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Differences in size distribution of marine phytoplankton in presence versus absence of jellyfish support theoretical predictions on top-down control patterns along alternative energy pathways

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Abstract

While theoretical food web studies highlight the importance of alternative energy pathways in shaping community response to bottom-up and top-down forcing, empirical insight on the relevance of the predicted patterns is largely lacking. In marine plankton food webs differences in food size spectra between ciliates and copepods lead to alternative energy pathways, one expanding from small phytoplankton over ciliates to copepods, the other from large edible phytoplankton directly to copepods. Correspondingly, predation pressure by copepods leads to an increase of small phytoplankton through top-down control of copepods on ciliates, but to a decrease of large phytoplankton through direct predation by copepods. Hence, food web theory predicts a shift from dominance of large to small algae along an enrichment gradient. This prediction clearly deviates from the general assumption of a shift from small fast growing to larger slow growing phytoplankton taxa with increasing nutrient availability. However, if copepods themselves are under top-down control by strong predation through planktivores such as fish or jellyfish, dominance of large algae is expected throughout the enrichment gradient. We tested these predictions by analyzing the phytoplankton composition from numerous marine lakes and lagoon sites located on the archipelago of Palau covering a wide range of nutrient levels, comparing sites lacking large numbers of higher trophic levels with sites harboring high densities of jellyfish. The observed patterns strongly support that higher trophic levels influence the phytoplankton size distribution along a nutrient enrichment gradient, highlighting the importance of alternate energy pathways in food webs for community responses.

Introduction

The interplay between bottom-up and top-down control in shaping community composition has been under debate for decades (Hairston et al. 1960, Hunter and Price 1992, Hessen and Kaartvedt 2014). Food chain theory proposes an alternating pattern of bottom-up and top-down control from top consumers down to primary producers, where only trophic levels under bottom-up control respond to increased nutrient availability (Fretwell 1985, Oksanen et al. 1981). Adding or removing the top trophic level leads to a cascading effect down the food chain, due to the shift in bottom-up and top-down control along the food chain (Oksanen et al. 1981). In freshwater systems strong top-down control and corresponding trophic cascades have been frequently observed (Carpenter et al. 1985, Shurin et al. 2002), however, results are not as conclusive in the marine environment (Shurin et al. 2002). One argument in explaining the lack of trophic cascades from top-consumers down to primary producers in marine systems is, that biodiversity at each trophic level is much higher compared to most freshwater systems, leading to attenuation of top down effects (Hessen and Kaartvedt 2014). Indeed, examples of clear trophic cascades in marine systems come from areas with low species diversity, dominated by a few strong interactors (Daskalov et al. 2007, Myers et al. 2007; Casini et al. 2008). However, it has been also argued that trophic cascades, while present, may be masked at the total phytoplankton level due to opposite responses of ‘small’ versus ‘large’ phytoplankton to bottom-up and top-down forcing along parallel food chains (Stibor et al. 2004). It was shown that differences in food size spectra between ciliates and copepods lead to alternative energy flow pathways, one expanding from small pico- and nano-phytoplankton over ciliates to copepods, the other from larger edible nano- and microphytoplankton directly to copepods (Stibor et al. 2004, Sommer and Sommer 2006). Accordingly, high predation pressure by copepods leads to an increase of small phytoplankton through top-down control on ciliates, but to a decrease of larger phytoplankton through direct predation (Stibor et al. 2004). In the absence of any predation on copepods, copepod biomass will increase with nutrient availability, leading to increasing predation pressure on ciliates and large algae, while small algae are released from predation pressure by ciliates as well as from resource competition with large algae. Correspondingly, theoretical investigations on the dynamic features of this food web module predict dominance of large phytoplankton at low nutrient availabilities and a shift to smaller sized phytoplankton with increasing nutrient availability (Fig. 1a, Wollrab and Diehl 2015). This prediction is opposite to the general assumption - based on nutrient uptake dynamics - that phytoplankton cell size should increase with enrichment, shifting from small fast growing species to larger slow growing taxa, mediated through increasing predation pressure on small fast growing species (Chisholm 1992, Kiørboe 1993, Thingstad 1998). Furthermore theory predicts that in the presence of planktivore predators such as fish/jellyfish, exerting strong top-down control on copepods, the response at the phytoplankton level is reversed and, in line with general assumptions, larger sized phytoplankton increases with enrichment (Fig. 1b, Wollrab and Diehl 2015). However, it is difficult to achieve data from comparable systems with and without presence of predators along a gradient of resource availability. Hence, until now no study exists confronting these general predictions from food web theory (Fig. 1, Wollrab and Diehl 2015) with data from natural communities.

