea show diversity of life-history strategies.

Paper III: **Leidenberger S**, Panova M, Jonsson PR (Manuscript)
Phylogeography of the Baltic *Idotea* spp. (Crustacea: Isopoda)
– the history of a post-glacial colonization.

Paper IV: **Leidenberger S,** Bourlat SJ, De Giovanni R, Kulawik R (Manuscript)
Mapping predicted distribution for a meso-grazer guild in the Baltic Sea: climate change will force a northern shift with possible genetic isolation.

* The article is re-printed with the kind permission of The Crustacean Society (2012).

Related articles not included in the thesis:

Gutow L, **Leidenberger S**, Boos K, Franke H-D (2007) Differential life history responses of two *Idotea* species (Crustacea: Isopoda) to food limitation.
Marine Ecology Progress Series 344:159-172

Introduction

1. The genus *Idotea*

Marine isopods of the genus *Idotea* Fabricius 1798 consist of approximately 30 different species (Appeltans et al. 2013). Brusca (1984) regarded *Idotea* a cosmopolitan genus, but which is absent from the warm and tropic seas in both the Pacific and the Atlantic oceans. Most of the *Idotea* species are endemic and restricted to shorelines in Europe, North America or Asia. Only two species, *Idotea balthica* and *Idotea metallica*, have a cosmopolitan distribution and are typical rafters (Brusca 1984, Naylor 1955a). *Idotea* is living in the littoral (eulittoral/intertidial zone and sublittoral/neritic zone) and is often associated to many species of seaweeds. Occasionally all *Idotea* species can show a pelagic lifestyle through rafting.
At present the molecular-based taxonomy of *Idotea* is very limited (Xavier et al. 2010), but under construction (Leidenberger et al. unpublished). Furthermore, despite often being very abundant the overall knowledge about *Idotea* species distribution, habitat segregation, and differences in life histories or population structure is scare.

In Europe eight different species of *Idotea* can be found: *I. balthica*, *I. chelipes*, *I. emarginata*, *I. granulosa*, *I. linearis*, *I. metallica, I. neglecta* and *I. pelagica* (Fig. 1). *I. metallica* was first restricted to British waters (Naylor 1955a), but was recently found in the North Sea as a consequence of increased sea surface temperature (Franke et al. 1999). Sexual dimorphism in *Idotea* is known for morphological characters, size and behaviour patterns, like habitat and food choice as well as mobility (Gruner 1965, Merilaita & Jormalainen 2000, Jormalainen et al. 2001).

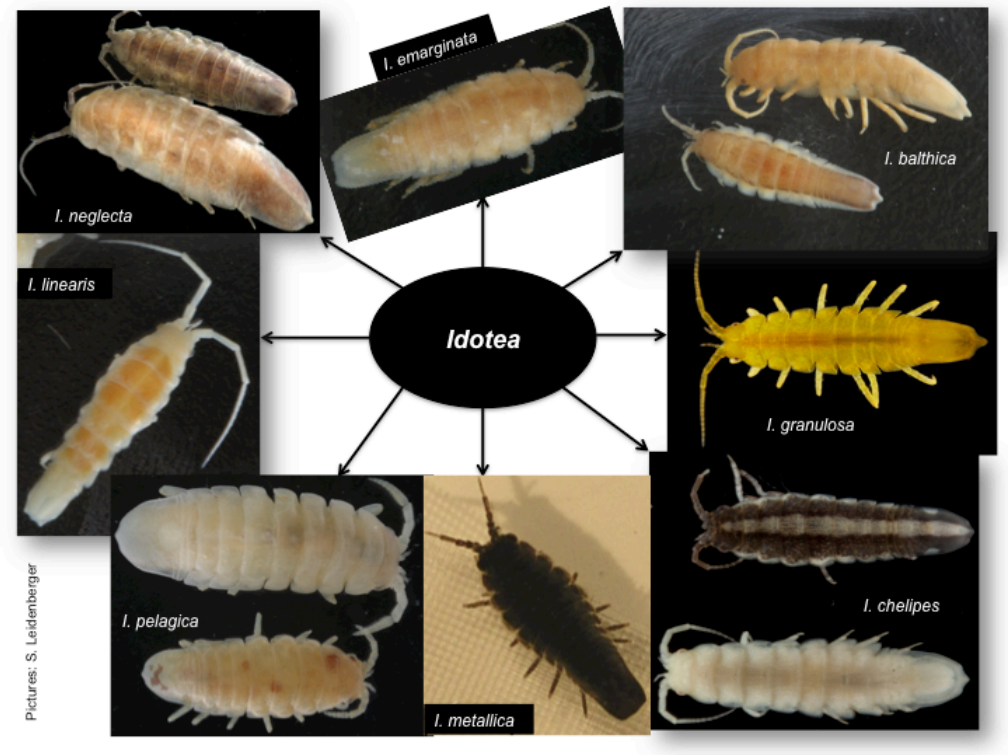


Figure 1: The eight *Idotea* species that can be found in Europe.

All species are generally described as omnivorous (Gruner 1965), but different preferences among the species exist and seem to depend on the local habitat. *I. pelagica,* for example, has a tendency to be carnivorous (Sheader 1977) and *I. neglecta* is described as a scavenger (Kjennerud 1950). *I. balthica* is known as an important grazer on different macro- and microalgae.

