Ecological Representativity of Marine Protected Areas along the Swedish West Coast

– Evaluating the effectiveness of the existing network and identifying expansion opportunities in the Skagerrak

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Abstract

Marine protected areas (MPAs) are recognised worldwide as an important tool to combat biodiversity loss. The European union (EU) has recently adopted a new strategy aiming at protecting at least 30% of Europe's marine environment and inferring strict protection for one third of the protected area. Examples of strict protection are no-take zones, a complete ban on commercial fishing. This study aimed to evaluate the efficiency of the current MPA network along the Swedish west coast and expansion opportunities were identified in the coastal zone of the Skagerrak in Västra Götaland county. By using monitoring data from samples of juveniles, habitat distribution for 21 species of fish and crustaceans were mapped using Esri ArcGIS Pro. The ecological representativity, i.e., the proportion of protected habitat (%) for each species, was calculated and compared against the goals set by the EU. Anthropogenic disturbances were also mapped to identify overlap of areas with high species richness and high anthropogenic pressure, focussing on endangered and commercially important species. The pressure data was further used as a cost-matrix to prioritise protection of habitats under high pressure, when analysing expansion opportunities using the conservation planning tool Marxan. Two target levels (40% and 50% habitat protection, based on results from the calculated ecological representativity) and two different scenarios were tested with Marxan; one unbiased solution with no spatial constraints, and one biased solution forcing already protected habitats to be included and thus focusing on expanding from existing MPAs. Results show that the ecological representativity provided by the current MPA network is sufficient in protecting ≥30% of the species habitat on the west coast, but in the Skagerrak, it fails to provide protection for the two-spotted goby (9%). The Marxan-analysis showed that it is possible to enhance protected habitat to >50% for all species in the Skagerrak. A best conservation solution was obtained when endangered and commercially important species were ranked as more important to protect than other species. Additionally, using the biased solution and instructing Marxan to emphasise MPA compactness yielded the most cost-efficient conservation solution with 39% less total reserve area required compared to 49% for the unbiased solution. Expansion opportunities should focus on the coastal area from Gothenburg northward to Orust where a large part of unprotected habitats are situated. Even though the ecological representativity is good for most of the species, many are endangered and a small frequency of occurrence in the fishing samples, suggests that merely establishing MPAs might not be enough. Inferring stricter protection such as no-take zones may be required, both from a species-perspective and as a measure to achieve the goal set by the EU. Thus, future work should focus on amending regulations in existing MPAs as well as expanding the current MPA network and include no-take zones.

Keywords: ecological representativity, ecological coherence, species richness, marine protected areas, Marxan, no-take zones

Populärvetenskaplig sammanfattning

Marina skyddade områden (MPAs) används över hela världen som ett viktigt verktyg för att skydda biologisk mångfald. Skyddet kan innebära mer eller mindre strikta restriktioner kring mänskliga aktiviteter som påverkar arter och deras livsmiljöer (habitat). På grund av den fortgående förlusten av biodiversitet och det effektiva verktyg som MPAs utgör, har Europeiska unionen (EU) nyligen antagit ett regelverk med målet om att skydda minst 30% av EUs havsmiljö samt införa ett strikt skydd för 10% av havsmiljön. Exempel på strikt skydd är ett fullständigt förbud mot kommersiellt fiske. En viktig parameter för att analysera om MPAs är effektiva är att mäta den ekologiska representativiteten. Detta görs genom att beräkna hur stor andel av en arts habitat är skyddat sett till det totala habitatet i regionen. Denna studie syftar till att utvärdera effektiviteten hos det nuvarande MPA-nätverket längs den svenska västkusten, med fokus på kustzonen i Skagerrak i Västra Götalands län. Fördelningen av habitat för 21 provfiskade arter (18 fiskar och 3 kräftdjur) analyserades med det geografiska informationsverktyget ArcGIS Pro, där den ekologiska representativiteten beräknades för varje art och jämfördes med de mål som EU etablerat. Data över mänskliga störningar i Skagerrak har använts för att identifiera överlapp med habitat med hög artrikedom. Dessa dataset har vidare använts i beslutsstödsverktyget Marxan, där potentiella expansionsmöjligheter för MPAs analyserades. Marxan strävar efter att leverera den mest kostnadseffektiva lösningen, där kostnaden i denna studie utgjordes av påverkan av mänsklig störning. Habitat som utsatts för höga störningar prioriterades genom att tilldelas en låg kostnad och vice versa. Två målnivåer (40% och 50% skyddat habitat, baserade på resultat från beräkning av den ekologiska representativiteten) infördes för respektive art och två olika scenarier testades; en analys utan rumsliga begränsningar och en analys som tvingade redan skyddade habitat att inkluderas i lösningen. Utöver detta testades även möjligheten att prioritera skydd för de arter som är hotade och/eller kommersiellt viktiga genom två analyser: en där de hotade arterna rankades högst följt av de kommersiellt viktiga arterna och lägst de resterande arterna samt en analys där alla arter rankades som lika viktiga. Resultatet visar att den ekologiska representativiteten som tillhandahålls av det nuvarande MPA-nätverket är tillräckligt för att skydda ≥30% av habitatet för hela västkusten. I Skagerrak misslyckas det nuvarande nätverket med att ge tillräckligt skydd för en art (den sjustråliga smörbulten), där endast 9% av habitatet är skyddat. Med Marxan påvisades möjligheten att förbättra skyddet för den sjustråliga smörbulten (och övriga arter), då båda målnivåerna uppnåddes. Den mest kostnadseffektiva lösningen uppnåddes när hotade och kommersiellt viktiga arter rankades som viktigare att skydda samt när redan skyddade habitat inkluderas som utgångspunkt för analysen. Denna lösning krävde 39% mindre yta än det nuvarande MPA-nätverket. En stor del av oskyddat habitat som Marxan anser är viktiga att skydda återfinns i kustområdet mellan Göteborg och Orust. Även om den ekologiska representativiteten är bra (jämfört med EUs mål), är ändå många arter hotade. En låg förekomst i provfisket kan tyda på att det inte är tillräckligt att enbart bilda MPAs, utan att strängare skydd, i form av ett fullständigt förbud mot kommersiellt fiske, behöver införas i befintliga och nya MPAs. Detta är viktigt både ur ett artbevaringsperspektiv och som åtgärd för att uppnå EU:s mål om skyddad havsmiljö. Därför bör framtida arbeten fokusera på att både utvidga det nuvarande MPA-nätverket, för att inkludera viktiga oskyddade habitat, samt att stärka existerande restriktioner genom att inkludera zoner med fiskeförbud.

Nyckelord: ekologisk representativitet, ekologisk koherens, biologisk mångfald, marina skyddade område, fiskefria områden, Marxan, fiskefria zoner

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Abbreviations

AIS	Automatic Identification System
AUC	Area Under Curve
BLM	Boundary Length Modifier
CBD	Convention on Biological Diversity
EU	European Union
IUCN	International Union for Conservation of Nature and Natural Resources
MPA	Marine Protected Area
SAC	Special Areas of Conservation
SLU	Swedish University of Agricultural Sciences
SPA	Special Protection Areas
SPF	Species Penalty Factor

1. Introduction

The concept of *representativity* is often used to determine if a subsample used to answer a question is representative of the whole. The idea is applicable across multiple disciplines. For example, in sociology, when analysing public opinion on national matters (e.g., are Swedish citizens for or against increased immigration?), a sample may be considered representative if the variation in the participants reflect the demographics of the Swedish population. A similar interpretation of the concept is applied in conservation science when designating areas for environmental protection. In this context, representativity refers to the proportion of a species or habitat that is protected within a reserve network relative to unprotected areas (Kukkala and Moilanen, 2013; Almany *et al.*, 2009; Austin and Margules, 1986). By estimating the ecological representativity of conservation features (species or habitats) in a protected area, suitability and effectiveness of conservation efforts can be analysed. Estimating ecological representativity for individual species is important but it is also crucial to consider multiple species, in order to maintain a wider biodiversity perspective on conservation efforts (Belbin, 1993).

Biodiversity is defined by the Convention on Biological Diversity (CBD) as the variability among living organisms, including intra- and interspecific variability (within a species versus between different species) and among ecosystems (United Nations, 1992). CBD was formed in 1993 as a response to the accelerating rate of global biodiversity loss, threatening both economic and social development and the wellbeing of current and future generations. However, biodiversity loss is not a recent phenomenon, but something which has occurred continuously since the introduction of hominins (*Homo sapiens* and its forefathers) on Earth (Pace *et al.*, 1999; Smith *et al.*, 2018). Both terrestrial and marine environments have suffered from long-term biodiversity loss, with loss on land being the most severe. During the past few centuries, especially since the 1970s, marine biodiversity have also experienced rapid declines in species and populations, with overfishing being the single largest contributing factor (Jackson *et al.*, 2001). Today, global biodiversity loss is occurring at an alarming rate and combating these losses requires global action and cooperation between countries (Ceballos *et al.*, 2015).

Biodiversity loss does not only affect species individually, but also affects species composition when interspecific interactions is altered, changing the dynamics of the trophic system, which in turn affects the function and structure of ecosystems (Gislason, 1994; Dayton *et al.*, 1995; Baum and Worm, 2009; Ritchie and Johnson, 2009). Conservation efforts must therefore target both individual species and communities of species. One method incorporating both of these objectives is the establishment of protected areas, a measure recognised as a key tool to combat biodiversity loss and achieve conservation goals set by the CBD and the 2030 Agenda for Sustainable Development (see goal 14 and 15; United Nations, 2016). A protected area is defined by the International Union for Conservation of Nature and Natural Resources (IUCN) as:

> *"a geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long term conservation of nature with associated ecosystem services and cultural values"* (Dudley and Stolton, 2008)

There are many categories of protected areas depending on the objectives and the spatial scale of protection. To facilitate universal standards for governments legislating protected areas, classification of categories has been produced by the IUCN (Dudley, Shadie and Stolton, 2013). This system has been recognized by the United Nations and other international bodies as the global standard of defining and classifying protected areas. The IUCN-categories include protection and management objectives for land-/seascapes, species, habitats, landforms, and natural resources.

Using the IUCN-classification, the European Union (EU) has developed the Emerald Network, a programme aiming to create an ecological network of protected areas where special conservation is required (European Union, 2016). The Emerald Network was introduced under the Bern Convention in 1989, aiming to create "long term survival of the species and habitats of the Bern Convention requiring specific protection measures" (European Union, 2016). The program laid the foundation for the Habitats Directive in 1992 followed by the introduction of the Natura 2000 network (The Council of the European Communities, 1992; Sundseth, 2008). Together with the Birds Directive adopted by the EU in 1979 (European Union, 2009), these policy instruments constitute an important framework on protecting, conserving and sustainably managing species, habitats and land-/seascapes in the EU.

Additionally, EU has adopted two frameworks regarding the marine environment: The Marine Strategy Framework Directive (European Union, 2008) and the Framework for Maritime Spatial Planning (European Union, 2014). Both frameworks aim at protecting the marine environment and streamlining marine spatial planning to reduce land- and ocean-based pollution and ease pressures from anthropogenic activities. Because the marine environment is shared across territorial borders, cooperation between states is important, as measures may be unproductive if not all states bordering the targeted area make coordinated protection and conservation efforts (Hayashi, 1993; Guerreiro *et al.*, 2010).

The same applies to marine species, as many are mobile and migrate long distances during their life cycle. Marine vertebrates, such as fish, are examples of organisms that require different types of habitat throughout their juvenile state and their adult and reproductive state (Jonsson and Jonsson, 1993). Food limitation and predation pressure may also affect migration (Jonsson and Jonsson, 1993). Furthermore, there is inter- and intraspecific variation in migration distances between species and individuals, and their migration routes may cross multiple marine territorial borders (Chapman *et al.*, 2011). This emphasizes the need for international collaboration when species targeted for conservation plans have a wide migration pattern. Creating an ecologically representative network of marine protected areas (MPAs), therefore, requires cooperation between states to effectively manage and conserve targeted species.

In 2020, the EU adopted the *EU Biodiversity Strategy for 2030* for combating biodiversity loss and habitat degradation, with protected areas being a key tool (European Commission, 2020a). In this strategy, emphasis is placed on the network being ecologically coherent, a term often used to assess the effectiveness of protected areas. The definition of "ecologically coherent" varies but often includes examining the networks (Davenport *et al.*, 2008; Sciberras *et al.*, 2013):

- *representativity* (the degree to which the various habitat and species present in the region are represented and protected, relative to unprotected areas)
- *connectivity* (spatial distribution of protected areas must be close enough to facilitate dispersal among separated populations)
- *replication* (habitats should be represented in multiple protected areas to strengthen resilience)
- *adequacy* (spatial factors including size, shape, and location, to secure long-term survival of species and populations)

As the current network of MPAs in Europe is not adequately protecting biodiversity (European Commission, 2020a), two objectives in the new strategy are to expand the network and implement stricter regulations (European Commission, 2021). The goal of the new strategy is to protect at least 30% of Europe's marine environment by the year 2030, of which one third is to be strictly protected (European Commission, 2020a). However, the EU has not yet defined the term "strict protection", so it is still unclear what measures the member states must take to reach the goal. A goal of protecting a minimum of 30% is also inferred for species and habitats (registered in the Birds and Habitat directives), features important for conservation as they either suffer from declining populations or are expected to decline, due to increased habitat deterioration (European Commission, 2020a).

Every coastal member state is expected to contribute to the two goals. For Sweden, this requires actions to more than double the coverage of MPAs, as currently only 14% of the marine environment, including the economic zone, is protected (Statistics Sweden, 2020a). However, some regions have achieved over 30% coverage, such as in the Swedish west coast, where 32% of the marine environment is protected (Statistics Sweden, 2020a). Even though this surpasses the 30% goal, Sweden may still be required to increase the proportion of strict protection, when the type of regulations and actions needed to implement strict regulations is established.

The Skagerrak is a region where collaboration between states is particularly important for creating an ecologically representative network of MPAs. The Skagerrak is a straight connecting the Baltic Sea and the North Sea, approximately 240 km long and between 80 and 140 km wide (Figure 1). The Skagerrak is bordered by the Danish north coast, the Swedish west coast, and the southern coast of Norway. With water mixing from both the North Sea and the Baltic Sea, the Skagerrak is subject to both land and sea-based pollution, as currents carry nutrients and pollutants from the extensive Baltic Sea basin, which is bordered by nine countries. The strait is also an important maritime shipping route as it connects northern Europe with the rest of the world and the route is especially important for the Russian oil export (U.S. Energy Information Administration, 2017). In fact, a global map displaying cumulative anthropogenic pressures across 20 marine ecosystems distinguish the North Sea, including the Skagerrak, as one of the most heavily impacted regions in the world (Halpern *et al.*, 2008). Moreover, coastal environments are more vulnerable with both sea- and land-based anthropogenic activities that direct (development, overfishing, use of destructive fishing techniques, pollution) and indirect (eutrophication, enhanced sedimentation, acidification) affect ecosystems and biodiversity (Airoldi and Beck, 2007; Halpern *et al.*, 2008).

Ecological representativity of the MPA network in the Skagerrak is poorly understood, particularly from a habitat or species distribution perspective. There are a few studies analysing ecological coherence of the existing MPA network. However, these studies focus on larval connectivity (Moksnes *et al.*, 2014; Nilsson and Jonsson, 2011) and multiple species dispersal strategies (Jonsson, Nilsson Jacobi and Moksnes, 2016). With biodiversity loss, declining fish stocks, and degradation of habitats in the Skagerrak, it is important to include ecological representativity as a parameter for measuring the effectiveness and success of the MPA network. The rapid rate of biodiversity loss, along with the significant knowledge gap, highlight the importance of examining the ecological representativity of the MPA network in the Skagerrak.

1.1. Aims and objectives

The aim of this study is to analyse the efficiency of the current network of marine protected areas (MPAs) with regard to habitats protected for 21 species in the Skagerrak, focusing on the coastal zone of Västra Götaland. This study evaluates the representativity of the MPA network and explore possibilities for the establishment of new MPAs, expansion of existing MPAs, and discuss the strictness of protection within existing network. It is important to ensure that the network of MPAs is ecologically representative to promote the conservation of species subject to anthropogenic disturbances. It is especially crucial to mitigate cumulative effects of anthropogenic activities in coastal areas, as coastal habitats are crucial spawning, nursery, and nesting sites for various organisms including the 18 fishes and 3 crustaceans analysed in this study. The objectives of this study are:

1) Using existing habitat distribution maps, to produce maps of protected and non-protected habitats for a specific group of fish and crustaceans.
2) Combining habitat maps for all species, to produce a species richness map to analyse the distribution of high species richness areas.
3) Analysing the spatial distribution of species richness in relation to the spatial distribution of pressures, to identify high species richness areas subject to high anthropogenic pressure.
4) Estimating the ecological representativity of the MPA network using the aforementioned habitat maps.
5) Evaluating the current MPA network and expansion opportunities in the Skagerrak using the conservation planning tool Marxan, by creating one "biased" solution where existing MPAs are included, and one "unbiased" solution where inclusion of existing MPAs are not enforced. A dataset of spatial anthropogenic pressure will be used as a cost matrix to produce conservation solutions, prioritising habitats under high anthropogenic pressure.
6) Providing suggestions for the expansion of existing MPAs, and where new MPAs could be established to include unprotected areas with high species richness.

2. Background

2.1. Study area

The Skagerrak is a brackish strait connecting the Baltic Sea with the North Sea, and it is bordered by three countries: Sweden, Norway, and Denmark (Figure 1). The physiography of the Swedish coastal landscape of the Skagerrak consists of low-lying and undulating bedrock with granitic lithologies (SNA, 1992). The region houses several fjords, orientated in north-south directions but with varying depth and physical properties (SNA, 1992). Fjords are typically long, narrow inlets with steep coastal slopes and deep narrow trenches (Fonselius, 1990). Some fjords in the Skagerrak have steep coastal slopes (e.g., Gullmarsfjorden,) while others lack steep relief above water (e.g., Kosterfjorden; Figure 1; Fonselius, 1990; SNA, 2003). The Skagerrak's rocky coastal seascape provides a wide variety of habitats, from soft, shallow beds and rocky reefs to muddy deep-water trenches with depths of up to 247 m (SNA, 1992; Länsstyrelsen i Västra Götaland län, 2020). It's rich archipelago landscape of 3,000 islands and 4,500 islets and skerries makes the area popular for recreational activities and an attractive destination for tourists (Nationalencyklopedin, 2021; SNA, 2003).

There are two major oceanic currents in the Skagerrak, the Jutland stream and the Baltic stream (Figure 1). These currents affect water flow and environmental conditions, which in turn influences the habitat and species composition in the area. The Jutland stream brings low-temperature saline water from the North Sea as it runs east along the west coast of Denmark, splitting into two directions at the country´s northern tip (SNA, 1992; Fonselius, 1990). One stream continues towards the Swedish coast in the Skagerrak where it joins the northbound Baltic stream, the other stream rounds Denmark´s northern tip and then continues southward along the Danish east coast, towards the sea of the Kattegat (Figure 1; Fonselius, 1990). The Baltic stream runs north along the Swedish west coast until reaching the southern part of Norway where it continues westward towards the North Sea (Figure 1) (Fonselius, 1990). The Baltic stream brings brackish water from the Baltic Sea, through the Kattegat and subsequently into the Skagerrak (Figure 1) (Fonselius, 1990).

