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Sensitivity of Bacterioplankton to Environmental Disturbance: A Review of Baltic Sea Field Studies and Experiments

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Bacterioplankton communities regulate energy and matter fluxes fundamental to all aquatic life. The Baltic Sea offers an outstanding ecosystem for interpreting causes and consequences of bacterioplankton community composition shifts resulting from environmental disturbance. Yet, a systematic synthesis of the composition of Baltic Sea bacterioplankton and their responses to natural or human-induced environmental perturbations is lacking. We review current research on Baltic Sea bacterioplankton dynamics *in situ* (48 articles) and in laboratory experiments (38 articles) carried out at a variety of spatiotemporal scales. *In situ* studies indicate that the salinity gradient sets the boundaries for bacterioplankton composition, whereas, regional environmental conditions at a within-basin scale, including the level of hypoxia and phytoplankton succession stages, may significantly tune the composition of bacterial communities. Also the experiments show that Baltic Sea bacteria are highly responsive to environmental conditions, with general influences of e.g. salinity, temperature and nutrients. Importantly, nine out of ten experiments that measured both bacterial community composition and some metabolic activities showed empirical support for the *sensitivity* scenario of bacteria—i.e., that environmental disturbance caused concomitant change in both community composition and community functioning. The lack of studies empirically testing the *resilience* scenario, i.e., experimental studies that incorporate the long-term temporal dimension, precludes conclusions about the potential prevalence of resilience of Baltic Sea bacterioplankton. We also outline outstanding questions emphasizing promising applications in incorporating bacterioplankton community dynamics into biogeochemical and food-web models and the lack of knowledge for deep-sea assemblages, particularly bacterioplankton structure-function relationships. This review emphasizes that bacterioplankton communities rapidly respond to natural and predicted human-induced environmental disturbance by altering their composition and metabolic activity. Unless bacterioplankton are resilient, such changes could have severe consequences for the regulation of microbial ecosystem services.

Keywords: bacterial diversity, archaea, 16S rRNA, metabolic activity, ecosystem functioning, climate change

BACTERIOPLANKTON COMMUNITY AND FUNCTIONAL DYNAMICS

Bacterioplankton communities have a remarkable capability in responding to environmental disturbances, such as changes in temperature, salinity and nutrients (Allison and Martiny, 2008; Logares et al., 2013; Cram et al., 2015; Salazar et al., 2016). Rapid responses are made possible thanks to relatively short generation times, and involve both adjustments in metabolic activity and restructuring of *community composition* (**Box 1**; Allison and Martiny, 2008; Brettar et al., 2016). There is now ample evidence that bacterioplankton activity and community composition play central roles in regulating biogeochemical cycles of elements, with particular focus on carbon in the form of dissolved organic matter (DOM) and dissolved organic carbon (DOC; Azam and Malfatti, 2007; Falkowski et al., 2008).

Given the importance of bacterioplankton-driven cycling of carbon, a fundamental question in microbial ecology is whether shifts in bacterioplankton community composition resulting from changes in environmental conditions also lead to changes in ecosystem functioning (Loreau, 2000, 2004; Langenheder et al., 2010; Comte and Del Giorgio, 2011; Beier et al., 2017). Bacterioplankton communities could, in theory, respond to environmental disturbances according to three scenarios termed *sensitivity*, *resistance*, and *resilience* [**Box 2**; *sensu* Allison and Martiny (2008); Shade et al. (2012)]. Each of these scenarios have distinctly different implications regarding how we interpret the consequences of environmental disturbances on the linkages between shifts in community composition and changes in community functioning. Ecosystem stability is linked with a community's response to disturbance. The stability depends on the *sensitivity*, *resistance* (insensitivity to disturbance), and the *resilience* (ability to return to original condition after disturbance) of the ecosystem (Shade et al., 2012). A disturbance is an event that can influence the community in pulses (discrete short-term events) or presses (long-term or continuous events). Shade et al. (2012) carried out a literature review to investigate bacterioplankton community responses to such disturbances in a variety of habitats. The authors identified that bacterioplankton communities are, in general, sensitive to disturbances but highlighted that empirical tests of *resilience*, i.e., studies that explicitly and comprehensively included the temporal dimension, were lacking.

THE BALTIC SEA AND PREDICTED CLIMATE CHANGE

The shallow brackish Baltic Sea system, with an average depth of ~54 m, varies in both hydrology and physicochemical features; it consists of a 2,000 km long salinity gradient ranging from truly marine to freshwater conditions through several basins of which three are major (the *Baltic Sea Proper*, the *Bothnian Sea*, and the *Bothnian Bay*; Omstedt et al., 2014). In addition to strong shifts in salinity, Baltic Sea basins are affected by different magnitudes of river discharges, transferring freshwater, and terrestrial DOM, so-called allochthonous DOM (i.e., DOM transported into the sea from terrestrial sources; Kritzberg et al., 2004), to coastal waters,

with seasonal variation (Omstedt et al., 2014; Rowe et al., 2018). The Baltic Sea is periodically affected by seasonal phytoplankton blooms, including typical diatom/dinoflagellate spring blooms and massive blooms of cyanobacteria in summer (Legrand et al., 2015), producing so-called autochthonous DOM (i.e., DOM produced *in situ* by e.g., phytoplankton; Kritzberg et al., 2004).

Projections of human-induced climate change in aquatic environments, with global temperature increases of 1.4–5.8°C and a global atmospheric CO₂ increase of 400 atm, resulting in lower pH by ~0.4 units until 2,100, implicate that ecosystem changes of unparalleled extent will occur (Brettar et al., 2016). In the Baltic Sea region the Swedish meteorological and hydrological institute (SMHI) projects increased precipitation by up to 48% until 2,100, leading to lower salinities and increased output of allochthonous matter from river discharge (Meier, 2006). Moreover, cyanobacterial blooms are increasing in magnitude due to human-driven climate change and the hydrography of this semi-enclosed system (Omstedt et al., 2014; Legrand et al., 2015). Eutrophication brings excess nutrients to the microbial food web, stimulating phytoplankton blooms that in turn influence the bacteria, resulting in increased community respiration rates through the degradation of phytoplankton DOM that sinks and ultimately causes bottom water and sediment hypoxia (Tamelander et al., 2017). Decreasing oxygen levels (<2 mg ml⁻¹ O₂) at the seafloor and in sediments of the Baltic Sea have been documented in the last 100 years and decreases are predicted to intensify in the future (Carstensen et al., 2014). Taken together, future selective forces in the marine environment will include, among others, increased sea surface temperatures, lower pH, eutrophication, hypoxia, increased allochthonous carbon inputs, decreased salinity, and massive cyanobacterial blooms (Andersson et al., 2015). Thus, the Baltic Sea offers a unique study system to investigate, in depth, both the causes and consequences of shifts in bacterioplankton community composition and functioning responding to environmental perturbations.