Whereas *I. emarginata*, *I. neglecta* and *I. pelagica* can be found in the Skagerrak and the Kattegat (Wahrberg 1930, H.G. Hansson pers. comm.), only *I. balthica*, *I. chelipes* and *I. granulosa* enter into the Baltic Sea. The first description of *I. balthica* (= *Oniscus balthicus)* was published by Pallas (1772) along the Baltic German coast of Schleswig-Holstein. He clearly noted the differences of *I. balthica* to the species he found some years before in England (= *O. chelipes*). For *I. chelipes,* the junior synonym *I. viridis* Sars, 1899 is often found in older literature. An overview of the basionym and junior synonyms for the three Baltic *Idotea* species is given in Table 1.

Many species of *Idotea* show high intra-specific variability and already Pallas (1772) mentioned the numerous colorations of the *I. balthica* specimens he found, but polymorphism is known for several *Idotea* species (*I. chelipes*: Sywula 1964, *I. granulosa*: Salemaa & Ranta 1991, *I. neglecta*: Kjennerud 1950).

Table 1: Basionym and junior synonyms for *Idotea balthica, chelipes* and *granulosa* (after Holthius 1949, Appeltans et al. 2013). The last table row presents the names of described subspecies existing in literature, but they are accepted as the species name.

Genus ***Idotea*** JC Fabricius, 1798
Family **Idotidae** Samouelle, 1819
Suborder **Valvifera** Sars, 1882
Ordo **Isopoda** Latreille, 1817

I. balthica[+] (Pallas)		***I. chelipes*** (Pallas)		***I. granulosa***, Rathke	
*Oniscus balthicus**	Pallas, 1772	*Oniscus chelipes**	Pallas, 1766	*Idothea granulosa**	Rathke, 1843
Oniscus tridens	Scopoli, 1763	*Oniscus viridis*	Slabber, 1769	*Idotea granulosa*	Tatersall 1911
Stenosoma irrorata	Say, 1818	*Idotea phosphorea*	Hoek, 1889	*Idotea cretaria*	Dahl, 1916
Idothea tricuspidata	Desmarest,1825	*Idothea salinarium*	Sars, 1899		
Idotea basteri	Audouin, 1826	*Idothea viridis*	Sars, 1899		
Stenosoma pusilla	Eichwald, 1942	*Idotea chelipes*	Holthius, 1949		
Idothea marina	Miers, 1881				
Idothea baltica	Sars, 1899				
Idotea sarsi	Collinge, 1917				
Idotea marina	Holthius, 1949				
I. b. baltica		*I. c. bocqueti* Rezig, 1977			
I. b. basteri Audouin, 1826		*I. c. mediterranea* Charfi-Cheikhrougha 1996			
I. b. marina					
I. b. stagnea, Tinturier-Hamelin, 1960					
I. b. tricuspidata Audouin, 1826					

+ The often found spelling of *I. baltica* is a misspelling – the accepted status of the species is *Idotea balthica* (Appeltans et al. 2013)
* basionym

In total, six major phenotypes and a number of combinations of those are described (Tinturier-Hamelin 1963, Salemaa 1978, Hull et al. 2001). The phenotype diversity is highest in more heterogeneous habitats (Salemaa 1978, Hull et al. 2001). In general, this polymorphism is heritable and modified by natural selection. Salemaa (1978) suggested frequency-dependent selection by predators (= fish) and that the substrate mosaic of the littoral are the main reasons for the camouflage in *I. balthica*. Distinct pigments (melanin granules/melanophores, crystalline purines/leucophores) in the chromatophores and in the eye are supposed to be responsible for the light-dark adaptation (Peabody 1939, Salemaa 1978).

All three *Idotea* species that have colonized the Baltic Sea are characterised by a broad salinity tolerance (Naylor 1955b, Harvey et al. 1973). The main salinity ranges based on published field data for *I. balthica*, *I. chelipes* and *I. granulosa* for the Baltic Sea are summarized in Figure 2.
More generally, *I. chelipes* is described as a brackish-water species, tolerating 3.5 to >50 PSU (Naylor 1955b, Naylor & Slinn 1958, Vlasblom et al. 1977), and mainly lives in shallow lagoons, estuaries or creeks. *I. granulosa*, in contrast, prefers more open exposed wasters, like the intertidal zone, with high oxygen content and turbulent waters (Naylor 1955b, Izquierdo & Guerra-García 2011). Sywula (1964) found *I. granulosa* mostly on overgrown rocky sea bottoms, with strong water movements. *Idotea balthica* is found in various habitats (shallow to fully exposed) and seems to be more flexible in its habitat choice than other *Idotea* species (Sywula 1964, Franke et al. 2007). It is also the only species that often can be found together with one of the other *Idotea* species. In studies on species interaction (Franke et al. 2007) or colonization patterns (Clarkin et al. 2012) *I. balthica* showed less propensity to choose between habitats compared to congeners.

