

Ocean Acidification (OA) in the Baltic Sea from a Swedish perspective

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Background

This report is produced as part of the project “Baltic Sea Acidification Mitigation” (BALSAM), supported by the Swedish Institute. The aim of this report and other, corresponding reports (produced for the other countries participating in BALSAM) is primarily to inform environmental NGOs and other stakeholders interested in environmental issues. The aim of this country report is to provide information on Ocean Acidification (OA) in the Baltic Sea with special emphasis on Swedish waters, and to provide an insight into the research and monitoring that are the basis of the current understanding of OA in these waters. This is done as support for campaigning towards mitigation of greenhouse gases and protection of the seas. Whereas this document is not a comprehensive literature review, it is intended as a timely guide to the concept of OA, and does contain key publications and links to further in-depth reading and sources of additional information.

Introduction

Ocean acidification (OA) comes in the wake of climate change as the result of increased atmospheric CO₂, which is taken up by the oceans. About 30 % of the CO₂ that is emitted to the atmosphere because of human activity ends up in the waterbodies. Part of the CO₂ reacts with water, and forms carbonic acid. Some of the carbonic acid dissociates, resulting in bicarbonate and in hydrogen ions. This process leads to acidification (lower pH, i.e. higher concentration of hydrogen ions). Organisms in the oceans are adapted to the pH-conditions that have prevailed in the seas prior to this human driven acidification-process. Especially calcifying organisms are sensitive to acidification, but the physiology of many other organisms can be affected as well, as can the complex ecological interactions between organisms. In a global setting, ongoing and projected effects of OA have been extensively described in several IPCC reports (e.g. IPCC, 2018, 2019).

In Sweden, an interdisciplinary review on causes and consequences of OA in the Swedish Seas (including both the Baltic Sea and the more saline waters of Skagerrak at the Swedish west coast), as well as knowledge gaps, was published relatively recently as part of work supported by the Royal Swedish Academy of Sciences (Havenhand et al. 2017). Additionally, in the same context, a scientific review focusing on the ecological consequences of OA was

published by Havenhand et al. in 2019. A policy brief¹ on OA in the Baltic Sea was furthermore published in 2020 by The Baltic Sea Centre of Stockholm University (Gustafsson & Winder 2020). This policy brief provides a general view of OA as support for policy making.

Here, we make use of the two publications by Havenhand et al. (2017, 2019) and additional literature to piece out a summary-view particularly on ecological issues related to OA, bearing in mind also the socio-economic importance of the Baltic Sea. Our aim is to provide an overview on the science behind the current understanding of OA to enable environmental NGOs (and other possible stakeholders) to meaningfully engage in advocacy in this matter. This is done with a popularized approach and we believe this combination of scientific information (at citation level) and summarized conclusions will complement the above earlier analyses especially to the benefit of the civil society. Clearly, all interpretations of each study are our own, and are based on our views on information we believe is important to convey to the civil society. We do encourage everyone who is either interested in a comprehensive, in depth scientific review or in a more generalized policy perspective to read also the two excellent studies by Havenhand et al. (2017, 2019) and/or the equally excellent policy brief (Gustafsson & Winder 2020), respectively.

Apart from our summary-view of earlier work, we also briefly touch upon the research and monitoring landscape to highlight to the civil society (and others) where the important work of studying OA is carried out.

Ocean Acidification in Sweden: Why it poses a threat from a socio-economic perspective

As pointed out by Havenhand et al. (2017), Sweden has a coastline that is over 3 000 km long and its waters represent one of the world's longest salinity gradients². It is also noted in the same study that half of Sweden's population lives within 10 km of the coastline (SCB 2014; cited in Havenhand et al 2017). Consequently, the coast is important for the wellbeing of people and for the economy, and based on data from Vinnova (2013), Havenhand et al. (2017) report that marine and maritime activities are worth 95 billion SEK annually and taken together support over 200 000 jobs.

Some sectors, such as shipping, are not a likely to be directly impacted by OA, although shipping is connected to a discourse on OA as a local acidification source due to emissions (Havenhand et al. 2017). Other sectors, such as fisheries, are at risk of being affected at first hand. This is exemplified rather drastically by stock recruitment models for cod: when experimental OA data (see section on Ecological consequences below) were used in these models, the outcome was a predicted 90 % reduction in recruitment for the Western Baltic Sea because of OA (Stiasny et al. 2016).

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https://www.su.se/polopoly_fs/1.493644.1585729224!/menu/standard/file/PB_Acidification_200331.pdf

² Including also Skagerrak, which connects the North Sea to the Baltic Sea

A wide variety of ecosystems is represented along the Swedish coastline due to the salinity and other gradients or variabilities in local conditions. Clearly, numerous ecosystem services could be affected by OA, including services that are part of the economic figures above. Furthermore, this variety in ecosystems is largely the foundation of the biodiversity along the Swedish coast, and the effects of OA (and other human induced effects) can also be seen from a conservation perspective.

