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# Baltic Sea genetic biodiversity: Current knowledge relating to conservation management

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## Abstract

1. The Baltic Sea has a rare type of brackish water environment which harbours unique genetic lineages of many species. The area is highly influenced by anthropogenic activities and is affected by eutrophication, climate change, habitat modifications, fishing and stocking. Effective genetic management of species in the Baltic Sea is highly warranted in order to maximize their potential for survival, but shortcomings in this respect have been documented. Lack of knowledge is one reason managers give for why they do not regard genetic diversity in management.

2. Here, the current knowledge of population genetic patterns of species in the Baltic Sea is reviewed and summarized with special focus on how the information can be used in management. The extent to which marine protected areas (MPAs) protect genetic diversity is also investigated in a case study of four key species.

3. Sixty-one species have been studied genetically in the Baltic Sea, but comprehensive genetic information exists for only seven of them. Genetic monitoring shows genetic stability in some species but fluctuations and genetic changes in others. About half of the scientific studies published during the last 6 years provide conservation advice, indicating a high interest in the scientific community for relating results to practical management.

4. Populations in MPAs do not differ genetically from populations outside MPAs, indicating that MPAs in the Baltic Sea do not protect genetic diversity specifically, but that populations in MPAs are a representative subset of populations in the Baltic Sea.

5. Recommendations are provided for cases where genetic information is available but not used in management, particularly for non-commercial species with important ecosystem function.

6. Improved channels for effective communication between academia and practical management on Baltic Sea genetic biodiversity are needed. A web page that can be used for knowledge transfer is highlighted here.

KEYWORDS

algae, alien species, brackish, conservation evaluation, fish, conservation genetic monitoring, genetic diversity, mammals

## 1 | INTRODUCTION

Genetic diversity is the foundation for all biological diversity; the persistence and evolutionary potential of species rely on it for adaptation to natural and human-induced selective pressures (Allendorf, Luikart, & Aitken, 2013). Research during the past decade has shown links between variation at the DNA level within species (genetic diversity) and biological productivity and viability (Lindley et al., 2009; Reusch, Ehlers, Hammerli, & Worm, 2005), resilience to environmental stressors (Frankham, 2005; Hellmair & Kinziger, 2014)

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and adaptation to changing environmental features such as climate change (Barshis et al., 2013; McGinnity et al., 2009). Understanding of the importance of genetic biodiversity is reflected in international conservation policies such as the Convention on Biological Diversity (CBD), which specifically calls for conservation and sustainable management of genetic diversity (www.cbd.int). The particular importance of maintaining genetic diversity of species of socio-economic value is highlighted in the Aichi Target 13 of the CBD Strategic Plan for 2011–2020 (UNEP/CBD/COP/DEC/X/2; www.cbd.int/sp/targets).

In species-poor environments, genetic diversity is considered to be of particular importance (Johannesson, Smolarz, Grahn, & André, 2011; Laikre et al., 2008) because it can have similar effects on ecosystem functioning as species diversity (Hughes, Inouye, Johnson, Underwood, & Vellend, 2008; Schindler et al., 2010). The brackish Baltic Sea represents one such species-poor system where genetic diversity is expected to be of particular concern (Johannesson, Smolarz et al., 2011). The Baltic Sea is evolutionarily young and has existed in its present stage for only 8000–9000 years. It is highly heterogeneous and comprises several sub-basins with restricted water exchange among them, and there are pronounced environmental gradients in, for example, declining salinity and temperature from the south-west towards the north (Voipio, 1981).

Relatively few marine and freshwater species have adapted to the Baltic Sea environment. For both types of species, however, this adaptation has resulted in genetically unique make-ups. Marine species typically are genetically divergent from, and show lower levels of genetic variation than, their conspecifics in the North Sea (Johannesson & André, 2006), whereas Baltic Sea populations of typical freshwater species may exhibit larger genetic variation than conspecific populations inhabiting freshwater habitats (Bekkevold, Jakobsen, Hemmer-Hansen, Berg, & Skov, 2015). Species-specific patterns of genetic variation within the Baltic Sea apparently reflect a variety of evolutionary histories and patterns of genetic drift and gene flow (DeFaveri, Shikano, Ghani, & Merilä, 2012; Wennerström et al., 2013).

Human-induced pressures on the Baltic Sea are extensive and have contributed to high levels of pollutants, eutrophication, large areas of oxygen-depleted sea beds, extensive fishing and stocking, spread of alien species and rapid climate change (Björklund & Almqvist, 2010; Diaz & Rosenberg, 2008; Ducrotoy & Elliott, 2008; Jansson & Dahlberg, 1999; Lehtonen & Schiedek, 2006; Neumann, 2010). These pressures are expected to increase the importance of genetic variation as a basis for population and species adaptation and resilience (Johannesson, Smolarz et al., 2011; Salo, Reusch, & Boström, 2015). Thus, incorporation of knowledge of genetic diversity in management and conservation efforts is of importance in this region, and would, for example, include that genetically distinct populations are identified and maintained at sufficient sizes and with sufficient degree of genetic exchange among them (connectivity) to assure long-term viability. However, shortcomings in this respect have recently been found; explicit mention of genetic biodiversity is almost non-existent in management plans for marine protected areas (MPAs) in the Baltic Sea (Laikre et al., 2016; Sandström, Lundmark, Jansson, Edman, & Laikre, 2016), indicating that earlier noted lack of incorporation of genetic information in aquatic management (Laikre, Palm & Ryman, 2005; Ryman, Utter, & Laikre, 1995) still remains.

Although both international and national policies that govern Baltic Sea biodiversity identify genetic diversity as an essential component for conservation, and MPAs as a means for conserving such diversity, management plans for MPAs in the Baltic Sea are largely devoid of goals and strategies for genetic biodiversity (Laikre et al., 2016). Sandström et al. (2016) explored why this is the case by interviewing regional managers in the area and found that there are several possible explanations including lack of knowledge of genetic variation and how it can be used in management. Apparently, awareness that genetics can be used to understand population viability, pinpoint the scale of isolation/connectivity among populations and areas, and identify valuable populations for long term survival (Allendorf & Ryman, 2002; Allendorf et al., 2013) is not yet wide spread among managers.

Here, current knowledge on genetic diversity of species in the Baltic Sea is reviewed and synthesized with particular focus on how this knowledge can be used in conservation management. The aim is to summarize information that can aid in increasing the implementation of existing policies with respect to gene level biodiversity in the management of Baltic Sea species. In particular, the recommendations that the scientists themselves have recently provided for separate species are highlighted. Further, we provide a, to our knowledge, first case study of how well Baltic Sea MPAs protect genetic diversity using georeferenced genetic datasets that we were able to locate for four species (northern pike, three-spined stickleback, bladderwrack and turbot) allowing comparison of genetic diversity and divergence within and outside MPAs.

## 2 | METHODS

The Web of Science™ search facility was used to gather all published scientific studies on population genetics of species in the Baltic Sea. The search was conducted in January 2016, thus including studies published up until the end of 2015. Search strings included several word combinations together with some exclusion criteria: 'genetic* AND (differen* OR structure OR divergen*) AND Baltic Sea' and 'genomic* AND (differen* OR structure OR divergen*) AND Baltic Sea'. These searches yielded 599 studies, which were manually scrutinized for relevant hits. To explore genetic patterns within the Baltic Sea, only studies including at least two spatially and/or temporally separated population samples from the inner Baltic Sea region were accepted (bordered by Darss and Limhamn underwater ridges; as defined by Johannesson & André, 2006; Figure 1). The search was limited to aquatic species; studies of seashore plants and waterfowl were excluded. Moreover, a study had to include a clear within-species component, and carry out novel genetic analyses; i.e. studies exclusively referring to results of previous work were not included. In total, 214 studies fulfilled all the search criteria and a full reference list is given in Supporting information, Appendix S1.

For each organism studied, the level of available genetic information was classified as 'good', 'reasonable', or 'limited' based on three categories; *spatial coverage of sampling*, *type and number of genetic markers used*, and *degree to which temporal variation has been considered*. The classification was made using scores from 1 to 3 for each category as shown in Figure 2.
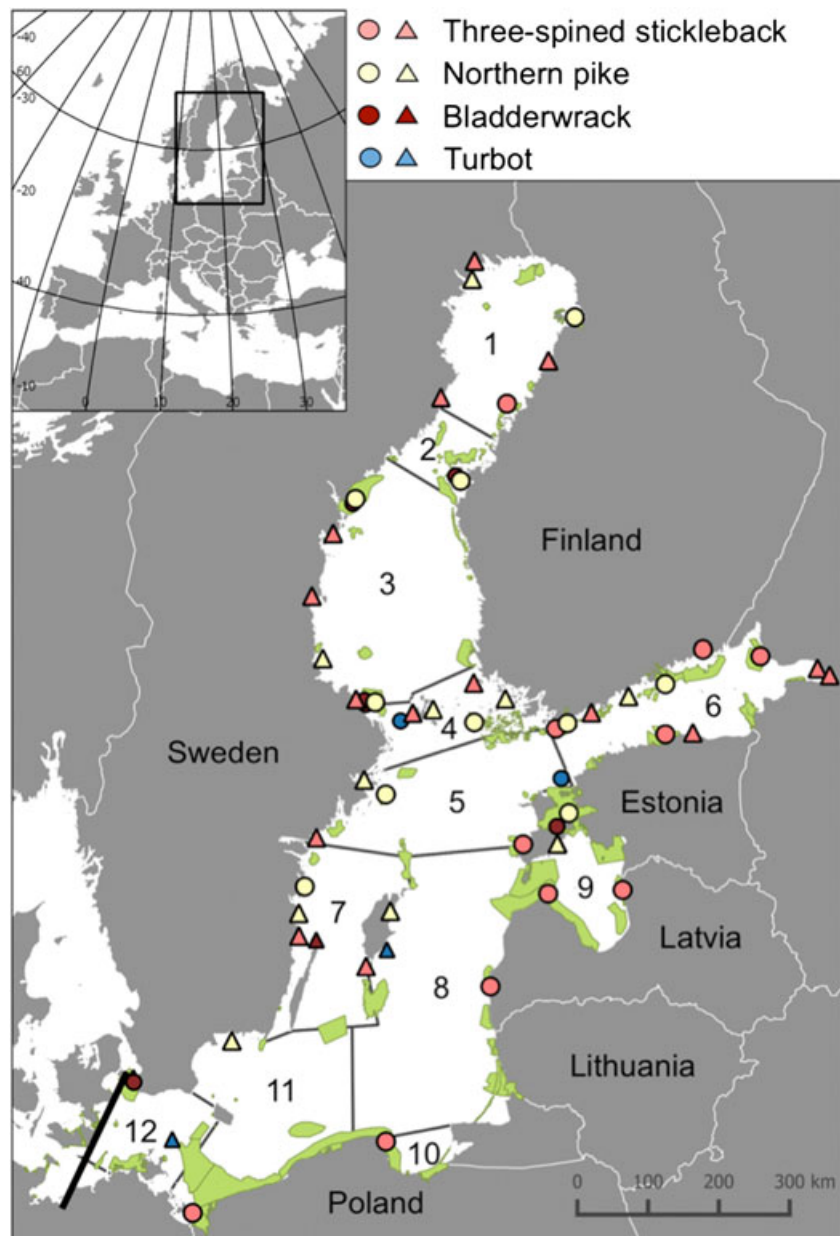
**FIGURE 1** The Baltic Sea with HELCOM MPAs colored in green and the border to the Baltic Sea (Johannesson & André, 2006) marked with a black line. Samples from four species taken inside MPAs (circles) and outside MPAs (triangles) are marked. Numbers denote major basins in the Baltic Sea: 1. Bothnian Bay, 2. The Quark, 3. Bothnian Sea, 4. Åland Sea, 5. Northern Baltic proper, 6. Gulf of Finland, 7. Western Gotland Basin, 8. Eastern Gotland Basin, 9. Gulf of Riga, 10. Gdansk Basin, 11. Bornholm Basin, 12. Arkona Basin