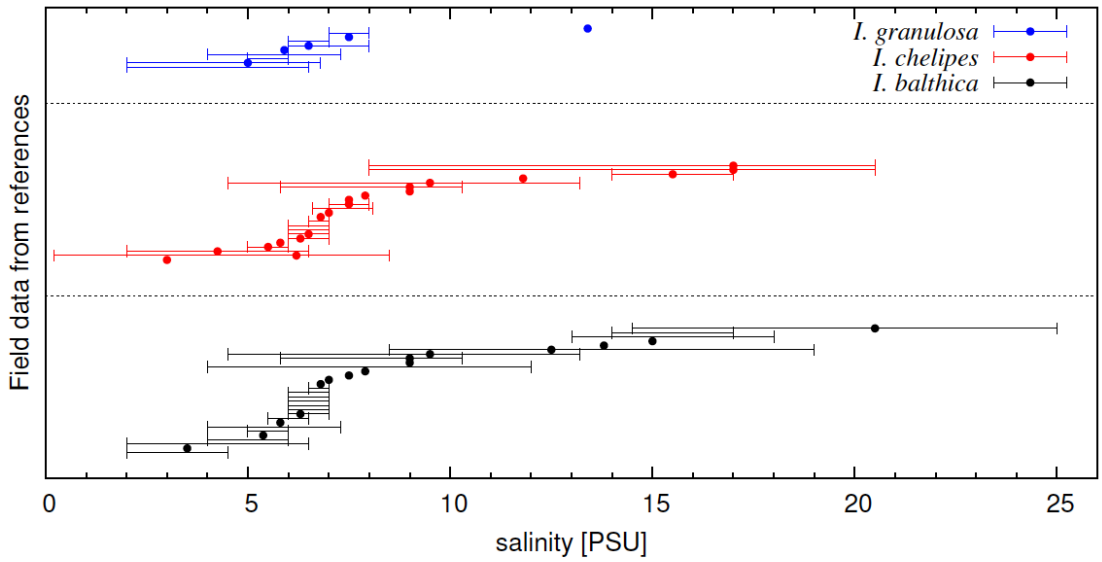


Figure 2: Reported salinity for *BA*, *CH* and *GR* in the Baltic Sea (the dot indicates the mean, the lines the ranges of salinity where the species were studied in field).

The genus is lacking a pelagic larval stage, and the females brood and give birth to juveniles looking like small adults and are not morphologically distinguishable between species or sex until they reach a length of 6-7 mm. Dispersal of *Idotea* is passive via drifting algae, wood and plastic debris (Thiel & Gutow 2005), or active on short distances by swimming and crawling from alga to alga.

The three *Idotea* species in the Baltic Sea that I have intensively studied in this thesis, have a distribution range in Europe from the Mediterranean Sea up to northern Norway and Iceland.

2. The ecological niche – restriction to a habitat?

To determine the niche of a species is a multifaceted task, since complex combinations of environmental factors allow a species to exist in a given geographical area or in a given community (Peterson et al. 2011). Hutchinson (1957) defined the fundamental niche of the species as a "set of points in an abstract n-dimensional space" (hypervolume), whereas the "realized niche" often only is a subset of the fundamental niche.

For marine species, salinity and temperature are the most important environmental variables determining their distribution ranges (Paavola et al. 2005, Gogina & Zettler 2010). For the isopod genus *Idotea* the Baltic Sea offered a new habitat/ecological niche under its formation after the deglaciation 8,000-10,000 years ago (Berglund et al. 2005). The environment the invading species faced in the new habitat differed clearly from the ancestral habitat. As one of the world´s largest brackish environment, the Baltic Sea has a strong, and fairly stable, salinity gradient from 25 PSU in the Skagerrak to nearly freshwater in the northern parts. Additionally, the temperature regime is colder during long winters, and the northern parts are often covered with ice, compared to full marine waters in northern Europe.

Holt et al. (2005) suggested that for successful invaders the population growth might be a key to rapid evolution. Invasion of a site A (Fig. 3) containing the ancestral habitat means that initial growth will be rapid and the selective environment is assumed to be similar to that of the native domain. The invasion to a site B, may force a slower growth rate and considerable variation may be lost, through stressful conditions near the boundary of the species potential niche. Outside the boundaries, the invaders will fail because population growth is too slow or negative (Fig. 3). Sites A and B can be regarded as "source habitats", whereas sites C and D are "sink habitats".

