



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 faecal 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 of 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 Zeebrugge (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 Zeebrugge (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 m³. 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
<i>Acartia clausi</i>	<i>A. clausi</i>	# individuals per m ⁻³	10.7	685.9
Surface water temperature	TEMP	°C	5.27	26.23
Chlorophyll <i>a</i>	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	µg L ⁻¹	1.05 * 10 ⁻⁴	5.48 * 10 ⁻⁴

nitrite-N and nitrate-N), silicate (Si) and polychlorinated biphenyls (PCBs) were queried from the Belgian Marine Data Centre (BMDC, 2016; Table S1). Dissolved inorganic nitrogen concentrations were used to represent nitrogen as DIN is an important factor in the regulation of the primary production (De Galan et al., 2004; Malerba et al., 2012). Silicate was chosen to represent silicon concentrations as for some phytoplankton species, in particular diatoms, Si is an essentiality (Rousseau et al., 2002). Note that in the BPNS the availability of Si is often limiting the diatom growth (Muylaert et al., 2005). When this situation occurs, the excess of nitrogen and phosphorous can lead to blooms of dinoflagellates such as *Phaeocystis globosa*. Despite its high levels of CHFLa, *P. globosa* is a poor source of energy for higher trophic levels (and copepods in particular). To account for this, we calculated the molar ratio between DIN and Si as in Turner et al. (1998). If the DIN/Si ratio is low (i.e. < 1:3) conditions are favorable for diatoms. On the contrary, high DIN/Si (> 1:1) are beneficial for dinoflagellates which are a poor food source for copepods (Turner et al., 1998). The organic chemicals included concentrations of seven PCBs (i.e. PCB 28, PCB 52, PCB 101, PCB 118, PCB 138, PCB 153 and PCB 180) which were reported to be of concern in the selected study area (Ghekiere et al., 2013). In the BPNS, PCBs were measured in the sediment fraction < 63 μm (reported as $\mu\text{g g dw}^{-1}$) and the organic carbon – water partitioning coefficient and a 2% organic carbon content of the sediment (Zaborska et al., 2008) was used to convert sediment concentrations to aqueous concentrations (i.e. $\mu\text{g L}^{-1}$; Table S2). The selected PCB congeners are often used as model compounds to study the environmental behavior and ecological effects of hydrophobic chemicals (De Laender et al., 2010) and listed in the priority list of the convention for the protection of the marine environment of the North-East Atlantic (OSPAR convention).

2.2. Multimodel inference with generalized additive models

To quantify the relative importance of abiotic variables on the density of *A. clausi* in Belgian coastal waters, we applied GAMs. GAMs are more powerful and a more flexible alternative for the traditionally used generalized linear models (GLMs). The main advantage of GAMs is that they do not require the assumption of a fixed functional form, and thus more complex dynamics can be captured (Hastie and Tibshirani, 1986). GAMs can, as an extension of GLMs, estimate linear trends as well as non-monotonic responses such as seasonal cycles. As changes in zooplankton abundances can span several orders of magnitude in Belgian marine waters, GAMs were very well suited to analyze the data of the present research. Covariates used to model the trends were: CHFLa, TEMP, SAL, DIN/Si ratio, and PCBs. In the present research, a complete version of the GAM that incorporated each of the oceanographic as well as the pollution variables (listed in Table 1) was defined as:

$$\log_{10}([Acartia\ clausi]) = b_x + f_{1,x}(\text{CHFLa}) + f_{2,x}(\text{TEMP}) + f_{3,x}(\text{SAL}) + f_{4,x}\left(\frac{\text{DIN}}{\text{Si}}\text{-ratio}\right) + f_{5,x}(\text{PCB}) + \varepsilon_x \quad (1)$$

[*Acartia clausi*] is the abundance of *A. clausi* measured at one station close to the harbor of Zeebrugge. A model-specific intercept is b_x , and $f_{i,x}$ ($i = 1$ to 5) are predictor-specific smooth functions (cubic splines with maximum four degrees of freedom) describing the partial additive effect of the predictor variable on the abundance of *A. clausi*. Note that the model as formulated in Eq. (1) is the full version of the GAM. While running the multimodel inference every possible combination of predictors will be implemented and model fit will be quantified (see further). A normal distributed and independent noise term is ε_x (Eq. (1)). Additive models were fitted using the *mgcv* package in R (R Development Core Team R, 2016).

