ORIGINAL ARTICLE

Mapping present and future potential distribution patterns for a meso-grazer guild in the Baltic Sea

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ABSTRACT

Aim The Baltic Sea is one of the world's largest semi-enclosed brackish water bodies characterized by many special features, including endemic species that may be particularly threatened by climate change. We mapped potential distribution patterns under present and future conditions for a community with three trophic levels. We analysed climate-induced changes in the species' distribution patterns and examined possible consequences for the chosen food web.

Location Baltic Sea and northern Europe.

Methods We developed two open-source workflow-based analytical tools: one for ecological niche modelling and another for raster layer comparison to compute the extent and intensity of change in species' potential distributions. Individual ecological niche models were generated under present conditions and then projected into a future climate change scenario (2050) for a food web consisting of a guild of meso-grazers (*Idotea* spp.), their host algae (*Fucus vesiculosus* and *Fucus radicans*) and their fish predator (*Gasterosteus aculeatus*). We used occurrence data from the Global Biodiversity Information Facility (GBIF), literature and museum collections, together with five environmental layers at a resolution of 5 and 30 arc-minutes.

Results Habitat suitability for *Idotea balthica* and *Idotea chelipes* in the Baltic Sea seems to be mostly determined by temperature and ice cover rather than by salinity. 2050 predictions for all modelled species show a northern/north-eastern shift in the Baltic Sea. The distribution ranges for *Idotea granulosa* and *G. aculeatus* are predicted to become patchier in the Baltic than in the rest of northern Europe, where the species will gain more suitable habitats.

Main conclusions For the Baltic Sea, climate-induced changes resulted in a gain of suitable habitats for *F. vesiculosus*, *I. chelipes* and *I. balthica*, whereas lower habitat suitability was predicted for *I. granulosa*, *F. radicans* and *G. aculeatus*. The predicted north-eastern shift of *I. balthica* and *I. chelipes* into the distribution area of *F. radicans* in the Baltic Sea may result in increased grazing pressure. Such additional threats to isolated Baltic populations can lead to a higher extinction risk for the species, especially as climate changes are likely to be very rapid.

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INTRODUCTION

Ecological niche modelling (ENM) has become a widely used approach for analysing species distributions and predicting changes in biodiversity patterns (Guinan *et al.*, 2009; Kulhanek *et al.*, 2011). Niche modelling techniques aim to recover the ranges of suitable habitat for a species by identifying environmental conditions associated with the species'

occurrence (Peterson *et al.*, 2011). Potential distribution (PD) models can be generated using relatively few variables to characterize the abiotic environment of the species. These variables are held in the form of geo-referenced raster layers. Biotic factors such as predation and/or competition also determine the niche of species, but in marine ecosystems abiotic factors (e.g. salinity and temperature) are considered the major features limiting the distribution of many species at the macroscale (Paavola *et al.*, 2005; Gogina & Zettler, 2010). Because species' ranges conform closely to their thermal limits in aquatic systems, ecological niche modelling can yield a more accurate prediction of range shifts than on land (Sunday *et al.*, 2012).

The Baltic Sea (BS) is one of the world's largest semi-enclosed brackish water bodies and is characterized by numerous special environmental features. Temperature and salinity, for instance, have very different ranges than in most other marine waters of the world, which results in unique water layer dynamics (Stipa & Vepsäläinen, 2002). The transition from the North Atlantic via the Skagerrak, Kattegat and Belt Sea to the entrance of the BS is characterized by a salinity gradient of 33–15 psu (practical salinity units). This gradient continues in the Baltic Proper with salinities around 10–8 psu in the Arkona Basin up to the Bothnian Bay and nearly freshwater in the Gulf of Finland (Fig. 1).

Following the latest deglaciation (*c.* 8–10 ka), immigrating species must have evolved a broad salinity tolerance to survive. Most of the marine species that have invaded the Baltic have gone through a bottleneck during colonization, with known losses in genetic variation, such as in the herring *Clupea harengus* and the harbour seal *Phoca vitulina* (Johannesson & André, 2006).

Biodiversity in the BS declines with the salinity gradient for species of both marine and freshwater origin (Bonsdorff, 2006). As the BS is a species-poor environment, communities tend to be less complex and often consist of only a few key species (Leidenberger *et al.*, 2012). In this paper, we model climate-induced distribution changes in a community consisting of three trophic levels: two primary producers, three grazers and a predator.

Two important key taxa in the BS are the meso-grazers of the isopod genus *Idotea* and the macroalgae *Fucus vesiculosus* Linnaeus, 1753 and *Fucus radicans* Bergström *et al.*, 2005 (Kautsky *et al.*, 1992; Leidenberger *et al.*, 2012). The bladder wrack (*F. vesiculosus*) has a wide distribution in the Northern Hemisphere. In the Baltic, it is the only perennial, canopy-forming macroalga, forming an important habitat in the littoral zone, down to around 10 m in depth. The endemic *F. radicans* (narrow wrack) is thought to have recently evolved from *F. vesiculosus* in the BS during the last 400 years (Bergström *et al.*, 2005; Pereyra *et al.*, 2009). Regarding the marine isopods, among the eight European *Idotea* species, three – *Idotea balthica* (Pallas, 1772), *Idotea chelipes* (Pallas, 1766) and *Idotea granulosa* Rathke, 1843 – have successfully colonized and adapted to the BS. Whereas *I. balthica* has a cosmopolitan distribution, the other species are restricted to European coastlines. In the BS, *Idotea* spp. graze heavily on macro- and microalgae and are important prey (Leidenberger *et al.*, 2012), for example for the three-spined stickleback, *Gasterosteus aculeatus* Linnaeus, 1758, a small predatory teleost living in marine and freshwater habitats in the Northern Hemisphere.

In the Baltic Proper, grazing by *Idotea* can lead to a dramatic decline of *Fucus* populations (Nilsson *et al.*, 2004). The high grazing pressure of *Idotea* has driven selection for increased grazer resistance in Baltic populations of *F. vesiculosus* compared with populations outside the BS (Nylund *et al.*, 2012). *Idotea* is also suggested to limit the southern distribution range of *F. radicans* in the BS through intense grazing effects (Gunnarsson & Berglund, 2012).

One level up in the trophic chain, *G. aculeatus* is known to be able to control benthic meso-grazers on Swedish coastlines (Eriksson *et al.*, 2009). As a consequence of heavy commercial fishing for larger predatory fish (e.g. *Gadus morhua*, *Esox lucius*), small predatory fish, such as *G. aculeatus*, now dominate most of the sheltered-coast Baltic communities (Eriksson *et al.*, 2011). Top-down and bottom-up effects on coastal ecosystems are multifaceted and become even more complex when human impacts and climate change are taken into account.

Studies using ENM to predict changes in distribution patterns of marine key species due to climate change are still rare. Many studies on changes in marine species distribution focus on invasive species (Peterson, 2003; Ba *et al.*, 2010), or are motivated by the economic importance of fish stocks (Lenoir *et al.*, 2011). In this study, an ENM-based approach was used to determine the potential species distribution for six species of a Baltic trophic chain. Using the PD maps obtained, temperature and/or salinity effects on the distribution pattern of *Idotea* spp. were analysed to answer the following questions. (1) Which environmental factors most influence the distribution range of the grazers in the BS and northern Europe? (2) What climate-induced changes are predicted for the meso-grazers, the host algae and the fish predator under a climate change scenario for 2050? (3) What might be the consequences for this food web?