OVERVIEW OF BALTIC SEA BACTERIOPLANKTON STUDIES

We identified a total of 86 articles carrying out field studies and/or experiments focusing on bacterioplankton community composition in the Baltic Sea, as summarized in **Table 1** and **Figure 1**. Studies performed in the Skagerrak and Kattegatt seas were examined (**Supplementary Table 1**), but were not included in the main analyses. Among the Baltic Sea studies, 48 were categorized as research performed *in situ* and 38 were experimental studies at different scales (micro- or mesocosms; **Table 1**). Twenty-six articles included samples from deep-waters/sediments. Among all articles, one third ($n = 29$) included some form of activity measurement and among the *in situ* studies less than one fifth ($n = 9$) measured metabolic activity. A majority of the articles focus on spatial distributions for *in situ* data ($n = 27$; 56% of all *in situ* studies) and on the effect of nutrient additions for experimental data ($n = 22$; 58% of all experimental studies; **Table 1**). The conducted studies have been performed throughout the Baltic Sea and include empirical evidence of shifts

BOX 1 | Determining bacterioplankton community composition.

Marine bacteria and archaea, collectively known as *bacterioplankton*, are a fundamental part of the planktonic food-web and imperative for ecosystem functioning (Falkowski et al., 2008). *Bacterioplankton community composition* refers to the taxonomic identity of organisms and their frequency distribution in the ecosystem. However, phenotypic identification of bacterioplankton is problematic since only a small fraction of all bacterioplankton are easily cultivable and these typically do not mirror the complete bacterioplankton diversity (Pedros-Alio, 2006; Hagström et al., 2017). Microbial ecologists therefore use culture-independent genetic identification techniques to differentiate bacterioplankton taxa (see e.g., Hugerth et al., 2015; Sunagawa et al., 2015; Beier et al., 2017; Celepli et al., 2017). In general, identification of individual bacterioplankton taxa is done by sequencing of the 16S rRNA gene, ITS (Internal Transcribed Spacer) or similar genetic fragments, processing raw *sequence reads* using bioinformatic methods (see e.g., Edgar, 2013; Callahan et al., 2015) and clustering these into specific phylotypes or *operational taxonomic units* (OTUs), followed by taxon delineation at a specific sequence identity threshold (typically 97–99% sequence identity; Hugerth and Andersson, 2017). Taxonomic annotation of these OTUs is then performed by matching a type- or centroid sequence of the OTU cluster against a database with taxonomic information (see e.g., Quast et al., 2013).

Technical advances in the last decade in the form of high-throughput sequencing have increased the sequencing resolution and thereby the detection levels of individual OTUs by several orders of magnitude at rapidly decreasing costs (Poisot et al., 2013; Hugerth and Andersson, 2017). As a result, the field of microbial ecology has advanced from primarily describing major bacterioplankton groups or a few dominant populations to resolving the distribution of thousands of populations over different temporal and spatial scales. This makes bacterioplankton attractive also for monitoring and thus important for stakeholders and marine management.

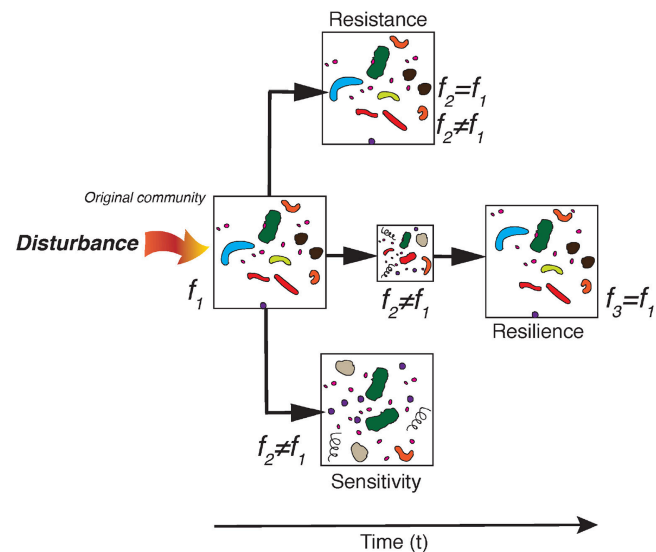
BOX 2 | Bacterioplankton community responses to environmental disturbance

Below follows a brief description of three theoretical responses that bacterioplankton assemblages may undertake in the light of natural or human-induced changes in environmental conditions, *sensu* Allison and Martiny (2008), (Shade et al., 2012). The figure is laid so that it emphasizes the temporal dimension on the x-axis in the *resilience* scenario.

Sensitivity—when community composition is altered by environmental disturbance and the resulting community functioning (f_2) is typically different from the initial functioning (f_1).

Resistance—when community composition is not altered by environmental disturbance and community functioning (f_2) may be different from, or the same as the initial f_1 .

Resilience—when community composition is initially altered by environmental disturbance but returns to the original composition and f_2 is typically temporally different from the initial f_1 but community functioning over time “returns to” f_3 similar to the initial f_1 .



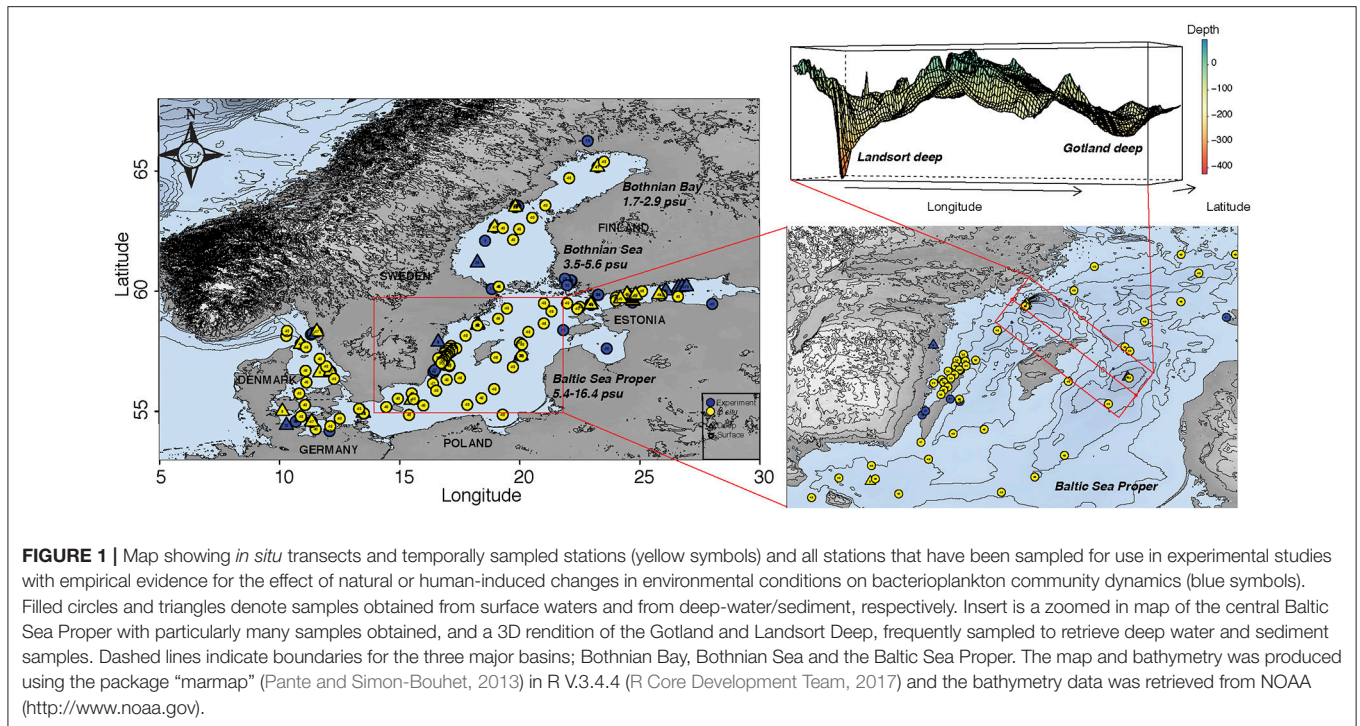
in bacterioplankton community composition in different basins (Figure 1). It is noteworthy that detailed temporal studies are typically limited to two sites in the Baltic Sea Proper (i.e., the Landsort Deep in the central Baltic Sea and at the Linnaeus Microbial Observatory off the coast of the island Öland in the Baltic Sea Proper) and that many deep-water/sediment samples have primarily been obtained from only two locations in the central Baltic Sea Proper (the Landsort and Gotland deeps in the central Baltic Sea; $n = 10$; 40% of all deep-water/sediment studies; Figure 1).