The Skagerrak has a stable halocline at a depth of 10-15 meters, with a salinity of 25 ‰ in the surface water, increasing to >30 ‰ under the halocline (SNA, 2003; Havsmiljöinstitutet, no date). Because of the high salinity and good oxygenation (due to the constant water exchange with the North Sea), species richness is relatively high, and the strait houses many endangered species including the rare cold-water coral Lophelia (*Lophelia pertusa*) (Swedish Environmental Protection Agency, 2014). Along the Swedish coast of the Skagerrak (Figure 1), a large portion of the coral reef has died, primarily due to detrimental fishing practices such as bottom trawling, but also because of anchoring, acidification, and consequences of climate change (increased water temperature, lower salinity due to increased precipitation). The remaining living coral is situated in Kosterfjorden, a part of the Swedish marine national park Kosterhavet (Figure 1).

Coral reefs and other important habitat forming species such as mussel reefs (Hirst, Clark and Sanderson, 2012), are important for biodiversity as they act as nurseries and provide protection from predators for a large number of vertebrates and invertebrates. Many of the species found in Kosterhavet are endemic, meaning they have not been found elsewhere in Sweden or the rest of the world. Besides the unique composition of flora and fauna in Kosterhavet, the Skagerrak is an important region for the Swedish fishing industry, because most commercial fisheries are located on the Swedish west coast (Waldo and Blomquist, 2020). Due to the great ecological and economic importance of productive habitats in the Skagerrak, this study focuses on the Swedish coastal and marine environment of the Skagerrak (Figure 1). However, the framework developed and used in this study is not exclusive to this region but is applicable to other parts of the world and other types of species.

The county administrative board of Västra Götaland is responsible for managing the marine environment in the Swedish part of the Skagerrak (Figure 1). Marine features with high conservation values have been identified and mapped to some extent, enabling a prioritisation of habitats and species with particularly high conservation values (Länsstyrelsen i Västra Götaland län, 2019). These include Natura 2000 and OSPAR sites, and habitats with rare, threatened, endangered, and key species. Some of the species prioritised by Västra Götaland county are included in this study: European eel (*Anguilla anguilla*), Atlantic cod (*Gadus morhua*) and European lobster (*Homarus Gammarus*). However, there is a knowledge gap regarding the distribution of costal habitats and species and what environmental conditions they require as well as insufficient data about the presence and extent of marine features with high conservation values (Länsstyrelsen i Västra Götaland län, 2019).

Västra Götaland county have several ongoing processes regarding expansion of the existing MPA network and establishing new MPAs, including habitats in deep water and shallow coastal areas important for spawning, and as nursery grounds for many fish species. Furthermore, it has been suggested that a new marine national park should be established in Gullmarsfjorden (Figure 1), because the region contains unique marine values important to preserve (Länsstyrelsen i Västra Götaland län, 2020). In addition to managing and developing the MPA network, Västra Götaland county collaborates with the administrative boards of Halland and Skåne counties. The three counties have produced a joint "Strategy for protection and management of marine environments and species in the North Sea" (Länsstyrelsen i Västra Götaland län, 2020). The collaboration recognises the importance of common management for marine environments and species, including cross-border establishment of MPAs to encompass habitats stretching over county borders.

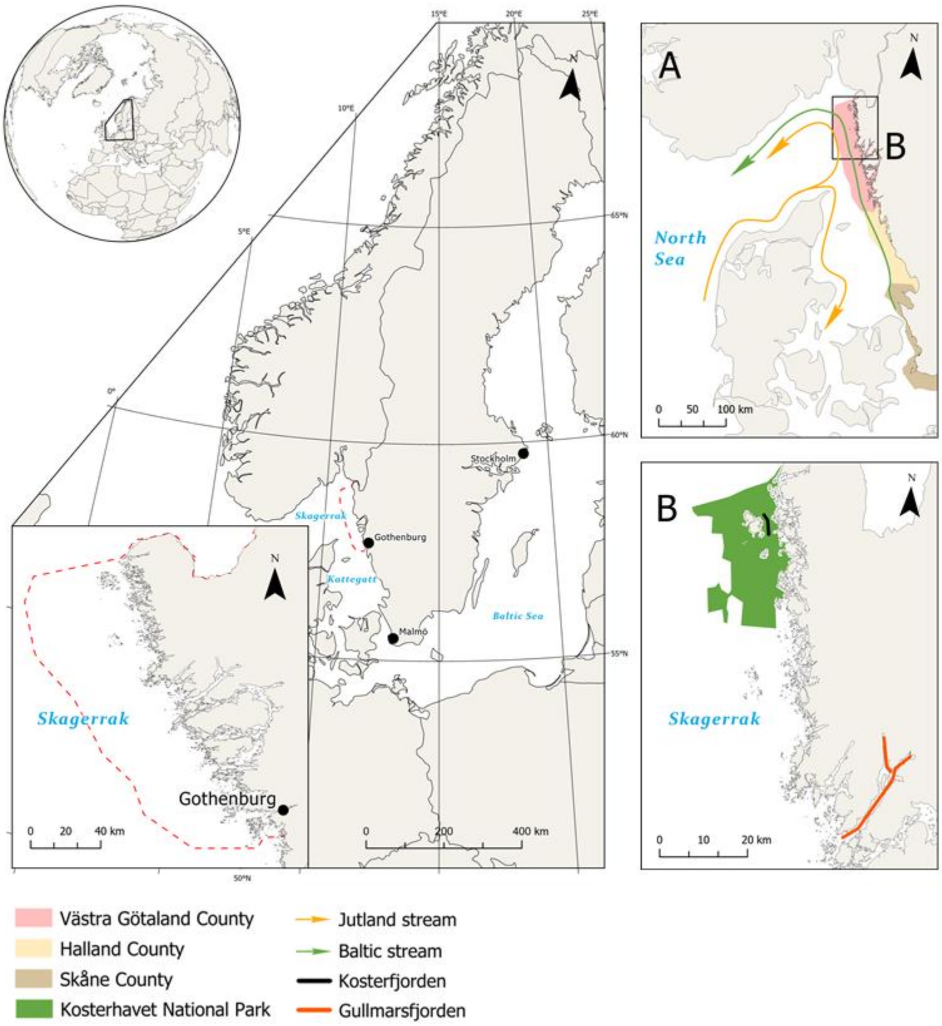


Figure 1. Map of the study region. The study area is indicated with dashed lines in red. Panel A displays the two major oceanic currents, the Jutland stream (orange arrow) and the Baltic stream (green arrow), affecting the environmental conditions in the Skagerrak. The coastal boundaries of featured counties are also shown in this panel. The black box in panel A shows the map extent of panel B. The marine national park of Kosterhavet is displayed in panel B together with the two fjords, Kosterfjorden and Gullmarsfjorden.

2.2. Anthropogenic disturbances

The Skagerrak is susceptible to multiple disturbances sourcing from both marine and land-based anthropogenic activities. Some of these disturbances are discussed here, including: i) discharge-pollution, ii) fishing pressure, iii) physical disturbance, and v) dispersal of pollutants.

There are many studies investigating effects of anthropogenic disturbances on the marine environment (Jägerbrand *et al.*, 2019). For example, discharge-pollution, the intentional and unintentional spill of oil and other chemicals, have a direct effect on the physiology of fish, such as liver damage, reduced growth, and increased mortality (Peterson, 2001; Rogowska and Namieśnik, 2010). Global maritime transportation also promotes species dispersal, as species enclosed in the ballast water of the ships or attached to the hull, are released in new areas, introducing invasive species to local environments (Blakeslee *et al.*, 2010; Seebens, Gastner and Blasius, 2013). Consequences for local species include increased competition or enhanced predation pressure, leading to changes in the trophic system as abundance of organisms in one trophic level decreases, affecting food supply for organisms higher up in the food chain (Fleeger, Carman and Nisbet, 2003). Discharge-pollution can be difficult to mitigate by establishing MPAs, because this disturbance can be either unintentional or intentional, meaning MPAs have little effect. Instead, a more effective measure is increased environmental monitoring.

Pressure from the fishing industry includes unsustainable yields and detrimental fishing methods. Overfishing of top predators induces top-down trophic cascades when natural predators decline in abundance, enhancing the survival success for species lower in the trophic system (Worm and Myers, 2003; (Frank *et al.*, 2005; Moksnes *et al.*, 2008; Baum and Worm, 2009; Östman *et al.*, 2016). One of the most destructive fishing methods is bottom trawling which implies scraping the bottom for fish (Gislason, 1994; Dayton *et al.*, 1995). Using this aggressive method results in not only the fish of interest being caught but also other organisms living on the bottom, species that are of no value to the fishing industry (so-called bycatch), which is often discarded back to the ocean with variable chances of survival (Gislason, 1994; Dayton *et al.*, 1995; Blaber *et al.*, 2000). Besides the removal of individuals, habitats are destroyed as the trawled area is left bare and unhospitable. Here, MPAs can play a vital role as fishing methods like unsustainable bottom trawling may be prohibited and methods that are less harmful are promoted. Commercial fishing may be limited to low yields or banned (periodically or continuously) from the area, enabling populations to recover, and maintain healthy and stable.

Apart from discharge-pollution and fishing pressure, marine environments are also subjected to physical damage. Construction of piers and ports to support anthropogenic activities have negative impacts on important habitat forming species such as eelgrass (*Zostera marina*), which inhibits soft and shallow beds, and large brown algae, the primary habitat forming vegetation inhibiting rocky seascapes (SNA, 2003). Shading from these constructions impair light penetration which in turn affects the species ability to photosynthesise, causing habitat degradation (Eriander *et al.*, 2017). Species using these habitats as nursery grounds and to hide from predators, is consequently affected by less suitable habitat available (Blaber *et al.*, 2000; Sandström *et al.*, 2005; Sundblad and Bergström, 2014). Furthermore, boating activities in these areas may physically harm species and habitats by anchoring, propeller cutting and by prohibiting light penetration as propellers stir up sediments (Short and Wyllie-Eciieverria, 1996; Sagerman, Hansen and Wikström, 2019). In addition to imposing ship/boat- and fishing-free zones, MPAs can protect unexploited areas from future exploitation and prevent further development in already exploited areas. This is especially important for coastal regions, because habitats in these areas act as nursery grounds for many fish species (Blaber *et al.*, 2000; Sandström *et al.*, 2005).

The previously described disturbances are more severe in coastal and nearshore regions than offshore regions because these environments are subject to both marine- and land-based disturbances. Major disturbances sourced from land-based activities are sediment and nutrient run-off. Deposition of sediment is induced by human activities (e.g. deforestation, construction, dredging) and natural phenomena (although amplified by human influence) such as coastal erosion and river discharge (Airoldi, 2003). Sediment loading in coastal areas deteriorates habitats by smothering underlying vegetation or prohibiting light penetration as water clarity is reduced (Airoldi, 2003; Thrush *et al.*, 2014). Nutrient run-off mostly originates from agriculture, where important fertilisers such as nitrogen and phosphorus are added to increase productivity and yields. These nutrients are released to the marine environment by leakage from arable fields to nearby water streams which carry the nutrients to coastal outlets where it is dispersed (Anderson, Glibert and Burkholder, 2002). The excessive nutrient inputs can cause eutrophication, a process in which algae growth is amplified, inducing oxygen depletion, which in turn affects organisms inhibiting the area as the environmental conditions required by the organisms are changed (Rosenberg, Bonsdorff and Karlson, 2002).

Multiple anthropogenic disturbances can occur simultaneously and in some cases act synergistically, ranging in spatial and temporal scale, and have consequences for the marine environment, such as degradation of habitats and decline in species richness and abundance (Dayton *et al.*, 1995; Blaber *et al.*, 2000). Coastal regions are known for high species richness and their important function as nurseries for a number of marine species (Blaber *et al.*, 2000; Sandström *et al.*, 2005). Habitat forming species in the Skagerrak’s coastal environments include seagrass, mussel reefs and large brown algae, important providers of shelter, and spawning and feeding grounds for fish. Habitat forming vegetation also stabilise sea beds, and counteract bed erosion by decreasing the motion of currents (Nyqvist *et al.*, 2009). They are especially important for demersal spawners (organisms who deposits eggs on substrates), including many fish species which are commercially important. Thus, availability and quality of these habitats are highly valuable not only from an ecological perspective but also from a socio-economic perspective. Finally, as with many other marine species, coral reefs and seagrass distribution and abundance are declining due to anthropogenic activities (Pihl *et al.*, 2006).

2.3. Marine Protected Areas

There are three main categories of MPAs present on the west coast, including one type of national park, and multiple types of nature reserves and Natura 2000 protected areas. Figure 2 outlines the different categories, their sub-types of protection, and the associated international conventions, which include some of the MPA types.

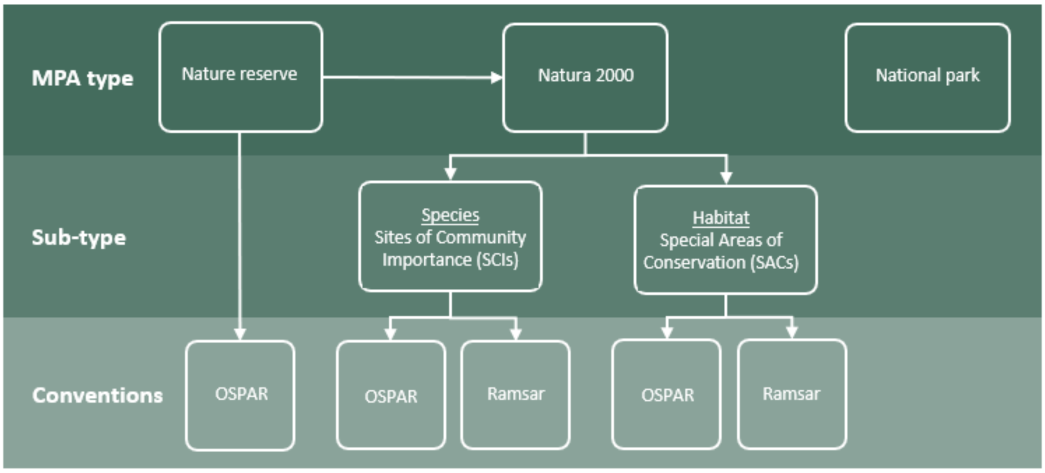


Figure 2. Diagram of MPA categories and their sub-types. Ramsar and OSPAR are two conventions ratified by Sweden and some of the MPAs in the study area are included in their management programmes.

2.3.1. National park

There is currently only one strictly marine national park in Sweden (Kosterhavet national park), located outside the northern coast of Västra Götaland county (Swedish Agency for Marine and Water Management, 2018). National parks aim to protect large-scale areas of specific landscape types with particularly high conservation values, as well as preserving their natural states for future generations (Swedish Environmental Protection Agency, 2020a). In a national park, the land is owned by the state and active land management is only performed in areas which have been subject to traditional management for a long period of time. Specific regulations vary between different national parks because variations are typically based on landscape characteristics and conservation values. For national parks that include marine or limnic landscapes, regulations may impact fishing activities by banning (Swedish Agency for Marine and Water Management, no date):

- specific species being fished
- specific fishing gears being used
- fishing in specific areas and/or during specific time periods (periodically or continuously)
- admission to specific areas and/or during specific time periods (periodically or continuously)

However, in Kosterhavet national park, the destructive fishing method bottom trawling is allowed, causing deprivation of high conservation values (Swedish Agency for Marine and Water Management, 2018). The process of establishing a national park involves many stakeholders, including government agencies, municipalities, county administrative boards, NGOs, residents, and the commercial sector (Swedish Environmental Protection Agency, 2015). The process stretches over several years with the Swedish parliament making the final decision (Swedish Environmental Protection Agency, 2015).

2.3.2. Nature reserve

Nature reserves are a more common type of MPA that is less time-consuming to establish and can be inferred on smaller spatial scales than national parks. Nature reserves can be established to protect both terrestrial and marine environments at a wide range of scales. The objectives of nature reserves are often to protect specific species or habitats, or preserving biodiversity in areas with special conservation values, or to protect, restore and create habitats for species with high conservation values (Swedish Environmental Protection Agency, 2010). In Sweden, there are over 5,000 nature reserves and 94 of these are marine (Swedish Agency for Marine and Water Management, 2017; Statistics Sweden, 2020), of which 32 are located on the west coast. Regulations may differ between individual reserves, but like national parks, they may include restrictions on fishing and other types of anthropogenic activities affecting marine and coastal habitats. Examples of restrictions include banning (Swedish Environmental Protection Agency, 2007):

- dredging (the process of removing bottom substrate due to e.g., pollution)
- anchoring (may be site-specific in the nature reserve and/or time-restricted to specific periods and/or lengths
- boat traffic (speed-limitations or prohibition from passing specific routes)

- new constructions or modification of existing constructions

There might be several stakeholders involved in the process of establishing a new nature reserve. However, the final decision is made by either a county administrative board or a municipality, making the decision-chain shorter and less time-consuming than with national parks (Swedish Environmental Protection Agency, 2007).

2.3.3. Natura 2000

Already established nature reserves can be included in a European network called Natura 2000. The network includes sites with species and/or habitats considered to have high conservation values, and to be unique to a particular region within the European Union (EU) member state (Mézard, Sundseth and Wegefelt, 2008). Depending on the objectives of the protection, there are two types of Natura 2000 sites: 1) Special Protection Areas (SPAs) are sites pertaining to the Birds Directive aiming at protecting breeding and resting habitats important for threatened bird species and migratory bird species (European Commission, 2020b); and 2) Special Areas of Conservation (SAC) are sites pertaining to the Habitats Directive which includes rare habitats, plants, and animal species with high conservation values (European Commission, 2020b). Member states continuously propose sites to be designated as SPAs and/or SACs. Once a site has been proposed, the member state must incorporate a long-term plan for the sustainable management of the site and implement measures to preserve and restore ecosystem components, if necessary. The proposal is processed by an expert panel during seminars aided by the European Environment Agency, with the purpose of ensuring that the member states propose sites of adequate conservation value.

As of 2019 there were 4,539 Natura 2000 sites registered in Sweden (Statistics Sweden, 2019). Only 61 of these are located on the west coast of Sweden and include marine environments. Earlier mentioned restrictions for national parks and nature reserves may also apply for Natura 2000 sites. In addition to national regulations, Sweden must adhere to the Birds Directive and the Habitats Directive which can imply stricter measures to meet the objectives (European Commission, 2007).

2.3.4. OSPAR

In addition to the EU-lead Natura 2000 network, Sweden has ratified two international conventions regarding the protection of marine environments – OSPAR and Ramsar. Both programs promote cooperation between states to achieve sustainable use of our shared marine and aquatic environments and ensure that they obtain good environmental status.

OSPAR (a fusion of the Oslo-Paris conventions) is a regional convention aiming at protecting marine environments in the North-East Atlantic sea, including the Skagerrak and parts of the Kattegat (OSPAR Commission, 2006). The work programme consists of five schemes of which one focus is to protect valuable marine and coastal areas to promote biodiversity and conserve important habitats. Marine sites with high conservation values are selected by each nation and then enrolled in the program, following monitoring and assessment schemes to track the condition of the protected area and ensure that measurements are implemented to achieve a good environmental status. There are 10 sites in Sweden enrolled in the OSPAR programme (all are Natura 2000 sites located on the west coast); two of these are also nature reserves (OSPAR Commission, 2020). Guidelines on how to manage the OSPAR sites are undertaken by the OSPAR Commission, who generate decisions (legally binding for all member states and must be incorporated into national law), recommendations, and agreements (neither legally binding).

