

# Experimental evidence for shaping and bloom inducing effects of decapod larvae of *Xantho poressa* (Olivi, 1792) on marine phytoplankton

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*To study zooplankton–phytoplankton relationships in the diatom-dominated plankton communities of the northern Adriatic we performed feeding experiments with diatoms and zoea I larvae of the brachyuran Xantho poressa. We found that zoea I of X. poressa feed on diatoms of different forms (centric, pennate, colony forming, single celled, with or without setae) and size classes. In a laboratory setup, we presented the zoeas with a mix of diatom species similar to communities observed during blooms regularly found in the northern Adriatic. We report that the grazing activity resulted in a decrease of the relative abundance of the toxic diatom Pseudo-nitzschia calliantha. For the colonial, bloom-forming diatom Skeletonema marinoi our results show a chain length reduction in the presence of zoea I. Of particular interest is the observation that the presence of larvae also resulted in an increased growth rate and abundance of S. marinoi, which resembles bloom induction by grazer presence.*

**Keywords:** *Xantho poressa*, grazing, Decapoda, zoea I, *Skeletonema marinoi*, *Pseudo-nitzschia calliantha*, *Pleurosigma planctonicum*, *Chaetoceros didymus*, *Bacillaria paxillifera*, diatoms, chain length, bloom induction

Submitted 30 April 2018; accepted 4 June 2018; first published online 26 July 2018

## INTRODUCTION

Marine phytoplankton is thought to be under constant predatory pressure, and zooplankton grazing is considered a major part of this pressure. Zooplankton not only has an adverse effect on microphytoplankton abundances but also is reported to have a shaping effect on the microphytoplankton community composition (Strom *et al.*, 2001). Selective feeding behaviour and the species-specific adaptations of microphytoplankton to evade grazing are reported to play a major role in the selection for successful phytoplankton bloom formation (Irigoiien *et al.*, 2005).

Grazing can be a major mechanism in the context of benthic-pelagic coupling as well (Mussap & Zavatarelli, 2017). For some benthic decapod species filter feeding of adults on plankton is known. Some sessile benthic filter feeders are reported to have significant impacts on the phytoplankton community and its composition (Lucas *et al.*, 2016). Other filter feeders might have different interactions with the phytoplankton surrounding them. For a sponge species

(*Aplysina aerophoba*, Nardo 1886) virtually no grazing on eukaryotic phytoplankton could be observed (Pfannkuchen *et al.*, 2009). However, carbon uptake from the water column was shown for two Mediterranean sponge species including *A. aerophoba* (Coppari *et al.*, 2016).

The Adriatic Sea is a north-eastern, semi-enclosed area of the Mediterranean Sea. Its eastern coast has over 1000 small islands along the coastline effectively resulting in a very large euphotic benthos area where benthic-pelagic coupling can involve direct interaction between benthic animals and phytoplankton. A special case is the northern Adriatic Sea, where depths never exceed 45–50 m, resulting in an enormous area where the seafloor is euphotic. This, in turn, results in a very large area, where the benthos is in direct contact with the phytoplankton of the euphotic zone of the water column. The research reported here is motivated by the assumption that in the northern Adriatic benthic-pelagic coupling might be directly linking the phytoplankton and the benthos in a particular way. Moreover, direct interaction between benthic organisms and phytoplankton might be a significant part of these processes.

The complex structure of the eastern Adriatic coastline also results in a high density of benthic habitat types that ultimately allows a comparably high diversity of benthic life forms, such as benthic decapods (Melzer *et al.*, 2016). Very

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little is known about the effect of benthic decapods on the phytoplankton community. While most adult benthic Decapoda are grazing or preying mainly on benthic biomass, their early larval stages are planktonic. Those planktonic stages feed on plankton. The importance of algal food sources in the diet of early decapod zoea stages was for a long time underestimated, but research has now demonstrated phytoplankton (including diatoms) to be a significant food source of, particularly, early zoea stages (Fileman *et al.*, 2014, and citations therein). Later zoea stages are reported to start feeding on zooplankton organisms and hence become predators (Anger, 2001). To further understand the interaction between the larval stages of benthic Decapoda and phytoplankton we decided to investigate larvae of a common crab from the northern Adriatic, *Xantho poressa* (Olivi, 1792) (Rodriguez & Martin, 1997).

