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Rapid effects of a fishing closure on whitefish (*Coregonus maraena*) in the northern Baltic Sea

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Areas closed to fishing year-round (no-take zones, NTZs) or during spawning time (spawning closures) are used as a management tool to increase declining fish populations. We evaluated the effects of a 147 km^2 NTZ and a 3980 km^2 spawning closure on whitefish populations in the northern Baltic Sea, and also accounted for fish consumption by seals and cormorants. Fish monitoring with multimesh gillnets in 2011–2016 showed a significant increase in catch per unit effort (CPUE) of mature whitefish (> 30 cm) both in the spawning closure and the NTZ compared with the reference area open to fishing. The rate of increase was significantly higher in the NTZ than in the spawning closure. Our results suggest that NTZs may strengthen coastal fish populations in temperate regions and that also seasonal closures under a critical period of the life cycle may benefit the populations.

Introduction

Fish populations are declining worldwide and attempts to hamper decline has failed in many places including Northern Europe and the Baltic Sea (Zeller *et al.* 2011; Pauly & Zeller 2016; Froese *et al.* 2018). In the last decade, there has been some reversal in the downward trend for the internationally managed stocks in the North East Atlantic (Fernandez & Cook 2013; Fernandez et al 2017), however, 69% of 397 European stocks are still subjected to ongoing overfishing (Froese *et al.* 2018). No-take zones (NTZs), areas where no fishing or other extractive use is allowed, may be a useful regulation to protect and increase these declining fish populations. This type of regulation has been suggested as a central management tool in ecosystem-based management and marine spatial planning by providing means of achieving both conservation and fisheries management objectives, where fish abundance and biomass is expected to increase within the NTZ during the time of closure (Jennings 2009; Gaines *et al.* 2010; Halpern *et al.* 2010). From a fisheries perspective, the core mechanisms underlying the success of NTZs is a build-up of fish densities

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and an increase of mean individual sizes, which in turn may elevate larval production and export to surrounding areas. Additionally, an increase of fish densities in NTZs may lead to spill-over of fish to surrounding areas (Halpern *et al.* 2009). However, if body growth is density-dependent, the build-up of fish densities may reduce in size at a given age within the NTZ because of competition, thereby counteracting the positive effects (Gårdmark *et al.* 2006). NTZs may also safeguard populations against evolutionary effects of size-selective fishing, i.e., lower individual growth rates and earlier maturation, and restore ecosystem structure and function (Babcock *et al.* 2010; Baskett & Barnett 2015; Pereira *et al.* 2017). A large number of studies around the world show positive effects of areas closed to fishing on densities, biomasses and body sizes of targeted fish (Lester *et al.* 2009). Furthermore, size, duration and placement of NTZs are considered important elements affecting the success of a fishery closure (Halpern & Warner 2002; Claudet *et al.* 2008; Molloy *et al.* 2009; Vandeperre *et al.* 2011). The majority of studies have, however, been conducted in tropical regions where Marine Protected Areas (MPAs) including NTZs are more common (Wells *et al.* 2016). Partially or seasonally closed areas, e.g., during spawning when fish aggregate at predictable locations and times, are common in the extensive fisheries management schemes of northern Europe (van Overzee & Rijnsdorp 2015, Eero *et al.* 2019), while NTZs are not. There is a widespread notion that NTZs are not suitable for temperate waters since many fishes are more mobile and have greater dispersal ranges than their tropical counterparts (Laurel & Bradbury 2006; Florin *et al.* 2013; Breen *et al.* 2015). Laurel and Bradbury (2006) therefore highlighted the need to scale up NTZs in temperate waters and not use tropical NTZs as direct scalar templates in temperate regions. However, recent findings suggest that several temperate NTZs do enhance fish and lobster abundance and/or biomass (Thorbjørnsen *et al.* 2018; Thorbjørnsen *et al.* 2019; Moland *et al.* 2013). When designing NTZs, home ranges of targeted species and movement patterns during different life-stages should hence be considered when planning the size and placement of NTZs (Palumbi 2003; Green *et al.* 2014).

The North East Atlantic and the Mediterranean Sea are governed by the European Common Fisheries Policy (CFP), a policy which has been the subject of debate for many years (Salomon *et al.* 2014). Many stocks are overfished and profit margins of fishers are continuously in decline (Khalilian *et al.* 2010; Froese *et al.* 2018). In 2013, the CFP underwent substantial reforms by including the concept of Maximum Sustainable Yields (MSY) and to ensure that the exploitation of marine resources restores and maintains populations of harvested stocks above levels that can produce the MSY (Salomon *et al.* 2014). The Total Allowable Catches (TACs), particularly for offshore species, is the major regulatory mechanism of fish catches in the North East Atlantic and Baltic Sea. Coastal species, however, are instead nationally managed. There is a tradition of separating nature conservation and fisheries management in nationally managed areas in Northern Europe (Sørensen & Thomsen 2009), hampering effective protection from fisheries and habitat degradation. Coastal species are more subjected to land use changes and changes to shallow benthic habitats. The implementation of NTZs could therefore be a valuable management strategy to increase populations of declining coastal and offshore species and protect the habitats they rely on. Studies on commercially important flatfish in the Baltic Sea and lobsters and cod in the North Atlantic and Skagerrak have found positive effects of NTZs on density and sizes of targeted species, suggesting that implementing NTZs in Northern Europe may be a successful management strategy (Florin *et al.* 2013; Moland *et al.* 2013; Howarth *et al.* 2017).

The expected positive effects of NTZs may be reduced by increasing populations of large predators such as marine mammals and birds (Fanshaw *et al.* 2003; Ward *et al.* 2012). Abundances of grey seals (*Halichoerus grypus*) and great cormorants (*Phalacrocorax carbo sinensis*) have been shown to be negatively correlated with fish abundance (Vetemaa *et al.* 2010; O'Boyle & Sinclair 2012; Östman *et al.* 2014; Cook *et al.* 2015) and may prevent the recovery of depleted fish stocks. In the Baltic Sea, the population sizes of grey seals and great cormorants have increased markedly during the last decades (HELCOM 2014, 2016). The consump-

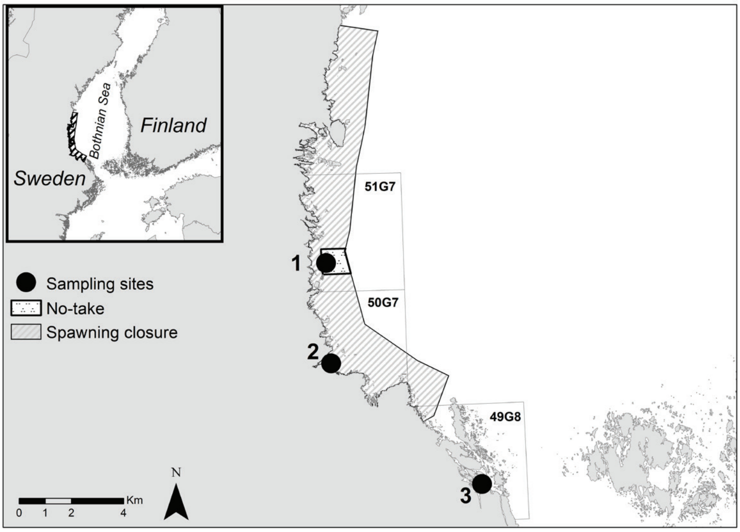

Fig 1. Map of sampling sites in the Bothnian Sea (northern Baltic Sea) including the: 1) no-take zone (NTZ); 2) spawning closure; and 3) reference area. ICES SD quadrats 49G8, 50G7 and 51G7, where commercial and recreational landings have been estimated, are shown.

tion of several coastal species by these piscivores can be substantial, and for whitefish it has been estimated to the same level or even exceeding the combined commercial and recreational fishery landings (Hansson *et al.* 2017). The estimated predation from grey seal and great cormorant on whitefish therefore needs to be compared between areas open and closed to fishing when evaluating the effects of NTZs in the Baltic Sea. This high level of predation in relation to fisheries catches in the Baltic Sea may be exceptional, and in many other coastal regions predation on commercially important species can be expected to be much lower than catches in fisheries (see e.g., Nilssen *et al.* 2019).

The present study sets out to evaluate the effects of a smaller (147 km^2) NTZ and a larger (3980 km^2) spawning closure on the salmonid European whitefish *Coregonus maraena* in the temperate northern Baltic Sea. The NTZ was designed with the whitefish's life-history and mobility (limited spawning- and ontogenetic migrations, generally below 20 km) in mind, why the NTZ was expected to protect a considerable part of a local population. The larger spawning closure, on the other hand, was expected to cover the full geographic range of a population, but with protection only during the spawning period. By comparing the development of the local whitefish populations in these two areas with an area open to fishing year-round, we thus explore the relative effects of a smaller, fully closed area with a larger seasonal closure.