2.3.5. Ramsar

Ramsar is an international convention aiming at protecting valuable wetlands and aquatic environments including shallow marine environments (UNESCO, 1971). These areas provide humans with important ecosystem services such as water purification, carbon sequestration and regulation of water flows (Ramsar Convention Secretariat, 2016). Migratory bird species and many fish species use these sites for resting, nesting or as nurseries, signifying their importance for biodiversity. As these environments are subject to high anthropogenic disturbance due to historical land use change, dredging, and implications of climate change, the Ramsar convention is an important tool to enhance the quality of our marine and aquatic environments and reassure a sustainable development (Ramsar Convention Secretariat, 2016). Climate change induces changed weather patterns with increasing droughts in some regions and more frequent events of heavy precipitation in others (Ramsar Convention Secretariat, 2002). This will adversely affect the ecological attributes and functioning of wetlands and impair sustainable use of the services they provide. The contracting parties are obligated to select at least one site to enrol in the programme and in the context of global conservation efforts, the selected site(s) must be of significant value. Sweden has enrolled 68 sites and seven of these are marine environments located on the west coast (Ramsar Convention Secretariat, 2015). All Ramsar sites are also Natura 2000 sites, strengthening the protection of the sites.

2.3.6. Shoreline protection

In addition to the above mentioned MPA types, the entire Swedish coastline is subject to a national protection called “the shoreline protection” (Boverket and

Naturvårdsverket, 2010). It includes the marine and terrestrial environment extending 100 m seaward and 100 m landward from the shoreline (the county administrative board have the authority to expand the area of protection of up to 300 m; Boverket and Naturvårdsverket, 2010). The shoreline protection was established in the 1950s with the intent to secure long-term public access to coastal areas and ensure good environmental conditions for species, both animals and plants, inhabiting both terrestrial and marine coastal environments (Boverket and Naturvårdsverket, 2010). The shoreline protection prohibits ground excavations, as well as establishing new buildings and modifying old ones, in a way that would severely deteriorate living conditions for species present in the area (Boverket and Naturvårdsverket, 2010).

However, municipalities and county administrative boards are authorized to make exemptions if special reasons are presented and if the purpose of the shoreline protection is not impeded (Boverket and Naturvårdsverket, 2010). They can also repeal specific areas from the shoreline protection, enabling exploitation in these areas without seeking approval of exemption (Boverket and Naturvårdsverket, 2010). Reports comprising data on granted and rejected applications of exemptions from the Shoreline protection is compiled by the Swedish Environmental Protection Agency yearly and show a widespread acceptance of exemptions (Swedish Environmental Protection Agency, 2018). During 2019, 568 applications were granted by county administrative boards and 5,055 by municipalities (Swedish Environmental Protection Agency, 2020b). While the numbers are high for 2019, the year is no exception as granted application rates has steadily increased since 2011 (Swedish Environmental Protection Agency, 2020b), discerning a trend of neglecting the very foundation of which the shoreline protection was established for – ensuring good environmental conditions for species inhabiting coastal areas.

3. Methods

3.1. Habitat maps

For this study, habitat distribution raster data from Fredriksson, Erlandsson and Bergström (2020), with a resolution of 250 m x 250 m, was used. Data was provided by the Swedish University of Agricultural Sciences (SLU) and consists of predicted distributions of nursery habitats for 21 species (18 fishes and 3 crustaceans; Table 1) in areas with a water depth of <30m. Four of the species: the European eel (critically endangered), pollock (critically endangered), Atlantic cod (vulnerable) and whiting (vulnerable), are threatened and red listed species in Sweden (SLU Artdatabanken, 2020). The red list is a classification system developed by the IUCN for assessing conservation status and extinction risk (IUCN Species Survival Commission (SSC), 2012) (Figure 3).

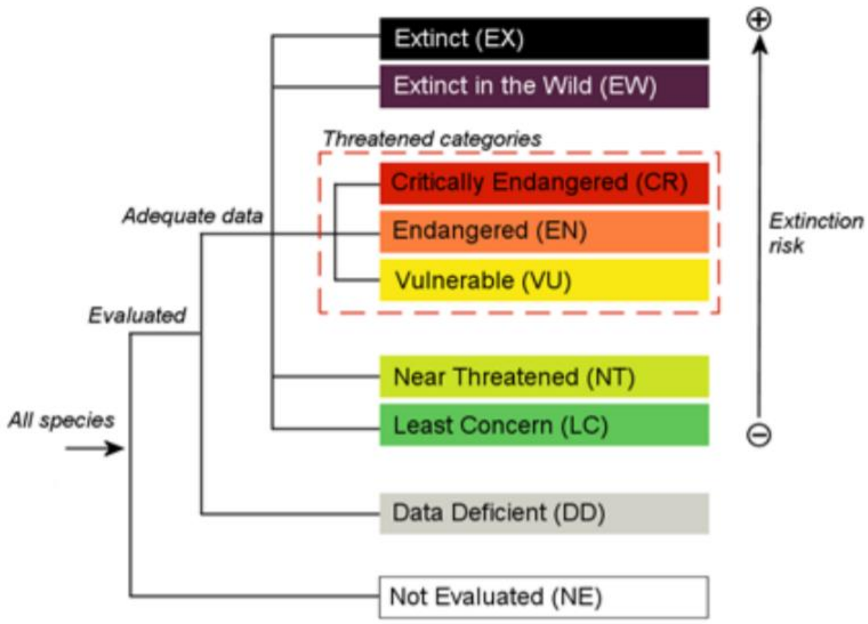


Figure 3. IUCN classification system for assessing extinction risk of species (IUCN Species Survival Commission (SSC), 2012).

The four endangered species, listed above, are also commercially important species for the Swedish fishing industry, together with the European lobster, saithe, brown crab, European plaice, European flounder, brill, and common sole (SLU, 2021). This subset of species is thus described in more detail in the subsequent analyses and discussion. The other species analysed in this study are common species in the Skagerrak, with important roles in the ecosystem, especially in the shallow areas.

Table 1. List of species used in the analysis. Frequency of occurrence refers to the species presence in the total fishing samples along the entire west coast. The Atlantic cod and European plaice were divided into two classes as there was a distinct age difference in the samples.

Species	**Frequency of occurrence (%)**
European shore crab (*Carcinus maenas*)	*89*
Goldsinny wrasse (*Ctenolabrus rupestris*)	*66*
European eel (*Anguilla anguilla*)	*57*
Viviparous eelpout (*Zoarces viviparus*)	*53*
Corkwing wrasse (*Symphodus melops*)	*49*
Atlantic cod (*Gadus morhua*) >20 cm	*44*
Black goby (*Gobius niger*)	*39*
European flounder (*Platichthys flesus*)	*38*
Atlantic cod (*Gadus morhua*) ≤20 cm	*31*
European plaice (*Pleuronectes platessa*) ≤13 cm	*20*
Longspined bullhead (*Taurulus bubalis*)	*16*
Saithe (*Pollachius virens*)	*16*
Common sole (*Solea solea*)	*14*
Whiting (*Merlangius merlangus*)	*14*
Brown crab (*Cancer pagurus*)	*6*
Fivebeard rockling (*Ciliata mustela*)	*5*
European plaice (*Pleuronectes platessa*) >13 cm	*4*
Ballan wrasse (*Labris bergylta*)	*4*
Brill (*Scophthalmus rhombus*)	*3*
Rock cook (*Centrolabrus exoletus*)	*3*
Pollock (*Pollachius pollachius*)	*2*
Two-spotted goby (*Gobiusculus flavescens*)	*2*
European lobster (*Homarus gammarus*)	*1*

The habitat distribution raster data are part of the ongoing project “National marine mapping”, operated by the Swedish Agency for Marine and Water Management (HaV, 2019). The project aims to produce distribution maps of benthic habitats for the entire coastal area of Sweden. The habitat data maps of fish and crustaceans were produced by SLU during the autumn of 2020 using monitoring data from fish samples of juveniles with fyke nets, carried out in May-Sept between 2002-2017.

A total of 5,146 samples along the Swedish west coast were obtained, and presence and abundance of juveniles were recorded (Figure 4). Of the 5,146 samples, 2,272 were in the coastal areas of Västra Götaland county.

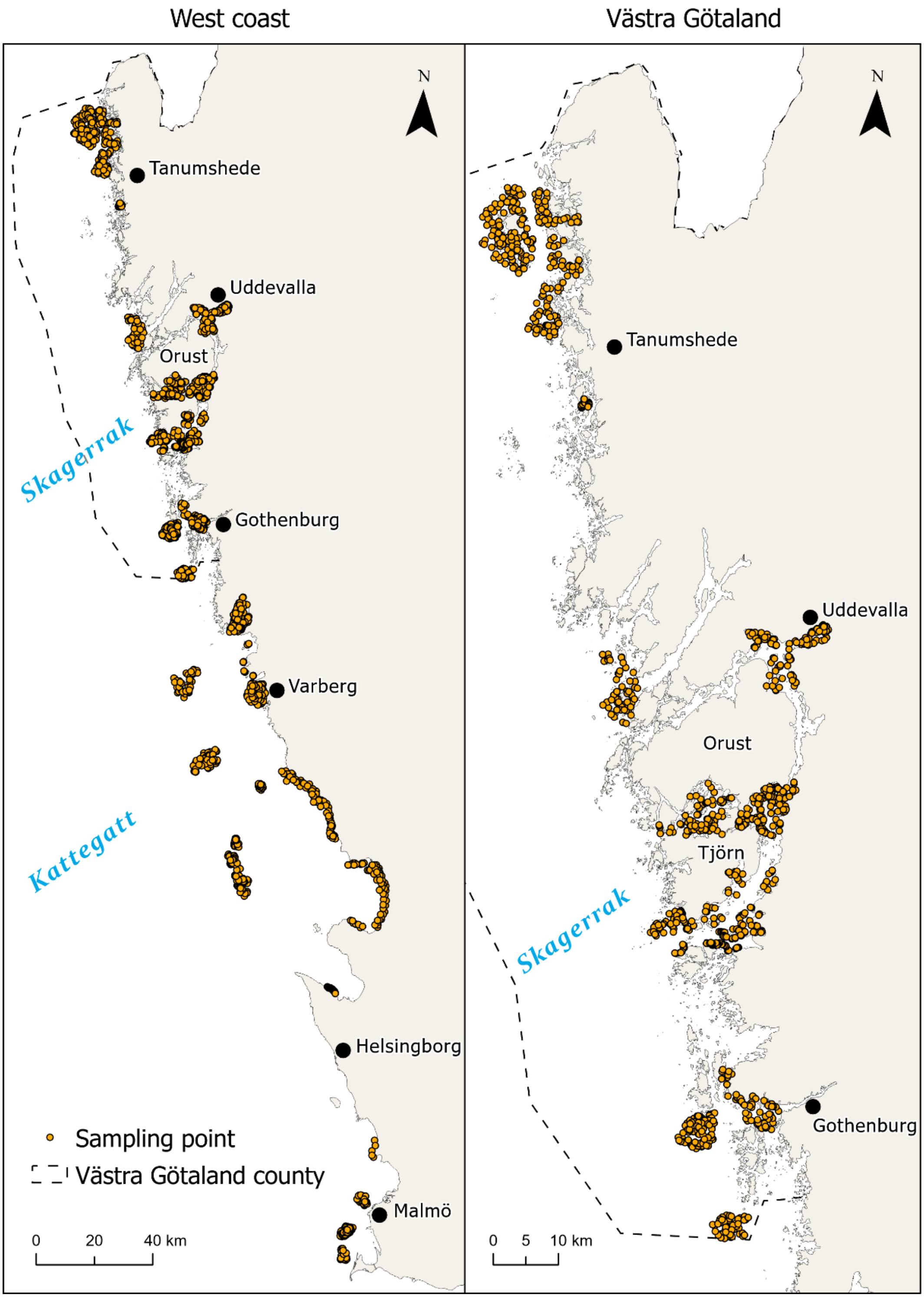


Figure 4. Map of juvenile fish and crustacean sampling sites. Fishing took place in May-Sept between 2002-2017.

The probability of the presence and distribution of juvenile habitats in areas between sampling points were derived by Fredriksson, Erlandsson and Bergström (2020), using spatial statistical modelling where the relationship between each species and five environmental variables (depth, wave exposure, rugosity, bottom temperature, and salinity) were analysed. A suitable habitat does not only require certain physical attributes but needs to meet environmental conditions optimal for the species. For example, ballan wrasse and corking wrasse (two species belonging to the family *Labridae*) both require habitats in shallow areas with rocky bottoms, but their physiological requirements differ. For ballan wrasse, rugosity is the most important environmental factor, affecting the distribution of suitable habitats, while for corking wrasse, temperature is the most important factor (Fredriksson, Erlandsson and Bergström, 2020).

The statistical modelling resulted in a habitat distribution raster dataset with cell values ranging between 0-1000 (probability of presence 0-100%) (Fredriksson, Erlandsson and Bergström, 2020). The authors tested model performance by evaluating AUC (Area Under Curve; Hosmer and Lemeshow 2013) and by the sensitivity and specificity values (the proportion of correctly predicted presences and absences). Thereafter, the authors calculated a cut-off value for each species to reclassify the habitat distribution into two classes: presence and absence (Fredriksson, Erlandsson and Bergström, 2020). They determined the cut-off value for each species using the True Skill Statistic (Allouche, Tsoar and Kadmon, 2006), where the cut-off value indicates the probability threshold where the sum of sensitivity and specificity is greatest. The cut-off values deriving from the work done by Fredriksson, Erlandsson and Bergström (2020), was used in this study to reclassify the habitat distribution into two classes: suitable and non-suitable habitat, using ESRI ArcGIS® Pro™ 2.5.0. In total, 23 suitable habitat maps were produced for 19 species and for two species with two size classes each, totalling 21 species.

3.2. Calculating ecological representativity

Ecological representativity is the proportion (%) of habitat that is protected. The suitable habitat data were used to estimate both the representativity of each species separately in the MPA network and all species combined. Maps of MPAs on the Swedish west coast was provided by the Swedish Agency for Marine and Water Management. The data includes MPAs established as of 2019. Thus, MPAs implemented during 2020 and later, are not included in the dataset and subsequently not analysed. The current MPA network on the west coast and the different MPA categories are displayed in Figure 5. The total area along the entire west coast currently under protection is ~6,310 km^2, of which ~1,375 km^2 is in Västra Götaland county. No distinction was made between different MPA categories in the subsequent analysis, as the representativity of the combined MPA coverage was analysed for each respective species.

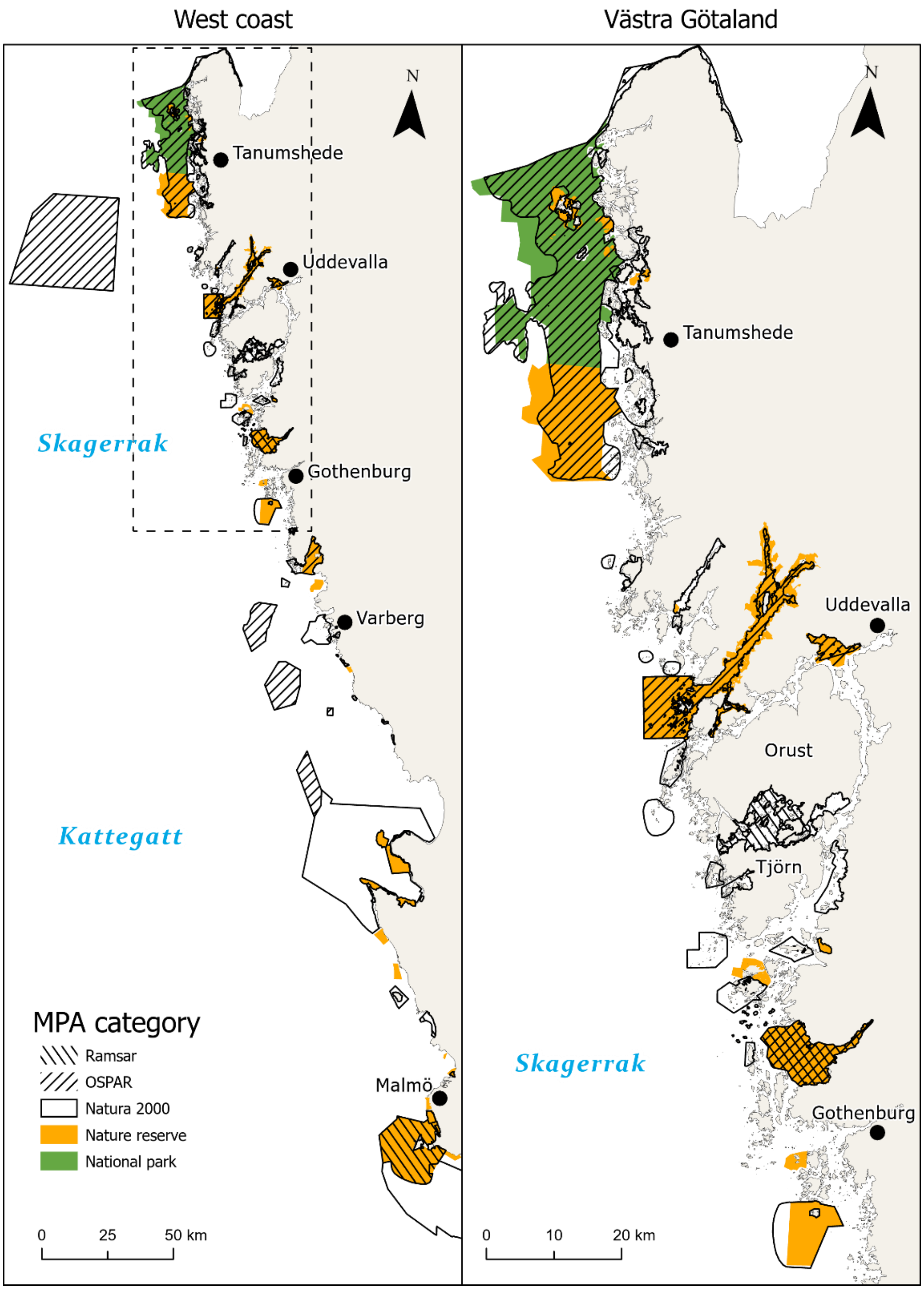


Figure 5. Maps of MPA categories and sites included in the Ramsar and OSPAR conventions. The dashed box indicates the extent of the right map, showing MPAs in Västra Götaland county.

The representativity of each species was calculated by comparing total habitat area (km^2) with habitat area (km^2) protected by MPAs, giving the proportion of protected habitats (%). A conceptual model of the approach is illustrated in Figure 6. The ecological representativity of the MPA network was estimated by calculating the mean representativity of all species.

