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Methane Emissions From Nordic Seagrass Meadow Sediments

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Shallow coastal soft bottoms are important carbon sinks. Submerged vegetation has been shown to sequester carbon, increase sedimentary organic carbon (C_{org}) and thus suppress greenhouse gas (GHG) emissions. The ongoing regression of seagrass cover in many areas of the world can therefore lead to accelerated emission of GHGs. In Nordic waters, seagrass meadows have a high capacity for carbon storage, with some areas being recognized as blue carbon hotspots. To what extent these carbon stocks lead to emission of methane (CH₄) is not yet known. We investigated benthic CH₄ emission (i.e., net release from the sediment) in relation to seagrass (i.e. Zostera marina) cover and sedimentary C_{org} content (%) during the warm summer period (when emissions are likely to be highest). Methane exchange was measured in situ with benthic chambers at nine sites distributed in three regions along a salinity gradient from ∼6 in the Baltic Sea (Finland) to ∼20 in Kattegat (Denmark) and ∼26 in Skagerrak (Sweden). The net release of CH₄ from seagrass sediments and adjacent unvegetated areas was generally low compared to other coastal habitats in the region (such as mussel banks and wetlands) and to other seagrass areas worldwide. The lowest net release was found in Finland. We found a positive relationship between CH₄ net release and sedimentary C_{org} content in both seagrass meadows and unvegetated areas, whereas no clear relationship between seagrass cover and CH₄ net release was observed. Overall, the data suggest that Nordic Zostera marina meadows release average levels of CH₄ ranging from 0.3 to 3.0 µg CH₄ m⁻² h⁻¹, which is at least 12–78 times lower (CO₂ equivalents) than their carbon accumulation rates previously estimated from seagrass meadows in the region, thereby not hampering their role as carbon sinks. Thus, the relatively weak CH₄ emissions from Nordic Z. marina meadows will not outweigh their importance as carbon sinks under present environmental conditions.

Keywords: seagrass, greenhouse gas, blue carbon, nordic, Zostera marina
INTRODUCTION

Methane (CH$_4$) is a very potent greenhouse gas (GHG), with a global warming potential 28 times higher than carbon dioxide (CO$_2$) per mole of CO$_2$ released (100-year period) (Myhre et al., 2013). CH$_4$ emissions have been estimated that about half of the global CH$_4$ emissions are generated from aquatic sources, although there is high variability between regions and ecosystems (Saunois et al., 2020; Roestreter et al., 2021). Oceanic shelves, although marginal in area compared to deep oceans, contribute about 75% of global CH$_4$ emissions from oceans worldwide (Bang et al., 2019). Methane in the marine environment is mainly produced in sediments during anaerobic degradation of organic matter by methanogenic archaea (Bakker et al., 2014; Wilson et al., 2020). The produced CH$_4$ may be oxidized in the water column (King et al., 1990), but if the conditions are right, CH$_4$ can be reoxidized in the water column by methane-oxidizing bacteria (MOBs) (Laanbroek, 2010). Up to 90% of the CH$_4$ produced in sediments with submerged vegetation can be globally oxidized by MOBs in the water phase (Laanbroek, 2010). Photosynthetically derived oxygen from submerged plants can potentially be used by methanogenic bacteria (MOBs) to convert CH$_4$ to CO$_2$ and thereby hinder methanogenesis. During their passage through the water column and the extent of this process depends on the bubble size and water depth (Weber et al., 2019). This explains why almost all CH$_4$ emissions are derived from the nearshore coastal environment, where there is less likelihood that the CH$_4$ is oxidized before reaching the atmosphere (Weber et al., 2019).

Natural wetlands, e.g., vegetated ecosystems where the soil is water-saturated for most of the year and which store large amounts of carbon in their soils (accounting for 20–30% of the global yearly CH$_4$ emissions and are thus the single largest non-anthropogenic source of CH$_4$), are global hotspots for blue carbon (Dahl et al., 2016; Röhr et al., 2018). Vegetation loss or alteration in macrophyte species composition may also stimulate methanogenesis in the sediment (Oremland and Taylor, 1975; Holmer and Kristensen, 1994; Sela-Adler et al., 2017).