Diatoms generally dominate the northern Adriatic microphytoplankton (Marić *et al.*, 2012; Godrijan *et al.*, 2013). The steep ecological gradients within the northern Adriatic allow for a relatively high planktonic diversity. Regular phytoplankton blooms and their succession are related to riverine nutrient inputs as well as stratification and mixing of the water column (Ivančić *et al.*, 2012; Ivančić *et al.*, 2016; Marić Pfannkuchen *et al.*, 2017). With diatoms dominating the northern Adriatic microphytoplankton and diatoms having been demonstrated to at times be a major part of the diet of decapod zoea, we decided to study the effect of *Xantho poressa* larvae on the northern Adriatic plankton. We chose five characteristic and common diatom species. *Bacillaria paxillifera* (O.F. Müller) T. Marsson is a regular, medium-sized diatom in the northern Adriatic phytoplankton. It forms compact, motile colonies. *Chaetoceros didymus* Ehrenberg is a colony forming centric diatom with long setae that are speculated to be evasive adaptations against grazing (Pickett-Heaps *et al.*, 1994). *Pleurosigma planctonicum* Cleve-Euler is a large diatom found in both the water column and benthic environments. *Pseudo-nitzschia calliantha* Lundholm, Moestrup & Hasle is a thin and elongated, toxic diatom that forms elongated chains (Lundholm *et al.*, 2003). This species is a significant threat to maricultures, for example of shellfish. Finally, *Skeletonema marinoi* Sarno & Zingone, 2005 is a rather small chain-forming diatom. It can form elongated chains and is regularly observed to form massive blooms in coastal areas with riverine nutrient inputs.

We here report results from feeding experiments, where zoea I of *X. poressa* were presented with the abovementioned species. In one series, each species was presented on its own, while in another series, a mix of the species was presented. To observe the growth dynamics of *S. marinoi* its growth *in vitro* was observed with and without *X. poressa* present in the culture medium.

## MATERIALS AND METHODS

### Establishment of monoclonal microphytoplankton cultures

Vertical net hauls were performed with a phytoplankton net (opening diameter 50 cm, length 2.50 m, mesh size 52 µm) from 15 m of depth to the surface. Diatom cells were manually isolated with a micropipette from such live net samples collected at various stations in the northern Adriatic Sea. Cells were grown into monoclonal batch cultures in 100 ml f/2 medium (Guillard, 1975) and incubated at 18 °C and 75 µmol photons m<sup>-2</sup> s<sup>-1</sup> on 12:12 h light/dark photoperiod. We here report results on experiments with five diatom species. Table 1 gives taxonomic information as well as information on their size and chain forming capacity. Figure 1 depicts the diatom species used in the grazing experiments.

