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Published in:
Environmental Science and Policy

Link to article, DOI:
10.1016/j.envsci.2023.103622

Publication date:
2024

Document Version
Publisher's PDF, also known as Version of record

Citation (APA):
Stounberg, J. L., Timmerman, K., Dahl, K., Pinna, M., & Svendsen, J. C. (2024). Comparing biogenic blue mussel (*Mytilus edulis*) reef definitions in Northern Europe: implications for management and conservation. *Environmental Science and Policy*, *151*, Article 103622. https://doi.org/10.1016/j.envsci.2023.103622

Environmental Science and Policy 151 (2024) 103622

Contents lists available at ScienceDirect

Environmental Science and Policy

journal homepage: www.elsevier.com/locate/envsci

Comparing biogenic blue mussel *(Mytilus edulis)* reef definitions in Northern Europe: Implications for management and conservation

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ARTICLE INFO

Keywords:
Biogenic reef
Blue mussels
EU Habitat Directive
Conservation
Natura 2000
Shellfish

ABSTRACT

To combat biodiversity loss, the European Union (EU) established a network of protected areas to be implemented by 2000, termed Natura 2000 (N2000). However, several N2000 sites remain unmapped, and various habitats remain undefined. Delayed implementation allows continued habitat degradation and biodiversity loss. Targeting biogenic reefs by blue mussels (*Mytilus edulis* and *Mytilus trossulus*), this study 1) compared blue mussel reef definitions across EU member states surrounding the North Sea and Baltic Sea, 2) scrutinized biological mechanisms underpinning the habitat definitions, and 3) provided suggestions for harmonized habitat definitions, respecting spatial and biological variation. By comparing official definitions of blue mussel reefs applied in Denmark, Sweden, The United Kingdom, and Germany, this study revealed A) decadal delay in implementation, B) reef definitions varying significantly regarding number of parameters used for identification (e.g., mussel seabed area (m^2), and proportion seabed mussel coverage (%)) and the associated parameter limits (e.g., 2.500 m^2, and 30%, respectively). Specifically, parameter limits for identification of reefs range between 1 and 10,000 m^2 for mussel area and between 5% and 30% seabed mussel coverage. The study failed to identify biological mechanisms justifying this variation. Variable habitat definitions, unjustified by biological and spatial variation, may result in uneven protection levels across borders, potentially compromising connectivity of the N2000 network. To avoid this scenario, our study highlights the need for compatible biogenic reef definitions reflecting spatial and biological properties and suggests moving from protection of individual reefs to protection of areas where habitat forming blue mussels are regularly occurring.

1. Introduction

Coastal degradation, and the associated habitat and biodiversity loss, is a major threat to marine ecosystems (van der Ouderaa et al., 2021). In Europe, 85% of the coastline is considered degraded (European Environment Agency, 1999), as a result of anthropogenic pressures (Bugnot et al., 2021; Connell et al., 2008; L. Benedetti-Cecchi, 2001), including eutrophication (Lotze et al., 2006), fishing (Beck et al., 2011; Cook et al., 2013; Guidetti et al., 2003; Thrush and Dayton, 2002), resource extraction (Suchanek, 1994), coastal construction (Bugnot et al., 2021; Reise, 2005), and climate change (Lotze et al., 2006).

In response to biodiversity loss, the European Union (EU) launched the Bird Directive (BD) (79/409/EEC) in 1979 and the Habitats Directive (HD) in 1992 (92/43/EEC). The directives are among the oldest in existence and form the cornerstone of Europe's nature conservation policy. The BD aims at conserving wild bird species, mainly through habitat conservation and species protection. The HD aims at ensuring biodiversity through the conservation of natural habitats and wild fauna and flora. The directives have been continually updated and amended, with addition of species, habitats, and supplemented with more detailed habitat descriptions in a series of guidelines to better achieve the objectives (European Commission, 2007, 2013). The habitats protected under HD form the Natura 2000 (N2000) network, an EU wide network counteracting continued deterioration of European territory and biodiversity loss. Member states (MS) are under article 3 of the HD obligated to contribute to the N2000 network with a proportion

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https://doi.org/10.1016/j.envsci.2023.103622
Received 3 March 2023; Received in revised form 9 October 2023; Accepted 18 October 2023
Available online 1 November 2023

representative of the natural habitats, as well as habitats of protected species, which occur within their territory. The proportion is by most MS adjusted to 30% of the natural habitats, in line with the EU 2030 biodiversity strategy goals of protecting 30% of EU sea (European Commission, 2013).

Despite the amendments to the directives, and the guidelines for habitat selection, the N2000 network is still not fully implemented or efficiently managed, and the goals of the directives are not reached, despite the name hinting at a coherent network established by 2000 (Ferranti et al., 2010; Fraschetti et al., 2018; Gerovasileiou et al., 2019). Furthermore, different interpretations of elements within the Habitat Directive among member states (Evans, 2010) may introduce additional conservation in-effectiveness. The delay exceeding 20 years means that protection of several habitats remains incomplete, and the designated N2000 sites are still not forming coherent ecological networks (European Commission, 2007).

Biogenic reefs are globally one of the most threatened marine habitats (Airoldi et al., 2008) and are included in the Annex 1 of the HD: reefs (1170) covering reef structures of both geogenic and biogenic origin. Biogenic reefs consist of hard matter of biological origin e.g., shells, encrustations or corallogenic (European Commission, 2013; Fariñas-Franco et al., 2023). The reefs are often topographically distinct from the surrounding seabed, and the reefs can grow substantially in height and diameter, providing habitat for numerous species. In the seas surrounding Europe, common reefs building species include mussels (*Modiolus modiolus, Mytilus sp.),* polychaetes (e.g., *Sabellaria spinulosa*), cold water corals (e.g., *Lophelia pertusa*), European flat oyster (*Ostrea edulis*) and the invasive pacific oyster (*Crassostrea gigas*) (European Commission, 2013).