Main findings, with special focus on results important from a management perspective, were summarized for species for which 'good' or 'reasonable' genetic information exist. Recently published studies (2010–2015, $n$ = 85) were examined specifically also for the extent to which the authors provided management advice, or if they discussed their findings in a wider perspective relevant to conservation or management of aquatic populations.

## 2.1 | Genetic variation in marine protected areas (MPAs)

HELCOM marine protected areas (HELCOM MPAs) is a network of protected areas in the Baltic Sea (Figure 1) governed within the framework of the Baltic Marine Environment Protection Commission (Helsinki Commission or HELCOM; www.helcom.fi). The overall objective for HELCOM MPAs is to protect biological diversity and the MPAs are aimed to be interconnected (Laamanen, 2013).

Genetic data for four species with a good spatial sampling coverage of the Baltic Sea and with at least two samples collected both inside and outside the HELCOM MPAs was used to address the capacity for HELCOM MPAs to protect Baltic Sea genetic diversity. Of the more than 200 published scientific studies identified in the literature search, this type of data was available only for four species; northern pike (*Esox lucius*), three-spined stickleback (*Gasterosteus aculeatus*; DeFaveri, Jonsson, & Merilä, 2013), bladderwrack (*Fucus vesiculosus*) and turbot (*Scophthalmus maximus*; Vandamme et al., 2014). The pike data were generated by ourselves (Wennerström, Olsson, Ryman, & Laikre, 2017) and the bladderwrack data were kindly provided by Professor Kerstin Johannesson and colleagues, Gothenburg University. Data for three-spined stickleback and turbot were available in the Dryad data repository (www. datadryad.org).

Genetic variation (allelic richness and expected heterozygosity) for each population was estimated using the *Fstat* software (Goudet,
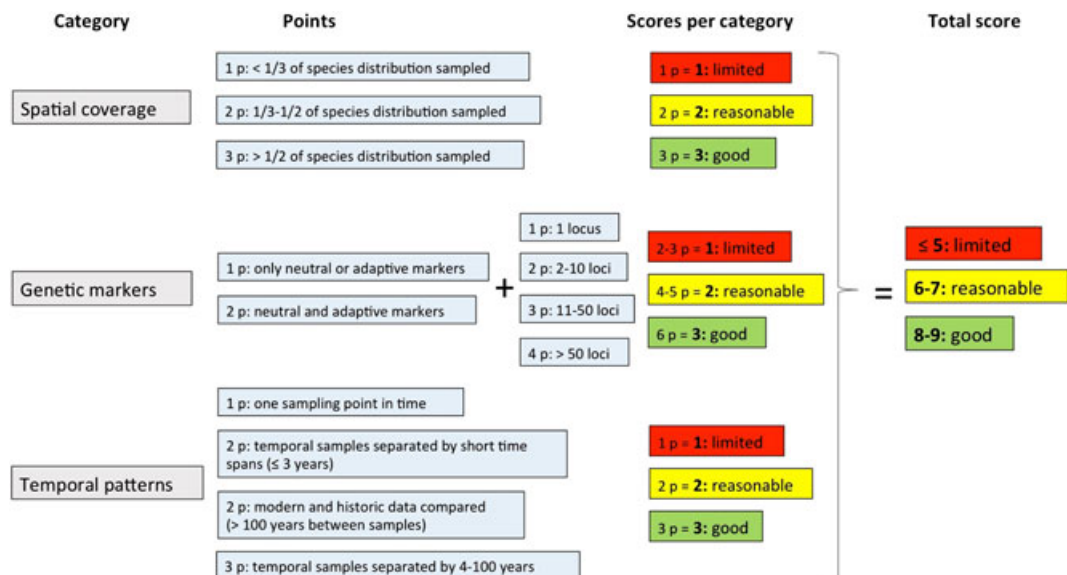
**FIGURE 2** The scoring system applied to classify the degree of genetic knowledge of Baltic Sea species. Scores for the *Spatial coverage* category are based on the proportion of the species distribution over the Baltic Sea that has been studied. The *Genetic markers* category classification is based on a combination of numbers and of type of markers (putatively neutral or selected or both) and number of loci. *Temporal patterns* are important for monitoring genetic diversity. The highest scores are given to studies with time spans that cover more than one generation (typically > 5 years) and are short enough to be of relevance for management and monitoring time frames (< 100 years). See Table 1 for scoring results for separate species (cf. Supporting information Appendix S2 for all data)

1995). Good spatial sampling was available for pike and three-spined stickleback with around 10 samples for both categories (MPA/non-MPA). More sparse samples were available for bladderwrack and turbot (Figure 1). Statistical tests to compare genetic variation inside and outside protected areas were thus only performed for pike and stickleback. Analyses of molecular variance (AMOVA) as implemented in the program *Arlequin* (Excoffier & Lischer, 2010) were performed with the hierarchical organization protection/populations/individuals. Contribution of each population sample to total genetic diversity was estimated following the method of Petit, Mousadik, and Pons (1998) as implemented in the software *MolKin* (Gutiérrez, Royo, Álvarez, & Goyache, 2005). This method was used to estimate how much each sampled population contributes to total genetic variation of the species in the Baltic Sea in terms of genetic diversity within the population and genetic uniqueness of the population, and thus how much of this variation that would be lost if the sampled population was removed.

## 3 | RESULTS

The number of population genetic studies in the Baltic Sea has increased almost exponentially since the beginning of the 1990s (Supporting Information, Figure S1). In total, 214 studies concerning 61 species (including three invasive alien species) were found and included in this review. The majority of the studies (n = 122, 57%) concerned fish species, and among these studies more than 40% (n = 51) focused on salmonids. Thus, salmonid fishes are by far the most well studied group of species with respect to genetic biodiversity in the Baltic Sea.

When the 61 species were classified according to level of knowledge, 11% (n = 7) were classified as 'good', 20% (n = 12) as 'reasonable' and 69% (n = 42) were classified as 'limited' (Table 1). Summary information on spatial coverage of studies and markers used are provided in Supporting Figures S2–S4. All collected data are presented in Appendix S2.

### 3.1 | Genetic information and its applicability in management for different organism groups

Genetic information useful for conservation management is available for several Baltic Sea species and is briefly summarized below. Key genetic information and management advice for the 19 species for which genetic knowledge is classified as 'good' or 'reasonable' (Table 1) are summarized in Table 2, together with six species classified as 'limited' but which are of high conservation concern and with management advice available.

Delimitation of population genetic structure in order to identify more or less isolated populations is of importance to define management units. Such information exists for fish species including Atlantic salmon (*Salmo salar*; Koljonen, Jansson, Paaver, Vasin, & Koskiniemi, 1999; Säisä et al., 2005), northern pike (*Esox lucius*; Laikre, Miller, et al., 2005; Wennerström et al., 2017), whitefish (*Coregonus lavaretus*; Olsson, Florin, Mo, Aho, & Ryman, 2012) and for habitat forming species such as bladderwrack (*Fucus vesiculosus*; Johannesson, Johansson et al., 2011). Also, identification of local adaptations is of particular importance in variable environments such as that of the Baltic Sea. Baltic Sea populations of cod (*Gadus morhua*), Atlantic herring (*Clupea harengus*) and three-spined stickleback (*Gasterosteus aculeatus*) have been shown to be genetically adapted to the low

