



# Temperature-induced copepod depletion and the associated wax of *Bellerochea* in Belgian coastal waters: Implications and shifts in plankton dynamics

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## ARTICLE INFO

### Keywords:

Data reusability  
Phytoplankton bloom  
Integrative use of data  
Zooplankton depletion

## ABSTRACT

Since 2018, severe and recurrent copepod depletions have been observed in Belgian coastal waters. These depletions have been described as temperature-induced mass mortality events. This paper confirms the relation of copepod abundance anomalies with periods of high temperature based on new data. Although severe, the effects, consequences and implications of this depletion remain unknown. Our study suggests that the absence of zooplanktonic predators in autumn, together with the availability of nutrients discharged via the Scheldt estuary, allowed a bloom of the diatom *Bellerochea*, in a season otherwise characterised by low phytoplanktonic activity. Although the bloom reaches high abundances, its effects on the marine environment are not yet visible. The enormous abundances are likely to induce small-scale oxygen depletions which might further translate to the environment. Communities of Calanoida, Canuelloida and Cyclopoida tend to recover from the annual autumn depletion, although the typical autumn peak is entirely missing in the years subject to severe heat waves and associated high water temperatures. As a result, copepod dynamics have drastically changed since the first observed depletion and associated bloom of *Bellerochea* in 2018.

## 1. Introduction

Marine ecosystems are under threat by human induced environmental changes, including those arising from climate change. For instance, temperature rise, pollution, eutrophication, oil spills and nuisance of invasive species are known to disrupt the ecological balance (Hoegh-Guldberg and Bruno, 2010). Climate change, and associated heat waves especially, have proven to alter marine ecosystems leading to regime shifts (e.g., Beaugrand, 2004; Capuzzo et al., 2017), oxygen depletion (e.g., Richardson, 2008), mass mortality events (e.g., Roberts et al., 2019; Garrabou et al., 2022), acidification (e.g., Blackford and Gilbert, 2007), habitat degradation and phytoplankton blooms (e.g., de Rijcke, 2017; Nohe et al., 2020). These issues are frequently and increasingly studied in marine scientific papers, for their obvious

importance to society.

The response of marine zooplankton to climate change, and rising sea surface temperatures, is of critical importance to the oceanic food web and fish stocks (Chivers et al., 2017). Zooplankton is a critical link between phytoplankton and higher trophic levels in the pelagic zone through predation; and to the benthic zone through sedimentation of faecal pellets (Wexels Riser et al., 2002). So, effects of changing zooplankton communities will translate to other communities (Mitra et al., 2014; Heneghan et al., 2020). Furthermore, zooplankton are crucial contributors to the carbon cycle and climate regulation as they actively participate in the biological pump. They play a vital role in this process by assisting in the uptake and transfer of carbon dioxide: initially, CO<sub>2</sub> is absorbed and converted into organic matter by phytoplankton; followed by zooplankton consuming this organic matter,

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<https://doi.org/10.1016/j.seares.2024.102523>

Received 30 April 2024; Received in revised form 29 July 2024; Accepted 31 July 2024

Available online 2 August 2024

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contributing to the formation of marine snow. Consequently, carbon is deposited through this sedimentation process (Wexels Riser et al., 2002; Richardson, 2008) or consumed by higher trophic levels if not sedimented (Lampitt et al., 1993). Because zooplankton is known to rapidly respond to environmental changes due to their rapid life cycles, they are applicable as bio-indicators of ecosystem change (Chiba et al., 2018).

In autumn 2018, a severe copepod depletion was observed in the coastal waters of the Belgian part of the North Sea (BPNS), suggested to be induced by high sea surface temperatures, which exceeded the thermal physiological threshold of the most dominant zooplankton species in this region, i.e. the calanoid copepod *Temora longicornis* (Mortelmans et al., 2021; Semmouri et al., 2023). This threshold of 22.5 °C (Halsband-Lenk et al., 2002; Sahota et al., 2022) was exceeded for the first time since the start of the temperature time-series in 2002, in the summer of 2018 (Flanders Marine Institute (VLIZ), Belgium, 2024). The major shortfall in Mortelmans et al. (2021) is the low taxonomic resolution of the considered dataset, and the reason for depletion could only be made at the level of orders. Therefore, this autumn anomaly was further examined on the level of species: the depletion in 2018 was proven to be related to the absence of *Temora longicornis* (Semmouri et al., 2023). Strikingly, the anomaly proved to be recurrent and in 2022 calanoid copepod abundances in nearshore regions dwindled towards zero (Semmouri et al., 2023). Both events were found to be temperature related (Semmouri et al., 2023), but other factors might also contribute to the observed dynamics.

Finally, temperature will not only affect zooplankton, but most likely also phytoplankton. Most common and best-known blooms from the southern bight of the North Sea, are those of *Phaeocystis* (Rousseau et al., 2000; Daro et al., 2008) and *Noctiluca* (Vasas et al., 2007; Ollevier et al., 2021). Favourable conditions, often enhanced by the environmental changes discussed above, might trigger species of phytoplankton to bloom (Anderson et al., 2017). Although these blooms are not necessarily negative (Da Silva et al., 2021), they are often detrimental to marine communities especially because the associated bacterial activity on decaying phytoplankton depletes dissolved oxygen, causing hypoxia (Harrison et al., 2017; Mohd-Din et al., 2020) and associated dead zones (Altieri and Diaz, 2019). Furthermore, blooming species can drastically

change the environment by accumulation of toxins in the food web (Richlen et al., 2010; Hallegraeff and Bolch, 2016); and are often considered nuisance as they might form foams or high cell densities that can clog the filter apparatuses and gills of fish (Hallegraeff, 2003).

In this study, we use imaging techniques to explore how copepod autumn depletions affect associated planktonic communities. Digitized samples allow to retroactively go back in time and work on historically scanned samples. Unlike stored physical samples, which can quickly decay, scanned samples are preserved indefinitely. From the BPNS, a recent time series on zooplankton has been created with observations since 2014 (see Mortelmans et al., 2021). Alongside the measured zooplankton abundances, information on *Bellerochea* was unintentionally collected, as this taxon appeared in the scans but was initially classified as 'detritus'. However, as *Bellerochea* is consistently measured by the device, it is now part of the image recognition algorithms to facilitate detection in the future. Here, 569 samples from 5 stations between 2014 and 2022 were processed, to detect *Bellerochea* (see Fig. 1A, B). From the resulting dataset, we aimed to map and explore *Bellerochea* dynamics and obtain first insights in the association with the observed environmental changes and copepod dynamics.

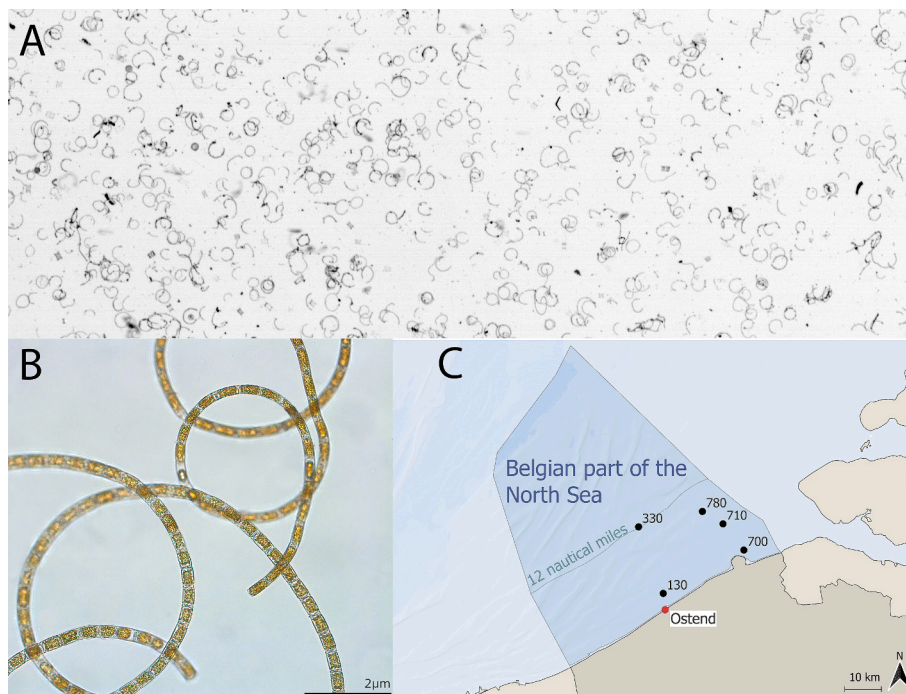
## 2. Material and methods

### 2.1. Study area

The Belgian part of the North Sea is one of the most intensively used seas in the world. The BPNS is part of the Southern Bight of the North Sea and covers ~3.447 km<sup>2</sup> (Fig. 1) and is characterised by a series of subtidal sandbank systems (Verfaillie, 2008; Lescrauwaet et al., 2013). On average, the BPNS has a shallow depth around 20 m with maximum depths up to 45 m (Lescrauwaet et al., 2013). The entire region is heavily impacted by anthropogenic activities: shipping, tourism, fisheries, wind farms and pollution (Lescrauwaet et al., 2013).