Seagrass meadows have been reported to naturally emit low levels of moderate levels of CH$_4$ ranging from 0.00004 to 378 μg m$^{-2}$ h$^{-1}$ (Garcia-Bonet and Duarte, 2017). This is substantially lower than what has been observed in other marine habitats. For example, saltmarshes can emit up to 10,000 μg m$^{-2}$ h$^{-1}$ (Whiting and Chanton, 1993). However, stressors such as high reductions in habitat fragmentation, salinity warming, and dramatically increasing CH$_4$ emissions in seagrass meadows can dramatically increase CH$_4$ emissions (Al-Haj and Fulweiler, 2020). In the Nordic region, seagrass meadows have high capacity for storing large amounts of carbon in their sediments. In particular, some sites along the Swedish Skagerrak coast are suggested to be global hotspots for blue carbon (Dahl et al., 2016; Röhr et al., 2018; Moksnes et al., 2021). Seagrasses are previously known coastal soft bottom sediments in in the Baltic Sea area (Heyer and Berger, 2000) and therefor could be of particular interest to study blue carbon habitats in such as seagrass meadows that may store large amounts of organic carbon (C$_org$) in their sediments. Understanding the fate of stored carbon in seagrass sediments and potential sources for GHG emissions is thus of great importance.
MATERIALS AND METHODS

Study Area

Nordic coastal areas are of particular interest since they stretch from the Baltic Sea, which is a semi-enclosed waterbody and one of the largest brackish water areas in the world, to the marine environments of Skagerrak and Kattegat through the Danish Strait (Storebælt, Lillebælt, and Oresund) of the region. Therefore, characterized by strong large-scale salinity gradients from freshwater conditions (0–2) in the Bothnian Bay (marine conditions of ~34) in the North Sea (Helcom 2017-2018). Coastal shallow habitats in northern areas are deemed by climate scenario models to be exposed to faster warming than the global average with an expected temperature increase ranging from ~2°C in the southern part of the Baltic Sea to ~4°C in the northern part by the end of this century (i.e., 2050; Andersson et al., 2015), which may influence CH4 emissions from coastal blue carbon habitats in the future. Further, the coastal water of the Baltic Sea, Skagerrak, and Kattegat are surrounded by nine countries and human activities in the area, adding pressure on seagrass ecosystems (Boström et al., 2014). For instance, severe seagrass losses of about 60% have been reported in the Swedish west coast between 1980 and 2000 (Baden et al., 2003; Nyqvist et al., 2009). From some of these areas in Sweden, where historical losses have occurred, it has been estimated that the resulting loss of sea carbon from these sediments could be up to 30% of Mg C ha–1 (Moksnes et al., 2021).

The current study was carried out during a warm summer period with water temperatures ranging from 20 to 23.5°C (see Supplementary Table 1) in August 2018 in Z. marina meadows and adjacent unvegetated areas within three regions along the salinity gradient stretching from the Baltic Sea archipelago west of Turku in Finland (three sites) to the fjord east of Fyn Odense in Denmark (two sites) and the Kullaberg fjord on the Swedish Skagerrak coast (four sites) (see Figure 1 and Table 1). The three Finnish study areas Z. marina grows in the lowest salinity (salinity propagation limit ~6), while the Danish sites have intermediate salinities (~20) and the Swedish sites have salinities varying between 8 and 34 in the surface waters with a yearly average of ~26. Water temperatures were between 20 and 23.5°C in the study area during the sampling period. In Finland, the sites are moderately exposed, and the sediment consists mainly of fine to coarse sand with low levels of organic content. In Denmark, the Nyborg site is exposed to easterly winds and the sediment is sandy with low organic content, while the Holckenhavn fjord is sheltered, and the sediment is silty with low organic content. In Sweden, the sites are situated in shallow bays exposed to different levels of hydrodynamic forces and the topmost layers in the sediments are sandy, silty, or muddy.

Incubation Chambers for Sampling CH4 at Sediment–Water Interface

Incubation chambers produced by transparent Plexiglas cores (inner diameter: 5.8 cm, height: 45 cm; Figure 2) containing an air-filled gas pocket with a gas-tight septum for extraction of
TABLE 1 | Sampling design showing number of replicates, water depth and water temperature in seagrass meadows and adjacent unvegetated habitats at the different sampling sites, and mean salinity for each of the three sampling regions.