**TABLE 1** Summary of current knowledge on the genetic diversity of Baltic Sea species (214 scientific studies covering 61 species published up to the end of 2015). Status of knowledge is based on the following three criteria (Figure 2). (I) *spatial coverage of sampling* (how well sampling covers the distribution area of the species in the Baltic Sea, and how large sample sizes have been used); (II) *type and number of genetic markers used* (have neutral and/or adaptive markers been used and how many loci were scored) and number of genetic markers; and (III) *degree to which temporal variation has been considered* (analyses backwards in time from modern samples and/or sampling at different time points). Colour codes refer to number of knowledge points: red = 1, yellow = 2, green = 3 (see text for details). HELCOM Redlist (2013) category refers to threat status, LC = Least concern, NT = Near threatened, VU = Vulnerable, EN = Endangered, CR = Critically endangered, RE = Regionally extinct, *non-indigenous invasive species. Full references for studies of separate species can be obtained from Appendix S1 via the reference number in the rightmost column

| Group | Common name | Scientific name | HELCOM Redlist category | I | II | III | | Number of references | Reference number in Appendix S1 |
|---|---|---|---|---|---|---|---|---|---|
| **Algae** | Red alga | *Ceramium tenuicorne* | | red | red | yellow | limited | 1 | 1 |
| | Green alga | *Cladophora rupestris* | | red | red | yellow | limited | 1 | 2 |
| | Narrow wrack | *Fucus radicans* | | green | red | green | reasonable | 5 | 3-6, 8 |
| | Serrated wrack | *Fucus serratus* | LC | yellow | red | red | limited | 1 | 7 |
| | Bladderwrack | *Fucus vesiculosus* | LC | green | red | yellow | reasonable | 7 | 4-6, 8-10, 214 |
| | Black carageen | *Furcellaria lumbricalis* | LC | green | yellow | red | reasonable | 2 | 11-12 |
| | Diatom | *Skeletonema marinoi* | | red | red | red | limited | 1 | 13 |
| | Gutweed | *Ulva intestinalis* | | green | red | red | limited | 1 | 14 |
| **Angiosperms** | Fennel pondweed | *Potamogeton pectinatus* | | green | yellow | red | reasonable | 2 | 15-16 |
| | Beaked tassleweed | *Ruppia maritima* | LC | red | yellow | red | limited | 1 | 17 |
| | Eelgrass | *Zostera marina* | LC | yellow | red | red | limited | 4 | 18-21 |
| **Fish** | Atlantic sturgeon | *Acipenser oxyrinchus* | RE | red | yellow | red | limited | 2 | 22-23 |
| | European eel | *Anguilla anguilla* | CR | yellow | red | red | limited | 1 | 24 |
| | Atlantic herring | *Clupea harengus* | LC | green | green | green | good | 14 | 25-37, 214 |
| | Whitefish (spp.) | *Coregonus lavaretus* | EN | green | yellow | green | good | 9 | 38-45, 214 |
| | Bullhead | *Cottus gobio* | LC | yellow | yellow | red | limited | 2 | 46-47 |
| | Northern pike | *Esox lucius* | LC | green | yellow | green | good | 3 | 48-49, 214 |
| | Cod | *Gadus morhua* | EN | green | green | green | good | 15 | 50-64 |
| | 3-spined stickleback | *Gasterosteus aculeatus* | LC | green | green | green | good | 9 | 65-72, 214 |
| | Fourhorn sculpin | *Myoxocephalus quadricornis* | LC | red | yellow | red | limited | 1 | 73 |
| | Round goby * | *Neogobius melanostomus* | | red | red | red | limited | 1 | 74 |
| | Smelt | *Osmerus spp.* | LC | red | red | red | limited | 1 | 75 |
| | Perch | *Perca fluviatilis* | LC | yellow | yellow | green | reasonable | 7 | 76-82 |
| | Flounder | *Platichthys flesus* | LC | green | yellow | yellow | reasonable | 5 | 83-87 |
| | Plaice | *Pleuronectes platessa* | LC | red | red | yellow | limited | 2 | 83, 88 |
| | Sand goby | *Pomatoschistus minutus* | LC | red | yellow | red | limited | 1 | 89 |
| | 9-spined stickleback | *Pungitius pungitius* | LC | green | yellow | red | reasonable | 6 | 69, 90-93, 214 |
| | Atlantic salmon | *Salmo salar* | VU/EN | green | green | green | good | 28 | 94-121 |
| | Brown trout | *Salmo trutta* | VU/EN | green | green | green | good | 14 | 98, 116, 122-133 |
| | Pikeperch | *Sander lucioperca* | LC | yellow | yellow | red | limited | 2 | 134-135 |
| | Turbot | *Scophthalmus maximus* | NT | green | yellow | yellow | reasonable | 3 | 136-138 |
| | Sprat | *Sprattus sprattus* | LC | yellow | yellow | red | limited | 2 | 139-140 |
| | Grayling | *Thymallus thymallus* | CR | yellow | yellow | red | limited | 3 | 141-143 |
| | Eelpout | *Zoarces viviparus* | NT | yellow | yellow | red | limited | 4 | 144-147 |
| **Mammals** | Grey seal | *Halichoerus grypus* | LC | yellow | yellow | red | limited | 2 | 148-149 |
| | Ringed seal | *Phoca hispida* | VU | yellow | yellow | red | limited | 1 | 150 |
| | Harbour seal | *Phoca vitulina* | LC | yellow | yellow | red | limited | 3 | 151-153 |
| | Harbour porpoise | *Phocoena phocoena* | CR | yellow | yellow | red | limited | 3 | 154-156 |
| **Molluscs** | Baltic clam | *Macoma baltica* | | yellow | green | yellow | reasonable | 6 | 157-162 |
| | Mussels | *Mytilus* spp. | | yellow | green | yellow | reasonable | 11 | 163-172, 214 |
| **Bristle worms** | Ragworm | *Hediste diversicolor* | | yellow | yellow | red | limited | 2 | 173-174 |
| | Mud worms * | *Marenzelleria* spp. | | green | red | red | limited | 3 | 175-177 |
| | Tubeworm | *Pygospio elegans* | | red | red | yellow | limited | 2 | 178-179 |

**TABLE 1** (Continued)

| Group | Common name | Scientific name | HELCOM Redlist category | Status of genetic knowledge I / II / III | Number of references | Reference number in Appendix S1 |
|---|---|---|---|---|---|---|
| **Arthropods** | Ostracod | *Cyprideis torosa* | | limited | 1 | 180 |
| | Copepod | *Eurytemora* spp. | | limited | 2 | 181-182 |
| | Gammarid | *Gammarus duebeni* | | limited | 1 | 183 |
| | Leaf beetle | *Macroplea mutica* | LC | reasonable | 1 | 184 |
| | Opossum shrimps | *Mysis* spp. | | limited | 4 | 185-188 |
| | Pseudocalanus | *Pseudocalanus* spp. | | limited | 1 | 189 |
| | Crab* | *Rhithropanopeus harrisii* | | limited | 1 | 190 |
| | Amphipod | *Monoporeia affinis* | | limited | 1 | 191 |
| **Comb jelly** | Warty comb jelly* | *Mnemiopsis leidyi* | | limited | 2 | 192-193 |
| **Bacteria** | Actinobacteria | *Actinobacteria* | | limited | 1 | 194 |
| | Cyanobacteria | *Anabaena* | | limited | 1 | 195 |
| | Cyanobacteria | *Nodularia* | | limited | 2 | 196-197 |
| | Freshwater cyanobacteria | *Microcystis aeruginosa* | | limited | 1 | 198 |
| | Shewanella | *Shewanella baltica*/spp. | | limited | 2 | 199-200 |
| | Bacterial communities | | | | 7 | 201-207 |
| **Dinoflagellates** | Dinoflagellate | *Alexandrium ostenfeldii* | | reasonable | 2 | 208-209 |
| **Other** | Penis worm | *Halicryptus spinulosus* | | limited | 1 | 210 |
| | Proboscis worm | *Echinorhynchus gadi* | | limited | 1 | 211 |
| | Microsporidium | *Hamiltosporidium tvaerminnensis* | | limited | 1 | 212 |
| | Eukaryotic microbes | | | | 1 | 213 |
| | Multiple species** | | | | 1 | 214 |

salinity conditions in the area (Berg et al., 2015; DeFaveri et al., 2013; Lamichhaney et al., 2012). The use of markers undergoing selection (so-called adaptive markers) has proven to give more detailed information on population genetic structure than putatively neutral genetic markers (Barrio et al., 2016; Berg et al., 2015; DeFaveri et al., 2013; Lamichhaney et al., 2012).

Combining genetic information with oceanographic data and morphological information and life-history data has proven to be successful for identifying management units in several species including the harbour seal (*Phoca vitulina*; Olsen et al., 2014) and the harbour porpoise (*Phocoena phocoena*; Sveegaard et al., 2015). Results from recent studies that have used new genetic/genomic methods on Baltic Sea populations are compiled in Supporting information, Appendix S3. Below, some important genetic findings of relevance for management for different organism groups in the Baltic Sea are summarized (cf. Table 2).

### 3.1.1 | Fish

Genetic uniqueness of Baltic Sea populations relative to North Atlantic populations has been shown for several fish species such as salmon (Nilsson et al., 2001; Ståhl, 1987), cod (Nielsen, Hansen, Ruzzante, Meldrup, & Gronkjaer, 2003), flounder (*Platichthys flesus*; Florin & Höglund, 2008) and herring (Lamichhaney et al., 2012). Genetic differences between brackish and freshwater populations are also present and have been documented for grayling (*Thymallus thymallus*; Swatdipong, Vasemägi, Koskinen, Piironen, & Primmer, 2009) and northern pike (Bekkevold, Jakobsen, et al., 2015). Management advice presented in the scientific literature include identification of the size

of management units of pike (Laikre, Miller, et al., 2005), identification of cod stocks in the eastern Baltic Sea and hybrid zones between stocks in the eastern and western Baltic Sea (Nielsen et al., 2003; Poćwierz-Kotus et al., 2015), genetic differentiation among demersal and pelagic spawners in flounder (Florin & Höglund, 2008) genetically distinct populations of salmon and trout in separate rivers (and areas within rivers) warranting management of each river flowing into the Baltic Sea separately (Ståhl, 1987; Ozerov et al., 2016), and low, but detectable, differentiation among stocks of herring, which promotes management on a more local level than currently applied (Barrio et al., 2016; Bekkevold, Heylar et al., 2015; Teacher, André, Jonsson, & Merilä, 2013). Of specific conservation interest is the identification of sturgeon (*Acipenser oxyrinchus*) populations from Canada suggested as the most suitable source populations for reintroduction programmes in Poland and Germany of the extinct sturgeon (Popović et al., 2014).

