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DECLINING POPULATIONS OF *MYTILUS* SPP. IN NORTH ATLANTIC COASTAL WATERS—A SWEDISH PERSPECTIVE

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ABSTRACT During the past 2–3 decades, the spatiotemporal distribution of *Mytilus* spp. in coastal waters of the North Atlantic has changed considerably. In general, reduced abundances of *Mytilus* are observed, but there is a great degree of local variation, and some areas are also experiencing recovery after declining events. In this review, hypotheses regarding the causes behind the changes are presented with focus on a Swedish perspective. Excessive exploitation of mussel banks combined with direct and indirect effects of climate change are most probably the main drivers of *Mytilus* spp. decline in large parts of the North Atlantic. On the Swedish west coast, the wild stocks have disappeared despite no overfishing. Paradoxically, they thrive in mussel farms and on other non-demersal substrates. Changes in predation from, for example, increased wintering populations of eiders (*Somateria molissima;* 10-fold) and green crabs (*Carcinus maenas;* 3-fold), alteration of natural substrates elicited by eutrophication, and exacerbated by climate change (increased sea surface temperature, precipitation and extreme weather events) are most likely the key factors for the decline. Most anthropogenic stressors may not be decisive by themselves, but combined effects can potentially be fatal to *Mytilus* spp. adults and larvae.

KEY WORDS: *Mytilus* spp. decline, North Atlantic, Swedish west coast, climate change, direct and indirect effects

INTRODUCTION

Blue mussels of the *Mytilus edulis* (L.) species complex (hereafter *Mytilus* or mussels) are reef-building foundation species (Dayton 1972). They are distributed along the coasts of the North Atlantic and adjacent sea areas, and the species complex includes three incompletely separated and hybridizing species: *M. edulis* occurs in the northeastern and northwestern Atlantic, *Mytilus trossulus* (Gould) occurs in northwestern Atlantic and the Baltic Sea, and *Mytilus galloprovincialis* (Lamarck) occurs in the Mediterranean and the warmer parts of the Atlantic coasts (see Genetic Drift and Hybridization section).

Mussel shells are found in archaeological excavations of kitchen middens from the Mesolithic period and have thus for thousands of years been taken for granted along littoral coasts. The mussels were important food items and bait for hunter-gathers and later also for agriculturalists (Gutieìrrez-Zugasti et al. 2011, Hood & Melsäther 2016, Lewis et al. 2016). It is an understatement to say that *Mytilus*, as well as other reef-building mussels, through time and space are considered to be of great ecological and socioeconomic significance.

Presently, *Mytilus* is regarded as an important ecosystem engineer as their multilayered beds create a complex habitat for a high biodiversity of invertebrates including juvenile *Mytilus*. Mussel beds are moist and cool through low tides and provide protection from waves through high tides (see Seuront et al. 2019 for review). They have a crucial ecological role as prime food for many sea birds, fish species, walruses, sea otters, and seals, and important nourishment for many invertebrates including crabs, sea stars, and whelks. Larvae of *Mytilus* are even cannibalized when getting too close to adult inhalant siphons (Troost et al. 2004, Newell et al. 2010, review by Beyer et al. 2017).

The paramount utility includes the use of *Mytilus* as a frequently used biomarker for environmental stress since they are sessile (providing local-specific information), filtering organisms, and highly tolerant of both natural and anthropogenic stressors. They act as vectors for pollution and infectious microbes in the water phase for further transmission to higher trophic levels (see Effect of Stressors section). Since the 1960s, mussels have been used frequently as sentinel organisms in coastal waters (Beliaeff et al. 1998, Cantillo 1998). The scientific literature on the key words "*Mytilus* * biomarker" gives 25,800 results (scholar.google.com, May 22, 2021). The use of *Mytilus* as biomarkers is well established and further standardized in mussel monitoring documents, for example, from UNESCO (1992), National Oceanic and Atmospheric Administration (Lanksbury et al. 2010, Lanksbury & West 2012), International Credential Evaluation Service (ICES) (Davies & Vethaak 2012), OSPAR (2012), and European Commission (EC 2014) (for review and references see Beyer et al. 2017 and Pollutants section).

Even hardy and tolerant organisms like *Mytilus* have tolerance limits and can be negatively affected when the environmental burden peaks. In addition to overfishing, changes in coastal ecosystems, increasing emission of anthropogenic pollutants, and recent climate change has also contributed to increased stress within the vital coastal zone. Climate change is already causing record sea surface temperatures (SST), reduced salinity caused by more rain and land runoff, ocean acidification (OA), increased wave exposure often in combination with extreme (locked) weather events (Bindoff et al. 2019, Collins et al 2019, IPCC 2019).

The general decrease in wild populations of *Mytilus* during recent decades has been reported from an increasing number of countries along the North Atlantic coast (more details described in North Atlantic Coastal Waters: Spatiotemporal Variation of *Mytilus edulis* Species Complex section). Recent, very concerning reports describe an almost total absence of

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adult and settling *Mytilus* in waters along the Swedish west coast. Paradoxically, settling still occurs in mussel farms and other floating artificial substrates, but not on natural substrates nearby.

This review summarizes investigations of the spatiotemporal changes of *Mytilus* with special emphasis on the Swedish west coast and draws upon the extensive knowledge and access to primary data of the authors. Hypotheses relevant for understanding the declining trend are presented and evaluated.

NORTH ATLANTIC COASTAL WATERS: SPATIOTEMPORAL VARIATION OF *MYTILUS EDULIS* SPECIES COMPLEX

The status of *Mytilus* beds in the European Atlantic zone was evaluated under the European commission between 2013 and 2016 with relation to degree of exposure and the subsequent type of substrate. No comprehensive maps for these mussel habitats exist. For many exposed mussel beds, temporal data are often lacking, but data from some locations indicate that these mussel beds are relatively stable. In the more sheltered littoral and sublittoral zones, there is stronger evidence for a large decline in the extent of *Mytilus* beds. In the littoral zone, the mussel beds have declined by more than 50% making these beds "endangered." In the sublittoral zone, the decline is greater than 30% being "near threatened" according to the European Red List of habitats (Gubbay et al. 2016). Significant declines in the extent and biomass of intertidal mussel beds have also been reported in the OSPAR Maritime Area and particularly in Region II (= "the Greater North Sea"). Recommendations for further protection of intertidal mussels in regions II and III are mentioned in OSPAR (2015). This review briefly complements the narrative of the spatiotemporal changes in the different sea areas of the North Atlantic (including the Baltic Sea) with special focus on the Swedish west coast.

Northwest Atlantic Coast

Along the northwest Atlantic coast, the distribution of *Mytilus* spans from the Arctic to North Carolina (Dall 1889, Gosner 1971). During the past 40 y, the mussels along the Gulf of Maine (450 km) have declined by approximately 60% (Sorte et al. 2017). Further, the southern range of *Mytilus* has contracted to 350 km northward from Cape Hatteras (North Carolina) during the last 50 y (Jones et al. 2010). The hypotheses for the decline are multifold, but dominated by overfishing and increasing water temperature. The mussels are abundant in coastal areas of the Atlantic Canada, West Greenland, and Iceland, but no reports on temporal and spatial changes were found. In the southern part of the Northwest Atlantic coast *Mytilus edulis* dominate whereas *Mytilus trossolus* as well as *Mytilus galloprovincialis* dominate in the northern part. Hybrids may contribute up to 30% of the population (Tam & Scrosati 2011, Mathiesen et al. 2016).

Northeast Atlantic Coast

On the Iberian coast along Portugal and Spain *Mytilus* is represented by *Mytilus galloprovincialis* mainly occurring in the sublittoral of exposed shores dominating the coast (Boaventura et al. 2002). The small-scale traditional fishery is dominating and the subsequent decrease in density of mussels results in larger individuals related to areas with more intense fishery in near urban areas (Rius & Cabral 2004, Veiga et al. 2020). Conversely, Bertocci et al. (2012) found no difference in total abundance, and abundance of larger individuals in explored areas compared with a nature reserve area. Spatiotemporal information on *M. galloprovincialis* along the Portuguese coast is lacking. A recent successful effort to fill this gap using drones with ground proofing showed bell-shaped variation in density with increasing wave exposure (Gomes et al. 2018). No reports on decline or mass mortality from the Iberian coast were found, but there are concerns for the wild mussel stocks and associated fauna caused by extensive seed mussel fishery from the rocky intertidal of NW Spain to supply floating rafts of mussel cultures (Pineiro-Corbeira et al. 2018).

In France, however, recurrent mass mortalities of mixtures of *Mytilus edulis* and *Mytilus galloprovincialis* have occurred the last decade. The reasons are still unclear, but Benabdelmouna and Ledu (2016) suggested genetic abnormalities due to hybridization whereas Lupo et al. (2021) in their review suggested elevated SST (despite the higher temperature tolerance for *M. galloprovincialis*), predation, and pathogens. On the French coast around Boulogne-sur-Mer, a series of 4–5 heat waves caused a mass mortality of intertidal *M. edulis* in August 2018 when 50%–60% of the annual commercial value was lost (Seuront et al. 2019).

North Sea

The Dutch and German Wadden Sea (Fig. 1) host vast areas of intertidal and subtidal *Mytilus edulis* beds. This part of the Wadden Sea is the only area where *Mytilus* is monitored using aerial photography and ground truthing since the 1960s, although less frequent in the early years of this period. The percentage coverage of intertidal mussels per tidal basin varies from 0% to 6% and is highest in the more sheltered flats of the eastern Dutch and western Lower Saxony Wadden Sea (Dijkema et al. 1989, Herlyn & Millat 2000, Folmer et al. 2014, 2019).

During the 1980s, the extension of intertidal mussel beds in the Dutch Wadden Sea decreased from approximately 42 km^2 to only 2 km^2 in 1990 (Dijkema 1989, Dankers et al. 2003), mainly because of overfishing (see Overfishing of Wild Mytilus Stocks section). Fishing of intertidal mussels has been partially prohibited since 1995 and completely since 2004. The area with mussels has slowly increased to about 10 km^2 *Mytilus* beds and 10 km^2 of so-called oyssel beds, i.e. a mixture of *Mytilus* and Pacific oyster [classified as *Magellana gigas* (Salvi & Mariottini) or *Crassostrea gigas* (Thunberg), of which the latter will be used in accordance with Bayne et al. 2017] with a total mussel biomass of approximately 40 kilotons (hereafter kt where 1 kt is 1,000 metric tons) (Reise et al. 2017, Folmer et al. 2019) (section Competition and Predation by the Invasive Pacific Oyster).

In the past, the majority of mussels in the Dutch Wadden Sea were subtidal. Between 1990 and 2004 the subtidal to intertidal stock of mussels decreased from 100% to 40%, with recovery of the intertidal mussels (Kats 2007). Interannual variations in subtidal mussel stocks are large and had a maximum of 180 kt in 1997. The subtidal mussel seed fishery was phased out after 2008 and the beds can now develop undisturbed (Bos & Tamis 2020).

Despite this recent recovering trend in the Dutch Wadden Sea, reinforced by strong spatfalls, great interannual variations

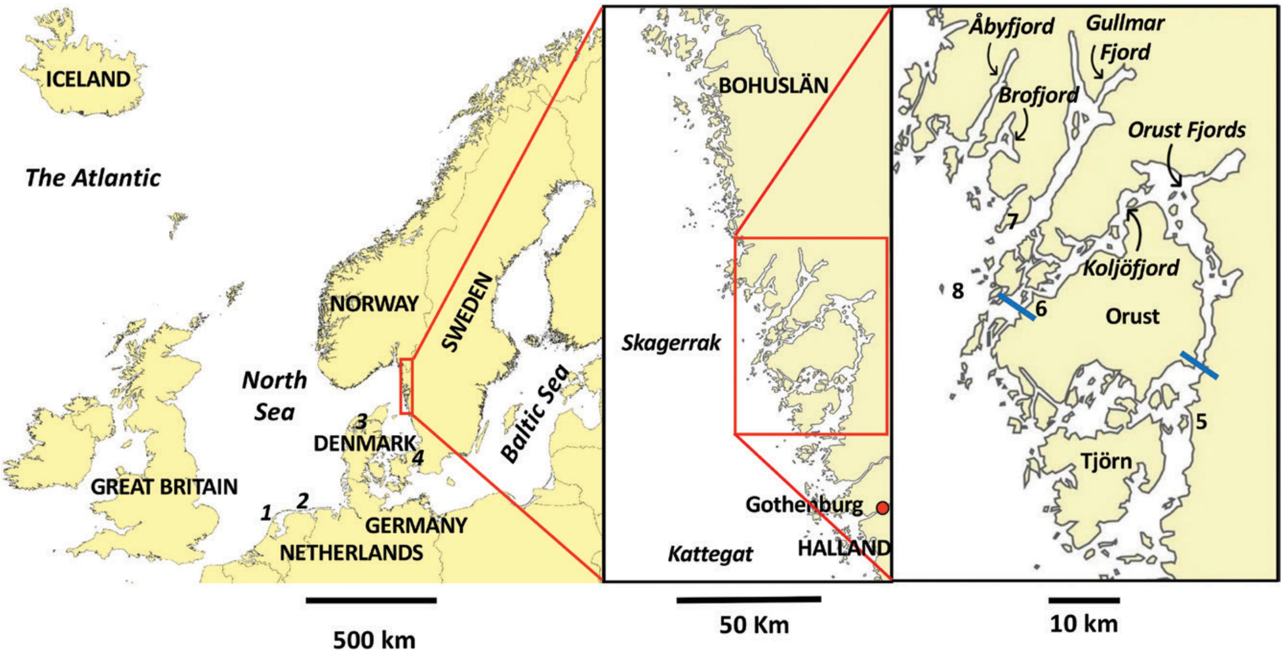

Figure 1. Map of Eastern North Atlantic (left), the Swedish west coast (middle), and a part of the west coast relevant to the text (right). (1) The Frisian Islands, (2) The Wadden Sea, (3) The Limfjord, (4) The Sound (Öresund), (5) Stenungsund, (6) Ellös, (7) Lysekil, and (8) Outer archipelago (Mittskär). The fjords on the inside of the island Orust are marked by two blue lines.

occur within the Sea (Folmer et al. 2014, van der Meer et al. 2019). An example is the southern Dutch Balgzand area of 50 km^2 where *Mytilus* decreased by 60% between 1997 and 2007. It was explained by overfishing and failing recruitment related to relatively high winter temperatures of the sea water, increasing predation from the crab *Carcinus maenas* (L.), and the sea star *Asterias rubens* (L.) arriving earlier in the season (Beukema & Dekker 2007) (Temperature Anomalies section).