Moreover, however, this variability has consequences for the way in which OA operates in the Baltic Sea, it causes some major differences in relation to the oceans, and to some extent it complicates the detection and predictions related to OA in the Baltic Sea. In the section below, we briefly discuss the concept of OA from a Baltic Sea perspective.

Understanding Ocean Acidification in the Baltic Sea³

Coastal Baltic Sea ecosystems have undergone drastic changes in the last decades, notably due to eutrophication and freshening. The potential importance of OA has only relatively recently been acknowledged, however, which at least partly may explain why the contribution of OA is not well known (Gattuso & Hansson 2011; cited in Havenhand et al. 2017).

Globally, the rate of release of CO₂, and hence the effects on marine carbon chemistry, is unprecedented in the last 300 million years (see e.g. Hönisch et al. 2012), and OA (together with other factors) has been associated with several extinction events in the earth's geological history (Harnik et al. 2012).

The buffer capacity is critical for the impact of increased CO₂ in the waters. In general, buffer capacity is associated with seawater salinity so that it is lower at lower salinities, due to lower alkalinity. In the Baltic Sea, this phenomenon can be exemplified in the Bothnian Bay, where salinity is low, and consequently the seasonal variability in pH is large. Unlike in the oceans, the relationship between salinity and buffering capacity is, however, complicated in the Baltic Sea through large variation in local geology that influences the alkalinity, as well by seasonality in runoff, and by extremely low salinities.

Large scale patterns in alkalinity due to geological differences cause, for instance, pronounced differences in mean pH between the Gulf of Riga and the Bothnian Bay, since the former is characterized by limestone bedrock, and the latter by granite. Mean pH, however, in the Swedish surface waters from Kattegatt to the Baltic Proper are relatively similar, due to similar alkalinities. Seasonal differences between these areas are, nevertheless, pronounced due to higher nutrient levels in the Baltic Proper. This causes larger variability in photosynthetic activity in the Baltic Proper - and thus binding of CO₂ - in comparison with Kattegatt. Further local variation stems from regional differences in runoff from land, which locally provides sources of organic carbon, which is microbially decomposed and can lead to further acidification from these land based carbon sources. As runoff from land is driven by precipitation, and as climate models (although with

³ Interpreted from comprehensive description of the chemical basis of OA in the oceans and in the Baltic Sea in Havenhand et al. (2017; section 3.2)

uncertainty) predict increased precipitation due to climate change, these landbased sources could become increasingly important contributors to OA in the Baltic, adding to the effect of excess atmospheric CO₂

Demonstrations of overall trends in pH in the Swedish coastal waters are thus far constrained by large seasonal variation and methodological challenges, but model work suggests a negative trend, notably demonstrated by falling winter minima of pH. This is exemplified by Havenhand et al. (2017) for the Eastern Gotland Basin, where wintertime pH minima are expected to drop to 7.8 within two decades, as compared to ca 8 in the 1980ies. Seasonally, acidified conditions could therefore be detected in Swedish waters relatively soon⁴.

What are the ecological consequences of Ocean Acidification in the Baltic Sea?

It is obvious from the literature (e.g. as reviewed by Havenhand et al. 2019) that OA can affect species and communities, as well as interactions between species, ecosystem processes etc. It is equally obvious (although perhaps not surprising), however, that the effects are highly variable, and different studies demonstrate either negative effects, no effects, or even positive effects. This variability stems, for instance, from different sensitivities among or within species and from what responses are being measured. Variability also stems from the duality of CO₂ (Connell et al. 2018), i.e. it can act both as a stressor and a resource for photosynthetic organisms and certain microbes.

Fish, benthic/littoral animals and zooplankton

Apparent direct negative effects are found among fishes and benthic (bottom living) and littoral (nearshore) animals, but partly also among zooplankton, although there is also variability within these groups.

In fish, these negative effects have been reported for growth of larval halibut, cod and herring (Franke and Clemmesen 2011; Frommel et al. 2013). However, there was no effect on sperm mobility of cod (Frommel et al. 2010), nor on swimming performance of adult cod (Melzner et al. 2009).

In benthic animals, negative effects have been found on embryonic and larval development in the bivalve *Limecola* (previously *Macoma*) *balthica* (Jansson et al. 2013, 2016), which is a key species in large parts of the Baltic Sea. Negative effects have also been shown for the littoral crustacean *Idotea balthica* in the form of oxidative stress caused by OA (Wood et al. 2016; see also section "Combined effects" below).