Mussel reefs commonly stretch from subtidal zone to the intertidal zone (Ricklefs et al., 2020) and are associated with a wide array of ecosystem services, including sediments stabilization, nutrient cycling, improved water quality, shoreline protection and food products (Commito et al., 2008, 2018; Heckwolf et al., 2021; Khalaman et al., 2021; Lefcheck et al., 2019; Nielsen et al., 2019).

The blue mussel (*M. edulis* and *M. trossulus*) is an important reef building organism capable of creating large three-dimensional structured habitats raising from the surrounding sea floor (Lefcheck et al., 2019). Blue mussels tolerate wide salinity (5–30 PSU) and temperature (0–25 °C) ranges, with *M.* trossulus being adapted to low salinity and *M. edulis* thriving at higher salinity (Knöbel et al., 2021; Pourmozaffar et al., 2020), and thus cover a large geographic range.

Blue mussel reefs are often associated with increased biodiversity (Bateman and Bishop, 2017; Romero et al., 2015) and serve as habitat and feeding grounds for several invertebrates, fish, and birds species (Commito et al., 2018; de Paoli et al., 2015; Díaz et al., 2015; Koivisto and Westerbom, 2012; Kristensen et al., 2015; Lauringson and Kotta, 2016; Norling et al., 2015; Schwartzbach et al., 2020; Sea et al., 2022; van der Ouderaa et al., 2021; van der Zee et al., 2012) and as nursing grounds for the critically endangered European eel *(Anguilla anguilla)* (Schwartzbach et al., 2020).

Habitat heterogeneity and complexity are considered key to understanding biodiversity patterns. Habitat heterogeneity and complexity often correlate with available refugia, quality and quantity of resources and ecological niches (Thomsen et al., 2022). Mussel areas' positive effects on biodiversity, are linked to the habitat provisioning, the structural heterogeneity of the habitat, and the hard substrate provided by the mussels (Tokeshi and Arakaki, 2012). In terms of biodiversity effects, it is also important to consider environmental conditions and ecological gradients, which may determine the specific importance of a biogenic reef for biodiversity. For example, when blue mussel reefs are part of a diverse habitat mosaic, or found in combination with a rocky reef, their impact on biodiversity might appear negligible, whereas blue mussel reefs found in a predominantly soft bottom environment often have drastic effects (Benjamin et al., 2022; Demmer et al., 2022; Khalaman et al., 2021; Koivisto et al., 2011; Rodil et al., 2020; Thomsen et al., 2022; Toone et al., 2023). Blue mussel beds can be subdivided into different habitats, depending on their tidal height (intertidal or subtidal), mussel patch size, and sedimentologic surroundings of which blue mussels can be found on both hard substrates (rocky shores, stones, chalk etc.) and softer sediments (sand, mixed etc.). These ecological characteristics, along with salinity, heavily influence the mussel area's three-dimensional structure and associated species community (Buschbaum and Saier, 2001; Khalaman et al., 2021; Knöbel et al., 2021; Saier, 2001, 2002). Furthermore, a variety of microhabitats are available in the dense mussel matrix of shells, byssal treads and debris and among the crevices between mussels, which creates a diverse habitat, sheltering many species of small crustaceans and fish (Commito et al., 2018; Fariñas-Franco et al., 2023; Orfanidis et al., 2021; Sea et al., 2022).

Degradation of structurally diverse habitats like blue mussel reefs is usually associated with a loss of ecosystem services and decreased biodiversity (Commito et al., 2006; de Paoli et al., 2015; Heckwolf et al., 2021; Lefcheck et al., 2019). Blue mussel reefs are slow to recover and rarely reappear if the basic reef structure is lost (Commito et al., 2006; de Paoli et al., 2015, 2017; Temmink et al., 2021, 2022). This is due to decreased habitat suitability caused by changes in abiotic factors, including current flow and sediment stability, but also a lack of suitable substrate for mussel recruits as they rely on adult conspecifics for settlement and protection from predation, by seeking refuge in the mussel matrix amongst the byssal threads and debris (Commito et al., 2006, 2018, 2019; Rodil et al., 2020). The formation of new mussel reefs from spatfall (i.e., the settlement and attachment of young mussels to the substrate) on bare substrate is therefore rare. Formation of new beds on bare substrate mainly occurs during years with exceptionally good recruitment (Commito et al., 2006; Essink et al., 2005; Nauta et al., 2023; Temmink et al., 2021), and these young beds may not persist. Conservation of fully developed reefs is therefore important for the preservation of this unique habitat, a key objective of the HD.

Fundamental for good connectivity, and the HD goal of favorable conservation status, is equal protection across EU MS. Similar issues have previously been addressed by the Commission (European Commission, 2007) and many authors (Goss-Custard et al., 2004; Marandi et al., 2014; Metcalfe et al., 2013; Ramirez et al., 2017).

The present study investigated the interpretation of the HD habitat "1170 reefs, subtype biogenic reefs of *M. edulis*" in northern Europe, specifically Denmark, Sweden, United Kingdom Offshore, Northern Ireland (UK), Wales (UK), Germany Offshore, Schleswig-Holstein (GER), and Lower Saxony (GER). As part of HD, blue mussel reefs must be defined, mapped, and protected within relevant N2000 areas. Importantly, good connectivity and equal protection across EU MS may be compromised if mussel reef definitions vary significantly between neighboring regions and countries. The overarching objectives of this study were to 1) compare national and regional definitions of blue mussel reefs in northern Europe, 2) assess the scientific basis for the definitions, including work by HELCOM and OSPAR, and 3) discuss management and conservation implications as well as outline approaches to provide operational and complimentary definitions reflecting variations in biological conditions across the North Sea-Baltic Sea transition zone.