The archipelago of Palau harbors numerous enclosed marine lakes and semi-enclosed coves covering a wide range of nutrient levels. The marine lakes, located within an area of approx. 50 km² on various islands within the archipelago, have only underground connections to the surrounding lagoon, resulting in strongly reduced immigration possibilities for animals such as fish or jellyfish (Colin, 2009; Hamner and Hamner 1998). As a result, many lakes are lacking large numbers of organisms at higher trophic levels (i.e. jellyfish or pelagic fish), while some of the lakes are famous for their high density of jellyfish of the genus *Mastigias* (Dawson and Hamner 2003). Mastigias is a zooxanthellate jellyfish, harbouring symbiontic dinoflagellates of the genus *Symbodinium*, but still assert strong top down control on zooplankton, especially on copepods (Graham et al. 2001, Dawson 2005). For these reasons, the archipelago of Palau offers a unique opportunity to look for patterns of cascading top down control on phytoplankton size distribution along an enrichment gradient in the presence vs. absence of large numbers of planktivore predators (jellyfish). The marine lakes can be seen as natural marine "mesocosms" which allow confronting/testing the above-described predictions of food web theory with phytoplankton communities of natural complexity and shared evolutionary history. Additionally, experimental mesocosms were set up in two of the marine lakes to characterize the cascading effects of jellyfish on phytoplankton in the marine lakes in a controlled and causal manner.

Methods

Sampling campaigns of marine lakes, coves and lagoons

During the summer period of four consecutive years (2010 - 2013) 44 lakes, coves and lagoon sites were sampled for phytoplankton community and nutrient analyses. All lakes, coves and lagoon sites are situated in the archipelago of Palau (table 1). Integrated water samples were collected with a 2 m long tube sampler from depths of 0 (surface) to 10 m, or from 0 to the bottom in lakes less than 10 m in depth. Samples were stored dark in a cooling box until further treatment in the laboratory. Total phosphorus measurements were performed after wet oxidation of water samples according to standard water chemical methods (Raimbault et al. 1999). Bioassay experiments performed in 2010 indicate phosphorus limitation for the majority of the studied lakes (see supplemental material S1). Initial phytoplankton size and community composition were analysed microscopically by using a standard Utermöhl technique with 50 - 100 ml sedimentation chambers (Utermöhl et al. 1958). 100 to 400 individuals per taxon were counted, 10 - 20 individuals were additionally measured in several dimensions and biovolumes were calculated based on geometric calculations. Cell counts were transformed to biovolume according to these measurements.

The presence or absence of jellyfish was verified by data from a Lake monitoring program (Dawson and Hamner 2005) and by visual surveys of sampling sites by snorkeling. Two of the lagoon sites were sampled twice, during low and high-tide (Table 1: lagoon 3 and lagoon 4). In the analysis they were treated as independent samples. However, adding or removing these data points from analyses did not influence the qualitative results of the study.

Mesocosm experiments:

Experimental set up:

Both experiments were set up using free floating mesocosms in a gradient design. In 2010 ten mescosms (4.3 m depth, 3.1m^3 volume, translucent PET foil) were filled randomly with unfiltered subsurface lake water (Lake Ongeim'l Tketau, OTM) by lifting up the empty mesocosm bags from ca. 5m depth to the lake surface. Subsequently, mesocosms received a population of the local *Mastigias* jellyfish ranging from 0 to 20 individuals/ mesocosm (all individuals ~10cm bell diameter). The experiment was run for 3 weeks with regular sampling (nutrients, copepods, phytoplankton) after one, two, and three weeks.