Methods

Study site and target species

An NTZ was established in 2011 in Storjungfrun-Kalvhararna at the Bothnian Sea coast, which includes an exposed archipelago area, i.e., an area with multiple cobs and islands, and part of a large (168.5 km^2) offshore bank, Storgrundet, in the northern part of the Baltic Sea, covering an area of 147 km^2. A general fishing ban during the whitefish spawning season (15 Oct–30 Nov) was also introduced along the coast covering an area of 3980 km^2 (Fig. 1). Five years later (2016) the NTZ was reopened, while the general fishing ban during spawning time is still in effect for both the previous NTZ and the area closed during whitefish spawning (spawning closure) along the coast. The selection of NTZ and spawning closure placement was done together with local fishers as well as on the basis of known spawning grounds identified in an extensive interview study (Gunnartz *et al.* 2011). Larval sampling with beach seine was performed at 25 sites during spring in the years 2012–2016 in the NTZ and spawning closure, and the presence of whitefish larvae confirmed that there were active spawning grounds in both sites. For the reference area, beach seine data from 2010 also confirmed the presence of active spawning grounds in the area (Florin *et al.*, unpublished).

A number of meetings with stakeholders were held in 2010 and 2011 before the establishment of the NTZ. Most participants agreed that the low catches of whitefish were worrying and that regulations were needed. However, they also believed that the consumption of whitefish by seals was a major problem for whitefish fisheries.

The establishment of the NTZ aimed to increase the populations of sea-spawning European whitefish. Whitefish is one of the most important species for commercial and recreational fisheries in the region. However, commercial catches have continuously decreased and are only about half the sizes of catches from the mid-1990s (Swedish Agency for Marine and Water Management 2018). This species is mainly fished during summer and autumn by commercial fishers, while recreational fishers mainly catch whitefish during spawning season in late autumn. The recreational fishery catches at least as much fish as the commercial fishery and 95% is classified as subsistence fishing, i.e., fishing carried out for personal consumption (Swedish Agency for Marine and Water Management 2016). Whitefish is also important in the Finnish fishery at the eastern coast of the Bothnian Sea, and similar to Sweden, catches have declined drastically (Verliin *et al.* 2013; Ozerov *et al.* 2016). Whitefish is classified as endangered in the Baltic Sea (HELCOM 2013), is listed in annex V in the EU habitats directive (Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora), and is listed on the IUCN Red List as vulnerable (IUCN 2017). There are two types of European whitefish in the Baltic Sea: the first are sea-spawning whitefish that spawn on shallow coastal sand or gravel bottoms, adapted to the brackish water of the area (4–6 psu in the Bothnian Sea); and the second are anadromous whitefish that migrate up rivers and creeks to spawn in late autumn (Himberg & Lehtonen 1995). The majority of sea-spawning whitefish migrate less than 10 km and up to 90% less than 20 km (Dahr 1947, Lehtonen *et al.* 1986, Saulamo *et al.* 2002), while the majority of anadromous whitefish migrate much further, up to 300 km in the Bothnian Sea and more than 300 km in the Bothnian Bay with maximum distances of 700 km (Lehtonen & Himberg 1992, Saulamo & Neuman 2002). The two types are difficult to separate morphologically and are caught mixed in the same fishery. Fish surveys in the present study were, however, performed during spawning season in order to maximize catches of sea-spawning whitefish and minimize catches of anadromous whitefish. Whitefish spawn in October to November and their demersal eggs remain in the spawning grounds until hatching in April to May, when the ice starts to break (Veneranta *et al.* 2013a). Samples of whitefish were examined using otolith chemistry following methods in Rohtla *et al.* (2017) and gill-rakers of a number of individuals were also counted following methods in Himberg *et al.* (2015) confirming that the majority of whitefish (67% otolith chemistry and 75–90% gill-raker counts) were from sea-spawning stocks (Florin *et al.*, unpublished data).

Commercial landings

Whitefish commercial landings in the counties Uppsala, Gävleborg and Västernorrland from 1914–2013 and in corresponding ICES SD 29 and 30 in years 2014–2016 were collated from Hentati-Sundberg (2017) and from Swedish official landing statistics, respectively. Whitefish commercial landings and effort (kg/gillnet and night) from gillnets in the Sea of Åland (SD 29) and the southern part of the Bothnian Sea (SD 30), matching the extent of the spawning closure, from 1999 to 2017 were also collected from mandatory fishing logbooks and journals from the Swedish Agency for Marine and Water Management. To compare changes over time between the spawning closure and the reference area a general linear model was applied, where "Area" was included as a fixed factor, "Year" as a covariate, and an interaction factor "Area × Year" to explore differences in the development over time between areas.

Fish monitoring

Surveys to monitor the effect of the NTZ on fish populations in the Bothnian Sea were done on a yearly basis from 2011 to 2016 with multimesh gillnets during whitefish spawning season (Oct–Nov) to avoid inclusions of river spawning whitefish. Gillnet fishing was performed in three locations: 1) within the NTZ (Storjungfrun-Kalvhararna); 2) in the spawning closure (Gävlebukten); and 3) in a reference area open to fishing (Galtfjärden, Fig. 1). In each location 30–40 random stations were sampled using gillnets; 5 within the depth range of 10-20 m and the rest equally distributed within the three depth strata 0–3 m, 3–6 m and 6–10 m. The survey gillnets consisted of 9 sections, 5 m long, with a geometrical mesh size series from 10–60 mm. Each station was fished overnight according to standard fishing practices for monitoring of Baltic Sea coastal fish stocks (HELCOM 2012). Mortality was 100% in the gillnets. The few fishes that were still alive after bringing the catch to land were quickly killed by a harsh blow to the head when the nets were emptied, following the procedure of the ethical permit. Depth, temperature and salinity were measured at each occasion and the whole catch was identified to species level. Lengths were measured to the closest cm.

The three treatments (NTZ, spawning closure, open to fishing) were not possible to replicate in this study, why potential site-specific effects could potentially affect the conclusions of the study. To accommodate this risk, we therefore estimated the potential impact of the other major whitefish mortality factors apart from fishing, which is predation from cormorant and grey seal (Hansson *et al.* 2017).

Predation by seals and cormorants

Consumption of whitefish by grey seal and great cormorant along the Swedish Bothnian Sea coast was estimated by combining cormorant and seal abundance data with information on diet composition and prey consumption. For cormorants, nest count data from 2014 was used to estimate abundance (see Supplementary Information Table S1.1, Fig. S1.1; Ageheim & Lindqvist 2015, Hjertstrand 2015, Alf Sevastik unpublished data). It was assumed that cormorants were present in the area during 180 days per year, in line with the estimate in Hansson *et al.* (2017; see Supplementary Information Table S2.2). Estimates of fish consumption were based on food requirements during breeding season (80 days) from Gremillet *et al.* (1995) and a prey consumption of 500 g × day^{-1} for breeding birds and fledglings outside the breeding season (100 days) as well as for non-breeding birds throughout the season (Keller & Visser 1999; Ridgway 2010). Each nest was assumed to represent two breeding adults, two fledglings and one non-breeding bird, resulting in an average daily food intake of 1987 g × nest^{-1} × day^{-1} (Gremillet *et al.* 1995). It was assumed that cormorants forage within 20 km from their nests (Grémillet 1997; Nelson 2005), and a kernel density function with a 20 km radius was applied in ArcGIS to estimate cormorant densities across the study areas. Whitefish was not found in the diet of cormorants feeding in the reference area, based on diet samples collected in Singöfjärden (approximately 8 km southeast of the reference area) 2013–2014 during the nesting period in May–June (*n* = 469; Ovegård *et al.* in prep.). For cormorants feeding in the NTZ and the spawning closure area, the weight proportion of whitefish in the diet was estimated to 1.75%, based on average estimates from diet samples collected in Lövstabukten April–August 2005 (*n* = 3002, Boström *et al.* 2012) and Gävlebukten April 2014 (*n* = 34, SLU unpublished data) in the middle of the study area.

For grey seal, abundance data from the national census, carried out by the Swedish Museum of Natural History, for year 2010–2015 was used (see Supplementary Information Table S1.2, Fig. S1.2). Seals were assumed to forage within a 60 km radius (Sjöberg & Ball 2000; Oksanen *et al.* 2014) and densities were estimated using a kernel density function, like for cormorants. A daily total fish consumption of 4.75 kg per seal was applied (Hammond & Grellier 2006; Hammond & Harris 2006). It was assumed that predation by seals was absent during 120 days/year due to ice cover. The weight proportion of whitefish in the seal diet was estimated to 11%, based on prey remains in grey seal digestive tracts collected in the Bothnian Sea 2001–2012 (*n* =151, SLU unpublished data).