The German Wadden Sea is divided into the coasts of Lower Saxony to the south and Schleswig-Holstein to the north. In the early 1990s, the mussel extension in Lower Saxony was approximately 27 km^2 (50 kt) decreasing to about 10 km^2 in 2004 whereafter only the mixed oyssel beds are recorded being 18 km^2 (containing 35 kt of mussels) in 2013. Along the coast of Schleswig-Holstein, data from around 1998 show a mussel extension of only approximately 10 km^2 (25 kt) decreasing to 5 km^2 of mussel and 5 km^2 oyssel beds in 2013 with a total mussel biomass of 20 kt (Folmer et al. 2019). Between Bremerhaven and Cuxhafen (a 50-km stretch close to Bremen), the mussels have been more or less absent since 1994 (Herlyn & Millat 2000). Since the recruitment was low, no real recovery has appeared, especially so in the northern part of the German Wadden Sea.

In the Danish Wadden Sea (Fig. 1), stock assessment of *Mytilus* has been carried out irregularly since 1980. The biomass of *Mytilus* reached a peak of 110 kt in 1993–1994. The stock was thereafter heavily overfished and the fishery closed in 2008. Between 2008 and 2016, no monitoring of the stock took place until 2017 when a recovery to 79 kt was seen. Simultaneously, the biomass of the invasive Pacific oyster increased to the same level (approximately 72 kt). The northern areas of the Danish Wadden Sea (around Esbjerg) have predominantly mussel beds, whereas the southern areas have oyssel beds (Nielsen et al. 2019a) (see Competition and Predation by the Invasive Pacific Oyster section).

In 2009, the Wadden Sea of Denmark, Germany, and the Netherlands became a world heritage site with far-reaching commitments to safeguard sustainable development of this unique ecosystem, explaining the recovery of the *Mytilus* in some parts of the Wadden Sea.

In the seas around Great Britain, *Mytilu*s is a widely distributed keystone species in littoral habitats of different exposure regimes and thus different substrates. Jones et al. (2000) reported that no significant decline in extent or quality was found for these habitats, nor for *Mytilus,* but that this requires further assessment. Through a more recent monitoring program, run by Marine Scotland Assessment (2020), six different habitats at 11 locations along the Scottish coast were visited in 2011 and again in 2018. Banks of *Mytilus* were only monitored in the outer part of Dornoch Firth. The area occupied by mussels at this location had declined from 218 ha (0.2 km^2) in 2010 to 1 ha in 2015 to 2016. This extreme loss was considered to have been caused by poor recruitment success and increased levels of post settlement mortality. Since 2000, no investigations on spatiotemporal distribution of *Mytilus* from Great Britain were found. Investigations on regional levels may exist to fill the gap.

Norwegian Sea

Frequent occurrences of disappearing and dead adult *Mytilus* have been reported from the entire Norwegian coast (Andersen et al. 2017). The observations include high mortality and lack of recovery after severe winters. Seed mussels have disappeared in some fjords (Andersen et al. 2017, Frigstad et al. 2018). In a questionnaire to the public, it appeared that *Mytilus,* in most cases, had disappeared suddenly within the last decade and from both exposed and sheltered locations (Andersen et al. 2017). Adult mussels are hard to find for environmental monitoring and scientific experiments (Green et al. 2019). Wild *Mytilus* have been red-listed as Category V (vulnerable) according to the Norwegian Biodiversity Information Centre (2018).

Danish Inner Waters

In the inner Danish coastal waters, *Mytilus* populations have been well investigated and show large spatiotemporal variations. The shallow Limfjord area (Fig. 1) has historically held the largest populations of *Mytilus*; however, in the central area of the Limfjord, the stock of *Mytilus* decreased from approximately 500 kt in 1990 to 10 kt in 2014, mainly caused by overfishing combined with hypoxia. A small recovery to approximately 20 kt had occurred in 2018 (Nielsen et al. 2018a), whereas in an adjacent southern area of the Limfjord, the stock of *Mytilus* increased from less than 1 kt in 2003 to 100 kt in 2016 (Nielsen et al. 2018b). The total catch from the entire Limfjord has decreased from 90 kt in the 1990s to present 25–30 kt (J. K. Petersen 2021, personal communication). In the Little Belt and the coastal area just north of Little Belt, the *Mytilus* stock biomass has been relatively stable at approximately 260 kt between 2009 and 2014. There were interannual variations, but no temporal trend (Nielsen et al. 2015, 2017). The *Mytilus* bank in the Sound (Öresund) is shared between Denmark and Sweden and is presently by far the largest (>100 km^2) in Europe, with an estimated biomass of 2–300 kt (Noren et al. 1999, Petersen et al. 2018). Unfortunately, no data on spatiotemporal changes in the Sound exist.

Baltic Sea

The Baltic Sea is one of the largest brackish water bodies in the world and is connected to the North Sea through the Kattegat and the narrow Danish straits. The salinity gradient is strong and *Mytilus* populations in the Baltic live at the margin of their distribution (Westerboom et al. 2019). Thus, mussels are small-sized caused by the physiological stress from low salinity reaching down to approximately 4–5 practical salinity units (S_p) in the northern part of the Baltic Proper (Maar et al. 2015). The mussel populations are dominated by *Mytilus trossulus* and are common on rocks and boulders in sublittoral zones (Gränö et al. 1999) between 3 and 12 m, but may occur even deeper (Vuorinen et al. 2002, Näslund 2013). Overall reports on temporal and spatial changes for *Mytilus* in the Baltic Proper are not found, but according to the red list of the Helsinki Commission the *Mytilus* biotopes in this area are categorized as Least Concern (Avellan et al. 2013). A recent investigation by Liénart et al. (2020) revealed that *Mytilus,* collected annually since 1993, but only from one location on the Swedish East coast, had increased in abundance but the individuals were smaller, which has resulted in a net decrease of population biomass. This was correlated with higher SST (see Temperature Anomalies section), lower salinity (see Hyposalinity and Physiological Stress section), and changes in food composition (more cyanobacteria and increased influx of terrestrial organic material) indicating a combination of climate change and eutrophication (Liénart et al. 2020) (see Food and Vitamin Supply section). In the southern Baltic Sea (Kiel and Lübeck Bights), *Mytilus* settlement was investigated between 2005 and 2015. The settlement on panels made of experimental concrete slabs declined after 2009 in all locations in the two Bights and recovered only in the Lübeck Bight (Franz et al. 2019).

Swedish West Coast

During the past two decades, the residents along the Swedish west coast (Fig. 1) have reported that wild *Mytilus edulis* in the archipelagos from north of Gothenburg to the Norwegian border have become very hard to find. The disappearance of mussels has been obvious for the general public in that rocks along the waterfront are no longer covered with remains of *Mytilus* dropped by seagulls in their efforts to crack the shells. Further, children fishing small crabs for fun no longer find mussels to use as bait. Previous mussel banks are now small clusters, if any. According to an inventory presented in 2007, mussel beds were scarce in the whole region, covering between 0.8% and 1.7% of the seabed (transects at 0–10 m depth) along the northern part of the coast and in the fjord system around the island of Orust (Stål & Pihl 2007) (Fig. 1). It should be noted that no historical or more recent studies from the area are available for comparisons. From the Wadden Sea, however, the coverage is up to 6% (see North Sea section).

In the mid-1980s, inventories of the shallow coastal areas in the archipelago along the Swedish west coast were carried out for coastal zone management purposes. Detailed mapping of habitats on the dominant sand-silt substrates pointed out *Mytilus* banks as important components in decisions on exploitation. In recent years, follow-up investigations and other inventories have all verified that many of the *Mytilus* banks present in the 1980s have disappeared (Thörnelöf & Lagenfelt 1982, Lagenfelt & Höglind 1983, Pihl et al. 1983, Ulmestrand & Pihl 1989, Alexandersson 2005, Miljöförvaltningen Göteborgs Stad 2007, 2020, Wernbo 2013, Länsstyrelsen Västra Götaland 2018a, 2018b). It can be summarized from all these observations that the disappearance of mussels probably began in the late 1990s, but the main drop of occurrence was during the 2000s. Typical for many of the localities revisited after 2000 was that remains of former mussel banks were dominated by large dead shells more or less covered by a gray fluffy layer of dead filamentous algae. The large shells indicated that the mussels were old when they died and absence of small shells indicated no resettling.

An example of mussel disappearance was documented from the Koljöfjord, north of Orust (Fig. 1). Previously, mussel banks at 1–5 m depth constituted a dominating part of the benthic ecosystem. In the 2000s, a mass mortality became obvious through the large amounts of shells on the beach in 2007 and 2009 (Fig. 2A). No large-scale or local hydrometeorological or other events have been identified as possible explanations for the high mortality of mussels. Mussels living on the traditional substrates have, in principle, become nonexistent since this event in the Koljöfjord area. Although there has been an obvious decrease of wild mussels in the Orust Fjord system (Fig. 1), no decrease in the settling of larvae has been observed in the mussel farms (A. Granhed 2020, personal communication). The residence time of the surface water (0–10 m) in the fjord system has been estimated to be about 1 mo (Björk et al. 2012). It is thus likely that the settling has been dominated by spawning of locally occurring farmed mussels, with minor or no support from local wild mussel stocks (see Settling Behavior and Growth section).

Figure 2. (A) Shells of *Mytilus* washed ashore in Koljöfjord 2007. Photo Inger Forsberg. (B) Mussels settling on artificial substrate. Photo Odd Lindahl. (C) *Mytilus* bed in the outer archipelago (Mittskär), Swedish west coast (Fig. 1, location 8). Photo Helen Sköld. (D) A representative picture of the establishment of Pacific oyster (*Crassostres gigas*) along the shallow coastline of Bohuslän where *Mytilus* previously was abundant. Photo Bodil Hernroth.

There are very few early documentations from the outer archipelago regarding the occurrence of *Mytilus*, except that blue mussels were very common and abundant "everywhere." In 2020, diving biologists and fishermen have reported on observations on the condition of mussel stocks in the outer archipelago of Bohuslän (e.g. Mittskär) (Fig. 1). The observations include abundant (Fig. 2C), weak, and extinct stocks (e. g. H. Skjöld and R. Johansson 2020, personal communications).

Along the more exposed Kattegat coast from south of Gothenburg to the Sound, marine biologists from the County Board of Halland (B. Gustafsson 2020, personal communication) have observed a decreasing occurrence of adult *Mytilus*. The effort to collect mussels for environmental analyzes has increased from being easy picking from a boat to now having to dive into deeper water. During some years, very dense settlings at 1–2 m without resulting in equivalent recruitment to adults have been observed. This decrease in *Mytilus* is documented in the Swedish Species Information Center (Artdatabanken 2021) and also mentioned in status reports from the Swedish Agency for Marine and Water Management (Bryhn et al. 2020). Due to the lack of systematic historic mapping, these observations of disappearing *Mytilus* can only partly be verified.

The observations of the authors indicate that the disappearance of *Mytilus* along the northern part of the Swedish west coast was a process ongoing for about a decade starting in the south and progressing to the north. It also seemed that the process was relatively fast (1–2 y) at a locality once it had started.

EFFECT OF STRESSORS

Introduction

Habitats for blue mussel beds are exposed to seasonal or dial fluctuations in temperature, salinity, oxygen, and nutrition supply, as well as exposure to air (when situated in the intertidal zone). Their coastal locations are also often affected by emissions from industries, land and forestry, and waste water treatment plants (Fig. 3). Thus, the mussels are considered exceptionally tolerant to a large range of physical and chemical conditions (reviewed by Bayne 1976, Mainwaring et al. 2014, Lacroix et al. 2015). Recently this assumption has changed owing the alarming decline in their extent and biomass, reported from OSPAR Maritime Area (OSPAR 2010, 2015).