The relative importance of predictors has often been quantified based on the “best” model using a stepwise testing procedure (e.g. Everaert et al., 2016). Variables in that “best” model are considered

important while excluded variables are considered not important. However, this may be too simplistic. Often, while the “best” model (in terms of lowest AIC) has the highest probability, its weight is often not substantially larger than the weight of the next rated models, which means that multiple models are nearly equally plausible (Burnham and Anderson, 2004). A more objective way to assess the importance of input variables is by inferring all possible models from the candidate set (Burnham and Anderson, 2002). Therefore, based on multimodel inference, we measured how much better the best approximating model was compared to the other models. To do so, we calculated the differences between the AIC_c of the best model and the AIC_c for each of the other models (Symonds and Moussalli, 2011). Note that the AIC_c is derived from the AIC with a correction for small sample sizes, and can also be used when the number of predictors is a relatively large fraction of the sample size (Hurvich and Tsai, 1989).

A first metric to quantify the relative strength of each candidate model was based on the evidence ratio (ER), which was calculated as:

$$ER = \frac{e^{-\frac{1}{2} * \Delta_{\text{best}}}}{e^{-\frac{1}{2} * \Delta_i}} = e^{\frac{1}{2} * \Delta_i} \quad (2)$$

where Δ_i is the absolute difference between the AIC_c of the best model and the AIC_c of model $_i$ and Δ_{best} is the difference for the best ranked model (i.e. = 0). The ER quantifies the model selection uncertainty and the weight of evidence for each model, or in other words how likely it is that the best model is better than model $_i$.

The Akaike weight (w_i) for a given model $_i$ was a second metric to quantify the relative strength of each candidate model, and was calculated as:

$$w_i = \frac{e^{-\frac{1}{2} * \Delta_i}}{\sum_{r=1}^R e^{-\frac{1}{2} * \Delta_{i_r}}} \quad (3)$$

where $\Delta_i = |\text{AIC}_c \text{ best model} - \text{AIC}_c \text{ model}_i|$; and where the denominator is the sum of these differences of all models in the set of models that have been tested (Δ_{i_r}). As such, the Akaike weight of model $_i$ is the weight of evidence that model $_i$ is the best model out of all models. The relative importance of a certain variable was quantified by summing the Akaike weights for each model in which that variable appears. So, a variable that shows up in lots of models with large weights will receive a high importance value and will tend towards 1. The higher the summed Akaike weights, the higher the probability that the corresponding variable is important (Burnham and Anderson, 2002). We used a confidence set of best models which is based on the 95% of the best-ranked models (the models which cumulative Akaike weight is smaller than or equal to 0.95; Symonds and Moussalli, 2011) to quantify relative importance of each variable. The latter means that this confidence set of models is the smallest subset of candidate models for which the Akaike weights sum to 0.95. Hence, this set includes those models for which we are 95% confident that the set contains the best approximating model to the true model if the data were to be collected again under the same circumstances (Whittingham et al., 2009). The summed Akaike weights of each variable are plotted in a bar chart. In this bar chart a vertical red line is drawn at 0.80 (on a scale between 0.00 and 1.00), which is an arbitrary cut-off to differentiate between important and less important variables (Whittingham et al., 2009; Terrer et al., 2016).

To illustrate the actual improvement of the model predictions when adding an extra predictor to the model configuration, we prepared a multi-panel plot as in Deschutter et al. (2017). In this multi-panel plot, we visualized the predicted (red line) and the observed densities (black dots) of *A. clausi* against the sampling date. The 95% confidence interval is fitted as a grey zone around the model fit. In the first panel, predictions are based on the most important predictor according to the Akaike weights (cfr. bar chart). In the second panel, predictions are based on the two most important predictors, i.e. the two top variables in the bar chart. We continue this process until all variables are in the

model, and by doing so we illustrate the added value of each predictor to the model.