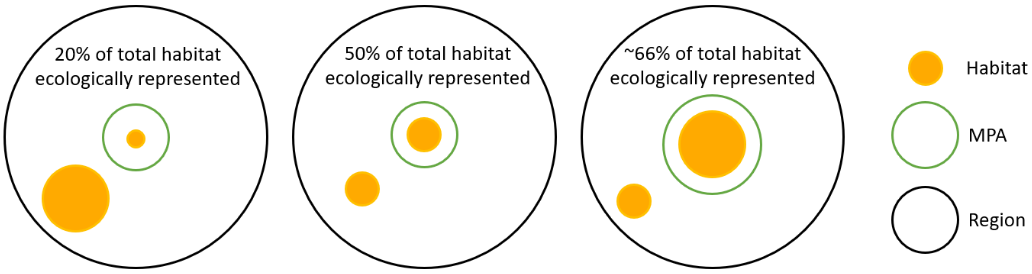


Figure 6. A conceptual model visualising the estimation of species representativity in MPAs.

3.3. Species richness and pressure maps

Using cell statistics, number of overlapping species habitats were calculated, producing a species richness map of the sub-set of species selected for this study. To identify areas subjected to high anthropogenic pressure and allow comparisons with the species richness map, a dataset from Törnqvist *et al.* (2020) was used. The dataset was produced for the Marine Strategy Framework Directive which is supervised by the Swedish Agency for Marine and Water Management. The framework aims at collecting, processing, and modelling physical disturbances, focusing on impact on connectivity, sea floor morphology and the hydrographical system, caused by anthropogenic activities in Swedish coastal environments (Törnqvist *et al.*, 2020). As part of this framework, Metria AB produced a dataset with quantified pressures classified into environmental impact rankings between 1 and 5 (low to high). The resolution of the dataset was 10 x 10 m and considers a vertical water depth limit of 15 m. The input data consisted of historical and contemporary orthophotos, registries, AIS (Automatic Identification System) data, satellite imagery, available geographical data and metadata retrieved from literature studies. The impact scale is, therefore, a compilation of assessments made by experts, using remote sensing analysis and datasets from previous studies.

The process of producing the impact dataset involved three steps (Törnqvist *et al.*, 2020). First, different pressures were identified and the feasibility of mapping these through a geographical information system were explored. Models of indirect pressures from shipping traffic were designed to estimate the extent and degree of impact, using information from observed traffic intensity, ship attributes, AIS-transponder signals and by analysing satellite imagery. Indirect pressures include bottom and shoreline erosion due to increased wave activity and deterioration of bottom habitat caused by anchoring, dredging, or resuspension from propellers.

Second, available datasets of pressures were collected and compiled with modelled pressures. Changes in the shoreline were studied by comparing historical orthophotos with contemporary orthophotos, focusing on detecting artificial landfills, excavations, and clearance of reed. Anthropogenic structures bordering the sea (buildings, bridges, piers, jetties etc.) were mapped, and objects absent in the available datasets but detected in the orthophotos, were digitalised. Dredged areas and dumping sites were mapped by discerning dredging vessels and their movement, from AIS data.

Finally, the pressure on bottom habitats was modelled by including impacts on connectivity, sea floor morphology, and the hydrographical system. In this way, the sensitivity of the abiotic conditions in the environment were considered and the cumulative effects of multiple pressures was identified. Connectivity impacts included impeded water exchange and impairment of species abilities to move in the area due to altered water flows, noise pollution or physical obstacles. Morphological impacts included changes in sediment composition and on the physical structure of the seabed. Hydrographic impacts include alteration in intensity and velocity of waves and water currents, subsequently affecting the habitats wave exposure. Together, these impacts affect habitat suitability for species present in the impact area, as the environmental conditions required by the species are altered. Furthermore, this may alter species composition and changes in the dynamics of the trophic system. The final data included three impact categories, based on connectivity, sea floor morphology and the hydrographical system. The cell values ranged between 1-5 (low-high) indicating the cumulative environmental impact for each category.

Previous sections describes the production of pressure maps performed by Törnqvist *et al.* (2020). The following section describes how the pressure maps have been processed and used in this study. To identify areas subjected to high anthropogenic pressure in Västra Götaland and allow comparison with the species richness map, the three pressure categories were summarised into one, resulting in cell values ranging between 1-15 (low-high). Two different pressure maps were produced for comparison with the species richness maps, the first map showed the raw summarised pressure data (10 x 10 m resolution), and the second map showed the data resampled to the same cell size as the species data (250 x 250 m), using block statistics and snapping the cell output to the species richness cells. The resampled map allowed for direct comparison between the species richness data and the summarised pressure data, while the map showing the raw summarised pressure data gave a more accurate picture of the spatial distribution of pressures.

3.4. MPA evaluation and identifying areas suited for expansion

Evaluation of the effectiveness of the existing network and identification of expansion opportunities in the Skagerrak, was performed using Marxan, a freely available conservation planning-tool used by organisations and institutions worldwide, to evaluate and design efficient networks of protected areas (Ardron, Possingham and Klein, 2010). The software was first developed to address terrestrial conservation planning in Australia (Ball, 2000), but has since been enhanced and is now used for conversation planning in all types of environments. With Marxan, decision makers can solve complex issues targeting multiple features and answer questions of where to establish nature reserves at minimum costs. For the reserve solution to be efficient, Marxan considers the conservation features complementarity meaning protected areas should complement each other in what species they protect so that redundancy (the same species being protected in all areas) is avoided. The tool can help both in identifying new areas of protection and evaluate if an existing network of protected areas is sufficient.

3.4.1. Planning units, conservation features and status

Marxan uses planning units to find the best reserve solution. Planning units are smaller regions of the total analysed area and are defined by for example, cell-size, grids, or ecological features such as water bodies or habitats. All planning units are assigned to the conservation features that the user wishes to protect. In this study, the conservation features are the 21 species listed in Table 1 and the planning units are their modelled habitats represented by individual pixels (250 m x 250 m). The total number of planning units (habitat cells) are 26 360. A status can be set to each unique planning unit to inform Marxan if the planning unit is inside or outside of an existing reserve. This setting is important as it helps to evaluate the existing network of protected areas (setting the status “not inside a reserve”) or if planning units located inside existing reserves must be included (as it is unrealistic that officials will make changes in reserve extent that excludes areas already protected).

3.4.2. Pressure as a cost metric

When selecting sites for protection, it is important to take possible pressures into consideration. For example, in marine conservation planning, pressures can be overfishing or changes in the morphology and/or hydrography (see section 2.2.2). In Marxan, the different levels of pressure endured by the habitats can be used as weights, enabling prioritising schemes as Marxan strives to deliver the most cost-effective solution. By using the *cost-function* in Marxan, the user can set different weights to each unique planning unit. The cost can reflect different types of economic, social, or ecological weights. In this study, the cost function was used to prioritise habitats with high species richness and high pressure. The resampled summarised pressure map was therefore used as a cost matrix, assigning each planning unit a cost ranging between 0-15 (low-high). This approach enabled Marxan to prioritise planning units according to biodiversity targets and the degree of experienced pressure for each planning unit. Species subjected to high pressure were considered important to prioritise and the cost was therefore set to 1 for planning units where the summarised pressure was 15, 2 for planning units with a summarised pressure of 14, and so on. Since Marxan always aim to provide the most cost-efficient solution, setting a low cost to planning units under high pressure instructs Marxan to prioritise these habitats as they are less costly to protect.

3.4.3. Conservation target, SPF, BLM, and repeated runs

A target can be set to instruct Marxan what proportion of the planning units per conservation feature must be included in the final reserve solution, for example 40 %. In addition to this, a Species Penalty Factor (SPF) can be added to different conservation feature-types. The SPF informs Marxan that it is more important to meet the conservation target for some conservation features than others and the model will therefore put greater emphasis on these species when opting for the most efficient reserve solution. This enables a prioritisation between conservation features which can be useful if, for instance, some of the conservation features are threatened, or if they are of greater social or economic significance.

Another important setting is the Boundary Length Modifier (BLM). It instructs Marxan on how much emphasis should be placed on making the network of reserves fragmented or compact, for example, “many small reserves” compared to “a few large reserves”. A low BLM enables Marxan to put greater emphasis on the cost, sacrificing compactness for more fragmented reserves to minimise the total cost. In contrast, a high BLM instructs Marxan to put greater emphasis on minimising number of reserves irrespective of the cost. Thus, setting the BLM will have a great impact on the final reserve solution and much consideration must therefore be given to this factor.

In this study, the BLM was set to 0 during experimental runs when evaluating performance of SPF, target levels and status (planning units inside or outside of existing reserves). Setting the BLM to 0 enabled Marxan to focus on achieving the targets at the lowest cost without consideration of reserve compactness. Originating from the best model performance, a method derived from Stewart and Possingham (2005) was used to deduce the most cost-efficient BLM. Using the same parameters for status, SPF and target, a sequence of twelve BLM values ranging from 0.0001 up to 1,000,000, using a fixed multiplier of 10, were tested. From each round, total boundary length of the reserve system and average cost of all solutions, was derived from the solution Marxan considered to be the most cost-efficient. Records of these values for each BLM-test were plotted in a diagram to find the BLM value generating minimum amount of reserve area to the lowest cost. This BLM value was further used to test model performance.

For each change in parameter (SPF, target, status, BLM), Marxan was instructed to execute 10,000 repeated runs. Each run is a proposed solution, meaning Marxan attempts to maximise the objective function using the iterative improvement and simulated annealing algorithms, which is then repeated iteratively. The objective function considers:

1. The number of conservation features and in which planning unit each occur.
2. The cost of protecting each planning unit.
3. The SPF and target for each conservation feature.
4. The pairwise shared boundary length between each planning unit.

After Marxan finished the 10,000 repeated runs, it calculated which of the 10,000 solutions gave the best conservation configuration. In other words, the most cost-efficient solution to reach the set conservation targets. Another important output Marxan produces is the selection frequency for each planning unit. With this information, the user can identify key planning units. The more frequently a planning unit is selected (during the 10,000 runs), the more important that planning unit is to reach the proposed targets for the reserve network. Planning units with a high selection frequency are likely to include multiple species or rare species, without which it is difficult to achieve the proposed targets. The combination of presenting both the best conservation solution and the selection frequency of planning units, is recommended by Ardron, Possingham and Klein, 2010. Interpreted individually, the best conservation solution provides the most cost-efficient configuration to meet the targets but since this solution is only based on one of the 10,000 runs, it is highly subjected to error as habitats important to protect might be disregarded in this very solution. The selection frequency provides the user with information on planning units' importance for an efficient network of protected areas and since the output utilises information from all 10,000 runs, it is less sensitive to errors.

3.4.4. Conservation solutions

The analysis resulted in two alternative solutions, one "unbiased" and one "biased". In the biased solution, Marxan was forced to include already protected planning units in the final solution. With this setting, Marxan presumably used already protected planning units as starting points and built on from them. In the unbiased solution, the status was set to "not inside a reserve" for all planning units, enabling Marxan to choose freely among the planning units, including those inside existing reserves. The analysis was divided into two steps (Figure 7) to evaluate model performance and deduce which settings returned the best result:

1) Two different target levels and two different SPF-settings were tested for both the unbiased and biased solution. BLM was excluded by setting it to zero meaning no emphasis was made on optimising the reserve compactness. Model performance was measured by the number of species for which targets were successfully met (Table 2).
2) Assuming from the best target and SPF-setting, a sequence of twelve BLM values were tested for both the unbiased and biased solution, to find the most cost-efficient BLM (Figure 8 and 9). The best BLM value was the turning point, for which after this value, the increase in cost is greater than the decrease in total reserve boundary length.

		Unbiased	Biased	40%	50%	SPF 1	SPF 2-4-8	BLM 0	BLM testing	BLM 0.01
Step 1	Table 2	x		x		x		x		
	Table 2		x	x		x		x		
	Table 2	x			x	x		x		
	Table 2		x		x	x		x		
	Table 2	x		x			x	x		
	Table 2		x	x			x	x		
	Table 2	x			x		x	x		
	Table 2		x		x		x	x		
		↓	↓		↓		↓		↓	
Step 2	Figure 8	x			x		x		x	
	Figure 9		x		x		x		x	
		↓	↓		↓		↓	↓		
Selection frequency	Figure 14 (left panel)	x			x		x	x		
	Figure 14 (right panel)		x		x		x	x		
		↓	↓		↓		↓			↓
Best solution	Figure 15 (left panel)	x			x		x			x
	Figure 15 (right panel)		x		x		x			x

Figure 7. Flow chart of the two steps taken to evaluate model performance and deduce which settings returned the best result. The figure showing selection frequency is based on a 50% target and a non-uniform SPF (2-4-8) with no emphasis on compactness (BLM = 0). The figure showing the best solution is based on 50% target, a non-uniform SPF (2-4-8) and a BLM value of 0.01.

The different SPF-settings tested were a) a uniform where the SPF was the same for all species meaning they are all equally important to protect, b) a non-uniform SPF where a fixed multiplier of two was used to rank the importance of the species. For the commercially important species (European lobster, saithe, brown crab, European plaice, European flounder, brill, and common sole), the SPF was set to four and for the endangered species (the European eel, pollock, Atlantic cod, and whiting) the SPF was set to eight, the SPF for the remaining species was set to two. The motivation for testing two different SPF-settings was that species of commercial interest and species at higher risk of extinction should be prioritised.

Two target levels, 40% and 50%, were used to test conservation capacity and evaluate model performance. The target levels were based on results from the calculated ecological representativity in section 3.3.2. To deduce which of the two alternatives (the unbiased or biased) was the most efficient solution for the MPA network in the Skagerrak, a comparison between the total reserve area in each solution was measured. The one with the lowest area was considered the most efficient, since the least possible area is required to satisfy the protection target of the species. Furthermore, the total reserve area in the two conservation solutions was compared to the total reserve area in the current MPA network, facilitating an evaluation of its effectiveness. Finally, expansion of existing MPAs and establishment of new MPAs were proposed by visually identifying clusters of planning units in the best conservation solution.

3.4.5. Evaluating model performance

For the SPF parameter, the best performance was achieved by using a non-uniform SPF (2-4-8; Table 2). There was no difference in model performance for the unbiased or biased settings, using non-uniform SPF, as both solutions delivered satisfying results for both target levels. There was no problem in satisfying both targets for the biased solution, irrespective of SPF. However, the success rate for the unbiased solution was inferior with two species (saithe and pollock) missing the 40% target and three species (the European eel, pollock, and two-spotted goby) missing the 50% target. The model performed best using a biased solution with a non-uniform SPF. As the model succeeded in reaching the highest target of 50% for all species, this target and the non-uniform SPF were used in the forthcoming analysis.

The mean ecological representativity for the Skagerrak was 43% (Table 3) but as the aim of this study was to improve the current network of MPAs, the modelling exercise aimed for a target of 50%. Several species, including commercially important and endangered species, had an ecological representativity of <40%, and therefore the feasibility of enhancing their representativity to at least 40% was analysed.

The most cost-efficient BLM value was 0.01 for both the unbiased and biased solution as the turning point, for which after this value, the increase in cost is greater than the decrease in total reserve boundary length (Figure 8 and 9).

Table 2. Results from model calibration to find which settings produced the best conservation solution. The BLM was excluded from the analysis by setting it to zero. Yellow boxes indicates when Marxan failed to achieve targets for species.

	Uniform SPF (1)				**Non-uniform SPF (2-4-8)**			
	Target 40%		Target 50%		Target 40%		Target 50%	
Species	Unbiased	Biased	Unbiased	Biased	Unbiased	Biased	Unbiased	Biased
European shore crab	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*
Goldsinny wrasse	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*
European eel	*yes*	*yes*	*no*	*yes*	*yes*	*yes*	*yes*	*yes*
Viviparous eelpout	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*
Corkwing wrasse	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*
Atlantic cod >20 cm	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*
Black goby	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*
European flounder	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*
Atlantic cod ≤20 cm	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*
European plaice ≤13 cm	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*
Longspined bullhead	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*
Saithe	*no*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*
Common sole	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*
Whiting	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*
Brown crab	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*
Fivebeard rockling	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*
European plaice >13 cm	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*
Ballan wrasse	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*
Brill	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*
Rock cook	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*
Pollock	*no*	*yes*	*no*	*yes*	*yes*	*yes*	*yes*	*yes*
Two-spotted goby	*yes*	*yes*	*no*	*yes*	*yes*	*yes*	*yes*	*yes*
European lobster	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*	*yes*

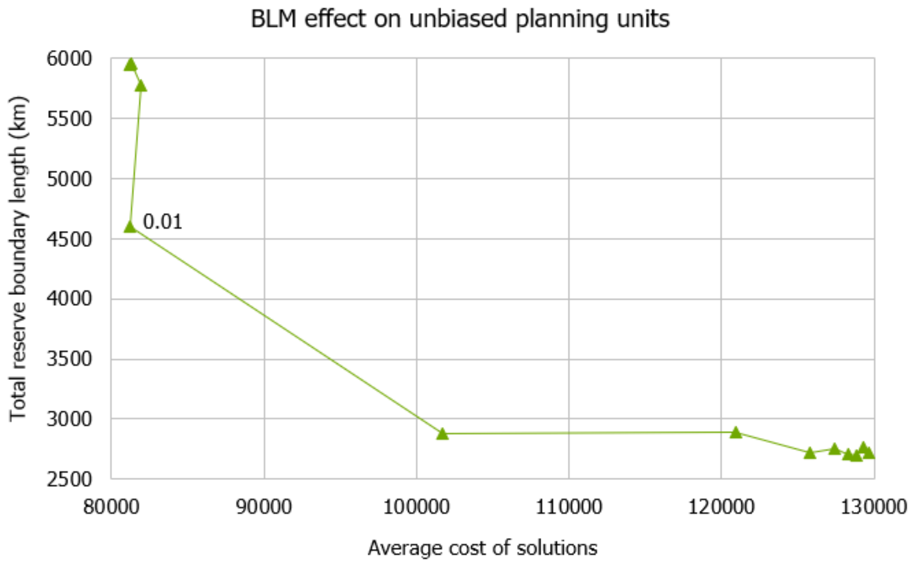


Figure 8. Diagram shows the effect of using different BLM values on total reserve boundary length and average cost of solutions, for the unbiased solution. The result from each round is plotted and the best BLM is 0.01 since succeeding BLM values results in a larger increase in average cost of solutions than decrease in total reserve boundary length.

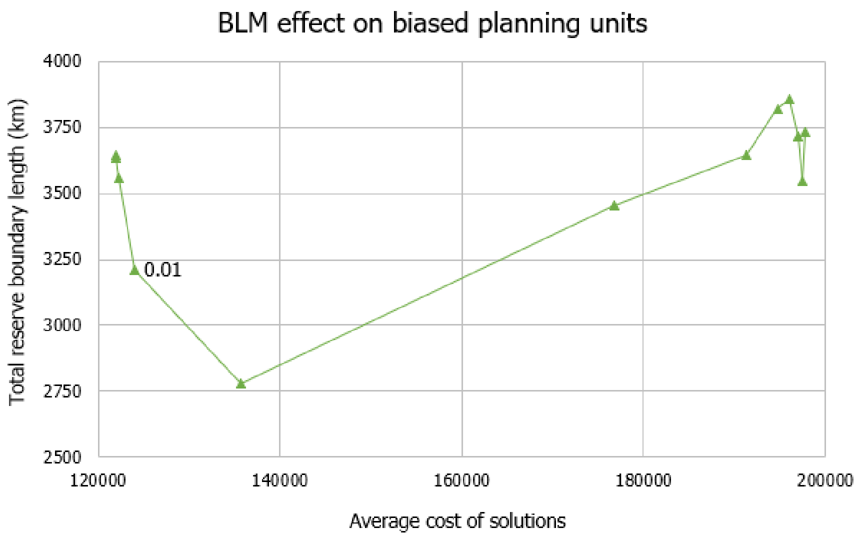


Figure 9. Diagram shows the effect of using different BLM values on total reserve boundary length and average cost of solutions, for the biased solution. The result from each round is plotted and the best BLM is 0.01 as the following BLM value results in a larger increase in average cost of solutions than decrease in total reserve boundary length.