### 2.2. Data collection

Data was collected monthly between 2014 and 2022 on 5 stations in



**Fig. 1.** Habitus of *Bellerochea*, as detected by the ZooScan (plot A). Habitus of *Bellerochea*, as detected by light microscopy (plot B). Sampling locations (130: 51.27083 N, 2.905 E; 330: 51.43333 N, 2.808333 E; 700: 51.376667 N, 3.22E; 710: 51.44083 N, 3.138667 E; 780: 51.47117 N, 3.058 E) (plot C).

the Belgian part of the North Sea: three stations (700, 710 and 780) perpendicular to the coast in front of Zeebrugge, which are influenced by the Scheldt estuary especially, and two (130 and 330) in front of Oostende, which have influence from more clear, nutrient poor waters coming from the Atlantic Ocean (Fig. 1C). On each of these stations, mesoplankton (including *Bellerochea*) was sampled with a 200- $\mu\text{m}$  WP2 net, which was deployed vertically and equipped with a flowmeter, following the protocol of Mortelmans et al. (2019). Zooplankton collected in the cod-end was sedated by soda water and fixated in 4% formaldehyde solution. In the lab, the fixative was changed to 70% ethanol solution. The samples were digitized by the ZooScan plankton imaging device (Hydroptic, ZooScan M3) and processed by ZooProcess and Plankton Identifier in order to detect and classify the digitized objects (Grosjean et al., 2004; Gorsky et al., 2010). Images were manually checked and validated to the 25 taxonomic categories (full list is found in Mortelmans et al., 2019). Throughout the manuscript, we will use 'Calanoida-group' for the group consisting of Calanoida, Canuelloida, Cyclopoida, as these taxa were not discriminated on the collected images. The existing data series on zooplankton was entirely reprocessed to detect occurrences of *Bellerochea*. On each of these stations, profiles data on conductivity (S/m), temperature ( $^{\circ}\text{C}$ ), depth (m), salinity of the water body (Practical Salinity Units), the density of the water body ( $\text{kg}/\text{m}^3$ ), the pressure of the water body (decibel), the sound velocity through the water body (m/s), the optical backscatter (OBS) and the turbidity of the water body (Nephelometric Turbidity Units) were collected with a Seabird SBE25plus CTD. Finally, data from the underway systems aboard the RV Simon Stevin are recorded nearly continuously, with temperature ( $^{\circ}\text{C}$ ) being measured using a Seabird SBE38. Only data around a 2 km buffer around the five stations is considered. All data is published via Flanders Marine Institute (2020). In addition, heat waves, as measured by the Royal Meteorological Institute (Royal Meteorological Institute (RMI), 2023) are included in the dataset as well.

To assess historic prevalence of *Bellerochea*, the dataset provided by Nohe et al. (2018) was explored to obtain counts of this genus. Nohe et al. (2018) provided a compilation of phytoplankton data from different research projects focused on the BPNS from Harden-Jones, 1968 to Hoegh-Guldberg and Bruno, 2010 and is considered as a valuable resource for historic data.

### 2.3. Taxonomic account of *Bellerochea*

The genus *Bellerochea* consists of six species: *B. horologicalis*, *B. indica*, *B. polymorpha*, *B. spinifera*, *B. malleus* and *B. yucatanensis* (Hasle and Syvertsen, 1997). The species are widespread and occur around the globe (Stosch von Stosch, 1977). The species *Bellerochea malleus* is extremely variable in morphology, as indicated by Hustedt (1930) and von Stosch (1977, 1987), making species identification very difficult. Although scanning electron microscopy allowed the authors to identify the Belgian bloom to be *B. horologicalis*, we remain careful with species identifications of this genus in literature and rather use *Bellerochea* throughout this manuscript. The ZooScan images do not allow for species recognition. To date, only *B. malleus* and *B. horologicalis* are mentioned to occur in the BPNS (Van Heurck, 1884; Nohe et al., 2018; Lagaisse, 2020).

### 2.4. Downstream analysis

Plankton abundances and distributions through the water column were visually represented in R (V 2023.06.1 + 524) in the RStudio environment (RStudio Team, 2023), using the following packages: Dplyr 1.0.9 (Wickham et al., 2022), ggplot2 3.3.6 (Wickham, 2016), ggpubr 0.4.0 (Kassambara, 2020), hrbrthemes 0.8.0 (Rudis, 2020), Hmisc 4.7.2 (Harrell, 2022), lattice 0.20.45 (Deepayan, 2008), lubridate 1.8.0 (Grolemund and Wickham, 2011a, 2011b), magrittr 2.0.3 (Bache and Wickham, 2022), mgcv 1.8.40 (Wood, 2017), PerformanceAnalytics 2.0.4 (Peterson and Carl, 2020), reshape 0.8.9 (Wickham., 2007), scales

1.2.0 (Wickham and Seidel, 2022), TidyR 1.2.0 (Wickham and Girlich, 2022), and tidyverse 1.3.2 (Wickham et al., 2019).

### 2.5. Statistics

To assess the parametric assumptions of our dataset, we performed several statistical tests. The Shapiro-Wilk test for normality indicated significant deviation from normal distribution ( $W = 0.171, p < 2.2\text{e-}16$ ), supported by the Kolmogorov-Smirnov test ( $D = 0.443, p < 2.2\text{e-}16$ ). Levene's test for homogeneity of variances across stations yielded a non-significant result ( $F = 1.55, p = 0.187$ ), suggesting variances were approximately equal. The assumption of normality was not met although variances were homogeneous. Based on the assumptions a Kruskal-Wallis test was used to examine the differences in the abundance of *Bellerochea* between the years before or equal to 2017 and after 2017.