Predominantly neutral effects in benthic animals include studies on the barnacle (larval development) *Balanus improvisus* from the Kiel Fjord in the western Baltic Sea, where pH-variation is naturally high due to upwellings (Pansch et al. 2014). In the higher salinity waters of Skagerrak (outside the Baltic Sea), with low natural pH-variation, there were, however,

⁴ In this context, we also want to note that in Finnish waters (Western Gulf of Finland), a decrease in winter time pH has already been reported (Almén et al. 2017).

significant effects on survival, growth and reproduction (Pansch et al. 2018), suggesting that populations are differently affected depending on prevailing natural pH-conditions. Similar results have been obtained for the bivalve *Mytilus edulis* (Thomsen et al. 2017), when the performance of animals from the Kiel Fjord where compared to animals from the North Sea (low natural pH-variation) under different experimental pH-conditions. The results showed that effects were more pronounced in the North Sea population, indicating evolutionary adaptation in the Kiel Fjord population. There was also a transgenerational tolerance effect, although to a limit. Furthermore, Thomsen and Melzner (2010) have shown for Kiel Fjord *M. edulis* that although shell growth is reduced under acidified conditions, the animals are able to adjust their physiology so that their metabolism is maintained.

In zooplankton, several studies report large phenotypic buffering, i.e. individuals are (to a limit) able to “buffer” the effects of OA by adjusting their physiology. This was, for instance demonstrated for egg hatching in the copepod *Acartia* sp.⁵ in a study showing that egg hatching success was highest if females produced their eggs under the same pH conditions as hatching took place (Vehmaa et al. 2012), although the size of the females was negatively affected by acidified conditions (see also Vehmaa et al. 2016). A study by Almén et al. (2016) revealed no effects of OA on another copepod species, namely *Eurytemora affinis*. In some cases, the effect of OA is dependent on other environmental conditions (see section on “Combined effects” below).

Phytoplankton, bacterioplankton and macrophytes

Studies on direct species level effects on phytoplankton show high variability. Cyanobacteria, for instance, exhibit negative, positive and no effects (Czerny et al. 2009; Eichner et al. 2014). In a toxin producing dinoflagellate (*Alexandrium ostenfeldii*) from the Baltic Sea, growth rates were strain specific and similarly included negative, positive or no effects, whereas toxin production was generally enhanced under elevated CO₂ (Kremp et al. 2012).

Highly variable effects are also found in community level studies on bacterio- and phytoplankton. In bacterioplankton, the effects are primarily indirect ones, exemplified by both smaller shifts (Lindh et al. 2013, Bergen et al. 2016) and more substantial ones (Hornick et al. 2017). Similarly, small shifts have been reported for phytoplankton communities (Sommer et al. 2015, Paul et al. 2016 a, b). However, effects on non-dominant species were reported to be more substantial (Sommer et al. 2015). It has also been shown that community respiration can be reduced through the effect of OA (Spilling et al. 2016).

There is evidence from neighboring seas that OA can shift phytoplankton communities towards dominance of picophytoplankton (Spizbergen, Schultz et al. 2013; Kattegatt, Bach et al. 2016) when nutrients are not limiting. Such shifts could lead to an increased importance of the microbial loop, reducing the amount of energy that is transported to zooplankton and fish (North Sea, Endres et al. 2014; Bermúdez et al. 2016). A study from the western Baltic Sea (Rossoll et al. 2012) furthermore showed that OA can impact the composition of fatty acids (which are important dietary components for animals feeding on phytoplankton) in phytoplankton and reduce their nutritional value for zooplankton, with negative implications

⁵ *Acartia* release their fertilized eggs into water, where they hatch

for their reproduction. Such effects through the food-webs could have impacts on abundances and species composition of fish stocks in the Baltic Sea, and negatively influence also the transfer of energy to benthic animals.

Effects of OA on macrophytes have mainly been studied on bladderwracks (*Fucus* spp.) and green- and red-algae. As these macroalgae can benefit from the added carbon availability provided by increased CO₂, positive effects such as increased growth (red- and green algae; Pajusalu et al. 2013) and increased carbon storage (*Fucus*; e.g. Takolander et al. 2019) have been found, albeit effects in *Fucus* are season dependent, and a few negative effects have also been reported (e.g. nitrogen uptake in winter; Takolander et al. 2019). Further examples for bladderwrack are given in the section on Combined effects below.

Combined effects

OA operates in tandem with other processes that are at least in part related to GHGs, such as warming, freshening, and deteriorated oxygen conditions, and hence it is important not only to consider the effects of OA alone, but also in combination with other environmental drivers.

Warming

There are a few studies that have demonstrated negative interactive effects between warming and OA. For instance, Vehmaa and co-workers found that a combination of these two factors negatively affected the oxidative balance in the copepod *Acartia bifilosa* (Vehmaa et al. 2013), and decreased the production of eggs and nauplii⁶ (Vehmaa et al. 2012). Studies by Al-Janabi et al. (2016a, 2016b) showed that the combined effect of warming and OA reduced the survival and growth in the bladderwrack *Fucus vesiculosus*, although the effects varied depending on nutrient levels and genetic factors. Another example on *Fucus* shows strong negative, season dependent direct and indirect (via the food web) warming effects that overwhelmed those of OA (Werner et al. 2016).

In other cases, only small or no interactive effects of OA and warming have been reported (barnacles, Pansch et al. 2012; cod, Frommel et al. 2013).