2. Methods

2.1. General approach

This study compared blue mussel reef definitions developed by EU MS bordering the North Sea or the Baltic Sea, specifically Denmark, Sweden, United Kingdom Offshore, North Ireland (UK), Wales (UK), Germany Offshore, Schleswig-Holstein (GER), and Lower Saxony (GER). Information on MS reef definitions was extracted from governmental webpages, as well as scientific and grey literature identified using snowball and chain referral techniques (Lecy and Beatty, 2012), a recognized approach used by previous studies (Montenero et al., 2021;

Smith et al., 2021). The collected information (Table 1) was validated by email correspondence with government officials and advisors (Table 2). The email addresses were obtained through government websites. We contacted the most relevant party, whether the contact information was for the head of department, or more ideally an environmental subdivision working with N2000 and coastal ecology directly (Table 2). In cases where only a general email address was available, an email stating the purpose of the study was sent along with a request to forward the message to a governmental specialist on the topic. Detailed contact information will be provided on request, provided consent from participants.

2.2. Blue mussel reef definitions by EU Member States

Definitions of blue mussel reefs were identified using a comprehensive web search. Firstly, relevant governmental departments, environmental consultancies and websites were identified with numerous key words, including "*biogenic reef*," Mytilus *edulis reefs*", "*mussel reefs*", and "*1170 reefs*". If the search provided no useful result, relevant personnel were contacted directly. A definition was considered valid when either an official statement was publicly available on government websites, or when verified by relevant professional personnel, including government officials and legal advisors. Verification was often necessary as some definitions remain unpublished and therefore not directly available.

Table 2
Information on respondents obtained through government websites and emails correspondences.

Institution	Department	Region/ country
Natural Resources Wales	Specialist Advisor – Marine Ecologist	Wales
Miljøstyrelsen (Danish Environmental Protection Agency)	Arter og natur (Species and nature)	Denmark
Sveriges Landbrugsuniversitet (Swedish University of Agricultural Sciences)	Environmental assessment and Marine habitats	Sweden
Havs- och vattenmyndigheten (Swedish Agency for Marine and Water Management)	Enheten för biologisk mångfald (Aquatic biodiversity)	Sweden
Agriculture, Environment and Rural Affairs	DAERA Marine and Fisheries Division, Marine Conservation and Reporting Team	Northern Ireland
Nationalparkverwaltung Niedersächsisches Wattenmeer (National Park administration Lower Saxony Wadden Sea)	Muschelbank monitoring und management (mussel bank monitoring and management)	Germany
Joint Nature Conservation Committee	Marine Evidence and Monitoring Management	United Kingdom

Table 1
International, national and regional definitions of biogenic reefs. The most commonly used parameters to identify biogenic reefs are mussel coverage of the sea floor and a minimum area size requirement. Stability of the reef is applied, among some member states (MS), with three MS using age and three MS using cohorts. Most of the definitions have been formulated from 2013 and later.

	Coverage	Minimum size	Stability	Placement	Other	Year of formulation	Reference
OSPAR	30%	–	–	Intertidal	Mussels binding the underlying substrate and providing habitat for infauna and epibiotic species	2008	(OSPAR, 2008, 2010, 2015)
Helcom	10%	–	–	Subtidal or uninterrupted from subtidal to intertidal		2013	(Helcom, 2013g, 2013f, 2013e, 2013d, 2013c, 2013a, 2013b, 2013p, 2013m, 2013n, 2013l, 2013k, 2013j, 2013i, 2013h, 2013o)
Trilateral Wadden Sea Cooperation (TWSC)	5%	–	–	Intertidal	> 25 m between beds	2002	(Essink et al., 2005)
EUNIS	-	-	-	Differentiated subtidal, intertidal		2019*	(European Commission, 2013; European Environment Agency, 1999)
Denmark	30%	2500 m^2	3 cohorts	Unspecified		2018	(Miljøstyrelsen, 2018)
Sweden	10%	-	-	Subtidal		2014	(Naturvårdsverket, 2000, 2011, 2012, 2014)
UK offshore (JNCC)	-	-	> 2 years	Subtidal		2014	(Fariñas-Franco et al., 2014)
North Ireland (UK)	30%	2 m^2	> 2 years	No differentiation ***		2014	(Fariñas-Franco et al., 2014)****,
Wales (UK)	30%	10 m^2*	> 2 years	No differentiation ***	Protruding 2–30 cm	2014	(Fariñas-Franco et al., 2014)****
Germany offshore	5% (North Sea), 10% (Baltic Sea)	100 m^2 along a 25 m axis	2–3 vintages (cohorts)	Subtidal (Sublittoral)	Core cover of 100%	2018	(Hendrischke, 2018)
Schleswig-Holstein (GER)	10%	10,000 m^2	2–3 vintages (cohorts)	Subtidal	Protruding 20 cm, less than 25 m between beds	Not fully formed	Email contact with Landesbetrieb für Küstenschutz, Nationalpark und Meeresschutz Schleswig-Holstein
Lower Saxony (GER)	5%	–	–	Subtidal	Less than 25 m between beds	2020	(von Drachenfels, 2020)

* *25 m^2 in practices due to mapping abilities.
* in 2012 and amended in 2019,
*** Special Areas of Conservation cannot be designated on the basis of intertidal reefs
**** Not differentiated but intertidal and subtidal beds are considered different habitats.