2.3. Simulations

Multimodel inference was used to identify and quantify the important environmental variables for zooplankton densities (cfr. 2.2). Based on the outcome of the multimodel inference, we selected the best configuration to perform future-oriented, scenario-based simulations of the densities of *A. clausi*. In these simulations we compared the situation of the year 2009 with simulations performed for the year 2050. The scenarios used were based on the IPCC (2007) for surface water temperature, predictions of Breivik et al. (2007) for PCBs, coastal management plans for concentrations of DIN, Si and CHFLa and predictions of Durack et al. (2012) for salinity changes. For example, regarding surface water temperature changes, we assumed a year-round increase of 1 °C and 2 °C according to scenarios RCP 2.6 and RCP8.5 of the IPCC (2007). For the potential future changes in CHFLa concentrations, we followed three tracks. First, according to Boyce et al. (2010), there is a global decrease of phytoplankton biomass of about 1% per year. Hence, if we pursue this reasoning until the year 2050 this means that the CHFLa levels will be at about 70% of the current day levels. However, specifically at the North Sea, Edwards et al. (2001) noted an increasing trend of phytoplankton biomass. Therefore, regarding our second track for simulated CHFLa concentrations, we assumed an increase in phytoplankton biomass of 1% per year. The latter would mean that by 2050, CHFLa levels will be at about 142% of the current day levels. Finally, we also considered a third CHFLa scenario in which the concentrations remained unchanged compared to the levels of 2009.

3. Results and discussion

3.1. Relative contribution of predictors to the abundance of *Acartia clausi*

Based on multimodel inference with GAMs we quantified the relative importance of environmental variables to the density of *A. clausi*, a marine copepod species. We found that CHFLa concentrations and TEMP were the most important predictors to explain the variability of density of *A. clausi* as their summed Akaike weights exceed 0.80 (Fig. 1), which is used as a cut-off to differentiate between important and less important variables. The best model contained only CHFLa and TEMP and had a w_i of 0.535 (Table 2), which must be interpreted as that there is 53.5% chance that a model including CHFLa and TEMP as covariates is truly the best approximating model. This finding is confirmed based on the evidence ratio (ER), i.e. the first model (CHFLa and TEMP) is 2.6 and 4.8 times more likely to be the best approximating model than the second (CHFLa + TEMP + DIN/Si) and third model (CHFLa + TEMP + SAL), respectively (Table 2). An ER lower than 2 is a threshold often used to discriminate between models that are equally plausible (Symonds and Moussalli, 2011).

As *A. clausi* is a thermophilic species (Corkett and McLaren, 1979) it was expected that water temperature would be amongst the most important predictors (Fig. 1). The water temperature in spring is one of the main regulators of the reproduction rate of *A. clausi*, i.e. higher temperatures shorten the development time and hence stimulate population growth (Landry, 1975; Chinnery and Williams, 2004). This ecological feature is clearly represented in our analysis as the smoother for temperature shows an overall positive trend, which suggests that higher water temperatures stimulate the abundance of *A. clausi* (Fig. S1). Moreover, these findings are in line with Zervoudaki et al. (2014) reporting positive effects of warming (16 °C to 20 °C) on the respiration and excretion rate of *A. clausi*. The fact that Garzke et al. (2016), found that the abundance and biomass of adult copepods was negatively affected by warming (9 °C to 15 °C), and that this effect was most obvious for nauplii and copepodites seems contradictory to our results. However, that is not the case, since the smoother for temperature is negative