In 2011 mesocosm materials, procedures and dimensions were the same as in 2010 except for the jellyfish gradient design: 14 mesocosms were set up in lake *Uet era Ngermeuangel* (NLK), 7 thereof were stocked with *Mastigias* from the lake (ranging from 0 to 16 individuals/ mesocosm, bell diameter ~6cm). In both lakes, the jellyfish gradients were at the lower end of average natural jellyfish densities. The experiment was run for 2 weeks with regular sampling (nutrients, copepods, phytoplankton) after one and two weeks. In both years, the integrity of mesocosms and the vitality of medusae were regularly controlled.

Sampling procedures, counting, measurements, chemical analyses

After one, two, (and three in 2010) weeks, depth-integrated water samples (10 litres) were taken from each mesocosm to determine phytoplankton biomass and to measure nutrients. 100ml of sampled water was immediately fixed with Lugol iodine for microscopic phytoplankton and ciliate identification and counting. Phytoplankton and ciliates were identified and counted by inverted microscopy using Utermöhl chambers aided by scanning electron microscopy (SEM). Cell counts were converted into biovolumes [μm^3 L^{-1}] using measured or published specific cell volumes. Samples for seston nutrient analyses were poured through a net (225µm mesh size) to retain zooplankton and large detrital particles. Algal biomass POC and PON, were determined subsequent to filtration onto pre-combusted and acid-washed glass-fibre-filters (Whatman GF/C, Whatman International Ltd.) by Elemental Analysis (Elemental Analyser, EA 1110 CHNS, CE Instruments). Algal biomass particulate phosphorus (PP) was measured after sulphuric acid digestion followed by a molybdate reaction. Copepod sampling was performed using a plankton net (188 litres per net haul, 250µm mesh size).

Jellyfish fresh weight calculations

At the end of each experiment, all jellyfish were removed from the mesocosms and bell diameters were measured to assess the effective number and biomass of jellyfish per mesocosm (some small medusae might have been trapped accidentally during filling of the bags, likewise trapped polyps could have had strobilated during the experiment). Jellyfish biomass was calculated using the following non-linear regression equations for fresh weight-to-bell diameter relationships, obtained from medusae not used in the experiments:

Mastigias fresh weight [g] = 0.15*bell diameter [cm]$^{2.92}$, $r^2=0.993$, $p<0.0001$, $n=34$.

Data analysis of field data

For each sampling site total phytoplankton biovolume was calculated and linear regression was used to investigate the pattern of total phytoplankton biovolume with increasing phosphorous levels. According to a meta-analysis on food size ranges of copepods and protozoa across different marine habitats by Sommer and Sommer (2006), phytoplankton with an equivalent spherical diameter (ESD) smaller than 10 µm (~523 µm^3) belong to the preferred food size range of ciliates, whereas phytoplankton with an ESD larger than 10 µm belong to the preferred food size range of copepods. Accordingly we summed the biovolumes of ‘small’ (<523 µm^3) and ‘large’ (>523 µm^3) phytoplankton for each sampling site (Sommer and Sommer 2006). Phytoplankton larger than 74000 µm^3 was considered inedible, restricting the summed large phytoplankton to cell sizes between 523 µm^3 and 74000 µm^3. Total phytoplankton biovolume per lake was calculated using the complete range of detected cell sizes. We investigated the correlation of total phytoplankton biovolume and of small and large phytoplankton with TP level for sites with and without jellyfish using the non-parametric Kendall correlation method, which measures the correspondence between the ranking of x and y variables. Kendall correlation test was done on the absolute biovolume data for small and large phytoplankton as well as on the relative contribution of small and large algae to total phytoplankton per site.

Data analysis and plotting was performed with the Software R (Version 3.1.1) using the packages *car*, *plyr*, *ggpubr, cowplot* and *gtools*.

Data analysis of mesocosm experiment

For both experiments (OTM in 2010 and NLK in 2011), the effect of the presence or absence of jellyfish on the abundance or biovolume (N) of copepods, ciliates and phytoplankton was assessed by calculating an effect value. For example, for copepods, the effect size (ES_{Cop}) has been calculated as:

$$ES_{Cop} = Ln\left(N_{encl-i}^{Cop}/N_{Control}^{Cop}\right) \quad (1)$$

Where N_{encl-i}^{Cop} is the copepod abundance (on the final sampling day) in the enclosure 'i' which contained a manipulated number of jellyfishes; $N_{Control}^{Cop}$ is the copepod abundance in the enclosure with no jellyfish on the last sampling day. Similarly, the effect size for ciliates (ES_{Cil}, based on abundance) and phytoplankton (ES_{Phyt}, based on cell biovolume) were calculated as follow:

$$ES_{Cil} = Ln\left(N_{encl-i}^{Cil}/N_{Control}^{Cil}\right) \quad (2)$$

and,

$$ES_{Phyt} = Ln\left(N_{encl-i}^{Phyt}/N_{Control}^{Phyt}\right) \quad (3)$$

Two size-classes were distinguished for phytoplankton, i.e. phytoplankton with cell biovolume <