2.3. Blue mussel reef definitions by intergovernmental organizations

EU MS reef definitions are often referring to definitions by intergovernmental organizations. Key environmental organizations covering the target area (i.e., North Sea and Baltic Sea) were identified via the literature from MS reef definitions (i.e., the snowball technique; Lecy and Beatty, 2012). The technique involves searching back in time via citations until the primary literature is identified. After identifying intergovernmental organizations, and primary literature, organization websites were examined for additional information using similar key words as previously (Section 2.1).

3. Results

3.1. Implementation of the Habitat Directive

The N2000 network was formed with the formulation of HD and its combination with the BD, as a measure to combat biodiversity loss. According to Articles 4.1 and 4.2 in the HD, MS must formulate a list of Annex 1 habitats within its territory. The list was to be transmitted to the Commission within three years of the HD's notification, together with information on each site. Within six years of the notification of the HD, the listed habitats were to be established in the network. These deadlines occurred in the late 1990 s and early 2000 s, however the implementation of the N2000 has been delayed, especially for marine habitats (European Commission, 2007) as addressed by the EU commission in 2007 with a set of marine guidelines (European Commission, 2007) and an interpretation manual in 2013 (European Commission, 2013). The delayed implementation of the HD by MS has been well documented during recent decades and several obstacles such as lack of political will, conflicts and resistance, lack of common understanding, acceptance, and compliance as well as contradictions between EU and national legislation have been identified (Ferranti et al., 2010; Fraschetti et al., 2018; Weber and Christophersen, 2002). The biogenic blue mussel reefs provide an example of the delayed implementation related to the Habitat Directive as only six of the countries bordering the North Sea and Baltic Sea have a blue mussel reef definition – a prerequisite for mapping and protection of the habitat. Furthermore, the definitions investigated here have all been formulated from 2008 and onwards (Table 1), with the Schleswig-Holstein reef definition still in progress.

3.2. Biogenic reefs in the HD

According to the HD interpretation manual (European Commission, 2013), biogenic reefs are characterized by 1) ***Biogenic concretions***, reef structures originating from dead or live animal material, creating hard bottom habitats supporting epibiotic species, 2) ***Topography***, which means that the reef must be distinct from the surrounding seafloor, 3) ***Associated biota***, mainly relevant in cases with overlying mobile sediment, where the biota must be dependent on hard substrate, and 4) ***Zonation***, because the reef may extend from the subtidal (sublittoral) uninterruptedly into the intertidal (littoral) zone or may only occur in the sublittoral zone. Importantly, mussels only located in the intertidal zone are associated with the HD habitat 1140 mudflats, as a characteristic species community, not 1170 reefs (European Commission, 2013). Specifically, intertidal reefs are only classified as 1170 reef according to HD, if there is an unbroken link between subtidal and intertidal components (European Commission, 2013). This is a crucial differentiation, because tidal placement strongly influences the structure of blue mussel areas (Brinkman et al., 2002; Buschbaum and Saier, 2001; Saier, 2001, 2002), associated communities and biodiversity (Buschbaum and Saier, 2001, 2003; Saier, 2002).

3.3. Biogenic reef definitions for the North Sea and Baltic Sea

In total, this study identified 12 definitions of biogenic reefs by blue mussel provided by governmental and intergovernmental organizations relevant for the North Sea and Baltic Sea area (Table 1). Many of the blue mussel reef definitions include the parameters: minimum area (m^2 of seabed with mussels), seabed mussel coverage (% seabed covered by mussels), a stability indicator (age of the reef (years) or numbers of mussel cohorts) and distinguish between intertidal and subtidal locations (Table 1). Four definitions have added further specification, including protrusion (2–30 cm), core cover (100%) and maximum distance (>25 m) between individual mussel beds. Denmark, North Ireland, and Wales have not specified the tidal elevation (intertidal and subtidal; Table 1).

Five of the nine definitions from the six countries include the parameter "minimum area" (m^2). Large variation in parameter limit was revealed by the present study with minimum area limits ranging from 2 m^2 to 10,000 m^2, a difference representing several orders of magnitude (Table 1).

Likewise, seabed mussel coverage limits used for reef identification vary substantially between MS definitions. Specifically, mussel coverage limits varied between 5% and 30% (Table 1). OSPAR's definition for intertidal blue mussel beds was used for the 30% mussel coverage limit in the reef definitions applied by Denmark (Miljøstyrelsen, 2018), North Ireland (Fariñas-Franco et al., 2014) and Wales (Fariñas-Franco et al., 2014). Blue mussel reef definitions applied by the remaining countries, all bordering the Baltic Sea, use a mussel coverage of 10%, or less, in line with the guidelines and habitat descriptions provided by HELCOM. The German reef definitions differentiate between the North Sea and Baltic Sea by using different mussel coverage limits for the North Sea (5%) and Baltic Sea (10%) to accommodate the environmental differences (Hendrischke, 2018).

Six definitions (50%) specify a parameter for reef stability, either as the age of the mussel area (years), or the number of cohorts present in the mussel bed. Denmark and Schleswig-Holstein use three and two cohorts, respectively, as stability indicator, whereas the remaining four definitions use the age of the mussel area (>2 years), making age the most applied stability indicator. At the age of two years, blue mussels are considered sexually mature (Saurel et al., 2004), and predation pressure significantly decreases (Buschbaum and Saier, 2001; Saier, 2001; Saurel et al., 2004).

The documented differences in the number of parameters, and the remarkable variation in parameter limits, indicate substantial differences among MS in the number and extend of biogenic reefs identified, mapped, and added to the N2000 network for protection.