MATERIALS AND METHODS

We used the Taverna Workflow Management System (Hull *et al.*, 2006) to create a pipeline (workflow) of existing tools and web services. Workflows were executed using the Taverna portal (https://portal.biovel.eu/), a web interface built through the BioVeL project (http://www.biovel.eu/) that allows users to run workflows without installing the Taverna workbench (http://www.taverna.org.uk/) (accessed 25 February 2013).

For this study, we used two novel workflows: one for ENM and one for statistical analysis of potential-distribution maps (raster layers). All versions of the ENM workflows can be downloaded from the MyExperiment repository (http://purl.ox.ac.uk/workflow/myexp-3355.20; accessed 2 December
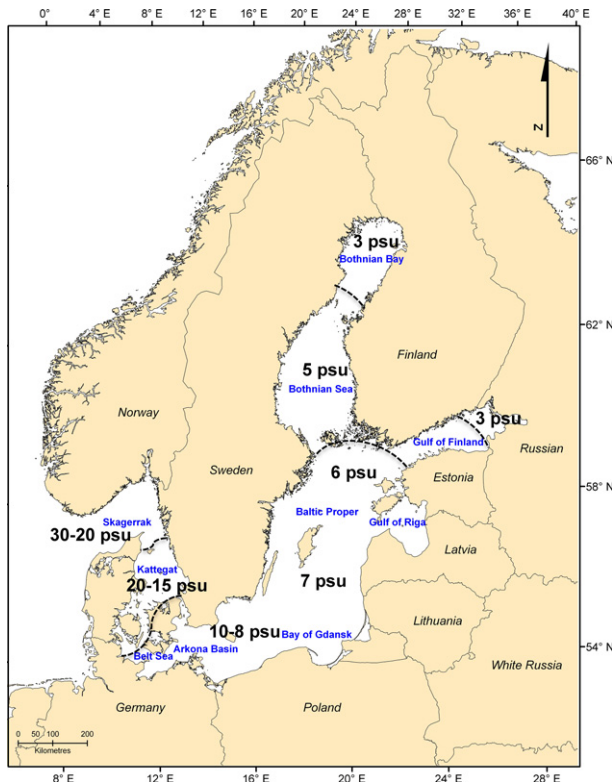
Figure 1 Study area of the meso-grazer guild. Mean sea-surface salinity values show the characteristic salinity gradient of the Baltic Sea. psu = practical salinity unit.

2013). Version 20 of the ENM workflow was used in our analyses. The ENM workflow uses occurrence and environmental data to model ecological niches using a web service based on openModeller, a library that provides a variety of algorithms to model species distribution patterns (http://openmodeller.sf.net/) (Muñoz *et al.*, 2011). The second workflow, the ENM Statistical Difference Workflow (ESW DIFF) (http://purl.ox.ac.uk/workflow/myexp-3959.2; accessed 23 January 2014) allows the spatial computation of changes in PD maps by calculating the differences between two raster layers using the R statistical environment 3.0.2 (R Core Team, 2013).

Occurrence data

Occurrence data for all species were extracted from GBIF (Global Biodiversity Information Facility; http://gbif.org/) during spring 2013 (see Appendix S1 in Supporting Information) (Table 1). For the *Idotea* spp., additional occurrence records were gathered through an extensive literature survey and manually geo-referenced (Appendix S2) as well as obtained from museum collections (FMNH Helsinki; GOM Stralsund; SMF Frankfurt; SMNH Stockholm; ZIN St. Petersburg; ZMB Berlin; ZMH Hamburg) and through our own sampling (Appendix S3). For *F. vesiculosus* and *F. radicans*, GBIF records were either concentrated in a small area of the Baltic that is not representative of the species' full distribution

range, or were too few (< 50). Consequently, additional occurrence points were created by geo-referencing in the known distribution range from the literature (Bonsdorff, 2006; Schagerström, 2013) (Table 1, Appendix S2). All occurrence data collected for this study have been submitted to the OBIS database (http://www.iobis.org/) (http://www.vliz.be/nl/imis?module=dataset&dasid=4607; title of data set 'Observations of three *Idotea* species (*I. balthica*, *I. chelipes* and *I. granulosa*) in northern Europe, including the Baltic Sea').

Environmental data

Environmental layers that are likely to affect the distribution of the species were chosen based on the literature (Table 1). Global marine layers came from Bio-Oracle (http://www.bio-oracle.ugent.be/; data downloaded 14 August 2013) at a resolution of 5 arc-minutes (Tyberghein *et al.*, 2012), and from AquaMaps (http://www.aquamaps.org/download/main.php; data downloaded 1 April 2008) at a resolution of 30 arc-minutes (Kaschner *et al.*, 2010). Layers for mean annual sea-surface salinity (SSS) and sea-surface temperature (SST) were available at a resolution of 5 arc-minutes for the present only, so we combined them with 30 arc-minute layers from AquaMaps for sea ice concentration (SIC), mean distance to land (DL) and maximum depth (MD) (Table 1). For the 2050 projection, only 30 arc-minute layers from AquaMaps were used. Present-day datasets from AquaMaps were built from long-term averages of temporally varying environmental variables (Ready *et al.*, 2010), whereas BioOracle layers were based on monthly level-3 pre-processed satellite data from NASA (Tyberghein *et al.*, 2012). For the PD under 2050 climate conditions, the AquaMaps layers were derived from the ECHAM5 A1B climate change scenario (Jungclaus *et al.*, 2006; IPCC *et al.*, 2007).

To address the question of which environmental factors mostly influence the distribution range of the grazers, we used a jackknife leave-one-out procedure (Peterson *et al.*, 2011) based on area under the curve of a receiver operating characteristic plot (AUC) values for SIC, SST and SSS for the Baltic and the known distribution area of the species (Table 2). In this procedure, for each environmental variable a model was created without it, and then model assessments were compared across the different layer sets. The most influential variable was considered the one that, when not included in the model, produced the lowest assessment value.

Occurrence point filtering

Occurrence data were filtered for environmentally unique points by running an initial BioClim workflow also based on the openModeller web service, using the same environmental layers as in the ENM workflow. This procedure avoids passing redundant information to niche modelling algorithms later. Besides filtering the points, the workflow generated a BioClim model (Busby, 1986; Nix, 1986) to calculate the environmental range for each variable (Table 3). The

Table 1 Table showing the origin of the data and the parameters used for ecological niche models (ENMs) for all study species in the Baltic Sea and their maximum distribution range. The table shows the total number of occurrence records before filtering, information on the species' biology from the literature, and the environmental layers selected. DL, distance to land (km); MD, maximum depth (m); SIC, sea ice concentration (30 arc-min); SSS, sea- surface salinity (psu); SST, sea-surface temperature (°C) (5 arc-min). All layers are mean annual values, except MD.