Other aspects of fish genetics that have potential value for managers are identification of deep water acting as barriers to gene flow in perch (*Perca fluviatilis*; Olsson, Mo, Florin, Aho, & Ryman, 2011) and whitefish (Olsson et al., 2012), local adaptations with respect to salinity and time of spawning that have been shown for herring (Barrio et al., 2016; Lamichhaney et al., 2012), and local adaptation connected to the Baltic Sea salinity and temperature gradient in three-spined stickleback (DeFaveri et al., 2013; Guo, DeFaveri, Sotelo, Nair, & Merilä, 2015). Extensive genetic baselines for stock identification are maintained for both salmon and trout (*Salmo trutta*) in the Baltic Sea (Koljonen, Gross, & Koskiniemi, 2014; Koljonen et al., 1999), and can be used to determine how much each genetically distinct population contributes to catches (so-called mixed stock analysis; Koljonen et al., 2014) and for

**TABLE 2** Brief summary of population genetic information of relevance for conservation management of separate species. Species included are those for which knowledge is classified as 'good' (seven) or 'reasonable' (twelve), and six species for which knowledge is classified as 'limited' but where important conservation management advice is still available (four mammal species, the important habitat-forming eelgrass, and the alien invasive warty comb jelly; Table 1). The species have been grouped according to their main ecological function

| Species | Knowledge on genetics | Threats to genetic biodiversity | Conservation genetic management advice | Reference |
|---|---|---|---|---|
| **Top predators** | | | | |
| Grey seal *Halichoerus grypus* | Baltic Sea population distinct from North Atlantic one. Within Baltic Sea clear genetic differences between breeding areas in the Bothnian Bay, Stockholm Archipelago, and Estonia. | Culling without knowing which population individuals belong to. Risk of overharvesting separate genetic group. | Treat different genetic groups from different breeding areas within the Baltic Sea. Separately monitor and safeguard breeding grounds and assure genetic viability within each group. More information needed on population structure within the Baltic Sea. | Graves et al., 2009 |
| Ringed seal *Phoca hispida* | Baltic Sea populations distinct from Arctic ones. No genetic divergence detected between Gulf of Finland and Gulf of Bothnia within the Baltic Sea. | Loss of genetic diversity due to small population size particularly in gulf of Finland ($N \sim 150$); $N_e$ at this breeding ground estimated as well below 50. | Conservation measures for the Gulf of Finland population needed. General protection of breeding grounds needed and population size needs to increase. National conservation and management plans need to be developed. | Palo, Mäkinen, Helle, Stenman, & Väinölä, 2001 |
| Harbour seal *Phoca vitulina* | Some genetic divergence between the Baltic Sea populations in Kalmar Sund vs those in South-Western Baltic Sea. Little divergence among south-western populations. | Loss of genetic diversity due to small population size in the Baltic Sea. Diseases have decreased the population substantially. | Baltic Sea populations should be a separate management unit from seals in Kattegat and Skagerrak. Protect breeding grounds and support populations. | Stanley et al., 1996; Goodman, 1998; Olsen et al., 2014 |
| Harbour porpoise *Phocoena phocoena* | Indications of a separate population in the Baltic Sea with a transition zone in the Arkona Basin into a Belt Sea population based on genetic, morphologic, and tracking data. | Baltic Sea population very small thus risk of loss of genetic diversity. Bycatches are unsustainably large. | Monitor and conserve the Baltic Sea population separately from populations in the Belt Sea and further west. Maintain/increase population size and protect breeding areas. | Wiemann et al., 2010; Sveegaard et al., 2015; Carlén et al., in prep. |
| **Major piscivores** | | | | |
| Northern pike *Esox lucius* | Genetic patterns appear to differ between pike spawning in the brackish Baltic Sea and those spawning in adjacent fresh water. Isolation by distance pattern for brackish spawners, distinct populations for freshwater spawners. Potential cross-Baltic Sea gene flow via Åland Islands occurs for brackish spawners. Genetic cores in Estonian and Stockholm Archipelagos, Bothnian Bay and the Swedish Quark. | Decline of local populations. Stocking occur in some areas and is not documented or monitored. | Ensure connectivity among spawning grounds to maintain a metapopulation of brackish spawners. Restore spawning grounds when needed. Both local and large-scale management needed. Pay particular attention to genetic core areas. Avoid stocking except to conserve weak populations. Monitor such releases and use genetically similar populations. | Laikre, Miller, et al., 2005; Bekkevold, Heylar et al., 2015; Wennerström et al., 2013, 2017 |
| Cod *Gadus morhua* | Genetically distinct Baltic Sea groups documented to reflect genetic adaptations to brackish water environment. Hybrid zone between Baltic and North Sea cod in Arkona Basin. Genetically separate spawning stocks west and east of Bornholm Island. | Eastern stock may not be replaced if depleted. High immigration of eastern cod into western management unit may mask poor state of western stock. Both western and eastern populations overfished which is expected to affect genetics. | Monitor eastern and western stock separately and assure large populations of each stock. The western stock should potentially be divided into several stocks. Continue and expand genetic monitoring of the stocks. | Nielsen et al., 2003, 2009; Eero, Hemmer-Hansen, & Hüssy, 2014; Poćwierz-Kotus et al., 2015; Hüssy et al., 2016 |

**TABLE 2** (Continued)

| Species | Knowledge on genetics | Threats to genetic biodiversity | Conservation genetic management advice | Reference |
|---|---|---|---|---|
| Perch *Perca fluviatilis* | Isolation by distance indicates gene flow mainly over short (<100 km) distances. Deep water acts as dispersal barrier. Estonian populations influenced by introgression from other populations. | Introgression from unknown populations in Estonia associated with high fishing pressure. Some local population declines and reduced effective sizes in Western Baltic Proper, Gulf of Riga, and Väinameri Archipelago. | Management units of less than 100 km and possibly different management strategies in different basins. Avoid intense fishing. Develop large scale management plans. | Olsson et al., 2011; Pukk, Kuparinen, Järv, Gross, & Vasemägi, 2013 |
| Atlantic salmon *Salmo salar* | Baltic Sea salmon genetically unique and includes three evolutionary units. Strong genetic substructure within the Baltic Sea; at least one genetically distinct population per river. Baseline data for genetic assignment to Baltic Sea rivers exist. Loss of genetic variation in hatchery stocks maintained to compensate for lost reproduction documented already in early 1980s. | The majority of natural populations lost, some of remaining ones threatened. Mixed fisheries, and large- scale releases threaten remaining gene pools and naturally spawning stocks. Genetic homogenization from releases documented and likely to have functional consequences. Global and local effective sizes depleted. Hatchery breeding often use too small populations, and large-scale releases threatens wild populations. Subjected to large-scale fishing which is expected to affect genetics. | Protection of populations of each river. Mixed open sea fisheries and large scale stocking should be avoided. Restore spawning habitats. Phase out large-scale releases. For conservation releases to support or reestablish weak/extinct population use local, genetically close populations. Genetic monitoring of effects of stocking and population losses needed. | Koljonen et al., 1999; Koljonen, Tähtinen, Säisä, & Koskiniemi, 2002; Ståhl, 1987; Pocwierz-Kotus et al., 2015; ICES, 2015; Palmé, Wennerström, Guban, Ryman, & Laikre, 2012; Ozerov, Gross et al., 2016 |
| Brown trout *Salmo trutta* | Strong genetic substructure with distinct populations; at least one per river/creek. High proportion of long distance migrants in mixed sea fisheries. Metapopulation structure documented in restricted areas (e.g. around islands Bornholm and Gotland). | Risk of depletion of weak stocks through mixed stock fisheries. Loss of spawning grounds. Large scale hatchery breeding and release risks genetic contamination of remaining wild populations. | Avoid stocking except for strict conservation purposes and then only use genetically similar populations. Protect and restore spawning grounds. Make use of available baseline information on stocks to monitor stock composition. Manage water systems as metapopulations. | Østergaard, Hansen, Loeschcke, & Nielsen, 2003; Laikre et al., 2002; Bernas, Burzyński, Debowski, Pocwierz-Kotus, & Wenne, 2014; Koljonen et al., 2014; ICES, 2015 |
| **Mesopredators** | | | | |
| Whitefish *Coregonus lavaretus/ C. maraena* | Baltic Sea whitefish forms an evolutionary significant unit (ESU) genetically distinct from non-Baltic Sea populations. Gene flow predominantly among neighboring populations. Isolation by distance pattern along Swedish coast. Sea- and river spawners form two different ecotypes further divided into genetically divergent populations. | Drastic decline of northern populations in the Baltic Sea. Introgressive hybridization from stocked European whitefish into Baltic Sea whitefish in the southern Baltic Sea. Mixed-stock fishery. | Local management with a regional context is suitable. Genetic monitoring of stocked populations is needed to assess effects on native populations. Maintain and restore spawning habitat. Avoid stocking except for conservation purposes and then only use genetically close populations. Use mixed-stock analysis based on genetics and gill-raker counts to avoid overexploitation of separate populations. | Olsson et al., 2012; Dierking et al., 2014; Ozerov, Himberg, Debes, Hägerstrand, & Vasemägi, 2016 |
| Atlantic herring *Clupea harengus* | Genetic adaptation to the Baltic Sea environment confirmed. Adaptive differences between spring and autumn spawning herring in the Baltic Sea also documented. | Risk of loss of local adaptations if some populations are depleted. Strong fishing pressure can affect genetic biodiversity. | Spring and autumn spawning herring should be genetically monitored as separate units and assure and large populations of both groups should be reassured. | Larsson et al., 2007; Lamichhaney et al., 2012; Barrio et al., 2016 |
| Three-spined stickleback *Gasterosteus aculeatus* | Little genetic differentiation in neutral genes but strong structuring in genes associated with physiology. Isolation by distance over Baltic Sea. | No immediate threats to populations or genetic variation. | No particular genetic management advice communicated. | DeFaveri et al., 2013 |