To compare extraction of whitefish by grey seals and cormorants with commercial and recreational whitefish landings in adjacent areas, fish extraction was estimated from mandatory fishery logbooks, journals from the Swedish Agency for Marine and Water Management and Statistics Sweden for ICES quadrats 49G8, 50G7, and 51G7 including only the water surface area from land up to 4 nm outside the baseline (the border between archipelago and open sea), to cover the main whitefish fishing area (Fig. S1.3 in Supplementary Information). Quadrat 49G8 represents whitefish landings around the reference area, 50G7 represents landings in the spawning closure and 51G7 represents landings in the NTZ. The estimates are based on data prior to the establishment of the NTZ, as no fishing was allowed within the area during the evaluation period).

Data analysis

To compare changes over time between the NTZ, the spawning closure and the reference area a generalized linear model was applied, using individual stations as replicates. "Area"was included as a fixed factor in the analyses, "Year" as a covariate, and an interaction factor "Area × Year" to explore differences in the development over time between areas. Focusing on the interaction term, rather than on differences between areas and years, allowed testing the hypothesis that the difference in fishing pressure between the two areas would be evident as differences in the catch trajectories over the short evaluation period. A negative binomial error distribution was used, as this distribution was found to fit the zero-inflated data best. The analyses were performed in R (ver. 3.6.1) using the *glm.nb* function (R Core Team 2019). Only undisturbed fishing events were used for data analysis. Sometimes fishing stations were disturbed by seals and hence removed from the statistical analyses. Fish > 30 cm were considered mature and classified as adults based on both fisheries data and our own fish monitoring data. In the analyses, results from individual stations were used as replicates for the analyses of catch per unit effort (CPUE).

To estimate the effect size of the 5-year full closure of fisheries on whitefish, we calculated the change in CPUE over time in the NTZ compared to the reference area from the generalized linear model of CPUE over time in each area separately. The change within each area was calculated by dividing the predicted value from the model for 2016 with the predicted value for 2011. By using the predicted values rather than the actual CPUE estimates, the effects of a between-year variability could be reduced.

Results

Commercial catches over time

From 1914 to the 1940s, the Swedish commercial landings of whitefish in the Bothnian Sea were stable with catches of 30–80 tons/year. However, there was a rapid increase in catches following the introduction of nylon in fishing nets after World War II. Catches peaked in the 1950s with 150–250 tons/year, and show a second peak in the 1990s with catches of almost the same magnitude. Since the 1990s the catches have decreased markedly, to around 50 tons/year the last ten years (Fig. 2). This declining trend has also been acknowledged among the local fishers in the region, and is reflected by the decline in CPUE in commercial landings. However, since the NTZ and spawning closure were established, commercial landings have significantly increased in the coastal area covered by the spawning closure compared to the adjacent Sea of Åland, where the reference area is situated (factor Area × Year, $F = 6.60$, $p = 0.02$, df = 14, Fig. 3) between 2011 and 2019.

Gillnet monitoring

Overall, 30 species were caught in the yearly gillnet survey and roach (*Rutilus rutilus*) and herring (*Clupea harengus*) were the most abundant species followed by ruffe (*Gymnocephalus cernuus*), perch (*Perca fluviatilis*) and fourhorn

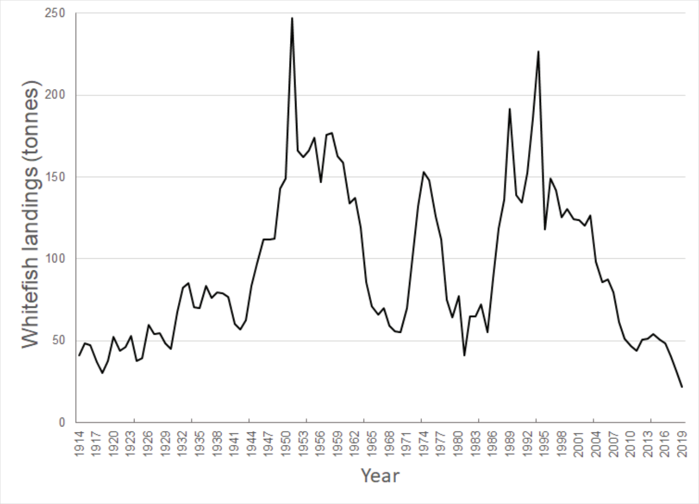

Fig 2. Whitefish commerial landings in the Bothnian Sea (counties Uppsala, Gävleborg and Västernorrland) 1914–2013 (from Hentati-Sundberg 2017) and in corresponding ICES SD 29 and 30 in years 2014–2019 (from Swedish official landing statistics).

Fig 3. Whitefish commercial landings in gillnet fisheries from 1999 to 2019 in the Sea of Åland (SD 29) and the part of the Bothnian Sea (SD 30) with a spawning closure (data from mandatory fishery logbooks and journals from the Swedish Agency for Marine and Water Management).

sculpin (*Triglopsis quadricornis*) (see Supplementary Information Table S2). Whitefish catches were generally low despite a high fishing effort, and depth distributions differed between locations and years, likely due to timing in relation to fish spawning activity, and therefore all depth zones were merged in analyses.

A significant increase over time in CPUE in mature whitefish (> 30 cm) was found in both the NTZ (factor Area × Year, $F = 38.04$, $p = 1.675\text{e-}09$, df = 407) and the spawning closure (factor Area × Year, $F = 12.09$, $p = 0.000563$, df = 399) compared to the reference area (Fig. 4). There was also a significant difference in CPUE in whitefish between the NTZ and spawning closure (factor Area × Year, $F = 7.09$, $p = 0.0080$, df = 456). For details of the statistical analyses, see Supplementary Information Table S3.1, Figs. S3.1–3.3. Whitefish populations increased by a factor of 9 in the NTZ and a factor of 2 in the spawning closure compared to the start of the regulations. At the same time the whitefish population decreased by a factor of 3 in the reference area.

Predation on whitefish by seals and cormorants

Due to the long distance to breeding colonies, the kernel density function resulted in absence of cormorants, and thus no fish con-

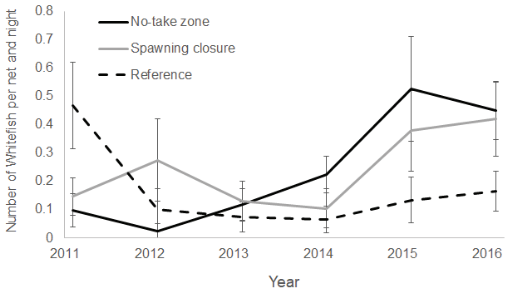

Fig 4. Changes in mean CPUE of adult whitefish (> 30 cm) within the no-take zone (NTZ), spawning closure and reference area open to fishing in the northern Baltic Sea from 2011 to 2016. Error bars depict SE.

sumption by these, in the NTZ. In the spawning closure and reference area, the estimated fish consumption by cormorants was 9 and 6 kg × hectare^{-1} × year^{-1}, respectively. Based on available diet data, cormorants extracted whitefish only from the spawning closure area: 0.15 kg whitefish per hectare and year. The estimated fish consumption by grey seals was 0.8 kg × hectare^{-1} × year^{-1} in the NTZ, 0.2 in the spawning closure area and 2.6 in the reference area. The extraction of whitefish by grey seals was estimated to 0.1 kg × hectare^{-1} × year^{-1} in the NTZ, 0.03 in the spawning closure and 0.3 in the reference area. The total estimated extraction of whitefish from seals and cormorants (kg × hectare^{-1} × year^{-1}) was lower in the NTZ (0.1), compared to the spawning closure (0.18) and the reference area (0.3). In comparison, estimated extraction of whitefish from the commercial fisheries was lower than that of seals and cormorants. The commercial fisheries extracted 0.03 kg × hectare^{-1} × year^{-1} of whitefish in the NTZ, 0.09 in the spawning closure and 0.07 in the reference area (Table S1.3 in Supplementary Information).

Discussion

As expected, a significant and large increase of adult whitefish over time was found in the NTZ compared to the reference area. Considering the short time frame of the closure, the increase was surprisingly large. A similar rapid positive effect within five years of closure has been found in other studies, the majority of them from the tropics (e.g., Roberts *et al.* 2001; Galal *et al.* 2002; Denny *et al.* 2004), although examples from temperate regions exist (e.g., Florin *et al.* 2013, Moland *et al.* 2013). Several meta-analyses have also found that the higher average values of density, biomass, organism size, and diversity inside reserves (relative to controls) plateaued within a few years (Halpern & Warner 2002; Halpern 2003; Babcock *et al.* 2010).