523 μm^3, or cell biovolume > 523 μm^3, no cells larger than 74000 μm^3 were detected.

Results

Patterns of total phytoplankton biovolume with enrichment for marine sights in presence vs. absence of jellyfish

Total phytoplankton biovolume is significantly positively correlated with nutrient enrichment for both, sites with and without jellyfish (Fig. 2, lakes with jellies: $r = 0.45$, $N = 25$, $p < 0.\ 01$, lakes without jellies: $r = 0.32$, $N = 19$, $p < 0.1$). Thereby the increase of total phytoplankton with total phosphorus is more pronounced in the presence of jellyfish compared to in the absence of jellyfish.

Patterns of small vs. large phytoplankton for marine sights along enrichment gradient in presence vs. absence of jellyfish

Overall, the summed biomasses of small and large phytoplankton are significantly positively correlated with increasing TP-levels (Fig. 3a and c). In the presence of jellyfish (Fig. 3a), the increasing trend is significant for large algae ($r = 0.41$, $N = 25$, $p < 0.01$) and small algae ($r = 0.57$, $N = 24$, $p < 0.001$), with higher biomass of large algae throughout the enrichment gradient. In the absence of jellyfish (Fig. 3c), the increasing trend is only significant for small algae ($r = 0.38$, $N = 19$, $p < 0.05$), but not for large algae ($r = 0.1$, $N = 19$, $p > 0.1$).

Looking at the relative contributions of small vs. large phytoplankton to total phytoplankton biovolume for each sampling site (Fig. 3b and d), in the absence of jellyfish (Fig. 3d), the relative contribution of large algae is significantly negatively correlated with increasing TP-levels ($r = -0.39$, $N = 19$, $p < 0.05$), whereas the relative contribution of small algae is significantly positively correlated with increasing TP-levels ($r = 0.3$, $N = 19$, $p < 0.1$). In addition we observe a shift from dominance of large algae to dominance of small algae for the highest investigated TP-levels. In the presence of jellyfish (Fig. 3b), in line with the absolute values, large algae dominate throughout the enrichment gradient for most sites. However, no significant correlation between total phosphorus and relative biovolume of large vs. small phytoplankton could be found (large phytoplankton, $r = -0.02$, $N = 25$, $p > 0.1$; small phytoplankton, $r = 0.0065$, $N = 24, p > 0.1$).

The size fraction above 73000 µm³, considered to be inedible, dominated the phytoplankton community only at one site (Lake New 1, see table 1). At sites where this size fraction was detected ($N = 11$ for lakes with jellyfish and $N=3$ for lakes without jellyfish), in most cases it contributed less than 20% to total phytoplankton (see supplemental material, Fig. S2). Additionally, no significant correlation between the abundance of large inedible algae and enrichment (inedible algae in presence of jellyfish: $r = -0.38$, $N=11$, $p = 0.1$, inedible algae in the absence of jellyfish: $r = 1$, $N = 3$, $p > 0.1$).

Experimental evidence for trophic cascades mediated by Mastigias

Increasing *Mastigias* biomass in the mesocosms established in the two different lakes resulted in a significant reduction of copepod abundances (Fig. 4a). Decreasing copepod abundances resulted in positive effect sizes of jellyfish on ciliates (Fig. 4b) and phytoplankton (Fig. 4c,d). The positive slope of increasing jellyfish on ciliate abundances was however not significant on a 5% level (Fig. 4b). Both, small and large phytoplankton groups showed positive responses to increasing jellyfish abundance. The effect size on large algae was considerably higher compared to the effects on small algae, the slope of effect sizes vs. jellyfish fresh weight was about twice as high for large phytoplankton (Fig. 4c,d).