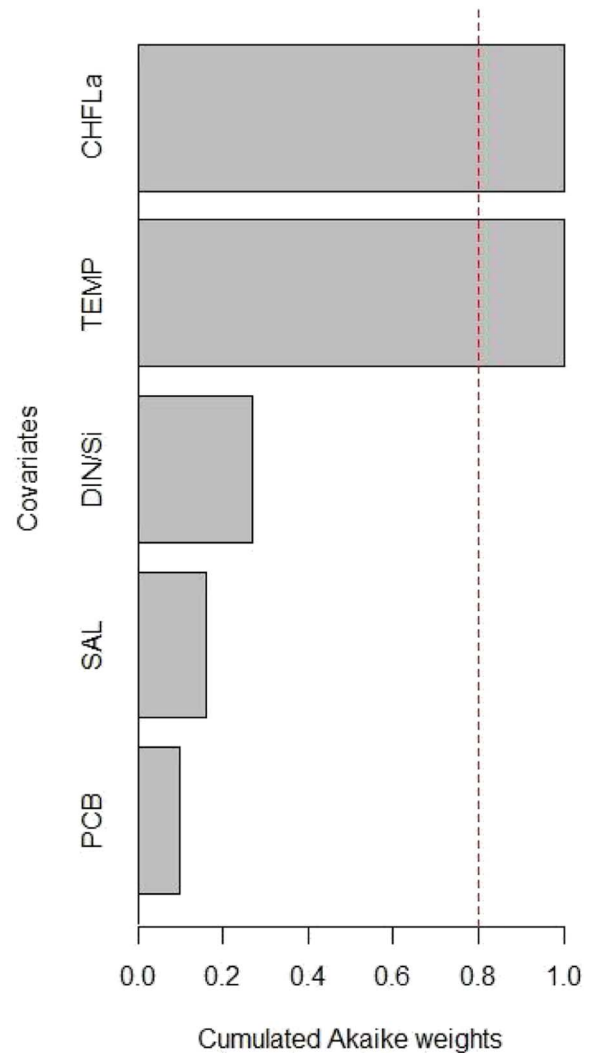


Fig. 1. Relative importance of the chlorophyll *a* concentration (CHFLa; 1.00), water temperature (TEMP; 1.00), ratio between dissolved inorganic nitrogen and silicate (DIN/Si; 0.27), salinity (SAL; 0.16), and concentrations of polychlorinated biphenyls (PCBs; 0.10) on the density of *Acartia clausi* in the Belgian part of the North Sea. A variable that shows up in models with large weights will receive a high summed Akaike weight and is considered important. The vertical red line is drawn at 0.80, which is used as a cut-off to differentiate between important and less important variables. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

95% confidence set of best-ranked models (the models whose summed Akaike weight, $\text{acc } w_i \leq 0.95$) examining effect of abiotic variables on the density of *Acartia clausi* in Belgian marine waters. Variables assessed are water temperature (TEMP), chlorophyll *a* concentration (CHFLa), ratio between dissolved inorganic nitrogen and silicate (DIN/Si), salinity (SAL), and concentrations of polychlorinated biphenyls (PCBs). The metrics used to quantify the relative strength of each model are based on the difference between the Akaike Information Criterion for small datasets (AIC_c) of the best model and the AIC_c of model_{*i*} (Δ_i). The evidence ratio (ER) quantifies how likely it is that the best model is better than model_{*i*}.

Candidate models	AIC_c	Δ_i	w_i	$\text{acc } w_i$	ER
TEMP + CHFLa	17.967	0.000	0.535	0.535	
TEMP + CHFLa + DIN/Si	19.904	1.937	0.203	0.738	2.63
TEMP + CHFLa + SAL	21.091	3.124	0.112	0.851	4.77
TEMP + CHFLa + PCB	21.661	3.694	0.084	0.935	6.34
TEMP + CHFLa + SAL + DIN/Si	22.854	4.887	0.046	0.981	11.51
TEMP + CHFLa + PCB + DIN/Si	24.695	6.728	0.019	1.000	28.90

in the temperature range tested by Garzke et al. (2016) (Fig. S1). Overall, regarding the effect of temperature our model results confirm what has been found based on laboratory experiments. In addition to the smoother of temperature, also the smoother of CHFLa suggests a positive effect of increasing CHFLa concentrations on the abundance of *A. clausi* (Fig. S1). This pattern is explained by the fact that increased food availability will stimulate the population growth of *A. clausi*. However, note that the standard deviation around the smoother of CHFLa increases considerably when exceeding 5 mg L^{-1} . This indicates that uncertainty of the positive effect of CHFLa increases above this threshold (Fig. S1). Indeed, a continued increase of CHFLa may be related to a bloom of *P. globosa* in Belgian coastal waters. *P. globosa* is a dinoflagellate species which forms colonies that are resistant to zooplankton grazing, and are thus not a good source of energy for higher trophic levels such as *A. clausi* (Hamm et al., 1999; Schoemann et al., 2005). After the spring diatom bloom large amounts of nitrogen (N) and phosphorus (P) are available and used by the dinoflagellate *P. globosa* to bloom (Muylaert et al., 2006). In general, increasing levels of CHFLa are suggested to have a positive effect on the density of *A. clausi*, but the transition from the nutritious spring diatom bloom to the inedible *P. globosa* bloom is not distinguishable by looking at CHFLa alone (Muylaert et al., 2006). The latter is likely to be the reason for having the ratio between DIN and Si (DIN/Si) as the third most important predictor variable (Fig. 1). Based on the Akaike weights and the ER, CHFLa concentration and TEMP were selected as the most important predictors for the abundance of *A. clausi* (Fig. 2). A model that only uses TEMP as predictor (Fig. 2A) results in a seasonal cycle of *A. clausi* that