Freshening

Freshening in the Baltic Sea, i.e. the gradual decrease in salinity that has been related to increased precipitation in climate models (Meier et al. 2006, Gräwe et al. 2013), is highly important to consider also in the context of OA. The distribution of many keystone marine species in the Baltic Sea is regulated by salinity, and there are vital physiological processes that could be interactively affected by salinity and OA. For instance, the bivalve *M. edulis* only occurs in parts of the Baltic Sea where salinity is high enough, and in parts where it does occur, size is smaller than in the oceans. Novel research suggests that the reduced size is due to high costs of calcification (rather than osmotic stress as previously believed) at low salinities (Sanders et al. 2018), and as calcifying organisms are in general at risk from OA, the effects of freshening should also be considered in this context. Similarly, risks for combined

⁶ Crustacean larvae are called nauplii (sing. nauplius)

effects can be inferred for another keystone species, namely the bladderwrack *Fucus vesiculosus*, the successful reproduction of which is dependent on sufficient salinity levels and other physiologically vital conditions (Serrão et al. 1999)⁷.

It has also been shown by Wood et al. (2016) that a marine population and a Baltic Sea population of the crustacean *Idotea balthica* responded very differently to OA. For instance, the osmoregulative capacity of the Baltic Sea population (although inherently higher from the beginning) was significantly reduced compared to the marine population under OA. At the same time, the Baltic Sea population upregulated its metabolic activity, while that of the marine population was depressed. Although the exact consequences of such phenomena for species and their different populations in future OA scenarios may be difficult to predict, such examples do demonstrate that historic salinity conditions and local adaptations to these conditions are vital to take into consideration both when it comes to OA and when it comes to the freshening that takes place concurrently.

Although among the few studies conducted so far on the interaction of freshening and OA in the Baltic Sea we find an example where no significant interactions were demonstrated (bacterioplankton; Wulff et al. 2018), we suggest that the baseline importance of salinity for marine species distribution and the possible physiological interplay between salinity and OA merit increased attention to this interaction in the future.

Oxygen deficiency

For poor oxygen conditions, there is evidence for negative combined effects from the Skagerrak (crustaceans, Hernroth et al. 2015), but in the Baltic Sea, interactive effects have been either absent or even positive (bivalves, Jakubowska and Normant 2015; Jansson et al. 2015, respectively). Overall, however, it seems that much like for freshening, this important interaction is underrepresented in studies in the Baltic Sea.

Who is doing what on OA in Sweden?

It is vital for the understanding of OA (as for any environmental change) to perform monitoring of relevant variables. In the case of OA, the overall responsibility of monitoring is with the Swedish Agency for Marine and Water Management, who has appointed the Swedish Meteorological and Hydrological Institute as data host. Relevant data for OA, such as pH and alkalinity are publicly available at <https://sharkweb.smhi.se/>. Three national monitoring contractors (Swedish Meteorological and Hydrological Institute, Department of Ecology, Environment and Plant Sciences at Stockholm University, Umeå Marine Sciences Centre at Umeå University) carry out sampling, analyses and data provisioning within the national pelagic monitoring programme.

Academic research is (evidently) carried out at Swedish universities with marine programs. An exhaustive list is virtually impossible to provide. However, much of the experimental work that relates to ecological effects, as well as field and experimental work on carbon chemistry, is carried out at marine field stations, such as the [Sven Lovén Centre for Marine](#)

⁷ For both *M. edulis* and *F. vesiculosus*, see also sections above

[Infrastructure](#) (University of Gothenburg), the [Askö Laboratory](#) (Baltic Sea Centre, Stockholm University), and the [Umeå Marine Sciences Centre](#) (Umeå University) and by staff at institutions of the respective universities. The [Baltic Sea Centre](#) at Stockholm University has a special role in conducting both research and conveying science to policy makers, other stakeholders and the general public.

Much of the research work is collaborative among universities and countries around the Baltic Sea, as evidenced also from many of the citations in this report. A number of these citations come from work carried out in mesocosms, i.e. experimental units where parts of nature can be enclosed to study experimental manipulations (such as OA). The performance of such - frequently highly labor intensive - experiments is facilitated by research consortia, such as [AQUACOSM-plus](#), which is a consortium dedicated to maintaining and developing mesocosm infrastructure, and collaboration related to such.

Conclusions and policy context

It is evident from the literature that ongoing OA poses a socio-economic and ecological threat in the Baltic Sea. Nevertheless, OA is rarely mentioned in media and does not have a strong position in public debate or within national environmental policy (Havenhand et al. 2017). In this respect, the situation in Sweden is similar with that of most countries at least within the EES, as recently analysed by Galdies et. al. (2020). This analysis showed that although OA is recognized for instance in the UN:s Sustainable Development Goals (SDGs; in particular SDG 14) and is integrated in the work of the IPCC, there is virtually no national European legislation to support specifically the mitigation and management of OA. Within the EU, this shortcoming seems be non-compliant with for instance the Marine Strategy Framework Directive (MSFD) and Water Framework Directive (WFD), and hence with the aim to achieve Good Environmental Status (GES) of EU waters. It is noteworthy in that the MSFD does not include monitoring descriptors that concern OA specifically.