						Selected layers	
Species	Total GBIF records distribution	GBIF records Baltic	Other records Baltic*	Origin	Salinity tolerance [psu]	5 arc-min† (Bio-Oracle, Tyberghein, *et al.*, 2012)	30 arc-min (Aqua-Maps, Kaschner *et al.*, 2010)
Fucus vesiculosus	11072	575	332	Marine	4–35	SSS	(SSS), SIC, DL, MD
Fucus radicans	1	1	249	Brackish	3–7	SSS	(SSS), SIC, DL, MD
Idotea balthica	173	94	765	Marine	3–35	SSS, SST	(SSS, SST), SIC, DL, MD
Idotea chelipes	518	44	376	Marine	3–35	SSS, SST	(SSS, SST), SIC, DL, MD
Idotea granulosa	1105	26	149	Marine	5–35	SSS, SST	(SSS, SST), SIC, DL, MD
Gasterosteus aculeatus	24891	1384	0	Fresh–Marine	0–34	SSS, SST	(SSS, SST), SIC, DL, MD

*Data collected by S. Leidenberger, data from museum collections and literature.
†Used in the present projection only; for the 2050 projection, 30 arc-min layers were used exclusively.

workflow can be downloaded from http://purl.ox.ac.uk/work-flow/myexp-3725.2; last accessed 2 September 2013.

Main ENM workflow

The niche modelling workflow (Fig. 2) uses occurrence data as input combined with a set of environmental layers (correlative approach) and a modelling algorithm defined by the user. A manual interaction step in the workflow allows algorithm and parameter selection. In this study, we used Mahalanobis distance (Mahalanobis, 1936; Farber & Kadmon, 2003) by means of the openModeller Environmental Distance algorithm with a set of parameters indicating the centroid of the input points to be used as a reference for distance calculation, and forcing distances to be translated into chi-square probability distribution values. Although not widely used in ENM studies, Mahalanobis distance has some interesting and useful features when compared with other algorithms. Among them is the fact that model shapes produced by this algorithm are *n*-dimensional ellipsoids, better reflecting the principle of central tendency in niche theory (Farber & Kadmon, 2003) and matching convex representations as hypothesized by Soberón & Nakamura (2009). Additionally, only presence points are required, with no need to generate pseudo-absence or background points, therefore not requiring prior knowledge of the species' origin and dispersal ability for model calibration, according to a recent study (Barve *et al.*, 2011). Such requirement applies to most of the other algorithms being used in ENM, as their results are clearly influenced by the choice of the region from where pseudo-absence or background points are sampled.

Models were created using each species' maximum distribution range and then projected into (1) the BS and (2) northern Europe. For *F. vesiculosus*, *I. granulosa* and *G. aculeatus*, the number of occurrence points was very unequal between the maximum distribution and the BS (i.e. there were many more

points outside), which led to a weak PD in the Baltic. To handle this documented problem of semi-enclosed seas (Ready *et al.*, 2010), ENM projections for these species were based on models generated with filtered data points from the BS only (and not on data from the whole distribution; see Table 3).

For each species, we ran one model where we combined environmental layers with different resolutions (Table 1), to be able to predict species distribution on a more local scale whenever possible through the generated model. The present model was also projected into a future scenario. Model performance was assessed using 10-fold cross-validation measuring the AUC and omission error. This means that for each species all points were randomly partitioned into 10 sets of equal size. For each set, a model was created using points from all other nine sets and then tested with points from the selected set. This technique is considered more robust than sub-sampling or bootstrapping, as it guarantees that all points are evenly used in both model creation and model testing. Therefore, prediction capability was assessed by means of multiple external tests, measuring the model's discriminatory power by averaging the AUC values. Because no absence data were used in this study, AUC values were

Table 2 Results of the jackknife analysis (AUC values) for the sea-surface salinity (SSS), sea-surface temperature (SST) and the sea ice concentration (SIC) for *Idotea* spp. in the Baltic Sea (BS) and the known distribution (KD) of the species. The most influential variable is in bold.

Layers/area	*Idotea balthica*		*Idotea chelipes*		*Idotea granulosa*	
	BS	KD	BS	KD	BS	KD
SIC	**0.690**	0.940	**0.762**	0.937	0.803	0.943
SST	0.701	0.952	0.791	**0.908**	0.808	**0.901**
SSS	0.745	**0.933**	0.795	0.920	**0.797**	0.940

calculated using the proportional area approach (Phillips et al., 2006) based on 10,000 background points randomly sampled across each mask. A model was only considered useful when the average AUC was ≥ 0.75 (Tables 3 & 4). Besides the AUC, omission errors were calculated during cross-validation for each species using the lowest presence threshold (LPT). In LPT, the lowest model value across all training points is used as the suitability threshold, ensuring that all training points fall within suitable areas. This threshold criterion was chosen because all occurrence points were reviewed and considered valid before being used. The results of the ENMs are presented as maps showing the PD for each species.

Post-processing

The ENM Statistical Difference Workflow (ESW DIFF) (Fig. 2) was used to compute the extent and intensity of change in species PD by measuring the differences between two raster layers using R 3.0.2 (R Core Team, 2013). The difference file was computed from two input files, in our case the present projection (combined 5 and 30 arc-minutes) and the 2050 projection (30 arc-minutes). The difference between each corresponding raster cell value was computed and stored in the difference file, regardless of the input files' geographical extent and origin. When files had a different geographical extent and/or origin, the workflow automatically

cropped them to the same extent and resampled the values using the 'nearest neighbour' method, resulting in a perfect cell match between the two rasters without changes in the values (Fig. 2).

In the difference file the resulting value range (−254, 254) is directly associated with the range of the input files (0, 254) to capture the maximum possible variation in both directions. Difference values were categorized into five positive and five negative classes depicted in gradients from green to red (increase) and green to blue (decrease), respectively. This allows regions of change to be clearly identified for each species as a heat map, while the range (−2, 2) is kept transparent. Overall coverage, overall intensity and the difference in intensity or coverage between the two raster layers were computed. Overall coverage was computed as the percentage of raster cells with values > 0, and overall intensity was computed as the sum of all cell values divided by the number of raster cells.

RESULTS

Environmental parameters limiting the distribution of the grazers in the Baltic

Our jackknife analysis shows that SIC (followed by SST) determines the northern distribution limit in the BS for *I.*

Table 3 Summary of the ranges of abiotic parameters obtained with the BioClim algorithm, ecological niche model (ENM) statistics for all study species, including AUC and omission error values for the potential distribution maps (*modelled with Baltic points only; †modelled with all distribution points) and coverage and intensity of habitat suitability (DIFF statistic %).