explains 47.4% of the variability in the data (Fig. 2A). When adding CHFLa as a predictor 73.1% of the deviance is explained (Fig. 2B). Adding DIN/Si ratio, SAL and PCB as predictor does only marginally (from 73.1% to 77.6%) improve the model predictions (Fig. 2C–E).

We found that PCBs were the least important factor when modelling *A. clausi* as their cumulated weight was only 0.10 (on a scale between 0.00 and 1.00) which is considerably lower than the threshold of 0.80 (Fig. 1). Moreover, the difference in deviance explained between a model including PCBs (77.6%; Fig. 2E) and without PCBs (77.0%; Fig. 2D) suggests that the relative contribution of PCBs is low ($< 1\%$; Fig. 2). As such, PCBs are suggested not to be very important in the population dynamics of *A. clausi*. Although a different methodology was used, these findings are in line with Everaert et al. (2015b), who reported only a small growth limitation due to hydrophobic chemicals of marine phytoplankton in the BPNS (ca. 1%). In the present research, focus was on the zooplankton, i.e. a trophic level above phytoplankton used in Everaert et al. (2015b). As such, due to the bioaccumulative properties of PCBs (Escher et al., 2011), we had expected that the calculated contribution of PCBs could have been higher than those calculated for phytoplankton. However, it is important to note that only concentrations of PCBs have been included in our analyses. PCBs are often used as model compounds for anthropogenic chemicals in the marine environment, but we acknowledge that currently about 100,000 chemicals are available on the EU market (Roose et al., 2011) of which a large group have a totally different mode of action than PCBs. In this context, Crain et al. (2008) synthesized 171 studies that manipulated two or more stressors in marine and coastal systems and suggested that