4. Results

4.1. Ecological representativity

The two-spotted goby had the least habitat protected (9%) in the Skagerrak while the Atlantic cod >20 cm had the most habitat protected (55%; Table 3). Along the entire West coast, the longspined bullhead had the most habitat protected (63%) while the European lobster had the least (32%; Table 3). Overall, no trend could be discerned in number of species having more habitat protected in the Skagerrak compared to the entire West coast or vice versa, the share was approximately 50/50. However, for those species having higher ecological representativity in the West coast than in the Skagerrak, there is a larger difference in representativity (Table 3). For example, the two-spotted goby (+34%), the viviparous eelpout (+17%) and the European plaice (+10%; Table 3). The mean ecological representativity, for all species combined, was 45% for the entire west coast and 43% for the Skagerrak. With regards to the EU goal of protecting ≥30% of non-prosperous species and habitats, the target was met for all species when examining the entire west coast. In the Skagerrak, the target was met for all species except for the two-spotted goby with only 9% habitat protected (highlighted with yellow in Table 3).

Table 3. Habitat area (km^2) and ecological representativity (proportion of protected habitats in %) for each species in the Skagerrak and summarized for the entire west coast. The species are listed according to frequency of occurrence in the total sample along the west coast. The yellow box highlights the only species with ecological representativity <30%.

	Total Habitat (km^2)		**Habitat in MPA (km^2)**		**Ecological representativity (%)**	
Species	West coast	Skagerrak	West coast	Skagerrak	West coast	Skagerrak
European shore crab	*1541*	*749*	*623*	*294*	*40%*	*39%*
Goldsinny wrasse	*909*	*652*	*432*	*288*	*47%*	*44%*
European eel	*600*	*297*	*284*	*133*	*47%*	*45%*
Viviparous eelpout	*2189*	*141*	*299*	*51*	*53%*	*36%*
Corkwing wrasse	*580*	*334*	*244*	*136*	*40%*	*41%*
Atlantic cod >20 cm	*566*	*81*	*873*	*44*	*49%*	*55%*
Black goby	*398*	*238*	*139*	*78*	*35%*	*33%*

European flounder	*612*	*241*	*281*	*110*	*48%*	*46%*
Atlantic cod ≤20 cm	*1764*	*882*	*957*	*398*	*44%*	*45%*
European plaice ≤13 cm	*764*	*457*	*318*	*195*	*42%*	*43%*
Longspined bullhead	*566*	*198*	*359*	*108*	*63%*	*54%*
Saithe	*1552*	*1096*	*673*	*503*	*43%*	*46%*
Common sole	*967*	*245*	*1632*	*126*	*49%*	*51%*
Whiting	*3348*	*598*	*379*	*248*	*39%*	*41%*
Brown crab	*2082*	*1035*	*844*	*467*	*41%*	*45%*
Fivebeard rockling	*753*	*358*	*376*	*172*	*50%*	*48%*
European plaice >13 cm	*1559*	*445*	*808*	*186*	*52%*	*42%*
Ballan wrasse	*571*	*447*	*281*	*214*	*49%*	*48%*
Brill	*639*	*34*	*312*	*18*	*49%*	*51%*
Rock cook	*1269*	*547*	*545*	*282*	*43%*	*52%*
Pollock	*1671*	*996*	*653*	*407*	*39%*	*41%*
Two-spotted goby	*1135*	*17*	*491*	*2*	*43%*	*9%*
European lobster	*1918*	*857*	*607*	*328*	*32%*	*38%*

4.2. Species richness vs. pressure

The 23 habitat maps were combined to illustrate species richness (Figure 10) of the sub-set of species selected for this study. Areas with high species richness were found mostly along the coastline and by the fjord inlets near Tjörn and Orust, with especially high values found in the Skagerrak (Figure 10). Within the confinement of the fjords, species richness was low to medium (Figure 10). There were areas found with overall low species richness but of high importance for single species like the European lobster (Figure 10). Maximum number of overlapping habitats was 18, which indicates that there were no areas containing habitats for all 21 species.

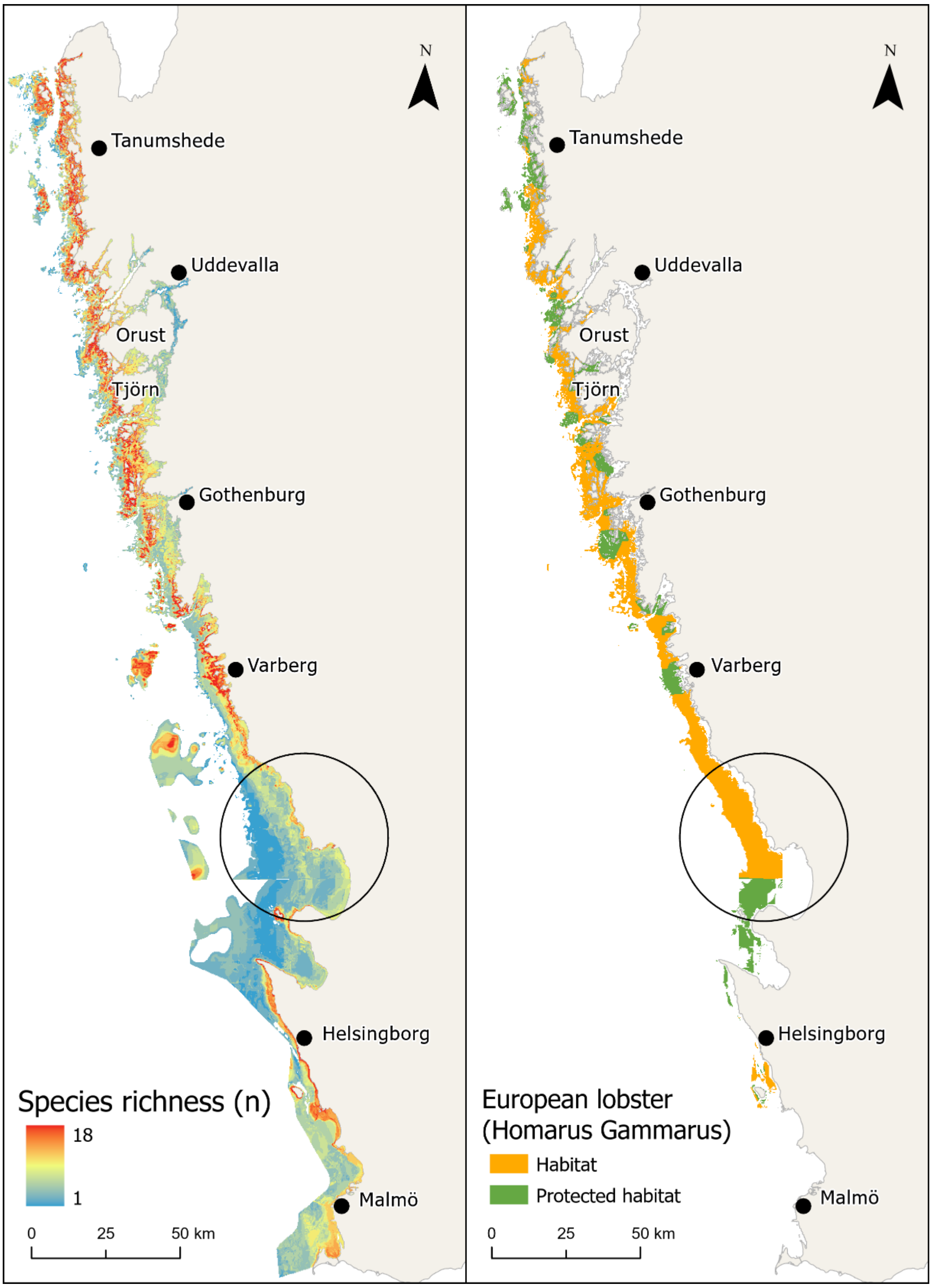


Figure 10. The left panel shows species richness (n≤18). The right panel shows protected and non-protected habitats for the European lobster (Homarus Gammarus). The black circle indicates a region with low species richness but a large extent of non-protected lobster habitat.

In general, pressures were concentrated near shorelines and close to the mainland coast (Figure 11). Species richness was also generally high close to shorelines but tended to concentrate along islands rather than the mainland coastal area (Figure 10). This was particularly apparent in area A, where there was almost no overlap between high species richness and high pressure (Figure 11a). In contrast, area B had overlap between high species richness and high pressure (Figure 11b), implying harsher living conditions for the many species inhabiting these areas. In area C, high species richness was found near islands but mostly along west-facing shorelines, while high pressure was mostly concentrated on the south-facing side of the islands (Figure 11c). High species richness and pressure did, however, overlap around islands located in the north-western part of the area, where a higher species richness was concentrated on the east-facing side of the islands (Figure 11c). Overall, areas where high species richness and the highest pressure overlapped were relatively few along the entire West coast.

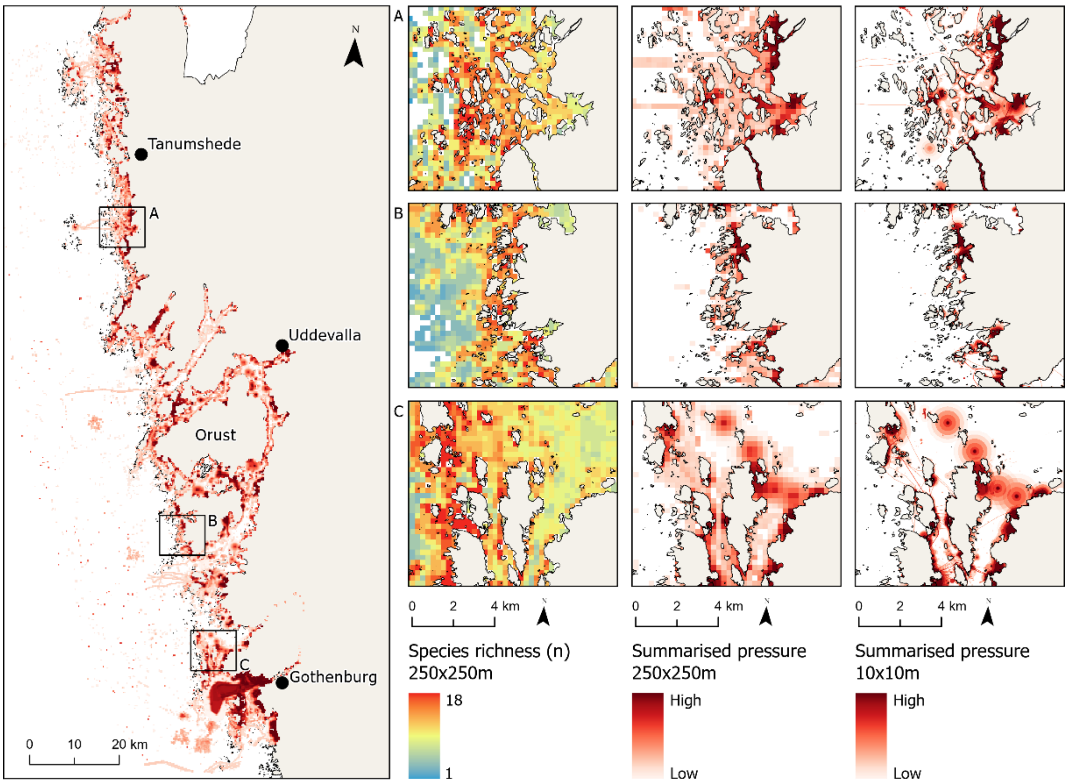


Figure 11. Resampled summarised pressure distribution in Västra Götaland county. Three example areas (box A, B and C) were selected because they exhibit high pressure and medium to high species richness. Both the raw summarised pressure (10 x 10m) and the resampled (250 x 250m) summarised pressure is shown for each example area. The resampled pressure data enables a direct pixel-to-pixel comparison with the species richness data.

Figure 12 and 13 further plot a pixel-by-pixel comparison between endangered and commercially important species and their experienced pressure. Proportion of habitat subjected to different pressure intensities differs between the species.

Pollock (Figure 12) and brown crab (Figure 13) had a large proportion of habitats subjected to low pressure while the European eel (Figure 12) and the European flounder (Figure 13) had a small proportion of habitat under low pressure. Both the European eel and the European flounder only had ~12% of habitat located in no-pressure areas (with current pressure data) and ~11% in areas with the second highest summarised pressure (Figure 12 & 13). Large specimens of Atlantic cod had just over 45% of its habitat in no pressure areas and smaller juveniles just under 35% (Figure 12). As the summarised pressure increases, proportion of habitat decreases for both small and large Atlantic cod, with an exemption for the small Atlantic cod where proportion of habitat increases slightly in areas with the second highest summarised pressure (Figure 12). In general, all species display a dramatic decrease in habitat proportion from zero pressure to areas with the lowest pressure class (Figure 12 & 13). Areas with a summarised pressure of three seems to be a cluster for high species richness of the sub-set of species selected for this study, as almost all species exhibit a temporary peak in habitat proportion (Figure 12 & 13).

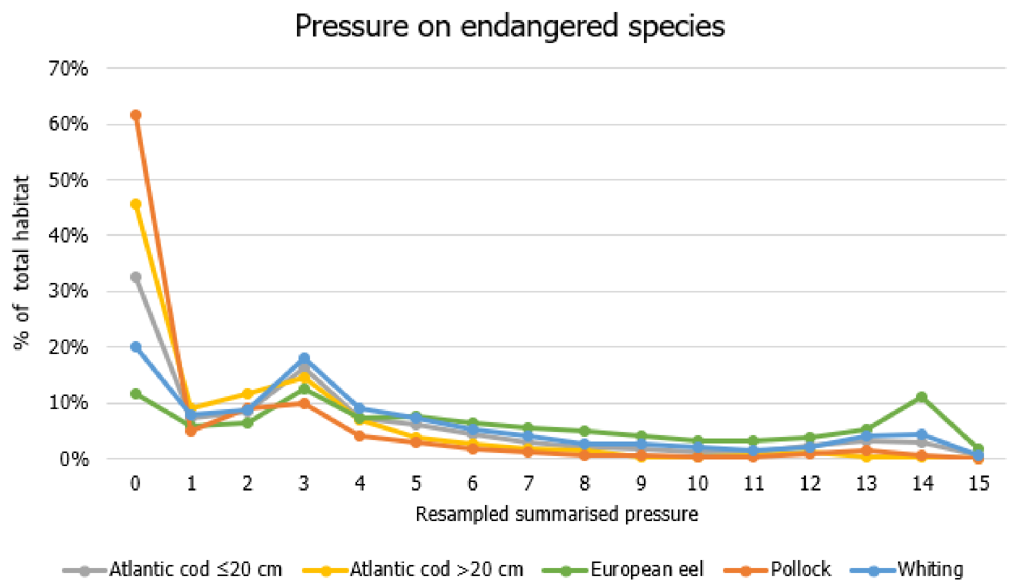


Figure 12. The summarised pressure experienced in situ for endangered and commercially important species, and the proportion of their habitat subject to a range of summarised pressure classes using the resampled data (250m x 250m). Zero pressure might not indicate that there are no anthropogenic disturbances in these habitats, but that data on potential pressure is missing.

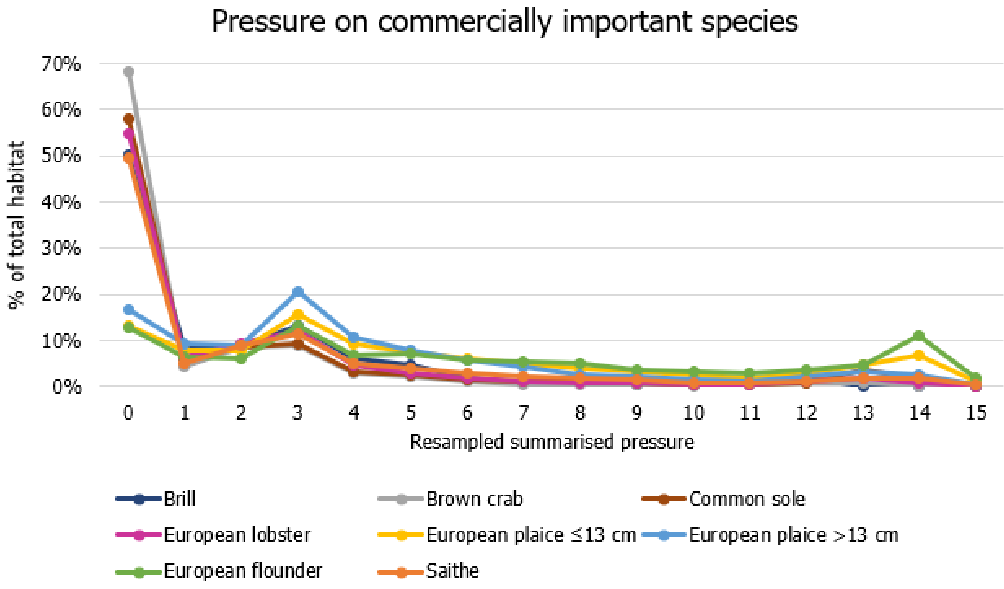


Figure 13. The resampled summarised pressure experienced in situ for commercially important species and the proportion of their habitat subject to a range of summarised pressure classes using the resampled data (250m x 250m). Zero pressure might not indicate that there are no anthropogenic disturbances in these habitats, but that data on potential pressure is missing.

4.3. Best conservation solutions and expansion opportunities

4.3.1. Best conservation solution

For the unbiased solution (when Marxan choses freely among the planning units), a large part of the planning units had a high selection frequency (Figure 14). The biased solution (when Marxan was constrained to include already protected planning units) delivered a more nuanced solution as the selection frequency was streamlined, making deduction of important planning units more distinct (Figure 14). The coastal areas enclosed by the red circles exemplifies areas with drastic differences in distribution of important planning units between the unbiased and biased solution (Figure 14). The total reserve area for all planning units selected in the unbiased solution was ~1 585 km^2 and ~1 427 km^2 for all planning units in the biased solution. The most cost-efficient solution for the MPA network in the Skagerrak was therefore the biased solution, as less protected area was required to reach the target. However, this solution required 4% more protected area than the current MPA network (~1 375 km^2). This was expected as the protection rate for most species (see Table 3 in 4.4.1) was less than the target of 50%.