### Hatching and harvesting of zoea I of *X. poressa*

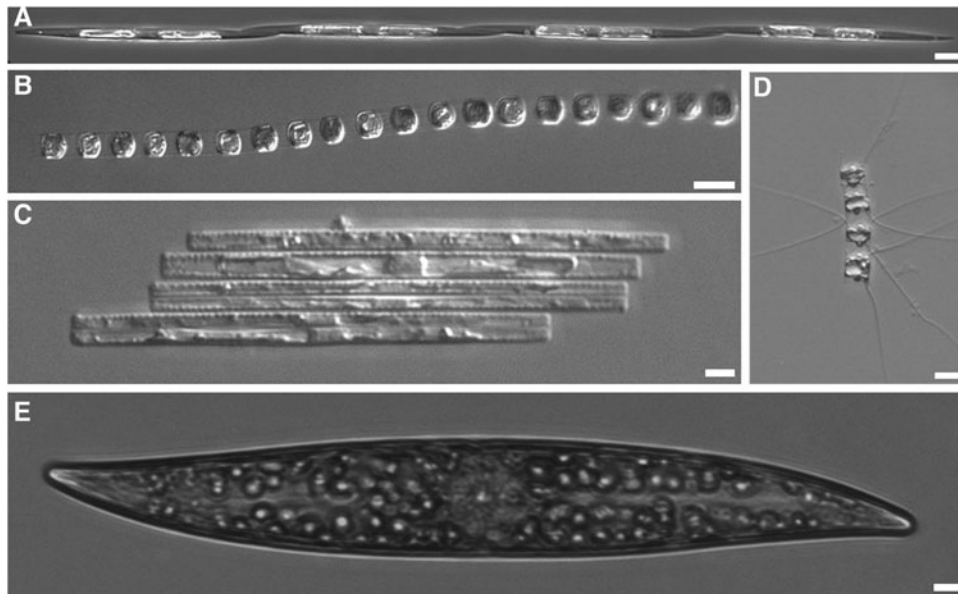
Adult, female and ovigerous specimens of *X. poressa* were collected manually, snorkelling or by apnea diving from the eastern coast of the northern Adriatic near the city of Rovinj. The specimens were transported in water buckets to the Centre for Marine Research in Rovinj and transferred into a flow-through system that consisted of a series of high-walled, 1-litre chambers. A continuous flow-through of seawater was generated. Hatched larvae were held back by 50 µm meshes. Hatched larvae were harvested manually with pipettes and transferred to phytoplankton chambers for subsequent experiments.

### Feeding experiments

For feeding experiments, 100 larvae were transferred to 250 ml transparent culture bottles. A set of 30 larvae was checked for the absence of fluorescence in the larvae. Diatoms were added to a final concentration of 10<sup>5</sup> cells l<sup>-1</sup>. The autofluorescence of the diatom cells was quantified using a Zeiss Axiovert epifluorescence microscope, filter set 14 (Zeiss, Oberkochen, Germany) and averaged across 30 cells. The same filter set was used to quantify fluorescence in the digestive tract of the larvae at the end of the feeding experiment. Excitation intensity and exposure time were adjusted so that control larvae before feeding showed no fluorescence signal. Larvae and diatoms were incubated at 18 °C and 75 µmol photons m<sup>-2</sup> s<sup>-1</sup> for 90 min and subsequently larvae were manually isolated and immobilized between object carrier and cover glass for life microscopy. Fluorescence intensities were calculated in Axiovision 4.8 (Zeiss). We calculated the number of ingested cells as

Table 1. List of diatom species and morphological characteristics.

Species	Length/height (µm)	Width (µm)	Growth form/Chain formation
<i>Bacillaria paxillifera</i> (O.F. Müller) T. Marsson	120	8	Pennate colony forming
<i>Chaetoceros didymus</i> Ehrenberg	20	10	Centric with long setae, chain forming
<i>Pleurosigma planctonicum</i> Hasle	150	30	Pennate single celled
<i>Pseudo-nitzschia calliantha</i> Lundholm, Moestrup & Hasle	120	5	Pennate chain forming
<i>Skeletonema marinoi</i> Sarno & Zingone	15	8	Centric, chain forming



**Fig. 1.** Light micrographs of diatoms species used in the grazing experiments. (A) *Pseudo-nitzschia calliantha*. (B) *Skeletonema marinoi*. (C): *Bacillaria paxillifera*. (D) *Chaetoceros didymus*. (E) *Pleurosigma planctonica*. Scale bars represent 10  $\mu\text{m}$ .

fluorescence intensity ( $\text{FI}_{\text{digestive tract}}$ ) accumulated in the digestive system divided by the fluorescence intensity per cell ( $\text{FI}_{\text{single cell}}$ ):  $\text{FI}_{\text{digestive tract}}/\text{FI}_{\text{single cell}}$ .