| Variables/Species BioClim (ranges)	Fucus vesiculosus	Fucus radicans	Idotea balthica	Idotea chelipes	Idotea granulosa	Gasterosteus aculeatus
Known distribution	Northern Hemisphere	Baltic Sea (endemic)	Cosmopolitan	Europe	Europe	Northern Hemisphere
n	1792	–	485	316	508	1634
DL [km]	0–137	–	0–796	0–796	0–796	0–871
MD [m]	1–1773	–	1–4951	1–4500	2–4500	1–7504
SIC	0–0.27	–	0–0.44	0–0.20	0–0.13	0–0.85
SST [°C]	(1.60–13.55)	–	4.07–29.36	6.47–19.46	3.08–18.26	−0.25–26.97
SSS [psu]	4.28–35.28	–	4.50–39.24	4.90–37.41	5.67–36.33	2.99–38.25
Baltic Sea						
n	313	184	265	124	69	123
DL [km]	0–84	0–51	1–118	1–118	4–118	0–87
MD [m]	1–372	2–362	2–372	3–372	11–372	1–372
SIC	0.01–0.25	0.04–0.25	0.0007–0.22	0.0007–0.20	0.0007–0.12	0.055–0.29
SST [°C]	(5.17–11.08)	(4.69–9.49)	6.20–11.08	6.77–10.95	6.92–10.55	4.19–10.67
SSS [psu]	4.28–13.51	4.07–6.83	4.50–13.38	4.90–13.48	5.67–12.90	2.99–12.21
ENM						
AUC	0.90 ± 0.03*	0.81 ± 0.05†	0.90 ± 0.02†	0.93 ± 0.04†	0.93 ± 0.05*	0.89 ± 0.05*
Omission error (%)	0.65	1.05	1.33	1.91	5.71	2.59
DIFF statistic (%)						
Coverage 2013	63.48	42.14	91.25	79.69	58.58	64.90
Coverage 2050	72.05	46.02	97.85	92.93	59.84	70.17
2050–2013	8.57	3.88	6.60	13.24	1.26	5.27
Intensity 2013	24.97	13.55	42.08	24.83	16.18	21.32
Intensity 2050	35.43	15.07	51.54	32.53	9.86	15.18
2050–2013	10.46	1.52	9.46	7.70	−6.32	−6.14

(a)

(b)
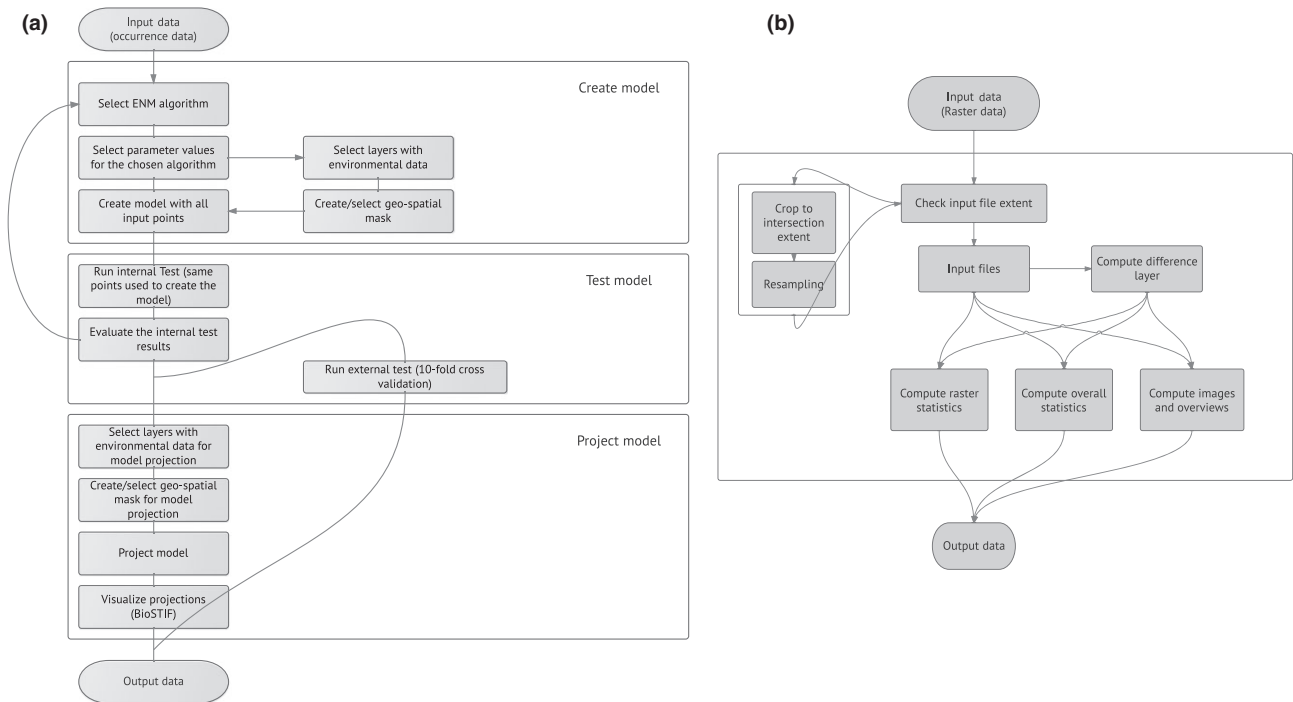
Figure 2 Diagrams of the workflows used in this study. (a) The ecological niche modelling (ENM) workflow takes as input a file containing species occurrence points to create a model with the openModeller web service. Algorithm, environmental layers and mask are selected during the workflow. The model is tested (internal test and optional cross validation external test) and then projected one or more times. Cross validation calculates the mean AUC and/or omission error. Model projection outputs are geotiff files with suitability values ranging from 0 to 254 (no data = 255). (b) The ENM Statistical Difference Workflow (ESW) allows the computation of the extent and intensity of change in species potential distribution through calculation of the differences between two raster layers using the R statistical environment (R Core Team, 2013). The difference file is computed from two input files (in this case present projection and 2050 projection) coming from the ecological niche modelling (ENM) workflow.

balthica and *I. chelipes* (Table 2, Fig. 3). In the PD map for *I. balthica* using SST and SIC the area of suitability is much more restricted in the northern Baltic (Fig. 3a). *Idotea granulosa*, however, is more restricted by SSS (Table 2). Outside the BS, our jackknife results show that SST is the most important environmental factor for *I. chelipes* and *I. granulosa*, whereas for *I. balthica* it is not.

Present potential distribution

The three marine isopods showed a widespread PD in the BS under present climate conditions (Fig. 4, Table 3). Whereas *I. balthica* has a PD deep into the Bothnian Sea (to 62° N) and into the Gulf of Finland, *I. chelipes* and *I. granulosa* are more restricted to the Baltic Proper and the Arkona Basin

Table 4 Summary of ecological niche model (ENM) statistics for the northern Europe projections of potential distribution for the study species modelled with all distribution points and the coverage and intensity of habitat suitability (DIFF statistic %).

Europe	*Fucus vesiculosus*	*Idotea balthica*	*Idotea chelipes*	*Idotea granulosa*	*Gasterosteus aculeatus*
ENM					
AUC	0.91 ± 0.01	0.94 ± 0.02	0.92 ± 0.03	0.92 ± 0.02	0.90 ± 0.02
Omission error (%)	0.73	2.27	1.58	1.18	1.36
DIFF statistic (%)					
Coverage 2013	16.71	48.17	33.87	27.71	60.38
Coverage 2050	23.96	52.79	38.87	32.83	63.95
2050–2013	7.25	4.62	5.00	5.12	3.57
Intensity 2013	8.11	13.52	10.01	8.30	21.38
Intensity 2050	11.21	17.37	12.98	10.14	22.94
2050–2013	3.10	3.85	2.97	1.84	1.56

(Fig. 4). The prediction strength was highest for *I. balthica*, followed by *I. chelipes* and *I. granulosa* (Table 3), which coincides with their frequency and dominance in the benthic ecosystem (Leidenberger *et al.*, 2012).