**TABLE 2** (Continued)

| Species | Knowledge on genetics | Threats to genetic biodiversity | Conservation genetic management advice | Reference |
|---|---|---|---|---|
| Flounder *Platichthys flesus* | Genetically unique Baltic Sea populations. Genetic differences between demersal and pelagic spawners within the Baltic Sea. | Risk of loss of local adaptations (e.g. demersal or pelagic spawners). Hybridization with plaice occurs to an extent that is unclear. | Two management units in the Baltic Sea should be considered, one in the northern Baltic Sea (demersal spawners) and one in the southern Baltic Sea including the Öresund straits (pelagic spawners). Hybridization with plaice needs genetic monitoring and further investigation to avoid misclassification of catches. | Florin & Höglund, 2007; Kijewska, Burzyński, & Wenne, 2009; ICES, 2015 |
| Nine-spined stickleback *Pungitius pungitius* | Two genetically distinct lineages meet in Danish straits. Isolation by distance indicates limited dispersal within Baltic Sea resulting in fine-scaled structuring. Levels of diversity and differentiation differ from that of threespined. | None known. | No particular genetic management advice communicated. | DeFaveri et al, 2012 |
| Turbot *Scophthalmus maximus* | Unique genetic group in the Baltic Sea. No clear population structure within the Baltic Sea. | Strong regional fishing pressure. | Important to safeguard the Baltic Sea population and assure good population status throughout the species coastal distribution area. Current data insufficient for management. | Florin & Höglund, 2008; Vandamme et al, 2014; ICES, 2015 |
| **Habitat forming species** | | | | |
| Narrow wrack *Fucus radicans* | Endemic to the Baltic Sea. Some clones widespread. Some areas with high genetic diversity have been identified. | Endemic to the Baltic Sea, cannot be replaced if eradicated. Loss of widespread clones. Low sexual reproduction in some areas. | Protect specifically this endemic Baltic Sea species. Assure large populations and connectivity among locations. Specific protection of Estonian populations known to harbour large variation including sexually reproducing populations. | Bergström, Tatarenkov, Johannesson, Jönsson, & Kautsky, 2005; Pereyra, Bergström, Kautsky, & Johannesson, 2009; Johannesson, Johansson et al., 2011; Schagerström, Forslund, Kautsky, Pärnoja, & Kotta, 2014 |
| Bladderwrack *Fucus vesiculosus* | Large genetic differences between Baltic Sea and North Sea populations. Fine-scale structure with significant genetic differences between populations as little as 1 km apart within the Baltic Sea. Higher clonality in northern populations. Several barriers to gene flow identified within Baltic Sea. Stable population structures over the last 10 years. | Historical declines of populations mostly due to habitat destruction. Loss of xgenetic variation in marginal areas of the Baltic Sea. | Protect populations of high clonal richness (predominantly southern populations). Maintain large population sizes and connectivity over the Baltic Sea. Consider for specific genetic monitoring due to ecological importance. Management plans are needed. | Tatarenkov, Jönsson, Kautsky, & Johannesson, 2007; Johannesson, Johansson et al, 2011; Wennerström et al, 2013 |
| Black carageen *Furcellaria lumbricalis* | Baltic Sea populations genetically unique relative to Atlantic. Little differentiation within the Baltic Sea. Contrasting divergence pattern between Baltic Sea and Atlantic populations indicate that low salinity has affected genetic variation. | Risk of losing locally adapted populations. | Suggested as a possible model for studying genetic variation over environmental gradients. Management plans are needed. Monitor occurence and assure connectivity among populations | Kostamo, Korpelainen, & Olsson, 2012; Olsson & Korpelainen, 2013 |

**TABLE 2** (Continued)

| Species | Knowledge on genetics | Threats to genetic biodiversity | Conservation genetic management advice | Reference |
| --- | --- | --- | --- | --- |
| Baltic clam *Macoma balthica* | Hybrid zone between Atlantic and Baltic Sea types in the Öresund straits and the western Baltic Sea. | No communicated threats. | Assure large populations and connectivity among populations. | Nikula, Strelkov, & Väinölä, 2008; Luttikhuizen, Drent, Peijnenburg, van deer Veer, & Johannesson, 2012 |
| Blue mussel *Mytilus spp* | Hybridization between *M. trossulus* (mostly Baltic Sea) and *M. edulis* (mostly North Sea). Hybrid zone at the entrance of the Baltic Sea. Hybrid swarm in Baltic Sea populations. | No apparent threats described in the scientific literature but risk of loss of marginal populations with strong *M. trossulus* profile. | Assure large populations and connectivity among populations. Monitor *M. trossulus* populations in northern Baltic Sea. | Väinölä & Strelkov, 2011; Zbawicka, Sañko, Strand, & Wenne, 2014 |
| Fennel pond weed *Potamogeton pectinatus* | Baltic Sea populations genetically separated from freshwater populations. | No apparent threats. | No particular genetic management advice communicated. | Nies & Reusch, 2005 |
| Eelgrass *Zostera marina* | Baltic Sea populations genetically unique. Genetically diverse populations documented to be positively associated with biomass production, plant and faunal abundance, resistance to disturbance and recovery potential. | Declining in some areas, e.g. the Puck Bay in Poland. | Assure large populations and connectivity among them. Use local strains for reintroductions (specifically for the Puck Bay in Poland). Consider for specific genetic monitoring due to ecological importance. | Reusch, Stam, & Olsen, 2000; Reusch et al., 2005; Gonciarz, Wiktor, Tatarek, Węgleński, & Stanković, 2014 |
| **Evertebrates** | | | | |
| Leaf beetle *Macroplea mutica* | Baltic populations not highly differentiated from other populations in Europe. Passive dispersal. | No apparent threats. | No particular genetic management advice communicated. | Mende, Biström, Meichssner, & Kölsch, 2010 |
| Dinoflagellate *Alexandrium ostefeldii* | Current species definitions are not resolved. | Not threatened, but poses a threat to other species due to toxic algae blooms. | No particular genetic management advice communicated. | Kremp et al, 2014 |
| **Alien invasive** | | | | |
| Warty comb jelly *Mnemiopsis leidyi* | Population in Baltic Sea comes from xat least two different invasions. Genetic diversity decreased in eastern distribution (Bornholm Basin) over 2008–2010 | Invasive species that is identified as a threat to the Baltic ecosystem. | Improve handling of ballast water to prevent further introductions. Use genetics to monitor occurrence, invasive histories, and for evaluating if and where selfsustaining populations have established. | Reusch, Bolte, Sparwel, Moss, & Javidpours, 2010; Bolte et al. 2013 |

monitoring genetic effects of stocking (Ozerov et al., 2016; Vasemägi et al., 2005).

### 3.1.2 | Mammals

Genetic data, combined with satellite and acoustic tracking and morphology, support the existence of a unique Baltic proper population of harbour porpoise, and another population in the south-west Baltic and Belt Seas (Sveegaard et al., 2015; Wiemann et al., 2010). These small and endangered populations should be monitored and conserved separately from North Sea harbour porpoise (Sveegaard et al., 2015). Genetically unique Baltic Sea populations have also been reported for harbour seal (*Phoca vitulina*; Johannesson & André, 2006) and grey seal (*Halichoerus grypus*; Graves et al., 2009).

Combining genetics with other life-history and demographic data has been a successful approach also for harbour seal; Olsen et al. (2014) identified management units in the southern Baltic Sea and in Denmark and the Swedish west coast that differ substantially both in size and location from current management units that are based mainly on habitat characteristics.

### 3.1.3 | Arthropods

Examples of studies of Baltic Sea arthropods with clear management implications are the identification of the North American invasive species *Eurytemora carolleeae* from its naturally occurring sister species (*Eurytemora affinis*) in the Baltic Sea by means of genetic barcoding. Genetic data are more precise than morphologic data in such situations (Sukhikh, Souissi, Souissi, & Alekseev, 2013). In a pilot study of *Monoporeia affinis*, a species used in ecotoxicological monitoring programmes, variation in mtDNA showed indices of lower genetic variation on polluted sites compared with non-polluted reference sites. The authors recommended adding the use of genetic data in the ongoing monitoring programme (Guban, Wennerström, Elfwing, Sundelin, & Laikre, 2015).

### 3.1.4 | Molluscs

Two species of blue mussel (*Mytilus*) are present in the Baltic Sea; *Mytilus edulis*, which is mainly occurring in the southern Baltic Sea and *Mytilus trossulus*, mainly in the northern part. There is substantial hybridization between the species and the taxonomy in the Baltic Sea is still not completely resolved (Riginos & Cunningham, 2005; Steinert, Huelsken, Gerlach, & Bininda-Emonds, 2012). A parallel case of high levels of hybridization between two genetically distinct lineages of Baltic clam (*Macoma balthica*) is also present in the Baltic Sea (Nikula et al., 2008). The hybridization is so extensive that the entire Baltic Sea population could be viewed as a hybrid swarm (Nikula et al., 2008).

### 3.1.5 | Macrophytes (algae and angiosperms)

Habitat-forming macrophyte communities in the Baltic Sea are dominated by a few species, among which the macroalgae *Fucus vesiculosus* and *F. radicans* and the eelgrass (*Zostera marina*) are particularly widespread and important (Gonciarz et al., 2014; Wikström & Kautsky, 2007). High levels of clonality in both *Fucus* species and in *Z. marina* make Baltic Sea populations vulnerable and unlikely to be replaced by

Atlantic populations if eradicated (Johannesson, Smolarz et al., 2011). *Fucus radicans* is a newly evolved species and endemic to the Baltic Sea (Bergström et al., 2005). One single clone of *F. radicans* dominates large areas in the Baltic Sea. Sexual reproduction is more widespread among Estonian populations where genetic diversity is subsequently higher (Johannesson, Johansson et al., 2011; Pereyra et al., 2009). For *Z. marina* genetic data have been used for identification of suitable donor populations for a reintroduction programme in Puck Bay, Poland (Gonciarz et al., 2014).

### 3.1.6 | Bacteria and invasive species

Bacterial communities in the Baltic Sea shift in response to season, salinity, anthropogenic actions, etc. (Dupont et al., 2014; Koskinen, Hultman, Paulin, Auvinen, & Kankaanpää, 2010; Tamminen, Karkman, Corander, Paulin, & Virta, 2011). Monitoring of this basal ecosystem level is important in order to understand trophic interactions and anthropogenic influences in the Baltic Sea (Tamminen et al., 2011), and might also be of use for climate modelling (Dupont et al., 2014).