Several anthropogenic stressors have been identified as driving forces weakening the stocks of *Mytilus* spp. through overfishing (Overfishing of Wild Mytilus Stocks section) and the state of health through, for example, disrupted metabolism, reproduction, and immunity or modified feeding behavior (Marigómez et al. 2013, Parisi et al. 2021). Sublethal effects of single stress factors can, however, increase to more drastic effects when the stressors occur in combination, such as the interaction between poor nutritional status, toxic chemicals, and invading pathogens, and not least progressing climate change (Couillard et al. 2008). For example, unusually high spawning activities followed by a *Phaeocystis* mass occurrence caused two mass mortality events in the Dutch Oosterschelde in 2016 and 2019. This was associated with high prevalence of granulocytomas indicating cumultative stress in the mussels (Capelle et al. 2021). Climate change results in higher water temperature, and OA as well as extreme weather events exacerbate the prevailing stressors as described earlier (Petoukhov et al. 2016, Bindoff et al. 2019, Collins et al. 2019). As reviewed by Beyer et al. (2017) many studies point out the necessity to adopt a holistic view involving both subcellular and whole organism responses to the complex environment when evaluating potential biological effects on mussels. There is, however, still a lack of knowledge concerning the influence of multiple stressors on the fitness of mussels and how stressors may vary in time and space at local scales (Sebens et al. 2018). Since the stressors in most cases act in concert it is appropriate to shed light on the single factors one by one to evaluate the combinatory effects. For the schematic overview of cause and effects involved in *Mytilus* decline, see Figure 3.

Overfishing of Wild Mytilus Stocks

The global catch of, for example, wild *Mytilus edulis* registered since 1950 reached a peak in 1992 to 1993 of approximately 170 kt. The 2017 catch was approximately 60 kt (FAO FishStat 2020). Despite the decline of wild *Mytilus* the annual aquaculture production of *M. edulis* and *Mytilus galloprovincialis* has increased steadily between the 1950s and 1980s and then stabilized approximately 200 kt and 100 kt, respectively (FAO FishStat 2020).

From the section North Atlantic Coastal Waters: Spatiotemporal Variation of *Mytilus edulis* Species Complex it is clear that overfishing of both adult and juvenile (to be used as seed) *Mytilus* has taken place in many areas during the last couple of decades and may explain the *Mytilus* decline to some extent. This is especially the case in the international Wadden Sea shared by the Netherlands, Germany, and Denmark, as well as the Gulf of Maine (United States), where an intensive fishery in the intertidal zone decreased the stocks mainly in the 1980s to 1990s (Beukema & Dekker 2007, Sorte et al. 2017). Since then, intertidal *Mytilus* beds on mixed and sandy sediments are categorized as a habitat under threat and/or in decline in OSPAR Regions II and III (OSPAR 2010). As the Wadden Sea is declared a World Heritage site since 2009, a restoration plan is in place (https://www.waddensea-worldheritage.org/). Commercial fishing in the subtidal zone is allowed (Bos & Tamis 2020). Although regular intertidal mussel beds are hard to reestablish, slow recovery has taken place in some areas, especially in the Dutch and Danish parts of the Wadden Sea (e.g., Folmer et al. 2014, Nielsen et al. 2018b, Folmer et al. 2019).

Fishing for mussels has, since historical times, taken place in the sheltered archipelago along the Swedish west coast. The mussels were mainly used as bait, but during the period 1950 to 1970 mussels were also collected for the canning industry. Unfortunately, there are only available data or reports of the mussel collection from the period 2007 to 2018. The largest biomass fished was 233 t in 2009 decreasing to 0.2 t in 2018 (www.jordbruksverket.se). The drop in harvesting was especially obvious after 2013, and after 2017 fishing of blue mussels more or less ceased because it was no longer profitable. Fishing never took place on sparse occurrences of mussels, earlier more widely present all over the archipelago. Thus, it can be concluded that fishing in this area may have reduced the dense populations, but not the sparser occurrences. Commercial longline mussel farming around the island of Orust (Fig. 1) is a valuable supplement and replacement of wild mussel fishery since mid-1970s. According to official statistics (2007 to 2017), the annual yield of harvested mussels from aquaculture in Sweden showed no temporal trend and ranged between 1459 and 2264 t (www.jordbruksverket.se).

Pollutants

Beyer et al. (2017) reviewed the principal routes for uptake of environmental contaminants in mussels, and conclude that it is dependent on several factors, including physiochemical properties of both the contaminants and the ambient seawater, as well as of the condition of the mussel itself. Subcellular effects, such as oxidative stress, have long been used as biomarkers for estimating the contaminants effects on mussels. International Credential Evaluation Service has recently agreed on a more holistic method, so-called integrated ecosystems assessment, involving monitoring of biological responses at subcellular, tissue, and whole organism levels of mussels (Davies & Vethaak 2012). Most countries have not yet implemented this type of complex monitoring and there is a great lack of knowledge concerning the extent to which the pollutants could affect the mussel stocks.

Within the European Union, emerging pollutants are defined in, for example, Directive 2013/39/EU and the Water Framework Directive (WFD). Specific guidelines exist for industrial chemicals, human and veterinary pharmaceuticals,

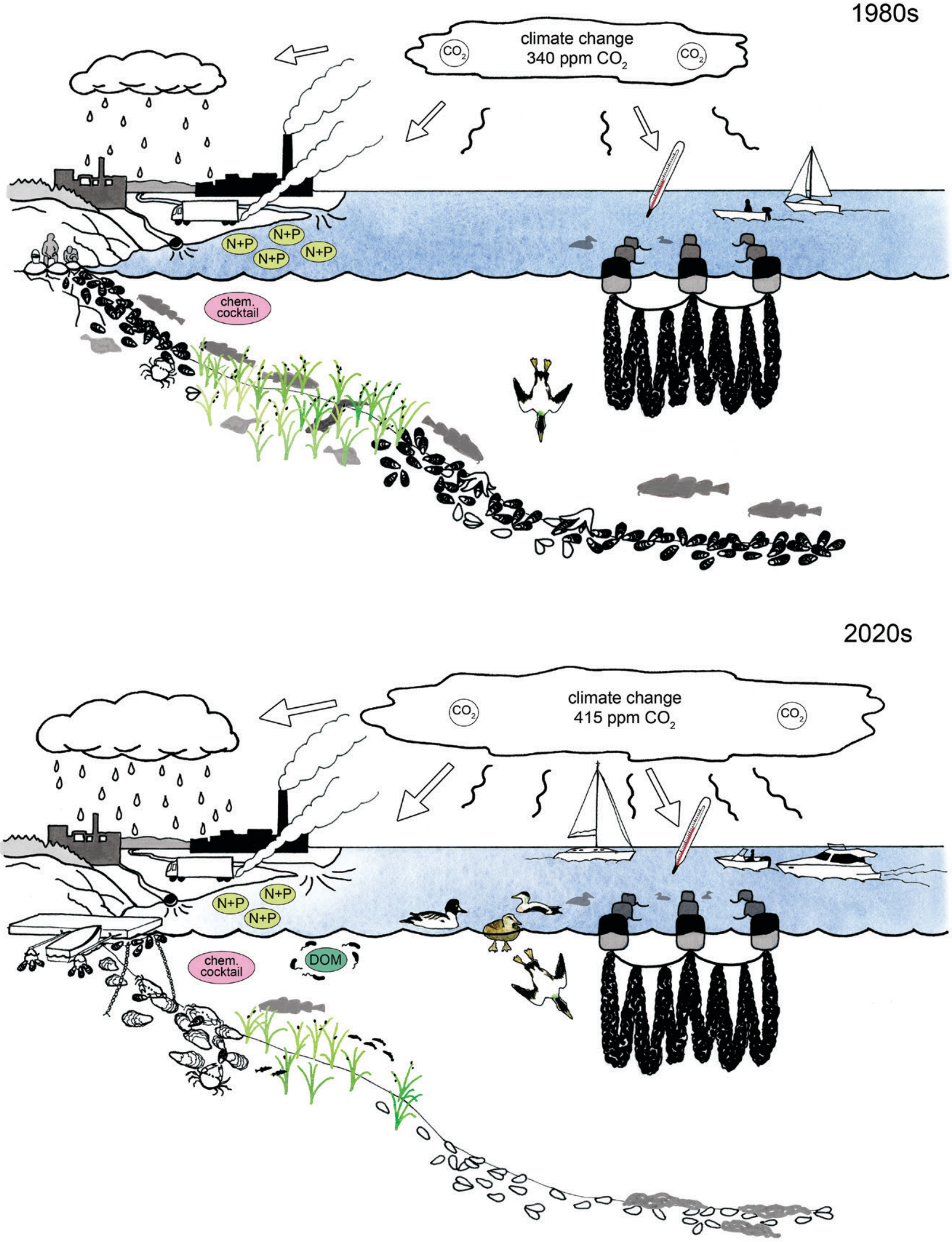

Figure 3. Schematic illustration of the near coastal zone of the Swedish west coast in the 1980s and 2020s. Factors potentially affecting the *Mytilus* beds are illustrated. Between 1980s and 2020s atmospheric CO_2, air and water temperature, precipitation, wintering eiders, shore crab and the invasive pacific oyster and leisure boat traffic increased whereas near coastal surface salinity, nutrients (and thus primary production), fish stocks, seagrass, and finally mussels decreased. For details see Effect of Stressors section and conclusions. Illustrations by Maj Persson.

biocides for disinfestation, and phyto-protection as well as other WFD priority pollutants. Threshold values, that is, concentrations that should not be exceeded to avoid adverse effects are, however, stated only for individual substances. Recently, it has been argued that the environmental threshold values that apply within the EU should take into account effects caused by the mixture of chemicals biota are exposed to (Kortenkamp et al. 2019).

According to the OSPAR Commission Quality Status Report (OSPAR 2012) antifouling substances and heavy metal contaminants have been identified as intermediate threats to mussel beds. Due to the lipophilic and constant nature of these compounds, bioaccumulation in biota and negative effects on *Mytilus* spp. have been noted, on both the reproductive and immune systems (St-Jean et al. 2002, David et al. 2010, Smolarz et al. 2017). A study of water samples from the Swedish west coast, in 2012, showed widespread, diffuse emissions of a mixture of anthropogenic organic substances whereof antifouling products, such as the biocides Irgarol and tributyl-tin, exceeded the stated environmental thresholds (Gustavsson et al. 2017). Other dominating organic pollutants were anionic surfactants used in, for example, boat cleaning products and commonly present in wastewater inputs, phatalate esters used as plasticizers, as well as chlorinated volatile organic compounds (VOC) and polycyclic aromatic hydrocarbons (PAH). Both VOC and PAH are also associated with boat traffic and emissions from, for example, oil refineries. Polycyclic aromatic hydrocarbons are considered highly toxic and known for causing oxidative damage (Altenburger et al. 2003) and DNA alterations in mussels (Pérez-Cadahia et al. 2004). In 2006 and 2016, both sediment and blue mussels from the Swedish west coast were analyzed with respect to heavy metals and organic pollutants (Bergkvist & Magnusson 2016). High concentrations of PAH were detected in the sediment of the Brofjord, where an oil refinery is situated. At all sampling sites, the levels of the PAH congener fluoride in mussels were below the current level for environmental quality standard. There is, however, a substantial contribution from the increasing extent of leisure boats and marinas (Moksnes et al. 2019). The number of these boats has quadrupled since 1980s and the engines have become increasingly more powerful (Swedish Maritime Administration). Two-stroke engines, mostly emitting their exhaust by the cooling or propeller water, have not been completely phased out. It has been estimated that during the period 2015 to 2019 roughly 1,000 t of PAH were annually emitted to southern Swedish coastal waters (Lagerqvist 2020). These "small-scale" PAH emissions may have serious consequences because the activity is greatest during the mussel reproductive period. This is, however, contradicted by the observations that it is still often possible to find plenty of mussels on the floating jetties at the marinas.

The report by Bergkvist and Magnusson (2016) pointed to flame retardants (polybrominated diphenyl ethers) as the most common organic pollutant in the mussels, exceeding the environmental quality standard at all sampling sites. Highest concentrations were seen where refineries are situated in Gothenburg and in the Brofjord (140 km north of Gothenburg) (Fig. 1). Damaging effects on the digestive glands and gills of mussels (Cappello et al. 2013, Vidal-Liñán et al. 2016, Espinosa Ruiz et al. 2019) as well as impairment of their immunity (Espinosa Ruiz et al. 2019) have been reported from experimental studies at environmentally realistic levels.

Microplatics (MP) characterized as plastic debris less than 5 mm and nanoparticles representing a diverse class of xenobiotics are contaminants of growing concern (Marine Strategy Framework Directive, Descriptor 10—Marine Litter: Decision 2017/848/EU) due to their widespread distribution and interaction, not least with filter feeders. A main concern is that plastics are carrying diverse chemical compounds and hydrophobic organic contaminants. As reviewed by Beyer et al. (2017) several studies have revealed accumulation of MPs in *Mytilus* spp. and physiological impacts of MPs have been assessed. There are indications of adverse effects on filtration capacity and immunity, but the results are contradictory (reviewed by Wright et al. 2013). According to the meta-analysis of Foley et al. (2018) there are no significant effects on growth, reproduction and survival of mollusks.