At present, both algal species are absent from the Bothnian Bay. Whereas *F. vesiculosus* has suitable habitats in nearly the whole BS, *F. radicans* is restricted to the north-east (Fig. 5). The ranges of abiotic parameters (temperature, salinity) for those species were very large, showing a wide tolerance of extreme environmental conditions, with lower extremes for *F. radicans* (Table 3). For *G. aculeatus*, the PD covers nearly the whole BS with its highest intensity in the Baltic Proper (Fig. 5). Of all modelled species, this species has the highest tolerance of low salinity, reflecting its capacity to live even in freshwater habitats (Table 3). A plot of occurrence points shows that the fish predator mostly overlaps in its habitat with the grazer *I. balthica* (Fig. 6), whereas the endemic alga *F. radicans* does not overlap with the grazer.

PD in northern Europe (Fig. 7) showed suitable habitats in the BS only for *I. balthica* and *I. chelipes*. Besides those two species, *I. granulosa*, *F. vesiculosus* and *G. aculeatus* showed a strong PD with high intensity along nearly all northern European coastlines.

All statistics (AUC, omission error, coverage, intensity) for the projections are summarized in Tables 2 and 3. All of the ENMs generated good to excellent predictions, as shown by their high AUC values (> 0.80). Omission errors (%) were excellent (< 5%) for all models, the only exception being the ENM for *I. granulosa* (5.7%).

2050 potential distribution

Under the 2050 climate scenario, the projections suggest a significant northern movement for *Idotea* spp., both in the BS and northern Europe (Figs 4 & 7). PD in the BS shifts eastwards into the Gulf of Finland, which seems to become a more suitable habitat for all species (Figs 4 & 5). *Fucus radicans* showed almost no difference in the 2050 PD. Coverage for *I. balthica* and *I. chelipes* was higher than for *I. granulosa*,

and higher for *F. vesiculosus* than for *F. radicans*. *Idotea balthica* had the highest intensity, whereas *I. granulosa* and *F. radicans* had the lowest (Table 3).

The northern shift in the Baltic coincides with the trend seen for the modelled species in northern Europe (Fig. 7). Here *I. granulosa* and *G. aculeatus* show less suitable habitats in southern regions.

Changes in species distribution

The most dramatic changes in distribution were predicted for the Baltic Proper. Here, *G. aculeatus* showed the most significant decrease in intensity, together with the meso-grazer *I. granulosa* (Figs 4 & 5, Table 3). Even *F. vesiculosus*, as well as *I. balthica* and *I. chelipes*, are predicted to lose suitable habitat in this area (Figs 4 & 5). For *F. radicans* the changes did not appear as clear as for the other species investigated, with suitable habitats decreasing or increasing slightly in different parts of the BS.

In general, all species show a slight increase in coverage in 2050. PD coverage differs between the 2050 predictions and the present most for *I. chelipes* and *F. vesiculosus* and least for *I. granulosa* and *F. radicans*. The intensity of habitat suitability (2050–2013) increased most for *F. vesiculosus* and *I. balthica*, whereas *I. granulosa* and *G. aculeatus* show a loss in intensity (Table 3). In contrast, those values were not so different for species in the northern European projection (Table 4). All modelled species are predicted to lose suitable habitats in the south and shift northwards (Fig. 7).

DISCUSSION

PD patterns modelled for the chosen species were only based on a few geographical and abiotic factors. It is important to note that other fundamental biotic interactions associated with resource availability can influence life-history traits and population dynamics (e.g. nutrient load for algae, predator risk or other food web interactions). These were not included in the model, as it is known that the inclusion of
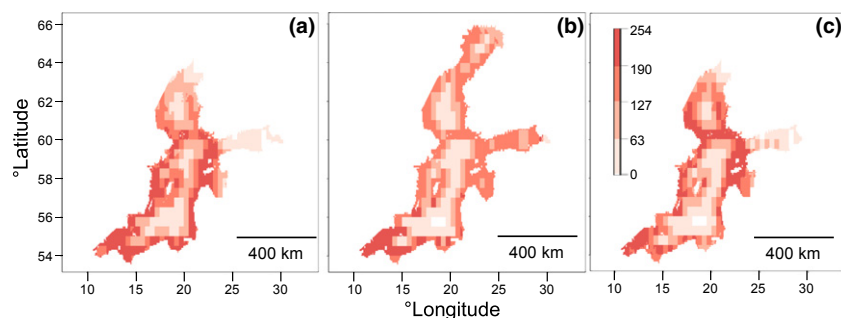

Figure 3 The potential distribution (PD) for *Idotea balthica* in the Baltic Sea using the following layers: (a) sea-surface temperature (SST), sea ice concentration (SIC), maximum depth (MD) and distance to land (DL) (AUC: 0.90, omission error: 1.34%), (b) sea-surface salinity (SSS), MD, DL (AUC: 0.91, omission error: 1.13%), and (c) SST, SIC, SSS, MD and DL (AUC: 0.90, omission error: 1.32%). The colour scale indicates habitat suitability, ranging from 0 (unsuitable, in white) to 254 (maximum suitability, in dark red).
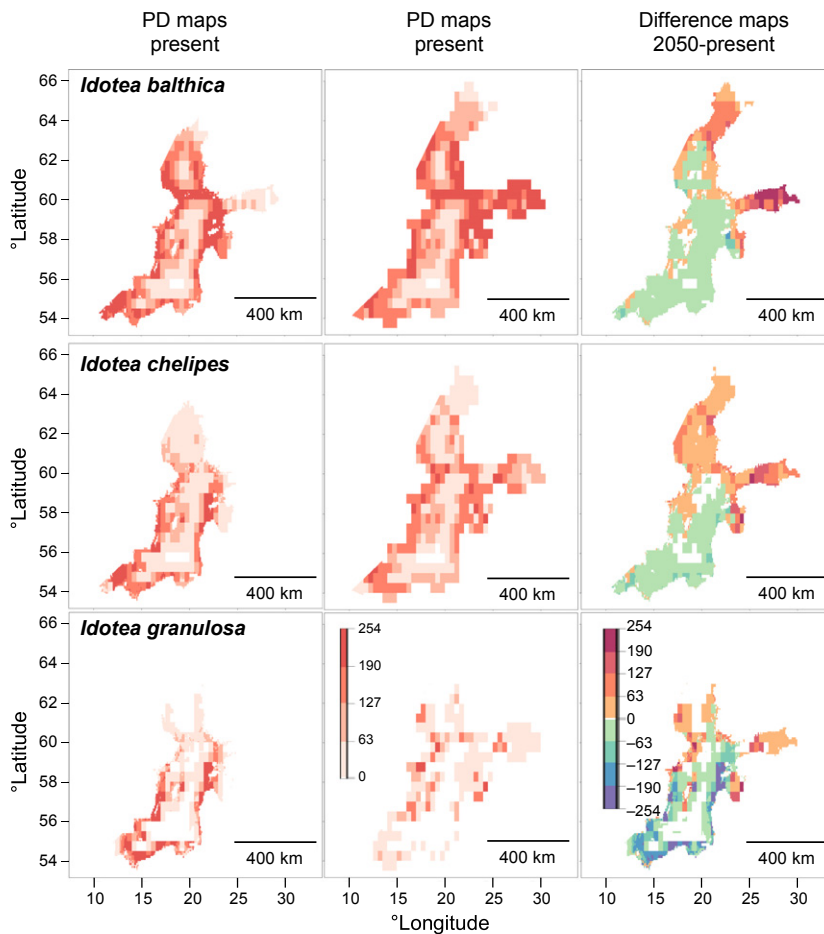
Figure 4 Maps showing the potential distribution for *Idotea balthica*, *I. chelipes* and *I. granulosa* in the Baltic Sea. The colour scale in the potential distribution (PD) maps indicates habitat suitability, ranging from 0 (unsuitable, in white) to 254 (maximum suitability, in dark red). On the difference maps (2050–present) colours from green to red indicate an increase in habitat suitability and those from green to blue indicate a decrease.

too many parameters can increase the uncertainty of models and the risk of multicollinearity (Lenoir *et al.*, 2011). Moreover, it is difficult to get layers for all those parameters.