The rapid positive response is likely due to intense fishing pressure in the area before closure as well as an adequate design in terms of size and placement of the reserve for whitefish in the Bothnian Sea. The strongest effects of NTZs are generally seen for targeted species that are heavily fished (Mosqueira *et al.* 2000; Micheli *et al.* 2004; Sciberras *et al.* 2015), like the whitefish populations in the present study. We present data showing that whitefish commercial landings have decreased substantially since the 1950s. Furthermore, whitefish is classified as endangered in the Baltic Sea (HELCOM 2013) and is also listed on the IUCN Red List as vulnerable (IUCN 2017). However, we also show that the whitefish catches per unit effort in the commercial fishery has increased significantly in the coastal area covered by the spawning closure and the no-take zone compared to the adjacent Sea of Åland, where the reference area is situated, since the establishment of the closed area, indicating a general population increase following the closure. Species may respond differently to protection depending on the intensity of exploitation they are exposed to outside the NTZ and prior to its establishment (Micheli *et al.* 2004). A strong negative relationship between fishing intensity and biomass of targeted fish species was found by Jennings *et al.* (1995) in the Seychelles, suggesting that if fishing intensity is high outside NTZs the potential for finding enhanced biomass within NTZs is greater. This was further demonstrated in California by Iacchei *et al.* (2005), who recorded a 3% increase in lobster density within the protected area compared to the recreationally fished control areas, but a 57% increase when compared with a commercially fished area. Roberts and Polunin (1992) and Edgar *et al.* (2009) found no differences between NTZs and fished areas in the Red Sea and Tasmania because pre-existing fishing pressure was low, depressing stocks only slightly. On the contrary, McLean *et al.* (2010) found very little change between protected and unprotected populations of emperors in New Zealand because previous high levels of exploitation combined with low recruitment years led to large reductions of abundances across the whole region, despite being protected for 15 years. These examples demonstrate that the effects of NTZs vary with preconditions of fishing intensity and hence the large positive effect of the NTZ on whitefish abundance is likely due to a strong decrease in fish mortality combined with viable reproduction areas in or in the vicinity of the NTZ, as evidenced by whitefish survey data presented following closure in the present study.

Seals and cormorants are common in the region and, like humans, contribute to fish mortality. We estimated predation on whitefish by these predators and found the estimated consumption to be slightly higher than estimated commercial fish landings in all areas. No local-scale estimates of recreational fisheries were available, but estimates for the whole Bothnian Sea (including Finnish catches) suggest that the catches of whitefish in commercial fisheries is three times more than the whitefish catches in recreational fisheries (Hansson *et al.* 2017). Estimates from Swedish landings in the Bothnian Sea suggest that catches from the recreational fisheries has, at times, been twice that of commercial fisheries. The estimated consumption of whitefish by seals and cormorants was about three times higher in the reference area compared to the NTZ, which may also have contributed to the differences found between the reference area and the NTZ. However, the consumption estimates for grey seal and cormorant in the different areas are coarse, mainly due to limitations in the abundance and diet data. For a more detailed picture of the predatory impacts of seals and cormorants on whitefish in the areas, covering intra- as well as inter-annual variability, additional monitoring of prey choice and presence of the predators is needed. For example, estimation of fish removal based on interpolation of colony breeding numbers does not include large scale movements of cormorants outside the breeding season, and diet samples collected during the breeding season may not be representative of post-breeding diet (Salmi *et al.* 2015). Also, possible predation by the large ringed seal population in the Gulf of Bothnia was not considered due to a lack of abundance and diet data. In some areas, seals and cormorants have been shown to impact fish stocks and have been suggested to compete with fisheries and prevent recovery efforts of salmonid species of conservation concern (Koed *et al.* 2006; Winfield *et al.* 2007; Thomas *et al.* 2016; Chasco *et al.* 2017; Jensen *et al.* 2018), even though there are exceptions (Boström *et al.* 2009; Nilssen *et al.* 2019). The predatory potential of the present large populations of seals and cormorants in the Baltic Sea motivates further assessments of their impacts on fisheries and fish stocks (Hansson *et al.* 2017).

Environmental change may also have contributed to the large-scale decline in whitefish populations in the Bothnian Sea. Veneranta *et al.* (2013a) studied nursery grounds of whitefish in the Bothnian Sea and Bothnian Bay and highlighted that climate change and related higher temperatures and shorter ice-covered periods can affect the recruitment of sea-spawning whitefish, by decreasing the hatching success of the eggs of this cold-water adapted species (Veneranta *et al.* 2013b). These large environmental changes and predation by seals and cormorants may contribute to the declines generally observed in the area. On the contrary, stocking of whitefish fry and larvae may have a positive effect on whitefish populations and affect annual catches (Jokikokko & Huhmarniemi 2014). However, stocking is mainly done in Finnish waters in the northern parts of the Gulf of Bothnia and has decreased since the late 90s. Moreover, stocking is mainly of river-spawning whitefish and sites are most likely too far away (more than 500 km) to have any major impact on CPUE in the present study (Jokikokko & Huhmarniemi 2014). Some stocking is also done north of the NTZ in Swedish waters but stocking has been constant throughout the years with no major changes that would affect the results. The presence of river-spawning whitefish ecotypes in samples may also add to some variation in the data as well as strong year classes. The majority of fish in samples were, however, found to be sea-spawning whitefish, based on otolith chemistry and gill-raker counts (Florin *et al.*, unpublished). Additionally, variation in year classes is likely linked to fluctuating climate which will affect all areas equally (Lehtonen & Lappalainen 1995). Instead, our results, demonstrating how reduced fishing within the NTZ and the spawning closure can give increases of whitefish over time, suggest that fishing is a major factor contributing to the declines of whitefish in the Bothnian Sea.

The mobility of whitefish and the spatial distribution of suitable habitat was taken into account, by using published information on habitat preferences and migration distances, when planning and establishing the NTZ in the present study. As sea-spawning whitefish in the area are expected to migrate around 10 km and up to 90% less than 20 km (Dahr 1947, Lehtonen *et al.* 1986, Saulamo & Neuman 2002), the 147 km^2 NTZ was expected to protect the majority of a local whitefish population during its life cycle. Life-history characteristics (Micheli *et al.* 2004; Claudet *et al.* 2010) and movement patterns during different life-stages have been highlighted as important features to consider when designing the shape, size, spacing and placement of NTZs (Kramer & Chapman 1999; Palumbi 2003; Green *et al.* 2014). The results show that the size of the NTZ (147 km^2) is likely large enough to protect sea-spawning whitefish. Thorbjörnsen *et al.* (2019) found that a small no-take zone (1.5 km^2) in a Norwegian fjord protected a large part of the sea trout population residing within its boundaries. Tagged fish displayed home ranges that were, on average, smaller than the reserve (< 0.5 km^2). However, the results from previous meta-analyses on the effects of NTZ size on fish populations are mixed. While some found that rapid biological responses within NTZs were independent of reserve size, indicating that even small reserves can enhance populations of targeted species (e.g., Côté *et al.* 2001; Halpern & Warner 2002; Halpern 2003; Micheli *et al.* 2004), others found clear effects of reserve size (Claudet *et al.* 2008; Edgar *et al.* 2014). These different outcomes likely reflect the importance of a species mobility in relation to the NTZ size. In a meta-analysis from the Mediterranean, Claudet *et al.* (2008) showed that the response of commercial species to protection was reserve-size dependent and that increasing the size of the NTZ resulted in increased density of commercial fishes within the NTZ compared to outside. They argue that the lack of size response in previous meta-analyses were due to data being synthesized across vastly different ecosystems, possibly obscuring the effects of reserve design within regions. Even though tagging studies show that some individuals may migrate up to 200 km and that migration may be population specific, sea-spawning whitefish generally have home ranges between 20 and 40 km, and hence the NTZ size (147 km^2) is likely adequate for the sea-spawning population (Lehtonen & Himberg 1992; Saulamo & Neuman 2002). A 360 km^2 NTZ around the island Gotska Sandön in the central Baltic Sea was successful in protecting and increasing stocks of flatfish with home ranges (10-20 km) similar to that of whitefish (Florin *et al.* 2013). A lot smaller NTZs in the Baltic Sea (1.7–3.7 km^2) have also been found successful in increasing populations of pike (*Esox lucius*), perch (*Perca fluviatilis*) and pike-perch (*Sander lucioperca*) despite these closures being smaller than the target species' home ranges (Bergström *et al.* 2016). These findings combined suggest that NTZs in the Baltic Sea are generally successful in increasing fish population sizes as long as they are large enough to protect a substantial proportion of the local populations during their life cycles.