The only metal exceeding the stated limit value was mercury (Hg) detected in mussels from the Gothenburg, Stenungsund, and Lysekil areas (Bergkvist & Magnusson 2016). Contents of other heavy metals in mussels showed low to moderate levels, but with an increasing tendency for arsenic (As), cadmium (Cd), and zinc (Zn) at all sampling sites. Moreover, in Sweden, copper (Cu) is the only biocide that occurs in antifouling paints for leisure boats. Other reports have shown that the content of Cu in sediment from marinas exceeded the limit value for "extensive acute toxic" effects ($>147\ \text{mg}\cdot\text{kg}^{-1}$ dry weight) in six of seven marinas along the Swedish west coast in 2010 and 2012 (Bengtsson & Cato 2011, Nordberg et al. 2012). Mussels tend to accumulate metals in their tissues altering biochemical and physiological processes (Bolognesi et al. 1996, Fasulo et al. 2008). For example, combined effects of nanomolar concentrations of Cd, Cu, and Hg cause genotoxic effects with DNA damage in gill structures of *Mytilus galloprovincialis* (Varotto et al. 2013). Both Cu and Cd can induce genotoxicity in the digestive gland (Pytharopoulou et al. 2013) and the genotoxicity of Cu has also shown negative effects on the reproductive system (Lettieri et al. 2019) of *M. galloprovincialis*.

Detoxification mechanisms, such as metallothioneins, can help protect mussels (Domouthsidou et al. 2004, Amiard et al. 2006), but the response may vary between seasons, potentially influencing the sensitivity to pollutants. The vulnerability of mussel larval stages is less investigated, but in Pacific oysters it has been recorded that As has retardation effects of embryonic development. The embryos had a narrower range of tolerance to both salinity and temperature at very low concentrations of As (Moreira et al. 2018).

In sea water sediments, naturally occurring metals are bound to normoxic sediment in oxidized states. Among these, manganese (Mn) is one of the most abundant. During hypoxia (<20% of air saturation), the dominating four-valent colloid state of manganese (MnO_2) becomes reduced and released into bioavailable forms (mainly Mn^{2+}). It has been recorded in the Skagerrak area that Mn can increase by a factor of 1,000 and reach approximately $20\ \text{mg}\cdot\text{L}^{-1}$ (Magnusson et al. 1996). This is in contrast to, for example, Cd, Cu, Pb, and Zn, which get more strongly bound during hypoxia (Gerringa 1991). Although Mn, as a trace metal, is essential for many physiological activities, such as skeletal formation, digestion, reproduction, and immune and nervous systems (ASTDR 2008, Aschner et al. 2009), it is toxic to organisms at elevated levels (Santamaria 2008, Michalke & Fernsebner 2014). Several reports have verified accumulation of Mn in marine biota, also in gills, hemolymph, and hepatopancreas of blue mussels (Baden & Eriksson 2006). Such elevated levels of Mn have shown immunosuppressive to mussels and significantly reduce their bactericidal capacity (Oweson & Hernroth 2009). Thus, it cannot be ruled out that this common metal can have negative effects at least on mussel beds in deeper waters.

Most toxic substances highlighted here have been detected in concentrations that do not exceed the acute toxicity limits, but these are poorly tested on mussel larvae. Moreover, potential sublethal effects of the cocktail of pollutants that mussels are exposed to may weaken immune and stress response and reproductive success. The fact that mussels still settle on artificial surfaces in contaminated areas such as, for example, marinas indicates that the pollutants have not been of decisive importance for the disappearance of wild stocks, at least not in Sweden.

Ocean Acidification

Extensive studies concerning effects of OA on marine organisms have been published over the past 20 y (reviewed by Gattuso & Hansson 2011) with particular attention to organisms producing calcareous structures (Orr et al. 2005, Gazeau et al. 2007). The pH shift decreases the available carbonate pool (Gattuso & Lavigne 2009) and increases the rate of dissolution of the crystalline forms of $CaCO_3$. This is considered critical for, for example, molluscs whose shells consist of a large proportion of aragonite, more soluble than, for example, the calcitic shell of crustaceans (Mucci 1983). When *Mytilus edulis* was exposed to OA for 4 mo, experimentally modified to a level predicted by IPCC (2014) to be reached at the end of this century (Δ −0.4 pH units), the average shell growth was reduced by 40% compared with the control group kept in ambient seawater. Confirmation by scanning electron microscopy images showed partially dissolved prisms at the edge of the OA-exposed shells, which is the growth zone, not repairable by the mantle tissue (Asplund et al. 2013).

Shell dissolution is of great concern as it weakens the outer barrier needed for protection against invading pathogens (Gutiérrez et al. 2003). Bivalves possess both humoral and cellular immunity mainly delivered by circulating hemocytes. These have a high capacity of phagocytosis and encapsulation and produce vital bactericidal compounds such as lyzosomal enzymes, reactive oxygen species, and antimicrobial peptides (AMP) (Cheng 1983, Leippe & Renwrantz 1988, Pipe 1992, Girón-Pérez 2010).

When OA exposed (Δ −0.4 pH units), mussels became more susceptible to infection when encountering the shellfish pathogen *Vibrio tubiashii* (Asplund et al. 2013), and AMPs expressed on the gills significantly reduced its bactericidal capacity against *Vibrio parahaemolyticus* (Hernroth et al. 2016). Bibby et al. (2008) found that OA suppressed phagocytosis of *Mytilus.* Likewise, OA suppressed both total hemocyte counts (THC) and phagocytic capacity of *Mytilus galloprovincialis*, especially so when temperature was raised from 22°C to 28°C (Matozzo et al. 2012). Altogether, the future climate scenario with increasing OA does not seem to have reached an acute fatal situation for the mussels, but they may become more susceptible to infections, which can result in mass mortality.

Experimental studies provide, however, only a static and narrow window into the vulnerability of the organisms, making it difficult to interpret the results and can hide possible bottlenecks and adaptations (Hendriks et al. 2009, Dupont et al. 2010, Waldbusser & Salisbury 2014, Hall-Spencer et al. 2015, Kroeker et al. 2019). To evaluate effects of mussels from the climate-driven situation achieved so far, the control animals of the different experiments can give insights. These were kept in ambient seawater without negative effects on, for example, growth or immunity. Conversely, it can be concluded that temporary reductions in seawater pH may produce similar effects that could be seen in the OA experiments. In nearshore shallow areas, a dynamic fluctuation of carbonate chemistry is likely driven by a combination of biotic factors, such as photosynthesis and respiration, and abiotic factors, such as oxygen variation and low salinity caused by land runoff. The short-term pH variability often occurs with a circadian rhythm but may persist for several days (Santos et al. 2012) and this occurs on top of the long-term baseline changes due to OA. Kapsenberg et al. (2018) reported that short-term variability of pH impaired early larval development by affecting shell construction and transition from the first to the second larval stage of *Mytilus galloprovincialis*. When Mangan et al. (2017) exposed *Mytilus edulis* to a near-future OA scenario, it induced significant acid–base disturbances and lipid peroxidation compared with the static today conditions, but the metabolic rate was not affected. When exposed to variable pH conditions, the metabolic rate was, however, significantly higher than those exposed to static pH under both current and the near-future OA scenario. This indicates that the physiological response to pH fluctuations is more energetically costly than a static pH, even if the static is lower than what mussels normally experience at present.

It can be concluded that alteration of carbonate chemistry that can occur in shallow, near-shore areas affected by land runoff may constitute an important factor for mussel fitness. In areas with more frequent extreme weather, these events may already now inhibit mussel larval development, though it occurs on a short term.

Temperature Anomalies

Physiological Stress

As intertidal species, mussels generally show high temporal and latitudinal variation in thermal tolerance. In temperate regions, they exhibit a seasonal cycle with lower physiological activities, such as feeding, locomotion, growth, and reproduction during winter and with increasing activities in line with the seasonal rise of temperature (Schulte 2015). This also includes the ability of *Mytilus* to activate the immune system. Experimental studies of *Mytilus edulis* have demonstrated a significantly higher antimicrobial capacity of hemocytes at 20°C compared with that of 6°C. This has been revealed both through investigation of hemocyte activity against *Salmonella enterica* serotype Typhimurium (*S. enterica*) (Hernroth 2003a) and the activity of AMP (extracted from hemocytes) against *Escherichia coli* (Hernroth 2003b). Mackenzie et al. (2014) have shown increasing THC and phagocytic capacity in *M.*

edulis when rising the temperature from approximately 12°C to approximately 16°C. When reaching a high critical temperature threshold, the oxygen regulation by enhancing ventilation and heartbeat rates is disrupted. Then oxygen levels in the organisms will be insufficient, depressing physiological activities (Jansen et al. 2009, reviewed by Pörtner 2010).

The increase in SST has resulted in the expanded northern distribution of *Mytilus* populations, especially by shifting the biogeographic distribution of the different taxa (Berge et al. 2005, Jones et al. 2010, Sorte et al. 2011, Wenne et al. 2016). At present, the more warm-water-tolerant *Mytilus galloprovincialis* can be found in regions where the colder water adapted *Mytilus edulis* and *Mytilus trossulus* used to dominate (Braby & Somero 2006, Lockwood & Somero 2011). Their respiratory plasticity indicates a potential for a successful biogeographic distribution, and it makes it indeed difficult to evaluate what constitutes a stressful temperature. The annual average European surface air temperature anomalies for 1950 to 2020 relative to the 1981 to 2010 reference period clearly demonstrates that the mean temperature has increased by about 2°C (climate.copernicus.eu 2021) (Fig. 4). The temperature increase in Europe has occurred during all seasons. Along the Swedish west coast, a trend analysis of the water temperature over the period 1990 to 2011 found that SST slowly increased over time at several of the coastal stations in the Bohuslän archipelago (Fig. 1) (Swedish Meteorological and Hydrographical Institute, SMHI 2013). The annual increase was in the range 0°C–1°C. Moreover, according to SMHI (2021a), most of the winters in Sweden during the past 20 y have been mild or very mild, and may determine limits of reproduction for *Mytilus.* It can be assumed that this change in temperature can be one of the main causes for the decrease of the mussel stocks in Sweden as well as in Europe. Gonad resorption and oocyte atresia in male and female, respectively, may occur during elevated temperature in winter to cover requirements of the raised basal metabolism under limited energy intake (Bayne et al. 1978, Tremblay et al. 1998, Mugica et al. 2015). The indirect effects from increased SST on mussels are described in sections Genetic Drift and Hybridization and Predation by Birds.

In the Bohuslän Archipelago, the daily tidal cycle is about 0.2 m. Changes in atmospheric pressure and wind impact have a greater effect on water surface level than the tide. Thus, a weekly or monthly variation can often be in the range of 1 m, and extremes can be up to 2 m (SMHI 2021b). As mentioned in Introduction, climate change can generate weather extremes according to changes in large-scale atmospheric circulation patterns, so-called locked weather events (Petoukhov et al. 2016, Collins et al. 2019). These may result in unusually long periods of high or low air pressure with the consequences on hydrometeorological conditions of extreme air exposure (desiccation), salinity, and temperatures. During winter, *Mytilus edulis* normally has the possibility to resist cold temperatures by the use of cryoprotecting agents in the haemolymph (Aunaas 1982); however, when subjected to air exposure during extended time, they may experience potentially lethal freezing conditions. Also, summer heat waves are likely to cause physiological stress. Molecular studies have shown that such events significantly increase caspase activity in hemocytes and gill tissues of *Mytilus* spp. (Yao & Somero 2012, Zhang et al. 2014). Activation of the caspase cascade induces double- and single-stranded breaks in DNA and downstream regulatory responses, and might play an important role in determining cellular thermal tolerance limits. Heat waves have shown devastating consequences as in France, around Boulogne-sur-Mer, where serial heat waves in August 2018 caused mass mortality of intertidal *Mytilus*, with a 50%–60% loss of the annual commercial value (Seuront et al. 2019). It is observed that *Mytilus* seemed to withstand a few heat waves, but not the 4–5 as occurred that year.