3.3.1. Scientific documentation used in biogenic reef definitions

MS rely on work by intergovernmental organizations including OSPAR, HELCOM and the Trilateral Wadden Sea Cooperation (TWSC) when defining blue mussel reefs (Table 1). The definition provided by OSPAR (OSPAR, 2008, 2010, 2015) is specifically intended for intertidal mussel reefs in the Northeast Atlantic Ocean and requires 1) 30% minimum seabed coverage of blue mussels (Table 1) 2) mussels binding the underlying substrate, and 3) mussels providing habitat for infauna and epibiotic species (OSPAR, 2015). The habitat is strictly intertidal, found on mid-lower shore or in the lower tide-swept parts of the shores (OSPAR, 2015). The definition and background material by OSPAR do not include minimum mussel area (Table 1), with stability only mentioned regarding the exclusion of beds formed from periodic spatfall (Table 1).

HELCOM consists of MS with only Russia not being part of EU and targets marine protection and conservation of the Baltic Sea, including Kattegat situated between Denmark and Sweden. HELCOM considers blue mussel a habitat forming species and provides several descriptions of mussel dominated habitats (Helcom, 2013g, 2013f, 2013d, 2013e, 2013c, 2013b, 2013a, 2013n, 2013m, 2013l, 2013k, 2013j, 2013i). The definitions require a minimum of 10% cover of epibenthic bivalves, and the bivalves must be more prevalent than any other perennial erect group (e.g., *Fucus*). Furthermore, Mytilidae must constitute at least 50%

of the biomass (Helcom, 2013g, 2013f, 2013d, 2013e, 2013c, 2013b, 2013a, 2013n, 2013m, 2013l, 2013k, 2013j, 2013i) (Table 1).

TWSC targets mussel beds, not biogenic reefs per se, and differentiates intertidal and subtidal mussel beds, based on biological and structural differences (Essink et al., 2005). A definition of subtidal beds remains unavailable (Essink et al., 2005). Intertidal mussel beds are defined by TWSC as collections of mussel clusters, with the blue mussel seabed cover exceeding 5% with > 25 m between patches (Table 1) (Fig. 1). TWCS operates with two different terms for stability: 1) stable sites 2) stable beds. Stable sites are areas where mature beds (>2 years) regularly form (Essink et al., 2005) (Table 1). Stable beds are defined as blue mussel areas that are recognizable over several years (Essink et al., 2005).

4. Discussion

Targeting definitions of biogenic reefs formed by blue mussel (*Mytilus edulis* and *Mytilus trossulus*), this study revealed A) decadal delay in defining biogenic blue mussel reefs with implications for the implementation of the Habitat Directive, B) blue mussel reef definitions varying significantly regarding the number of parameters (e.g., mussel seabed area (m^2) and proportion seabed mussel coverage (%)) and the associated parameter limits (e.g., 2.500 m^2 and 30%, respectively) for reef identification. This variation seems arbitrary as it rarely reflects the spatial e.g., tidal height (Saier, 2001, 2002), physical e.g., salinity (Knöbel et al., 2021), submersion time (Brinkman et al., 2002), and substate (Commito et al., 2006, 2008; de Paoli et al., 2015; Díaz et al., 2015; Koivisto and Westerbom, 2010) and ecological e.g., mussel size (Khaitov, 2013; Svane and Ompi, 1993), recruitment (Beukema and Dekker, 2007; Mutti et al., 2021), and predation (Buschbaum and Saier, 2001; Commito, 1987; Lauringson and Kotta, 2016; Ricklefs et al., 2020; Saier, 2001, 2002) variation characteristic for the North Sea and Baltic Sea areas.

4.1. Unjustified and excessive variation in definition parameters and their limits threatens connectivity

With the N2000 Network designed to cover all EU MS, ecological and physical variation should be reflected in the national definitions. The observed variation in definitions of biogenic reefs may become problematic if it does not reflect environmental differences. Large variation should therefore not occur between neighboring MS sharing an inlet, an estuarine area, or similar. Considering the proximity of the MS in this study, the variations in the number of parameters (e.g., mussel seabed area (m^2) and proportion seabed mussel coverage (%)) and the associated parameter limits (e.g., 2.500 m^2 and 30%, respectively) are striking, and likely to exceed the ecological variance. With no known detailed studies investigating specifically at what mussel area size, % seabed coverage, and age a blue mussel area is a blue mussel reef, parameters and parameter limits should be based on recent research, case studies and what is operationally feasible.

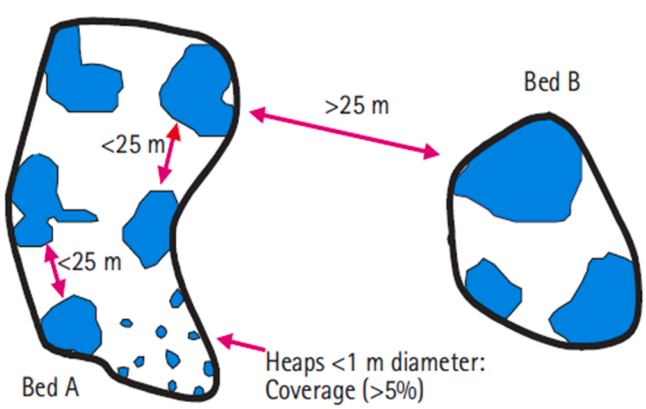

Fig. 1. Bed A and B are considered separate as there is more than 25 m between them. The standardized surface area of each bed is indicated by the black enveloping lines. The small heaps are considered part of bed A as their cover exceeds 5% and they are less than 25 m to the remainder of the bed. Seabed coverage is calculated as % seabed coverage = (sum of patch surfaces / total surface of bed envelope) x 100% (Essink et al., 2005).
Modified from Marencic (2009).