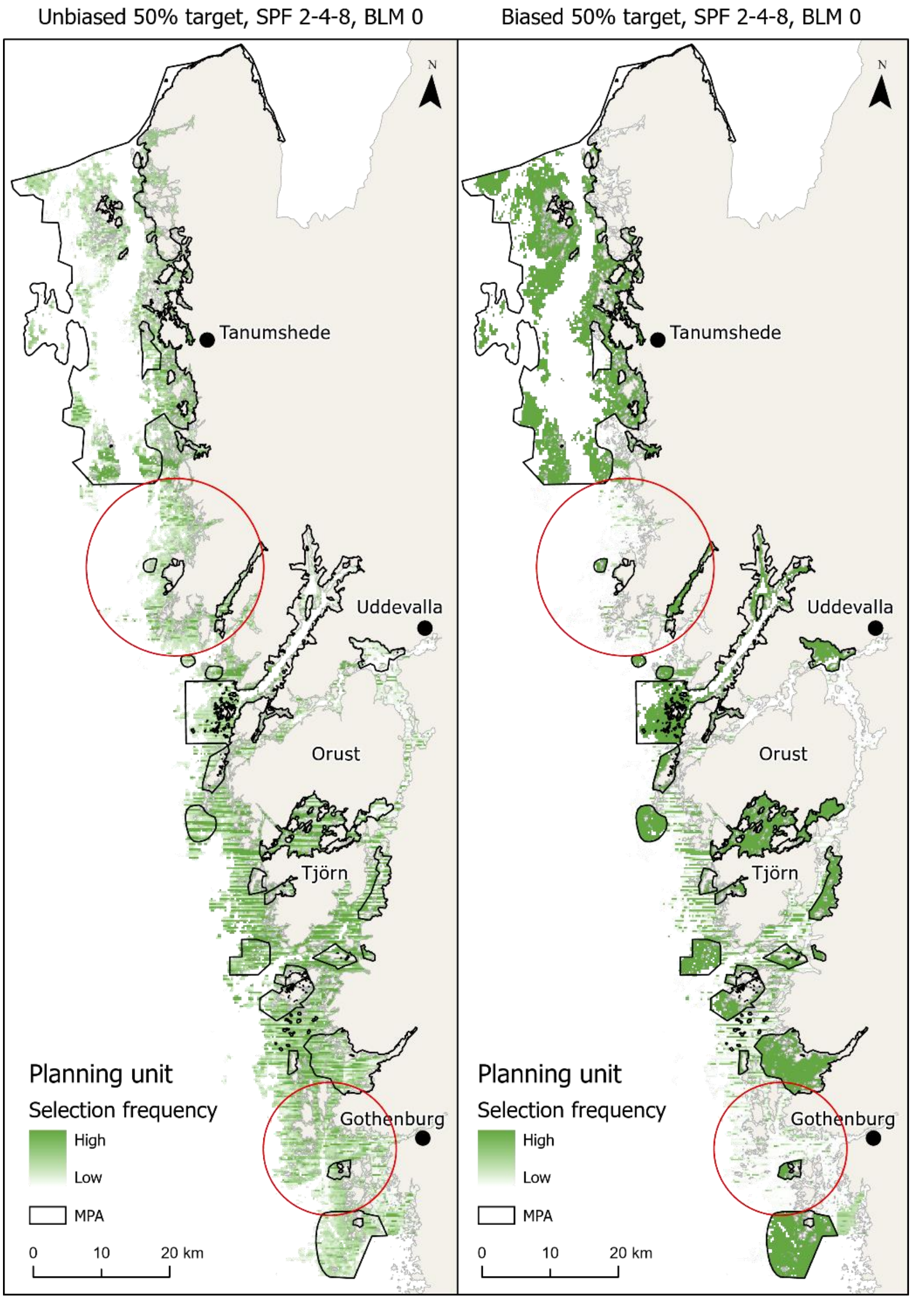


Figure 14. Selection frequency of each planning unit when running the unbiased solution (Marxan chose freely among the planning units) shown in the left panel, and the biased solution (Marxan had to include already protected planning units) shown in the right panel, using the non-uniform SPF, a BLM of 0 and a target of 50%. The scale of low–high indicates the importance of a particular planning unit for the reserve network. The selection frequency shows how many of the 10,000 repeated runs, each planning unit was selected. A higher selection number implies the importance of that planning unit for the reserve network. Red circles indicates areas with distinct difference in distribution of important planning units between the unbiased and biased solution.

Using the most cost-efficient BLM value of 0.01, the best conservation scenario for the unbiased and biased solutions could be displayed (Figure 15). A large part of the planning units in the unbiased solution were located outside MPAs while planning units in the biased solution was predominantly located inside MPAs

(Figure 15). For both solutions, there was a high concentration of unprotected planning units along the coast from Gothenburg northward to Orust (Figure 15). The calculated reserve area for the unbiased solution was 709 km^2 and for the biased solution 844 km^2. Overall, less reserve area was required when using a BLM value than excluding it from the analysis. Comparing with reserve area in the current MPA network (~1 375 km^2), both solutions required less reserve area (-49% for the unbiased and -39% for the biased), suggesting the current reserve network has been streamlined.

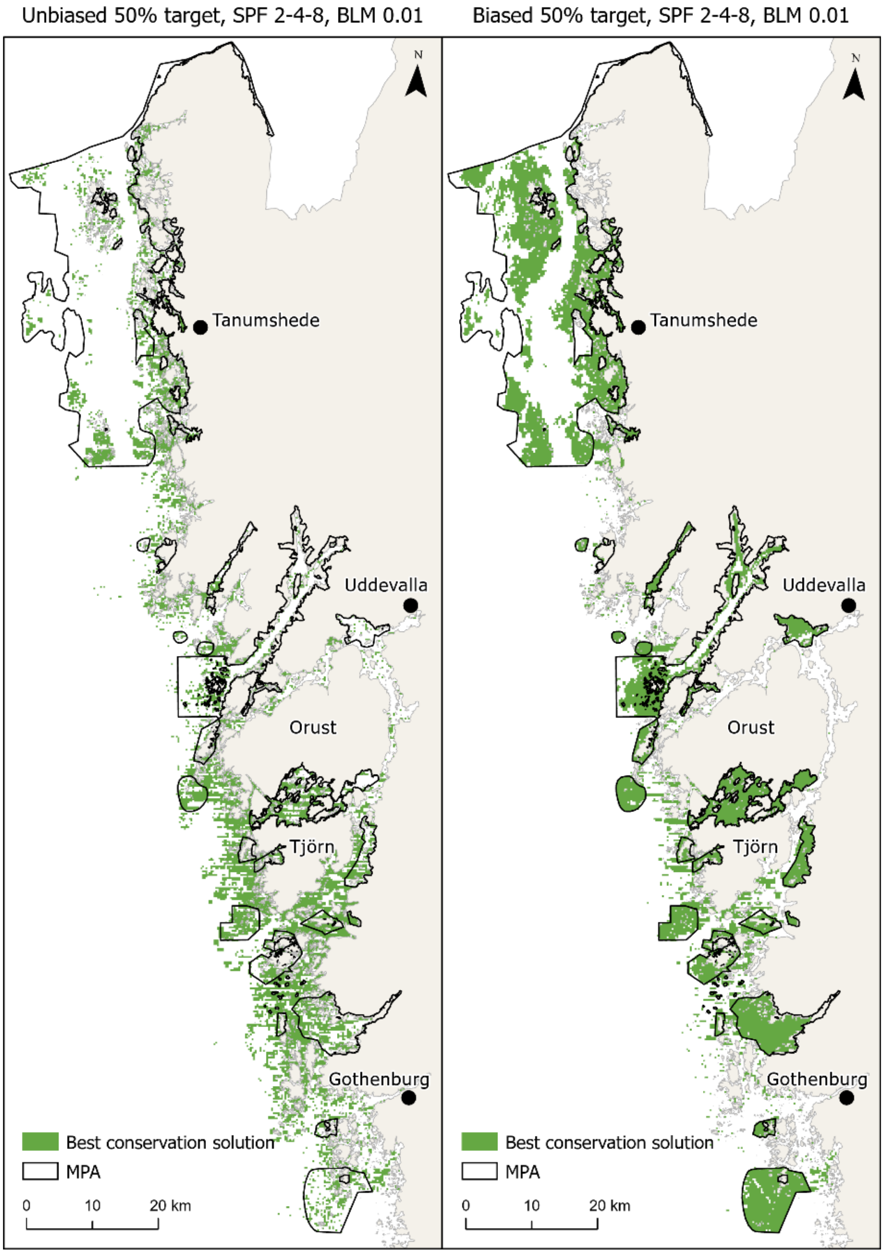


Figure 15. The best conservation scenario for the unbiased solution (left panel) and the biased solution (right panel), using the non-uniform SPF, a BLM of 0.01 and 50% target. The green areas represent planning units (= habitats) important to protect to achieve the target for all species.

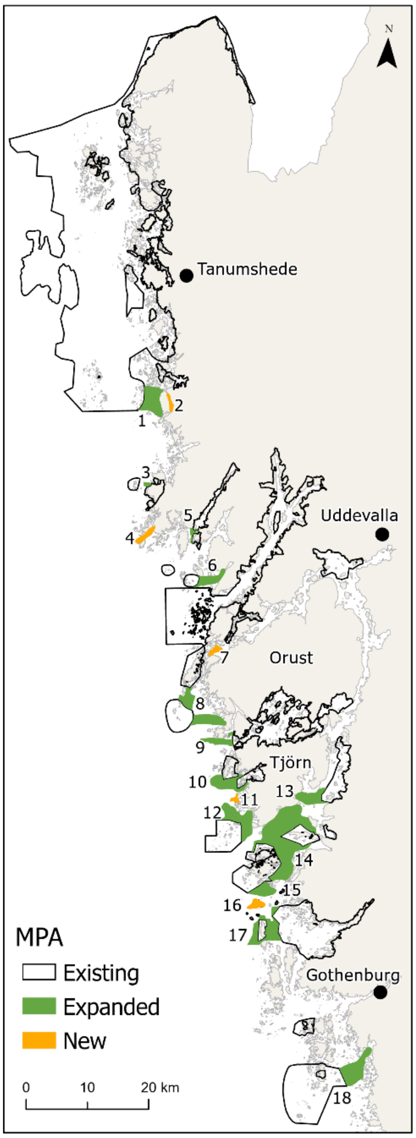
If the current MPA network would expand according to the best conservation solution proposed by using the biased setting, the mean ecological representativity in the Skagerrak would increase from currently 43% to 54% (Table 4). This would also entail increased habitat protection for most species including the two-spotted goby, which currently only had 9% of its habitat protected (Table 3). However, amending the current MPA network to follow the best conservation solution would implicate a decrease in protected habitat for the black goby (-5%), pollock (-1%) and the European shore crab (-2%; Table 4).

Table 4. Habitat area (km^2) and ecological representativity (proportion of protected habitats (%)) in the Skagerrak for the current MPA network and the optimised MPA network proposed by Marxan. The species are listed according to frequency of occurrence in the total sample along the west coast.

	Total habitat (km^2)	**Habitat in MPAs (km^2)**		**Ecological representativity (%)**		**Frequency of occurrence (%)**
Species		Current	Optimised	Current	Optimised	
European shore crab	*652*	*293*	*358*	*39%*	*55%*	*89%*
Goldsinny wrasse	*297*	*141*	*160*	*44%*	*54%*	*66%*
European eel	*141*	*55*	*71*	*45%*	*50%*	*57%*
Viviparous eelpout	*334*	*140*	*175*	*36%*	*52%*	*53%*
Corkwing wrasse	*81*	*44*	*49*	*41%*	*61%*	*49%*
Atlantic cod >20 cm	*238*	*82*	*119*	*55%*	*50%*	*44%*
Black goby	*241*	*117*	*133*	*33%*	*55%*	*39%*
European flounder	*882*	*405*	*484*	*46%*	*55%*	*38%*
Atlantic cod ≤20 cm	*457*	*203*	*248*	*45%*	*54%*	*31%*
European plaice ≤13 cm	*198*	*109*	*123*	*43%*	*62%*	*20%*
Longspined bullhead	*1096*	*510*	*610*	*54%*	*56%*	*16%*
Saithe	*245*	*126*	*141*	*46%*	*58%*	*16%*
Common sole	*598*	*255*	*320*	*51%*	*53%*	*14%*
Whiting	*358*	*173*	*205*	*41%*	*57%*	*14%*
Brown crab	*445*	*189*	*228*	*45%*	*51%*	*6%*
Fivebeard rockling	*447*	*216*	*256*	*48%*	*57%*	*5%*
European plaice >13 cm	*34*	*18*	*19*	*42%*	*55%*	*4%*
Ballan wrasse	*547*	*282*	*327*	*48%*	*60%*	*4%*
Brill	*996*	*408*	*498*	*51%*	*50%*	*3%*
Rock cook	*749*	*304*	*374*	*52%*	*50%*	*3%*
Pollock	*1035*	*467*	*545*	*41%*	*53%*	*2%*
Two-spotted goby	*857*	*329*	*429*	*9%*	*50%*	*2%*
European lobster	*17*	*1*	*8*	*38%*	*50%*	*1%*

4.3.2. Expansion opportunities

Expansion of existing MPAs and the establishment of new MPAs are proposed in Figure 16. Clusters of planning units in the best conservation solution (see right panel in Figure 15) were visually identified to either be included in an existing MPA by extending it, or by establishing a new MPA. Thirteen sites are suggested to be included in existing MPAs (marked green in Figure 16) and new MPAs are suggested for five sites (marked orange in Figure 16).



Expansion of adjacent MPAs

1) Väderöarna
3) Ramsvikslandet
5) Åbyfjorden and Näverkärr
6) Malmöfjord
8) Härmanö and Måseskär
9) Stigfjorden
10) Härön and Breviks kile-Toftenäs
12) Pater Noster-skärgården
13) Stenungsundskusten
14) Älgön-Brattön, Marstrand and Sälöfjorden
15) Sälöfjorden
17) Sälöfjorden and Nordre älvs estuarium
18) Vrångöskärgården

New MPAs

2) Hamburgsund
4) Smögen
7) Gullholmen
11) Tjörn
16) Halloreskären

Figure 16. Proposal for MPA expansion based on visually delineating major clusters of planning units considered conservation worthy by Marxan, the best conservation scenario for the biased solution, using the non-uniform SPF, a BLM of 0.01 and 50% target. Clusters of planning units important to protect is either proposed to be included in existing MPAs (green) by expanding adjacent MPAs, or by establishing new MPAs (orange). The numbers refer to either existing MPAs suited for expansion to encompass proposed green sites or refers to a local relevant place name for the proposed new MPAs (orange sites).

5. Discussion

The mean ecological representativity was 45% for the entire west coast and 43% for the Skagerrak. For the west coast and the Skagerrak, all individual species had an ecological representativity of >30% except for the two-spotted goby which had only 9% habitat protected in the Skagerrak. Proportion of habitat subjected to different pressure intensities differs between species. For example, the European eel, whiting, the European flounder and the European plaice experienced more stress as they had the smallest share of habitats located in low pressure areas. Examples of species experiencing minor stress were the pollock and brown crab which had a high share of habitats located in low pressure areas.

When excluding BLM from the Marxan analysis, the most cost-efficient solution for the MPA network in the Skagerrak was provided by the biased solution, since less protected area was required to reach the target. However, this solution, still required 4% more protected area than the current MPA network. Including BLM in the Marxan analysis yielded solutions (both the unbiased and biased) that required less protected area than the current MPA network. From a cost-efficiency perspective, the biased solution was preferable as the planning units were concentrated within existing MPAs, thus reducing expansion efforts and allocation of monetary resources. Thirteen existing MPAs are suggested to be expanded and five new MPAs are suggested. Expansion opportunities are mainly suggested for habitats along the coasts between Gothenburg and Orust, where there was a high concentration of important unprotected planning units (habitats).

5.1. Ecological representativity and protection measures

This study has shown that the current MPA network provides an ecological representativity of >30% for the majority of investigated species in the Skagerrak. This suggests that the EU goal of ≥30% protection is already achieved but since several of the species in this study are endangered and experiencing a population decline, the question of whether it is important to enhance current protection rate is important. By comparing ecological representativity in the current MPA network with frequency of occurrence in the fish monitoring samples, some conclusions regarding the status of populations can be made. For instance, brill and rock cook, currently have >50% habitat protected and yet, they were only caught in 3% of the fish monitoring samples. This suggests that the populations are small, and that concern of their status should be raised. Two main factors might explain low occurrence despite high ecological representativity, 1) environmental conditions specific to the species are unfavourable in this region and 2) the quality of the habitat is poor which can be attributed to anthropogenic disturbances. A low frequency of occurrence despite a high proportion of protected habitat, can imply that the current protection regime is insufficient and that stricter regulations like fishing bans, are imperative. Future protection measures should therefore focus on adjusting regulations in current MPAs, rather than expanding them, to include a stricter protection.

Amending current regulations is more cost-effective as all pre-work required when investigating where new MPAs should be established, is redundant. Also, inferring stricter protection is recognised by the EU as a key tool to combat biodiversity loss (European Commission, 2020a). Currently, only 1% of the sea in EU is strictly protected and the goal is to increase this to ≥10% by 2030 (European Commission, 2020a). The EU has yet to define what strict protection entails but presumably so called *no-take zones* will be included. A no-take zone is an area where all or specific activities involving extracting or removing natural features, is prohibited (Florin *et al.*, 2013). No-take zones are intrinsically a type of MPA with strict fishing regulations but are not included in the MPA network on the Swedish west coast. Instead they are considered a complement to MPAs (Bergström *et al.*, 2016).

There are currently three no-take zones in the Skagerrak (Vinga, Havstensfjorden and Kåvra) of which none are located within any of the existing MPAs (Bergström *et al.*, 2016). Several of the no-take zones protect species that are analysed in this study including the European lobster, Atlantic cod and the European plaice (Bergström *et al.*, 2016). The no-take zones have had positive impacts on local populations, individual sizes and spill-over effects of the European lobster (Moland *et al.*, 2013; SLU, 2021). For the Atlantic cod and the European plaice, there were no significant effects on the populations as of 2016 (Bergström *et al.*, 2016). A plausible factor as to why only the European lobster is experiencing a positive trend, may be a too short evaluation time, considering the longevity of these species, and age at which they reach sexual maturity. Also, the fish stock was heavily over-exploited at the time of the establishment of the no-take zones, which will affect recovery time. Therefore, no conclusions can be made yet regarding the success of the existing no-take zones in the Skagerrak.

Despite the negative population trends for the Atlantic cod and the European plaice, extending the network of no-take zones in the Skagerrak is a robust approach as there is an ample supply of studies supporting no-take zones (Pipitone *et al.*, 2000; Côté, Mosqueira and Reynolds, 2001; Ecoutin *et al.*, 2014). Prohibiting fishing has shown to, even in short-term (<4 years), increase species richness, abundance and biomass of fish communities as well as size-augmentation and increased populations of apex predators (Pipitone *et al.*, 2000; Côté, Mosqueira and Reynolds, 2001; Ecoutin *et al.*, 2014). As populations for high trophic level species increases, predation pressure changes in the trophic system accentuating top-down effects (Aburto-Oropeza *et al.*, 2011). Furthermore, low level species such as phytoplankton will decrease, which in turn has a positive effect on water clarity and reduced oxygen depletion as less organic matter is deposited on the bottom (Heck and Valentine, 2007; Garpe, 2008).