For immobile species, the ability to adapt to elevated temperatures is a determining factor in survival. Since the temperature can vary greatly depending upon depth and on water currents, it can be assumed that there can be relatively large differences between temperature stress affecting mussels that grow on floating substrates and those that grow on bottoms in

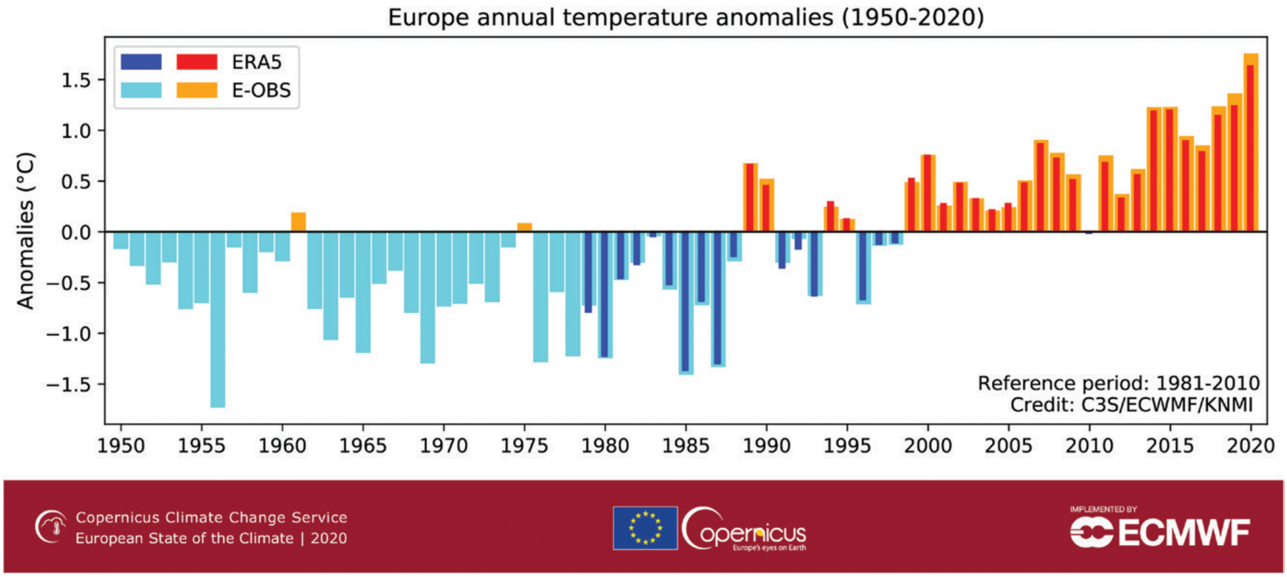

Figure 4. Annual average European surface air temperature anomalies for 1950 to 2020 relative to the 1981 to 2010 reference period (climate.copernicus.eu 2021).

shallow water. Long-term ice or air exposure during winter, as well as heat stress, are more pronounced during locked weather events, most likely with greater effects on mussels situated on bottoms at 1–2 m depth.

Infectious Diseases

As reviewed by Destoumieux-Garzón et al. (2020) mussels are considered more resistant to infections, in particular vibrioses, compared with that of oysters. Climate change, both in terms of increase in water temperature and/or lowered pH conditions, is, however, predicted to change pathological conditions, parasite abundance and diversity and bacterial incidence also in *Mytilus edulis* (Mackenzie et al. 2014). A great variety of pathogens (bacteria, viruses, fungi, and parasites) has been registered in oysters (Zannella et al. 2017), but this review focuses only on those reported from Europe and detected also in mussels from the Swedish west coast.

In France, mass mortalities have often been reported from oyster cultures and hatcheries, while *Mytilus* in the same area did not appear to be affected. Since 2010 mass mortalities in mussel farms have been reported with increased frequency (Eggermont et al. 2017). Inconsistently, *Vibrio* belonging to the *Splendidus* clade was isolated during these events and was shown capable of escaping the immune defense of adult mussels (Ben Cheikh et al. 2016). Most interesting, Eggermont et al. (2017) demonstrated that these vibrios isolated from wild-caught adult mussels were capable of inducing mass mortality in mussel larvae. The abundance and persistence of vibrios in water and sediment increase with temperature and nutrient supply (Duan & Su 2005, Collin & Hernroth 2020), and are thus expected to increase in line with climate change (DePaola et al. 1990, Daniels et al. 2000, Vezzulli et al. 2013). As a consequence, pathogenic *Vibrio* spp. have expanded their distribution in the Baltic and the North Sea area during the last decades (Vezzulli et al. 2016, Baker-Austin et al. 2017). This is of particular interest as it also carries an increased risk of being transmitted to humans through sea bathing or shellfish consumption (Baker-Austin et al. 2013, Hernroth & Baden 2018). In the Swedish west coast area, *Vibrio* spp. are not included in any monitoring of mussels and seawater, but through sporadic sampling high numbers of *Vibrio* pp. have been found both in mussels and sediments (Collin & Rehnstam-Holm 2008, B. Hernroth, personal communication 2021). In addition, *Vibrio parahaemolyticus* has been isolated from mussels collected along the west coast. These strains were used in research projects where they were able to infect blue mussels in a dose-dependent manner (Oweson & Hernroth 2009), particularly so at high temperature (Hernroth et al. 2009). In these "*in vitro*" experiments, high concentrations of the bacteria were lethal for adult mussels, indicating that this could be a realistic phenomenon also for mussels exposed to *Vibrio* "*in vivo*."

The oyster herpesvirus-1 (OsHV-1) and variants have increasingly been recorded for causing high mortality rate in Pacific oyster cultures in Europe since 2008 (Segarra et al. 2010, EFSA AHAW Panel 2015, Martenot et al. 2015). After the warm summer of 2014, high mortalities of *Crassostrea gigas* occurred in a hatchery and in wild populations at the Swedish west coast and the nearby Norwegian south coast (Mortensen et al. 2017). All size classes were affected, and the disease seemed to be a combined infection of OsHV-1 and pathogenic *Vibrio* species (mainly *Vibrio aestuarianus*) in combination with increased physiological stress (after spawning) and elevated temperature. The virus was also found in the native oyster *Ostrea edulis* and in blue mussels, but these remained healthy. Recently, it was shown that during elevated temperature events, wild mussels at *C. gigas* culture sites can transmit the virus to oysters (O'Reilly et al. 2017).

According to OIE notifiable diseases (https://www.oie.int/animal-health-in-the-world/oie-listed-diseases-2020/) pathogenic species of the parasites *Bonamia*, *Martelia*, *Perkinsus*, and *Xenohaliotis* are listed as disease agents in molluscs, predominantly found in oysters. Sporadic detection of *Bonamia* in flat oysters has been reported from Norway (OIE 2009) and from the Limfjord in Denmark (Madsen 2017, ICES 2018), but so far it has not been found in mussels; however, *Martelia refringes* known as an oyster parasite in Southern Europe has also caused decline and even extinction of local *Mytilus* beds in France. This species has thus far not been detected north of France, but a survey in the UK, Norway, and the Swedish west coast identified a closely related genotype, distinguished as *Marteilia pararefringes* (Kerr et al. 2018), thus far only detected in mussels. Infection levels and prevalence of both *M. refringes* and *M. pararefringes* peak during summer. Their success is most likely related to the distribution and life cycle of intermediate hosts, such as the *M. refringes* related copepod *Paracartia* (*Acartia*) *grani* (G. O. Sars) (Audemard et al. 2001).

Healthy mussels are inhabited by abundant microbial communities that stay in balance with the host immune system. When sudden and patchy extinction of mussel beds occur, disease outbreaks should be suspected, as it could be caused by opportunistic pathogens taking advantage of a certain situation. In general, pathogenicity is highly dependent upon the host immune capacity, its developmental stage, number of pathogens, and on environmental factors. In Sweden, there is no control program performed to detect mussel pathogens, but there is a duty to report suspected cases to the Swedish Veterinary Institute. The negative observations of rapid changes in the mussel populations call for a more active approach. The state of present knowledge shows that even the robust mussels can suffer from diseases, particularly the larvae. It is also known that environmental factors can benefit the presence of, for example, pathogenic *Vibrio*. In combination with local environmental stress factors or when the mussels are also infected with other pathogens, this may be a tipping point. Thus, more studies including relevant stress factors are needed particularly during larval and juvenile vibriosis to clarify the impact on mussel survival.

Increased Precipitation

According to the EEA Report No 1/2017 (Jol & Füssel 2017), the precipitation pattern of Europe has changed because of climate change since the 1960s. Along the Atlantic shoreline of the Iberian Peninsula, the annual mean precipitation has decreased significantly, whereas it gradually has increased with higher latitudes. The west coast of Sweden has experienced an annual increase of approximately 30 mm per decade, and the 30 y annual mean value has recently been upregulated by approximately 100 mm by SMHI (2020a). Total land runoff to the Swedish sea areas, including the Baltic and Bothnian Seas, was in periods during the 1990s and 2000s above the long-term mean (1961 to 1990), and for example in 2008, it resulted in a 33% increased supply of fresh water to the Kattegat and Skagerrak areas (Fig. 1) (Naturvårdsverket 2009)

Hyposalinity and Physiological Stress

As a consequence of the increasing precipitation, lower salinity of the coastal waters of the North Atlantic has been reported (Durack et al. 2012, Jol & Füssel 2017, Bindoff et al. 2019, Lettieri et al. 2019). Also, in Swedish Skagerrak surface coastal waters and fjords, a significant trend of decreased salinity during the period 1992 to 2012 was identified (Moksnes et al. 2015). Most salinity recordings are profiles from deeper water, but Pihl and Rosenberg (1982) showed that during spring time weekly means in the Gullmar Fjord at the bottom of about 0.7 m mean depth could be as low as 8–10 S_P in some years. Normal salinity of surface water measured in the archipelago is 18–25 S_P. According to the trends described in both Durack et al. (2012) and IPCC (2019), it is likely that the salinity has decreased even further since the 1980s, potentially impacting the settlement of juvenile *Mytilus* in shallow water. Increasing land runoff can, besides the direct effect of hyposalinity, also cause indirect consequences for *Mytilus* by changing the nutritional composition and light conditions and thus their substrates and food supply.

Hyposalinity is considered one of the most significant environmental stressors for marine bivalves and has a great influence on several physiological parameters in mussels, such as filtration activity, heartbeat rate, immune parameters, and growth rate affecting their maximum size (Shumway 1977, Riisgård et al. 2013, Wu et al. 2018). Although adults are euryhaline, they are more susceptible to pollutants in the brackish Baltic water than those living in marine water (Tedengren et al. 1999).

Normally, fertilization of *Mytilus* occurs in a wide range of salinities (15–40 S_P**)** (Bayne 1964, Bayne 1976). According to the Canadian study by Qiu et al. (2002) the embryonic development of *Mytilus edulis* requires relatively high salinity and no completed development was recorded below 15 S_P. Juveniles, and adults of *Mytilus* spp. can close their shells as protection against temporary hyposaline events (Shumway 1977, Qiu et al. 2002). The veliger stages of both *M. edulis* and *Mytilus trossulus* were shown most vulnerable and were not able to survive when salinity was restored (27–29 S_P). Moreover, adults were less tolerant of hyposalinity during the reproductive period with high mortality at salinities of 10–15 S_P. The authors suggest that differences in salinity tolerance may act as a selective factor for abundance and size structures of wild mussel populations.

Genetic Drift and Hybridization

As the tolerance to decreasing salinity varies between species of *Mytilus* there are differences in their distribution. The *Mytilus* species complex generally expresses a high degree of phenotypic plasticity, which makes it difficult to make distinctions based on morphological characteristics. In areas of overlapping occurrence as well as when non-native species have been translocated for aquaculture activities, hybridization is possible (Gosling 1992, Seed 1992, Bierne et al. 2003). Recently, Wenne et al. (2020) genetically investigated the species complex at 53 locations covering the entire distribution area. The degree of hybridization is high, but *Mytilus edulis* is dominant along the coast of the USA and southern Canada (mostly, the North American *M. edulis*) and in northern Skagerrak and the North Sea (European *M. edulis*), whereas *Mytilus trossulus* prefer lower salinity than *M. edulis.* A study on genetic differentiation of *Mytilus* populations along a transect from the North Sea to the inner Baltic (Kijewski et al. 2019) demonstrated a significant shift from *M. edulis* to *M. trossulus* at a salinity of 12 $S_{P.}$ The hybridization (*M. edulis* × *M. trossulus*) zone in Sweden is concentrated in the Baltic area, along the Sound and the shoreline of Kattegat (Michalek et al. 2016).

The extent of hybridization is inhibited by several factors, such as hydrodynamic barriers, spawning synchrony, and local adaptation (Michalek et al. 2016). In addition, postzygotic barriers may affect the success of the hybrids by reducing their viability and reproductive capacity (Bierne et al. 2003), also generating functionally sterile F1 hybrid males and hermaphrodites (Kenchington et al. 2019).

Potential negative effects of hybridization have been reported, for example, from the hybridization zone between *Mytilus edulis* and *Mytilus galloprovincialis* at the Atlantic coast of France. In 2014, mass mortalities of cultured *M. edulis* × *M. galloprovincialis* occurred and heavy genomic abnormalities were discovered (Benabdelmouna & Ledu 2016). This was manifested by continuously dividing neoplastic cells in the hemolymph, giving rise to a fatal leukemia-like disease, replacing the normal hemocyte populations and in the late stages penetrating the tissues (Barber 2004, Carballal et al. 2015). It was not determined if hybridization causes the genomic abnormality, other hypotheses such as effects of pollutants have also been discussed. Another potentially negative effect was noted by Beaumont et al. (2004) who demonstrated that hybrid larvae (*M. edulis* × *M. galloprovincialis*) grew slower than larvae of the pure species. Slow growth could increase predation of the larvae with possible selection against hybrids. In Scotland, hybrids between the native species *M. edulis* and the nonnative *M. galloprovincialis* have been successfully cultivated. This was interrupted in 2004, when pure species of *Mytilus trossulus* as well as hybrids of all three genotypes were, for the first time, found in the area (Beaumont et al. 2008). Then, the harvesting process resulted in 50% loss caused by fragile shells. The invading *M. trossulus* is now listed as a commercially damaging species (Scottish Government 2014). The threat to the local mussel industry may, however, persist as this low-salinity species is more associated with farm sites compared with natural intertidal habitat (Dias et al. 2009) and may expand its distribution in line with increasing rainfall (Hyposalinity and Physiological Stress section).

