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Multimodel inference to quantify the relative importance of abiotic factors in the population dynamics of marine zooplankton

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ABSTRACT

The effect of multiple stressors on marine ecosystems remains poorly understood and most of the knowledge available is related to phytoplankton. To partly address this knowledge gap, we tested if combining multimodel inference with generalized additive modelling could quantify the relative contribution of environmental variables on the population dynamics of a zooplankton species in the Belgian part of the North Sea. Hence, we have quantified the relative contribution of oceanographic variables (e.g. water temperature, salinity, nutrient concentrations, and chlorophyll *a* concentrations) and anthropogenic chemicals (i.e. polychlorinated biphenyls) to the density of *Acartia clausi*. We found that models with water temperature and chlorophyll *a* concentration explained ca. 73% of the population density of the marine copepod. Multimodel inference in combination with regression-based models are a generic way to disentangle and quantify multiple stressor-induced changes in marine ecosystems. Future–oriented simulations of copepod densities suggested increased copepod densities under predicted environmental changes.

1. Introduction

Since the anthropocene, marine ecosystems have been exposed to changing environmental conditions, such as changing temperatures and sea level rise (Levitus et al., 2012), salinity changes (Durack and Wijffels, 2010), coastal eutrophication (Ryther and Dunstan, 1971) and an increasing amount of chemicals (Dachs and Méjanelle, 2010). Evidence is growing that these changing environmental conditions have negative effects on the biodiversity and functioning of marine zooplankton (Johnston et al., 2015). Changes in the zooplankton community structure may lower the overall functioning of the marine ecosystem as zooplankton represents an important connection in marine food webs by linking autotrophs and higher trophic levels. For example, zooplankton contributes significantly to biogeochemical cycles, most notably by grazing on phytoplankton and by exporting carbon to deep-sea through their faecel pellets (Bathmann et al., 1987). However, in spite of their key role in marine ecosystems, the combined effects of environmental and human-induced stressors and their relative contribution to the total impact on marine zooplankton have been poorly assessed so far (Crain et al., 2008; Johnston et al., 2015). Although there is an increasing number of studies that investigate and review the impact of multiple stressors on marine environments (e.g. Gunderson et al., 2016; Johnston et al., 2015), we still face a poor quantification of their combined effects as chemical pollution is one of the least-studied stressors in ecology (Lawler et al., 2006; Rockstrom et al., 2009).

Most of the multiple stressor-related research has been performed in laboratories with unclear potential for extrapolation towards in situ conditions. A big advantage of laboratory experiments is that model species are often kept in optimal conditions (temperature, nutrients, light etc.) to isolate the effects of the stressor in question (e.g. Walker et al., 2001). The inevitable consequence of those standard test conditions is that the conversion of laboratory-based conclusions towards field conditions is hampered as organisms rarely experience those optimal conditions in their natural settings (Holmstrup et al., 2010). In addition to these laboratory-specific conditions, also the development stage of the organisms (i.e. for zooplankton: larval nauplius, juvenile copepodite, and adult) can alter their response making intercomparability between studies more complex especially if different development stages have been used in different laboratory experiments. For example, Mayor et al. (2015) found that adult *Calanus* copepods (Crustacea) remain unaffected by projected environmental changes (i.e. ocean acidification and warming). However, younger development

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stages of zooplankton are known to be more sensitive to ocean acidification (Cripps et al., 2014). Another advantage of using field data is that natural background variation of bottom-up drivers of marine ecosystems is implicitly included in the results that are obtained (Coull and Chandler, 1992). In this context, natural variations in the physical-chemical conditions of marine sediments and surface waters due to, for example, seasonal and daily cycles of solar radiation as well as tidal cycles, continuously alter the multiple stressor environment. Even though such continuously changing multiple stressor environment can have both direct and indirect effect to the species living there, it is not easily mimicked under laboratory conditions. In terms of indirect effects, a well-known example relates to the biological pump, which is the transfer of plankton-bound organic chemicals to deeper water and sediment. When phytoplankton blooms, dissolved-phase organic chemicals can be depleted while sediment concentrations of these chemicals increase. The latter is a seasonal process and results in variable concentrations of chemicals in the environmental compartments (Newman and Unger, 2003; Everaert et al., 2015a). Hence, when using in situ data, the natural background variation is implicitly embedded. In our opinion, depending on the research question, the use of in situ data can thus have advantages over laboratory experiments. However, regardless the context and the actual aim of the research, most of the information that is available to date is still based on experimental studies (Johnston et al., 2015) that rarely incorporated natural physical-chemical variation into their designs (Gunderson et al., 2016). Moreover, multiple–stressor related research that did include chemical contaminant effects often dealt with marine pelagic phytoplankton and it is not clear to what extent that these findings are valid for higher trophic levels. Indeed, out of the 264 studies that were reviewed by Johnston et al. (2015), 79 focused on pelagic primary producers, and only 19 studies were dealing with marine zooplankton. Although phytoplankton related research may yield interesting quantifications of multiple stressor environments under laboratory conditions, it remains unclear what the real outcome will be for species living at higher trophic levels in the marine environment.