Although the sea-spawning whitefish is not considered a highly mobile species, it is still more mobile than most tropical and sub-tropical species that often are rather site attached and for which most studies show positive effects of NTZs. Fish tend to be more mobile in temperate waters because of strong seasonality and spatial variation in productivity and hence stocks move between locations to exploit the richest food resources (Breen *et al.* 2015). Furthermore, factors like temperature, depth and salinity play a major role in the distribution of species, including spawning and nursery grounds (Rose 2005). Mobile fish, capable of moving long distances, are not expected to benefit from protection. However, Gell and Roberts (2003) highlighted that intra-species differences in movement behaviour may still allow mobile species to benefit from NTZs of small sizes (1–5 km^2). In many fish species, a large proportion of the population might remain within a relatively small area, while the rest undertake longer movements (Gell & Roberts 2003). This pattern has been observed in a number of fish species from New Zealand (Willis *et al.* 2003), South Africa (Griffiths & Wilke 2002), Jamaica (Munro 2000), and the Baltic Sea (Florin & Franzén 2010).

Life-history characteristics and ecological traits such as body size, maturity and habitat use have also been pointed out as important features effecting the responses of different fish species to protection (Claudet *et al.* 2010). Whitefish is a demersal spawner and reaches maturity at the age of 3–5 years with a distribution restricted to shallow coastal areas (Froese & Pauly 2018, Lehtonen & Himberg 1992). Spawning and larval habitats mainly consist of sandy and gravelly bottoms close to the shoreline (Veneranta *et al.* 2013a). The NTZ in the current study is placed to include suitable habitats for all life stages. Furthermore, an additional closure during spawning season is present around the NTZ, protecting mature adults while migrating to spawn. The home range of sea-spawning whitefish being smaller than the NTZ size, together with a growth to maturity within 3-5 years, allows for growth and reproduction to occur within the time frame of this study. Larval dispersal has also been highlighted as an important characteristic impacting the effectiveness of NTZs (Palumbi 2003; Green *et al.* 2014). Species with benthic eggs, like whitefish, will have more limited dispersal abilities than pelagic spawners and hence benefit more from fisheries closure (Jennings 2000; Mosqueira *et al.* 2000). Furthermore, sea-spawning whitefish spawn in suitable nursery areas where larvae can flourish without having to move far (Veneranta *et al.* 2013a). Information on whitefish larval dispersal is limited in the Baltic Sea, however, a study on the river spawning ecotype indicated that larval dispersal is rather limited in this species and does not contribute much to its dispersal (Lehtonen *et al.* 1992). Additionally, Olsson *et al.* (2012) studied the genetic structure of European whitefish in the Baltic Sea and found evidence of regional differentiation and isolation by distance, confirming limited dispersal in this species.

Biological and physical factors are not the only factors influencing the effects of NTZs. Social, cultural, economic and political factors can also be highly influential, and positive attitudes towards the establishment of NTZs are necessary for successful management (Gall & Rodwell 2016). Effective management and enforcement may be strongly influenced by the social acceptability of the designation and in the present study the compliance of local fishers may have contributed to the success of the NTZ. The spawning closure in the present study was initiated by the fishers themselves, despite running the risk of temporary lowered catches compared to previous years. A science-based, top-down approach has most often been applied when establishing NTZs, however, community-based, bottom-up approaches are becoming more common and highlighted as more successful (Voyer *et al.* 2012; Voyer *et al.* 2015). Finding a "middle ground" between these two approaches is a challenge and requires an honest acknowledgment of the trade-offs involved in achieving conservation outcomes (Voyer *et al.* 2012). In the current case, the county board and municipality in the area were deeply involved from the beginning of the process and the spawning closure is still in effect due to the continued support from local fishers. A recent study by Bostedt *et al.* (2020) also found that the benefits outweighed the costs after the establishment of the NTZ. Although the NTZ has been successful and reopened, it is of great importance to continue monitoring salmonid populations in the area to evaluate whether the spawning closure alone will be enough to support viable stocks in the future.

We investigated if NTZs can be an efficient method to rapidly strengthen depleted salmonid stocks in coastal areas and found evidence that this was successful. Many species targeted by commercial and recreational fisheries, including whitefish, are, however, subjected to additional anthropogenic pressures and are highly dependent on healthy coastal nursery and feeding grounds (Sundblad *et al.* 2014; Kraufvelin *et al.* 2018). Simultaneously the health of coastal habitats has been shown to depend on strong stocks of predatory fish (Östman *et al.* 2016; Donadi *et al.* 2017). Many coastal species are nationally managed, while their habitats have low protection due to the tradition of separating nature conservation and fisheries management in Northern Europe (Sørensen & Thomsen 2009; Seitz 2014). Given the mutual benefits of protecting habitats and fish, a fruitful way forward may be to merge the two management strategies, particularly in relation to NTZs and other MPAs. This would secure the success of protecting not only target species, but the environment where they thrive and the ecosystem to which they belong (Grip & Blomqvist 2017). Thus, while temporarily closed areas like spawning closures can serve fisheries management objectives, permanent closures where habitats are simultaneously protected may offer broader conservation benefits, in line with current policies aiming for an ecosystem approach to management.

Conclusion

In conclusion, we demonstrated rapid positive effects of an NTZ on the abundance of a mobile temperate species, European whitefish, suggesting that NTZs may be a useful tool for management of coastal fish stocks in Northern Europe and other temperate regions. Additionally, a large spawning closure was also found to have positive effects on the abundance of whitefish, although less pronounced than the NTZ, showing that also seasonal closure under a critical period of the life cycle may benefit important target species of fisheries. Our study concurs with previous findings and highlights that NTZs may be particularly useful in heavily fished areas where other management attempts have failed. Furthermore, dispersal and life-history characteristics should be accounted for when planning and establishing an NTZ, as well as engaging local stakeholders to ensure compliance.

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References

Ageheim S. & Lindqvist S. 2015. *Förvaltningsplan för skarv i Gävleborgs län,* Länstyrelsen Gävleborg Rapport 2015:8, 30pp. available.

Babcock R.C., Shears N.T., Alcala A.C., Barrett N.S., Edgar G.J., Lafferty K.D., McClanahan T.R. & Russ G.R. 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *P. Natl. A. Sci.* 107: 18256–18261.

Baskett M.L. & Barnett L.A.K. 2015. The ecological and evolutionary consequences of marine reserves. *A. Rev. Ecol. Evol. System.* 46: 49–73.

Bergström U., Sköld M., Wennhage H. & Wikström A. 2016. *Ekologiska effekter av fiskefria områden i Sveriges kust- och havsområden.* Aqua reports 2016:20. Institutionen för akvatiska resurser, Sveriges lantbruksuniversitet, Öregrund. 207pp. available.

Bostedt G., Berkström C., Brännlund R., Carlén R., Florin A-B., Persson L., Bergström U. 2020. Benefits and costs of two temporary no-take zones. *Mar. Policy.* 117:103883.

Boström M.K., Lunneryd S.-G., Karlsson L., Ragnarsson B. 2009. Cormorant impact on trout (*Salmo trutta*) and salmon (*Salmo salar*) migrating from the river Dalälven emerging in the Baltic Sea. Fisheries Research 98: 16–21.

Boström M.K., Östman Ö., Bergenius M.A.J. & Lunneryd S.-G. 2012. Cormorant diet in relation to temporal changes in fish communities. *ICES J. Mar. Sci.* 69: 175–183.

Breen P., Posen P. & Righton D. 2015. Temperate marine protected areas and highly mobile fish: a review. *Ocean Coast. Manage.* 105: 75–83.

Chasco B.E., Kaplan I.C., Thomas A.C., Acevedo-Gutiérrez A., Noren D.P., Ford M.J., Hanson M.B., Scordino J.J., Jeffries S.J., Marshall K.N., Shelton A.O., Matkin C., Burke B.J. & Ward E.J. 2017. Competing tradeoffs between increasing marine mammal predation and fisheries harvest of Chinook salmon. *Sci. Rep.* 7: 15439.

Claudet J., Osenberg C.W., Benedetti-Cecchi L., Domenici P., García-Charton J.-A., Pérez-Ruzafa A., Badalamenti F., Bayle-Sempere J., Brito A., Bulleri F., Culioli J.-M., Dimech M., Falcón J.M., Guala I., Milazzo M., Sánchez-Meca J., Somerfield P.J., Stobart B., Vandeperre F., Valle C. & Planes S. 2008. Marine reserves: size and age do matter. *Ecol. Lett.* 11: 481–489.