For environmental NGOs, there is clearly a mission to raise the general awareness on OA, and to efficiently campaign for the inclusion of OA in relevant policies.

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Literature

Al-Janabi, B., Kruse, I., Graiff, A., Winde, V., Lenz, M., Wahl, M. (2016a) Buffering and Amplifying Interactions among OAW (Ocean Acidification & Warming) and Nutrient Enrichment on Early Life- Stage *Fucus vesiculosus* L. (Phaeophyceae) and Their Carry Over Effects to Hypoxia Impact. *Plos One* 11, e0152948. doi:10.1371/journal.pone.0152948

Al-Janabi, B., Kruse, I., Graiff, A., Karsten, U., Wahl, M. (2016b) Genotypic variation influences tolerance to warming and acidification of early life-stage *Fucus vesiculosus* L. (Phaeophyceae) in a seasonally fluctuating environment. *Marine Biology* 163, 1–15. doi:10.1007/s00227-015-2804-8

Almén, A.-K., Vehmaa, A., Brutemark, A., Bach, L., Lischka, S., Stuhr, A., Furuhaugen, S., Paul, A., Bermúdez, J. R., Riebesell, U., Engström-Öst, J. (2016) Negligible effects of ocean acidification on *Eurytemora affinis* (Copepoda) offspring production. *Biogeosciences* 13, 1037–1048. <https://doi.org/10.5194/bg-13-1037-2016>

Almén, A.-K., Glippa, O., Pettersson, H., Alenius, P., Engström-Öst, J. (2017) Changes in wintertime pH and hydrography of the Gulf of Finland (Baltic Sea) with focus on depth layers. *Environmental Monitoring and Assessment* 189(4), 147. doi:10.1007/s10661-017-5840-7

Bach, L.T., Taucher, J., Boxhammer, T., Ludwig, A., The Kristineberg KOSMOS Consortium, Achterberg, E.P., et al. (2016) Influence of Ocean Acidification on a Natural Winter-to-Summer Plankton Succession: First Insights from a Long-Term Mesocosm Study Draw Attention to Periods of Low Nutrient Concentrations. *PLoS ONE* 11(8): e0159068. <https://doi.org/10.1371/journal.pone.0159068>

Bergen, B., Endres, S., Engel, A., Zark, M., Dittmar, T., Sommer, U., Jürgens, K. (2016) Acidification and warming affect prominent bacteria in two seasonal phytoplankton bloom mesocosms. *Environmental Microbiology* 18, 4579-4595. <https://doi.org/10.1111/1462-2920.13549>

Bermúdez, J., Riebesell, U., Larsen, A. *et al.* (2016) Ocean acidification reduces transfer of essential biomolecules in a natural plankton community. *Scientific Reports* 6, 27749. <https://doi.org/10.1038/srep27749>

Czerny, J., Barcelos e Ramos, J., Riebesell, U. (2009) Influence of elevated CO₂ concentrations on cell division and nitrogen fixation rates in the bloom-forming cyanobacterium *Nodularia spumigena*. *Biogeosciences* 6, 1865–1875. <https://doi.org/10.5194/bg-6-1865-2009>

Connell, S.D., Doubleday, Z.A., Foster, N.R., Hamlyn, S.B., Harley, C.D.G., Helmuth, B., Kelaher, B.P., Nagelkerken, I., Rodgers, K.L., Sarà, G., Russell, B.D. (2018) The duality of ocean acidification as a resource and a stressor. *Ecology* 99, 1005-1010. <https://doi.org/10.1002/ecy.2209>

Eichner, M., Kranz, S.A., Rost, B. (2014) Combined effects of different CO₂ levels and N sources on the diazotrophic cyanobacterium *Trichodesmium*. *Physiologia Plantarum* 152, 316-330. <https://doi.org/10.1111/ppl.12172>

Endres, S., Galgani, L., Riebesell, U., Schulz, K.-G., Engel, A. (2014) Stimulated Bacterial Growth under Elevated pCO₂: Results from an Off-Shore Mesocosm Study. *PLoS ONE* 9(6), e99228. <https://doi.org/10.1371/journal.pone.0099228>

Franke, A., Clemmesen, C. (2011) Effect of ocean acidification on early life stages of Atlantic herring (*Clupea harengus* L.). *Biogeosciences*, 8, 3697–3707. <https://doi.org/10.5194/bg-8-3697-2011>

Frommel, A. Y., Stiebens, V., Clemmesen, C., Havenhand, J. (2010) Effect of ocean acidification on marine fish sperm (Baltic cod: *Gadus morhua*). *Biogeosciences* 7, 3915–3919. <https://doi.org/10.5194/bg-7-3915-2010>

Frommel, A.Y., Schubert, A., Piatkowski, U., Clemmesen, C. (2013) Egg and early larval stages of Baltic cod, *Gadus morhua*, are robust to high levels of ocean acidification. *Marine Biology* 160, 1825–1834. <https://doi.org/10.1007/s00227-011-1876-3>