TEMPORAL AND SPATIAL VARIABILITY IN BACTERIOPLANKTON

Extended temporal studies are scarce in the Baltic Sea, but there are four published reports of bacterioplankton dynamics extending over ≥ 1 year at semi- to high-resolution (Pinhassi and Hagström, 2000; Riemann et al., 2008; Andersson et al.,

2010; Lindh et al., 2015c). They all show pronounced shifts in bacterioplankton community composition with fairly distinct spring, summer and autumn communities. In general, Bacteroidetes dominate in spring during the diatom and dinoflagellate bloom. In summer, particular populations of e.g., Verrucomicrobia increase in abundance, associated with pronounced blooms of picocyanobacterial populations and filamentous Cyanobacteria. In autumn, actinobacterial populations proliferate, potentially following changes in temperature, mixing of the water column, and/or autumn phytoplankton blooms. Changes in temperature over the yearly cycle typically explain around 0.45 (Pearson r) of total variation in community composition (Andersson et al., 2010; Lindh et al., 2015c).

There have been three major transects studies of bacterioplankton community composition across the entire salinity gradient of the Baltic Sea, showing that changes in salinity is the major driver of the distribution of bacterial populations (OTUs) at large spatial scales in the Baltic Sea



(Herlemann et al., 2011, 2016; Dupont et al., 2014; Larsson et al., 2014; Celepli et al., 2017). Notably, salinity explained almost all of the observed variation in bacterioplankton community composition with r values ranging from 0.78 to 0.97. In contrast, in a transect across one particular basin, the Baltic Sea Proper, Bunse et al. (2016a) found that, instead of salinity, the advancing phytoplankton spring bloom had a substantial influence in structuring the bacterial community (i.e., the distribution of specific OTUs). The authors emphasized how interactions between bacterioplankton and phytoplankton populations may influence carbon cycling to higher trophic levels thus extending the importance of bacterioplankton dynamics for ecosystem services. In addition, there have been several transects performed at high-resolution spatial scales of which two locations are particularly well-studied; the western Gotland Sea (Bertos-Fortis et al., 2016; Lindh et al., 2016, 2017) and the Gulf of Finland (Laas et al., 2014, 2015, 2016). For example, Bertos-Fortis et al. (2016) show that Cyanobacteria have plastic responses to changes in environmental conditions where opportunistic picocyanobacteria and N_2 -fixing cyanobacteria may be able to utilize nutrients from filamentous Cyanobacteria during the summer bloom (Bertos-Fortis et al., 2016). An approach using metacommunity theory (Leibold et al., 2004) found that local environmental conditions rather than dispersal-driven assembly is the main mechanism for structuring bacterioplankton assemblages in the Baltic Sea (Lindh et al., 2016). Similarly, bacterioplankton communities in areas such as the Pacific Ocean and East China Sea are also mainly shaped by environmental factors and to a less extent by spatial factors (Yeh et al., 2015; Lindh et al., 2018). Moreover, deep-water bacterioplankton communities in the Gulf

of Finland are structured by seasonally anoxic conditions where redox-specialized bacterioplankton populations proliferate (Laas et al., 2015). Surface seawater communities in that study, on the other hand, were largely assembled following variation in phytoplankton succession. Collectively, these studies indicate that whereas the salinity gradient sets the boundaries for bacterioplankton composition, regional environmental conditions at a within-basin scale, including the level of hypoxia and phytoplankton succession stages, may significantly tune the composition of bacterioplankton.

EXPERIMENTAL MANIPULATION OF ENVIRONMENTAL CONDITIONS

Salinity

The *in situ* studies described above dictate that grand scale spatial distributions of particular OTUs in the Baltic Sea are driven by changes in salinity. In accordance, manipulated changes in salinity in micro- and mesocosm experiments also show that salinity can significantly shape bacterioplankton community composition (Langenheder et al., 2003; Kaartokallio et al., 2005; Sjöstedt et al., 2012b; Lindh et al., 2015a). For example, shifts in bacterioplankton community structure occurred in response to salinity changes following the experimental melting of sea ice (Kaartokallio et al., 2005). Compositional shifts occurred in response to a change in salinity and DOM conditions using chemostats, showing how rare or inactive taxa already present in the “seed bank,” proliferated over time (Sjöstedt et al., 2012b). Moreover, a transplant experiment showed how transfer of bacterioplankton assemblages from ambient to changed salinity (brackish compared to near freshwater) and DOM conditions

TABLE 1 | Summary of Baltic Sea bacterioplankton studies in which data on community composition is available ($n = 83$).