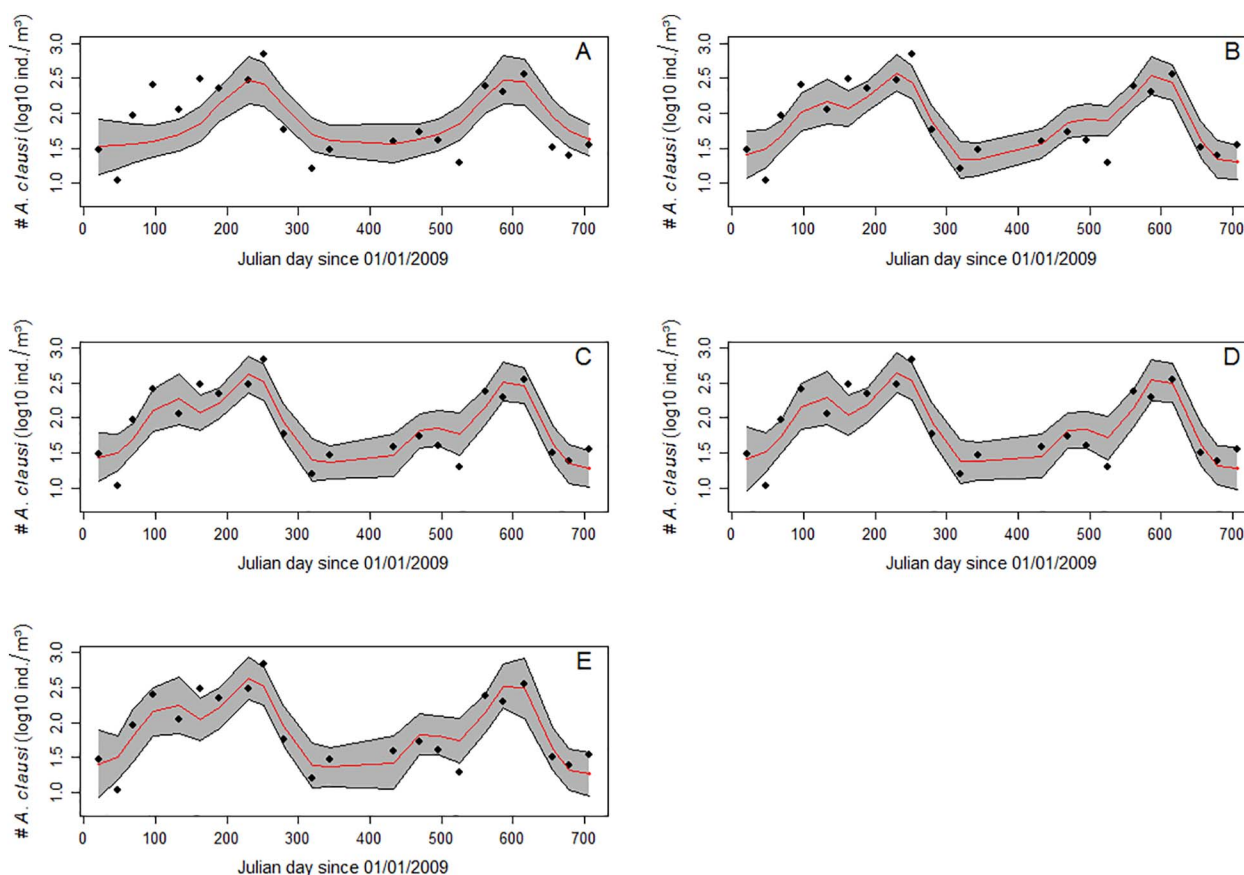


Fig. 2. Predicted (red line) versus observed (black dots) abundances of *Acartia clausi*. Five different model configurations have been used based on the outcome of the summed Akaike weights (cfr. Fig. 1). Hence, the first configuration models the densities of *A. clausi* solely based on water temperature, the second configuration consists of water temperature and chlorophyll *a* concentrations (B), the third of water temperature, chlorophyll *a* concentrations, and the ratio between DIN and Si (C), the fourth of water temperature, chlorophyll *a* concentrations, the ratio between DIN and Si, and salinity (D) and the fifth of water temperature, chlorophyll *a* concentrations, the ratio between DIN and Si, salinity and concentrations polychlorinated biphenyls (E). Deviance explained is 47.4%, 73.1%, 75.9%, 77.0%, and 77.6% for panel A, B, C, D, and E respectively. The grey polygon delimits the 95% confidence interval around the predictions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