To mimic a typical situation for the northern Adriatic (a bloom event of *Pseudo-nitzschia calliantha*; Maric *et al.*, 2011) we presented 100 larvae in 250 ml with a mix of four species: *Pseudo-nitzschia calliantha* (84%), *Chaetoceros didymus* (7%), *Preurosigma planctonicum* (3%) and *Bacillaria paxillifera* (6%) at a total concentration of  $10^5$  cells  $\text{l}^{-1}$ . After 90 min of incubation at 18 °C and 75  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  the diatom cells were counted. We analysed triplicates for culture chambers with larvae and without larvae.

### Growth dynamics of *Skeletonema marinoi*

We inoculated 250 ml of F/2 medium with a final concentration of 47,000 cells  $\text{l}^{-1}$  of *S. marinoi* and grew the cultures at 18 °C and 75  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  on a 12:12 h light/dark photoperiod. Triplicates of such cultures were grown without larvae, and triplicates were grown with 30 larvae present in 250 ml. Larvae became inactive after  $\sim 2$  days in culture and were replaced manually by new larvae every second day. *Skeletonema* cells were daily counted microscopically, the number of cells per chain was noted.

## RESULTS

### Larval feeding on single diatom species

We presented zoea I of *X. poressa* with five different diatom species from the northern Adriatic. After 90 min of feeding, we quantified the ingested amount of cells in the digestive tract of the larvae ( $N = 30$ ). Figure 2 shows ingestion and the number of ingested cells for each of the species as well as a representative micrograph of a stage 1 larva after 90 min exposure to *S. marinoi*. We found that the larvae on

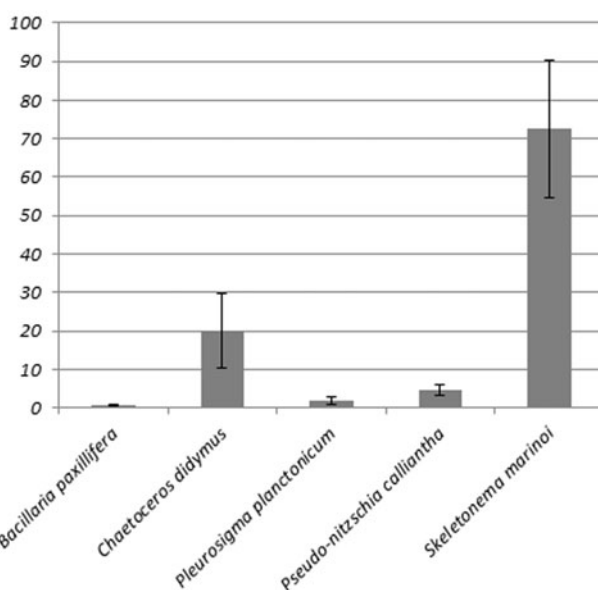
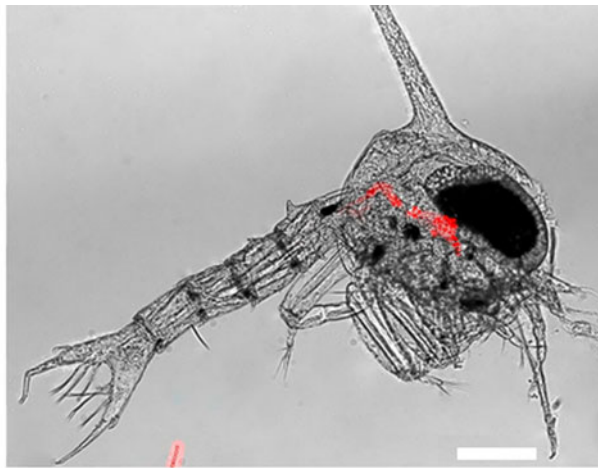
average ingested 0.58 cells of *B. paxillifera* ( $\text{SD} = 0.28$ ), 20 cells of *Ch. didymus* ( $\text{SD} = 9.78$ ), 1.9 cells of *P. planctonicum* ( $\text{SD} = 0.98$ ), 4.53 cells of *Pseudo-nitzschia calliantha* ( $\text{SD} = 1.47$ ) and 72.53 cells of *S. marinoi* ( $\text{SD} = 17.82$ ) in 90 min.