Study	Type		Water source [¶]	Include activity measurements?*	Factor tested	Total community or specific group
Glaubitx et al., 2009		▲	Central Baltic Sea	YES	Dark CO ₂ fixation	Total community
Holmfeldt et al., 2009	●		Northern Baltic Sea	YES	Spatial	Actinobacteria
Lindh et al., 2015c	●		Baltic Sea Proper	YES	Temporal	Total community
Pinhassi et al., 1997	●		Northern Baltic Sea	YES	Temporal	Total community
Piwosz et al., 2013	●		Baltic Sea Proper	YES	Temporal	Total community
Rieck et al., 2015	●		Baltic Sea	YES	Particle associated compared to free-living	Total community
Riemann et al., 2008	●		Central Baltic Sea	YES	Temporal	Total community
Andersson et al., 2010	●		Central Baltic Sea	NO	Temporal	Total community
Bengtsson et al., 2017	●		Western Baltic Sea	NO	Epibiont	Total community
Bergen et al., 2014	●		Baltic Sea	NO	Spatial	Spartobacteria
Bertos-Fortis et al., 2016	●		Baltic Sea Proper	NO	Spatiotemporal	Cyanobacteria
Brettar et al., 2012	●		Baltic Sea	NO	Spatial	Total community
Bunse et al., 2016a	●		Baltic Sea Proper	NO	Spatiotemporal	Total community
Buongiorno et al., 2017		▲	Baltic Sea	NO	Molecular methods (Spatial)	Total community
Celepli et al., 2017	●	▲	Baltic Sea	NO	Spatial	Cyanobacteria
Dupont et al., 2014	●	▲	Baltic Sea	NO	Spatial	Total community
Eiler and Bertilsson, 2006	●		Baltic Sea	NO	Spatial	<i>Vibrio</i>
Eiler et al., 2006	●		Baltic Sea	NO	Spatiotemporal	<i>Vibrio</i>
Golebiewski et al., 2017	●		Baltic Sea Proper	NO	Spatial	Total community
Grote et al., 2012		▲	Central Baltic Sea	NO	Spatial	<i>Sulfurimonas</i>
Hagström et al., 2000	●		Northern Baltic Sea	NO	Spatial	Total community
Herlemann et al., 2011	●	▲	Baltic Sea	NO	Spatial	Total community
Herlemann et al., 2016	●	▲	Baltic Sea	NO	Spatial	Total community
Hoffe and Brettar, 1995	●		Central Baltic Sea	NO	Spatial	Total community
Hu et al., 2016	●		Baltic Sea	NO	Spatial	Total community
Kaartokallio et al., 2008	●		Northern Baltic Sea	NO	Temporal	Total community

(Continued)

TABLE 1 | Continued

Study	Type	Water source ^{ff}	Include activity measurements?*	Factor tested	Total community or specific group	
Kisand and Wikner, 2003	●	Northern Baltic Sea	NO	Allochthonous DOM	Total community	
Klier et al., 2018						
		▲	Baltic Sea	NO	Spatial	Total community
Koskinen et al., 2011	●	Northern Baltic Sea	NO	Spatiotemporal	Total community	
Laas et al., 2016	●	▲	Gulf of Finland	NO	Spatiotemporal	Total community
Laas et al., 2014	●	▲	Gulf of Finland	NO	Spatiotemporal	Total community
Laas et al., 2015	●	▲	Gulf of Finland	NO	Spatial	Total community
Larsson et al., 2014	●	▲	Baltic Sea	NO	Spatial	Cyanobacteria
Lindh et al., 2016	●		Baltic Sea Proper	NO	Spatiotemporal	Total community
Lindh et al., 2017	●		Baltic Sea Proper	NO	Spatiotemporal	Total community
Lindroos et al., 2011	●		Northern Baltic Sea	NO	Spatiotemporal	Total community
Pinhassi and Hagström, 2000	●		Northern Baltic Sea	NO	Temporal	Total community
Rahlf et al., 2017	●		Baltic Sea	NO	Wind speed (spatial)	Total community
Reindl and Bolatek, 2017						
		▲	Baltic Sea Proper	NO	Methane production	Archaea
Reunamo et al., 2013	●		Baltic Sea Proper	NO	Petroleum hydrocarbon	Total community
Reyes et al., 2017						
		▲	Baltic Sea	NO	Fe and S Reducing Bacteria	Total community
Salka et al., 2008	●		Baltic Sea	NO	Spatial	Aerobic anoxygenic phototrophic bacteria
Salka et al., 2014	●		Baltic Sea	NO	Spatial	Actinobacteria
Simu and Hagström, 2004	●		Baltic Sea Proper	NO	Single cell life strategy	Oligotrophic bacteria
Stolle et al., 2011	●		Western Baltic Sea	NO	Bacterioneuston	Total community
Tiirik et al., 2014	●		Baltic Sea	NO	Antibiotic resistance (spatial)	Total community
Tuomainen et al., 2006	●		Gulf of Finland	NO	<i>Nodularia</i> sp. (Cyanobacteria) Aggregates	Total community
Zinke et al., 2017						
		▲	Baltic Sea	NO	Activity of deep sea microbes	Total community



















(Continued)

TABLE 1 | Continued

Study	Type	Water source [¶]	Include activity measurements?*	Factor tested	Total community or specific group
Berg et al., 2013	▲	Central Baltic Sea	YES	Carbon substrate and trace metals	Total community
Berg et al., 2015	▲	Central Baltic Sea	YES	Ammonia oxidation	Archaea
Bergen et al., 2016	●	Western Baltic Sea	YES	Acidification	Total community
Brettar et al., 2006	●	Central Baltic Sea	YES	Denitrification	<i>Thiomicrospira denitrificans</i>
Camarena-Gómez et al., 2018	●	SW Coast of Finland	YES	Phytoplankton/ Autochthonous DOM	Total community
Dinasquet et al., 2013	●	Northern Baltic Sea	YES	DOC	Total community
Glaubitz et al., 2014	▲	Central Baltic Sea	YES	Carbon substrate	<i>Sulfurimonas</i>
Gomez-Consarnau et al., 2012	●	Baltic Sea Proper	YES	Carbon substrates	Total community
Grubisic et al., 2012	●	Northern Baltic Sea	YES	DOM and stratification depth	Total community
Hannig et al., 2007	▲	Central Baltic Sea	YES	Denitrification and anammox	Annamox bacteria
Herlemann et al., 2014	●	Western Baltic Sea	YES	Allochthonous DOM	Total community
Kaartokallio et al., 2005	●	Northern Baltic Sea	YES	Salinity	Total community
Labrenz et al., 2005	▲	Central Baltic Sea	YES	Different electron donor/acceptor combinations	Total community
Lindh et al., 2015a	●	Baltic Sea	YES	Salinity, Autochthonous and Allochthonous DOM	Total community
Reunamo et al., 2017	▲	Baltic Sea	YES	Petroleum hydrocarbon	Total community
Stolle et al., 2010	●	Western Baltic Sea	YES	Bacterioneuston, low wind	Total community
Tammert et al., 2012	●	Gulf of Finland	YES	Nutrient limitation and DOC	Total community
Traving et al., 2017	●	Northern Baltic Sea	YES	Allochthonous DOM	Total community
Vaquier-Sunyer et al., 2015	●	Baltic Sea Proper	YES	DON	Total community
Vaquier-Sunyer et al., 2016	●	Baltic Sea Proper	YES	Wastewater treatment plant effluent input	Total community

(Continued)