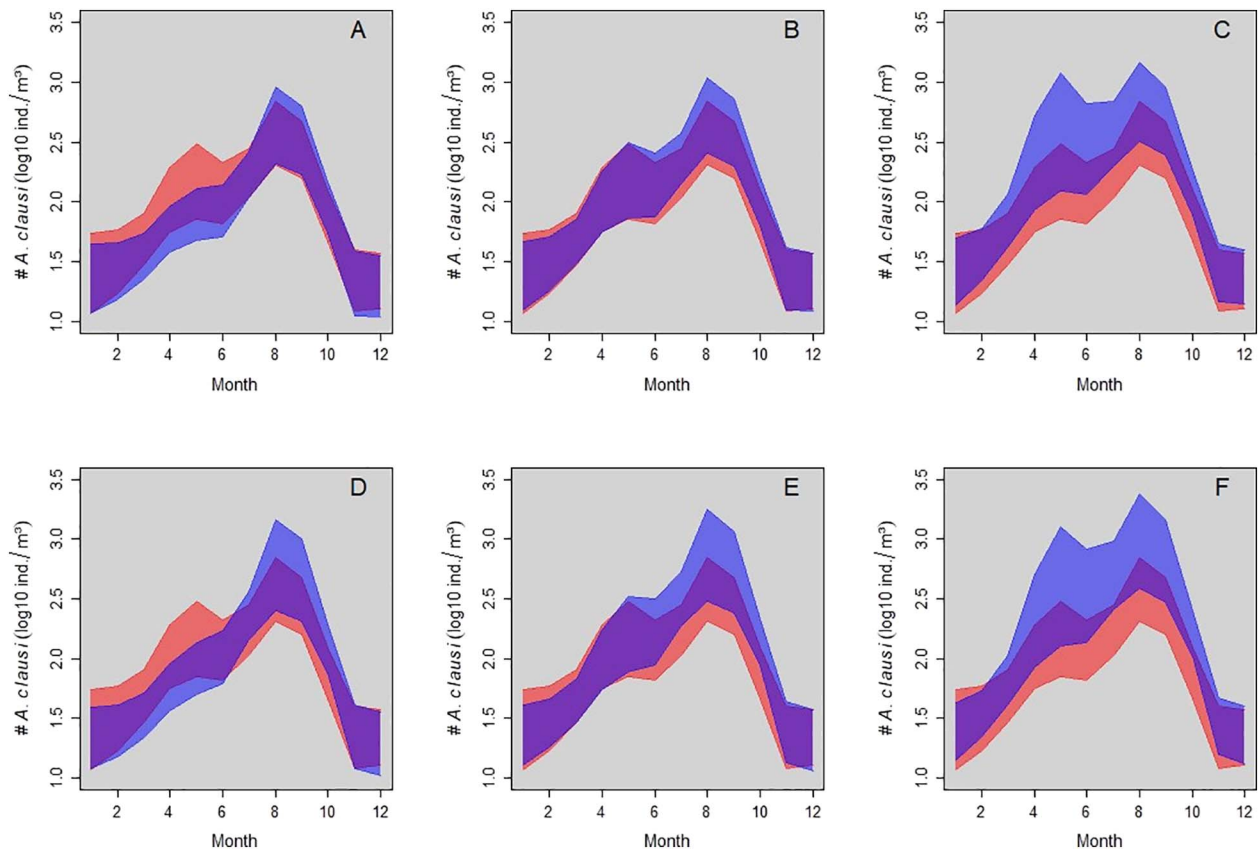


Fig. 3. Simulated densities of *Acartia clausi* (blue polygons) based on water temperature and chlorophyll *a* concentrations. The red polygon represents the densities of *A. clausi* in 2009 and are shown for comparison. To perform simulations for the year 2050, six scenarios have been used; a year-round increase of the water temperature with 1 °C by 2050 according to the RCP2.6 scenario (panels A, B and C), a year-round increase of the water temperature with 2 °C by 2050 according to the RCP8.5 scenario (panels D, E and F); a 1% yearly decrease of the phytoplankton biomass suggesting that chlorophyll *a* levels will be at 70% of the current day levels by 2050 (panels A and D), a constant phytoplankton biomass suggesting that chlorophyll *a* levels by 2050 will be the same as the current day levels (panels B and E), and a 1% yearly increase of the phytoplankton biomass suggesting that chlorophyll *a* levels will be at 142% of the current day levels by 2050 (panels C and F). The purple colour indicates the overlap between the red and blue polygons. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

synergistic interactions are common in nature and should be taken into account in ecological studies. As not a lot of research is done yet on the combined toxic effects of pollutants on marine zooplankton, it is difficult to predict how persistent organic pollutants (POPs) will affect marine copepods. Therefore, in future research we suggest not only to include conventional OSPAR priority substances, but also emergent compounds that may cause adverse ecological effects such as pharmaceuticals (Backhaus, 2014).

Although the impact of the hydrophobic compounds (i.e. PCBs) seems limited, our results should be carefully interpreted as a slight restructuring in the food web due to changing environmental conditions may change the trophic ratio (Chust et al., 2014) and/or cause a mismatch in seasonal events of different species. These changes are very likely to alter marine ecosystem functioning and services (Richardson and Schoeman, 2004) as a small deviance of a few percentages of the zooplankton densities due to the presence of PCBs may have serious implications for the entire planktonic community. A change in zooplankton densities of a few percentages may already lead to a competitive (dis)advantage for particular species. As such, although the present research yields interesting quantifications, patterns and trends for one single marine copepod species, it is necessary to further validate the results in a mesocosm experiment (i.e. under realistic test conditions, including multiple species and different trophic levels) or under field conditions. In this context, we acknowledge that the dataset was small as only one marine copepod has been assessed that was sampled in two years at one sampling location. Different (copepod) species may react differently to changing environmental conditions (Deschutter et al., 2017), and due to these species-specific stressor interactions,

extrapolation to other species (or regions) should be avoided. Therefore, we encourage future studies to use larger sets of data both in terms of spatial and temporal coverage.