<table>
<thead>
<tr>
<th>Sampling regions</th>
<th>Seagrass replicates (n)</th>
<th>Unveg. replicates (n)</th>
<th>Seagrass depth (m)</th>
<th>Unveg. depth (m)</th>
<th>Temp. (°C)</th>
<th>Salinity (mean)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Finland (Fin)</td>
<td>Fårö</td>
<td>6</td>
<td>2</td>
<td>2</td>
<td>20</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Hummelskär</td>
<td>6</td>
<td>2.1–2.2</td>
<td>2.3–2.4</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ångsö</td>
<td>6</td>
<td>2–2.3</td>
<td>2–2.1</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td>Denmark (Den)</td>
<td>Holckenhavn Fjord</td>
<td>6</td>
<td>2</td>
<td>2</td>
<td>21</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>Nyborg</td>
<td>5</td>
<td>2.5</td>
<td>2.5</td>
<td>23.5</td>
<td></td>
</tr>
<tr>
<td>Sweden (Swe)</td>
<td>Getevik</td>
<td>6</td>
<td>2.2</td>
<td>2.6</td>
<td>21.5</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>Kristineberg</td>
<td>6</td>
<td>3.1</td>
<td>3.5</td>
<td>21.6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Skalhavet</td>
<td>6</td>
<td>2.2</td>
<td>2</td>
<td>22.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Gåsö</td>
<td>6</td>
<td>2.5</td>
<td>2.7</td>
<td>23.5</td>
<td></td>
</tr>
</tbody>
</table>

FIGURE 2 | Deployed incubation chamber in a seagrass meadow (left) and collection of a gas sample (top right). Illustration (bottom right) of the sampling methodology using an incubation chamber inserted 15 cm into sediment with a 20 cm water column above the sediment. On the top, a 5 cm air-pocket is connected to a gas-tight septum from where a gas-sample (including methane) released from the sediment could be collected (using a syringe). Gas-samples were extracted periodically after insertion from the chamber and stored in gas-tight exetainers until analyzed with gas-chromatography (GC). Photos: K. Gagnon.
Analysis of Methane

The gas in the collected exetainers samples were analyzed by means of headspace analysis and gas chromatography (GC). Briefly, the headspace was injected into a gas chromatograph (GC5A, Shimadzu Corporation) equipped with a Porapak-N column (60–100 mesh) and a flame ionization detector (FID). The carrier gas for the FID was nitrogen, while the fuel gas was hydrogen and the oxidant air. For calibration, certified standards at atmospheric concentration (1 ppm) and with 49.99 ppm CH₄ (Air Liquide gas AB) were used. Using this deal with gas laws (PV = nRT) the ppm concentrations were converted into molar concentrations (µmol CH₄ g⁻¹), which were plotted against incubation time. The CH₄ emissions per surface area of the sediments were calculated as the total amount of CH₄ accumulating over time within the gas-filled pocket of the incubation chamber and reported as µg CH₄ m⁻² h⁻¹. Since measurements were only conducted during daytime, values were not extrapolated to full diurnal estimates.

Collection of Sediment Cores

After incubation, sediment cores were collected adjacent to each incubation chamber using a shiver core sampling device (0–60 cm). The cores were sliced into three different depth sections: 0–1 cm representing the oxidized zone, 1–15 cm representing the rhizospheric and clowd, and 15–50 cm representing the sediments without living seagrass. Sediment compression was accounted for by measuring the distance from the top of the cores to the sediment surface inside and outside of the cores after being inserted into the incubation chamber and reported as µg CH₄ m⁻² h⁻¹. Since measurements were only conducted during daytime, values were not extrapolated to full diurnal estimates.