5.2. Anthropogenic pressure and protection measures

In this study, protecting habitats subjected to high anthropogenic pressure in the Skagerrak, has been prioritised by setting a low cost in Marxan for these planning units (habitats). Appointing a low cost to high pressure areas instructs Marxan to prioritise these planning units in the final conservation solution. Prioritising habitats in high-pressure areas is not an obvious measure. For example, it can be ineffective to protect habitats under high pressure as their deterioration might have proceeded during longer time periods and the damage might be too severe or costly to remedy. Also, coastal anthropogenic activities such as industries and wastewater treatment plants, will most likely continue their operation for an unforeseeable future and proceed with effluents into coastal waters.

As the Swedish population is expected to increase with 7,4% from 2019 to 2030 (Statistics Sweden, 2020b), this will put more strain on the coastal environment with higher visitor rates and increased housing development. In addition to this, a revision of the “shoreline protection” was recently proposed (SOU, 2020), implicating a weakening of development restrictions which will impact numerous species as the coastal area includes crucial spawning, nursery, and nesting sites for multiple organisms (Blaber *et al.*, 2000; Sandström *et al.*, 2005). At the same time, housing developments in coastal areas can be used as an argument for protecting habitats in high-pressure areas as they provide people with recreational values such as recreational fishing. Additionally, a healthy coastal environment (no or reduced eutrophication) attracts people to take part in leisure activities such as swimming and scuba diving.

On the other hand, it might be more efficient to protect habitats under minor anthropogenic pressure as these sites can offer environments with better conditions and better prerequisites for a sustainable development of local populations. A study by Brander *et al.* (2020) showed that it is more cost-efficient to focus protection measures on high species richness habitats under minor anthropogenic pressure, as the expected return is threefold the investment. Furthermore, benefits from the investment can create positive feedbacks spilling over to other non-targeted species and populations (Côté, Mosqueira and Reynolds, 2001). Migration of individuals in targeted populations can source other populations at risk of extinction, the so-called rescue effect (Hanski, 1991), and induce geneflow which reduces the risk of inbreeding and subsequently extinction (Pérez-Ruzafa *et al.*, 2006). Source populations can re-colonize patches formerly inhabited by extinct populations and thus increase survival rates of the species (Hanski and Simberloff, 1997). The downside with prioritising conservation efforts for populations in low-pressure areas is that resources (time, money) is spent on protecting areas that do not need protection from anthropogenic activities. Also, vulnerable species inhabiting high-pressure areas can be neglected, potentially reducing biodiversity as species go extinct (Brooks *et al.*, 2006). These species might be predators crucial in sustaining a top-down predation pressure in the food web or the populations might be the only one left of that species. Hence, a balance of the trade-offs should be made when deciding where to focus conservation efforts.

Regardless of whether low- or high-pressure areas are being targeted for protection measures, other spatial aspects must be considered, which will influence the success of protection measures. For instance, reserve size has been shown to have a positive effect on abundance and species richness (Claudet *et al.*, 2008) although there are also studies not showing a strong link (Côté, Mosqueira and Reynolds, 2001; Halpern, 2003). Depending on the conservation feature, life history traits and habitat requirements, some species benefit from a single large reserve while others benefits from several smaller ones ("the SLOSS theory") (Diamond, 1975). Additionally, one of the more widespread theories in ecology is the species-area-relationship theory (SAR), which implies a positive correlation between conservation area size and species richness (Arrhenius, 1921). Creating large reserves is also more economically sound as the cost per unit area decreases as the area of an MPA increases (Brander *et al.*, 2020).

Finally, if the objective is to protect and preserve multiple species from an ecological representativity perspective, as is the approach in this study, protecting a larger area is preferable as it is more cost-efficient; more of the targeted species are included and edge effects are reduced. This leads to less spill-over as there is less total habitat edge which leads to a higher degree of conservation features being maintained within the MPA (Abesamis and Russ, 2005). However, for the fishing industry, several small reserves is preferable as it increases the total habitat edge and thus higher spill-over (Halpern, Lester and Kellner, 2009; Gaines *et al.*, 2010).

5.3. Comparing species richness with anthropogenic pressure

This study found several spatial patterns in species richness and anthropogenic pressure. High species richness, were mostly identified along the coastline of islands and by large fjord inlets. High pressure areas are also concentrated near the coastal zone as pressure sources such as industries, wastewater treatment plants, ports, and jetties, are typically located along the coast. There are some overlaps between high pressure- and high species richness areas, primarily by the coastal mainland. However, the difference in spatial coverage of the habitat and pressure data might emphasise areas of overlap located near shorelines. The mapped pressure distribution is predominantly located near the shorelines as the data cover depths up to 15 m, while the spatial distribution of the habitat data covers depths up to 30 m. This discrepancy in the range of depth will affect the comparison between spatial distributions of species richness and pressure, since the applied habitat data encompass a larger region. Because the spatial extent of the pressure data is limited in comparison to the habitat data, it might be inaccurate to interpret a high proportion of habitat experiencing no or low pressure as them being undisturbed and thus unworthy of conservation efforts. Also, the lack of pressure data at depths >15 m, might cause habitats potentially experiencing higher anthropogenic pressure to be overlooked in the Marxan-analysis, as Marxan focuses on achieving conservation targets at the lowest cost. Therefore, habitats with high species richness experiencing no or low pressure (which were assigned a high cost), were likely de-prioritised to favour conservation of low cost-areas with high species richness.

5.4. Using ecological representativity and Marxan to explore expansion opportunities

Total reserve areas for conservation solutions produced by Marxan were used together with ecological representativity to explore expansion opportunities. The specific settings specified in Marxan affect the results. When BLM (parameter instructing Marxan to emphasis reserve compactness) was excluded from the analysis, the unbiased (+15%) and the biased solutions (+4%) had a greater total reserve area, respectively, than the current MPA network. This does not imply that the current MPA network is efficient in protecting minimum 50% of the species habitat (assuming the highest target used in the analysis). The results rather indicate the importance of including BLM in the analysis because when added, total reserve area becomes 49% less for the unbiased solution and 39% less for the biased solution, compared to the current MPA network. This suggests that with a streamlining of current MPAs, it is possible to achieve a minimum of 50% representativity. Also, less required reserve area for the unbiased solution does not mean it was the most efficient solution. With more planning units located outside existing MPAs, a vast expansion of the current network would be required which in reality is not feasible, thus the unbiased solution was ineffective from a cost-efficiency perspective.

The different results gained by excluding or including BLM, demonstrate the importance of individual parameter settings in Marxan. The same effect was seen with the SPF (a setting ranking the importance of meeting the conservation target for all species). When using a uniform SPF (all species had the same value), Marxan failed to meet both target levels (40% and 50%) for all species. In contrast, using a non-uniform SPF, the conservation target for all species was achieved irrespective of target level. When forcing Marxan to include protected planning units and specified BLM and SPF values, the system was not only able to achieve both targets, but it also provided a solution which is more effective than the current MPA network. This suggests that Marxan performs better when given constraints. Thus, in terms of expansion opportunities, giving Marxan constraints, provides a more realistic and practical result, since governing agencies are more likely to expand existing reserves than creating completely new ones (Roberts *et al.*, 2003).

The best conservation solution was achieved with the biased setting, using a non-uniform SPF and a BLM of 0.01. Even though a BLM was used, the proposed solution of which planning units should be protected, is still fragmented. If greater emphasis is placed on compactness, the final solution should be more frugal as a more concentrated network is more cost-efficient to manage and expanding already existing MPAs is less demanding as regulations and other necessary components are already in place. Roberts *et al.* (2003) also recognises that it is easier to enforce larger reserves as allocation of monetary resources is concentrated. Also, fewer (but larger) reserves facilitates compliance to boundaries and regulations (Roberts *et al.*, 2003). The downside of putting more emphasis on compactness is that important habitats with high conservation values located far from existing MPAs, might be ignored as Marxan prioritises habitats in and within proximity to existing MPAs (when using the biased setting). Protecting remote habitats with high conservation values may contribute to enhanced connectivity between MPAs, an important factor for an ecologically coherent MPA network.

Because the most cost-efficient solution (the biased one) requires less total reserve area (-39%) than the current MPA network, this indicates that a more effective network could be developed, even though, three species would suffer a decrease in ecological representativity: The black goby (-5%), pollock (-1%) and the European shore crab (-2%). This raises an important question: are some species more important to protect than others? Different stakeholders would provide different answers. The fishing industry would almost certainly agree, as for them some species are truly more valuable, from an economic perspective. However, from a conservation science perspective, each species holds an important role in the ecosystem. In this study, the investigated species were ranked according to their commercial importance, conservation status and risk of extinction. From both a commercial and a conservation perspective, all three factors should be considered, as many species at risk of extinction are commercially important. Equally, some of the commercially important species are top predators (such as the Atlantic cod, the European flounder, and saithe), species crucial for asserting top-down pressure in the trophic system and maintaining the functional structure of an ecosystem. Thus, both commercial and conservation stakeholders benefit from MPAs, although from different objectives (Halpern, Lester and Kellner, 2009).

Even if the most cost-efficient conservation solution results in a decrease in protected habitat, the species would still have >50% of their habitat under protection. Similar results were obtained by Geange *et al.* (2017) using the conservation planning tool Zonation, where a decrease in ecological representativity for some features did not impede an increase on the whole. This might seem like a good trade-off but values of ecological representativity must be analysed based on their real-life sufficiency. The EU goal of ≥30% protection refers to species and habitats registered in the Birds and Habitat directives but by applying this goal on the species in this study, the current MPA network is adequate at protecting all species except the two-spotted goby. The most cost-efficient conservation solution produced by Marxan shows that it is possible to enhance habitat protection for the two-spotted goby without implicating a <50% protection for the other species.

By considering the SAR-theory (discussed in section 5.5.2) together with the results from this study and the discussion above, the primary objective should be to expand the current MPA network by enlarging already existing MPAs, to include important habitats. This approach was already mimicked by Marxan, since this is the case for the biased solutions, when planning units (habitats) located inside existing MPAs are forced to be included in the final conservation solution. This setting increased the probability of Marxan using already protected planning units as starting points and thus, focusing on expanding existing MPAs rather than finding remote areas suited for protection. In order to simplify the Marxan produced maps for potential end users, Figure 16 provides examples of potential MPA expansion opportunities and the potential for establishing new reserves. The map was created by visually delineating major clusters of planning units considered conservation worthy by Marxan. In line with the SAR-theory, focus was on enlarging existing MPAs as well as providing few larger expansions as opposed to several smaller ones.

Finally, future analyses should include more anthropogenic disturbances in the cost-matrix other than those used in the current study (coastal development, dredging and boat traffic), specifically fishing pressure (intensity, gears, methods, capacity) and nutrient loadings causing eutrophication, activities known to stress species and deteriorate habitats. The estimated success of prioritising habitats under high or low pressure must be considered and accounted for when determining conservation approach, as protecting habitats under high pressure may be futile. Furthermore, it is important to include connectivity and minimum reserve-size as they are integrated parts of making MPA networks ecological coherent (Roberts *et al.*, 2003). Using conservation planning-tools like Marxan to evaluate and expand reserves, enables decision makers to streamline conservation efforts and ensure best practice to secure sustainable use of resources.

6. Conclusions

This study reveals that the ecological representativity of the Skagerrak is satisfactory for all but one species (the two-spotted goby), if taking the EU goal of ≥30% protection into consideration. Results from the Marxan analysis shows that it is possible to enhance ecological representativity for all species to 50%, focusing on expansion of existing MPAs. The best conservation solution, obtained with the biased setting, suggests that opportunities for expansion of the MPA network is concentrated to sites along the coast from Gothenburg northward to Orust. The coastal habitats can be protected by expanding 13 existing MPAs and creating five new ones. Since several species already have >30% habitat protected but are nonetheless endangered or have a low frequency of occurrence in fish monitoring samples (suggesting small populations), establishing MPAs may not be enough. Besides expanding the MPA network, amending current regulations to include stricter protection such as no-take zones, is suggested in order to achieve the EUs goal of strictly protecting one third of the total MPA coverage by the year 2030.

7. References

Abesamis, R. A. and Russ, G. R. (2005) 'Density-dependent spillover from a marine reserve: Long-term evidence', *Ecological Applications*, 15(5), pp. 1798–1812. doi: 10.1890/05-0174.

Aburto-Oropeza, O. *et al.* (2011) 'Large recovery of fish biomass in a no-take marine reserve', *PLOS ONE*, 6(8). doi: 10.1371/journal.pone.0023601.

Airoldi, L. (2003) 'The effects of sedimentation on rocky coast assemblages', *Oceanography and Marine Biology*, 41, pp. 161–236.

Airoldi, L. and Beck, M. W. (2007) *Loss, status and trends for coastal marine habitats of Europe*, *Oceanography and Marine Biology*. doi: 10.1201/9781420050943.ch7.

Allouche, O., Tsoar, A. and Kadmon, R. (2006) 'Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS)', *Journal of Applied Ecology*, 43(6), pp. 1223–1232. doi: 10.1111/j.1365-2664.2006.01214.x.

Almany, G. R. *et al.* (2009) 'Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs', *Coral Reefs*, 28(2), pp. 339–351. doi: 10.1007/s00338-009-0484-x.

Anderson, D. M., Glibert, P. M. and Burkholder, J. . (2002) 'Harmful algal blooms and eutrophication: Nutrient sources, composition, and consequences', *Estuaries*, 25, pp. 704–726. doi: 10.1007/BF02804901.

Ardron, J. A., Possingham, H. P. and Klein, C. J. (2010) *Marxan Good Practices Handbook, Version 2*. Second, *Pacific Marine Analysis and Research Association*. Second. Victoria, BC, Canada. Available at: www.pacmara.org.

Arrhenius, O. (1921) 'Species and Area Author (s): Olof Arrhenius Published by : British Ecological Society Stable URL : http://www.jstor.org/stable/2255763', *Journal of Ecology*, 9(1), pp. 95–99.

Austin, M. P. and Margules, C. R. (1986) 'Wildlife Conservation Evaluation', in Usher, M. B. (ed.) *Wildlife Conservation Evaluation*. London: Chapman and Hall, pp. 45–67. doi: 10.1007/978-94-009-4091-8.

Ball, I. R. (2000) *Mathematical applications for conservation ecology : the dynamics of tree hollows and the design of nature reserves*. Adelaide, Australia: The University of Adelaide. Available at: https://digital.library.adelaide.edu.au/dspace/handle/2440/19542.

Baum, J. K. and Worm, B. (2009) 'Cascading top-down effects of changing oceanic predator abundances', *Journal of Animal Ecology*, 78(4), pp. 699–714. doi: 10.1111/j.1365-2656.2009.01531.x.

Belbin, L. (1993) 'Environmental representativeness: Regional partitioning and reserve selection', *Biological Conservation*, 66(3), pp. 223–230. doi: 10.1016/0006-3207(93)90007-N.

Bergström, U. *et al.* (2016) *Aqua reports 2016 : 20 Ekologiska effekter av fiskefria områden i Sveriges kust- och havsområden*, *Aqua reports*. Öregrund.

Blaber, S. J. M. *et al.* (2000) 'Effects of fishing on the structure and functioning of estuarine and nearshore ecosystems', *ICES Journal of Marine Science*, 57(3), pp. 590–602. doi: 10.1006/jmsc.2000.0723.

Blakeslee, A. M. H. *et al.* (2010) 'A hitchhiker's guide to the Maritimes: Anthropogenic transport facilitates long-distance dispersal of an invasive marine crab to Newfoundland', *Diversity and Distributions*, 16(6), pp. 879–891. doi: 10.1111/j.1472-4642.2010.00703.x.

Boverket and Naturvårdsverket (2010) *Strand Skydd*. Available at: https://www.naturvardsverket.se/Om-Naturvardsverket/Publikationer/ISBN/8400/978-91-620-8473-8/.

Brander, L. M. *et al.* (2020) 'The global costs and benefits of expanding Marine Protected Areas', *Marine Policy*, 116(March), p. 103953. doi: 10.1016/j.marpol.2020.103953.

Brooks, T. M. *et al.* (2006) 'Global Biodiversity Conservation Priorities', *Science*, 313(5783), pp. 58–61.

Ceballos, G. *et al.* (2015) 'Accelerated modern human-induced species losses: Entering the sixth mass extinction', *Science Advances*, 1(5). doi: 10.1126/sciadv.1400253.

Chapman, B. B. *et al.* (2011) 'The ecology and evolution of partial migration', *Oikos*, 120(12), pp. 1764–1775.

Claudet, J. *et al.* (2008) 'Marine reserves: Size and age do matter', *Ecology Letters*, 11(5), pp. 481–489. doi: 10.1111/j.1461-0248.2008.01166.x.

Côté, I. M., Mosqueira, I. and Reynolds, J. D. (2001) 'Effects of marine reserve characteristics on the protection of fish populations: A meta-analysis', *Journal of Fish Biology*, 59(SUPPL. A), pp. 178–189. doi: 10.1006/jfbi.2001.1752.

Davenport, J. *et al.* (2008) *Challenges to Marine Ecosystems*, *Hydrobiologia*. doi: 10.1007/978-1-4020-8808-7.

Dayton, P. K. *et al.* (1995) 'Environmental effects of marine fishing', *Aquatic Conservation: Marine and Freshwater Ecosystems*, 5(3), pp. 205–232. doi: 10.1002/aqc.3270050305.

Diamond, J. M. (1975) 'The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves', *Biological Conservation*, 7(2), pp. 129–146. doi: 10.1016/0006-3207(75)90052-X.

Dudley, N., Shadie, P. and Stolton, S. (2013) *Guidelines for Applying Protected Area Management Categories*, *International Union for Conservation of Nature and Natural Resources*. Gland, Switzerland. doi: 10.1103/PhysRevB.38.10724.

Dudley, N. and Stolton, S. (2008) *Defining protected areas: An international conference in Almeria, Spain Mayo 2007*, *IUCN Protected Areas Categories Summit*. Gland, Switzerland. Available at: http://cmsdata.iucn.org/downloads/almeria_proceedings_final.pdf.

Ecoutin, J. M. *et al.* (2014) 'Ecological field experiment of short-term effects of fishing ban on fish assemblages in a tropical estuarine MPA', *Ocean and Coastal Management*, 100, pp. 74–85. doi: 10.1016/j.ocecoaman.2014.08.009.

Eriander, L. *et al.* (2017) 'The effects of small-scale coastal development on the eelgrass (Zostera marina L.) distribution along the Swedish west coast – Ecological impact and legal challenges', *Ocean and Coastal Management*, 148, pp. 182–194. doi: 10.1016/j.ocecoaman.2017.08.005.

European Commission (2007) *Guidelines for the establishment of the Natura 2000 network in the marine environment.*, *Application of the Habitats and Birds Directives*. Available at: http://ec.europa.eu/environment/nature/natura2000/marine/index_en.htm.

European Commission (2020a) *EU Biodiversity Strategy for 2030*. Brussels.

European Commission (2020b) *Natura 2000 sites designation*. Available at: https://ec.europa.eu/environment/nature/natura2000/sites/index_en.htm (Accessed: 23 November 2020).

European Commission (2021) *Draft Technical note on criteria and guidance for protected areas deignations*.

European Union (1992) 'Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora', *Official Journal of the European Communities*, pp. 1–44. doi: 10.1017/cbo9780511610851.039.

European Union (2008) 'Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive)', *Official Journal of the European Union*, pp. 1–22.