Salinity is a major determinant for blue mussel growth, with low salinity often dwarfing mussels (Beyer et al., 2017; Kautsky et al., 1990; Pourmozaffar et al., 2020; Tedengren and Kautsky, 1986). Mussel size influences reef topography (Saier, 2002), and structural differences in blue mussel reefs are therefore expected between the North Sea and the Baltic Sea, with mussel reefs in the Baltic Sea consisting of smaller mussels due to the suboptimal living conditions (i.e., suboptimal salinity) (Beyer et al., 2017; Kautsky et al., 1990; Pourmozaffar et al., 2020; Tedengren and Kautsky, 1986), often with a lower seabed mussel coverage (%) common for subtidal mussel (Brinkman et al., 2002; Buschbaum and Saier, 2001; Saier, 2001, 2002). In the subtidal transition zone between the North Sea and Baltic Sea, less is known about typical mussel densities, however densities from 0 to > 90% coverage have been reported. MS bordering both the North Sea and Baltic Sea e.g., Denmark and Germany, should account for the ecological differences with unique definitions reflecting the salinity gradient between the two seas.

Reef structure is heavily affected by tidal placement due to differences in submersion time (Benjamin et al., 2022; Brinkman et al., 2002; Saier, 2002), predation (Goss-Custard et al., 2004; Lauringson and Kotta, 2016; Norling and Kautsky, 2007, 2008; Saier, 2001; van der Zee et al., 2012) and recruitment (Capelle et al., 2017; Mutti et al., 2021; Saier, 2002) (Fig. 2). The intertidal zone is an unstable enviroment often dominated by dense, low diversity communites of species tolerant of air exposure, such as blue mussel, as they experience less interspecific competition. Intertidal mussel areas are therefore denser, less diverse and relatively species poor compared to the subtidal counterparts Indeed, these findings are supported by systematic reviews (Buschbaum and Saier, 2001, 2003; Saier, 2002). Intertidal mussels exhibit lowered growth rates, largely due to their inability to feed during air exposure and are therefore often smaller than subtidal mussels (Brinkman et al., 2002; Buschbaum and Saier, 2001; Saier, 2001, 2002). In addition, intertidal mussels are often more overgrown by barnacles than subtidal mussels, lowering predation by sea stars (*Asterias rubens*) (Buschbaum and Saier, 2001) and increasing recruitment (Saier, 2001), both adding to the differences in mussel coverage and structure between intertidal and subtidal mussel areas (Fig. 2).

It is therefore important to differentiate between intertidal and subtidal mussel areas when defining a biogenic reef. The two types of mussel areas are clearly differentiated in the N2000 habitats interpretation manual with intertidal mussel areas strictly associated with the HD habitat 1140 mudflats as a characteristic species community, whereas subtidal mussel areas are considered as 1170 reefs, subtype biogenic (European Commission, 2013). Importantly, intertidal reefs are only considered part of 1170 reef if there is an unbroken link between subtidal and intertidal mussel areas (European Commission, 2013). It is therefore surprising that several nations and regions, including Denmark, Wales, and North Ireland, use OSPAR background material intended for intertidal mussel areas as justification for a 30% mussel coverage when defining 1170 biogenic reef (OSPAR, 2015). However, tides are small in many Danish waters, and tidal mussel beds are mainly common in the Danish Wadden Sea. Furthermore, the protection of only the densest mussel areas, can be perceived as a failure to recognize the existence of less dense, but nevertheless ecologically very important mussel settlements, which may be considered counterproductive when the aim is to ensure biodiversity through a network of natural habitats.

Not only is the OSPAR material meant for intertidal mussel areas, but the material is also targeting the Northeast Atlantic region, a high saline

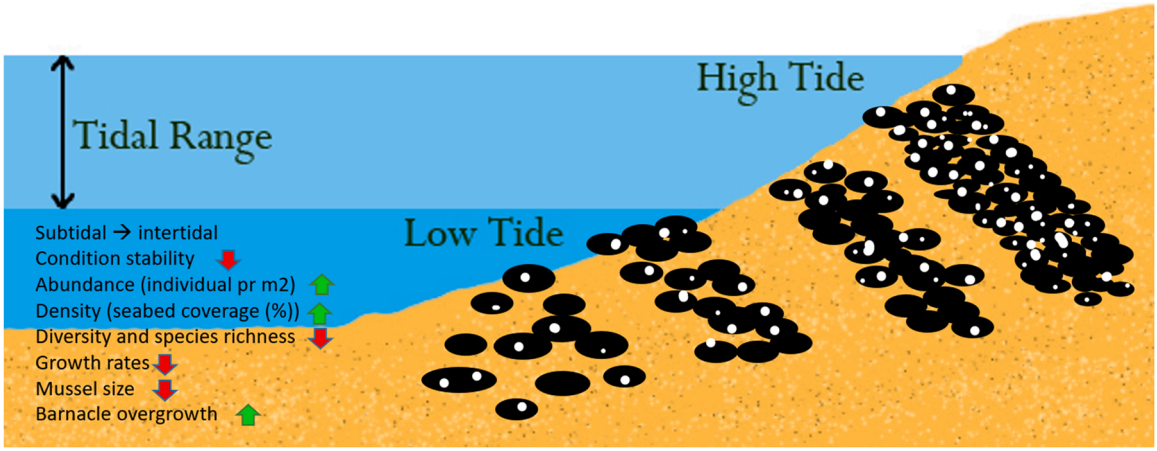

Fig. 2. Variations in mussel habitats moving from subtidal to intertidal. Modified from (Buschbaum and Saier, 2001; Saier, 2001, 2002).