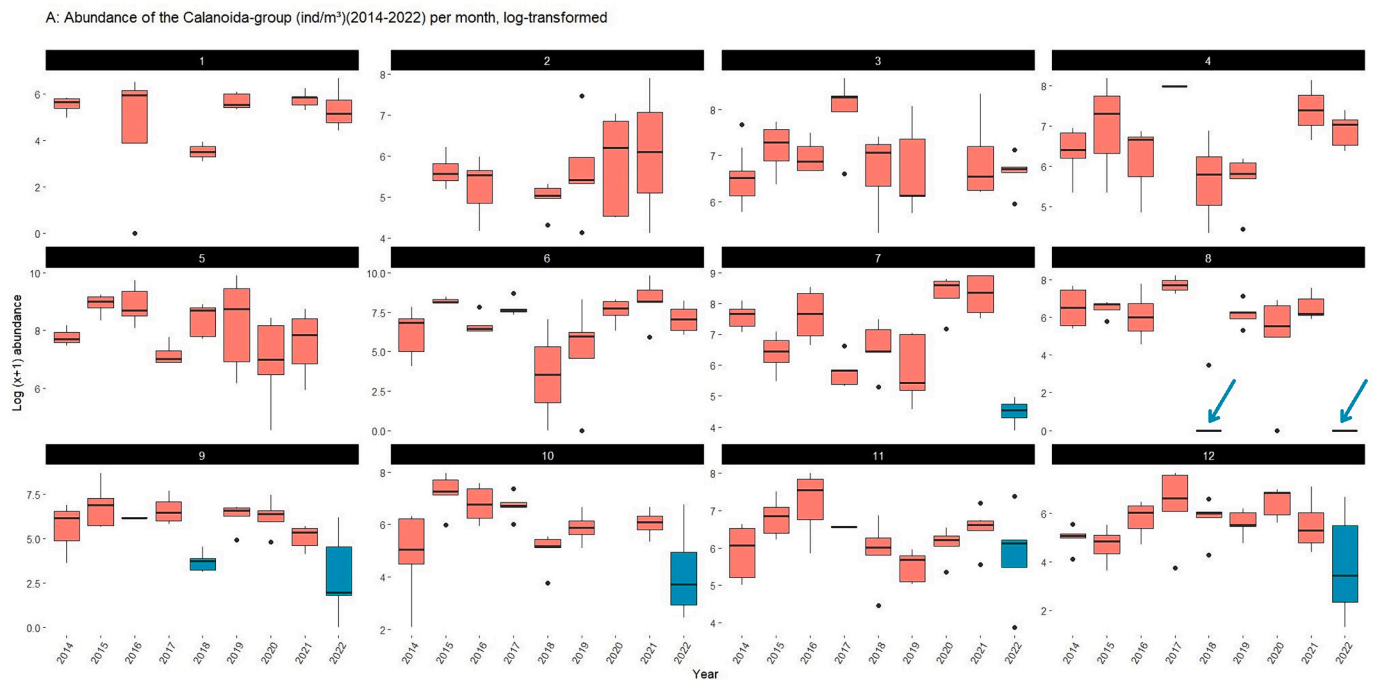
Seasonal generalized additive mixed models (GAMM) are applied to the Calanoida-group: two for nearshore stations (700, 130, 710) before and after January 2018; and an additional two for offshore stations (330, 780) before and after January 2018. One cubic regression spline was used to model the seasonal trend across one year. This approach employs a smoothing technique that maintains continuity throughout the year, ensuring that the trend's value transitions smoothly from the start to the end of each observed time period (Zuur et al., 2009). Covariates used in the GAM models were month and year. The variable "station" was added to both sets as a random mixed effect, excluding any spatial autocorrelation. The model fit of the GAMs was assessed following the method of Zuur et al. (2009), i.e., using the Akaike Information Criterion (AIC) and inspecting the homogeneity and normality of the model residuals. The minimum AIC was used to select the best-fit GAM model.

## 3. Results

### 3.1. Dynamics of the Calanoida-group

Abundances for the Calanoida-group are presented on a log-transformed scale (Fig. 2). The seasonal pattern consisted of prominent spring peaks in March, a secondary peak in May, and a third very small one in October. These spring peaks were each time followed by a subsequent decline in abundances. During December and January abundances were at their lowest, rising again from February onwards to the first spring peak. Notably, from January to June, the abundance levels are stable without major discrepancies between the years. However, in August and September 2018, a first depletion of the Calanoida-group is seen, whose abundances only recovering in October 2018. The next, more severe, depletion occurred from July to October 2022, recovering only in November 2022.

The dynamics of species abundance were analyzed using GAMM (Fig. 3). In the nearshore stations, the period before January 2018 exhibited a consistent increase in abundances from January to May, peaking in late May and maintaining relatively high levels through the summer months (Fig. 3A). In contrast, the period after January 2018 showed a similar increase from January to May but experienced a decline from June to September, stabilizing through December (Fig. 3B). This shift indicates an alteration in autumn abundance dynamics post-2018 compared to the earlier period. For offshore stations, before January 2018, three distinct peaks in abundance were observed: March, June, and October, followed by a decline to winter levels in December (Fig. 3C). After January 2018, a similar peak pattern persisted, but with declines in August and September, followed by a recovery towards the end of the year (Fig. 3D). The fitted lines are provided, highlighting per subset the main trend of the trends provided: a first set shows the fitted line for nearshore stations, in which the period after 2018 has a major depletion in autumn months (where it had been much higher before 2018), recovering towards end of the year (Fig. 3E). A second set shows the fitted line for offshore stations, in which the period after 2018 has a



**Fig. 2.** Log-transformed ( $x + 1$ ) abundances of the Calanoida-group over the month, per year, in order to visualize variation per month. Boxplots indicated in green are considered as striking events with reduced/absent abundances. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

major depletion in autumn months (where it had been much higher before 2018), recovering much faster compared to nearshore stations and abundances increase to pre-2018 levels in November (Fig. 3F).

### 3.2. *Bellerochea* dynamics

Abundances for *Bellerochea* are presented on a log-transformed scale (Fig. 4A). In the years 2014 to 2017 only low abundances were observed for *Bellerochea*. In the years 2018 to 2022 a shift is seen: the taxon became very abundant from July to October, only depleting in November. The year 2017 is a transition, with only one month of high abundances. From January to June the taxon is present in very low abundances only. The results of the Kruskal-Wallis showed a significant difference in abundance of *Bellerochea* before 2018 and after or equal to 2018 ( $p < 0.001$ ).

Finally, absolute abundances of *Bellerochea*, presented as a barplot (per month, per year), are combined with sea surface temperatures and heat waves (Fig. 5A). Over the time series air-heatwaves are seen in 2015 (6 days, 30.5 °C), in 2016 (5 days, 30.2 °C), one in 2017 (5 days, 30.6 °C), two in 2018 (15 days, 28.9 °C and 10 days, 30.1 °C), three in 2019 (8 days, 28.4 °C; 5 days, 33.8 °C; 6 days, 30.2 °C), one in 2020 (12 days, 31.3 °C), and one in 2022 (8 days, 30.2 °C) (Royal Meteorological Institute (RMI), 2023) (Fig. 5A). A section of Fig. 5A is given in Fig. 5B, only plotting the highest sea surface temperatures exceeding 21.21 °C. The horizontal line given in Fig. 5A is set at 22.5 °C, which is the thermal threshold for *Temora longicornis*: in 2018, 2020 and 2022 this line is crossed. The difference in abundance of *Bellerochea* before 2018 and after or equal to 2018 is obvious.

## 4. Discussion

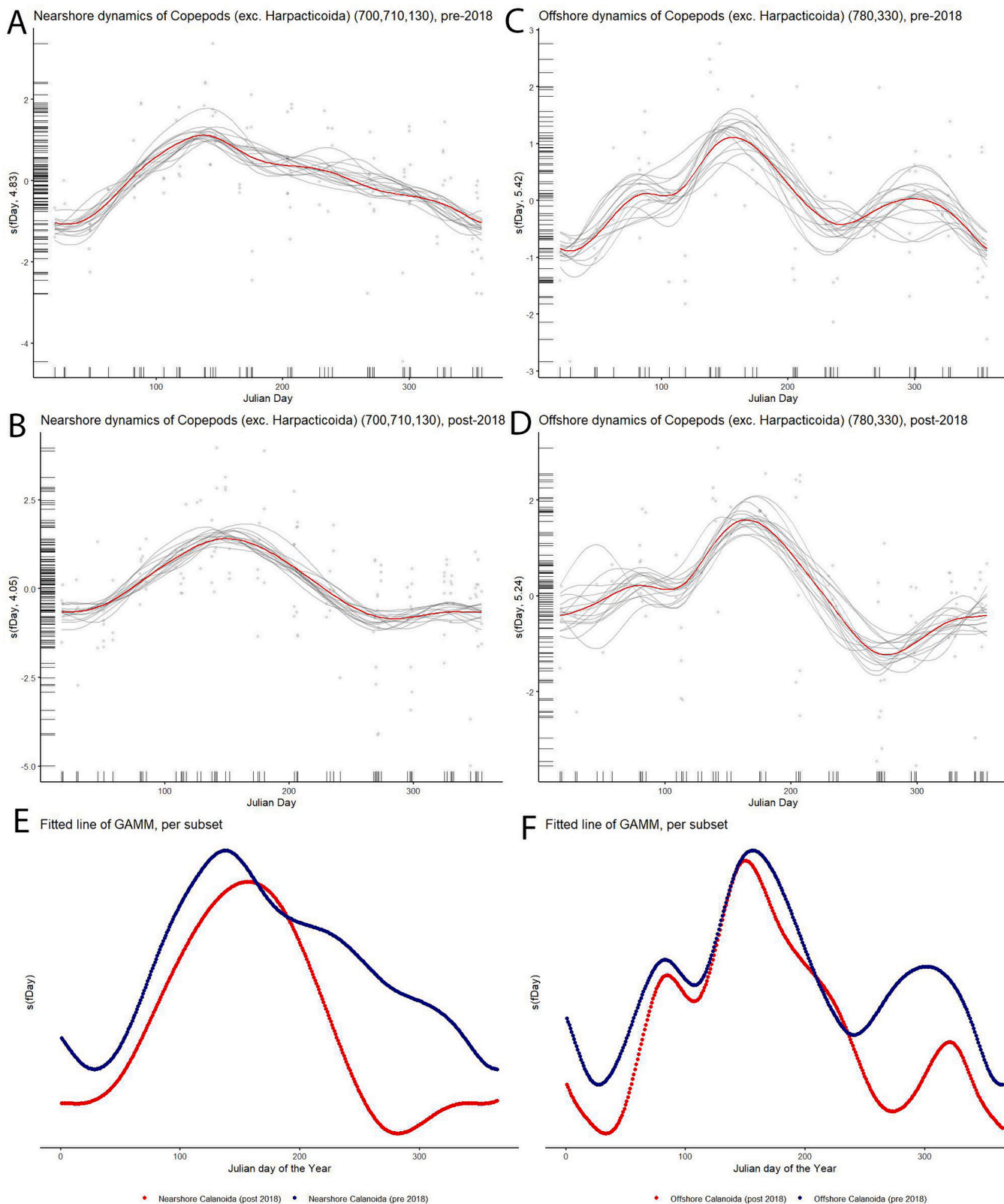
### 4.1. Autumn anomalies of the Calanoida-group