The environmental parameters were deemed to best reflect the habitat needs of the benthic *Idotea* spp. (Table 1), as they are known to have a major influence on the species' biology (e.g. size, fertility and age at maturity) (Leidenberger, 2013); the same applies to *G. aculeatus*. For four Baltic macrophytes, including *F. vesiculosus/radicans*, Sandman *et al.* (2013) emphasized the importance of depth on species' distribution, and that salinity is more important in archipelagos with a strong salinity gradient than in most coastal areas of the BS, where differences were too small to be a useful predictor for habitat suitability.

Generally, the present PD of *Idotea* spp. (Fig. 4) is in agreement with the observed distribution of the species (Leidenberger *et al.*, 2012). Its distribution seems to be more constrained by SIC/SST than by SSS in the BS (Fig. 3). All three species differ slightly in their ranges of abiotic parameters inside and outside the BS (Table 3). The environmental parameters have different effects depending on the area of interest (Table 2). For example, *I. balthica* showed the poorest tolerance of low salinities, and *I. granulosa* can be found at colder temperatures on North Atlantic coasts (Table 3, Fig. 7). The latter species is tolerant of more open exposed

waters, in contrast to *I. chelipes*, which is a meso-grazer of lagoons and estuaries in shallow coastal areas, preferring warmer temperatures. *Idotea balthica*, a cosmopolitan species, is known to have a more generalist lifestyle (Leidenberger *et al.*, 2012).

The Baltic distribution of the meso-grazer *I. balthica* is limited to the range of its host algae *F. vesiculosus* and *F. radicans*, which are currently both absent from the Bothnian Bay. *Fucus radicans* is reported only from the Swedish coast of the Bothnian Bay and north of Poori/Björneborg in Finland, as well as around Ösel island in Estonia (Bergström *et al.*, 2005; Schagerström, 2013) (Fig. 6). Schagerström (2013) explained the absence of this species on the east coast of the Bothnian Bay by intraspecific competition with *F. vesiculosus*. Our modelled distribution showed a potentially broader suitable area for *F. radicans* (Fig. 5) than where it can be observed today.

Interestingly, the current distribution limits of *F. radicans* and *I. balthica* overlap only slightly on the south-eastern coast of the Bothnian Sea. The grazer is more concentrated in the south of the Bothnian Sea and *F. radicans* in the north (Fig. 6). Habitat limitation caused by SIC/SST for *Idotea* might have provided a unique ecological niche for the recently evolved endemic narrow wrack in the northern Bothnian Sea. Up to now, no detailed studies on the physiology
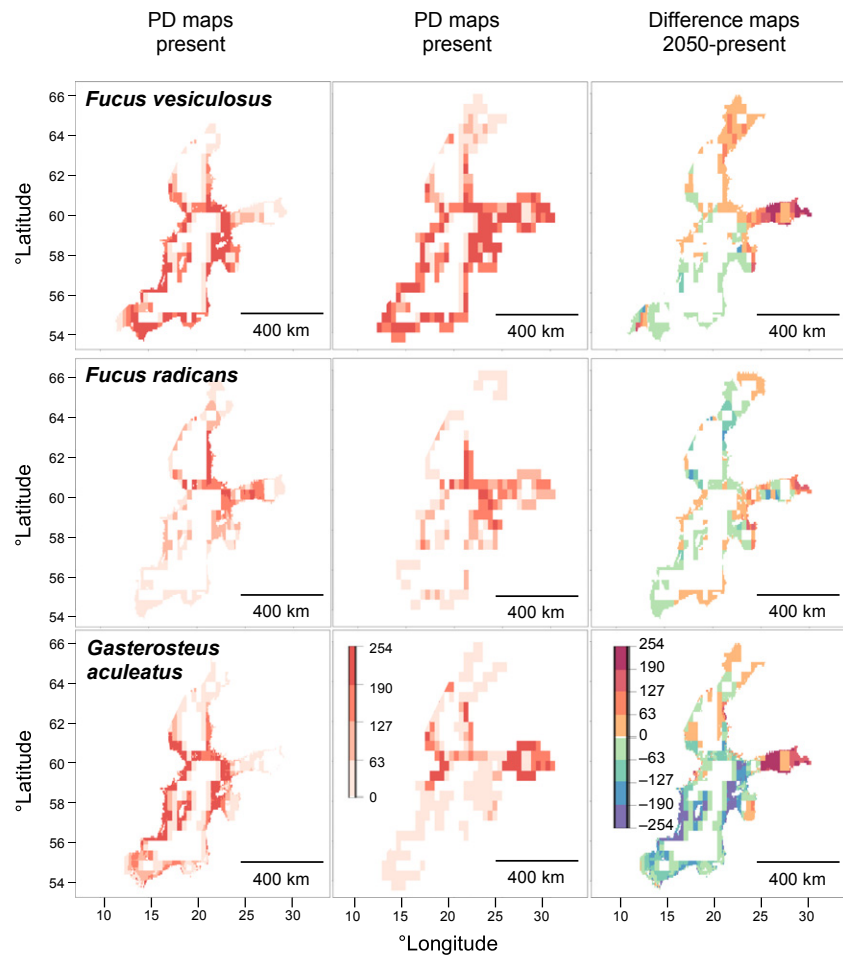
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Figure 5 The potential distributions for *Fucus vesiculosus*, *F. radicans* and *Gasterosteus aculeatus* in the Baltic Sea. The colour scale in the potential distribution (PD) maps indicates habitat suitability, ranging from 0 (unsuitable, in white) to 254 (maximum suitability, in dark red). On the difference maps (2050–present) colours from green to red indicate an increase in habitat suitability and those from green to blue indicate a decrease.

of *F. radicans* exist. Experimental studies have shown that *F. radicans* is highly sensitive to high grazing pressure, and that it was preferred as a food item by *Idotea* when given the choice between *F. vesiculosus* and *F. radicans* (Gunnarsson & Berglund, 2012). The overlapping habitat ranges of *Idotea* spp. and *F. vesiculosus* have forced a selection for high grazing-resistance in *F. vesiculosus* during colonization of the BS (Nylund *et al.*, 2012). This seems not to be the case for *F. radicans*.

The estimated distribution patterns modelled for the meso-grazer guild under the 2050 scenario followed the overall trend of a shift to more northerly regions as a response to rising SST (Perry *et al.*, 2005). This northern shift was seen in our predictions for both the BS and northern Europe projection (Figs 4, 5 & 7). The eastern shift may be a consequence of the regional climate changes predicted for the Baltic.