Claudet J., Osenberg C.W., Domenici P., Badalamenti F., Milazzo M., Falcón J.M., Bertocci I., Benedetti-Cecchi L., García-Charton J.A., Goñi R., Borg J.A., Forcada

A., de Lucia G.A., Pérez-Ruzafa Á., Afonso P., Brito A., Guala I., Diréach L.L., Sanchez-Jerez P., Somerfield P.J. & Planes S. 2010. Marine reserves: Fish life history and ecological traits matter. *Ecol. Appl.* 20: 830–839.

Cook R.M., Holmes S.J., Fryer R.J. & Frid C. 2015. Grey seal predation impairs recovery of an over-exploited fish stock. *J. Appl. Ecol.* 52: 969–979.

Côté I.M., Mosqueira I. & Reynolds J.D. 2001. Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. *J. Fish Biol.* 59: 178–189.

Dahr E. 1947. Biologiska studier över siken vid mellansvenska Östersjökusten. Medd. Från statens anstalt för sötvattensfisket. 28: 1–79. [In Swedish]

Denny C., M. , Willis T., J. & Babcock R., C. . 2004. Rapid recolonisation of snapper *Pagrus auratus*: Sparidae within an offshore island marine reserve after implementation of no-take status. *Mar. Ecol. Prog. Ser.* 272: 183–190.

Donadi S., Austin Å.N., Bergström U., Eriksson B.K., Hansen J.P., Jacobson P., Sundblad G., van Regteren M. & Eklöf J.S. 2017. A cross-scale trophic cascade from large predatory fish to algae in coastal ecosystems. *P. Roy. Soc. B Biol. Sci.* 284.

Edgar G.J., Barrett N.S., Crane K. & Bankroft K. 2009. *Ecosystem Monitoring of subtidal reefs in different management zones of the Jurien Bay Marine Park 1999–2007*. TAFI Internal Report, Tasmanian Aquaculture and Fisheries Institute, Hobart, available at http://ecite.utas.edu.au/60508.

Edgar G.J., Stuart-Smith R.D., Willis T.J., Kininmonth S., Baker S.C., Banks S., Barrett N.S., Becerro M.A., Bernard A.T.F., Berkhout J., Buxton C.D., Campbell S.J., Cooper A.T., Davey M., Edgar S.C., Forsterra G., Galvan D.E., Irigoyen A.J., Kushner D.J., Moura R., Parnell P.E., Shears N.T., Soler G., Strain E.M.A. & Thomson R.J. 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506: 216–220.

Eero M., Hinrichsen H.-H., Hjelm J., Huwer B., Hüssy K., Köster F.W., Margonski P., Plikshs M., Storr-Paulsen M. & Zimmermann C. 2019. Designing spawning closures can be complicated: Experience from cod in the Baltic Sea. *Ocean Coast. Manage.* 169: 129–136.

Fanshawe S., Vanblaricom G.R., Shelly A.A. 2003. Restored top carnivores as detriments to the performance of marine protected areas intended for fishery sustainability: a case study with red abalones and sea otters. *Cons. Biol.* 17: 273–283.

Florin A.-B. & Franzén F. 2010. Spawning site fidelity in Baltic Sea turbot (*Psetta maxima*). *Fish. Res.*102: 207–213.

Florin A.B., Bergström U., Ustups D., Lundström K. & Jonsson P.R. 2013. Effects of a large northern European no-take zone on flatfish populations. *J. Fish Biol.* 83: 939–962.

Froese R., Winker H., Coro G., Demirel N., Tsikliras A.C., Dimarchopoulou D., Scarcella G., Quaas M. & Matz-Lück N. 2018. Status and rebuilding of European fisheries. *Mar. Policy* 93: 159–170.

Gaines S.D., White C., Carr M.H. & Palumbi S.R. 2010. Designing marine reserve networks for both conservation and fisheries management. *P. Natl. A. Sci.* 107: 18286–18293.

Galal N., Ormond R.F.G. & Hassan O. 2002. Effect of a network of no-take reserves in increasing catch per unit effort and stocks of exploited reef fish at Nabq, South Sinai, Egypt. *Mar. Freshwater Res.* 53: 199–205.

Gall S.C. & Rodwell L.D. 2016. Evaluating the social acceptability of Marine Protected Areas. *Mar. Policy* 65: 30–38.

Gårdmark A., Jonzén N. & Mangel M. 2006. Density-dependent body growth reduces the potential of marine reserves to enhance yields. *J. Appl. Ecol.* 43: 61–69.

Gell F.R. & Roberts C.M. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends Ecol. Evol.* 18: 448–455.

Green A.L., Fernandes L., Almany G., Abesamis R., McLeod E., Aliño P.M., White A.T., Salm R., Tanzer J. & Pressey R.L. 2014. Designing marine reserves for fisheries management, biodiversity conservation, and climate change adaptation. *Coast. Manage.* 42: 143–159.

Gremillet D., Schmid D. & Culik B. 1995. Energy requirements of breeding great cormorants *Phalacrocorax carbo sinensis*. *Mar. Ecol. Prog. Ser.* 121: 1–9.

Grémillet D. 1997. Catch per unit effort, foraging efficiency, and parental investment in breeding great cormorants (*Phalacrocorax carbo carbo*). *ICES J. Mar. Sci.* 54: 635–644.

Griffiths M.H. & Wilke C.G. 2002. Long-term movement patterns of five temperate-reef fishes (Pisces: Sparidae): implications for marine reserves. *Mar. Freshwater Res.* 53: 233–244.

Grip K. & Blomqvist S. 2017. Establishing marine protected areas in Sweden: Internal resistance versus global influence. *Ambio* 47: 1–14.

Gunnartz U., Lif M., Lindberg P., Ljunggren L., Sandström A. & Sundblad G. 2011. *Kartläggning av lekområden för kommersiella fiskarter längs den svenska ostkusten — en intervjustudie. Finfo: 2011:3, 41 pp. Fiskeriverket, Öregrund*. available.

Halpern B.S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecol. Appl.* 13: 117–137.

Halpern B.S. & Warner R.R. 2002. Marine reserves have rapid and lasting effects. *Ecol. Lett.* 5: 361–366.

Halpern B.S., Lester S.E. & Kellner J.B. 2009. Spillover from marine reserves and the replenishment of fished stocks. *Environ. Conserv.* 36: 268–276.

Halpern B.S., Lester S.E. & McLeod K.L. 2010. Placing marine protected areas onto the ecosystem-based management seascape. *P. Nat. Acad. Sci.* 107: 18312–18317.

Hammond P.S. & Grellier K. 2006. *Grey seal diet composition and prey consumption in the North Sea. Final Report to Dept. for Environmental Food and Rural Affairs, Project MF0319, 54 pp*. available.

Hammond P.S. & Harris R.N. 2006. *Grey seal diet composition and prey consumption off western Scotland and Shetland. Final Report to Scottish Executive Environment and Rural Affairs Dept. and Scottish Natural Her-*

itage, 41 pp. available.

Hansson S., Bergström U., Bonsdorff E., Härkönen T., Jepsen N., Kautsky L., Lundström K., Lunneryd S.-G., Ovegård M., Salmi J., Sendek D. & Vetemaa M. 2017. Competition for the fish – fish extraction from the Baltic Sea by humans, aquatic mammals, and birds. *ICES J. Mar. Sci.* 75: 999–1008.

HELCOM. 2012. *Indicator based assessment of coastal fish community status in the Baltic Sea 2005–2009*. Balt. Sea Environ. Proc. No. 131, available at http://www.helcom.fi/Core%20Indicators/Population%20trends%20and%20abundance%20of%20seals_HELCOM%20core%20indicator%20report%202016_web%20version.pdf.

HELCOM. 2013. *Red list of fish and lamprey species*. Available at: http://www.helcom.fi/baltic-sea-trends/biodiversity/red-list-of-species/red-list-of-fish-and-lamprey-species.

HELCOM. 2014. *Baltic Sea Environment Fact Sheet, Population development of Great Cormorant*. Available at: http://www.helcom.fi/baltic-sea-trends/environment-fact-sheets/biodiversity/population-development-of-great-cormorant.

HELCOM. 2016. *Core indicator report, Population trends and abundance of seals*. Available at: http://www.helcom.fi/Core%20Indicators/Population%20trends%20and%20abundance%20of%20seals_HELCOM%20core%20indicator%20report%202016_web%20version.pdf.