The coastal ecosystem in the southern North Sea is changing. Both Mortelmans et al. (2021) and Semmouri et al. (2023) described severe depletions of copepods in the BPNS in autumn of especially 2018 and

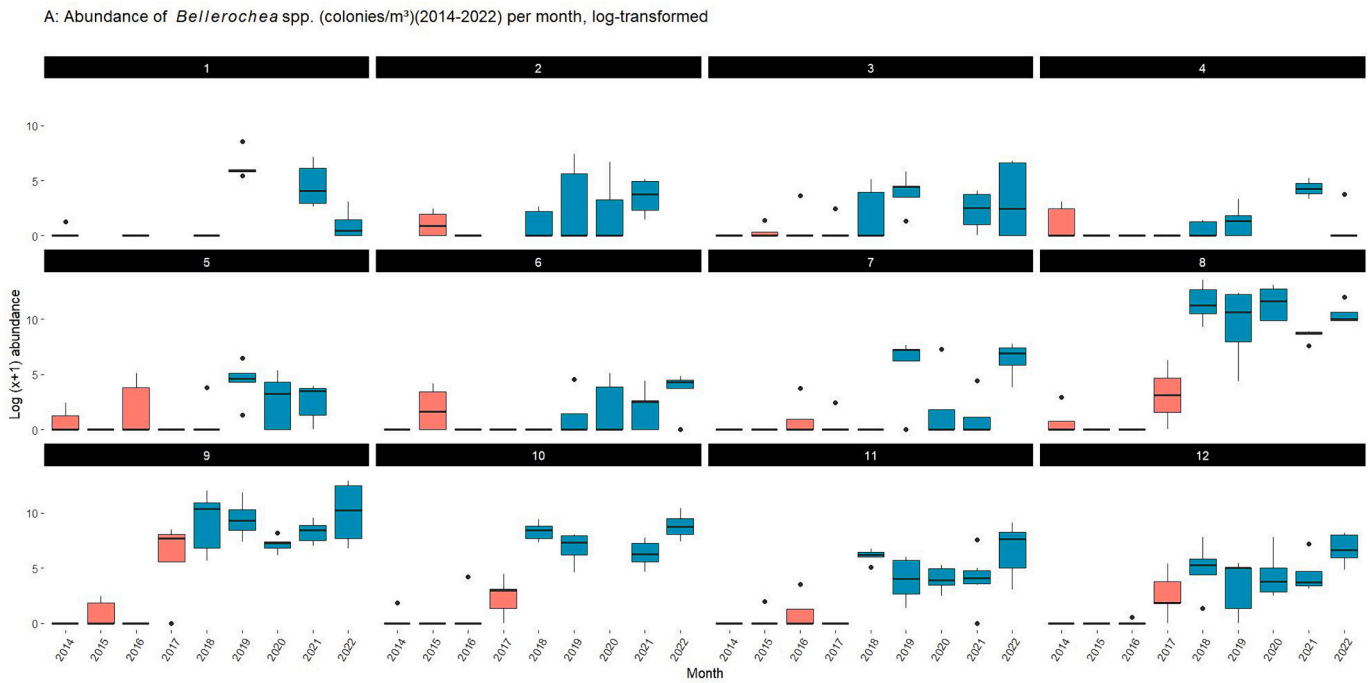
2022. These depletions were down to low abundances of four dominant calanoid taxa: *Temora longicornis*, *Acartia clausi*, *Centropages* spp. and *Calanus helgolandicus* (Semmouri et al., 2023). We argue these autumn depletions were distinct from regime shifts (Beaugrand, 2004; Alvarez-Fernandez et al., 2012; Capuzzo et al., 2017) or interannual variations (Greve et al., 2004; O'Brien et al., 2011) as an entire trophic level was lost in August and September 2018 and 2022, only to recover in October–November on nearshore locations. The main loss during the depletion could be attributed to *Temora longicornis* (Semmouri et al., 2023), previously identified as a sentinel species for climate change (Semmouri et al., 2019, 2020), and the dominant zooplankton species in the BPNS (Van Meel, 1975; Van Ginderdeuren, 2013; Deschutter et al., 2017; Semmouri et al., 2019, 2021). *Temora longicornis* is relatively well studied in the BPNS: it is an omnivorous calanoid copepod that is present all year round in coastal waters of the North Sea, with maximum abundances in spring (Fransz et al., 1992; Williams et al., 1994; Deschutter et al., 2017; Semmouri et al., 2023). Importantly, it has been shown that *T. longicornis* in Belgian waters is herbivorous during fall and winter, while during spring and summer it needs heterotrophic food to meet its energetic demands for egg production (Antajan et al., 2004; Gentsch et al., 2008). Since a dominant herbivorous species was entirely lost in autumn of 2018 and 2022, it is suggested its (phytoplanktonic) prey will now have lost a predator and might thrive if environmental conditions allow it. It is noteworthy that the depletion of 2022 had a temporally longer impact compared to 2018 – as the abundances only recovered in December (or even January 2023), where in 2018 abundances were back to normal in October.

### 4.2. Detection of *Bellerochea* by the ZooScan

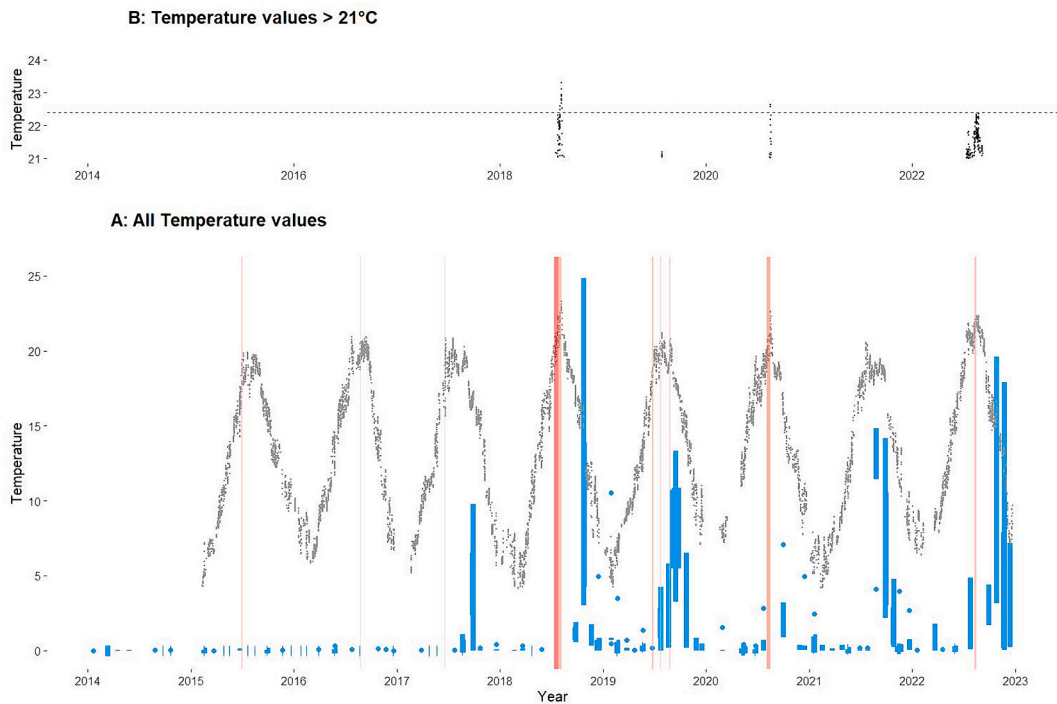
The abundances described here are underestimations of true abundances: the samples are collected over the entire water column, while colonies are especially seen in the surface layers, which implies an underestimation in terms of abundance. A further underestimation comes from the fact we measured colonies, not cells as in Nohe et al. (2020). Moreover, overlapping colonies on the scan were measured as one,