TABLE 1 | Continued

Study	Type	Water source [¶]	Include activity measurements?*	Factor tested	Total community or specific group
von Scheibner et al., 2014		Western Baltic Sea	YES	Temperature	Total community
von Scheibner et al., 2017		Western Baltic Sea	YES	Temperature	<i>Glaciecola</i> sp.
Anderson et al., 2013		Central Baltic Sea	NO	Grazing	<i>Sulfurimonas</i>
Broman et al., 2017a		Baltic Sea Proper	NO	Oxygen shifts	Total community
Broman et al., 2017b		Baltic Sea Proper	NO	Oxygen shifts	Total community
Degerman et al., 2013		Northern Baltic Sea	NO	Increased temperature and nutrients	Total community
Eiler et al., 2007		Central Baltic Sea	NO	Temperature and DOM	<i>Vibrio</i>
Kisand et al., 2002		Northern Baltic Sea	NO	Allochthonous DOM	Total community
Langenheder et al., 2004		Northern Baltic Sea	NO	Allochthonous DOM	Total community
Langenheder et al., 2003		Northern Baltic Sea	NO	Salinity and allochthonous DOM	Total community
Lindh et al., 2015b		Northern Baltic Sea	NO	Allochthonous DOM and temperature	Total community
Lindh et al., 2013		Baltic Sea Proper	NO	Acidification and increased temperature	Total community
Sipura et al., 2005		Northern Baltic Sea	NO	Inorganic nutrient addition	Total community
Sjöstedt et al., 2012a		Baltic Sea Proper	NO	Increased temperature	Total community
Sjöstedt et al., 2012b		Baltic Sea	NO	Salinity and DOC	Total community
Tank et al., 2011		Western Baltic Sea	NO	Temperature and salinity	Purple sulfur bacteria
Viggor et al., 2015		Gulf of Finland/Riga	NO	Petroleum hydrocarbon	Total community
Viggor et al., 2013		Baltic Sea Proper	NO	Petroleum hydrocarbon	Total community

Yellow symbols denote *in situ* transects and temporally sampled stations and blue symbols denote all stations that have been sampled for use in experimental studies with empirical evidence for the effect of natural or human-induced changes in environmental conditions on bacterioplankton community dynamics. Filled circles and triangles denote samples obtained from surface waters and from deep-water/sediments, respectively. The table is sorted according to (i) Field or experimental studies, (ii) include activity measurements, and (iii) author name.

[¶] A water source from the "Baltic Sea" denotes multiple locations across different basins.

*Activity measurements encompass uptake rates such as ³H-Leucine/Thymidine and enzymatic activities.

(allochthonous compared to autochthonous) has a major impact on composition and metabolic activity (Lindh et al., 2015a). Still, how such changes in salinity affect bacterioplankton community functioning, with potential implications for ecosystem services, remains largely unknown.

Temperature and pH

Seasonal variation in temperature significantly affects bacterioplankton community dynamics in the Baltic Sea (Andersson et al., 2010; Lindh et al., 2015c). Empirical evidence from micro- and mesocosm experiments highlights temperature as a major driver of compositional shifts in bacterioplankton (Muren et al., 2005; Sommer et al., 2007; Hoppe et al., 2008; von Scheibner et al., 2014; Vaquer-Sunyer et al., 2015). Typically, OTUs affiliated with Gammaproteobacteria such as *Glaciecola* spp. proliferate at higher temperatures (von Scheibner et al., 2017). Gammaproteobacteria also increased in relative abundance in warming experiments of bacterioplankton amended with dissolved organic nitrogen sources and incubated in higher temperatures (Vaquer-Sunyer et al., 2015). Here it is also worthwhile to mention that cell size is influenced by increasing temperatures (Sjöstedt et al., 2012a), as also observed in other marine ecosystems (Morán et al., 2015).

Evidence for the effect of ocean acidification on Baltic Sea bacterioplankton community dynamics are few (Bergen et al., 2016). Still, there are some indications of synergistic effects between increased temperature and pCO₂ levels (Lindh et al., 2013). This is in line with analyses from other systems suggesting that ocean acidification could affect bacterioplankton growth and physiology both directly and indirectly, e.g., by affecting DOM release and composition originating from higher trophic levels (Vega Thurber et al., 2009; Joint et al., 2011; Bunse et al., 2016b; Sala et al., 2016). Therefore, increased sea surface temperatures together with acidification due to climate change will likely affect the dynamics of particular bacterioplankton populations either alone or synergistically with potential amplification effects.

Nutrient Inputs

The quality and composition of DOM is partly dependent on its origin, which can be either *allochthonous* or *autochthonous* (Kritzberg et al., 2004; Nagata, 2008). Since bacteria are the main contributors to the biological transformation of marine DOM, much attention has been put into uncovering the role of bacterial community composition in this biogeochemical process. In the Baltic Sea, particular opportunistic bacterioplankton populations are capable of successfully utilizing elevated concentrations of labile, low-molecular weight (LMW) compounds (Gomez-Consarnau et al., 2012). Moreover, multiple studies report important effects of allochthonous DOM on Baltic Sea bacterioplankton responses in community composition (Kisand et al., 2002; Grubisic et al., 2012; Herlemann et al., 2014). An important and intriguing future challenge is to determine the relationship between DOM composition and bacterioplankton community composition and functioning. Curiously, we found few studies reporting on the direct effects of inorganic nutrient enrichments on Baltic Sea Bacterioplankton communities (but see Tammert et al., 2012). This is perhaps surprising given the

importance nitrogen and phosphorus plays in eutrophication of the Baltic Sea (Conley et al., 2009). Simple experiments with bacterioplankton assemblages and nitrogen and phosphorus additions will be a promising avenue of future research to couple changes in inorganic nutrients and DOM to shifts in bacterioplankton community structure and its relationship with Baltic Sea ecosystem function.

Opportunistic Gammaproteobacteria—Bottle Effects or True Dynamics?

OTUs affiliated with Gammaproteobacteria often increase in relative abundance in micro- and mesocosm experiments. Such dynamics are sometimes attributed to the so-called “bottle effect” in which confinement of water causes shifts in bacterioplankton community composition and physiological rates (Fuchs et al., 2000; Massana et al., 2001; Baltar et al., 2012). Such effects are typically detected by rapidly increasing proportions of copiotrophic gammaproteobacterial populations and metabolic activity (see e.g., Gomez-Consarnau et al., 2012; Sjöstedt et al., 2012b). However, we note that particular gammaproteobacterial OTUs also peak in relative abundance *in situ* (Andersson et al., 2010; Lindh et al., 2015c). This pattern does not only occur in the Baltic Sea but also in the North Sea and Mediterranean Sea (Fodelianakis et al., 2014; Alonso-Saez et al., 2015; Teeling et al., 2016). These findings suggest that Gammaproteobacteria could respond faster to environmental disturbances aided by their copiotrophic lifestyle and thus potentially become dominant more frequently due to increased incidence of perturbation *in situ*. It remains to be determined whether such changes would significantly alter microbial-driven carbon cycling or if these Gammaproteobacteria perhaps carry functional redundancy (see e.g., Pedler et al., 2014).