### Effect of larval grazing on a diatom community

To get an insight into the possible effect of larval grazing on a diatom community we presented larvae with a mix of four diatom species resembling a typical situation for the northern Adriatic. After an incubation time of 90 min, we analysed the relative abundance contributions of the four species to the total abundance in the mix and compared the results with the initial relative abundance contributions. Results are shown in Figure 3. On average ( $N = 3$ ) the relative contribution increased for *B. paxillifera* by 0.48%, for *P. planctonicum* by 0.048% and for *Ch. didymus* by 3.77%. For *P. calliantha* however, the relative contribution fell by 4.33%. There is a significant difference between the effect of larval grazing on *B. paxillifera*, *P. planctonicum*, *Ch. didymus* if compared with the effect on *P. calliantha* ( $t$ -test,  $P < 0.0001$ ).

### Effect of larval grazing on the growth dynamics of *S. marinoi*

To observe the effect of larval grazing on the growth dynamics of *S. marinoi* we added zoea I of *X. poressa* to a growing culture of *S. marinoi*. Figure 4A shows the development of average chain length (number of cells per chain) of *S. marinoi* during the growth experiment with and without zoea I present. Figure 4B shows the growth dynamics (cells  $\text{l}^{-1}$ ) during the growth experiment with and without larvae present. A significant decrease in chain length could be observed in the presence of larvae. Additionally, a significantly accelerated growth dynamic could be observed in the presence of larvae.



**Fig. 2.** Light micrograph of a zoea I of *X. poressa* after 90 min of grazing on *S. marinoi*. Chlorophyll autofluorescence is shown in red (scale bar = 100  $\mu\text{m}$ ). The graph shows number of cells ingested on average by zoea I of *X. poressa* in 90 min. Error bars show standard deviation. Number of larvae analysed: 30.

## DISCUSSION

Little is known about the interaction between marine phytoplankton communities and benthic species. It is generally accepted that benthic-pelagic coupling is a significant mechanism in the functioning of the marine ecosystem. In coastal marine ecosystems such as the northern Adriatic Sea, the relatively shallow water column and the relatively large euphotic benthos area results in a particular importance of benthic-pelagic coupling mechanisms (Mussap & Zavatarelli, 2017). Less is known about the interaction between marine phytoplankton communities and specific benthic species. Benthic filter feeders such as Bivalvia and Porifera have been investigated with respect to benthic-pelagic coupling, but the particular interaction between phytoplankton and benthic species has only rarely been detailed (Pfannkuchen *et al.*, 2009; Coppari *et al.*, 2016; Lucas *et al.*, 2016). One form of benthic-pelagic coupling is pelagic life stages of benthic organisms. Pelagic larval stages of benthic decapods often start out as herbivores and change their diet continuously during body