European Union (2009) 'Directive 2009/147/EC of the European Parliament and the Council of 30 November 2009 on the Conservation of Wild Birds', *Official Journal of the European Union*, pp. 1–19. doi: 10.1111/1467-9388.00079.

European Union (2014) 'Directive 2014/89/EU of the European Parliment and of the Council of 23 July 2014 establishing a framework for maritime spatial planning', *Offical Journal of the European Union*, pp. 1–11.

European Union (2016) *Convention on the Conservation of Wildlife and Natural Habitats, Council of Europe*. Strasbourg, France.

Fleeger, J. W., Carman, K. R. and Nisbet, R. M. (2003) ‘Indirect effects of contaminants in aquatic ecosystems’, *Science of the Total Environment*, 317(1–3), pp. 207–233. doi: 10.1016/S0048-9697(03)00141-4.

Florin, A. B. *et al.* (2013) ‘Effects of a large northern European no-take zone on flatfish populationsa’, *Journal of Fish Biology*, 83(4), pp. 939–962. doi: 10.1111/jfb.12097.

Fonselius, S. H. (1990) *Skagerrak - porten mot Nordsjön*.

Frank, K. T. *et al.* (2005) ‘Ecology: Trophic cascades in a formerly cod-dominated ecosystem’, *Science*, 308(5728), pp. 1621–1623. doi: 10.1126/science.1113075.

Fredriksson, R., Erlandsson, M. and Bergström, U. (2020) *Kartering av uppväxtområden för fisk och större kräftdjur i grunda områden i Västerhavet*, *Aqua reports*. Drottningholm, Lysekil and Öregrund.

Gaines, S. D. *et al.* (2010) ‘Designing marine reserve networks for both conservation and fisheries management’, *Proceedings of the National Academy of Sciences of the United States of America*, 107(43), pp. 18286–18293. doi: 10.1073/pnas.0906473107.

Garpe, K. (2008) *Ecosystem services provided by the Baltic Sea and Skagerrak*.

Geange, S. W. *et al.* (2017) ‘Integrating conservation and economic objectives in MPA network planning: A case study from New Zealand’, *Biological Conservation*, 210, pp. 136–144. doi: 10.1016/j.biocon.2017.04.011.

Gislason, H. (1994) ‘Ecosystem Effects of Fishing Activities in the North Sea’, *Marine Pollution Bulletin*, 29, pp. 50–51. doi: 10.1016/0308-597X(92)90055-T.

Guerreiro, J. *et al.* (2010) ‘Establishing a transboundary network of marine protected areas: Diplomatic and management options for the east African context’, *Marine Policy*, 34(5), pp. 896–910. doi: 10.1016/j.marpol.2010.01.014.

Halpern, B. S. (2003) ‘The impact of marine reserves: Do reserves work and does reserve size matter?’, *Ecological Applications*, 13(1 SUPPL.), pp. 117–137. doi: 10.1890/1051-0761(2003)013[0117:tiomrd]2.0.co;2.

Halpern, B. S. *et al.* (2008) ‘A global map of human impact on marine ecosystems’, *Science*, 319(5865), pp. 948–952. doi: 10.1126/science.1149345.

Halpern, B. S., Lester, S. E. and Kellner, J. B. (2009) ‘Spillover from marine reserves and the replenishment of fished stocks’, *Environmental Conservation*, 36(4), pp. 268–276. doi: 10.1017/S0376892910000032.

Hanski, I. (1991) ‘Single-species metapopulation dynamics: concepts, models and observations’, *Biological Journal of the Linnean Society*, 42(1–2), pp. 17–38. doi: 10.1111/j.1095-8312.1991.tb00549.x.

Hanski, I. and Simberloff, D. (1997) ‘The Metapopulation Approach, Its History, Conceptual Domain, and Application to Conservation’, in *Metapopulation Biology*. Elsevier, pp. 5–26. doi: 10.1016/b978-012323445-2/50003-1.

Havsmiljöinstitutet (no date) *Skagerrak, Havsmiljöinstitutet*. Available at: https://www.sverigesvattenmiljo.se/undersoka-vattenmiljo/skagerrak (Accessed: 2 April 2021).
Hayashi, M. (1993) 'The Management of Transboundary Fish Stocks under the LOS Convention', *The International Journal of Marine and Coastal Law*, 8(2), pp. 245–261. doi: 10.1163/157180893X00026.
Heck, K. L. and Valentine, J. F. (2007) 'The primacy of top-down effects in shallow benthic ecosystems', *Estuaries and Coasts*, 30(3), pp. 371–381. doi: 10.1007/BF02819384.
Hirst, N. E., Clark, L. and Sanderson, W. G. (2012) *The distribution of selected MPA search features and Priority Marine Features off the NE coast of Scotland, Scottish Natural Heritage Commissioned Report No.500*.
Hosmer, D. W. and Lemeshow, S. (2013) *Applied Logistic Regression Analysis*. Second, *John Wiley & Sons, Inc.* Second. doi: 10.2307/2988559.
IUCN Species Survival Commission (SSC) (2012) *IUCN Red List categories and criteria: Version 3.1*. Second edi. Gland, Switzerland and Cambridge. UK: IUCN, Gland, Switzerland. Available at: http://www.ncbi.nlm.nih.gov/pubmed/2734.
Jackson, J. B. C. *et al.* (2001) 'Historical overfishing and the recent collapse of coastal ecosystems', *Science*, 293(5530), pp. 629–637. doi: 10.1126/science.1059199.
Jägerbrand, A. K. *et al.* (2019) 'A review on the environmental impacts of shipping on aquatic and nearshore ecosystems', *Science of the Total Environment*, 695, p. 133637. doi: 10.1016/j.scitotenv.2019.133637.
Jonsson, B. and Jonsson, N. (1993) 'Partial migration: niche shift versus sexual maturation in fishes', *Reviews in Fish Biology and Fisheries*, 3(4), pp. 348–365. doi: 10.1007/BF00043384.
Jonsson, P. R., Nilsson Jacobi, M. and Moksnes, P. O. (2016) 'How to select networks of marine protected areas for multiple species with different dispersal strategies', *Diversity and Distributions*, 22(2), pp. 161–173. doi: 10.1111/ddi.12394.
Kukkala, A. S. and Moilanen, A. (2013) 'Core concepts of spatial prioritisation in systematic conservation planning', *Biological Reviews*, 88(2), pp. 443–464. doi: 10.1111/brv.12008.
Länsstyrelsen i Västra Götaland län (2019) *Regional handlingsplan för en grön infrastruktur*.
Länsstyrelsen i Västra Götaland län (2020) *Strategi för skydd och förvaltning av marina miljöer och arter i Västerhavet*.
Mézard, N., Sundseth, K. and Wegefelt, S. (2008) *Natura 2000: Protecting Europe's biodiversity*. Edited by D. E. Susanne Wegefelt, Nature & Biodiversity Unit. Office for Official Publications of the European Communities. doi: 10.1017/CBO9781107415324.004.
Moksnes, P.-O. *et al.* (2014) *Larval Connectivity and Ecological Coherence of Marine Protected Areas (MPAs) in the Kattegat-Skagerrak Region*,

Swedish Institute for the Marine Environment report no 2014:2. Gothenburg. Available at: http://hdl.handle.net/2077/35530.
Moksnes, P. O. *et al.* (2008) 'Trophic cascades in a temperate seagrass community', *Oikos*, 117(5), pp. 763–777. doi: 10.1111/j.0030-1299.2008.16521.x.
Moland, E. *et al.* (2013) 'Long-term decrease in sex-specific natural mortality of European lobster within a marine protected area', *Marine Ecology Progress Series*, 491, pp. 153–164. doi: 10.3354/meps10459.
Nationalencyklopedin (2021) *Bohuslän*. Available at: http://www-ne-se.ezp.sub.su.se/uppslagsverk/encyklopedi/lång/bohuslän (Accessed: 2 April 2021).
Nilsson, M. and Jonsson, P. R. (2011) 'Optimal networks of nature reserves can be found through eigenvalue perturbation theory of the connectivity matrix', *Ecological Applications*, 21(5), pp. 1861–1870.
Nyqvist, A. *et al.* (2009) 'Dynamics of seagrass meadows on the Swedish Skagerrak coast', *Ambio*, 38(2), pp. 85–88. doi: 10.1579/0044-7447-38.2.85.
OSPAR Commission (2006) *OSPAR convention on the protection of the marine environment of the North-East Atlantic*. doi: 10.1163/ej.9789004146174.i-394.38.
OSPAR Commission (2020) *MPA datasheets*. Available at: https://mpa.ospar.org/home-ospar/mpa-datasheets (Accessed: 24 November 2020).
Östman, Ö. *et al.* (2016) 'Top-down control as important as nutrient enrichment for eutrophication effects in North Atlantic coastal ecosystems', *Journal of Applied Ecology*, 53(4), pp. 1138–1147. doi: 10.1111/1365-2664.12654.
Pace, M. L. *et al.* (1999) 'Trophic cascades revealed in diverse ecosystems', *Trends in Ecology and Evolution*, 14(12), pp. 483–488. doi: 10.1016/S0169-5347(99)01723-1.
Pérez-Ruzafa, Á. *et al.* (2006) 'Effects of fishing protection on the genetic structure of fish populations', *Biological Conservation*, 129(2), pp. 244–255. doi: 10.1016/j.biocon.2005.10.040.
Peterson, C. H. (2001) 'The "exxon valdez" oil spill in alaska: acute, indirect and chronic effects on the ecosystem', *Advances in Marine Biology*, 39, pp. 1–103. doi: 10.1016/s0065-2881(01)39008-9.
Pihl, L. *et al.* (2006) 'Shift in fish assemblage structure due to loss of seagrass Zostera marina habitats in Sweden', *Estuarine, Coastal and Shelf Science*, 67(1–2), pp. 123–132. doi: 10.1016/j.ecss.2005.10.016.
Pipitone, C. *et al.* (2000) 'Fish biomass increase after a four-year trawl ban in the Gulf of Castellammare (NW Sicily, Mediterranean Sea)', *Fisheries Research*, 48(1), pp. 23–30. doi: 10.1016/S0165-7836(00)00114-4.
Ramsar Convention Secretariat (2002) *Resolution VIII.3 Climate change and wetlands: impacts, adaptation, and mitigation*.

Ramsar Convention Secretariat (2015) *Annotated List of Wetlands of International Importance Sweden*.
Ramsar Convention Secretariat (2016) *An Introduction to the Ramsar Convention on Wetlands, (previously The Ramsar Convention Manual)*. Available at: https://www.mendeley.com/viewer/?fileId=658dea6f-a739-d995-65b0-e9d2a5a9f4c6&documentId=158ad1b6-0317-3653-ac6d-fb0139511534.
Ritchie, E. G. and Johnson, C. N. (2009) 'Predator interactions, mesopredator release and biodiversity conservation', *Ecology Letters*, 12(9), pp. 982–998. doi: 10.1111/j.1461-0248.2009.01347.x.
Roberts, C. M. *et al.* (2003) 'Ecological criteria for evaluating candidate sites for marine reserves', *Ecological Applications*, 13(1 SUPPL.), pp. 199–214. doi: 10.1890/1051-0761(2003)013[0199:ecfecs]2.0.co;2.
Rogowska, J. and Namieśnik, J. (2010) 'Environmental implications of oil spills from shipping accidents', in Whitacre, D. M. (ed.) *Reviews of Environmental Contamination and Toxicology Volume 206*. New York: Springer New York, pp. 95–114. doi: doi.org/10.1007/978-1-4419-6260-7_5.
Rosenberg, R., Bonsdorff, E. and Karlson, K. (2002) 'Temporal and Spatial Large-Scale Effects of Eutrophication and Oxygen Deficiency on Benthic Fauna in Scandinavian and Baltic Waters', *Oceanography and Marine Biology*, 40, pp. 427–489. doi: 10.1201/9780203180594.ch8.
Sagerman, J., Hansen, J. P. and Wikström, S. A. (2019) 'Effects of boat traffic and mooring infrastructure on aquatic vegetation: A systematic review and meta-analysis', *Ambio*, 49, pp. 517–530. doi: 10.1007/s13280-019-01215-9.
Sandström, A. *et al.* (2005) 'Boating and Navigation Activities Influence the Recruitment of Fish in a Baltic Sea Archipelago Area', *AMBIO A Journal of the Human Environment*, 34(2), pp. 125–130. doi: 10.1639/0044-7447(2005)034.
Sciberras, M. *et al.* (2013) *Criteria for assessing ecological coherence of MPA networks : A review*.
Seebens, H., Gastner, M. T. and Blasius, B. (2013) 'The risk of marine bioinvasion caused by global shipping', *Ecology Letters*, 16(6), pp. 782–790. doi: 10.1111/ele.12111.
Short, F. T. and Wyllie-Eciieverria, S. (1996) 'Natural and human-induced disturbance of seagrasses', *Environmental Conservation*, 23(1), pp. 17–27. doi: 10.1017/s0376892900038212.
SLU (2021) *Fisk- och skaldjursbestånd i hav och sötvatten 2020, Havs- och vattenmyndighetens rapport 2021:6*. Edited by E. Von Wachenfeldt, R. Yngwe, and S. Bureborn. Havs- och vattenmyndigheten. Available at: https://www.slu.se/globalassets/ew/org/inst/aqua/externwebb/sidan-publikationer/resurs-och-miljo/resursoversikt_2018_mindre.pdf.
SLU Artdatabanken (2020) *Rödlistade arter i Sverige 2020*. Edited by W. Eide. Uppsala: SLU Artdatabanken, Uppsala. Available at:

https://www.artdatabanken.se/globalassets/ew/subw/artd/2.-var-verksamhet/publikationer/31.-rodlista-2020/rodlista-2020.
Smith, F. A. *et al.* (2018) 'Body size downgrading of mammals over the late Quaternary', *Science*, 360(6386), pp. 310–313. doi: 10.1126/science.aao5987.
SNA (1992) *Sveriges nationalatlas - Hav och kust*, *Sveriges nationalatlas - Hav och kust*. Edited by B. Sjöberg. Sveriges nationalatlas.
SNA (2003) *Sveriges nationalatlas - Västra Götaland*. Sveriges nationalatlas.
SOU (2020) *Tillgänglig stränder – ett mer differentierat strandskydd*. Stockholm.
Statistics Sweden (2019) *Natura 2000-områden, antal och areal efter region. År 2002 - 2019*. Available at: https://www.statistikdatabasen.scb.se/pxweb/sv/ssd/START__MI__MI0603__MI0603D/Natura2000N/ (Accessed: 23 November 2020).
Statistics Sweden (2020a) *Skyddad natur*. Available at: https://www.scb.se/hitta-statistik/statistik-efter-amne/miljo/markanvandning/skyddad-natur/ (Accessed: 23 November 2020).
Statistics Sweden (2020b) *Sveriges framtida befolkning 2020–2030*.
Stewart, R. R. and Possingham, H. P. (2005) 'Efficiency, costs and trade-offs in marine reserve system design', *Environmental Modeling and Assessment*, 10(3), pp. 203–213. doi: 10.1007/s10666-005-9001-y.
Sundblad, G. and Bergström, U. (2014) 'Shoreline development and degradation of coastal fish reproduction habitats', *AMBIO A Journal of the Human Environment*, 43(8), pp. 1020–1028. doi: 10.1007/s13280-014-0522-y.
Swedish Agency for Marine and Water Management (2017) *Marina naturreservat*. Available at: https://www.havochvatten.se/arter-och-livsmiljoer/atgarder-skydd-och-rapportering/skyddade-omraden/marina-naturreservat.html (Accessed: 20 November 2020).
Swedish Agency for Marine and Water Management (2018) *Marina nationalparker*. Available at: https://www.havochvatten.se/arter-och-livsmiljoer/atgarder-skydd-och-rapportering/skyddade-omraden/marina-nationalparker.html (Accessed: 18 November 2020).
Swedish Agency for Marine and Water Management (2019) *Nationell marin kartering - Miljöövervakning - Övervakning och uppföljning*. Available at: https://www.havochvatten.se/overvakning-och-uppfoljning/miljoovervakning/nationell-marin-kartering/nationell-marin-kartering.html (Accessed: 7 December 2020).
Swedish Agency for Marine and Water Management (no date) *Fiskereglering i skyddade områden*. Available at: https://www.havochvatten.se/arter-och-livsmiljoer/atgarder-skydd-och-rapportering/skyddade-omraden/fiskereglering-i-skyddade-omraden.html (Accessed: 18 November 2020).
Swedish Environmental Protection Agency (2007) *Skydd av marina miljöer med höga naturvärden*. Available at: http://www.naturvardsverket.se/Documents/publikationer/620-5739-1.pdf.

Swedish Environmental Protection Agency (2010) *Naturreservat i Sverige*. Available at: https://www.naturvardsverket.se/Documents/publikationer/620-8233-7.pdf?pid=3954.
Swedish Environmental Protection Agency (2014) *Rev av ögonkorall*.
Swedish Environmental Protection Agency (2015) *Så bildas en nationalpark*.
Swedish Environmental Protection Agency (2018) *Strandskyddsbeslut*. Available at: http://www.naturvardsverket.se/Miljoarbete-i-samhallet/Miljoarbete-i-Sverige/Uppdelat-efter-omrade/Naturvard/Skydd-av-natur/Strandskydd/Strandskyddsbeslut/ (Accessed: 18 November 2020).
Swedish Environmental Protection Agency (2020a) *Sveriges nationalparker*. Available at: https://www.naturvardsverket.se/Var-natur/Skyddad-natur/Nationalparker/ (Accessed: 18 November 2020).
Swedish Environmental Protection Agency (2020b) *Uppföljning av strandskyddet 2019*. Available at: http://www.naturvardsverket.se/upload/miljoarbete-i-samhallet/miljoarbete-i-sverige/regeringsuppdrag/2019/strandskydd/uppfoljning-strandskyddet-2019.pdf.
Thrush, S. F. *et al.* (2014) 'Muddy Waters: Elevating Sediment Input to Coastal and Estuarine Habitats', *Frontiers in Ecology and the Environment*, 2(6), pp. 299–306.
Törnqvist, O. *et al.* (2020) *Fysisk störning i grunda havsområden – Kartläggning och analys av potentiell påverkanszon samt regional och nationell statistik angående störda områden*.
U.S. Energy Information Administration (2017) *World Oil Transit Chokepoints*. Available at: https://www.eia.gov/beta/international/regions-topics.php?RegionTopicID=WOTC.
UNESCO (1971) *Convention on Wetlands of International Importance especially as Waterfowl Habitat*.
United Nations (1992) *Convention on Biological Diversity*, *Convention on Biological Diversity*. Rio de Janeiro. doi: 10.1016/B978-0-12-384719-5.00418-4.
United Nations (2016) *Arsenic and the 2030 Agenda for sustainable development*, *The 2030 Agenda for Sustainable Development*. doi: 10.1201/b20466-7.
Waldo, S. and Blomquist, J. (2020) *Var är det lönt att fiska? – en analys av fisket i svenska regioner*, *Fokus*. Lund.
Worm, B. and Myers, R. A. (2003) 'Meta-Analysis of Cod-Shrimp Interactions Reveals Top-Down Control in Oceanic Food Webs', *Ecology*, 84(1), pp. 162–173.

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