BACTERIOPLANKTON COMMUNITY FUNCTIONING IS CORRELATED WITH COMMUNITY DYNAMICS BUT DATA IS SCARCE

In this section we provide an overview of experimental studies that statistically tested the linkage between changes in bacterioplankton community composition and metabolic activity (i.e., functioning) upon environmental forcing (disturbance; **Table 2**). A few *in situ* studies have shown simultaneous shifts in bacterioplankton community composition and metabolic activity (Pinhassi et al., 1997; Riemann et al., 2008; Glaubitz et al., 2009; Holmfeldt et al., 2009; Piwosz et al., 2013; Lindh et al., 2015c; Rieck et al., 2015; **Table 1**), but as these measurements can be influenced by and/or auto-correlated to a number of undetermined environmental variables they were not included in the current analysis. A majority of experimental studies performed (non-quantitative) cluster-like analyses based on beta-diversity estimates that indicated shifts in composition (see e.g., Lindh et al., 2013; von Scheibner et al., 2014). Notably, most of the studies using cluster statistics methods show that functioning to some degree changes upon shift in composition. A number

TABLE 2 | Summary of Baltic Sea bacterioplankton studies in which experimental data with empirical testing of the effect of natural or anthropogenically induced disturbances on total bacterioplankton community composition and functioning have been determined concomitantly ($n = 10$).

Study*	Summary	Function change?	Composition shift?	Statistical tests	Indicated p -values
Bergen et al., 2016	Tested the effect of increased temperature and pCO ₂ levels on bacterioplankton communities. Found that warming and not pCO ₂ lead to changes in bacterioplankton community composition and metabolic activity.	YES	YES	Repeated measures ANOVA PERMANOVA/ Linear discriminant effect size	≤0.01 0.001/LDA values>3.6 (LEfSe)
Camarena-Gómez et al., 2018	Tested how bacterial physiology and community structure were affected by changes in phytoplankton community composition.	YES	YES	Tukey's b PERMANOVA	<0.05 <0.05
Dinasquet et al., 2013	Investigated how bacterioplankton communities respond to varying supply of bioavailable carbon (bDOC) and how this affected bacterioplankton community composition and functioning. Found that bDOC triggered a shift in community composition and changed the abundance of specific extracellular enzymes.	YES	YES	Factorial analysis of variance Mantel's test	0.005 0.017
Grubisic et al., 2012	Tested the effect of changed DOM quality and concentrations and stratification depth on bacterioplankton communities. Bacterioplankton community composition were influenced both by stratification depth and DOM but only stratification depth affected bacterial heterotrophic production.	YES	YES	MANOVA PLS analysis	<0.001 VIP-values > 1 (PLS)
Herlemann et al., 2014	Investigated potential biodegradation of experimentally added riverine DOM by bacterioplankton communities. Found no evidence of a direct link between bacterioplankton composition and community functioning responding to riverine DOM.	NO	NO	Repeated measures ANOVA two-way ANOSIM	>0.05 >0.05
Lindh et al., 2015a	Tested the impact of changed salinity and DOM quality on bacterioplankton communities, with a transplant experiment. Demonstrated shifts in bacterioplankton community composition coupled with changed metabolic activities responding to changes in the environmental conditions. After communities were re-transplanted to original environmental conditions they did not return to original composition nor functioning.	YES	YES	Repeated measures ANOVA PERMANOVA/Mantel's test	0.001 0.001
Tammert et al., 2012	Tested the effects of nutrient limitation and bioavailable DOC additions on bacterioplankton communities. bDOC changed bacterial heterotrophic production and led to shifts in community composition.	YES	YES	Generalized least squares models Permutations test	<0.001 <0.05
Traving et al., 2017	Investigated the effects of elevated levels of riverine DOM on bacterioplankton communities. DOM additions stimulated protease activity and specific operational taxonomic units responded significantly.	YES	YES	Linear mixed model GLM analysis	<0.0002 <0.05
Vaquier-Sunyer et al., 2015	Investigated synergistic effects of simultaneous DON additions and warming on bacterioplankton communities. Bacterioplankton community composition and metabolic rates changed in relation to temperature and DON additions.	YES	YES	Mixed-effects model Mantel's test	< 0.01 0.001
Vaquier-Sunyer et al., 2016	Tested the effects of wastewater treatment plant effluent inputs on bacterioplankton communities. Nutrient addition lead to shifts in bacterioplankton community composition linked with changed metabolic activity.	YES	YES	Repeated measures MANOVA Mantel's test	<0.0001 <0.001

Statistical tests of significant effects and indicated p -values are given for bacterioplankton functioning followed by community composition separated by "|". All studies consisted of samples obtained from the surface and not from the deep-water or sediments. None of the studies measured shifts in bacterioplankton community composition and functioning over a longer period of time, therefore we can only determine initial sensitivity and not resilience.

*Only studies with total community and with statistical testing of observed effects were included in this qualitative analysis.

of studies focused on changes in the relative or absolute abundance of particular taxa or groups of bacterioplankton such as *Sulfurimonas* GD-1, *Thiomicrospira denitrificans*, and

Glaciecola spp. and also measured metabolic activity of these populations (Brettar et al., 2006; Glaubitz et al., 2014; von Scheibner et al., 2017). Importantly, shifts in abundance of these

particular populations were typically coupled to pronounced changes in metabolic activity when exposed to environmental disturbance.

Relatively few studies have carried out statistical assessments with quantitative data for changes in both the overall bacterioplankton community composition and bacterial functioning (e.g., using multivariate statistics such as Mantel's test, PERMANOVA, or similar). We analyze in detail these studies to reach a general understanding of current quantitative data. We note a lack of deep-water or sediments studies that in a strict sense target such quantitative assessments. Consequently, only studies with surface water samples were included in this analysis (Table 2). Nine out of ten studies with measurements of total bacterioplankton community composition and metabolic activity show empirical evidence of concomitant shifts in community composition and functioning. One study, by Herlemann et al. (2014), found no significant effects on bacterioplankton community dynamics responding to riverine DOM additions, including limited growth, nor links between composition and functioning. Thus, a majority of studies highlight bacterioplankton assemblages responding to disturbances following the *sensitivity* scenario (Table 2; Box 2).

The studies showing statistical support for concomitant shifts in community composition and functioning essentially investigated the effect of nutrient amendments on bacterioplankton community composition dynamics and metabolic activity (Grubisic et al., 2012; Tammert et al., 2012; Degerman et al., 2013; Lindh et al., 2015a; Vaquer-Sunyer et al., 2015, 2016; Bergen et al., 2016; Traving et al., 2017; Camarena-Gómez et al., 2018). The Bergen et al. (2016) study emphasized how temperature significantly alters community composition and heterotrophic bacterial production but that pCO₂ had a more limited effect. The authors noted how these changes in bacterioplankton dynamics could be indicative of changed carbon fluxes in a future ecosystem where heterotrophy may become more important compared to today. Dinasquet et al. (2013) showed that bioavailable DOC triggered a shift in community composition and changed the abundance of specific extracellular enzymes suggesting that bacterioplankton communities can respond, following the *sensitivity* scenario, to varying supplies of DOC ultimately affecting heterotrophic respiration. Vaquer-Sunyer et al. (2015) also noted that nutrient inputs of dissolved organic nitrogen (DON) and changed temperature may lead to a more heterotrophic system. In a different study by Vaquer-Sunyer et al. (2016), they showed an effect of wastewater treatment plant effluent inputs on bacterioplankton dynamics, with an increase in the relative abundance of Cyanobacteria responding to the influx of wastewater with concomitant changes in metabolic activity. A recent study by Camarena-Gómez et al. (2018) investigated the relationship between phytoplankton bloom dynamics (different phytoplankton species) and bacterioplankton community function and taxonomic structure. Their work emphasized how bacterial metabolic activity and community composition were affected by changes in the phytoplankton community—in particular the divergent bacterial responses to phytoplankton dominated by diatoms compared to dinoflagellates. Amendment