**Fig. 3.** Four seasonal generalized additive mixed models (GAMM) are applied for the Calanoida-group: two for nearshore stations (700, 130, 710) before (plot A) and after January 2018 (plot B); and an additional two for offshore stations (330, 780) before (plot C) and after January 2018 (plot D). In red, the fitted line is given. In grey, the coincidence intervals. Finally, the fitted lines of each of the plots (A, B) are grouped in plot E; the fitted lines of each of the plots (C, D) are grouped in plot F. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 4.** Log- transformed (x + 1) abundances of *Bellerochea* over the year, per month, in order to visualize variation per year. Boxplots indicated in green are considered as striking events with high abundances. From July 2017 a distinct shift can be seen: before this date only marginal abundances of *Bellerochea* are seen (in red); after this date distinctly high abundances are observed (in blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 5.** Sea Surface Temperature time series (black dots), with indication of *Bellerochea* densities (blue bars) and heatwaves and their intensity (in red boxes; the larger, the more intense and longer the heatwave)(plot A). A subplot to plot A; and gives only temperature data above 21 °C to illustrate the high temperature values after the associated heatwaves. The critical temperature for *Temora longicornis*, 22.5 °C, is illustrated with a dashed line (plot B). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

further underestimating final abundances. Nevertheless, the measured abundances are consistently high compared to historic data from both Belgium (Nohe et al., 2018; Nohe et al., 2020), but also compared to other published records on the species (e.g., a maximum of 5000 cells/L

for *B. horologicalis* in the bay of Tunis (Yahia-kéfi et al., 2005)). For that reason, it is safe to say this is the first documented bloom of *Bellerochea* in the BPNS.

For the BPNS, historic mean abundances of *Bellerochea* are 325.99

cells/L, with a maximum of 21,000 cells/L detected 9th of May 1978 on station 'smeets\_west1' [directly in front of Ostend, 51.241667° N, 2.9111° E] (Nohe et al., 2018, Nohe et al., 2020). Although this maximum is higher to the maximum we observe, the reasons for our underestimation need to be considered. As noted in Nohe et al. (2020), there are no historic accounts available between 1978 and 1994; and between 2010 and 2018. The interrupted time series is therefore not indicating absences of *Bellerochea*, but absences in sampling. *Bellerochea*, interestingly, was described from Belgium by Van Heurck (1884), indicating the long-term presence of this genus in the BPNS.

Finally, as reported by von Stosch (1977), *Bellerochea malleus* grows well at 21 °C, but unfortunately von Stosch (1977) does not mention the optimal growth temperature. Von Stosch (1977) did mention optimal growth temperature for *B. yucatanensis*, which is set at an astonishing 29 °C, and a maximum near 34 °C in aerated cultures (von Stosch, 1977).

#### 4.3. *Bellerochea* in Belgium

In the BPNS, nutrient enrichments show a clear gradient for phosphates, nitrites, nitrates, silicates and ammonia with highest concentrations near the Scheldt estuary towards lowest concentrations in offshore regions (Rousseau et al., 2006; Otero et al., 2023). The abundances of *Bellerochea* are high over the studied stations, but especially near the mouth of the Scheldt Estuary highest abundances are seen. In the Mediterranean, *B. horologicalis* has been reported to occur in eutrophic waters such as the Nile delta (Dowidar, 1974) and the Gulf of Naples (Marino and Modigh, 1981) [both were initially published as *B. malleus*, but identifications have been rectified in Yahia-Kéfi et al. (2005) and Ismael, 2014], and *B. malleus* is reported from the eutrophic water in the Venice lagoon (Tolomio and Moschin, 1994). For that reason, the environment of the Belgian bloom in front of Zeebrugge is similar to blooms described in Dowidar (1974) and Marino and Modigh (1981): both documented blooms of *Bellerochea* in eutrophic waters. It is here argued that sufficient nutrient loads in this region allow *Bellerochea* to bloom, in the absence of potential predators. In the highly eutrophicated southern North Sea phytoplankton is controlled by grazing activities of zooplankton, as nutrients are ubiquitous. (Rousseau et al., 2006; Van Ginderdeuren, 2013; Otero et al., 2023).

The blooms of *Bellerochea* in 2018 to 2022 yielded enormous abundances over the considered stations, resulting in a visually altered state of the sea. During the several sampling campaigns, visual observations indicated a severe bloom of *Bellerochea*, especially in the nearshore region in front of Zeebrugge. In the field, especially in August, the bloom was visible as a dark green to brown, coherent mass floating in the water column. Despite the bloom, we did not experience any nuisance in smell.

#### 4.4. Foresight

It is impossible to predict how the coastal ecosystem of the BPNS will cope with recurrent copepod depletions or blooms of *Bellerochea*. We expect impacts on oxygen levels as decaying phytoplankton will increase activity of aerobic bacteria which at their turn will deplete oxygen (Schmidtke et al., 2017; Chen et al., 2021). The effects of hypoxia will likely translate into other trophic levels (Vaquer-Sunyer et al., 2008), and especially towards larval fish and zooplankton. In the well-mixed nearshore region of the BPNS (van Leeuwen et al., 2015), hypoxia is likely to affect benthic communities through benthic-pelagic coupling (e.g., Griffith et al., 2017). If decay of *Bellerochea* (or any bloom of phytoplankton in autumn) indeed triggers hypoxia, this hypoxia might further strengthen the depletion of zooplankton (not only Copepods, but also other taxa). Furthermore, as heatwaves are often associated with oxygen depletion (Grodzins et al., 2016) these effects are likely to be reinforced. Depletion of copepod abundances in August and September especially are expected to impact larval fish, as these coastal regions are often used as nurseries (Harden-Jones Harden-Jones, 1968). Especially Downs herring (*Clupea harengus*), a species of high socio-economic

interest, is of importance as it reproduces during winter in the Eastern English Channel (ECC) and Southern Bight of the North Sea (see Denis et al., 2016 and references within). Finally, it is not unlikely *Temora longicornis* or other calanoids, such as *Centropages* spp., will be replaced by more temperature resilient species in the BPNS, similar to what has been observed for *Calanus helgolandicus/finmarchicus* (Hirche, 1983; Bonnet et al., 2005). The LifeWatch dataserie on zooplankton, phytoplankton, water quality and *Bellerochea* abundance is constantly growing and will obviously allow us to make more predictions on the autumn anomalies and associated events. High temperatures do allow *Bellerochea* to thrive (von Stosch, 1977). It is important to track, monitor and quickly quantify ongoing changes as implications for aquaculture, fisheries and recreation are imminent. Right now, it is not yet known whether *Bellerochea* has toxic capacities when blooming.

## 5. Conclusion

The first effects of a temperature-induced copepod-depletion in 2018 and 2022 are becoming visible, in the shape of an autumn bloom of *Bellerochea*. This species was previously not documented to form blooms in the BPNS. The power of image-based datasets is illustrated, as it allows us to retroactively go back in time and work on unchanged samples not subject to decay or disintegration. The depletion of copepods and the subsequent bloom of *Bellerochea* are showing an increasingly pronounced intensity. In 2022, both the copepod depletion and the *Bellerochea* bloom presented longer durations compared to the conditions observed in 2018. Global warming-induced copepod depletion and *Bellerochea* blooms potentially lead to oxygen depletion, impacting trophic levels, larval fish, and zooplankton in the Belgian part of the North Sea and the ecosystem as a whole.