Recently, it was discovered that another *Mytilus trossulus* that originates from the North Pacific/Northwest Atlantic and is genetically distinct from those occurring in the Baltic Sea, and is widespread along North European coasts, including the Norwegian west coast (Väinölä & Strelkov 2011). In addition to thinner shells, *M. trossulus* is associated with lower meat content, showing a grayer character and reduced shelf life after harvest (Penney et al. 2007, 2008). Mussel farmers from Bohuslän (A. Granhed 2020, personal communication) made no such observations of hybrids nor has their harvest diminished. Whereas *M. trossulus* is mostly found at lower salinity (Beaumont et al. 2008), it cannot, however, be ruled out that wild mussel populations in the inner archipelago of Bohuslän are possibly affected by hybrids. Genetic comparisons will be necessary to clarify if *M. trossulus* has an effect on these populations.

Substrate Changes

Settling Behavior and Growth

At present, there are no studies available regarding the observation that normal benthic settling has more or less ceased in the Swedish fjords at the same time as settling continues to take place in mussel farms and on other artificial substrates and at some localities in the outermost archipelago (Fig. 2B). In prior *Mytilus* localities revisited during the 2010s, only remains of large dead shells and a gray fluffy layer of old, decaying filamentous algae were found. Obviously, the live mussels had been old and no resettling taken place, or alternatively, the resettled mussels had not survived. In fact, difficulties settling can be one of the main reasons why greater parts of the natural mussel populations have disappeared over time. Settling of *Mytilus* spp. is dependent on access to suitable substrates.

A mini survey in Koljöfjord in the northern part of the Orust Fjord system (Fig. 1) illustrates the observed difference between settling sites. In the littoral zone, very few mussels ranging in size 2–6 cm were found at places where dense populations were common 10–15 y ago. No settling and no small mussels (<2 cm) were found in the littoral zone except under a floating pontoon, where both small and large mussels were present in abundance. Just a few hundred meters from the site, two long-line mussel rigs have been operating for about 10 y by a commercial mussel farmer. On the rigs, using mussel webbing (woven 5-cm wide bands) as substrate and reaching to 6 m depth, settling of mussel larvae and growth of mussels have been relatively successful during most years, although with some interannual variability. Thus, this is a paradox with two very different situations of mussel settling and growth occurring parallel in time and just a few hundred meters apart. Settling on artificial, but not on natural, substrates has also been observed at other localities along the Bohuslän coast by the authors as well as by several other persons. Figure 2B demonstrates another example of the paradox: settling on artificial substrates on a boat, moored over summer in a marina just outside the Orust Fjord system. The underside of the buoy belonging to this boat was also covered with mussels. No mussels growing on natural substrates could be observed on the bottom of the marina or elsewhere in the nearby surroundings where a thick cover of filamentous algae was present.

The paradox has also been documented from Norway where *Mytilus* disappeared from hard bottoms, but not from the underside of floating jetties. Speculations about potential reasons include changed behavior of settlement (Andersen et al. 2017, Frigstad et al. 2018, Christie et al. 2020).

Biofilm Formation

Before settlement, pediveliger larvae need to be competent, that is, fully developed and able to metamorphose to plantigrades (Lutz & Kennish 1992). Reaching that stage requires specific environmental cues, such as appropriate temperature, salinity, texture of the substrate, biofilm, and coexisting species, indicating a suitable habitat (e.g., Bishop et al. 2006, Thiyagarajan 2010, Gribben et al. 2011). All immersed surfaces (natural and artificial) are rapidly colonized starting with bacteria, that through cell-to-cell communication (so-called quorum sensing) coordinate their swarming and adhesion. These initial colonizers are generally followed by diatoms, other algae, cyanobacteria, and invertebrate larvae, all surrounded by a matrix of extracellular polymeric substances (reviewed by Antunes et al. 2019). The constitution of metabolites and other chemical cues from the biofilm depends on influences of environmental factors (Battin et al. 2007) and may either stimulate or inhibit the larval settlement (Olivier et al. 2000); however, virtually nothing is known about biofilm-derived cues and the substances attracting *Mytilus* (Bao et al. 2007). The biofilm is certainly not the only factor regulating settlement. Other factors, such as the importance of the presence of phytoplankton, have shown more crucial for a successful settling (Toupoint et al. 2012a). In particular, the settlement success of *Mytilus* is dependent upon the lipid content of the premetamorphic larvae. This seems to explain why the major settlement peaks are synchronized with phytoplankton pulses rich in fatty acids (Toupoint et al. 2012b). If the settlement conditions are not good enough, larvae remain adrift and may delay metamorphosis for about 15 days (Martel et al. 2014). It reduces their energy reserves and results in poorer settlement success (Elkin & Marshall 2007).

Alteration of biofilm composition was raised as a hypothesis because of the observation that the mussels continue to settle on floating substrates but not on the bottom near land. In addition, mussel banks in the outer archipelago seems to remain intact. It has been recognized that climate change contributes to, for example, increasing inputs of terrestrial dissolved organic matter in coastal areas beneficial for heterotrophic bacteria (Eggermont et al. 2014, Soares et al. 2018). Increased land run-off in terms of fresh water (see Hyposalinity and Physiological Stress section) and harmful substances (see Pollutants section) can be assumed to affect areas close to the shore and can to some extent spread above the halocline. This may indicate that even if no clear changes in terrestrial emissions of nutrients have yet been identified through the regular monitoring programs, there may be local differences affecting biofilm compositions. Further, Sanil et al. (2015) identified, using "shotgun" metagenomic sequencing, the taxonomic composition of biofilms formed on test surfaces placed on different sites near the mouth of the Gullmar Fjord (Swedish west coast, see Fig. 1). The taxonomic structures were comparable between all sampling surfaces placed at 4–6 m depth, but these were deviant from those of the deepest test surface, placed on 10 m. In the same way, the depth difference between lagoons and open coast sites was shown to be the main explanation for differences in biofilm composition on *Zostera* leaves (Bengtsson et al. 2017). Such differences on a relatively small spatial scale strengthen the hypothesis that there may be a change in the settlement environment for the wild mussels.

Mytilus Early and Late Plantigrade Settlement

The planktonic pediveliger stage of *Mytilus* develops into an early and a late plantigrade (settlement) stage (nomenclature by Carriker 1961). In the intertidal and subtidal zones, the early plantigrade stage between 250 μm and 1–1.5 mm appears in filamentous algae and hydroids (Bayne 1964, Pulfrich 1995) and in *Zostera marina* (L.) (hereafter *Zostera*) meadows (Baden 1990, Reusch 1998, Newell et al. 2010) mainly in the early and midsummer period. According to Dobretsov and Wahl (2001) the veliger larvae seem to selectively avoid settling on some algae [e.g *Laminaria* spp. (Lamouroux) and *Chorda* spp. (Dumortier) possibly having repellants], but preferring *Zostera* and artificial substrates. De Blok and Taan-Maas (1977) also found that settlement of plantigrades greater than 500 µm was more frequent on thicker algal threads (>1 mm). Mussels are known to detach voluntarily and these settlements are temporary before drifting from the vegetation or hydroids using a long byssus thread especially made for drifting (Sigurdsson et al. 1976, de Blok & Taan-Maas 1977). Resettling occurs within areas of algae or seagrasses and finally as late plantigrades (mainly in August) on hard substrates or in the adult mussel beds (Pulfrich 1995). This strategy is speculated to be a predator protection since the smallest sizes of plantigrades easily get accidentially inhaled by filtering adult *Mytilus* and other predators not present among *Zostera* leaves and other preferred algae environments (Lutz & Kennish 1992, Dolmer & Stenalt 2010).

The preference of early plantigrades for macroalgae, large hydroids, or *Zostera* varies geographically (Pulfrich 1995). Along the Swedish west coast, early plantigrades (200 µm to 1.8 mm) arrive to *Zostera* during June and July and disappear in August. In July 1997, the mean abundance (±SE) per m^{-2} of plantigrades in 19 *Zostera* beds along the coast was 9,341 ± 3,360 individuals·m^{-2}. When revisiting the same meadows in July 2018, only 14 meadows remained and the plantigrade mean abundance had declined with 83% being 1,555 ± 805 individuals·m^{-2} (Riera et al. 2020). This is of certain concern since the vicinity of *Zostera* to mussel beds results in a 3-fold increase in recruitment (Reusch 1998).

The distribution of seagrasses in general and *Zostera* specifically has declined globally in recent decades (Waycott et al. 2009, Santos et al. 2019). Along the Swedish west coast, the prevalence of *Zostera* has decreased by more than 60% since the mid-1980s. It has largely been replaced by filamentous opportunistic algae dominated by *Ulva* (L.) and *Ectocarpus* spp. (Lyngbye). There has also been increased resuspension of sediments preventing recovery of *Zostera* (Baden et al. 2003, Moksnes et al. 2008, Baden et al. 2010, Moksnes et al. 2018). When no seagrasses or macroalgae of suitable texture are available, the larvae make the primary settlement among adult mussels despite the risk of being accidentally consumed by filtering adults (Dolmer & Stenalt 2010). It is likely that the decline in *Zostera* has affected the local recruitment of *Mytilus*, but to what extent remains to be investigated. It is also important to investigate the role of macroalgae surrounding the *Zostera* since, in the Wadden Sea, early plantigrades are found also among the macroalgae (Pulfrich 1995). Further, the fine filamentous algae [mainly *Ulva* spp. (L.) and *Ectocarpales* spp. (Setchell & N. L. Gardner)] often replacing the *Zostera* (Baden et al. 2010) may be a nuisance hampering the plantigrade feeding and movement or able to replace the function of *Zostera*.

When natural preferred settling surfaces of mussels are occupied by more or less degraded annual filamentous algae they may physically hamper settling (see Settling Behavior and Growth section). The final settling of *Mytilus* on hard substrates is considered to provide a high resistance to wave exposure. With softer sediment (sand to mud including building up of faeces/psuedofaeces under the bank), the resistance to exposure becomes weaker and in risk of being spoiled by storms (Connor et al. 2004, Mainwaring et al. 2014). In the Wadden Sea, Diederich (2006) found that in the competition for space between *Mytilus* and the invasive Pacific oyster, *Mytilus* had an advantage and could settle despite some fouling with *Fucus* on hard substrate and as well between the oyster*s* (Reise et al. 2017). No investigations on algal fouling hampering settlement of *Mytilus* were found.

Food and Vitamin Supply

Phytoplankton is an important food for mussels and climate change can cause indirect consequences for *Mytilus* through, for example, a change in the amount and composition of available food.

Access to Food for Mussels

As a filter-feeding organism, *Mytilus* is completely dependent on nutrient-rich particles from the surrounding water and phytoplankton constitutes a main food source. Phytoplankton dynamics, in turn, are dependent upon a balance between nutrient concentration and grazing, called bottom-up and top-down regulation, respectively. Excess nutrients, resulting in increased phytoplankton production, can act synergistically or antagonistically with changes in fish populations (e.g., overfishing). The effects depend on the number of trophic levels in the ecosystem and generate a downward cascade that regulates grazing zooplankton and thus the phytoplankton biomass. For many coastal waters the effect of increased concentrations of nutrients and overfishing were found equally important for the resultant plankton biomass (Casini et al. 2008, Baden et al. 2012, Östman et al. 2015, Tiselius & Möller 2017).

Measurements of primary production *in situ* have been carried out since 1985 in the Gullmar Fjord, a more wind exposed and ventilated site compared with the Orust fjord system (Fig. 1). Here the annual mean production during 1985 to 1994 was 240 g C·m^{-2}·y^{-1}, peaked at approximately 250 g C·m^{-2}·y^{-1} during the 1990s and decreased during the 2000s to 220 g C·m^{-2}·y^{-1} (Lindahl et al. 2009). From relatively few measurements in the Skagerrak and Kattegatt outside the Gullmar fjord between 1950 and 1970, it was estimated that the primary production in the Gullmar fjord was approximately 100 C·m^{-2}·y^{1} indicating a doubling of the primary production in a couple of decades (Lindahl et al. 2009). It was suggested that the primary production during 1985 to 1998 was controlled by the coupling of large climatic decadal patterns such as the NAO and the subsequent changes in the nutrient regime both in the central Skagerrak and at a regional scale (Belgrano et al. 1999). During 2010s, the primary production continued to decrease to approximately 170 g C·m^{-2}·y^{-1} toward the middle of the decade (Tiselius et al. 2016). A significantly decreasing trend in total nitrogen concentrations in the coastal surface waters was found for the period 1992 to 2012 (Moksnes et al. 2015), probably explaining the decreasing phytoplankton production.