Galdies, C., Bellerby, R., Canu, D., Chen, W., Garcia-Luque, E., Gašparović, B., Godrijan, J., Lawlor, P.J., Maes, F., Malej, A., Panagiotaras, D., Martinez Romera, B., Reymond, C.E., Rochette, J., Solidoro, C., Stojanov, R., Tiller, R., Torres de Noronha, I., Ušcinowicz, G., Vaidianu, N., Walsh, C., Guerra, R. (2020) European policies and legislation targeting ocean acidification in european waters - Current state. *Marine Policy* 118, 103947. <https://doi.org/10.1016/j.marpol.2020.103947>

Gattuso, J.-P., Hansson, L. (2011) Ocean acidification: background and history. In: Gattuso, J.-P. and L. Hansson (eds) *Ocean acidification*, OUP, Oxford. 1-20.

Gräwe, U., Friedland, R., Burchard, H. (2013) The future of the western Baltic Sea: two possible scenarios. *Ocean Dynamics* 63, 901–921. <https://doi.org/10.1007/s10236-013-0634-0>

Gustafsson, E., Winder, M. (2020) Emerging ocean acidification threatens Baltic Sea ecosystems. Policy brief, March 2020, Baltic Sea Centre, Stockholm University. Retrieved from: https://www.su.se/polopoly_fs/1.493644.1585729224!/menu/standard/file/PB_Acidification_200331.pdf

Harnik, P.G., Lotze, H.K., Anderson, S.C., Finkel, Z.V., Finnegan, S., Lindberg, D.R., Liow, L.H., Lockwood, R., McClain, C.R., McGuire, J.L., O’Dea, A., Pandolfi, J.M., Simpson, C., Tittensor, D.P. (2012) Extinctions in ancient and modern seas. *Trends in Ecology & Evolution* 27(11), 608-17. doi: 10.1016/j.tree.2012.07.010

Havenhand, J., Crépin, A.-S., Filipsson, H.L., Jagers, S., Langlet, D., Matti, S., Niiranen, S., Troell, M., Anderson, L.G. (2017) Acidification of Swedish seas in a changing environment: causes, consequences, and responses – an interdisciplinary review of current knowledge, knowledge gaps, and implementation needs. Report. The Environmental Committee, The Royal Swedish Academy of Sciences. 55 p. Retrieved from: https://s3.eu-de.cloud-object-storage.appdomain.cloud/kva-image-pdf/2017/04/Acidification-of-Swedish-Seas_170421.pdf

Havenhand, J.N., Filipsson, H.L., Niiranen, S., Troell, M., Crépin, A.-S., Jagers, S., Langlet, D., Matti, S., Turner, D., Winder, M., de Wit, P., Anderson, L.G. (2019) Ecological and functional consequences of coastal ocean acidification: Perspectives from the Baltic-Skagerrak System. *Ambio* 48, 831-854. doi:10.1007/s13280-018-1110-3

Hernroth, B., Krång, A.-S., Baden, S. (2015) Bacteriostatic suppression in Norway lobster (*Nephrops norvegicus*) exposed to manganese or hypoxia under pressure of ocean

acidification. *Aquatic Toxicology* 159, 217-224.
<https://doi.org/10.1016/j.aquatox.2014.11.025>.

Hornick, T., Bach, L.T., Crawford, K.J., Spilling, K., Achterberg, E.P., Woodhouse, J.N., Schulz, K.G., Brussaard, C.P.D., Riebesell, U., Grossart, H.-P. (2017) Ocean acidification impacts bacteria–phytoplankton coupling at low-nutrient conditions. *Biogeosciences* 14, 1–15.
<https://doi.org/10.5194/bg-14-1-2017>.

Hönisch, B., Ridgwell, A., Schmidt, D.N., Thomas, E., Gibbs, S.J., Sluijs, A., Zeebe, R., Kump, L., Martindale, R.C., Greene, S.E., Kiessling, W., Ries, J., Zachos, J.C., Royer, D.L., Barker, S., Marchitto, T.M. Jr, Moyer, R., Pelejero, C., Ziveri, P., Foster, G.L., Williams, B. (2012) The geological record of ocean acidification. *Science* 335(6072), 1058-63. doi: 10.1126/science.1208277. Erratum in: *Science* 335(6074), 1302.