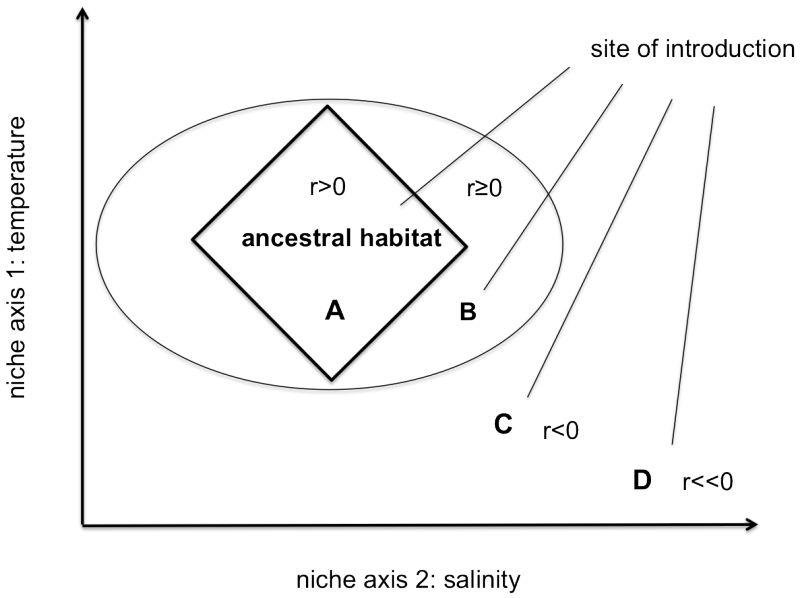


Figure 3: Schematic drawing of the niche definition after Holt et al. 2005. The rhombus shows the ancestral habitat where the conditions are inside the fundamental niche and permit deterministic persistence (e.g. population A) with high population growth. The ellipse represents conditions outside the niche, but where a population still can exist on its "margins" (e.g. B = near the niche). Outside the ellipse the population declines slowly or rapidly (e. g. C and D).

The *Idotea* species, *I. balthica*, *I. chelipes* and *I. granulosa* may have had a stronger evolutionary potential to invade the new habitat, "the Baltic Sea", compared to the other congeners of the genus that so far have failed. Johannesson et al. (2011) assumed that invaders, which colonized the early Baltic Sea, grew more and more adapted to the Baltic environment and this led to an increased differentiation from Atlantic populations. An alternative explanation is that the successful colonizers were sufficiently plastic to survive. Thus, an overall question is how much evolutionary adaptations have contributed to the persistence of Baltic populations compared to phenotypic plasticity.

3. What do we call for adaptation?

The terms "adaptation" and "plasticity" has been discussed in science for many decades, but more intensely with the expanding fields of population genetics/genomics and evolutionary ecology. Published papers with those terms increased from <50 in the early 1990´s to nearly 700 the last year, and citations including those two words increased to more than 20,000 in 2012 (Web of Science: plasticity*adaptation, April 2013). In the following paragraphs, the definition of the two terms and their relevance for my thesis will be addressed.

Phenotypic plasticity means a broad response of an organism to environmental changes through different phenotype expressions. For this set of expressed phenotypes, Stearns et al. (1991) introduced the term of reaction norm, but pointed out that even the expression of one single genotype as a function of one environmental variable can be called a

reaction norm. Adaptation, in contrast, is a trait that evolved by natural selection to improve the relative fitness (reproduction and survival) of an organism. If a population is locally adapted, the evolved trait provides individuals with an advantage under their local environmental conditions (Kawecki & Ebert 2004). To make things more complicated, the degree and strength of plasticity (reaction norm) can itself be under selection and thus considered an adaptation (Gotthard & Nylin 1995).

But how is it possible to distinguish between phenotypic plasticity and (local) adaptation? The obvious development of a morphological structure, like teeth in a cannibalistic lifestyle for instance, is a clear adaptation, in contrast to smaller size of an organism in response to low food levels, which is more unclear (Gotthard & Nylin 1995). A useful starting point can be comparative studies of reaction norms with respect to different habitats (Newman 1992) (paper I, II). Also comparisons between species and between populations within species can address adaptation questions (Curio 1973) (paper I, II, III). Another possible approach to this question is the reciprocal experiment, where genotypes from each site are transferred and showed to have the highest fitness at their own site of origin (Gotthard & Nylin 1995). However, this approach was not used in this thesis. Furthermore, common garden experiments where essential factors are manipulated under laboratory conditions while controlling for other factors (Kawecki & Ebert 2004) can be performed to test subsamples of different populations (paper II). And overall, the measurements of basic fitness parameters, like fecundity, the net reproductive rate, juvenile survival, can be used to detect local adaptations (Kawecki & Ebert 2004) (paper II).

To identify different traits under divergent selection it is also interesting to study their genetic bases. Here a good start is an overall identification of the population structure, like it is analysed in phylogeographic studies (paper III). With the advent of population genomics and next-generation sequencing, further studies may reveal selected domains and even suggest candidate genes for critical adaptations (Allendorf et al. 2010).

Aim of the thesis

The association and interactions between the macro-algae *Fucus* spp and meso-grazers like *Idotea* spp. have been intensively studied in the Baltic Sea for several decades. Many studies are focused on feeding choice and grazing pressure of *I. balthica* (Jormalainen et al. 2001, Kotta et al. 2006, Råberg & Kautsky 2007, Forslund et al. 2012), or on chemical defenses shown by the alga against the grazer (Wikström et al. 2006, Jormalainen et al. 2008, Haavisto et al. 2010). To date, only few papers have analyzed the physiology of Baltic *Idotea* or have investigated the two species *I. chelipes* and *I. granulosa* (Hørlyck 1973, Lapucki et al. 2005, Lapucki & Normant 2008). Recently, some studies were published analyzing the local adaptation and co-evolution of *I. balthica* to its host/food alga in the Baltic Sea (Hemmi & Jormalainen 2004, Jormalainen et al. 2008, Vesakoski et al. 2009, Nylund et al. 2012).
In my thesis, the main goal has been to understand the Baltic *Idotea* complex, consisting of three species and forming a guild of meso-grazers in a relatively species-poor ecosystem. I tried to clarify their different ecological niches and population structures along the salinity gradient that is characterizing the Baltic Sea and represents an extreme environment for the marine isopods.
The specific aims for each of the included papers in this thesis were:

Paper I: To review the distribution patterns and the ecology of the three Baltic *Idotea* species, through an intensive literature survey and meta-analysis, including information from museum collections around the Baltic Sea. The role of *Idotea* in the food web was outlined (bottom-up and top-down effects) and to try to understand the community dynamics involving the genus. How on-going environmental and human generated changes may impact populations of the *Idotea* spp. were also discussed.