Discussion

Trophic cascades

Our results support the importance of presence vs. absence of higher trophic levels in shaping quantitative and qualitative responses of primary producers to resource enrichment. Within the edible size range of phytoplankton for ciliates and copepods we observe clear differences between the abundance patterns of small vs. large phytoplankton, dependent on the presence or absence of jellyfish. In the presence of jellyfish, large edible phytoplankton dominates throughout the enrichment gradient, whereas in the absence of jellyfish, a shift from dominance of larger towards smaller size classes occurs. These observations are in line with theoretical predictions on contrasting top-down control patterns along the large algae-copepod chain vs. the small algae-ciliate-copepod chain (Wollrab and Diehl 2015) and highlight the relevance of parallel food chains within food webs for bottom-up and top-down response patterns (Armstrong 1994; Shin et al. 2010; Wollrab et al. 2012). While the dominance of large algae in the presence of jellyfish and their increase with total phosphorus levels is in line with theoretical predictions, the increase of small algae in presence of jellyfish is not predicted by theory. However, one has to take into account that the *in situ* natural food web complexity is higher than the model *in silico* complexity and direct and indirect interactions between food web compartments which are not part of the model structure, for example interactions between bacteria and algae, may lead to deviations from model predictions.

Our conclusions are based on detailed knowledge on the presence and absence of the top predator *Mastigias* sp. and quantitative analyses of the autotroph base of the food web (phytoplankton abundance and cell size distribution). The data used for the analyses originate from a sampling program investigating phytoplankton diversity in marine lakes, therefore we lack quantitative zooplankton data. However, our data from the two mesocosm experiments conducted in Palau lakes strongly support the idea that observed quantitative differences in phytoplankton community composition with respect to cell size are linked to changes in top-down control patterns dependent on the presence or absence of jellyfish. In the observed lakes, jellyfish, if present, are top-predators in the system and usually reach very large population sizes. For example in lake OTM the population of *Mastigias* can reach total densities of up to 24 million individuals (Dawson and Hamner 2005). While *Mastigias* are mixotrophic, they still need zooplankton as part of their diet and exert high predation rates and therefore strong top-down control on zooplankton (Fig. 4a; see also McCloskey et al. 1994). There is the possibility that in lakes without jellyfish, zooplanktivorous chaetognaths might get the dominant predators on zooplankton, however, their grazing impact is usually much lower (up to a few copepods per day, Oresland1987; Fulton 1984) in comparison to jellyfish grazing rates (McCloskey et al. 1994; Graham and Kroutil 2001; Bezio et al. 2018). Additionally, cannibalism is quite prevalent among chaetognaths, thereby strongly controlling their own population densities (Øresland 1987). Jellyfish, also mixotrophic ones, are well known to induce trophic cascades (Stibor et al. 2004; West et al. 2009), while such evidence is lacking for chaetognaths.

The search for trophic cascades in real systems has often been focused on whole trophic level responses (Carpenter et al. 1985; Shurin et al. 2002). Our study strengthens the necessity of recognizing alternative energy pathways and highlights the relevance of parallel food chains in mediating the response to bottom-up as well as top-down forcing at the phytoplankton level. The expectation, that phytoplankton communities shift from dominance of small, fast growing, to bigger, slow growing and less edible, cell sizes with increasing nutrient availability (Chisholm 1992; Kiørboe 1993; Arin et al. 2002; Irwin et al. 2006), is based on insight from food web theory according to which coexistence between competing prey species is only possible in the presence of a trade-off between resource use efficiency and edibility to a shared predator (Holt et al. 1994; Leibold 1996). Theory predicts that along an enrichment gradient there is a shift from the superior resource competitor to the inferior, but less edible, resource competitor, corresponding to a shift from dominance of resource to apparent competition (Holt et al. 1994; Leibold 1996). However, if alternative food chains are of different length, top-down control patterns related to apparent competition can deviate from the above described pattern, leading to counterintuitive predictions (Wollrab et al. 2012; Wollrab and Diehl 2015).