3.2. Simulations

We found that a year-round temperature increase of 1 °C and 2 °C of marine surface water will generally increase the zooplankton abundance as long as sufficient CHFLa is present (Fig. 3). Indeed, under the scenario that CHFLa levels are at 70% of the current day levels by 2050, the simulations suggest that the densities of *A. clausi* will be lower (−36% in case of a 1 °C temperature increase and −32% in case of a 2 °C temperature increase) from January to June than the current day levels (Fig. 3A and D, respectively). Between July and December, the decreased abundance of *A. clausi* due to less availability of CHFLa (70%) is compensated by the increase in *A. clausi* due to the temperature increase (Fig. 3A and D). The latter suggests that the diminished food availability due to a 30% reduction of CHFLa can be compensated in summer and autumn when the water temperature is most optimal for the growth of copepods. Under the second scenario, i.e. a 1 °C and 2 °C temperature increase and an increase of CHFLa concentrations up to 142% of the current day levels, we found that the densities of *A. clausi* will be considerably higher in the entire seasonal cycling (+90% and +139% on average; Fig. 3C and F, respectively). Under the intermediate scenario, in which the CHFLa concentrations are assumed unchanged between 2009 and 2050, a 1 °C increase of the surface water temperature would mean a 25% increase of the zooplankton abundance (Fig. 3B), and 2 °C increase of the temperature is

expected to increase the abundance of *A. clausi* with 60% (Fig. 3E). In both cases the increased abundance of *A. clausi* concentrates from July to October. Overall, increasing surface waters temperatures are expected to rise zooplankton abundances which corroborates with findings in literature. For example, Lewandowska et al. (2014) implemented projections from a global circulation model in a mesocosm experiment to examine the effect of temperature in a multi-trophic plankton community. They observed that warming treatments had a positive effect on the phytoplankton biomass and that the density of copepods was higher in warm mesocosms due to an accelerated growth rate. These observations seem in contrast with Chust et al. (2014) who estimated a global decrease of 11% in zooplankton biomass in the event of increased mean sea surface temperature (+2.29 °C). However, when specifically looking at the Belgian marine waters, findings of Chust et al. (2014) suggest an increase of both the mean phytoplankton and zooplankton biomass under scenario A1B of the IPCC. As such, these results corroborate with the conclusions of Lewandowska et al. (2014) and those of the present research. Although the trends found in the present research are supported by literature, we acknowledge that a doubling (i.e. 90–139% increase; Fig. 3C and F) of the density of *A. clausi* compared to the current day levels might be unrealistic. The main reason is that we have used statistical models to examine our research questions. Although it is very likely that increased levels of CHFLa will result in increased feeding rates and densities of *A. clausi* (Conover, 1956), at a certain point, e.g. once the feeding rate of the copepods reach their maximum levels, there is no further increase possible (Almeda et al., 2010). Conventional statistical models are often biologically naïve, in the sense that they do not take physiological limits into account (Serra-Diaz et al., 2013). Statistical models (such as for example GAMs) treat the time series data as a string of numbers ignoring any quantitative and qualitative information about the ecological system that has generated the time series (Kendall et al., 1999). Therefore, mechanistic models as those used by Everaert et al. (2015a, 2015b), which in their simplest form are composed of a set differential equations that are coupled according to food-web interactions (Franco et al., 2016), might be better alternatives if one is interested in the ecological mechanisms underlying the field data. Such mechanistic models also allow to include species interactions which are also likely to be altered under changing environmental conditions (Pacifci et al., 2015).

In conclusion, in the present research we have applied a novel technique to disentangle and quantify the relative importance of multiple stressors on the abundance of a marine copepod *A. clausi*. To do so, we applied multimodel inference with GAMs to a specific case of Belgian marine waters. We found that mainly surface water temperature and chlorophyll *a* concentrations play a key role and that the impact of the hydrophobic compounds (i.e. PCBs) was limited. The methodology that was implemented in this research was appropriate for answering our scientific questions, hence in future research multimodel inference with GAMs can be used to assess the similar data that have been collected at a wider spatial and temporal coverage. To unravel the ecological mechanisms underlying the field data, we recommend to use mechanistic modelling.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jmarsys.2018.02.009>.

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