Paper II: To analyze the life history traits of the three Baltic *Idotea* species, to better understand their life cycle and breeding ecology. In a common-garden experiment the growth, survival and fertility for all three species were compared. The population growth rate was estimated for each analyzed population, and used as a measurement of long-term fitness and compared with fully marine populations.

Paper III: To understand the history of post-glacial colonization of the three *Idotea* species into the Baltic Sea, a phylogeographic study based on a fragment of the mitochondrial COI gene was performed. The population structure along the Baltic salinity gradient was analyzed and splitting time between populations was calculated for each species.

Paper IV: To model the climate niche space of the Baltic *Idotea* spp. and *Fucus vesiculosus/radicans,* ecological niche modelling was performed. The data set for *Idotea* was based on distribution data from paper I. Predicted distributions of the present and future were mapped. Possible distribution changes for the grazer and its host algae as well as consequences for the *Fucus-Idotea* association were discussed.

Main results and discussion

1. Top-down and bottom-up effects – the role of Baltic *Idotea* spp.

The three Baltic *Idotea* spp. have a central functional role as grazers in the food web and may act as key species in the Baltic coastal ecosystem. They are among the dominant meso-grazers in the perennial canopy-forming *Fucus* belt as well as in *Zostera marina* beds (paper I). With impressive feeding rates on a range of epiphytes/filamentous algae, *Idotea* has a positive effect on the removal of epiphytes (paper I). But even if *Idotea* can control epiphyte growth on seagrass (Jaschinski & Sommer 2008), and a recently study could show that the presence of invertebrate meso-grazers mediate the effect of climate change on primary biomass production (Alsterberg et al. 2013), *Idotea* is not able to control the enormous mats of filamentous algae in the Baltic Sea (paper I).

On macrophytes, especially on *Fucus* spp., *Idotea* can also have a direct and negative grazing effect by destroying the whole algal habitat (Engkvist et al. 2004). Phlorotannin-rich algal species, like *Fucus vesiculosus*, seem to evolve local adaptations for Baltic populations through selection caused by the grazing pressure from *Idotea* (Hemmi & Jormalainen 2004, Nylund et al. 2012). Interestingly, the newly described endemic species *Fucus radicans,* which shows a restricted distribution to the northern parts of the Baltic Sea (Bothnian Sea), where *Idotea* is less present (paper I and IV), is the more preferred *Fucus* spp. in feeding experiments (Gunnarsson & Berglund 2012).

Beside top-down effects, we could also show, that *Idotea* is involved in numerous bottom-up effects, through its importance as prey for numerous fish species (paper I). The on-going shift to more small-sized fish caused by declining populations of overfished piscivores (Eriksson et al. 2009, Eriksson et al. 2011), can have cascading effects on the meso-grazer guild and deserves future studies. Local extinctions as recently observed for all three *Idotea* species (paper I and II) at different places in the Skagerrak-Kattegat region and in the Baltic Sea are discussed as one consequence of overfishing.

2. Habitat segregation and different life history strategies

The three *Idotea* spp. show more or less clear habitat segregation (paper I and II). Whereas *I. balthica* is more flexible in habitat and food choice, and should be considered as an omnivore in the Baltic Sea, *I. chelipes* and *I. granulosa* have more restricted niches. *I. chelipes* is generally found in the Baltic Sea closely to moderately exposed shores or in lagoons, mainly in the surface waters. In contrast, *I. granulosa* typically inhabits open waters with strong wave movements, where it often is the dominant species (paper I). These findings coincide with the general patterns of the three *Idotea* spp. described in the introduction part (see above). *I. balthica* often is found together with one of the other two species, but also all three species can coexist and compete for food resources and space (Korheina 1981).

From paper II it became clear, that the different habitats are also reflected by different life history strategies of the *Idotea* spp. Classical ecological theories (MacArthur & Wilson 1967, Pianka 1970) predict that ephemeral and variable habitats will select for fast growth rates (*r*-selection), and more stable habitats for a more efficient use of resources (*K*-selection). And indeed, *I. balthica* is with larger body size, a delayed reproduction, low fecundity, high juvenile mortality and slow population growth, more of a generalist and *K*-selected species in the Baltic Sea. *I. chelipes*, in contrast, is characterized by small body size, early reproduction, high fecundity and higher adult mortality (*r*-selected species) (paper II). The third species, *I. granulosa* seems to be less competitive in the Baltic Sea, since it inhabits adverse environments and was characterized by slower growth and deferred maturity (similar to an adversity strategy: Grime 1977 and Greenslade 1983) (paper II). According to Sywula (1964), *I. balthica* occupied the most favorable habitats in the Baltic Sea and may displace *I. granulosa* to less favorable habitats (paper I). Furthermore, this species died early after reproduction and showed the shortest lifespan. For, *I. chelipes* we found the longest breeding season and as the fast growth rate and the large reproductive effort, coincide with other reports in the Baltic Sea (Korheina 1981, Jazdzewski 1970).