Hentati-Sundberg J. 2017. *Svenskt fiske i historiens ljus – en historisk fiskeriatlas. Aqua reports 2017:4. Sveriges lantbruksuniversitet, Institutionen för akvatiska resurser, Lysekil. 56 s*. available.

Himberg M. & Lehtonen H. 1995. Systematic and nomenclature of coregonid fishes, particularly in Northwest Europe. *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* 46: 39–47.

Himberg M., von Numers M., Vasemagi A., Heselius S.H., Wiklud T., Lill J.O. & Hagenstrand H. 2015. Gill raker counting for approximating the ratio of river- and sea-spawning whitefish, Coregonus lavaretus (Actinopterygii: Salmoniformes: Salmonidae) in the Gulf of Bothnia, Baltic Sea. *Acta Ichthyol. Piscat.* 45: 125–13.

Hjertstrand G. 2015. *Skarv i Stockholms Skärgård 1994–2014. Levande skärgårdsnatur 2015. Skärgårdsstiftelsen i Stockholms län, 18–19*. available.

Howarth L.M., Dubois P., Gratton P., Judge M., Christie B., Waggitt J.J., Hawkins J.P., Roberts C.M. & Stewart B.D. 2017. Trade-offs in marine protection: multispecies interactions within a community-led temperate marine reserve. *ICES J. Mar. Sci.* 74: 263–276.

Iacchei M., Robinson P. & Miller K.A. 2005. Direct impacts of commercial and recreational fishing on spiny lobster, *Panulirus interruptus*, populations at Santa Catalina Island, California, United States. *New Zealand J. Mar. Freshwater Res.* 39: 1201–1214.

IUCN. 2017. *The IUCN Red List of Threatened Species: Coregonus maraena*. Available at: http://www.iucnredlist.org/details/135672/0.

Jennings S. 2000. Patterns and prediction of population recovery in marine reserves. *Rev. Fish Biol. Fisheries* 10: 209–231.

Jennings S. 2009. The role of marine protected areas in environmental management. *ICES J. Mar. Sci.* 66: 16–21.

Jennings S., Grandcourt E.M. & Polunin N.V.C. 1995. The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. *Coral Reefs* 14: 225–235.

Jensen L.F., Rognon P., Aarestrup K., Bøttcher J.W., Pertoldi C., Thomsen S.N., Hertz M., Winde J. & Svendsen J.C. 2018. Evidence of cormorant-induced mortality, disparate migration strategies and repeatable circadian rhythm in the endangered North Sea houting (*Coregonus oxyrinchus*): A telemetry study mapping the postspawning migration. *Ecol. Freshwater Fish* 27: 672–685.

Jokikokko E. & Huhmarniemi A. 2014. The large-scale stocking of young anadromous whitefish (*Coregonus lavaretus*) and corresponding catches of returning spawners in the River Tornionjoki, northern Baltic Sea. *Fisheries Manage. Ecol.* 21, 250–258.

Keller T.M. & Visser G.H. 1999. Daily energy expenditure of great cormorants *Phalacrocorax carbo sinensis* wintering at Lake Chiemsee, southern Germany. *Ardea* 87: 61–69.

Khalilian S., Froese R., Proelss A. & Requate T. 2010. Designed for failure: a critique of the Common Fisheries Policy of the European Union. *Mar. Policy* 34: 1178–1182.

Koed A., Baktoft H. & Bak B.D. 2006. Causes of mortality of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) smolts in a restored river and its estuary. *River Res. Appl.* 22: 69–78.

Kramer D.L. & Chapman M.R. 1999. Implications of fish home range size and relocation for marine reserve function. *Env. Biol. Fish.* 55: 65–79.

Kraufvelin P., Pekcan-Hekim Z., Bergström U., Florin A.-B., Lehikoinen A., Mattila J., Arula T., Briekmane L., Brown E.J., Celmer Z., Dainys J., Jokinen H., Kääriä P., Kallasvuo M., Lappalainen A., Lozys L., Möller P., Orio A., Rohtla M., Saks L., Snickars M., Støttrup J., Sundblad G., Taal I., Ustups D., Verliin A., Vetemaa M., Winkler H., Wozniczka A. & Olsson J. 2018. Essential coastal habitats for fish in the Baltic Sea. *Est. Coast. Shelf Sci.* 204: 14–30.

Laurel B.J. & Bradbury I.R. 2006. "Big" concerns with high latitude marine protected areas (MPAs): trends in connectivity and MPA size. *Can. J. Fish. Aquat. Sci.* 63: 2603–2607.

Lehtonen H., Böhling P., Hudd R. 1986. Siken och sikfisket i Kvarkenområdet. RKTL. Helsinki. Kalantutkimusosasto, monistettuja julkaisuja 47. 76 pp. (In Swedish)

Lehtonen H., Nyberg K., Vuoronen P.J., Leskelä A. 1992. Radioactive strontium (^{85}Sr) in marking whitefish [*Coregonus lavaretus* (L.)] larvae and the dispersal of larvae from river to sea. *J. Fish Biol.* 41: 417–423.

Lehtonen H. & Himberg M. 1992. Baltic Sea migration patterns of anadromous, *Coregonus Lavaretus* (L) S. Str., and sea-spawning European whitefish, C.L. Widegreni Malmgren. *Pol. Arch. Hydrobiol.* 39: 463–472.

Lehtonen H. & Lappalainen J. 1995. The effects of climate on the year-class variation of certain freshwater fish species. pp. 37–44. In: Beamish R. J. (ed), *Climate change and northern fish populations. Can. Spec. Publ. Fish Aquat. Sci.* 121

Lester S.E., Halpern B.S., Grorud-Colvert K., Lubchenco J., Ruttenberg B.I., Gaines S.D., Airamé S. & Warner R.R. 2009. Biological effects within no-take marine reserves: a global synthesis. *Mar. Ecol. Prog. Ser.* 384: 33–46.

McLean D.L., Harvey E.S., Fairclough D.V. & Newman S.J. 2010. Large decline in the abundance of a targeted tropical lethrinid in areas open and closed to fishing. *Mar. Ecol. Prog. Ser.* 418: 189–199.

Micheli F., Halpern B.S., Botsford L.W. & Warner R.R. 2004. Trajectories and correlates of community change in no-take marine reserves. *Ecol. Appl.* 14: 1709–1723.

Moland E., Olsen E.M., Knutsen H., Garrigou P., Espeland S.H., Kleiven A.R., André C. & Knutsen J.A. 2013. Lobster and cod benefit from small-scale northern marine protected areas: inference from an empirical before–after control-impact study. *P. Roy. Soc. B Biol. Sci.* 280.

Molloy P.P., McLean I.B. & Côté I.M. 2009. Effects of marine reserve age on fish populations: a global meta-analysis. *J. Appl. Ecol.* 46: 743–751.

Mosqueira I., Côté I.M., Jennings S. & Reynolds J.D. 2000. Conservation benefits of marine reserves for fish populations. *Anim. Conserv.* 3: 321–332.

Munro J.L. 2000. Outmigration and movement of tagged coral reef fish in a marine fishery reserve in Jamaica. *Proc. Gulf Carib. Fish. Inst.*: 557–568.

Nelson J.B. 2005. *Pelicans, Cormorants, and their Relatives the Pelecaniformes,* Oxford University press.

Nilssen K.T., Lindstrøm U., Westgaard J.I., Lindblom L., Blencke T.-R. & Haug T. 2019. Diet and prey consumption of grey seals (*Halichoerus grypus*) in Norway. *Marine Biology Research* 15: 137–149.

O'Boyle R. & Sinclair M. 2012. Seal–cod interactions on the Eastern Scotian Shelf: Reconsideration of modelling assumptions. *Fish. Res.* 115–116: 1–13.

Oksanen S.M., Niemi M., Ahola M.P. & Kunnasranta M. 2015. Identifying foraging habitats of Baltic ringed seals using movement data. *Movement Ecol.* 3: 33.

Olsson J., Florin A.-B., Mo K., Aho T. & Ryman N. 2012. Genetic structure of whitefish (*Coregonus maraena*) in the Baltic Sea. *Est. Coast. Shelf Sci.* 97: 104–113.

Ozerov M.Y., Himberg M., Debes P.V., Hägerstrand H. & Vasemägi A. 2016. Combining genetic markers with an adaptive meristic trait improves performance of mixed-stock analysis in Baltic whitefish. *ICES J. Mar. Sci.* 73: 2529–2538.

Palumbi S.R. 2003. Population genetics, demographic connectivity, and the design of marine reserves. *Ecol. Appl.* 13: 146–158.

Pauly D. & Zeller D. 2016. Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nat. Commun.* 7:10244.