## Funding

This work was supported by data and infrastructure provided by VLIZ as part of the Flemish contribution to LifeWatch [I000819N-LIFEWATCH, I002021N-LIFEWATCH].

## CRediT authorship contribution statement

**Jonas Mortelmans:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ilias Semmouri:** Writing – original draft, Conceptualization. **Michiel Perneel:** Writing – original draft, Conceptualization. **Rune Lagaisse:** Writing – original draft, Conceptualization. **Luz Amadei Martínez:** Writing – review & editing, Writing – original draft, Validation, Formal analysis, Conceptualization. **Zoe Rommelaere:** Validation. **Pascal I. Hablützel:** Formal analysis. **Klaas Deneudt:** Supervision, Project administration, Methodology, Funding acquisition.

## Declaration of competing interest

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

## Data availability

Data will be made available on request.

## Acknowledgements

We wish to thank Lennert Schepers, for his help in cleaning the underway temperature measurements. The crew of the RV Simon Stevin and fellow scientists for their assistance during the cruises. David Nicolás Marro Salazar and Naia Fernandez de Larrinoa for their aid in

scanning and validating over the course of their internships at MOC. This work makes use of data and infrastructure provided by VLIZ and is funded by the Research Foundation - Flanders (FWO) as part of the Belgian contribution to the LifeWatch program.