For the BS, a regional climate model was developed [the Rossby Centre Ocean Model (RCO)], to consider the extremes of this semi-enclosed sea (Döscher *et al.*, 2002). Meier *et al.* (2011) were able to show that in general circulation models (GCMs), such as the ECHAM model used in our analysis, simulations predicted warming bias of the BS due to a reduction of the ice-albedo feedback (a positive feedback climate process where a change in the area of snow-covered land or sea ice alters the albedo causing a reinforcement in the initial alteration in ice area). Different climate scenarios published in recent years resulting from the RCO, and using ECHAM (versions 4 and 5) as lateral boundary data, predict serious changes in SST, SSS, SIC and turbidity in the BS region (Meier *et al.*, 2011, 2012). The latest RCO simulation, using ECHAM5, clearly indicated that SST would increase with time. The biggest change is predicted for the central Bothnian Bay and Bothnian Sea during summer (+4 °C), and for the Gulf of Finland in spring and winter (Meier *et al.*, 2012). Salinity will be reduced through significantly increased runoffs into the BS. The largest decreases in SSS were predicted in the Baltic Proper (about 1.5–2 psu) (Meier *et al.*, 2012). Effects on ecological quality indicators, such as phytoplankton concentration, Secchi depth and bottom oxygen concentration are predicted to be larger under ECHAM5 (Meier *et al.*, 2012) than under previous scenarios (Meier *et al.*, 2011). Secchi depth is predicted to decrease by up to 1.5 m in the Baltic Proper. The BALTEX Assessment of Climate Change for the Baltic Sea Basin (BACC) working group has already recorded numerous examples of climate-related marine biodiversity changes on all trophic levels (BACC Author Team, 2009).
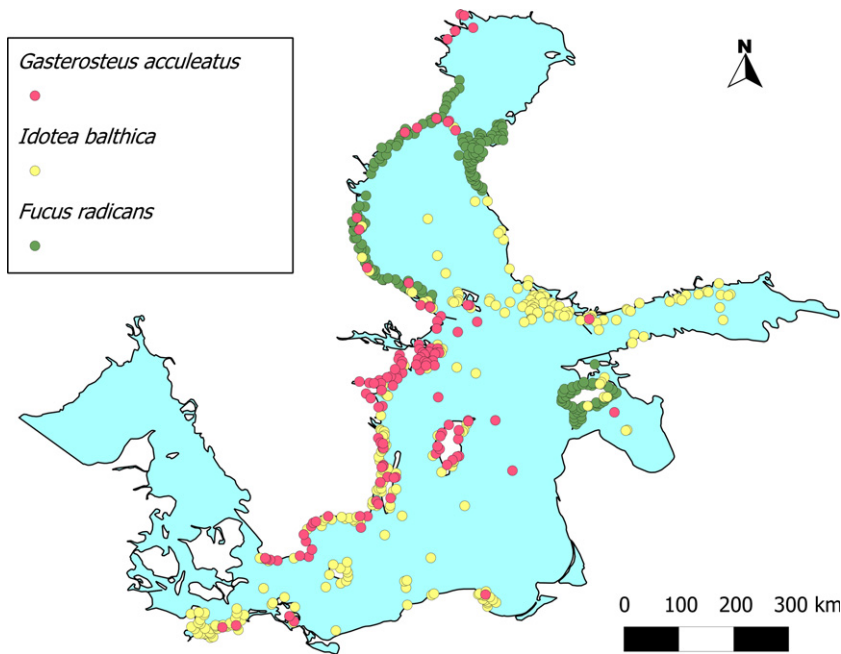
Figure 6 The overlap of current habitats in the Baltic Sea for the predatory fish (*Gasterosteus aculeatus*), the grazer (*Idotea balthica*) and the endemic alga (*Fucus radicans*), based on all the occurrence points used in this study.

Increased SST can have a direct effect on the physiology of species and may have indirect consequences through changes in food webs (Leidenberger *et al.*, 2012), especially in Baltic fish species (Eriksson *et al.*, 2011). If *G. aculeatus* coverage decreases as much as predicted in our model (Fig. 5), this will have a knock-on effect on *Idotea* meso-grazers, which will also lead to higher grazing pressure on the Baltic algae, especially *F. radicans*. Therefore, climate-induced changes pose an indirect extinction risk for this endemic species, as it does not seem to have evolved protection against high grazing pressure as has *F. vesiculosus*. *Fucus* species may not be affected by SST increase in the Baltic to the same degree as was observed for populations outside the BS (Jueterbock *et al.*, 2013; Nicastro *et al.*, 2013), but a predicted increase in the frequency of local heat-waves can increase stress. Jueterbock *et al.* (2013) found a northward shift for three *Fucus* species, with most habitat losses south of 45° N in the North Atlantic in the near future.

The combination of serious changes in nutrient load, oxygen concentration, SSS and SST predicted for the Baltic Proper, and a northern/north-eastern shift of species, may result in genetic separation of local populations. Phylogeographical studies have indicated that Baltic populations in general (Johannesson & André, 2006), and populations of *Idotea* spp., *F. vesiculosus* and *G. aculeatus* in particular, have lost genetic variation in contrast to populations from the Atlantic (Tatarenkov *et al.*, 2007; Nylund *et al.*, 2012; DeFaveri *et al.*, 2013; Leidenberger, 2013). A large population size with a high level of genetic variation can increase the capacity to adapt to environmental changes, in comparison with small isolated populations with low genetic diversity (Johannesson *et al.*, 2011). Indeed, local adaptation of *F. vesiculosus* to the low-salinity environment of the BS is associated with reduced stress tolerance (Pearson *et al.*, 2000) and the advent of asexual reproduction (Bergström *et al.*, 2005). For *Idotea*,

physiological studies on salinity and stress tolerance are still rare, but local adaptations to food algae are described inside and outside the BS (Vesakoski *et al.*, 2009; Bell & Sotka, 2012). An experimental heat wave scenario for *I. balthica* significantly decreased the immune-competence of the grazer (Roth *et al.*, 2010). A similar heat shock scenario (25 °C for 30 min) for specimens of both Baltic *Fucus* species indicated a higher sensitivity than for specimens from outside the BS (Lago-Lestón *et al.*, 2010). Outside the BS, the macroalga has already experienced an 11° northward shift in distribution on the North African coast (= 1250 km) as a consequence of a significant increase in coastal SST (Nicastro *et al.*, 2013), followed by extinction of a cryptic genetic clade. Local adaptation along an environmental gradient has also been shown for *G. aculeatus* (DeFaveri *et al.*, 2013).

The evolutionary potential of the species will determine how they will be able to cope with predicted future climate changes in the BS. The outcome of our models shows that the meso-grazer guild of *Idotea* is likely to be affected by distribution changes under a future climate scenario leading to knock-on effects in the Baltic food web.

As our statistical analyses show, the likely winners in the BS seem to be *F. vesiculosus* and the grazers *I. chelipes* and *I. balthica*, whereas the losers with less habitat suitability might be the grazer *I. granulosa*, *F. radicans* and the fish *G. aculeatus* (Table 3, Figs 4 & 5). In northern Europe all species analysed are predicted to have increased habitat suitability, even if this trend is reduced for *I. granulosa* and *G. aculeatus* (Table 4, Fig. 7).