Pereira T.J., Manique J., Quintella B.R., Castro N., de Almeida P.R. & Costa J.L. 2017. Changes in trophic ecology of fish assemblages after no take Marine Protected Area designation in the southwestern coast of Portugal. *Ocean Coast. Manage.* 137: 144–153.

R Core Team. 2016. *R: A language and environment for statistical computing.* R Foundation for statistical computing, Vienna, Austria. https://www.r-project.org/.

Ridgway M.S. 2010. A review of estimates of daily energy expenditure and food intake in cormorants (*Phalacrocorax* spp.). *Journal of Great Lakes Research* 36: 93–99.

Roberts C.M., Bohnsack J.A., Gell F., Hawkins J.P. & Goodridge R. 2001. Effects of marine reserves on adjacent fisheries. *Science* 294: 1920–1923.

Roberts C.M. & Polunin N.V.C. 1992. Effects of marine reserve protection on northern Red Sea fish populations. *P. 7th Int. Coral Reef Symp.* pp. 969–977.

Rohtla M., Svirgsden R., Verliin A., Rumvolt K., Matetski L., Hommik K., Saks L. & Vetemaa M. 2017. Developing novel means for unravelling population structure, provenance and migration patterns of European whitefish *Coregonus lavaretus* s.l. in the Baltic Sea. *Fish. Res.* 187: 47–57.

Rose G.A. 2005. On distributional responses of North Atlantic fish to climate change. *ICES J. Mar. Sci.* 62: 1360–1374.

Salmi J. A., Auvinen H., Raitaniemi J., Kurkilahti M., Lilja, J. & Maikola, R. 2015. Perch (*Perca fluviatilis*) and pikeperch (*Sander lucioperca*) in the diet of the great cormorant (*Phalacrocorax carbo*) and effects on catches in the Archipelago Sea, Southwest coast of Finland. *Fish. Res.* 164: 26–34.

Salomon M., Markus T. & Dross M. 2014. Masterstroke or paper tiger – The reform of the EU′s Common Fisheries Policy. *Mar. Policy* 47: 76–84.

Saulamo K. & Neuman E. 2002. *Local management of Baltic fish stocks — significance of migrations*. Fiskeriverket, Finfo 2002:9, 1–18, available.

Sciberras M., Jenkins S.R., Mant R., Kaiser M.J., Hawkins S.J. & Pullin A.S. 2015. Evaluating the relative conservation value of fully and partially protected marine areas. *Fish Fish.* 16: 58-77.

Seitz R.D. 2014. Value of coastal habitats for exploited species: introduction to a theme set of articles. *ICES J. Mar. Sci.* 71: 636–637.

Sjöberg M. & Ball J.P. 2000. Grey seal, *Halichoerus grypus*, habitat selection around haulout sites in the Baltic Sea: bathymetry or central-place foraging? *Can. J. Zool.* 78: 1661–1667.

Sundblad G., Bergström U., Sandström A. & Eklöv P. 2014. Nursery habitat availability limits adult stock sizes of predatory coastal fish. *ICES J. Mar. Sci.* 71: 672–680.

Swedish Agency for Marine and Water Management. 2016. *Recreational fishing in Sweden 2016*. Aqua reports 2017:4. Swedish University of Agricultural Sciences. 56 pp.

Swedish Agency for Marine and Water Management. 2018. *Fisk- och skaldjursbestånd i hav och sötvatten 2017. Resursöversikt.* Göteborg, 273p, available at https://www.slu.se/institutioner/akvatiska-resurser/sok-publikation/fiskbestand-och-miljo-i-hav-och-sotvatten/.

Sørensen T.K. & Thomsen L.N. 2009. A comparison of frameworks and objectives for implementation of marine protected areas in Northern Europe and in Southeast Asia. *Aquat. Ecosyst. Health Manage.* 12: 258–263.

Thomas A.C., Nelson B.W., Lance M.M., Deagle B.E. & Trites A.W. 2016. Harbour seals target juvenile salmon of conservation concern. *Can. J. Fish. Aquat. Sci.* 74: 907–921.

Thorbjørnsen S.H., Moland E., Huserbråten M.B.O., Knutsen J.A., Knutsen H. & Olsen E.M. 2018. Replicated marine protected areas (MPAs) support movement of larger, but not more, European lobsters to neighbouring fished areas. *Mar. Ecol. Prog. Ser.* 595: 123–133.

Thorbjørnsen S.H., Moland E., Simpfendorfer C., Heupel M., Knutsen H. & Olsen E.M. 2019. Potential of a no-take marine reserve to protect home ranges of anadromous brown trout (*Salmo trutta*). *Ecol. Evol.* 9: 417–426.

Vandeperre F., Higgins R.M., Sánchez-Meca J., Maynou F., Goñi R., Martín-Sosa P., Pérez-Ruzafa A., Afonso P., Bertocci I., Crec'hriou R., D'Anna G., Dimech M., Dorta C., Esparza O., Falcón J.M., Forcada A., Guala I., Le Direach L., Marcos C., Ojeda-Martínez C., Pipitone C., Schembri P.J., Stelzenmüller V., Stobart B. & Santos R.S. 2011. Effects of no-take area size and age of marine protected areas on fisheries yields: a meta-analytical approach. *Fish Fish.* 12: 412–426.

Wells S., Ray G.C., Gjerde K.M., White A.T., Muthiga N., Bezaury Creel J.E., Causey B.D., McCormick-Ray J., Salm R., Gubbay S., Kelleher G. & Reti J. 2016. Building the future of MPAs – lessons from history. *Aquat. Conserv. Mar. Freshwater Ecosyst.* 26: 101–125.

Veneranta L., Hudd R. & Vanhatalo J. 2013a. Reproduction areas of sea-spawning coregonids reflect the environment in shallow coastal waters. *Mar. Ecol. Prog. Ser.* 477: 231–250.

Veneranta L., Urho L., Koho J., Hudd R. 2013b. Spawning and hatching temperatures of whitefish (*Coregonus lavaretus* (L.)) in the Northern Baltic Sea. Advanc. Limnol. 64: 39–55.

Verliin A., Saks L., Svirgsden R., Vetemaa M. & Saat T. 2013. Whitefish (*Coregonus lavaretus* (L.)) landings in the Baltic Sea during the past 100 years: combining official datasets and grey literature. *Advanced Limnology* 64: 133–152.

Vetemaa M., Eschbaum R., Albert A., Saks L., Verliin A., Jürgens K., Kesler M., Hubel K., Hannesson R. & Saat T. 2010. Changes in fish stocks in an Estonian estuary: overfishing by cormorants? *ICES J. Mar. Sci.* 67: 1972–1979.

Ward E.J., Levin P.S., Lance M.M., Jeffries S.J., Acevedo-Gutiérrez A. 2012. Integrating diet and movement data to identify hot spots of predation risk and areas of conservation concern for endangered species. *Conserv. Letters* 5: 37–47.

Willis T.J., Millar R.B. & Babcock R.C. 2003. Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. *J. Appl. Ecol.* 40: 214–227.

Winfield I.J., Crawshaw D.H. & Durie N.C. 2007. Management of the cormorant, *Phalacrocorax carbo*, and endangered whitefish, *Coregonus lavaretus*, populations of Haweswater, UK. . In: Cowx I.G. (ed.), *Interactions between Fish and Birds: Implications for Management,* pp. 335–344.

van Overzee H.M.J. & Rijnsdorp A.D. 2015. Effects of fishing during the spawning period: implications for sustainable management. *Rev. Fish Biol. Fisheries* 25: 65–83.

Voyer M., Gladstone W. & Goodall H. 2012. Methods of social assessment in Marine Protected Area planning: is public participation enough? *Mar. Policy* 36: 432–439.

Voyer M., Gollan N., Barclay K. & Gladstone W. 2015. 'It's part of me'; understanding the values, images and principles of coastal users and their influence on the social acceptability of MPAs. *Mar. Policy* 52: 93–102.

Zeller D., Rossing P., Harper S., Persson L., Booth S. & Pauly D. 2011. The Baltic Sea: estimates of total fisheries removals 1950–2007. *Fish. Res.* 108: 356–363.

Östman Ö., Boström M.K., Bergström U., Andersson J. & Lunneryd S.-G. 2014. Estimating competition between wildlife and humans — a case of cormorants and coastal fisheries in the Baltic Sea. *PLoS ONE* 8: e83763.

Östman Ö., Eklöf J., Eriksson B.K., Olsson J., Moksnes P.-O. & Bergström U. 2016. Top-down control as important as nutrient enrichment for eutrophication effects in North Atlantic coastal ecosystems. *J. Appl. Ecol.* 53: 1138–1147.