size increase and often become predatory (Anger, 2001). The species and larval stage-specific dietary requirements or food preferences are only rarely known (Powell *et al.*, 2017). However, since microzooplankton as a functional group was already demonstrated to have a significant effect on marine phytoplankton (Franks, 2001; Strom *et al.*, 2001; Irigoien *et al.*, 2005; George *et al.*, 2015), in particular in coastal waters, we became interested in what possible role the planktonic larval stages of benthic Decapoda might have in shaping plankton communities. We decided to investigate the planktonic larvae of *X. poressa*, a common, benthic Decapoda in the northern Adriatic (Spivak *et al.*, 2010). As the northern Adriatic microphytoplankton is mostly dominated by diatom communities, we presented zoea I of *X. poressa* with a range of diatom species typical for the northern Adriatic. This selection included massive and large species like *Pleurosigma planctonicum*, the bulk colony-forming *Bacillaria paxillifera*, the small, centric and chain-forming *Skeletonema marinoi*, the centric, chain-forming and setae-bearing *Chaetoceros didymus*, as well as the delicate and toxic *Pseudo-nitzschia calliantha*. The largest diatom, *P. planctonicum* is larger than the mouth opening ( $\sim 20 \mu\text{m}$ ) of the larvae (Meyer *et al.*, 2004). However, larvae were feeding on this species. Microscopic observation showed that this diatom species was chewed upon and broken down before ingestion with a considerable amount of sloppy feeding (data not shown). The same feeding was observed for all other elongated, pennate diatoms tested (*B. paxillifera*, *P. calliantha*), as well as for the centric *Ch. didymus* that is adorned with long setae, which were speculated to help to evade grazers by steric obstruction (Pickett-Heaps *et al.*, 1994). Our results indicate that there is no significant hindering effect of setae on predation by decapod larvae (see Figures 1D and 2). However, our results show that all tested diatom species are ingested by zoea I of *X. poressa*. This allows the conclusion that the northern Adriatic, diatom-dominated microphytoplankton provides suitable food for early stage planktonic larvae of *X. poressa* and that those larvae might contribute to the shaping of the microphytoplankton community in the area.

The toxic diatom genus *Pseudo-nitzschia* is a common, frequent and abundant component of the northern Adriatic phytoplankton community (Ljubecic *et al.*, 2011; Maric *et al.*, 2011, 2012; Godrijan *et al.*, 2013). During bloom events, *Pseudo-nitzschia* species dominate the microphytoplankton, which is a particularly interesting phenomenon, as these toxic species pose a significant threat to shellfish farms. To imitate such a situation, we mixed four microphytoplankton diatom species with a strong domination of *Pseudo-nitzschia calliantha* and presented the community to zoea I of *X. poressa*. After 90 min of grazing, we determined relative abundances microscopically. Our results showed a significant difference in the development of relative abundances between *B. paxillifera*, *P. planctonicum* and *Ch. didymus* whose relative abundances increased and *P. calliantha*, whose relative abundance decreased significantly. This observation would indicate that decapod larval grazing activity might selectively reduce the relative contribution of toxic diatoms in microphytoplankton bloom events. This would be particularly important in areas with shellfish production or mariculture, hence a healthy and intact benthic environment that provides suitable habitats for benthic Decapoda might prove beneficial. However, *in situ* observations have not found a clear pattern in the interaction between grazers and toxic species so far (Turner & Tester, 1997).

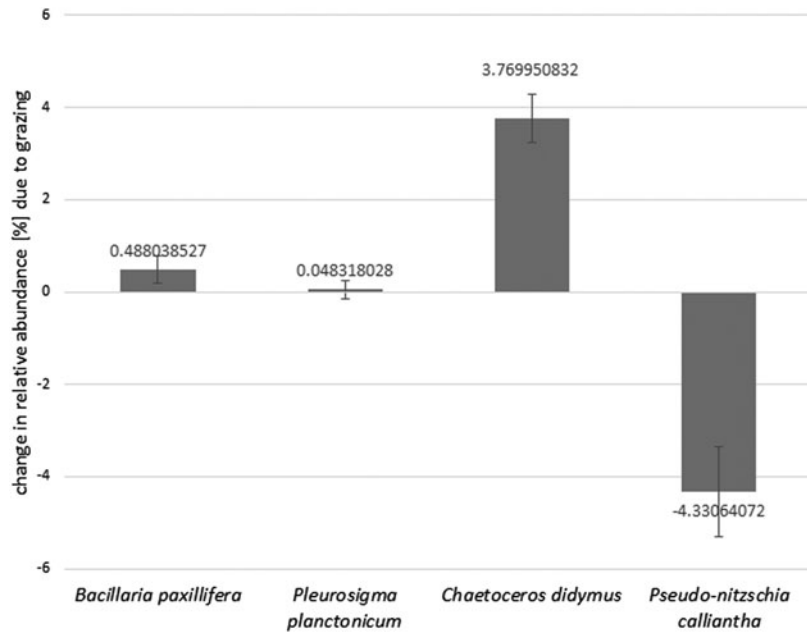


Fig. 3. Changes in relative abundance of four diatom species, that were presented as an artificial phytoplankton community to zoea I of *X. poressa*. Error bars show standard deviations. A positive value means an increase in relative abundance contribution to the total abundance.