Uncertainties in our analyses arise from the GCM, the climate scenario itself (ECHAM5 A1B) and other limitations of ENM, such as the number and distribution of occurrence points used to create the model, although the final number of points for all species was > 50, as recommended by Farber
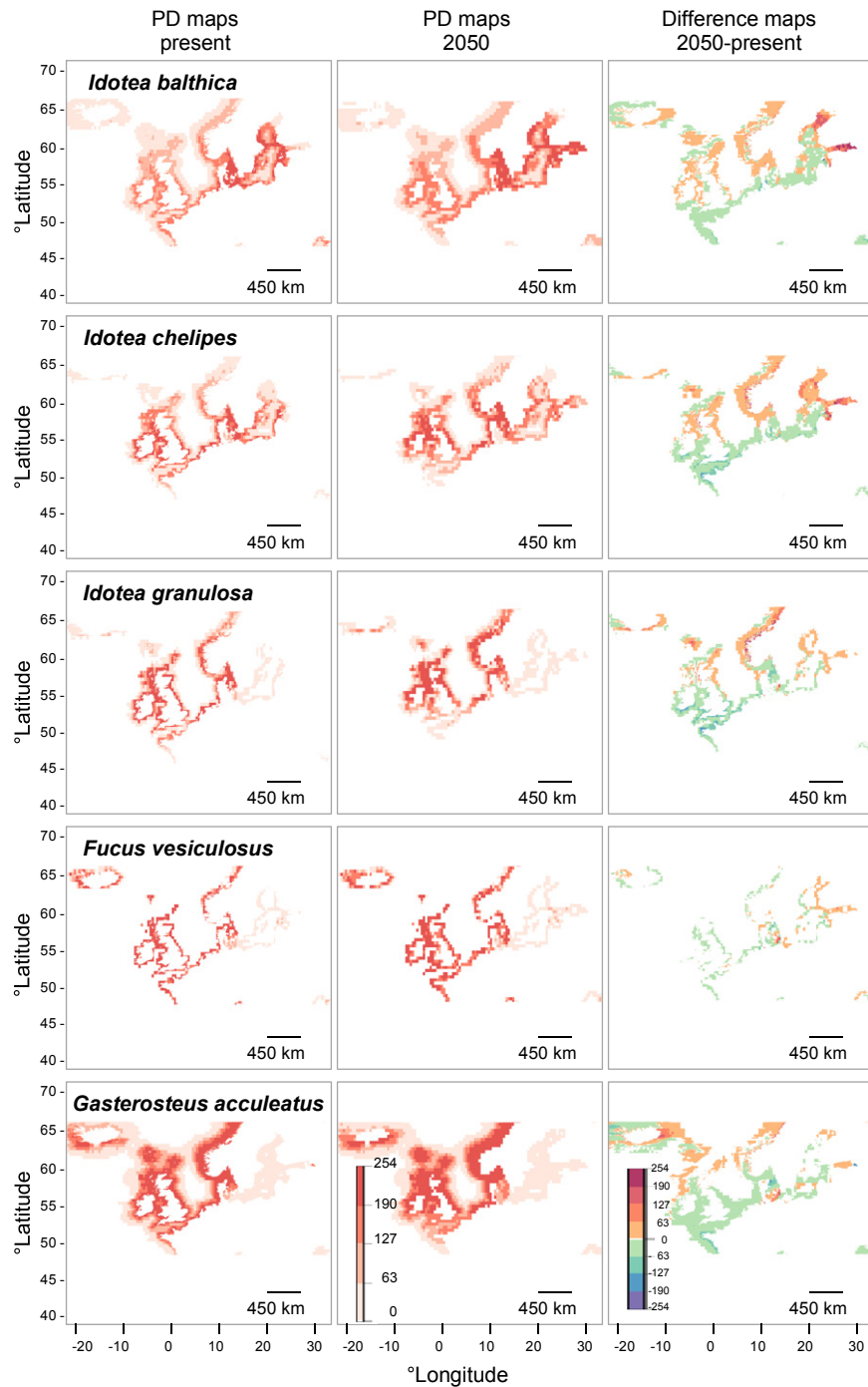
Figure 7 The potential distributions for *Idotea balthica*, *I. chelipes*, *I. granulosa*, *Fucus vesiculosus* and *Gasterosteus aculeatus* at the scale of northern Europe. The 'enclosed sea problem' as discussed in the main body of the text can be seen for *I. granulosa*, *F. vesiculosus* and *G. aculeatus*. Colour scale in the potential distribution (PD) maps indicates habitat suitability, ranging from 0 (unsuitable, in white) to 254 (maximum suitability, in dark red). On the difference maps (2050–present) colours from green to red indicate an increase and those from green to blue indicate a decrease in habitat suitability.

& Kadmon (2003) for the Mahalanobis distance algorithm. *Fucus radicans* and *I. granulosa*, for example, were two species where the number of occurrence points was low (Table 3), and the PD patterns (both for the present and 2050) are not as clear as for the other species modelled with

higher numbers of occurrence points (Table 3, Figs 4 & 5). For *I. chelipes*, which also has relatively low numbers of occurrence points (Table 3), the proportion of points inside and outside the BS was better distributed than for *I. granulosa*, resulting in a better model (Fig. 4).

Models projected on the European scale resulted in a weak PD for *I. granulosa*, *F. vesiculosus* and *G. aculeatus* in the BS (Table 4, Fig. 7). For those species, the number of occurrence points outside the BS was much higher (up to 13 times) than in the BS (Figs 4 & 5). This 'enclosed sea problem' is known for ENM in seas with distinct environmental conditions from surrounding areas (Ready *et al.*, 2010). For *I. granulosa*, occurrence points in the BS were too few, leading to a higher omission error (> 5%). More occurrence points would be needed to improve the models for this species (Table 3).

CONCLUSIONS

If our modelled meso-grazer guild is not able to deal with multiple stressors resulting from decreased genetic variability, dramatic effects on Baltic coastal ecosystems may result. The capability of isolated Baltic populations to cope with future climate changes may strongly depend on their evolutionary and adaptive potential; however, the time-scales of predicted climate changes are likely to be very rapid.

In the near future, interdisciplinary research is required both in terrestrial and marine habitats, to improve our overall knowledge of the consequences of environmental changes on species' distribution ranges and their population genetics. The development of novel computational tools combining data from different sources (species occurrence data, environmental data and genetic data) is necessary to allow the rapid observation and analysis of environmental changes, which can feed into environmental management and decision-making.

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Data provider names for occurrence records downloaded from GBIF.

Appendix S2 Data references from a literature survey for all study species (a) and occurrence records manually georeferenced by species (b–e).

Appendix S3 Occurrence records from museum material (a) and material collected by S. Leidenberger (b).

BIOSKETCH

Sonja Leidenberger is a postdoctoral researcher investigating species distribution in northern Europe for the EU-funded BioVel project (http://www.biovel.eu/). Her research interests range from life-history strategies, phylogeography and species distribution modelling, to the effects of climate change on marine benthic species.

Author contributions: S.L. and S.J.B. designed the study and collected the data. A.R.W., R.G. and R.K. built the work-flows. S.L., S.J.B., R.G. and R.K. performed the modelling. S.L. and S.J.B. wrote the first draft of the manuscript, and all authors contributed substantially to the revisions.

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