The clear and coherent patterns along the resource gradient that were found in our analyses of natural phytoplankton communities are even more reassuring, since between lake variation in terms of species composition is naturally high. The marine lakes and coves on Palau differ in their connectivity to the surrounding ocean, ranging from direct surface connections for lagoon sites and coves, to only underground connections for lakes (Hamner and Hamner 1998). Distance and characteristics of the connection to the marine environment put potential restrictions on species migration and invasion possibilities and thereby species distribution for marine lakes. This might be one reason that leads to the observed high between site variability in species composition and species richness, especially for sampling sites without jellyfish, which do not have direct surface connections to the ocean. Therefore it is hardly surprising that the highest variance in total phytoplankton biovolume was observed for mesotrophic lakes without jellyfish. The still coherent responses of phytoplankton along the enrichment gradient in the presence vs. absence of jellyfish, strongly point towards the generality of some of the predicted mechanisms of how top-down control influence primary producer community composition responses to resource availability by previous experimental (Stibor et al. 2004) and theoretical investigations (Wollrab and Diehl 2015).

While the situation of low numbers or even the absence of planktivorous predators as such will not be relevant for most marine systems, our results have several important implications for our understanding of food web functioning. First, removing or reducing of higher trophic levels within food webs (shifting the length of food chains) can result in opposite and unexpected responses at lower trophic positions to simultaneous nutrient enrichment. Such scenarios are not unrealistic at all following the large effects of anthropogenic stressors such as overfishing (depletion of upper trophic levels) (Pauly et al. 1998) and eutrophication of coastal waters (Rabalais et al. 2009). Second, effects of nutrient enrichment may not necessarily result in clear increases of primary producer biomass with increasing nutrient availability, but responses may differ between size classes of phytoplankton. It is therefore important to have knowledge about food web structure before using phytoplankton biomass as an indicator for eutrophication or over-fertilization (Garmendia et al. 2013).

In line with the approach of so called end-to-end models (Shin et al. 2010), our study shows that focusing on major energy pathways in the analysis of community response patterns to environmental forcing may be a useful way to derive valuable information on expected shifts. However, this requires data that encompass all trophic levels and information on within trophic level heterogeneity in terms of size distribution and food size ranges. Such data sets will enable to develop appropriate food web approximations and to confront predicted patterns on community structure with observed patterns in natural systems.

Compliance with Ethical Standards

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Conflict of Interest: All authors declare that he/she has no conflict of interest.

Ethical approval: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Experiments were approved by the Republic of Palau and the State of Koror, research permit holders were Herwig Stibor & Philippe Pondaven. Jellyfish were released into their natural habitat after the experiments.

Data availability

The datasets analysed during the current study are available from the corresponding author on reasonable request.

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Figure legends

Figure 1: Schematic figure of the plankton food web in the absence (a) versus presence (b) of jellyfish. Arrows connecting circles indicate feeding interactions pointing from prey to predator, circles represent R - shared nutrient P_S - small algae, P_L - large algae, Cil - ciliates, Cop - copepods and J - jellyfish. Thick arrows next to circles indicate the expected longterm response pattern with increasing total nutrient content following theoretical predictions from the analysis of the equilibrium response of a corresponding differential equation system in Wollrab & Diehl (2015).

Figure 2: Total phytoplankton biovolume [$\mu m^3\ L^{-1}$] per sampling site along the total phosphorus gradient [$\mu g\ L^{-1}$] for sites with (yellow triangles) and without (blue circles) jellyfish. All values are $\log_{10}$-transformed.

Figure 3: Absolute $\log_{10}$-transformed biovolumes (a. c) and relative (logit-transformed) contribution (b. d) of small (<523 μm^3. blue circles) and large (>523 μm^3. yellow triangles) phytoplankton per site [$\mu m^3\ L^{-1}$] along the total phosphorous gradient [$\mu g\ L^{-1}$] for sites with jelly fish (a. b) and for sites without jellyfish (c. d).

Figure 4: Effect size of jellyfish freshweight on (a) copepod. (b) ciliate. (c) small algae and (d) large algae from mesocosm experiments in 2010 (black circles) and 2011 (open circles).