3. *Idotea* ´s history of colonizing the Baltic Sea

As reviewed in paper I, Sywula (1964) proposed the idea, that *I. chelipes* was the first species that entered into the Baltic Sea, because of its preference for brackish environments. He argued, that the most probable moment for colonization was the transition from the Ancylus Lake to the Littorina Sea (around 7,500 years ago), and only later when the Baltic Sea was invaded by more marine species, *I. balthica* and *I. granulosa* followed and pushed *I. chelipes* into isolated estuaries again.

With the results of our phylogeographic study and reconstruction of the demographic history, we find exactly the opposite (paper III). Supposedly, after the Baltic Sea became a marine environment, *I. granulosa* invaded the new habitat first from populations outside the Baltic, followed by *I. balthica* and *I. chelipes*. Not only the coalescent model estimates but also the haplotype networks of the threes species suggested an early and rapid colonization for at least *I. granulosa* and *I. balthica*. Small estimated population sizes suggest that these species have gone through a bottleneck under colonization, which is conforming to several other Baltic species (reviewed by Johannesson & André 2006).
Furthermore, all three species were genetically distinct from populations outside the Baltic Sea (paper III), but the degree was around 10 times higher for *I. granulosa* and *I. balthica* than for *I. chelipes*. Interestingly, *I. chelipes* clearly differs from the genetic patterns that most of the other Baltic species show along the Baltic salinity gradient with lower levels of nucleotide and haplotype diversity (Johannesson et al. 2011). Another known exception is the Baltic clam *Macoma balthica*, which showed higher genetic diversity within the Baltic Sea through old genetic lineages (Luttikhuizen 2003, Nikula et

al. 2007). But for *I. chelipes*, the genetic diversity was nearly the same in all populations, thus haplotypes were shared or closely related to the diversity in other analyzed populations (paper III).

4. Future distribution patterns: salinity *versus* temperature

The review over the distribution patterns over the last 150 years for the *Idotea* spp. in the Baltic Sea indicated a fairly constant large-scale distribution (paper I). *I. balthica* is the most recorded species, maybe due to its high abundance at most parts of the Baltic Sea. The species probably lives close to its carrying capacity in the Baltic Sea (paper II). The northernmost described distribution is at 62°N. *I. balthica* does not enter into the low salinity areas of the Bothnian Bay and the Gulf of Finland (see Graphical Abstract), where also its host alga *Fucus vesiculosus* is absent. *I. chelipes* show similar distribution patterns to *I. balthica*, but does surprisingly not enter as deep into the Gulf of Finland or the west coast of the Bothnian Bay (paper I), even if it is known to have a broader salinity tolerance (see introduction above). *I. granulosa* differs clearly in its distribution pattern compared to the other two congeners. This species extends only to around the Åland Islands, and does neither enter into the Gulf of Finland nor into the Bothnian Bay (paper I).

Based on the recorded distributions of the *Idotea* spp. and modeled temperature and salinity patterns during the summer months (June-August) (paper I), we found that *I. chelipes* significantly occur at higher summer temperatures, and *I. balthica* significantly at lower salinities. This might be the reason, why *I. balthica* penetrates further into the Gulf of Finland and the Bothnian Bay than *I. chelipes* does. Vlasblom et al. (1977) suggested after experimental studies on osmoregulatory ability, that the interaction of temperature and salinity might limit *I. chelipes* distribution patterns.

In paper IV the predicted distribution of *I. balthica* through ecological niche modelling (using the environmental layers of mean salinity, mean sea surface temperature, mean distance to land and maximum depth), showed that the most suitable habitats are along the coasts of the Arkona Basin, the Baltic Proper and Gulf of Riga. In the Gulf of Finland and Bothnian Bay the suitability clearly decreased. Those results fit well the real distribution of the species described above (paper I). The ecological niche modelling could also show that the predicted distribution seems to be determined rather by temperature than by salinity (paper IV). In general, the mean sea surface temperature is coldest and the ice cover remains longest for the Bothnian Bay (Feistel et al. 2008). Whereas the predicted distribution for *I. balthica* and *I. chelipes* was quite similar (paper IV), the ecological niche model showed a higher suitability for distribution patterns to exposed open waters for *I. granulosa* in the Skagerrak, the west coasts of Denmark and Norway. Moreover, a broader distribution range for the narrow wrack *Fucus radicans* could be predicted compatible with its known distribution today.

5. Consequences of predicted climate changes

Climate changes have characterized the evolution on earth through the different geological stages, accompanied by extinctions of species (Futuyma 2009). Past temperature changes were thought to be no more than 1°C, but recent studies from Greenland and Antarctica have indicated intervals of rapid temperature changes (Botkin et al. 2007). In Europe, the temperature increased rapidly at the end of the last glaciation, when the shores of the North Atlantic allowed the Gulf Strom to reach the coastlines of Northern Europe. Future climate change scenarios under different greenhouse gas scenarios predict a global and rapid temperature increase, melting the ice cover at the poles, causing sea level rise and dryness in tropical areas (IPCC 2007).