IPCC (2018) Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. [Masson-Delmotte, V., P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J.B.R. Matthews, Y. Chen, X. Zhou, M.I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, and T. Waterfield (eds.)]. Retrieved from: <https://www.ipcc.ch/sr15/>

IPCC (2019) IPCC Special Report on the Ocean and Cryosphere in a Changing Climate. [H.-O. Pörtner, D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, N.M. Weyer (eds.)]. Retrieved from: <https://www.ipcc.ch/srocc/>

Jakubowska, M., Normant-Saremba, M. (2015) The Effect of CO₂-Induced Seawater Acidification on the Behaviour and Metabolic Rate of the Baltic Clam *Macoma balthica*. *Annales Zoologici Fennici* 52, 353-367. <https://doi.org/10.5735/086.052.0509>

Jansson, A., Norkko, J., Norkko, A. (2013) Effects of reduced pH on *Macoma balthica* larvae from a system with naturally fluctuating pH-dynamics. *Plos One* 8, e68198. doi:10.1371/journal.pone.0068198

Jansson, A., Norkko, J., Dupont, S., Norkko, A. (2015) Growth and survival in a changing environment: Combined effects of moderate hypoxia and low pH on juvenile bivalve *Macoma balthica*. *Journal of Sea Research* 102, 41–47. <https://doi.org/10.1016/j.seares.2015.04.006>

Jansson, A., Lischka, S., Boxhammer, T., Schulz, K.G., Norkko, J. (2016) Survival and settling of larval *Macoma balthica* in a large-scale mesocosm experiment at different f CO₂ levels. *Biogeosciences* 13, 3377-3385. <https://doi.org/10.5194/bg-13-3377-2016>

Kremp, A., Godhe, A., Egardt, J., Dupont, S., Suikkanen, S., Casabianca, S. and Penna, A. (2012) Intraspecific variability in the response of bloom-forming marine microalgae to changed climate conditions. *Ecology and Evolution* 2, 1195-1207. <https://doi.org/10.1002/ece3.245>

Lindh, M.V., Riemann, L., Baltar, F., Romero-Oliva, C., Salomon, P.S., Granéli, E. and Pinhassi, J. (2013) Climate change-induced shifts in microbial communities. *Environmental Microbiology Reports* 5, 252-262. <https://doi.org/10.1111/1758-2229.12009>

Meier, H. E. M., Kjellström, E., and Graham, L. P. (2006), Estimating uncertainties of projected Baltic Sea salinity in the late 21st century. *Geophysical Research Letters* 33, L15705. doi:[10.1029/2006GL026488](https://doi.org/10.1029/2006GL026488).

Melzner, F., Göbel, S., Langenbuch, M., Gutowska, M.A., Pörtner, H.O., Lucassen, M. (2009) Swimming performance in Atlantic Cod (*Gadus morhua*) following long-term (4-12 months) acclimation to elevated seawater P(CO₂). *Aquatic Toxicology* 92(1), 30-7. doi: 10.1016/j.aquatox.2008.12.011.

Pajusalu, L., Martin, G., Põllumäe, A., Paalme, T. (2013) Results of laboratory and field experiments of the direct effect of increasing CO₂ on net primary production of macroalgal species in brackish-water ecosystems. *Proceedings of the Estonian Academy of Sciences* 62, 148–154. doi: 10.3176/proc.2013.2.09

Pansch, C., Nasrolahi, A., Appelhans, Y.S., Wahl, M. (2012) Impacts of ocean warming and acidification on the larval development of the barnacle *Amphibalanus improvisus*. *Journal of Experimental Marine Biology and Ecology* 420–421, 48-55. <https://doi.org/10.1016/j.jembe.2012.03.023>

Pansch, C., Schaub, I., Havenhand, J., Wahl, M. (2014) Habitat traits and food availability determine the response of marine invertebrates to ocean acidification. *Global Change Biology* 20, 765-777. <https://doi.org/10.1111/gcb.12478>

Pansch, C., Hattich, G.S.I., Heinrichs, M.E., Pansch, A., Zagrodzka, Z., Havenhand, J.N. (2018) Long-term exposure to acidification disrupts reproduction in a marine invertebrate. *PLoS ONE* 13(2), e0192036. <https://doi.org/10.1371/journal.pone.0192036>

Paul, C., Sommer, U., Garzke, J., Moustaka-Gouni, M., Paul, A. and Matthiessen, B. (2016a) Effects of increased CO₂ concentration on nutrient limited coastal summer plankton depend on temperature. *Limnology and Oceanography* 61, 853-868. <https://doi.org/10.1002/lno.10256>

Paul, A. J., Achterberg, E. P., Bach, L. T., Boxhammer, T., Czerny, J., Haunost, M., Schulz, K.-G., Stühr, A., Riebesell, U. (2016) No observed effect of ocean acidification on nitrogen biogeochemistry in a summer Baltic Sea plankton community. *Biogeosciences* 13, 3901–3913. <https://doi.org/10.5194/bg-13-3901-2016>

Rossoll, D., Bermúdez, R., Hauss, H., Schulz, K.G., Riebesell, U., Sommer, U., et al. (2012) Ocean Acidification-Induced Food Quality Deterioration Constrains Trophic Transfer. *PLoS ONE* 7(4), e34737. <https://doi.org/10.1371/journal.pone.0034737>

Sanders, T., Schmittmann, L., Nascimento-Schulze, J., Melzner, F. (2018) High calcification costs limit mussel growth at low salinity. *Frontiers in Marine Science* 5, 352. doi: 10.3389/fmars.2018.00352

SCB (2014) Recreational fishing in Sweden 2013. JO – Jordbruk, skogsbruk och fiske 57 SM 1401. Swedish Central Bureau of Statistics, Sweden.