of a diatom dominated community resulted in a significantly changed bacterial heterotrophic production and shift in bacterioplankton community structure compared controls, while amendment of a dinoflagellate community had overall smaller impact on both community function and composition (Camarena-Gómez et al., 2018). It is noteworthy how the addition of riverine DOM could result in changed ecosystem function from shifts in bacterioplankton community dynamics toward a more heterotrophic system (Degerman et al., 2013; Figueroa et al., 2016). Also in the Gulf of Finland enrichment with labile DOC changed bacterial production and led to shifts in community composition, promoting filamentous bacteria - the authors indicate that this DOC source may impact diversity, food-web structure and biogeochemical processing of carbon (Tammert et al., 2012). Only three specific studies have directly determined the correlation between shifts in community composition and metabolic activity responding to environmental perturbations (Lindh et al., 2015a; Vaquer-Sunyer et al., 2015, 2016). These studies indicated that variation in bacterioplankton community functioning is often significantly explained by changes in metabolic activity explaining up to around 0.65 of the variance (Pearson r).

Although environmental disturbances can influence bulk bacterioplankton community composition, the replacement of sensitive taxa will occur at the individual OTU level. For example, although Bergen et al. (2016) implicated limited effects on bulk community dynamics resulting from increased pCO₂, there was a substantial influence on particular populations with statistical support from linear discriminant effect size (LEfSe). Traving et al. (2017) performed statistical tests (generalized linear models) to determine the coupling between specific OTUs and amendment of riverine DOM where several OTUs were significantly correlated with changed environmental conditions. Although these shifts in the relative abundance of particular OTUs were not coupled directly to metabolic activity there were concomitant significant changes in protease activity. Taken together, the nine studies emphasize the *sensitivity* scenario of bacterioplankton communities in Baltic Sea, where particular populations respond to different sets of environmental forcing. The causal loop diagram in Figure 2 summarizes the significant effects of changes in environmental conditions for community composition and functioning included in this review. Overall, the studies in this section highlight how changes in environmental forcing may significantly impact pelagic remineralization of organic carbon and result in a drastic reduction in the flow of organic matter through the microbial loop.

OUTSTANDING QUESTIONS

Although the Baltic Sea bacterial communities are fairly well studied, research to integrate bacterioplankton dynamics and its consequences in food-web and biogeochemical models is much needed. We infer that such integration is necessary to allow predictions and counter measures of detrimental future climate change effects on microbial food webs and their ecosystem services.

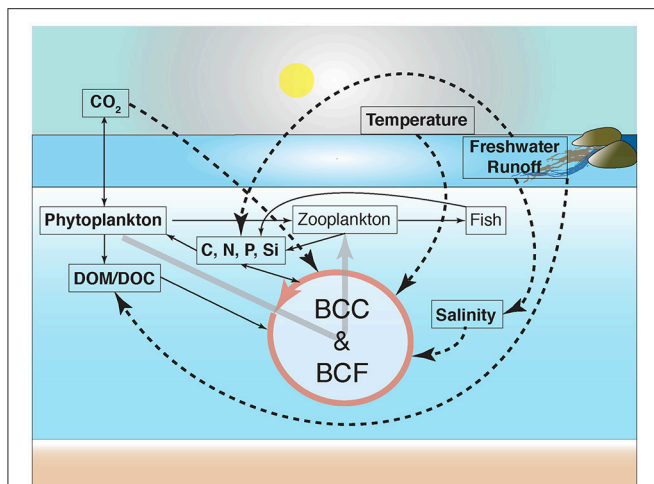


FIGURE 2 | Causal-loop diagram indicating potential ecosystem-wide effects in carbon cycling due to responses among bacterioplankton populations to natural and anthropogenic disturbances. Bacterioplankton community composition and functioning have been abbreviated to BCC and BCF, respectively. The figure is redrawn and modified from (Azam and Malfatti, 2007). Continuous and dashed arrows denote nutrient fluxes and changes in environmental variables with empirical evidence of significant effects on bacterioplankton community composition covered in this review, respectively. Changes in bacterioplankton community functioning, such as bacterial heterotrophic production and respiration, may occur due to increases in the availability of dissolved organic matter (DOM), resulting from, for example, increased freshwater runoff and phytoplankton blooms.

Recent work on bacterial populations and their activity at the seafloor of the Baltic Sea has shown a plethora of interesting dynamics and lifestyles including, an active community that was previously deemed unlikely (Glaubitz et al., 2009, 2014; Berg et al., 2013, 2015; Broman et al., 2017a,b; Reyes et al., 2017; Zinke et al., 2017). Detailed studies with concomitant measurements of bacterioplankton community composition and function are required in deep-waters and sediments of the Baltic Sea to determine the role of bacteria in key biogeochemical cycles (e.g., of C, N, P, and S) in general, and in relation to hypoxia in particular.

Seasonal *in situ* studies of bacterioplankton community dynamics have emphasized how communities return to a similar composition and functioning in specific seasons year after year (Fuhrman et al., 2006; Andersson et al., 2010; Lindh et al., 2015c). This could indicate that bacterioplankton communities are in fact resilient to recurrent pulse and press disturbances, but could also indicate that the environmental conditions over seasons are “repeated” and that the same bacterial populations are repeatedly selected for. Overall, there is a recognized need to incorporate the long-term temporal dimension when quantifying resistance and resilience of microbial communities (Shade et al., 2012; Fodelianakis et al., 2017; Liu et al., 2018). Only by including the temporal dimension can microbial ecologists fully understand the consequences of ocean change for bacterioplankton community dynamics,

and we urgently need more information on changes occurring over time, preferably long-term studies. In particular, for experimental studies, there is a lack of data that empirically test the scenarios of resistance and resilience for Baltic Sea bacterioplankton communities. Nevertheless, in one study using a transplant and re-transplant experimental design (Lindh et al., 2015a), we showed how bacterioplankton community dynamics remain altered even after returning to the same environmental conditions as the original community experienced. One of the most important questions to address in future studies in the Baltic Sea will therefore be to empirically test whether bacterioplankton communities remain sensitive to an environmental disturbance or if the community can return to a similar original community structure and function following the *resilience* scenario. Presently, we observe that a majority of the Baltic Sea studies point toward the sensitivity scenario, and that it is necessary to await future research to make definite conclusions regarding the extent of resilience. Thus, within the time frame of 2 weeks, the studies indicate that sensitivity is more developed than resistance. Nevertheless, natural temporal changes in environmental conditions for time frames of more than a month will alter the composition and functioning of bacterioplankton communities, likely interfering with interpretations of the scenarios of sensitivity, resistance and resilience.