The climate change is also expected to affect the Baltic Sea (Belkin 2009, Meier et al. 2011, Meier et al. 2012). Various climate scenarios predict different changes. Early models predicted a dramatic salinity decrease of 3-4 PSU (use of climate model ECHAM4: Meier 2006), while recent models predict more moderate changes of 1.5-2 PSU for the sea surface salinity through increased runoffs in the Baltic Proper (use of climate model ECHAM5: Meier et al. 2012). Both climate models clearly indicate an increase of sea surface temperature of up to +4°C for the central Bothnian Bay and Bothnian Sea (Meier et al. 2006, Meier et al. 2012).

In paper I, we used historical data from HELCOM (1960-2010) and the Rossby Center Oceanographic Model (Meier et al. 2003) to model temperature and salinity for the *Idotea* records during the summer months. The findings indicated an increased sea surface temperature of 0.06°C per year and a salinity decrease of 0.014 PSU per year (paper I). Even if it is speculative, we found a significant latitudinal southern shift of *I. granulosa* and *I. chelipes* from 1.5° and 1.15°. Interestingly, recently literature reports for changes in *Idotea* distribution exist and coincide with those results. *I. chelipes* is now rare in the Gulf of Riga, but more abundant in the Gulf of Gdansk (Kotta et al. 2000, Lapucki & Normant 2008). For *I. granulosa*, several local extinctions are reported at Falsterbo Peninsula, Sweden (paper II), the Bay of Puck and Bay of Gdansk in Poland (Zettler et al. 2000, Jazdzewski et al. 2005). Also dramatically declines of *Idotea* spp. along the Swedish West coasts are reported (Moksnes et al. 2008).

If the important habitat corridor between Atlantic and Baltic populations will disappear, Baltic populations will become more isolated. In paper IV ecological niche model predicted distribution patterns for *Idotea* spp. under a 2050 climate change scenario (ECHAM5), that showed a northern shift of the meso-grazers deeper into the Bothnian Bay. Such consequences may lead to overlapping habitats of the *Idotea* and *Fucus radicans*. Recently, the cold temperatures seems to restrict *Idotea* to the southern area of the Bothnian Bay (paper IV), which might have provided a unique ecological niche for the recently evolved endemic narrow wrack that seems less chemically protected against heavy grazing pressure like its mother species *F. vesiculosus* (Gunnarsson & Berglund 2012). Overlapping habitats of the grazer and the host alga, caused by climate changes,

can harbor the risk of extinction for the endemic *Fucus* species. A northern shift of populations may also force more genetic isolation from Atlantic populations. Johannesson et al. (2011) emphasized that high genetic variation increase the capacity to adapt to environmental changes. For *I. balthica* and *I. granulosa* we could show, that genetic variation were lost through the colonization of the Baltic Sea (paper III). Moreover, the demographic analysis in paper II suggested that all three *Idotea* spp. live close to their limits in the Baltic Sea. The obvious change in life history traits from the North Sea to the Baltic Sea can be a cost of acclimation or adaptation.

Plasticity in fecundity and numbers of broods in response to abiotic factors may have facilitated the colonization of brackish waters for the *Idotea* guild, since plasticity can allow populations to rapidly acclimate to new environmental conditions (Crispo 2008). Temperature definitely seems as an important factor not only for breeding time and reproductive effort of *Idotea* spp. (paper II), but also in determining distribution patterns for the meso-grazers (paper I and IV).

In my thesis, I clearly could show that there is evidence for local extinction of *I. granulosa* (paper I and II), where *I. balthica* and *I. chelipes* seem to be more tolerant to, e.g. organic pollution (paper I, Korheina 1981). *I. chelipes* as a typical *r*-selected species showed, for instance, high elasticity for juvenile mortality and high reproductive value that peaked early (paper II). This means an advantage in more variable environments, e.g. high temperatures, salinity changes and oxygen deficiency. Moreover, this species has not lost genetic variation as much like the other two species through its post-glacial colonization to the Baltic Sea (paper III), which may increase its capacity to adapt even to further predicted climate changes.

My studies on the Baltic *Idotea* spp. provide a clear example, how predicted environmental changes may force ecosystem changes as exemplified with a meso-grazer guild, especially in a species-poor ecosystem with likely low resilience capacity.
Future investigations on Baltic *Idotea* spp. should be concentrated on multi-stressor experiments (temperature x salinity) or on reciprocal experiments. Intensified studies on local adaptations of the three *Idotea* spp. may help us to understand their evolutionary potential, which seems to be key for how Baltic *Idotea* populations can cope with future climate changes that are predicted to alter the Baltic Sea on a very rapid timescale.

Conclusions

To summarize my PhD thesis, the following main findings can be pointed out:

* *I. balthica* and *I. granulosa*, but not *I. chelipes*, lost genetic variability during colonization of the Baltic Sea.

* Supposedly, *I. granulosa* was the first colonizer, followed by *I. balthica* and *I. chelipes*.