Figure 1

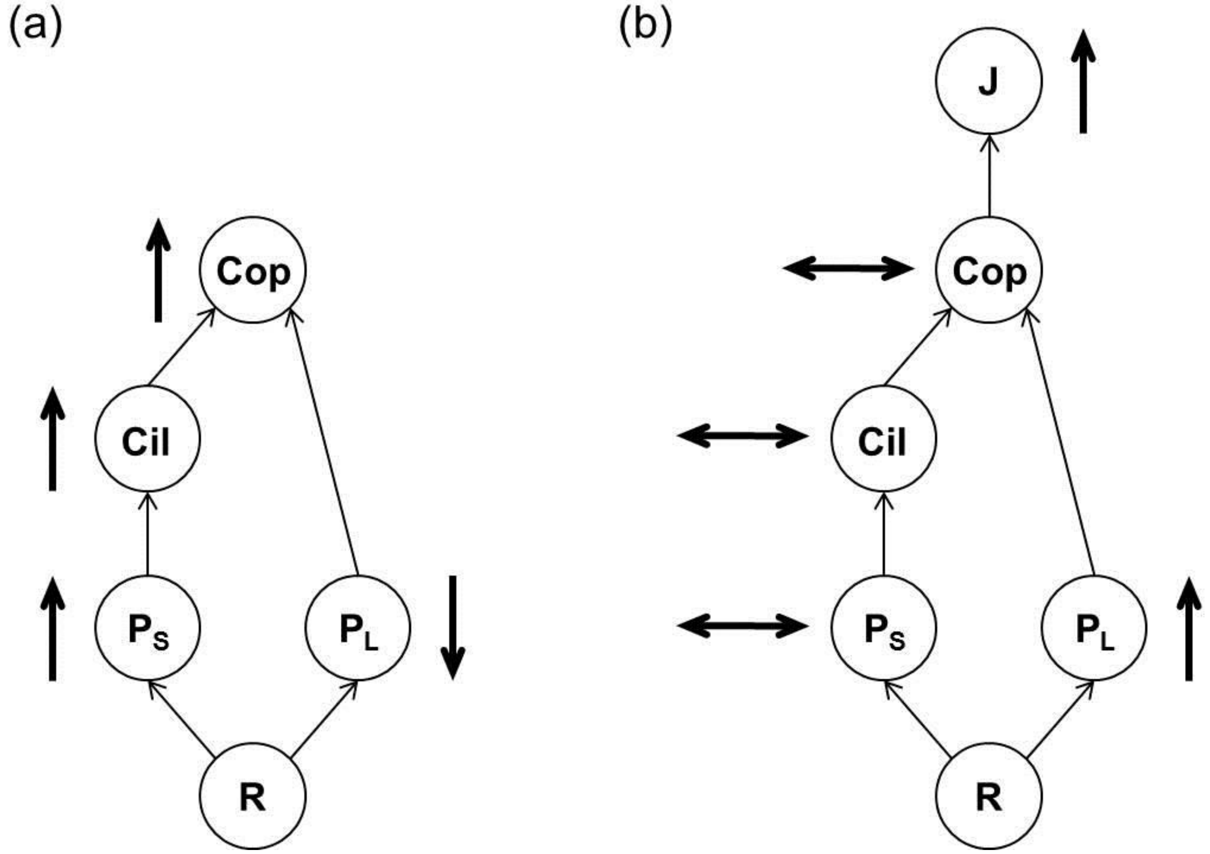


Figure 2

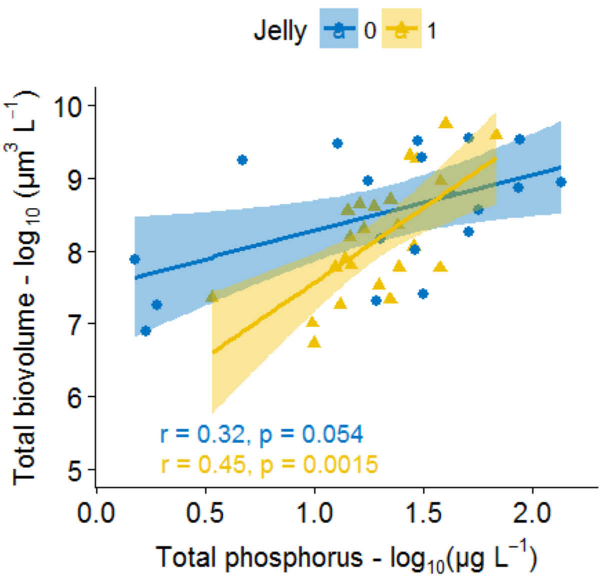

Jelly
0
1
Total biovolume - $\log_{10}$ (μm^3 L^{-1})
10
9
8
7
6
5
r = 0.32, p = 0.054
r = 0.45, p = 0.0015
0.0
0.5
1.0
1.5
2.0
Total phosphorus - $\log_{10}$(μg L^{-1})