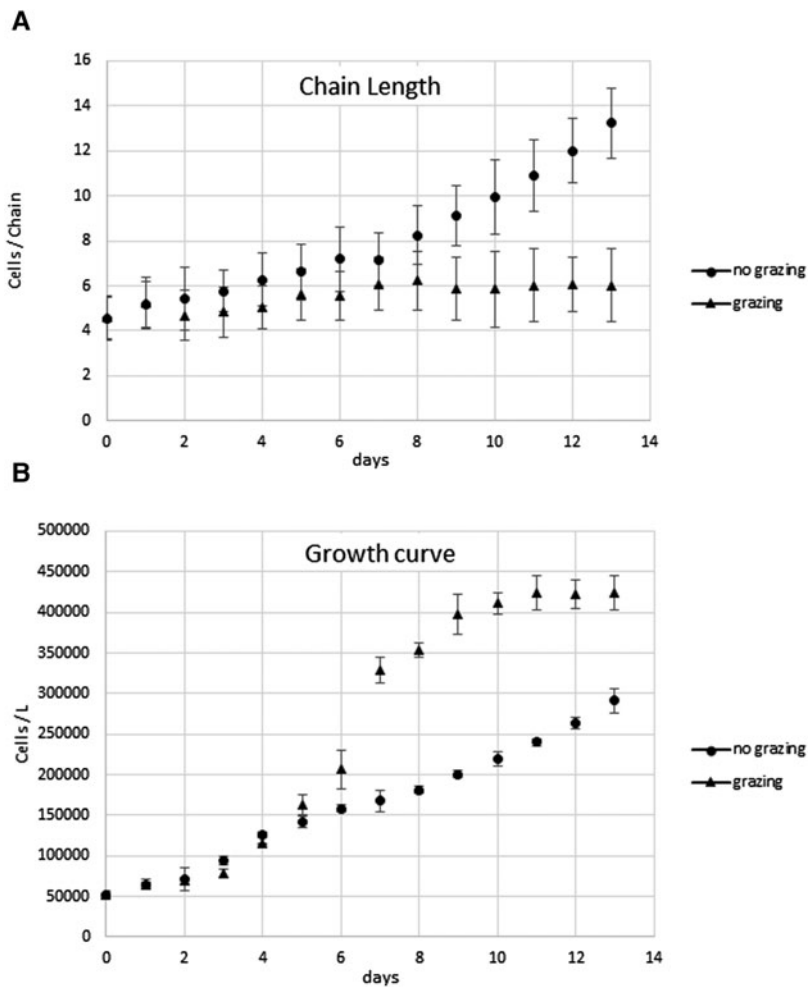


Fig. 4. Development of average chain length (A) during the growth of an *S. marinoi* culture with grazing pressure (*X. poressa*) (triangles) or without grazing pressure (circles). Growth dynamics (B) of an *S. marinoi* culture with grazing pressure (*X. poressa*) (triangles) or without grazing pressure (circles).