Genetic studies of invasive species can give information on source populations of the invasive populations and/or aid in species identification. Invasive species that have been studied in the Baltic Sea are the comb jelly (*Mnemiopsis leidyi*) and mudworms (*Marenzelleria* spp.). Genetic data have identified a direct invasion of comb jelly via ballast water from the US east coast to the Baltic Sea. It has also been shown that the current ballast water treatment is not sufficient to prevent future invasions (Reusch et al., 2010). Mudworms in the Baltic Sea consist of three different sister species that have invaded the area on different occasions. Morphological identification of these species is difficult, but genetic data have improved the potential for species identification (Bastrop & Blank, 2006; Blank, Laine, Jürss, & Bastrop, 2008). More detailed mapping of the distribution of these new species will now be possible.

## 3.2 | Temporal variation and genetically effective population size ($N_e$)

The genetically effective population size ($N_e$) has been estimated for 12 species in the Baltic Sea as reported in 16 scientific publications (Table 3). $N_e$ is a key parameter in conservation genetics monitoring because it quantifies the rate of inbreeding and loss of genetic diversity through random chance (so-called genetic drift; Crow & Kimura, 1970). As an example, if a population of 100 individuals (i.e. census size $N_c$ = 100) shows an inbreeding increase of 2 percent per generation ($\Delta F$ = 0.02) then the effective size of that population is 25 ($N_e = \frac{1}{2\Delta F}$). For conservation of genetic biodiversity it is typically the effective population size rather than the census size that is of concern. Thus, considerable research efforts have been devoted to $N_e$ including theoretical work on how to understand, model and estimate $N_e$ (Luikart, Ryman, Tallmon, Schwartz, & Allendorf, 2010; Waples, 2010, 2016) as well as empirical work on using the theory to estimate effective size of populations (Palstra & Fraser, 2012).

For nine of the 12 Baltic Sea species effective size estimates refer to $N_e$ in sampling localities within separate basins. Such estimates for present day populations range from 10 and below for perch to c. 2,000 for whitefish (Table 3). For three species attempts have been

**TABLE 3** Summary of published estimates of the genetically effective population size ($N_e$) for populations of species in the Baltic Sea

| Species | Sample location | $N_e$ point estimate (approximate) | Estimation method/comment | Reference |
|---|---|---|---|---|
| Atlantic herring *Clupea harengus* | *Northern Baltic Proper, 2 sites* Himmerfjärden | 1600 | Between 1979 and 2003; assuming migration into population (likelihood method; Wang & Whitlock, 2003) | Larsson et al., 2010 |
| | | >35 000 | Between 1979 and 2003; assuming isolated population (likelihood method, Wang, 2001) | |
| | Vaxholm | 450 | Between 2002 and 2003 (temporal method; Jorde & Ryman, 2007) | |
| | | 280 | Between 1979 and 2003; assuming migration into population (likelihood method; Wang & Whitlock, 2003) | |
| | | 420–710 | Between 1979 and 2003; assuming isolated population (likelihood method, Wang, 2001; temporal method, Jorde & Ryman, 2007; $F_c$, Nei & Tajima, 1981) | |
| | | 840 | Between 2002 and 2003 (temporal method; Jorde & Ryman, 2007) | |
| | *Bothnian Bay, 1 site* Kalix | 3060 | Between 1979 and 2003; assuming migration into population (likelihood method, Wang & Whitlock, 2003) | |
| | | >35 000 | Between 1979 and 2003; assuming isolated population (likelihood method; Wang, 2001) | |
| | | 420–4060 | Between 2002 and 2003 (temporal method, Jorde & Ryman, 2007; linkage disequilibrium method, Waples, 1989b) | |
| | All three sites | 2150 | Between 1979 and 2003; assuming migration into population (likelihood method, Wang & Whitlock, 2003) | |
| | | 6120–12 280 | Between 1979 and 2003 assuming isolated population (likelihood method, Wang, 2001; $F_c$, Nei & Tajima, 1981) | |
| | | 1470 | Between 2002 and 2003 (temporal method, Jorde & Ryman, 2007) | |
| Whitefish *Coregonus lavaretus* | *Bothnian Bay, 2 sites* Kiiminkijoki autumn run | 120–510 | Contemporary $N_e$ in 2006 autumn run (linkage disequilibrium, Hill, 1981; LDNe, Waples & Do, 2008; MCMC simulations in MSVAR, Beaumont, 1999, Storz & Beaumont, 2002) | McCairns et al., 2012 |
| | | 440–1750 | Between 1981 and 2006 (6 generations; temporal methods, Waples, 1989a, Wang, 2001) | |
| | | 87 000 | Historic $N_e$ over thousands of years from 2006 sample (MSVAR, Beaumont, 1999; Storz & Beaumont, 2002). | |
| | Tornionjoki Autumn + summer run | 44–1000 | Contemporary $N_e$ in year 2000 (methods as for Kiiminkijoki) | |
| | | 1300–1980 | Between 1981 and 2000 (5 generations; temporal methods Waples, 1989a, Wang, 2001) | |
| | | 104 300 | Historic $N_e$ over thousands of years from 2000 sample (as above) | |
| Northern pike *Esox lucius* | *Arkona Basin, 1 site* Stege nor | 400 | Between 1957 and 2007, approximate Bayesian approach (DIYABC, Cornuet, Ravigné, & Estoup, 2010) | Bekkevold, Jakobsen et al., 2015 |
| Cod *Gadus morhua* | *Bornholm Basin, 1 spawning site* | 840–1750 | Between c. 1930 and 1997 (~7 generations; temporal method, Waples, 1989a using NeEstimator; Peel, Ovenden, & Peel, 2004; likelihood method, Wang, 2001 using MNE; Wang & Whitlock, 2003); coalescent based method, Berthier, Beaumont, Cornuet, & Luikart, 2002) | Poulsen et al., 2006 |

(Continues)

**TABLE 3** (Continued)

| Species | Sample location | $N_e$ point estimate (approximate) | Estimation method/comment | Reference |
|---|---|---|---|---|
| Three-spined stickleback *Gasterosteus aculeatus* | *The Quark, 1 site* Sikeå | 50–450 | Samples from 2003, 2009 estimates using single sample methods (Tallmon, Koyuk, Luikart, & Beaumont, 2008; Wang, 2009) and several temporal methods (Berthier et al., 2002; Nei & Tajima, 1981; Pollak, 1983; Wang & Whitlock, 2003) | DeFaveri & Merilä, 2015 |
| | *Gulf of Finland, 2 sites* Tvärminne | 45–300 | Years and methods as above | |
| | Kotka | 55–260 | Years and methods as above | |
| | *Entire Baltic Sea, 11 sites* | 1700 | Single samples (year not provided), maximum likelihood method of MIGRATE (Beerli & Felsenstein, 2001) | DeFaveri et al., 2012 |
| Nine-spined stickleback *Pungitius pungitius* | *Entire Baltic Sea, 11 sites* | 990 | Single samples (year not provided), maximum likelihood method of MIGRATE (Beerli & Felsenstein, 2001) | DeFaveri et al., 2012 |
| Perch *Perca fluviatilis* | *Northern Baltic Proper, 1 site* Matsalu Bay | 80 | Cohorts 1981–1990 before fisheries induced collapse (maximum-likelihood method, MLNE, Wang & Whitlock, 2003) | Pukk et al., 2013 |
| | | 10 | Cohorts 1995–2008 after fisheries induced collapse (method as above) | |
| | *Western Gotland Basin, 13 sites* | 1.5–3.0 | Variance and inbreeding $N_e$ in 2005 from equation of Xu and Fu (2004) and from $F_{IS}$ values | Bergek & Björklund, 2009 |
| Atlantic salmon *Salmo salar* | *Bothnian Bay, 1 captive broodstock* Tornionjoki | 240 | Over two generations, temporal method of Pollak (1983) | Koljonen et al., 2002 |
| Brown trout *Salmo trutta* | *Bornholm Basin Slupia River drainage* Slupsk, wild | 290–550 | Single samples from 2008 in all four cases. All estimates based on linkage disequilibrium methods using LDNe (Waples, 1989b) and NeEstimator (Peel et al., 2004) | Bernas et al., 2014 |
| | Lower Slupia | 40–50 | | |
| | Kwacza (flowing into Slupia) | 22–50 | | |
| | *Gulf of Finland, 5 rivers* Rompeti River | 450 | Single samples from 2009 in all rivers. All estimates based on linkage disequilibrium (LDNe, England, Cornuet, Berthier, Tallmon, & Luikart, 2006; Waples, 1989b) | Poćwierz-Kotus et al., 2014 |
| | Jukkola River | 50 | | |
| | Loo River | 60 | | |
| | Valkla River | 200 | | |
| | Riguldi River | 70 | | |
| | *Eastern Gotland Basin, 1 river* Neman River | 25 | | |
| | *Gdansk Basin, 1 river* Vistula River | 180 | | |
| | *Bornholm Basin, 2 rivers* Slupia River | 160 | | |
| | Bornholm Island | 100 | | |
| | *Bornholm Basin,* 7 creeks on the island of Bornholm | 20–260 | Estimates for separate creeks assuming isolated populations (temporal method, MLNE; Wang & Whitlock, 2003) | Østergaard et al., 2003 |
| | | 8–23 | Estimates for separate creeks assuming migration between creeks (temporal method, MLNE; Wang & Whitlock, 2003) | |
| | *Western and Eastern Gotland Basins* 13 creeks on the island of Gotland | 30 | Average per creek female $N_e$ (temporal method; Jorde & Ryman, 1995, modified for mitochondrial DNA, Laikre, Jorde, & Ryman, 1998) | Laikre et al., 2002 |

(Continues)