Analysis of Organic Carbon Content in the Sediment

Sediment cores were weighed, homogenized, and sliced into subsamples (0–1 cm). Each depth section was then dried at 60°C for ~48 h until constant weight was achieved. The bulk density (g DW cm⁻³) was calculated as the ratio of dry sediment samples were grinded into powder using a Retch 400 mixing mill for subsequent carbon analyses. The total carbon and nitrogen content (µg C and % N) in each depth section was subsequently analyzed using a carbon–nitrogen elemental analyzer (Flash 2000, Thermo Fisher Scientific). Previous research in the studied regions have documented that the organic carbon and nitrogen content generally is low (<5%) and was therefore not accounted for (Röhr et al., 2016). However, these samples were also analyzed for their sedimentary C content and environmental variables such as sedimentary Corg content and seagrass shoot density, respectively, were tested with linear regression analysis. All data analyses were performed in IBM SPSS Statistics (version 27).

RESULTS

The CH₄ emissions were generally low but varied substantially both within and between sites. Emission rates of CH₄ to the air phase ranging from 0.1 to 6% g CH₄ m⁻² h⁻¹ at the Finnish sites to 2.0–2.5% g CH₄ m⁻² h⁻¹ at the Danish sites and 0.4–3.0% g CH₄ m⁻² h⁻¹ at the Swedish sites (Figures 1 and 2). Pairwise comparisons showed that the overall CH₄ emissions from seagrass meadows were significantly higher in both the Swedish and Danish sites when compared to the Finnish sites, while there was no significant difference between the Swedish and Danish sites (Table 2). For the unvegetated areas, CH₄ emissions were significantly higher in the Swedish sites compared to the Finnish sites (Table 2). Overall, there was no difference in emissions between seagrass covered- and unvegetated sediments, even though differences between these habitat types occurred in some sites within each region (Table 2 and Figure 3).

Methane emission increased along the salinity gradient (Figures 1 and 3), although this pattern likely also was reflecting the inherent conditions of the three regions. The mean integrated (0–15 cm) organic carbon (Corg) content of the sediments varied between 0.1% and 6%, with the largest levels found in the Swedish sites (Supplementary Tables 2 and 3). There were linear...
### Table 2: Summary of non-parametric Kruskal–Wallis tests of methane emissions among regions within (seagrass meadows and unvegetated areas) and between habitats.

<table>
<thead>
<tr>
<th>Pairwise comparison</th>
<th>Test statistic</th>
<th>Std. error</th>
<th>Std. test statistic</th>
<th>Adj p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Region-seagrass (total N = 51, df = 2, model p = 0.005)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fin vs Den</td>
<td>14.483</td>
<td>5.823</td>
<td>2.487</td>
<td>0.039</td>
</tr>
<tr>
<td>Fin vs Swe</td>
<td>-14.479</td>
<td>4.798</td>
<td>-3.018</td>
<td>0.008</td>
</tr>
<tr>
<td>Den vs Swe</td>
<td>0.004</td>
<td>5.413</td>
<td>0.001</td>
<td>1.000</td>
</tr>
<tr>
<td>Region-unvegetated (total N = 47, df = 2, model p = 0.002)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fin vs Den</td>
<td>7.321</td>
<td>5.443</td>
<td>1.345</td>
<td>1.000</td>
</tr>
<tr>
<td>Fin vs Swe</td>
<td>-16.010</td>
<td>4.635</td>
<td>-3.454</td>
<td>0.003</td>
</tr>
<tr>
<td>Den vs Swe</td>
<td>-8.688</td>
<td>5.103</td>
<td>-1.709</td>
<td>0.532</td>
</tr>
</tbody>
</table>

Habitat (total N = 98, df = 1, model p = 0.806

Significant values (p < 0.05) are shown in bold. Countries with bolded text indicate the higher values in the pairwise comparisons. Std. error, standard error; Adj p, Adjusted p-value.

### Supplementary Figure 1B

There was no significant relationship between the average seagrass shoot density and CH4 emission in the current study.

### Discussion

This study shows that CH4 emissions from cold-temperate Nordic seagrass meadows are relatively low when compared to seagrass areas worldwide. Nevertheless, differences in vegetation or shallow-water habitats in the Nordic region of the Baltic Sea and in other parts of the Baltic (e.g., Sweden) may further influence CH4 emissions from seagrass habitats worldwide. CH4 production and release of methane from seagrass meadows are relatively low in cold temperate areas compared to other regions of the world, which may be due to lower water temperatures and low productivity. This may explain the lower CH4 emissions from seagrass meadows in the Nordic region compared to other parts of the world.