area, in contrast to subtidal and low saline areas like the Baltic Sea. Because countries like Denmark are bordering both the North Sea and the Baltic Sea, the sole use of the OSPAR definition in Denmark may not capture biogenic reefs in the Baltic Sea part of the Danish waters. When comparing Denmark to Germany, the only other nation bordering both the Baltic Sea and the North Sea (including its special sub basin of the Wadden Sea), the differences in the definitions are striking. This study found Denmark to be the only nation bordering the Baltic Sea and requiring a 30% seabed mussel coverage, with Sweden and Germany requiring 10% in the Baltic Sea, in agreement with the HELCOM recommendation, and with Germany using 5% seabed mussel coverage for the Wadden Sea. Due to Denmark's 30% seabed mussel coverage requirement, mussel habitats in the Danish part of the Baltic Sea are likely not granted the same protection as in Sweden and Germany. Application of a lower mussel coverage in the reef definition will increase the probability of the mussel habitat to be included in the protection scheme. However, some data from the Danish national monitoring program (NOVANA) on reef locations in the Baltic Sea, east of the Gedser-Dars sill, document high coverage of mussels, perhaps due to limited predation pressure by common sea stars (*Asterias rubens*) in the area.

The Danish definition disregards empty shells and shells hash from the % seabed mussel coverage (Miljøstyrelsen, 2018). It remains unclear if this is the case for other 1170 biogenic reef definitions as well. Exclusions of empty shells and shell hash are problematic due to the importance of shells for mussel recruitment (Commito, 1987; Khaitov, 2013; Svane and Ompi, 1993), and recovery of lost mussel areas. Empty shells and shell hash are crucial, because mussel areas formed on bare substrate often degrade during the first winter season (de Paoli et al., 2015, 2017; Essink et al., 2005).

This study also found large definition variations in the parameter mussel area (m^2) with the parameter limit varying strikingly between 2 and 10,000 m^2 required for a mussel area to be considered a biogenic reef. North Ireland and Wales have the lowest area requirement of 2 m^2 and 10 m^2, respectively, significantly lower than the 10,000 m^2 required by Schleswig-Holstein (in Germany). Habitat topography and characteristics (e.g., % seabed mussel coverage and mussel size) (Commito et al., 2006; Díaz et al., 2015; Guichard and Bourget, 1998; Svane and Ompi, 1993), as well as species diversity (Koivisto and Westerbom, 2010; Koivisto and Westerbom, 2012; Lauringson and Kotta, 2016; Norling and Kautsky, 2007, 2008), recruitment and predation (Capelle et al., 2017) can change immensely between 2 and 10,000 m^2. The reasoning (Miljøstyrelsen, 2018) for mussel area size being an important factor is the notion that biodiversity often increases with habitat size, as indicated by some studies (Dittmann, 1990; Norling and Kautsky, 2007, 2008). However, biodiversity rarely increases indefinitely with area size (Dittmann, 1990; Norling and Kautsky, 2008; Tokeshi and Arakaki, 2012). Instead, biodiversity is typically plateauing at a certain size (van der Ouderaa et al., 2021). For example, a Swedish study reported biodiversity to increase with patch size up until around 4 m^2 where it leveled off and began to plateau (Norling and Kautsky, 2008), indicating little or no increase in biodiversity beyond 4–5 m^2. Studies have even indicated positive biodiversity effects of just a few mussels (Lauringson and Kotta, 2016; Norling and Kautsky, 2007, 2008). If the findings are representative for mussel areas in the Baltic Sea, the presence of mussel patch matters more than the size of the mussel areas for biodiversity (Benjamin et al., 2022; Lauringson and Kotta, 2016; Norling and Kautsky, 2007, 2008). Indeed, these findings are supported by systematic reviews (Bateman and Bishop, 2017; Romero et al., 2015), and studies investigating habitat heterogeneity effects on biodiversity (Hall et al., 2018; Soukup et al., 2022; Tokeshi and Arakaki, 2012; van der Ouderaa et al., 2021). The majority of studies cited in this paper describes the diversity of the associated species communities (Buschbaum and Saier, 2001; Commito et al., 2006, 2008; Koivisto and Westerbom, 2012; Saier, 2002), as few studies on the effect of mussel area size on biodiversity of fish, birds and marine mammals exist (Goss-Custard et al., 2004; Schwartzbach et al., 2020; van der Zee et al., 2012). The diversity of the associated communities will likely plateau faster than for larger more mobile species such as fish and seabirds, an understudied area beyond the scope of this article. In general, heterogenic habitats with large variation in sizes of crevices, different current exposures etc. support higher biodiversity but lower abundance than more uniform habitats, often harboring high abundances of a few species (Tokeshi and Arakaki, 2012). The positive correlation between habitat heterogeneity and biodiversity indicates a maximum biodiversity capacity for a given habitat, suggesting that habitat size matters less than its heterogeneity. To the best of our knowledge, there is no biological justification for blue mussel area size requirements above 5–10 m^2 if the target is biodiversity. Management of individual mussel areas of this size is not feasible and area size requirements must therefore be based on what is operational as well as biologically significant, a field beyond the scope of the present study.