Chlorophyll *a* (Chl-*a*) has been measured monthly at a number of near coastal and fjord stations along the Swedish north-west coast since 1990 (SMHI 2020b). The main overall trend is a significantly ($p < 0.05$) decreasing trend from 1990 and onward of the concentration of Chl-*a* in the surface water (0–10 m) at stations situated in the Orust Fjord system. At coastal stations situated in the outer archipelago a decreasing trend has been obvious since 2016. From the summary of the

Gullmar Fjord time series, the decrease of Chl-*a* concentrations has occurred mainly during autumn, from approximately 4–8 $mg \cdot m^{-3}$ (average 0–10 m) in the 1990s, over 4–6 $mg \cdot m^{-3}$ in the 2000s to 2–4 $mg \cdot m^{-3}$ in the 2010s. (Tiselius et al. 2016). A similar decline was also reported from the Danish coastal zone where the biomass of filter feeders [mainly *Mytilus edulis*, *Mya arenaria* (L.), and *Cerastoderma* spp. (Poll)] has decreased by a factor of three from 1985 to 2013 correlating to a halving of Chl-*a* annual mean concentration from about 6 $mg \cdot m^{-3}$ to 3 $mg \cdot m^{-3}$ as a result of reduced eutrophication (Riemann et al. 2016). A Chl-*a* concentration of 3–6 $mg \cdot m^{-3}$ was found to be optimal for *Mytilus* filtration by Franz et al. (2019).

The large decrease of the natural mussel stock and banks seems to have occurred mainly during 2000s, but the Chl-*a* data from the Swedish west coast presented above reveal no evidence that the mussels have suffered from a lack of supply of feed of such significance that more or less all wild mussels should have disappeared. This conclusion is further supported by the fact that no decrease in the production or impaired quality of farmed mussels has been observed. Small-scale spatial variations of the plankton community can, however, be expected to affect mussel settlement in areas close to the shore more affected by land runoff.

Thiamine Deficiency

Thiamine deficiency has recently been pointed out as a possible driver of wildlife population declines by the expert panel of the annual "Horizon Scan of Emerging Issues for Global Conservation and Biological Diversity" (Sutherland et al. 2018). Thiamine is a water-soluble vitamin (B_1) that is essential for the maintenance of basic cellular metabolism and neuronal functions in all vertebrates as it takes part as cofactor for many life-sustaining enzymatic systems. Thiamine or its precursors are synthesized only in bacteria, fungi, and plants, and to become functional in animals, thiamine requires phosphorylation within the cells. The dominating producers of thiamine in the aquatic food web are heterotrophic prokaryotes and photoautotrophs (although some are auxotrophic, requiring certain B vitamins) (Heliwell 2017).

Among the phytoplankton there is great versatility in thiamine content depending on species and cell size and the content may fluctuate over time. In general, phytoplankton communities dominated by the smallest primary producers, picophytoplankton, result in low flows of thiamine to higher levels in the food chain (Ejsmond et al. 2019). Abiotic factors such as salinity, temperature, and photon flux density have shown to affect the thiamine contents, but with different response in different species (Sylvander et al. 2013). Thus, shifts in the composition of phytoplankton communities through large-scale environmental changes, have the potential to alter the thiamine availability for higher trophic levels.

The thiamine levels in the oceans are generally low, mostly below picomolar concentrations. Released thiamine can be recycled but since it is water-soluble it cannot be stored in the animals and they rely on a continuous external supply (Sañudo-Wilhelmy et al. 2012, Suffridge et al. 2017). Episodic thiamine deficiency has been recorded across the Northern Hemisphere and from a wide range of taxonomic groups, such as fish, birds, and invertebrates (Balk et al. 2016, Harder et al. 2018, Sutherland et al. 2018). A model of the flow of vitamin B_1 through the food web in the Baltic indicated that climate change driven increased load of nutrient and dissolved substances in combination with overfishing initiate the reduction of the vitamin by altering the relation between populations of different planktonic organisms (Balk et al. 2016). The consequences of large-scale whole-ecosystem influences on thiamine production are, however, difficult to overview. It has been discussed, among other things, whether the deficiency is caused by a reduced supply or if the animals are affected by oxidative stress (e.g., from pollutants) increasing the consumption of thiamine as an antioxidant (Hylander et al. 2020). According to Balk et al. (2016) biochemical observations of normal proportions of the phosphorylated forms, do not indicate impaired phosphorylation. Rather, thiamine deficiency is caused by insufficient availabilities in the food web as indicated through the relationship between the common eider and its main prey, blue mussels.

Severe episodic thiamine deficiency has been recorded in *Mytilus* from the Baltic Sea (Balk et al. 2016) but data is limited, also from the Swedish west coast. The declining populations of mussels may, however, not be a direct effect of thiamine deficiency, sublethal effects should also be considered. The molecular alterations due to disrupt functions of thiamine-dependent enzymes will increase toxic metabolites, causing secondary effects on, for example, growth, immune defense, and reproduction (Balk et al. 2016). It is known that the deficiency can cause irreversible disorders, why also episodic thiamine deficiency may affect the health status of the populations. Thus, the hypothesis that thiamine deficiency may contribute to the declining mussel populations cannot be ruled out without further investigations.

Competition and Predation

This section focuses on feeding ecology and temporal trends of the main competitors and predators affecting *Mytilus*. Mussels of all life stages are attractive food items for numerous species explaining why especially predation on *Mytilus* has been a popular research topic since long, for example, in 1959 the quote "On the open coast *Mytilus* is sufficiently in balance with its predators to survive throughout a season" was expressed by Kitching et al. (1959). Since then, many marine ecosystems have changed due to human activities and thus affected the balance between *Mytilus*, invasive competitors, and predators (van der Heide et al. 2014).

Competition and Predation by the Invasive Pacific Oyster

The literature on the interaction between *Mytilus* and the invasive Pacific oyster (*Crassostrea gigas*) is extensive. For the Wadden Sea, the research on this interaction is described by Reise et al. (2017) and reviewed by Folmer et al. (2019). In the 1960s Pacific oyster was introduced by the aquaculture industry to several locations along the North Sea coast. The first feral oysters were reported from Texel in the Dutch Wadden Sea in 1983. Since then, there has been an increase in dominance of Pacific oyster and after a period of total dominance of oysters overgrowing *Mytilus*, the two species often coexist in relatively stable mixed oyssel beds. There, mussel*s* seem to "hide" from predators in the interspaces of oysters (Reise et al. 2017). The coexistence results in slower growth and worse general condition of the mussels (Eschweiler & Christensen 2011). The higher the proportion of Pacific oyster in a mixed oyssel bed, the lower the condition of *Mytilus* (Waser et al. 2016).

Folmer et al. (2019) concluded that many different environmental and biotic factors affecting competition between *Mytilus* and *Crassostrea* in the Wadden Sea making it hard to produce long-term predictions for the outcome. Both species are now regarded important in terms of biomass, ecological functioning, ecosystem engineering, and biodiversity. Oyster beds, for example, contain higher biodiversity and abundance of benthic organisms than both *Mytilus* beds and bare sand (Hollander et al. 2015).

In the Danish Limfjord where Pacific oyster was introduced in the early 1970s mussels and oysters have coexisted for about 50 y and there is no temporal and spatial niche separation (Strand & Lindegarth 2014, Laugen et al. 2015, Holm et al. 2016). In other parts of Scandinavia Pacific oyster has spread, especially after 2005 (Laugen et al. 2015). In 2007, the first *Crassostrea* were reported by the public along the Swedish west coast. The oysters mainly disappeared after a severe winter 2009 to 2010 but are now widely distributed along the Swedish west coast (Figs. 1 and 2D) and up along the Norwegian coast but it is not found in the southern part of Kattegat or in the Baltic (Strand & Lindegarth 2014, Laugen et al. 2015). They prefer shallow (<1.5 m) and sheltered coasts and are rare below 4 m (Strand & Lindegarth 2014, Laugen et al. 2015). A normal density is about 100 ind.$\cdot$m^{-2} and may reach 1,000 individuals$\cdot$m^{-2} especially in places with high water velocity (Laugen et al. 2015). Since the invasion of Pacific oyster to the Swedish west coast is relatively recent, coexistence with *Mytilus* may not yet have reached such an equilibrium as reported from the Wadden Sea and inner Danish waters. Joyce et al. (2019) suggested from experiments that the greatest ecological impacts and competition of Pacific oyster vis a vis *Mytilus* will occur on sediment with low flow velocity and low food level. The Swedish west coast has a relatively narrow strip of this type of suitable sediment, potentially exacerbating the competition (Stål & Pihl 2007, Laugen et al. 2015). Although Pacific oyster may not be the direct cause of the decline in the wild mussel populations along the Swedish west coast, it cannot be ruled out that the large distribution of the oysters may have affected recovery of mussel beds (Fig. 2D).

Predation by Invertebrates

Although the veliger larval stage of *Mytilus* is relatively small (approximately 150 μm) it is preyed upon, but not necessarily digested, by jellyfish such as *Aurelia aurita* (L.) (Hansson et al. 2005) and the ctenophore comb jelly which are efficient predators. Nelson (1925) noticed that in July, 75% of the ctenophore *Mnemiopsis leydei* (A. Agassiz) (hereafter *Mnemiopsis*) stomachs from New Jersey coastal waters contained *Mytilus* larvae far more frequently than any other food items of same size category. Along the temperate Atlantic coast of North and South America *Mnemiopsis* is native and has natural predators (Purcell et al. 2001). Despite these predators, the populations of *Mnemiopsis* occurred in vast amounts up to 60 mL$\cdot$m^{-3} in July–August of 1995 to 1998 (Purcell et al. 2001), and the zooplankton abundance was found to be inversely related to the biovolume of *Mnemiopsis* in most months as found in Chesapeake Bay (Burrell & Van Engell 1976). Between 2005 and 2007, *Mnemiopsis leydei* invaded the east Atlantic coast, and in 2006 the Skagerrak and the Kattegat (Hansson et al. 2005). In contrast to native ctenophores, *Mnemiopsis* has no natural predators on the eastern site of the Atlantic, and in the autumn of 2007 reached a mass occurrence with up to 5 times the biovolume than that in western Atlantic (Riisgård et al. 2007). For some distribution areas, *Mnemiopsis* can thus potentially be an important predator on *Mytilus* veliger larvae when they occur simultaneously. Along the Swedish west coast, the main settling of *Mytilus* plantigrade larvae is documented in seagrass in June (Baden 1990), meaning that the veliger larvae occur 4–6 wk earlier (Lutz & Kennish 1992). The first seasonal appearance of *Mnemiopsis* is reported from mid-July to August (Haraldsson et al. 2013, Tiselius & Möller 2017). Thus, there is a mismatch in time for being an efficient predator unless unreported small (<500 μm) *Mnemiopsis* actually appear earlier. Noteworthy, in both 2015 and 2020, a large spatfall of *Mytilus* occurred in the outer archipelago simultaneously with a mass occurrence of *Mnemiopsis* (Tiselius & Möller 2017, Baden pers. obs). In 2015, the *Mytilus* juveniles did, unfortunately, not survive the winter. These single observations may indicate a more complicated interdependence than simple predation and this calls for special attention.

The shore crab *Carcinus maenas* (L.) is omnivorous and a well-known predator of *Mytilus* (e.g., Elner 1978). In Swedish coastal waters, 0–1 group C*arcinus* prey mainly on *Crangon crangon* (L.), *Hydrobia* spp. (Hartmann) and *Mytilus* (Pihl 1985). Walne & Dean (1972) showed, *in vitro*, that *Carcinus* had a preferred size of *Mytilus* increasing linearly with the carapace length of the crab, and they can consume between 2 and 3 *Mytilus* per day when no other food sources are offered. This was verified by Kamermans et al. (2009) in experiments in the Wadden Sea. Crabs of 20 and 80 mm carapace length prefer *Mytilus* of 10 and 32 mm length, respectively. Predation of *Mytilus* by *Carcinus* as a possible interfering factor for the decrease of *Mytilus* along the Skagerrak coast of both W Sweden and S Norway was tested by Christie et al. (2020). In a rocky mesocosm environment and using natural densities of *Carcinus* and newly settled *Mytilus* (2–3 mm), they found that the mean *Mytilus* cover decreased by 30% within 5 h and to 0% within 24 h indicating an efficient predation. Along the Swedish west coast *Carcinus* has increased 2–3 times (observed from changes in CPUE of fyke nets) simultaneously with a crash of the cod population, being a main predator of *Carcinus* (Svedäng & Bardon 2003, Eriksson et al. 2011). Further, *Carcinus* is benefitted by an increase of intermediate biomass of filamentous algae caused by eutrophication (Wennhage & Pihl 2007). Their increase may thus be a contributing factor to a decrease in *Mytilus* populations. When seastars *Asterias rubens* (L.) prey on intact sublittoral *Mytilus* banks consisting of two size classes of mussels, they prefer the larger individuals in the top layer, or rather can only get access to the larger ones since the bank structure is a refuge for the smaller individuals. The size of *Asterias* ranged from 57 to 116 mm, and the size of predated mussels ranged from 14 to 59 mm (Dolmer 1998). On most banks *Asterias* showed to prefer *Mytilus* oriented with the hinge downward as is often the position in banks. In the Danish Limfjord, *Asterias* is trawled with a strictly regulated quota to decrease the predation on *Mytilus* (Nielsen et al. 2018a, 2018b). In wild seed beds of *Mytilus* in the Wadden Sea, *Carcinus* was shown to be a 23 times more voracious predator on these small mussels than *Asterias* (Kamermans et al. 2009). The starfish is associated with the mussel banks, and since the banks have more or less disappeared in the inner coastal zone of the Swedish west coast, they are now harder to find. The relative role of *Asterias* in the decline of *Mytilus* seems to vary between areas and is largely undocumented.