## References

- Altieri, A.H., Diaz, R.J., 2019. Dead zones: Oxygen depletion in coastal ecosystems. In: Sheppard, C. (Ed.), *World Seas: An Environmental Evaluation*, Second edition. Academic Press, pp. 453–473. <https://doi.org/10.1016/B978-0-12-805052-1.00021-8>. ISBN 9780128050521.
- Alvarez-Fernandez, S., Lindeboom, H., Meesters, E., 2012. Temporal changes in plankton of the North Sea: community shifts and environmental drivers. *Mar. Ecol. Prog. Ser.* 462, 21–38.
- Anderson, D.M., Boerlage, S.F.E., Dixon, M.B. (Eds.), 2017. *Harmful Algal Blooms (HABs) and Desalination: A Guide to Impacts, Monitoring, and Management*. IOC Manuals and Guides, vol. 78. UNESCO, Paris, 539 pp.
- Antajan, E., Gasparini, S., Daro, M.H., Tackx, M., 2004. Contribution of herbivory to the diet of *Temora longicornis* (Müller) in Belgian coastal waters. In: Antajan, E. *Responses of calanoid copepods to changes in phytoplankton dominance in the diatoms - Phaeocystis globosa dominated Belgium coastal waters* (pp. 85–108). PhD Thesis. Vrije Universiteit Brussel. Laboratorium voor Ecologie en Systematiek: Brussel. 147 pp.
- Bache, S., Wickham, H., 2022. Magrittr: a forward-pipe operator for R. R package version 2.0.3.
- Beaugrand, G., 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. *Prog. Oceanogr.* 60 (2–4), 245–262.
- Blackford, J.C., Gilbert, F.J., 2007. pH variability and CO<sub>2</sub> induced acidification in the North Sea. *J. Mar. Syst.* 64 (1–4), 229–241. <https://doi.org/10.1016/j.jmarsys.2006.03.016>.
- Bonnet, D., Richardson, A., Harris, R., Hirst, A., Beaugrand, G., Edwards, M., et al., 2005. An overview of *Calanus helgolandicus* ecology in European waters. *Prog. Oceanogr.* 65 (1), 1–53. <https://doi.org/10.1016/j.pocean.2005.02.002>.
- Capuzzo, E., Lynam, C.P., Barry, J., Stephens, D., Forster, R.M., Greenwood, N., McQuatters-Gollop, A., Silva, T., van Leeuwen, S.M., Engelhard, G.H., 2017. A decline in primary production in the North Sea over twenty-five years, associated with reductions in zooplankton abundance and fish stock recruitment. *Glob. Chang. Biol.* 24 (1), 1–13.
- Chen, C., Shiah, F., Gong, G., Chen, T., 2021. Impact of upwelling on phytoplankton blooms and hypoxia along the Chinese coast in the East China Sea. *Mar. Pollut. Bull.* 112288 <https://doi.org/10.1016/j.marpolbul.2021.112288>.
- Chiba, S., Batten, S., Martin, C.S., Ivory, S., Miloslavich, P., Weatherdon, L.V., 2018. Zooplankton monitoring to contribute towards addressing global biodiversity conservation challenges. *J. Plankton Res.* 40 (5), 509–518. <https://doi.org/10.1093/plankt/fby030>.
- Chivers, W.J., Walne, A.W., Hays, G.C., 2017. Mismatch between marine plankton range movements and the velocity of climate change. *Nat. Commun.* 8 (14434), 1–8.
- Daro, M.-H., Breton, E., Antajan, E., Gasparini, S., Rousseau, V., 2008. Do Phaeocystis colony blooms affect zooplankton in the Belgian coastal zone. In: Rousseau, V., et al. (Eds.), *current status of eutrophication in the Belgian coastal zone*, pp. 61–72.
- de Rijke, M., 2017. *The Current and Future Risk of Harmful Algal Blooms in the North Sea*. Ghent University, Faculty of Bioscience Engineering, Ghent, Belgium.
- Deepayan, S., 2008. *Lattice: Multivariate Data Visualization with R*. Springer.
- Denis, J., Vallet, C., Courcot, L., Lefebvre, V., Caboche, J., Antajan, E., Marchal, P., Loots, C., 2016. Feeding strategy of down herring larvae (*Clupea harengus* L.) in the English Channel and North Sea. *J. Sea Res.* 115, 33–46. <https://doi.org/10.1016/j.seares.2016.07.003>.
- Deschutter, Y., Everaert, G., De Schampelaere, K., De Troch, M., 2017. Relative contribution of multiple stressors on copepod density and diversity dynamics in the Belgian part of the North Sea. *Mar. Pollut. Bull.* 125 (1–2), 350–359. <https://doi.org/10.1016/j.marpolbul.2017.09.038>.
- Dowidar, N.M., 1974. The phytoplankton of the Mediterranean waters of Egypt. I-A checklist of the species recorded. *Bull. Inst. Oceanogr. Fish.* 4, 321–344.
- Flanders Marine Institute (VLIZ), Belgium, 2024. LifeWatch observatory data: nutrient, pigment, suspended matter and secchi measurements in the Belgian Part of the North Sea. <https://doi.org/10.14284/652>.
- Fransz, H.G., Gonzalez, S.R., Cadée, G.C., 1992. Long-term changes in the structure of a zooplankton community in the western Wadden Sea. *Neth. J. Sea Res.* 30 (1–2), 45–55.
- Garrabou, J., Gómez-Gras, D., Medrano, A., Cerrano, C., Ponti, M., Schlegel, R., Benoussan, N., Turicchia, E., et al., 2022. Marine heatwaves drive recurrent mass mortalities in the Mediterranean Sea. *Glob. Chang. Biol.* 28, 5708–5725. <https://doi.org/10.1111/gcb.16301>.
- Gentsch, E., Kreibich, T., Hagen, W., Niehoff, B., 2008. Dietary shifts in the copepod *Temora longicornis* during spring: evidence from stable isotope signatures, fatty acid biomarkers and feeding experiments. *J. Plankton Res.* 31 (1), 45–60. <https://doi.org/10.1093/plankt/fbn097>.
- Gorsky, G., Ohman, M.D., Picheral, M., Gasparini, S., Stemann, L., Romagnan, J.-B., 2010. Digital zooplankton image analysis using the ZooScan integrated system. *J. Plankton Res.* 32 (3), 285–303. <https://doi.org/10.1093/plankt/fbp124>.
- Greve, W., Reiners, F., Nast, J., Hoffmann, S., 2004. Helgoland roads meso- and macrozooplankton time-series 1974 to 2004: lessons from 30 years of single spot, high frequency sampling at the only offshore island of the North Sea. *Helgol. Mar. Res.* 58 (4), 274–288.
- Grodzins, M., Ruz, P., Keister, J., 2016. Effects of oxygen depletion on field distributions and laboratory survival of the marine copepod *Calanus pacificus*. *J. Plankton Res.* 38 (6), 1412–1419. <https://doi.org/10.1093/plankt/fbw063>.
- Grolemund, Garrett, Wickham, Hadley, 2011a. Dates and times made easy with lubridate. *J. Stat. Softw.* 40 (3), 1–25. <https://www.jstatsoft.org/v40/i03/>.
- Grolemund, G., Wickham, H., 2011b. Dates and times made easy with lubridate. *J. Stat. Softw.* 40 (3), 1–25.
- Grosjean, P., Picheral, M., Warembourg, C., Gorsky, G., 2004. Enumeration, measurement, and identification of net zooplankton samples using the ZOO SCAN digital imaging system. *ICES J. Marine Sci.* 61 (4), 518–525.
- Hallegraeff, G.M., 2003. Harmful algal blooms: A global overview. In: Hallegraeff, M., Anderson, D.M., Cembella, A.D. (Eds.), *Manual on Harmful Marine Microalgae*. Monographs on Oceanographic Methodology, 2nd edition. IOC-UNE-SCO, Paris, pp. 25–49.
- Hallegraeff, G., Bolch, C., 2016. Unprecedented toxic algal blooms impact on Tasmanian seafood industry. *Microbiol. Aust.* 37, 143–144.
- Halsband-Lenk, C., Hirche, H.-J., Carlotti, F., 2002. Temperature impact on reproduction and development of congeneric copepod populations. *J. Exp. mar. biol. Ecol.* 271(2): 121–153. [https://doi.org/10.1016/S0022-0981\(02\)00025-4](https://doi.org/10.1016/S0022-0981(02)00025-4). In: *Journal of experimental marine biology and ecology*. Elsevier: New York.
- Harden-Jones, 1968. *Fish Migrations*. Mishawaka, USA.
- Harrell, F., 2022. Hmisc: Harrell Miscellaneous. R package version 4.7–2.
- Harrison, P.J., Piontkovski, S., Al-Hashmi, K., 2017. Understanding how physical-biological coupling influences harmful algal blooms, low oxygen, and fish kills in the sea of Oman and the Western Arabian Sea. *Mar. Pollut. Bull.* 114, 25–34. <https://doi.org/10.1016/j.marpolbul.2016.11.008>.
- Hasle, G.R., Syvertsen, E.E., 1997. *Marine Diatoms*. In: Tomas, C.R. (Ed.), *Identifying Marine Phytoplankton*. Academic Press, San Diego, pp. 5–386.
- Heneghan, R.F., Everett, J.D., Sykes, P., Batten, S.D., Edwards, M., Takahashi, K., Suthers, I.M., Banchard, J.L., et al., 2020. A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. *Ecol. Model.* 435, 109265.
- Hirche, H., 1983. Overwintering of *Calanus finmarchicus* and *Calanus helgolandicus*. *Mar. Ecol.* 11, 281–290.
- Hoegh-Guldberg, Bruno, 2010. The impact of climate change on the World's marine ecosystems. *Science* 328 (5985), 1523–1528. <https://doi.org/10.1126/science.118993>.
- Hustedt, F., 1930. Die Kieselalgen Deutschlands, Österreichs und der Schweiz unter Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete. In: *Kryptogamen-Flora von Deutschland, Österreich und der Schweiz*. (Ed. By L. Rabenhorst), Band 7. Teil 1, pp. 1–920. Akademische Verlagsgesellschaft, Leipzig.
- Ismael, A.A., 2014. Coastal engineering and harmful algal blooms along Alexandria coast. *Egypt. J. Aquat. Res.* 40, 125–131.
- Kassambara, A., 2020. Ggpubr: 'ggplot2' based publication ready plots. R package version 0.4.0.
- Lagaisse, R., 2020. *Phytoplankton Biodiversity in the Belgian Part of the North Sea: A Microscopic and Molecular Inventory*. MSc Thesis. Ghent University, Biology Department, 117 pp.
- Lampitt, R.S., Wishner, K.F., Turley, C.M., Angel, M.V., 1993. Marine snow studies in the Northeast Atlantic Ocean: distribution, composition and role as a food source for migrating plankton. *Mar. Biol.* 116, 689–702.
- Lescauwae, A.-K., Pirlot, H., Verleye, T., Mees, J., Herman, R., 2013. *Compendium voor Kust en Zee 2013: Een geïntegreerd kennisdocument over de socio-economische, ecologische en institutionele aspecten van de kust en zee in Vlaanderen en België*. Oostende, Vlaams Instituut voor de Zee (VLIZ).
- Marino, D., Modigh, M., 1981. An annotated check-list of planktonic diatoms from the Gulf of Naples. *Mar. Ecol.* 2, 317–333.
- Mitra, A., Castellani, C., Gentleman, W.C., Jónasdóttir, S.H., Flynn, K.J., Bode, A., Halsband, C., Kuhn, P., et al., 2014. Bridging the gap between marine biogeochemical and fisheries sciences, configuring the zooplankton link. *Prog. Oceanogr.* 129, 176–199.
- Mohd-Din, M., Abdul-Wahab, F., Mohamad, S.E., Jamaluddin, H., Shahir, S., Ibrahim, Z., et al., 2020. Prolonged high biomass diatom blooms induced the formation of hypoxic-anoxic zones in the inner part of Johor Strait. *Environ. Sci. Pollut. Res.* 27, 42948–42959. <https://doi.org/10.1007/s11356-020-10184-6>.
- Mortelmans, J., Deneudt, K., Cattrijsse, A., Beauchard, O., Daveloose, I., Vyverman, W., Vanaverbeke, J., Timmermans, K., Peene, J., Roose, P., Knockaert, M., Chou, L., Sanders, R., Stinchcombe, M., Kimpe, P., Lammens, S., Theetaert, H., Gkritzalis, T., Hernandez, F., Mees, J., 2019. Nutrient, pigment, suspended matter and turbidity measurements in the Belgian part of the North Sea. *Sci. Data* 6 (1), 22.
- Mortelmans, J., Aubert, A., Reubens, J., Otero, V., Deneudt, K., Mees, J., (UGent), 2021. *Copepods (Crustacea: Copepoda) in the Belgian part of the North Sea: trends, dynamics and anomalies*. *J. Mar. Syst.* 220.
- Nohe, A., Knockaert, C., Goffin, A., Dewitte, E., De Cauwer, K., Desmit, X., Vyverman, W., Tyberghein, L., Lagring, R., Sabbe, K., Ugent- Laboratory of Protistology & Aquatic Ecology; Flanders Marine Institute; Belgian Marine Data Center, 2018. *Marine phytoplankton community composition data from the Belgian part of the North Sea, 1968-2010*. VLIZ. <https://doi.org/10.14284/320>.
- Nohe, A., Goffin, A., Tyberghein, L., Lagring, R., De Cauwer, K., Vyverman, W., Sabbe, K., 2020. Marked changes in diatom and dinoflagellate biomass, composition, and seasonality in the Belgian part of the North Sea between the 1970s and 2000s. *Sci. Total Environ.* 716, 136316.
- O'Brien, T.D., Wiebe, P.H., Hay, S., 2011. *ICES Zooplankton Status Report 2008/2009* (152 pp).