* Life history traits of Baltic *Idotea* spp., at least for *I. balthica* and *I. chelipes*, are affected by decreased salinities. All three species live at their limits (”margins”) with a population growth rate (lambda) close to one in the Baltic Sea.

* Life history strategies obviously differ between the three Baltic *Idotea* species, which is reflected by their habitat segregation.

* Different distribution patterns may be a result of salinity tolerance, which seems to be higher for *I. balthica* and *I. chelipes* than for *I. granulosa*, but temperature may also have a strong role in the Baltic Sea.

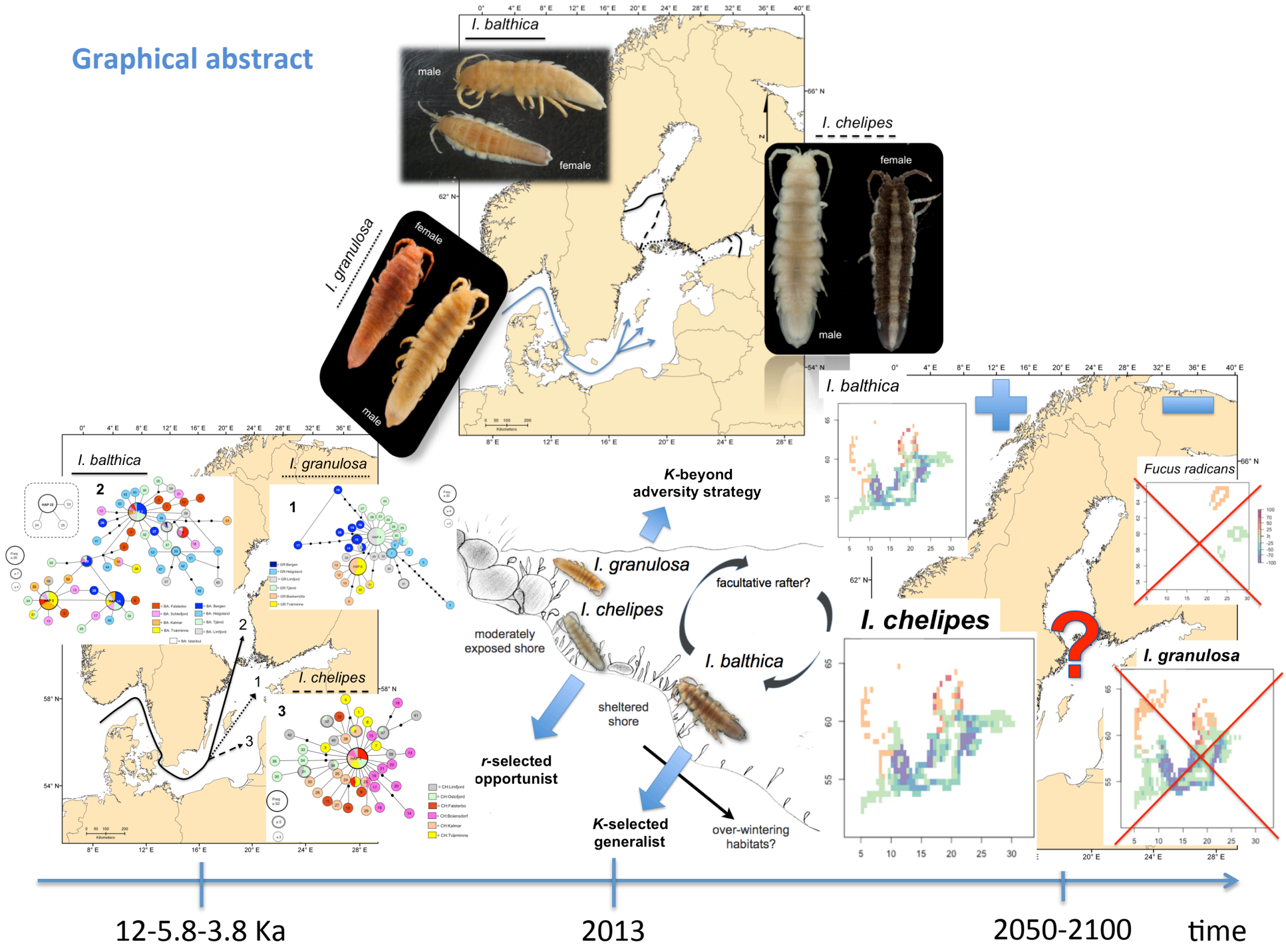
* On-going environmental and human-generated changes are affecting/will affect the meso-grazer guild. Whereas *I. granulosa* already is locally extinct in some areas, *I. chelipes* may have the greatest “buffer” against predicted changes.

* Predictions for *Idotea* spp. under a climate change scenario for the Baltic Sea showed a future northern shift of the species, which may increase the risk of extinction for *Fucus radicans*, because it seems more susceptible to high grazing pressure.

* The evolutionary potential and the presence of local adaptations may be the key for all of the three *Idotea* species to survive the predicted extreme environmental changes in the Baltic Sea.

* The Baltic *Idotea* species are suitable models for further investigations of rapid adaptations to extreme environments.

Graphical abstract



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