### Supplementary Table 3

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Model p</th>
<th>Adj p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nordic meadows</td>
<td>0.005</td>
<td>0.039</td>
</tr>
<tr>
<td>Unvegetated areas</td>
<td>0.002</td>
<td>0.003</td>
</tr>
</tbody>
</table>

Adjust p-value.

### Supplementary Figure 3

The relatively low CH4 emissions levels measured in our study agree well with those reported for coastal bare sediments (1.2–2.3 µg CH4 m⁻² h⁻¹) in the Baltic proper (Bonab et al., 2017). Those sediments had similar carbon content to the other Swedish coastal areas (5.5%) and similar salinities to the Finnish area (6.8). But these samples were collected in the summer at much higher temperature (8.0 °C) compared to our study range (20–23.5 °C).

### Supplementary Table 4

The good agreement rates may be explained by the fact that most of the CH4 generated in deep inside the sediments efficiently oxidized in the community to methane-oxidizing archaea and sulfate-reducing bacteria before it can reach the sediment-water interface (Orphan et al., 2001).

Up to 90% of the CH4 produced from marine sediments are consumed in the sediments, and the efficiency of the oxidation is dependent on the presence of reduced organic matter, and temperature and the microbial community composition.

Temperature and other factors significantly influence CH4 production both in tropical (Burkholder et al., 2020; George et al., 2020) and cold-temperate waters (Hoyer and Berger, 2000). However, in the present study, water temperature was similar across regions, whereas the differences in water temperature were more spatially and temporally dynamic, and could have influenced the variation in emission rates. Therefore, it is suggested that future studies should investigate these factors.
TABLE 3 | Sediment methane (CH₄) emission rates from seagrass meadows worldwide and other shallow-water habitats in Nordic waters, using sediment-to-air filled pocket chamber techniques, reported in the literature and in the current study.

<table>
<thead>
<tr>
<th>Region</th>
<th>Habitat type</th>
<th>Ranges (or average*) of emission rates, (µg CH₄ m⁻² h⁻¹)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seagrass worldwide</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Global estimation</td>
<td>Seagrass in general</td>
<td>54*</td>
<td>Rosentreter et al., 2021</td>
</tr>
<tr>
<td>Portugal, Atlantic coast</td>
<td>Zostera nolii (at night)</td>
<td>71</td>
<td>Bahmann et al., 2014</td>
</tr>
<tr>
<td>Florida bay</td>
<td>Thalassia testudinum</td>
<td>14–185</td>
<td>Barber and Carlson, 1993</td>
</tr>
<tr>
<td>France, Atlantic coast</td>
<td>Zostera spp</td>
<td>66*</td>
<td>Deborde et al., 2010</td>
</tr>
<tr>
<td>Red Sea</td>
<td>Halophila stipulacea and Halodule uninervis</td>
<td>16–74</td>
<td>Gascas-Bonet and Duarte, 2017</td>
</tr>
<tr>
<td>Western Indian Ocean</td>
<td>Thalassia hemprichii</td>
<td>50* (controls), 224–291 (disturbed)</td>
<td>Lyimo et al., 2018</td>
</tr>
<tr>
<td>Florida Keys</td>
<td>Syringodium sp.</td>
<td>2–5</td>
<td>Oremland, 1975</td>
</tr>
<tr>
<td>Thalassia testudinum</td>
<td>29–30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nordic waters</td>
<td>Zostera marina</td>
<td>0.3–3.0</td>
<td>Current study</td>
</tr>
<tr>
<td>Other shallow-water habitats in Nordic waters</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>North-Eastern Germany</td>
<td>Brackish fen, Phragmites australis</td>
<td>538–15,200</td>
<td>Koch et al., 2014</td>
</tr>
<tr>
<td>Gulf of Bothnia</td>
<td>Eustarine wetlands</td>
<td>8,583*</td>
<td>Likanen et al., 2009</td>
</tr>
</tbody>
</table>

It has been suggested that the higher levels of sulfate found in sediments of higher salinity will increase sulfate reduction, which in turn could inhibit CH₄ production in vegetated habitats (e.g., Koebischer et al., 2018). Methane emissions from marine areas could hence be expected to be lower. In contrast, seafloor sediments in Nordic and co-occurring Halophila and Enhalus may also be that the inhibitory effect of sulfate reduction plays a minor role in sulfide generation and methanogenesis (Gerber et al., 2015). Therefore, CH₄ production and carbon sequestration could be expected to be low. In conclusion, the relative high organic carbon content in sediments is also confirmed in the current study.