Zooplankton grazing is a mechanical disturbance that might have a shortening effect on diatom chain length. Several investigations have already demonstrated that the presence of grazers alone, via a proposed chemical signalling, reduces chain length in phytoplankton species, including *S. marinoi* (Bjærke *et al.*, 2015). However, those investigations used copepods as model grazers. This is to our knowledge the first report of decapod effects on diatom chain length. Our results confirm that a reduction in chain length is a diatom reaction to the presence of decapod grazers. Such size reduction appears to reduce clearance rates of grazers and hence helps evade grazing. While these results contradict the traditional idea of chain formation as an adaptation to evade grazing, investigations have so far concentrated on the grazing efficiency or clearance rates in relation to chain length. In addition, longer chains appear to be more accessible to grazing. In our experiment, we additionally followed the growth dynamics of *S. marinoi*. Our result shows a significant increase in growth rate as a reaction to the presence of grazers in the culture. Figure 3 clearly shows that the reduction in chain length is accompanied by an increase in growth rate. This means that the presence of (decapod) grazers can induce an increase in *S. marinoi* growth rate and possibly a bloom event. *In situ* data from a long-term data set for the northern Adriatic documents a regular *S. marinoi* bloom early in the year, when water temperatures are at a low (January to March) (Marić Pfannkuchen *et al.*, 2017). Kurian also reported peak abundances of decapod zoaea in the Adriatic plankton for the beginning of the year, between January and March, which coincides with the peak abundances of *S. marinoi* (Kurian, 1956; Marić Pfannkuchen *et al.*, 2017). González-Gordillo & Rodríguez (2003) reported peak abundance of *Xantho* spp. around May for Atlantic coastal waters off the south-western Iberian peninsula. Results from the British channel demonstrate diatoms to be part of the decapod zoea diet *in situ*. The temporal correlation of peak abundances together with the observation of zoea ingesting diatoms *in situ* as well as *in vitro*, suggests *in situ* significance of the interaction between zoea larvae and diatoms like *S. marinoi*. It, however, remains to be investigated to what extent the localized higher abundances of planktonic life stages of benthic animals are causal to the observation of coastal bloom events of *Skeletonema* species (Marić Pfannkuchen *et al.*, 2017). The abundances of zoea I larvae used in our experimental setups exceed abundances observed *in situ*. We chose to use higher abundances of grazers in our experiment, to shorten the necessary exposure times and thus to isolate the effect of grazing from other possible effects like allelochemical effects or effects of growth adaptations. We nevertheless expect that the results are of relevance for *in situ* mechanisms as grazing under natural conditions lasts significantly longer than our experiments and as *in situ* a number of species are present simultaneously. Ianora *et al.* (2004) reported experimental evidence of a negative allelochemical effect exerted by *S. marinoi* on copepod larvae and their development. A similar effect might explain the relatively short survival time of *X. poressa* zoea in *S. marinoi* cultures observed in our experiments.

From our results we can conclude that zoea I of *X. poressa* do graze on marine diatoms. If an artificial community is presented, decapod larval grazing can change the community composition. In our experimental setup the relative abundance of a toxic species (*P. calliantha*) was reduced, which

indicates that decapod larvae might have a positive effect in coastal areas or in maricultures by reducing the risk or impact of toxic phytoplankton blooms. Chain formation is traditionally presumed to be a feature that helps diatoms to evade predation. Earlier findings showed that the presence of copepod grazers induces chain length reduction in *S. marinoi*. Our results expand these findings and show also that the presence of zoea I of *X. poressa* induces chain length reduction in *S. marinoi*. In addition, we observed the growth dynamics of *S. marinoi* in the presence of grazers and demonstrated that the reduction in chain length is accompanied by an increase in growth rate which indicates that the presence of grazers might induce *S. marinoi* bloom events.

## ACKNOWLEDGEMENTS

We thank both anonymous reviewers for their helpful discussion and the resulting improvement of the manuscript.

## FINANCIAL SUPPORT

This work was supported by the Ministry of Science, Education and Sports of the Republic of Croatia as well as by the scientific project UIP-2014-09-6563 'Phytoplankton life strategies in the northern Adriatic'. This work was furthermore supported jointly by the German Academic Exchange Service and the Ministry of Science, Education and Sports of the Republic of Croatia through the bilateral project 'Phytoplankton-Zooplankton Interactions in the P-limited northern Adriatic. Integrating interspecies interactions into life strategy analysis'.

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