**TABLE 3** (Continued)

| Species | Sample location | $N_e$ point estimate (approximate) | Estimation method/comment | Reference |
|---|---|---|---|---|
| Grey seal *Halichoerus grypus* | *Bothnian Bay, 1 site* *Northern Baltic Proper, 2 sites* | 6100 | Historic $N_e$ c. 2000 generations ago (coalescent based, Bayesian computation (Beaumont, Zhang, & Balding, 2002; Bertorelle, Benazzo, & Mona, 2010; DIYABC software, Cornuet et al., 2008, 2010) | Klimova et al., 2014 |
| | *All three sites considered as one population in $N_e$-analyses* | 46 800 | Contemporary $N_e$ (method as above) | |
| | | 13 600 | Contemporary $N_e$ based on Bayesian computation using mitochondrial DNA data (IMA2, Hey, 2010) | |
| Copepod *Eurytemora affinis* | *Northern Baltic Proper, 1 site* | 0.6 | Contemporary female $N_e$ before population expansion (coalescent modelling of mitochondrial DNA sequence evolution, LAMARC, Kuhner, 2006) | Winkler, Souissi, Poux, & Castric, 2011 |
| | | $>7.81 \times 10^{10}$ | Contemporary female $N_e$ after population expansion (approach as above) | |
| Spionid polychaete *Pygospio elegans* | *Åland Sea, 1 site* Ängsö | 145–220 | Likelihood based method (MLNE; Wang & Whitlock, 2003) and moment based temporal method (NeEstimator, Ovenden et al., 2007) assuming isolated population | Kesäniemi, Mustonen, Boström, Hansen, & Knott, 2014 |
| | | 65 | Likelihood based method (MLNE; Wang & Whitlock, 2003) assuming non-isolated population | |
| | *Gulf of Finland, 1 site* Fårö | 145–190 | Methods as above assuming isolated population | |
| | | 45 | Methods as above assuming non-isolated population | |

made to estimate $N_e$ over the entire Baltic Sea providing estimates of c. 2000 and 1000 for three-spined and nine-spined sticklebacks, respectively, and thousands for grey seal (Table 3).

A rule of thumb in conservation genetics stipulates that a population should have a $N_e$ of at least 50 for short-term conservation, and one of at least 500 for long-term conservation to allow harbouring enough genetic variation to maintain the capacity of response to selective pressures and subsequently long-term survival (Allendorf & Ryman, 2002; Franklin, 1980). Short-term time frames typically refer to 5–20 generations or less than 100 years, whereas long term typically means longer periods, including over evolutionary time scales.

There are several local Baltic Sea populations with $N_e$ < 50 (Table 3). For example, effective size for perch in Matsalu Bay in Väinameri Archipelago, Estonia, was estimated as only 10 after a population collapse induced by fisheries (Pukk et al., 2013). Similarly, strikingly low $N_e$ estimates were observed for brown trout in a Lithuanian population (Poćwierz-Kotus et al., 2014) as well as in several creeks on the islands of Bornholm (Østergaard et al., 2003) and Gotland (Laikre et al., 2002). These low estimates underline the importance of managing populations as interconnected metapopulations assuring gene flow between local populations with small effective sizes. Similarly, there are several examples of $N_e$ estimates exceeding 50 but falling below 500, which also points to the need to assure large populations and connectivity among them over the Baltic Sea to secure maximum evolutionary potential for Baltic Sea species.

Long-term genetic monitoring over several decades carried out for populations of six Baltic species showed temporal stability of spatial genetic structuring in pike (Bekkevold, Jakobsen et al., 2015), herring (Larsson, Laikre, André, Dahlgren, & Ryman, 2010; Limborg et al., 2012) and whitefish (McCairns, Kuparinen, Panda, Jokikikko, & Merilä, 2012). In contrast, non-stable patterns, with considerable genetic fluctuations over decades, were observed for the Bornholm brown trout (Østergaard et al., 2003). For cod, Nielsen, MacKenzie, Magnussen, and Meldrup (2007) found stable genetic structure at both neutral markers and a single, coding marker over >6 decades, whereas Poulsen, Nielsen, Schierup, Loeschcke, and Grønkjaer (2006) report small but significant changes in the Bornholm Basin during the same time span. In heavily fished perch populations along the Estonian and Latvian coast, life history changes were observed and might be due to immigration of genetically different populations following population decrease (Pukk et al., 2013). Genetic homogenization of salmon in the River Vindelälven – one of few remaining wild, viable Baltic salmon populations – was observed between 1985 and 2003 as a result of a heavy stocking programme (Vasemägi, Nilsson, & Primmer, 2005).

Genetic monitoring over years within single decades shows a temporally stable structure and amount of genetic variation in pike, plaice, cod, and three-spined stickleback (DeFaveri & Merilä, 2015; Pampoulie, Stefánsson, Jörundsdóttir, Danilowicz, & Daníelsdóttir, 2008; Was, Gosling, & Hoarau, 2010; Wennerström et al., 2017), but with some temporal differences observed in turbot (Nielsen, Nielsen, Meldrup, & Hansen, 2004). Within-season genetic differences at herring spawning sites are interpreted as genetically different populations using the same spawning grounds (spawning waves; Jørgensen, Hansen, Bekkevold,

Ruzzante, & Loeschcke, 2005; Jørgensen, Hansen, & Loeschcke, 2005). Short-term genetic changes indicating drift have been observed in the species with low effective sizes (Table 3) and also in turbot and narrow wrack (Ardehed et al., 2015; Florin & Höglund, 2007).

In fourhorn sculpin (*Myoxocephalus quadricornis*) considerable genetic fluctuations were observed over a number of years in the Bothnian Bay and the Quark, particularly at polluted sampling sites. This suggests that sculpins are unable to maintain stable populations in polluted areas resulting in population turnovers (Gyllensten & Ryman, 1988).

### 3.3 | Management advice in the scientific literature

In 47 (55%) of the 85 studies published during 2010–2015 there is a conservation or management angle. Direct management advice based on genetic data is given for 15 species (Appendix S2). In 20 of the 47 studies with a management or conservation angle, specific advice for the species concerned is not given; rather, the authors generalize their findings within a larger conservation perspective, e.g. by stressing the importance of incorporating genetic data in management (Limborg et al., 2012; Olsson & Korpelainen, 2013). For non-threatened species without a commercial interest, methods and study approaches can be extended to other species that are in greater need of management. One example is the use of selected markers to identify population subdivisions in high gene-flow species, as applied for the three-spined stickleback (DeFaveri et al., 2013).

### 3.4 | Genetic variation in marine protected areas

No genetic patterns were found that differentiated between populations inside vs outside HELCOM MPAs for any of the four species considered in the case study; the amount of genetic variation, measured both as allelic richness and expected heterozygosity, was almost identical (Table 4). For pike and three-spined stickleback the number of sampled populations was large enough to permit statistical comparison of the level of genetic variation inside vs outside MPAs. There was no

difference in allelic richness or expected heterozygosity between populations sampled inside vs outside MPAs (pike, allelic richness: $t_{18} = 0.437$, $P = 0.667$, $H_e$: $t_{18} = 0.224$, $P = 0.826$; three-spined stickleback: allelic richness: $t_{24} = 1.234$, $P = 0.229$, $H_e$: $t_{24} = 0.645$, $P = 0.526$). Total contribution to genetic diversity did not differ between protected and unprotected areas for any of the species (pike: $F_{1, 18} = 0.014$, $P = 0.907$; three-spined stickleback: $F_{1, 24} = 0.082$, $P = 0.778$). The results from the AMOVAs showed that the amount of genetic variation explained by protection was 0% for all four species except for bladderwrack where protection explained 1% of the total genetic variation.

## 4 | DISCUSSION

Genetic information of direct relevance for conservation management is available for more than 20 Baltic Sea species and we recommend using this information in management (summarized in text and in Table 2). There is a clear interest among scientists to inform how research results are relevant to conservation and management; more than half of the studies published since 2010 consider conservation or management issues.

Recently, several studies have been successful in communicating results into conservation plans (Table 2). One of these projects involved the identification of suitable populations of eelgrass for reintroduction to protect declining populations in Puck Bay in Poland (Gonciarz et al., 2014). The results are already being implemented in practical conservation work (http://www.iopan.gda.pl/projects/Zostera/; Magdalena Gonciarz personal communication). Similarly, genetic information is used in stock assessments of some commercially fished species such as salmon, trout and cod (International Council for the Exploration of the Sea [ICES], 2015).

Other examples of recent genetic results already included in management plans, or expected to be so soon, include identification of genetically distinct units of seals and porpoise. New ways to analyse population genetic data jointly with data on individual movement and

**TABLE 4** Summary statistics of genetic diversity among populations of four species with samples grouped into those from protected areas and those outside such areas (Figure 1). Pop = number of populations sampled, n = number of individuals sampled (maximum and minimum sample sizes in parenthesis), Loci = number of genetic marker loci analyzed, allelic richness = measure of amount of genetic variation measured as alleles when sample size is taken into account. For allelic richness and $H_e$ the average for respective group is given, minimum and maximum values are given in parenthesis. Contr (%) is the sum of contribution in percent of each population to total genetic variation, i.e. the total proportion of variation that would disappear if all populations from the group were removed from the total sample (Petit et al., 1998)

| | Pop | n | Loci | Allelic richness | Expected heterozygosity | Contr (%) |
|---|---|---|---|---|---|---|
| **Pike (*Esox lucius*)** | | | | | | |
| Protected | 10 | 257 (10–59) | 11 | 2.78 (2.62–3.07) | 0.60 (0.55–0.66) | -0.406 |
| Unprotected | 10 | 402 (10–132) | 11 | 2.79 (2.64–2.91) | 0.59 (0.55–0.63) | 1.282 |
| **Three-spined stickleback (*Gasterosteus aculeatus*)** | | | | | | |
| Protected | 11 | 362 (31–36) | 20 | 7.38 (7.28–7.73) | 0.72 (0.69–0.73) | 0.331 |
| Unprotected | 15 | 522 (21–36) | 20 | 7.47 (6.80–7.74) | 0.72 (0.70–0.74) | -0.270 |
| **Turbot (*Scophthalmus maximus*)** | | | | | | |
| Protected | 2 | 118 (24–48) | 14 | 4.25 (4.07–4.43) | 0.63 (0.61–0.66) | 3.286 |
| Unprotected | 2 | 91 (45–46) | 14 | 4.41 (4.38–4.44) | 0.64 (0.64–0.65) | -0.756 |
| **Bladderwrack (*Fucus vesiculosus*)** | | | | | | |
| Protected | 4 | 112 (12–43) | 9 | 3.17 (2.36–4.31) | 0.57 (0.49–0.71) | 4.780 |
| Unprotected | 5 | 126 (9–42) | 9 | 3.37 (2.59–4.26) | 0.60 (0.52–0.69) | 4.759 |

morphology (Flannery et al., 2012; Sveegaard et al., 2015), or population viability analysis (Olsen et al., 2014) have proven successful in delineating population boundaries and identifying new management units. Recommendations based on these studies to treat Baltic Sea harbour porpoise as a separate management unit are expected to be incorporated in management plans and include suggestions to protect breeding areas within the EU Natura2000 framework (Swedish Government Decision, Ministry of Environment and Energy, 2016–12-14 M2015/02273/Nm; Mats Amundin, Linköping University, personal communication; Carlén et al. in prep.). For harbour seals results from genetic studies are already used by HELCOM and are expected to be included in Swedish and Danish national management plans (Morten T. Olsen, University of Copenhagen, personal communication).