SUMMARY

A majority of the studies included in this review show that bacterioplankton community composition is sensitive to changes in environmental conditions, in particular salinity and nutrient inputs, with empirical support for simultaneous changes also in community functioning. As noted also in other aquatic environments, pronounced shifts in composition and bacterial heterotrophic production occur following spring diatom and dinoflagellate blooms and summer blooms of filamentous Cyanobacteria. The sensitivity scenario and its impact on the microbial loop is highlighted in **Figure 3A**. Salinity singles out as a principal determinant of the distribution of bacterioplankton populations across basin-wide spatial scales in the Baltic Sea. Nevertheless, at regional (within-basin) scales, changes in nutrient availability and both autochthonous and allochthonous DOM influence the bacterioplankton community composition. Hence, this review provides a roadmap as to what ecological consequences climate change could have on the Baltic Sea ecosystem if bacterioplankton dynamics changes. Yet, although bacterioplankton communities are initially sensitive we know very little about the potential of resilience due to the lack of empirical studies testing this scenario (**Figure 3B**).

For quantifying the level of *sensitivity* or *resilience* of bacterioplankton communities to natural and human-driven changes in environmental conditions it is essential to investigate particular bacterioplankton populations and their responses to alternate physicochemical conditions and specific (in)organic nutrient sources, e.g., different DOM and DOC compounds.

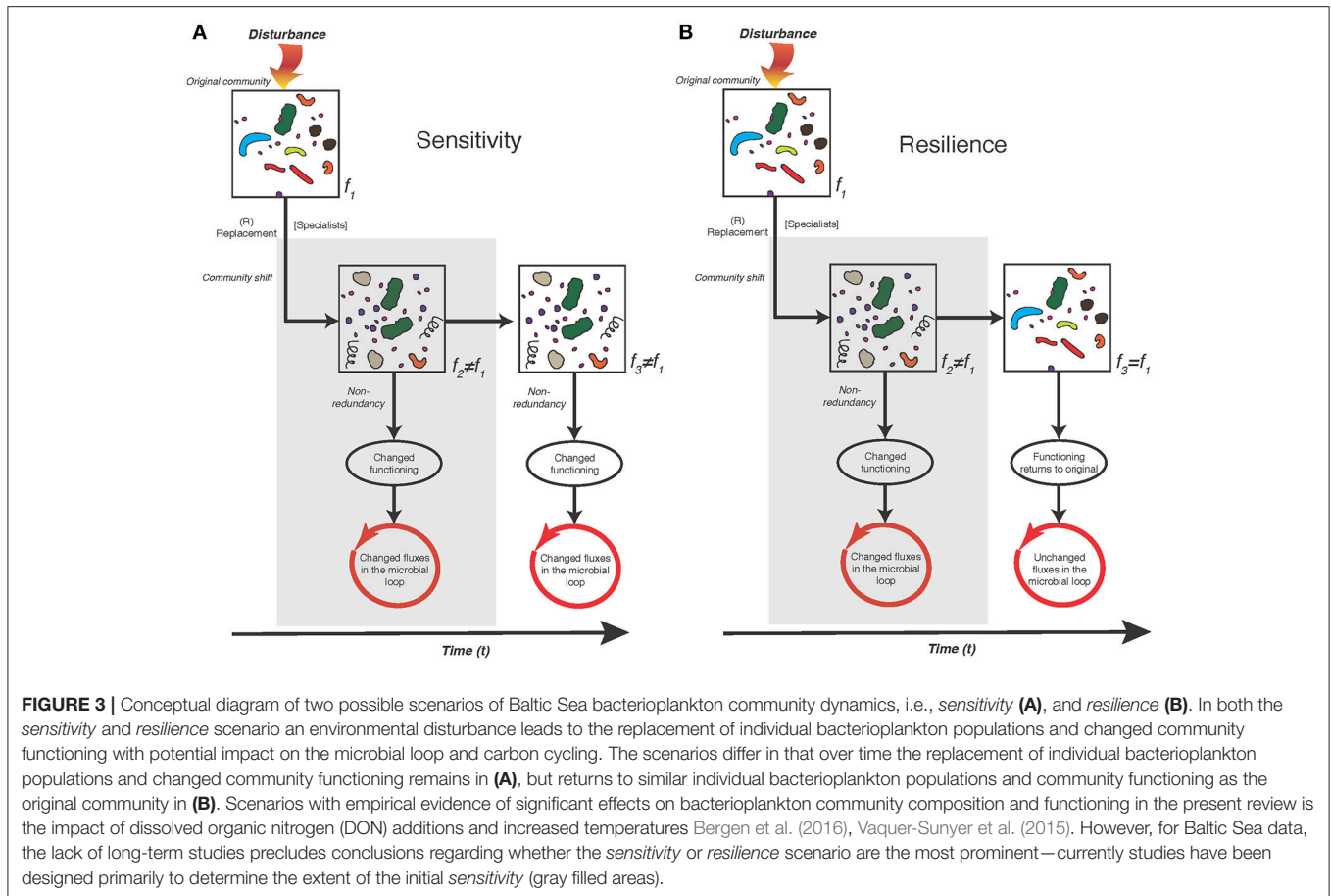


FIGURE 3 | Conceptual diagram of two possible scenarios of Baltic Sea bacterioplankton community dynamics, i.e., *sensitivity* (A), and *resilience* (B). In both the *sensitivity* and *resilience* scenario an environmental disturbance leads to the replacement of individual bacterioplankton populations and changed community functioning with potential impact on the microbial loop and carbon cycling. The scenarios differ in that over time the replacement of individual bacterioplankton populations and changed community functioning remains in (A), but returns to similar individual bacterioplankton populations and community functioning as the original community in (B). Scenarios with empirical evidence of significant effects on bacterioplankton community composition and functioning in the present review is the impact of dissolved organic nitrogen (DON) additions and increased temperatures Bergen et al. (2016), Vaquer-Sunyer et al. (2015). However, for Baltic Sea data, the lack of long-term studies precludes conclusions regarding whether the *sensitivity* or *resilience* scenario are the most prominent—currently studies have been designed primarily to determine the extent of the initial *sensitivity* (gray filled areas).

The *sensitivity* scenario has important implications for the Baltic Sea ecosystem: it dictates that environmental disturbances and climate change are likely to affect processes like the microbial-driven carbon pump and/or the general microbial regulation of energy and matter fluxes. We infer that knowledge of the linkages between bacterioplankton composition and bacterial cycling of carbon and other elements under varying environmental forcing is critically important for developing action plans to sustain microbial ecosystem services invaluable for all marine life.

AUTHOR CONTRIBUTIONS

ML and JP both participated in the study design, analysis, and writing of the article.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2018.00361/full#supplementary-material>

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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