Even though those emissions were measured from both vegetated and adjacent unvegetated sediments, the CH₄ emissions partly counteract the seagrass meadows’ capacity as functionally significant carbon sinks. Only published data on carbon accumulation rates from seagrasses in the Nordic area (Röhr et al., 2016) shows annual mean values of 0.03–0.001 g C m⁻² yr⁻¹ for Finland and 0.35 g C ha⁻¹ yr⁻¹ for Denmark. While all accumulation data for Sweden has been published, given the same units and calculated as CO₂/ha, WP100 (2015), Myhre et al. (2013), the CH₄ emission in this study ranged from 0.0007 to 0.0040 g CH₄ ha⁻¹ yr⁻¹ in Finland, from 0.0045 to 0.0056 g CH₄ ha⁻¹ yr⁻¹ in Denmark, and from 0.0095 to 0.0067 g CH₄ CO₂ ha⁻¹ yr⁻¹ in Sweden. Thus, the carbon accumulation rate in Finland was between 2 and 7 times higher, and in Denmark between 5 to 10 and 7–8 times higher, than the estimated emissions from CH₄ in the current study. Therefore, we conclude that the relative weak emission of CH₄ from Nordic seagrass meadows will not outweigh their importance as carbon sinks under present environmental conditions.

Climate simulations for the Baltic sea ecosystems indicate a 2–4°C warming under climate change, which is significant for increased precipitation by the year 2100 (Finn et al., 2019). This may have multifaceted effects on the carbon cycle. While healthy seagrass meadows contribute to mitigate the effects of runoff and capture part of the increased input of nutrients and organic matter, an increased organic content in the sediments might result in increased respiration and lower oxidation rates in the sediment. If lower oxidation will in turn favor anaerobic respiration, it might thus lead to increased production and emissions of CH₄ and other GHGs. A higher temperature is predicted to increase more drastically in the Nordic region than on a global scale (Andersson et al., 2015). This may accelerate the CH₄ emissions from blue carbon habitats such as seagrass meadows (Yvon-Durocher et al., 2011).

Methane emissions from seagrass sediments in the Nordic region have been shown to be higher than global estimates (Andersson et al., 2015). This may accelerate the CH₄ emissions from blue carbon habitats such as seagrass meadows (Yvon-Durocher et al., 2011). It has previously been shown in tropical seagrass sediments that CH₄ emissions more than doubled during high temperature stress (Georg et al., 2020). In the Nordic seagrass systems, today functioning effectively in less atmospheric CO₂, might thus be hampered by climate change effects. It has also been shown that the higher salinity of the sediments might result in increased respiration (Koebischer et al., 2018).
their capacity for natural carbon sinks. To fully understand the extent of methane emissions from microhabitats and other GHGs from Nordic coastal habitats, multiple spatial and temporal aspect should be considered in future studies.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material. Further inquiries and requests directed to the corresponding author.

AUTHOR CONTRIBUTIONS

MA, MB, SG, MM, DB, and MB conceived and designed the study. MA, MB, DD, MG, and MB carried out the laboratory and analysis. MA and MB wrote the first draft of the manuscript. With aid from MA, SB, and MB, DD carried out the fieldwork. MA, MB, DD, MG, CB, and KG carried out the lab work and analysis. All authors contributed to the final version of the manuscript and MB wrote the first draft of the manuscript with aid from MA, SB, and MB. DD carried out the lab work and analysis. MA, MB, DD, MG, CB, and KG carried out the fieldwork. MA, MB, DD, MG, BAI, and MB wrote the first draft of the manuscript. With aid from MA, SB, and MB, DD carried out the lab work and analysis. All authors contributed to the final version of the manuscript.

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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.2021.811533/full#supplementary-material.


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