An interesting topic for future research includes elucidating factors affecting adaptive management with respect to genetic diversity. For several species where genetic data are used, such as for salmon and brown trout, genetic information has been available for a long time and genetic management advice has been actively communicated by researchers for decades (Ryman, 1981; Ryman & Utter, 1987). In contrast, genetic information for the harbour porpoise and the harbour seal has been provided more recently.

Important knowledge gaps are also identified in this review (c.f. Table 1). For many of the commercially most important fish species in the Baltic Sea such as plaice (*Pleuronectes platessa*), sprat (*Sprattus sprattus*), dab (*Limanda limanda*), sole (*Solea solea*) and brill (*Scophthalmus rhombus*), information on population structure is sparse or completely lacking (ICES, 2015). These shortcomings were pointed out 10 ten years ago, as was the lack of population genetic data for common bream (*Abramis brama*), burbot (*Lota lota*), and vendace (*Coregonus albula*; Laikre et al., 2005). Generating data on basic population genetic structure of these species should be of high priority. There are also frequent time lags between available scientific data and practical management.

The estimates of effective population size and other temporal data that exist for Baltic Sea species (Table 3) indicate that loss of genetic diversity might be rather rapid, at least in local populations of some species. The results underline the importance of continued monitoring of genetic diversity and assuring gene flow between local populations as well as maintaining large populations of Baltic Sea species. They also highlight the need to adopt a metapopulation approach in management, which includes recognizing that affecting the genetic composition in one region through, for example, population reduction, or genetic changes through stocking, may affect genetic biodiversity also in other regions of the Baltic Sea. At the same time the $N_e$ estimates should be interpreted with some caution because estimating $N_e$ in substructured populations without detailed knowledge of the population structure and/or in situations with high rates of gene flow can give biased estimates (Ryman, Allendorf, Jorde, Laikre, & Hössjer, 2014).

For species without a clear commercial interest, genetic information is rarely used in management even when available. This is unfortunate since many of these species are important keystone species, such as the habitat-forming *Fucus vesiculosus*, *Fucus radicans* and *Zostera marina*. Correlations between genetic diversity and species richness, habitat quality and stability have been shown in other marine systems

(Selkoe et al., 2016) including with respect to *Z. marina* (Reusch et al., 2005). Thus, protection and monitoring of genetically diverse populations, such as *Fucus* populations in Estonia (Johannesson, Johansson et al., 2011), and large and interconnected populations of habitat forming species is likely to be important for the entire ecosystem.

In general, it is important to maintain large populations of naturally occurring species and assure genetic connectivity over the Baltic Sea to maximize each species´ potential for genetic adaptation to the changing environment. This is particularly important for species with a marine origin since increasing genetic data show that such species have developed unique genetic adaptations to the brackish environment. Current rapid climatic changes, which further decrease salinity levels while temperature is increasing, are expected to put elevated selective pressures on typically marine species in the Baltic Sea. The potential for further adaptation and survival of Baltic Sea species needs to be maximized through maintaining large gene pools on which selection can operate.

## 4.1 | MPAs and genetic conservation

Marine protected areas (MPAs) are widely advocated for being the most effective conservation tool in marine environments, including protection of genetic diversity (Claudet et al., 2008; Edgar, 2011; Palumbi, 2003). The fish *Diplodus sargus* in MPAs in the Mediterranean Sea have significantly higher genetic variation, estimated as allelic richness, than populations outside protected areas (Perez-Ruzafa, Gonzales-Wangüermert, Lenfant, Marcos, & García-Charton, 2006). MPAs have also been shown to be important for populations outside protected areas, because protected populations can contribute individuals to non-protected areas (Moland et al., 2013; Pujolar et al., 2013).

In the present study, there were no patterns of increased genetic variations for samples from MPAs compared with samples from non-protected areas, for the four species studied. Rather, samples from within MPAs seem to be a random and representative selection of populations in the Baltic Sea. Thus, even though HELCOM MPAs do not appear to be protecting populations of particular genetic importance for the species studied here, these MPAs appear to protect genetic diversity in proportion to the size of the area under protection.

The lack of obvious difference between samples from within vs outside MPAs can be due to several factors. First, for MPAs to be effective they need to be constructed with the specific biology of species and populations to be protected in mind (Bors, Rowden, Maas, Clark, & Shank, 2012). This is not the case for the MPAs studied here. Not only are Baltic Sea MPAs not constructed to protect genetic variation per se (Laikre et al., 2016), they also rarely focus specifically on marine organisms, although their general, broad aim includes conserving biodiversity at all levels. Second, MPAs should generally fulfill several of the following key features: no take allowed (i.e. no fishing, hunting, or other exploitation of species), well enforced legally, old, large, and isolated (Edgar et al., 2014). However, all of these features do not necessarily apply for all species, e.g. for species without a commercial interest such as bladderwrack in the present study a no take area is irrelevant since the species is not harvested at all. The general

features are not fulfilled for most of the Baltic Sea MPAs, and thus the effectiveness of Baltic Sea MPAs might be reduced (Sandström et al., 2016). A more comprehensive study, with a careful sampling design with samples in and outside MPAs including diverse species, would be needed for an in-depth assessment of genetic patterns and connectivity among MPAs in the Baltic Sea.

## 4.2 | New possibilities with genomic tools

With emerging genomic methods, the costs for genetic studies are dropping fast; new methods are sometimes already cheaper than more traditional approaches (Ovenden, Berry, Welch, Buckworth, & Dichmont, 2015; Shafer et al., 2015). The vast expansion of available genetic data enables more precise estimation of, for example, population census and genetically effective size and connectivity, while simultaneously opening up the possibility to identify genomic regions underlying adaptive trait variation in natural populations (Allendorf, Hohenlohe, & Luikart, 2010; Shafer et al., 2015). The genomic methods are currently reshaping our understanding of how marine populations are structured. Despite low genetic divergence among populations as seen with neutral genetic markers, selective differences occur in species within the Baltic Sea indicating the existence of genetic adaptation to this particular environment (Hemmer-Hansen, Therkildsen, Meldrup, & Nielsen, 2014; Limborg et al., 2012).

In marine environments genes behind adaptive divergence often code for protein variants reflecting adaptation to particular salinity and temperature conditions (Corander, Majander, Cheng, & Merilä, 2013; Limborg et al., 2012). Such adaptations are expected to be found among populations in the Baltic Sea, and have recently been documented for Baltic Sea species such as herring (Barrio et al., 2016; Lamichhaney et al., 2012), three-spined stickleback (DeFaveri et al., 2013) and cod (Hemmer-Hansen et al., 2014). Monitoring such genetic adaptive variation over time is highly warranted for these and other Baltic Sea species. In Appendix S3, major findings from 17 recent studies that have applied new genetic methods to Baltic Sea organisms are summarized.

## 4.3 | A webpage on Baltic Sea genetic biodiversity

As illustrated in this review, scientific information on genetic biodiversity of Baltic Sea species is accumulating fast and much of this information is of direct relevance for practical management (Tables 1–3; Figure S1). At the same time, management appears to be generally slow in incorporating new knowledge (see also Laikre et al., 2016; Sandström et al., 2016; Shafer et al., 2015), although some encouraging exceptions have been exemplified here.

To increase adaptability of management, improved and new platforms for knowledge transfer among scientists and managers are urgently needed (Ovenden et al., 2015). As an example, a webpage – the BaltGene Wiki (c.f. www.bambi.gu.se) – aimed at providing genetic information on Baltic Sea species has been constructed within a previous BONUS funded research programme BALTGENE (Baltic Sea Genetic Biodiversity; www.tmbl.gu.se/BaltGene/index.html; www. bonusportal.org/about_us/history/bonus_2009-2011/bonus_projects/ baltgene) and is being updated in the ongoing BONUS BAMBI research

programme, coordinated by Prof. Kerstin Johannesson, Gothenburg University (www.bambi.gu.se). Parts of the results and species summary information provided by the present review are planned to be made available on this website. Databases such as this web page, summarizing scientific progress in an easy to understand way is important in order to increase the communication between academia and managers. A problem with efforts like this is that they are typically funded by research projects only running for a few years, and the economic support for continuing the efforts after the research projects terminate is typically not available. It is important to find ways to support the maintenance of efforts from scientists to provide genetic guidelines to managers (Hoban et al., 2013; Stetz, Kendall, & Vojta, 2011). Furthermore, other types of fora providing means for knowledge transfer among scientists and managers are urgently needed. Lack of knowledge has been identified as one important reason why Baltic Sea public managers do not regard genetic diversity in practical management of Baltic Sea MPAs (Sandström et al., 2016), while knowledge communication efforts such as lectures and deliberative discussions have been shown to increase perception of genetic diversity among such managers (Lundmark, Andersson, Sandström, & Laikre, 2016). Increased research to understand what factors affect the incorporation of genetic information into management and how use of genetic information has affected successful management is warranted.

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## SUPPORTING INFORMATION

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