The gastropods *Nucella lapillus* (L.) and *Hinia reticulata* (L.) are predators of molluscs. The first choice of prey for *N. lapillus* up to 3 cm height is *Mytilus* of up to 2 cm length (Morgan 1972, Bayne & Scullard 1978). The main predator of *Nucella* is *Carcinus* (Feare 1970). The spatiotemporal and quantitative literature on *Nucella* and *Hinia* predation on *Mytilus*, is sparse. In Canada, the high correlation observed between the density of *Nucella* and overall mussel density across regions suggests that these predatory snails may not be controlling mussel abundance on the regional scale. Instead, their abundance seems to respond closely to variation in prey abundance across regions (Tam & Scrosati 2011).

Predation by Birds

Many waterbirds are important predators of *Mytilus* (Waser et al. 2016). In the east Frisien Islands (Fig. 1) bird predation on *Mytilus* was responsible for 7%–15% of the total elimination in the beginning of the 1990s (Hilgerloh 1997). More abundant oysters could be expected to affect several waterbirds normally preying on *Mytilus*. According to Waser et al. (2016), the only bird species affected by more abundant oysters in the littoral zone of the Wadden Sea, however, is the common eider *Somateria molissima* (L.). The abundance of eiders was positively correlated with increasing proportion of *Mytilus.*

In Sweden, eiders, goldeneyes *Bucephala clangula* (L.), Eurasian oystercatchers *Haematopus ostralegus* (L.), and some gulls, especially the herring gull *Larus argentatus* (Pontoppidan), are significant predators on *Mytilus* (Nyström et al. 1991, Laursen et al. 2009, Waser et al. 2016, Hönneland & Seip 2019). The Swedish breeding populations of these waterbirds have either decreased or stayed stable since 1975 (Björnås 2017, Green et al. 2018, Lindegarth et al. 2019). In the western Swedish archipelago, however, wintering eider and goldeneye have increased (Nilsson & Haas 2016). Wintering eider increased by a factor 10 from 2,900 to 30,000 individuals and goldeneye with a factor 7 from 1,000 to 6,800 individuals between 1971 and 2015, with a peak in 2004 of 37,000 eiders and 13,000 goldeneyes (Nilsson & Haas 2016). The breeding birds are difficult to count, but in an area around the islands of Orust and Tjörn 3,000 eiders were recorded in 2018, declining from 8,000 individuals since 1990s (Lindegarth et al. 2019).

Eiders can dive to 20 m (Zydelis & Richman 2015) and may thus be able to prey on mussels from intertidal and subtidal areas as well as in mussel aquaculture facilities. On the underside of floating objects, like jetties or buoys, it seems as mussels are not predated by eider according to the authors' observations. Eiders prey selectively and prefer relatively small *Mytilus* in the summer (approximately 20–35 mm) and larger in the winter (approximately 40–55 mm) to minimize the proportion of shell to meat (Hamilton et al. 1999). Goldeneyes can eat mussels up to 15 mm, but is mainly omnivorous and is reported to eat seeds and smaller gastropods from *Zostera marina* (Pehrsson 1976). Is it possible that the increase in wintering common eiders did exhaust the *Mytilus* populations in the Swedish archipelago? The daily winter consumption of *Mytilus* by common eiders was estimated to be 2,260 g ww per day in the Sound. Thus 30,000 overwintering eiders consume an equivalent of 14 kt *Mytilus* from October to April (Nilsson 2005, Nilsson & Haas 2016). The unknown predation in the summer months also has to be considered. This predicted amount of *Mytilus* lost to bird predation is about 7 times the harvest from aquaculture in the area (Overfishing of Wild Mytilus Stocks section).

The large predation on mussels from wintering eider populations in the area was also empirically verified by Svedberg (2017). In a replant experiment from December to April between Orust and Tjörn (Fig. 1) the small size classes (mean size 27–38 mm) were preyed upon to almost 0% survival in two out of three localities, whereas in the larger mean size of 58 mm, 20%–50% of the mussels survived. The eider predation on mussel aquaculture is also significant and creates large commercial losses for the culture industry (Lindegarth et al. 2019). As suggested by these authors, the aquaculture facilities could be an essential food resource for starving eiders. Thus, it is possible that this indirect effect of climate change with the large increase in wintering eiders, to a large extent can explain the serious decline of *Mytilus* populations—at least along the Swedish west coast.

CONCLUSIONS

The spatiotemporal development of the *Mytilus* spp. in the North Atlantic was evaluated and an overall decrease in distribution with local variations was verified. Different hypotheses linking factors of anthropogenic origin to explain this decrease have been scrutinized (Fig. 5). No single factor has been identified or demonstrated to account for the observed losses of mussel populations but in this review some factors were found more likely to play part in the mussel decline than others. Where *Mytilus* populations have declined, the dominant reasons reported were overfishing of mussel banks (particularly in the Wadden Sea during late 1980s) and climate change via direct effects (changes in temperature, salinity and extreme weather events) or indirect effects (higher abundance of predators and infectious agents). A multitude of anthropogenic factors can be involved in synergy, probably too demanding for different stages of the mussels. According to strict management of *Mytilus* populations in a few areas recovery, although slow, can be found (see North Atlantic Coastal Waters: Spatiotemporal Variation of *Mytilus edulis* Species Complex section).

On the Swedish west coast, where no intensive fishing for mussels has taken place, the stocks have nevertheless decreased drastically in recent decades. Amazingly, at the same time as no settlement or growing mussels can be found on natural substrates in the littoral zone, nearby situated (300 m) mussel farms have no problems with either settlement or growth to adulthood. In fact, floating artificial substrates such as the underside of floating jetties, hulls, ropes, and nets are favorable for all life stages of *Mytilus* from newly settled plantigrade larvae to adults. Moreover, mussel beds localized in the outer archipelago still occurs. Strong candidates behind the differences were evaluated (see Effect of Stressors section). The explanation seems to be that the natural substrates close to the mainland shore are either occupied or nonoptimal for the settling of late

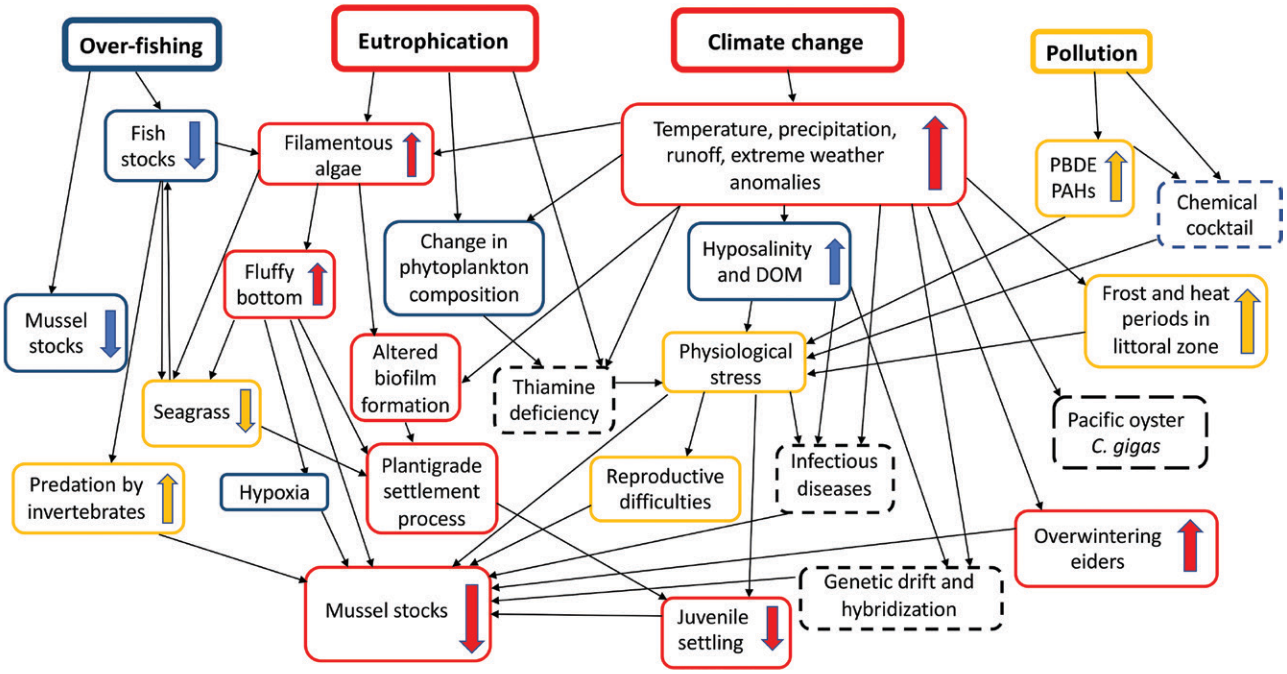

Figure 5. The dendogram demonstrates identified or suggested cause and effect parameters relevant for the decline of wild *Mytilus* along the Swedish west coast during 1990s to 2010s. Blue color means a light influence, orange color medium, and red color a strong influence. An arrow pointing upward means an increase, arrow pointing down means a decrease. A dashed frame means a hypothetical relation warranting further examination.

plantigrade larvae (Substrate Changes section) in combination with increased predation by birds and invertebrates.

It is concluded that differences between natural substrates in the littoral/demersal zones versus artificial substrate in the free water body and mussel beds in the outer archipelago may be caused by:

Position in the water column: Faster water turnover in the free water body and in the predominating coastal current of the outer archipelago may benefit the condition and health of the mussels.

Increasing land runoff may to a greater extent affect salinity, pH, deposition of terrestrial organic material, and thereby composition of nutrients, seston, and biofilm inhibiting mussel metamorphosis and settlement in the littoral zone.

Hyposalinity may in the initial stage hamper settlement or decrease survival of *Mytilus edulis* and in a longer perspective induce greater proportion of *Mytilus trossulus* or hybrids of *M. edulis* × *M. trossulus*, more susceptible to fluctuations with higher salinity.

Competition/Predation: Great dominance of *Crassostrea gigas* along the shores indicates that a mussel/oyster balance has not yet been established as seen in the Wadden Sea and the Limfjord. Mussels in the littoral zone are also more prone to predation from green crabs *Carcinus maenas* whose abundances have increased 3-fold since cod, being one of their main predators, has declined by more than 90%. The peak (×10) of wintering eiders, *Somateria molissima*, along with mild winters in the beginning of the century may have had the greatest effect on the mussel population in the littoral zone where they were more accessible to predation.

Consequences of changes in the seagrass and algal extension and composition: Reduced areas of seagrass *Zostera marina* and suitable macroalgae where mussel plantigrade larvae can seek protection before permanent settlement may decrease larvae survival in the littoral zone.

Increased deposition of degraded filamentous algae when annual species replace perennials may further impair the quality of the substrate.

Influence of extreme physical conditions during locked weather events: Long lasting air exposure during low water level, heat waves during summer, ice cover during winter have greater impact on the littoral zone and may cause mussel mortalities.

Emissions of pollutants can have a greater impact on physiologically stressed mussels in the littoral zone. In particular, the effects of chemical cocktails should be considered. This also applies to susceptibility to infection that may increase during stress and rising temperature.

GAPS OF KNOWLEDGE

As shown in this review, research on *Mytilus* is very extensive. Nevertheless, important knowledge gaps have been revealed and they need to be investigated to achieve a better understanding of the decline of *Mytilus* spp. in the North Atlantic.

Most importantly, the spatiotemporal distribution of *Mytilus* spp. should be regularly monitored all over the North Atlantic using internationally standardized programs (e.g. the ones developed and used in the Wadden Sea and Danish Inner waters). Further the degree of hybridization between *Mytilus* spp. is important knowledge for understanding the resistance to physical and biological demands. Hybridization is thoroughly investigated in many areas, but not in, for example, Sweden.

For *Mytilus* larval stages, the knowledge gap results in an insufficient understanding of the degree of predation from invasive species such as *Mnemiopsis* and *Crassostrea* and to what extent the massive establishment of *Crassostrea* in the littoral zone has prevented new settlement of *Mytilus*. In addition, studies on the dependence of plantigrade larvae access to seagrass and suitable macroalgae are needed since these might constitute a protective refuge before final settlement on natural or various artificial substrates.

After settlement, the spat and adult mussels are heavily preyed upon, especially by water birds. Along the Swedish west coast, wintering eiders (*Somateria molissima*) increased with a factor 10 following warm winters. In-depth studies on how climate change has affected the overall interaction between mussels and birds are essential to understand the impact on mussel populations.

The differences between mussel habitats in the near-coastal zone and those that have a position in the free water mass as well as in the outer archipelago should be investigated with regard to small-scale spatial differences in biofilm, species composition, and thiamine content of phytoplankton affected by physical and chemical changes exacerbated by climate change. The control programs of today do not include such small-scale sampling as would be needed to track these possible differences. Likewise, regular monitoring does not include the pathogens that can affect mussel stocks with increasing temperature.

It is unlikely that any single factor will be identified as responsible for the losses of *Mytilus* populations noted and multidisciplinary studies will be of critical importance.

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