Generalized additive models (GAMs) and the Akaike Information Criterion (AIC) model selection has been often used to infer relationships between environmental conditions and the biological responses. In many often these studies conclusions were based on the minimum adequate model, i.e. the model that contains the minimum number of predictors that satisfies some criterion (e.g. statistical significance; Whittingham et al., 2006). However, inappropriate focus on a single best model may result in biased modelling outcomes as explained by Whittingham et al. (2006). In this context, multimodel inference (Burnham and Anderson, 2002) has a lot of potential to avoid the pitfalls of the stepwise selection of regression-based modelling techniques. Multimodel inference has already provided useful quantifications of the relative importance of environmental conditions in terrestrial and freshwater ecology, but in spite of its robustness, i.e. no reliance on a single model, it was only applied few times in marine science. For example, Boyce et al. (2014) used multimodel inference with generalized additive models (GAMs) to infer long-term trends from global chlorophyll concentrations. However, as it was not their aim, Boyce et al. (2014) did not use the multimodel inference to unravel the multiple stressor conditions through the quantification of the relative importance of each of these environmental drivers of chlorophyll production. Bekkby et al. (2009) used GAM combined with multimodel inference to identify the most important variables to explain the distribution of kelp forest, but did not disentangle the contribution of each individual variable. Chang et al. (2012) used multimodel inference to investigate the growth of marine crustaceans and to determine the effect of environmental stress on their growth pattern. However, these authors did not use GAMs. As such, to our knowledge in the present research, we will present for the first time the use of multimodel inference with GAMs to quantify the relative importance of multistress conditions on marine zooplankton.

In the present research, we tested if we could apply multimodel inference on GAMs to quantify the effect of multiple stressors on marine ecosystems. Focus is on the Belgian part of the North Sea as it has a long history of chemical pollution and is globally amongst the most intensively monitored marine regions (Roose et al., 2011). We quantify the relative importance of the environmental conditions (water temperature, salinity, nutrient concentrations, chlorophyll *a* concentrations and concentrations of polychlorinated biphenyls) to the zooplankton population dynamics. To do so, we used a novel methodology (i.e. multimodel inference with generalized additive modelling) and applied it to the specific case of monthly zooplankton abundance data collected in 2009 and 2010 close to the sea harbor of Zeebruges (Belgium).

2. Materials and methods

2.1. Biological and physical-chemical data

We used zooplankton data that were collected by Van Ginderdeuren (2013) and that were retrieved from the biology data portal of the European Marine Observation and Data Network (EMODnet, https://doi.org/10.14284/55). In 2009 and 2010 Van Ginderdeuren (2013) sampled the zooplankton community monthly at ten sampling locations in the Belgian part of the North Sea (BPNS) with one station being close to the harbor of Zeebruges (51°22′30″N; 3°11′15″E). Samples were taken with a WP2 net (200 μm mesh size), fitted with a flow meter, which was towed from bottom to surface (Van Ginderdeuren, 2013). After fixing and preserving the samples in a 4% formaldehyde solution, taxa were identified to species level. Species densities were expressed as the amount of individuals of a species per m^3. For a full inventory of the zooplankton community in the BPNS we refer to Van Ginderdeuren (2013). Copepods are a key component in the pelagic food web of the BPNS and play a key role in the dynamics of economic important fish stocks (e.g. mackerel; Van Ginderdeuren et al., 2014). In the BPNS *A. clausi* (Giesbrecht, 1889) is one of the most prevalent calanoid species as confirmed during the sampling campaign. *A. clausi* is a neritic to oceanic species inhabiting near-surface water layers and is one of the most abundant copepod species in the North Sea (Van Ginderdeuren et al., 2014). Being an omnivorous species, *A. clausi* feeds on phytoplankton, microzooplankton, copepod eggs and nauplii (Wiadnyana and Rassoulzadegan, 1989). As the research vessel was not able to go out for sampling in two months due to bad weather conditions, in total 22 records (= 24 months of sampling − 2 months) of *A. clausi* are available (Table 1). These biological data were combined with oceanographic variables (see further) in one dataset based on sampling location and sampling time and a summary of the data is given in Table 1.

Water samples to quantify the water temperature (TEMP), salinity (SAL), chlorophyll *a* concentrations (CHFLa) were collected simultaneously with the zooplankton data (Table S1). Concentrations of dissolved inorganic nitrogen (DIN; sum of concentrations of ammonium-N,

Table 1
Summary of the dataset used to quantify the relative importance of environmental variables to the density of *Acartia clausi*, a marine zooplankton species. Apart from *A. clausi* (n = 22), for each variable 24 (24 months of sampling) records were available.

Variable	Abbreviation	Unit	Min. value	Max. value
Acartia clausi	*A. clausi*	# individuals per m^{-3}	10.7	685.9
Surface water temperature	TEMP	°C	5.27	26.23
Chlorophyll a	CHFLa	$mg\,m^{-3}$	1.08	13.64
Dissolved inorganic nitrogen	DIN	$mmol\,L^{-1}$	6.10	74.6
Silicon	Si	$mmol\,L^{-1}$	3.12	31.08
Salinity	SAL	psu	31.74	32.76
Polychlorinated biphenyls	PCB	$\mu g\,L^{-1}$	$1.05 * 10^{-4}$	$5.48 * 10^{-4}$