- Ollevier, A., Mortelmans, J., Aubert, A., Deneudt, K., Vandegheuchte, M.B., 2021. Noctiluca scintillans: dynamics, size measurements and relationships with small soft-bodied plankton in the Belgian part of the North Sea. *Frontiers in marine science* 8. <https://doi.org/10.3389/fmars.2021.777999>. Article 777999. Available at:
- Otero, V., Pint, S., Deneudt, K., De Rijcke, M., Mortelmans, J., Schepers, L., Martin-Cabrera, P., Sabbe, K., Vyverman, W., et al., 2023. Pronounced seasonal and spatial variability in determinants of phytoplankton biomass dynamics along a near-offshore gradient in the southern north sea. *J. of Marine Sci. and Engin.* 11, 1510. <https://doi.org/10.3390/jmse11081510>.
- Peterson, B.G., Carl, P., 2020. PerformanceAnalytics: econometric tools for performance and risk analysis. R package version 2.0.4.
- Richardson, A.J., 2008. In hot water: zooplankton and climate change. *65* (3), 279–295. Available at: <https://doi.org/10.1093/icesjms/fsn028>.
- Richlen, M.L., Morton, S.L., Jamali, E.A., Rajan, A., Anderson, D.M., 2010. The catastrophic 2008–2009 red tide in the Arabian gulf region, with observations on the identification and phylogeny of the fish-killing dinoflagellate *Cochlodinium polykrikoides*. *Harmful Algae* 9, 163–172.
- Roberts, S.D., Van Ruth, P.D., Wilkinson, C., Bastianello, S.S., Bansemmer, M.S., 2019. Marine heatwave, harmful algae blooms and an extensive fish kill event during 2013 in South Australia. *Frontiers in marine science* 6, Article 610. <https://doi.org/10.3389/fmars.2019.00610>.
- Rousseau, V., Becquevort, S., Parent, J.-Y., Gasparini, S., Daro, M.H., Tackx, M., Lancelot, C., 2000. Trophic efficiency of the planktonic food web in a coastal ecosystem dominated by *Phaeocystis* colonies. *J. Sea Res.* 43 (3–4), 357–372. [https://doi.org/10.1016/S1385-1101\(00\)00018-6](https://doi.org/10.1016/S1385-1101(00)00018-6).
- Rousseau, V., Park, Y., Ruddick, K., Vyverman, W., Parent, J.Y., Lancelot, C., 2006. Phytoplankton blooms in response to nutrient enrichment. In: Rousseau, V., Lancelot, C., Cox, D. (Eds.), *Current Status of Eutrophication in the Belgian Coastal Zone*. Presses Universitaires de Bruxelles.
- Royal Meteorological Institute (RMI), 2023. <https://www.meteo.be/nl/klimaat/klimaat-verandering-in-belgie/klimaattrends-in-ukkel/luchttemperatuur/gemiddelde/jaarlijks> (last accessed 27 July 2023).
- RStudio Team, 2023. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL. <http://www.rstudio.com/>.
- Rudis, B., 2020. Hrbthemes: additional themes, theme components and utilities for 'ggplot2'. R package version 0.8.0.
- Sahota, R., Boyen, J., Semmouri, I., Bodé, S., De Troch, M., 2022. An inter-order comparison of copepod fatty acid composition and biosynthesis in response to a long-chain PUFA deficient diet along a temperature gradient. *Mar. Biol. (Berl.)* 169 (133). <https://doi.org/10.1007/s00227-022-04121-z>.
- Schmidtko, S., Stramma, L., Visbeck, M., 2017. Decline in global oceanic oxygen content during the past five decades. *Nature* 542, 335–339. <https://doi.org/10.1038/nature21399>.
- Semmouri, I., Asselman, J., Van Nieuwerburgh, F., Deforce, D., Janssen, C., De Schampelaere, K., 2019. The transcriptome of the marine calanoid copepod *Temora longicornis* under heat stress and recovery. *Mar. Environ. Res.* 143, 10–23. <https://doi.org/10.1016/j.marenvres.2018.10.017>.
- Semmouri, I., De Schampelaere, K.A.C., Van Nieuwerburgh, F., Deforce, D., Janssen, C. R., Asselman, J., 2020. Spatio-temporal patterns in the gene expression of the calanoid copepod *Temora longicornis* in the Belgian part of the North Sea. *Mar. Environ. Res.* 160, 105037. <https://doi.org/10.1016/j.marenvres.2020.105037>.
- Semmouri, I., De Schampelaere, K., Willemsse, S., Vandegheuchte, M., Janssen, C., Asselman, J., 2021. Metabarcoding reveals hidden species and improves identification of marine zooplankton communities in the North Sea. *ICES J. Mar. Sci.* 78 (9), 3411–3427. <https://doi.org/10.1093/icesjms/fsaa256>.
- Semmouri, I., De Schampelaere, K., Mortelmans, J., Mees, J., Asselman, J., Janssen, C., 2023. Decadal decline of dominant copepod species in the North Sea is associated with ocean warming : importance of marine heatwaves. *Mar. Pollut. Bull.* 193. <https://doi.org/10.1016/j.marpolbul.2023.115159>.
- Silva, E., Counillon, F., Brajard, J., Korosov, A., Pettersson, L.H., Samuelsen, A., Keenlyside, N., 2021. Twenty-one years of phytoplankton bloom phenology in the Barents, Norwegian, and north seas. *Frontiers in marine science. Sec. Marine Biogeochemistry* 8. <https://doi.org/10.3389/fmars.2021.746327>. Article 746327. Available at:
- Tolomio, C., Moschin, E., 1994. Epilithic diatoms from different river habitats in the river dese watershed (northern Italy). *Arch. Hydrobiol.* 130 (4), 429–446.
- Van Ginderdeuren, K., 2013. Zooplankton and its Role in North Sea Food Webs: Community Structure and Selective Feeding by Pelagic Fish in Belgian Marine Waters. PhD Thesis. Ghent University, Ghent (xx, 266 pp).
- Van Heurck, A., 1884. Synopsis des diatomées de Belgique: Table alphabétique des noms génériques et spécifiques et de synonymes contenus dans l'atlas. Anvers, Henri Van Heurck, p. 120.
- Van Meel, L.L.J., 1975. La Mer du Nord M'ericionale, le Pas de Calais et la Manche. In: *Etude D'écologie Marine*. Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Principalement en ce qui Concerne le Microplankton. Vol. II Etude Planctonique (655 pp).
- Vasas, V., Lancelot, C., Rousseau, V., Jordán, F., 2007. Eutrophication and overfishing in temperate nearshore pelagic food webs: a network perspective. *Mar. Ecol. Prog. Ser.* 336, 1–14. <https://doi.org/10.3354/meps336001>.
- Verfaillie, E., 2008. Ontwikkeling en Validering van een Ruimtelijke Verspreidingsmodellen van Mariene Habitats, ter Ondersteuning van het Ecologisch Waarderen van de Zeebodem = Development and Validation of Spatial Distribution Models of Marine Habitats, in Support of the Ecological Valuation of the Seabed. PhD Thesis. Instituut voor de Aanmoediging van Innovatie door Wetenschap en Technologie in Vlaanderen/RCMG/Universiteit Gent: Brussel (207 pp Western Channel Observatory (2019)).
- von Stosch, H.A., 1977. Observations on *Bellerochea* and *Streptothecha*, including descriptions of three new planktonic diatom species. *Nova Hedwig. Beih.* 54, 113–166.
- von Stosch, H.A., 1987. Some marine diatoms from the Australian region, especially from port Phillip Bay and tropical North-Eastern Australia. II survey of the genus *Palmeria* and of the family *Lithodesmiaceae* including the new genus *Lithodesmioides*. *Brunonia* 9, 29–87.
- Wexels Riser, H., Amundsen, O., Riis, J.O., 2002. *Industry and Innovation: The Dynamics of Competitive Advantage*. Routledge.
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer.
- Wickham, H., Girlich, M., 2022. Tidy: tidy messy data. R package version 1.2.0.
- Wickham, H., Seidel, D., 2022. Scales: scale functions for visualization. R package version 1.2.0.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., et al., 2019. Welcome to the tidyverse. *J. Open Source Soft.* 4 (43), 1686. <https://doi.org/10.21105/joss.01686>.
- Wickham, H., Bryan, J., Yutani, H., Robinson, D., 2022. R for Data Science: Import, Tidy, Transform, Visualize, and Model Data. O'Reilly Media.
- Wickham, 2007. Reshaping data with the reshape package. *J. Stat. Softw.* 21 (12).
- Williams, R., Conway, D.V.P., Hunt, H.G., 1994. The role of copepods in the planktonic ecosystems of mixed and stratified waters of the European shelf seas. *Hydrobiologia* 292, 521–530.
- Wood, S.N., 2017. *Generalized Additive Models: An Introduction with R*, 2nd edition. Chapman and Hall/CRC.
- Yahia-kéfi, O.D., Souissi, S., Fernando, G., Daly Yahia, M.N., 2005. Effect of nutrient disturbances on the microphyto-plankton structure in the bay of Tunis (SW Mediterranean Sea). *Mediterr. Mar. Sci.* 6 (1), 17–34.
- Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer (ISBN 978-0-387-87457-9).