For conservation and management reasons, habitat stability is important, because MS, according to Article 4.4 of the HD, must maintain and/or restore a site to a favorable conservation status. The age and state of a blue mussel area affect the composition of species community, as well biodiversity (Commito et al., 2018; Koivisto et al., 2011; Koivisto and Westerbom, 2010; Ricklefs et al., 2020). The various methods used to assess the age of a mussel area vary in required time and effort. Age can be estimated by 1) the number of cohorts (Koivisto and Westerbom, 2010; Ricklefs et al., 2020), 2) monitoring the mussel area across time (Essink et al., 2005), or by 3) the presence of mature mussels (Essink

et al., 2005). Cohorts are commonly determined using mussel dredging (Ricklefs et al., 2020), an invasive method which can interfere with the integrity of the mussel area (de Paoli et al., 2015, 2017), increasing the risk of dislogment. Other issues regarding the use of cohorts when estimating age is the reduced growth when blue mussel reach maturity, potentially lumping several cohorts in one size group and blurring the true number of cohorts (Commito, 1987; Commito et al., 2006). In addition, recruitment failures have increased in recent times (Beukema and Dekker, 2007; Commito et al., 2018, 2019; Essink et al., 2005; Pogoda et al., 2020; Ricklefs et al., 2020), and there may be several years between detectable cohorts (Commito, 1987; Commito et al., 2006). This makes it difficult to accurately estimate mussel area age using cohorts, as the number of cohorts may not be equal to the age of the mussel area. Age and stability determination using annual monitoring provide the most precise estimate of reef stability, but it is expensive, difficult and time consuming (Essink et al., 2005; Ricklefs et al., 2020), often making it economically infeasible. This makes the presence of mature mussels the most feasible approach to indicate stability of a mussel area, due to the simplicity of the approach. In the North Sea and Baltic Sea, blue mussels are often around two years when they reach maturity (Saurel et al., 2004), associated with a significant drop in the predation pressure and the risk of dislodgement (Beukema and Dekker, 2007; Brinkman et al., 2002; Essink et al., 2005; Saurel et al., 2004). Mussel areas hosting mature mussels are therefore regarded as mostly stable (Essink et al., 2005).

As a bioengineered habitat, there are limits to mussel reef stability, because area covered (m^2) and % seabed coverage of the individual areas vary with recruitment (Commito, 1987; Dittmann, 1990; Mutti et al., 2021; Svane and Ompi, 1993), predation pressure (Buschbaum and Saier, 2001; Capelle et al., 2017; Goss-Custard et al., 2004; Saier, 2001; van der Zee et al., 2012) and mortality of aging mussels (Commito et al., 2018; Khaitov, 2013; Koivisto et al., 2011). Especially subtidal blue mussel beds in high saline areas seem to be less stable than for example intertidal mussel beds with an average survival time of less than 5 years (Troost et al., 2022). As the HD requires MS to maintain and restore habitats to a favorable conservation status, it may be considered problematic to protect a habitat declining by broad natural causes. Restoration of mussel areas is labor intensive and expensive, with high failure rates (de Paoli et al., 2015, 2017), potentially making the conservation of mussel areas resource demanding. For this reason, MS often aim to map and protect the most pristine and stable habitats. To better encompass the dynamic nature of blue mussel habitats, focus may be shifted from protecting individual reefs to protecting areas where mussel beds regularly occur. This would require an increased focus on 1) broader locations where dynamic habitats with changing boundaries occur within a broad area, and 2) how individual reefs and mussel patches are connected, for example by dispersal of eggs and larvae. This would resemble a recent approach applied for habitat conservation and management in urban and coastal areas (Holon et al., 2018; Nelli et al., 2022).

5. Final remarks and recommendations

This study highlights challenges associated with the use of rigid parameter limits to define and subsequently protect dynamic habitats engineered by a relatively short-lived species like the blue mussel. MS generally have vague definitions of biogenic reefs (e.g., Sweden and UK offshore) and none had a definition prior to 2014, and the offshore German definition remain under development. Clearly, such vague and incomplete definitions hamper identification and protection of biogenic reefs. The existing definitions of biogenic reefs show striking variation in the number of parameters e.g., mussel seabed area (m^2), mussel coverage (%), and age of the biogenic reef (years), and the associated parameter limits used for reef identification. The variation in parameter numbers and parameter limits is not justified by biological variation and will have implications for conservation of mussel beds in comparable environments, as less rigid definitions will allow for a wider range of mussel beds to be identified, mapped and protected. To avoid compromising the integrity of the N2000 network, we recommend a more harmonized approach to blue mussel reef definitions. Because positive biodiversity effects of the associated species community are plateauing when a mussel area exceeds a few m^2, the area size requirements should be kept correspondingly low, considering what is feasible and operational.

In subtidal, mussel dominated habitats, mussel coverage varies considerably in both time and space depending on the local environmental conditions. Whereas a mussel seabed coverage of 10% may accurately reflect the suboptimal living conditions (e.g., low salinity) in the Baltic Sea, and the OSPAR definitions of 30% coverage is suitable for intertidal mussel beds in the Northeast Atlantic Ocean, less is known for blue mussel coverage in the transition zone between the North Sea and Baltic Sea. However, considering the importance of empty shells and shell hash for recruitment and recovery of lost mussel areas, empty shells should be included in biogenic reef definitions.

The dynamic and occasionally unstable nature of blue mussel biogenic reefs remains a challenge for management and may question the suitability of individual (and possibly unstable) blue mussel reefs as a habitat *sensu* the Habitat Directive. In addition, measures of mussel bed stability such as age, size of individual mussels, and in particular number of cohorts, induce monitoring challenges and additional costs. Instead, we recommend moving from protection of individual blue mussel reefs to protection of areas where habitat forming blue mussels are regularly occurring. This will likely aid in site selection and associated management, ensuring the needed protection of blue mussel reefs, including the site-specific characteristics, unstable nature, and important ecosystem services.

Author statement

The work is original, and all authors approved the submitted manuscript J.C. Svendsen conceived the idea for the study and J. L. Stounberg conceived the study design and collected the data. J. C. Svendsen, K. Timmerman, K. Dahl and M. Pinna contributed with expert knowledge and J.L. Stounberg wrote the manuscript. All authors critically reviewed the manuscript and gave comments.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

No data was used for the research described in the article.

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