Schulz, K. G., Bellerby, R. G. J., Brussaard, C. P. D., Büdenbender, J., Czerny, J., Engel, A., Fischer, M., Koch-Klavsen, S., Krug, S. A., Lischka, S., Ludwig, A., Meyerhöfer, M., Nondal, G., Silyakova, A., Stuhr, A., and Riebesell, U. (2013) Temporal biomass dynamics of an Arctic plankton bloom in response to increasing levels of atmospheric carbon dioxide. *Biogeosciences* 10, 161–180. <https://doi.org/10.5194/bg-10-161-2013>

Serrão, E.A., Brawley, S.H., Hedman, J., Kautsky, L., Samuelsson, G. (1999) Reproductive success of *Fucus vesiculosus* (Phaeophyceae) in the Baltic Sea. *Journal of Phycology* 35, 254–269. <https://doi.org/10.1046/j.1529-8817.1999.3520254.x>

Sommer, U., Paul, C., Moustaka-Gouni, M. (2015) Warming and Ocean Acidification Effects on Phytoplankton—From Species Shifts to Size Shifts within Species in a Mesocosm Experiment. *Plos One* 10, e0125239. doi:10.1371/journal.pone.0125239

Spilling, K., Paul, A. J., Virkkala, N., Hastings, T., Lischka, S., Stuhr, A., Bermúdez, R., Czerny, J., Boxhammer, T., Schulz, K. G., Ludwig, A., Riebesell, U. (2016) Ocean acidification decreases plankton respiration: evidence from a mesocosm experiment. *Biogeosciences* 13, 4707–4719. <https://doi.org/10.5194/bg-13-4707-2016>

Stiasny, M. H., Mittermayer, F. H., Sswat, M., Voss, R., Jutfelt, F., Chierici, M., Puvanendran, V., Mortensen, A., Reusch, T. B. H., Clemmesen, C. (2016) Ocean Acidification Effects on Atlantic Cod Larval Survival and Recruitment to the Fished Population. *Plos One* 11, e0155448. doi:10.1371/journal.pone.0155448

Takolander, A., Cabeza, M., Leskinen, E. (2019). Seasonal interactive effects of pCO₂ and irradiance on the ecophysiology of brown macroalga *Fucus vesiculosus* L. *European Journal of Phycology* 54, 380–392. <https://doi.org/10.1080/09670262.2019.1572226>

Thomsen, J., Stapp, L. S., Haynert, K., Schade, H., Danelli, M., Lannig, G., Wegner, K. M., Melzner, F. (2017) Naturally acidified habitat selects for ocean acidification-tolerant mussels. *Science Advances* 3, e1602411. DOI: 10.1126/sciadv.1602411

Thomsen, J., Melzner, F. (2010) Moderate seawater acidification does not elicit long-term metabolic depression in the blue mussel *Mytilus edulis*. *Marine Biology* 157, 2667–2676. <https://doi.org/10.1007/s00227-010-1527-0>

Vehmaa, A., Brutemark, A., Engström-Öst, J. (2012) Maternal Effects May Act as an Adaptation Mechanism for Copepods Facing pH and Temperature Changes. *Plos One* 7, e48538. <https://doi.org/10.1371/journal.pone.0048538>

Vehmaa, A., Hogfors, H., Gorokhova, E., Brutemark, A., Holmborn, T., Engström-Öst, J. M. (2013) Projected marine climate change: effects on copepod oxidative status and reproduction. *Ecology and Evolution* 3(13), 4548–4557. <https://doi.org/10.1002/ece3.839>

Vehmaa, A., Almén, A.-K., Brutemark, A., Paul, A., Riebesell, U., Furuhagen, S., Engström-Öst, J. (2016) Ocean acidification challenges copepod phenotypic plasticity. *Biogeosciences* 13, 6171–6182. <https://doi.org/10.5194/bg-13-6171-2016>

Werner, F.J., Graiff, A., Matthiessen, B. (2016) Temperature effects on seaweed-sustaining top-down control vary with season. *Oecologia* 180, 889–901. <https://doi.org/10.1007/s00442-015-3489-x>

Wood, H.L., Sundell, K., Almroth, B.C., Skold, H.N., Eriksson, S.P. (2016) Population-dependent effects of ocean acidification. *Proceedings of the Royal Society B-Biological Sciences* 283: 7. <https://doi.org/10.1098/rspb.2016.0163>

Wulff, A., Karlberg, M., Olofsson, M., Torstensson, A., Riemann, L., Steinhoff, F.S., Mohlin, M., Ekstrand, N., Chierici, M. (2018) Ocean acidification and desalination: climate-driven change in a Baltic Sea summer microplanktonic community. *Marine Biology* 165, 63. <https://doi.org/10.1007/s00227-018-3321-3>