Figure 3

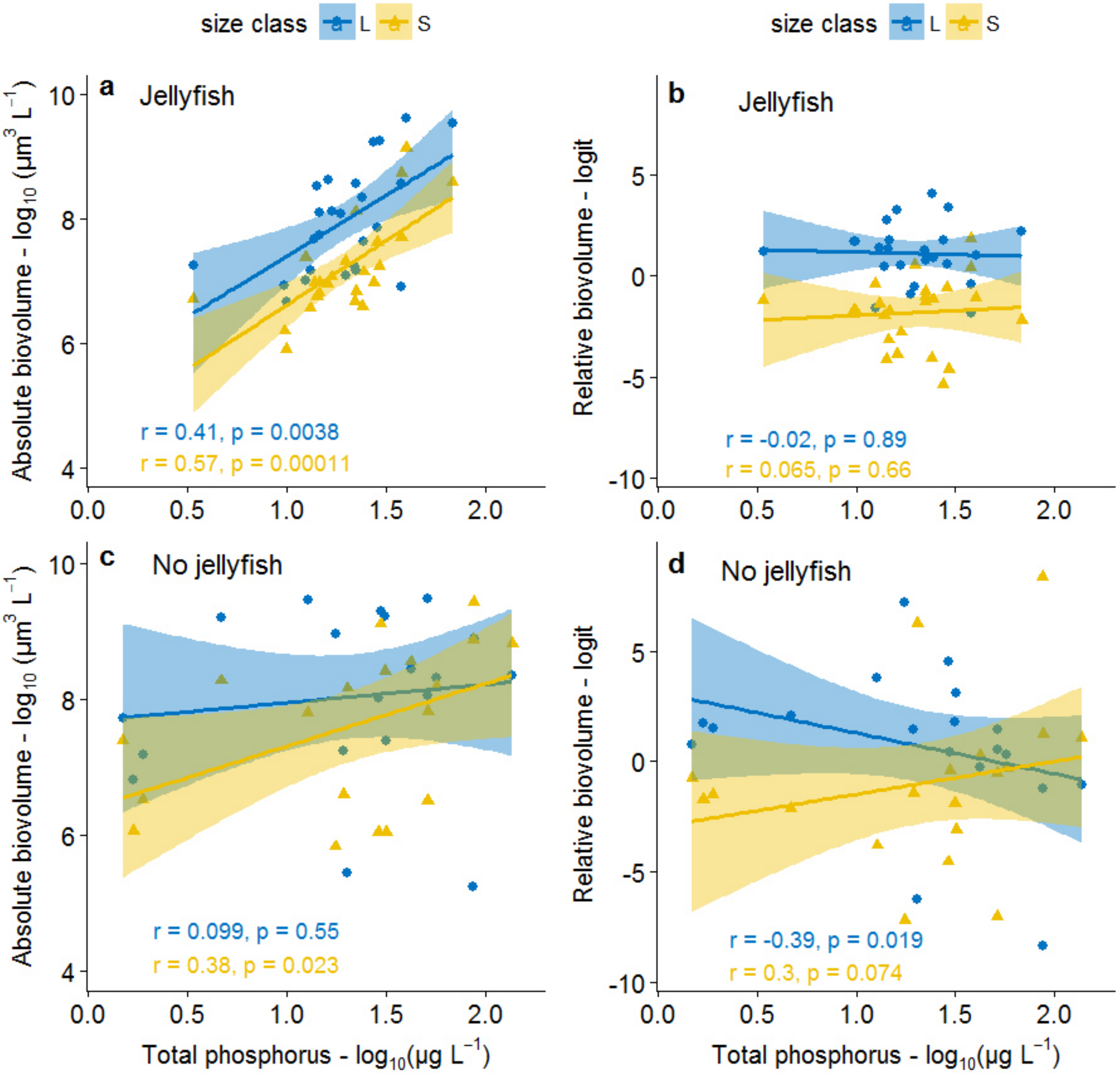
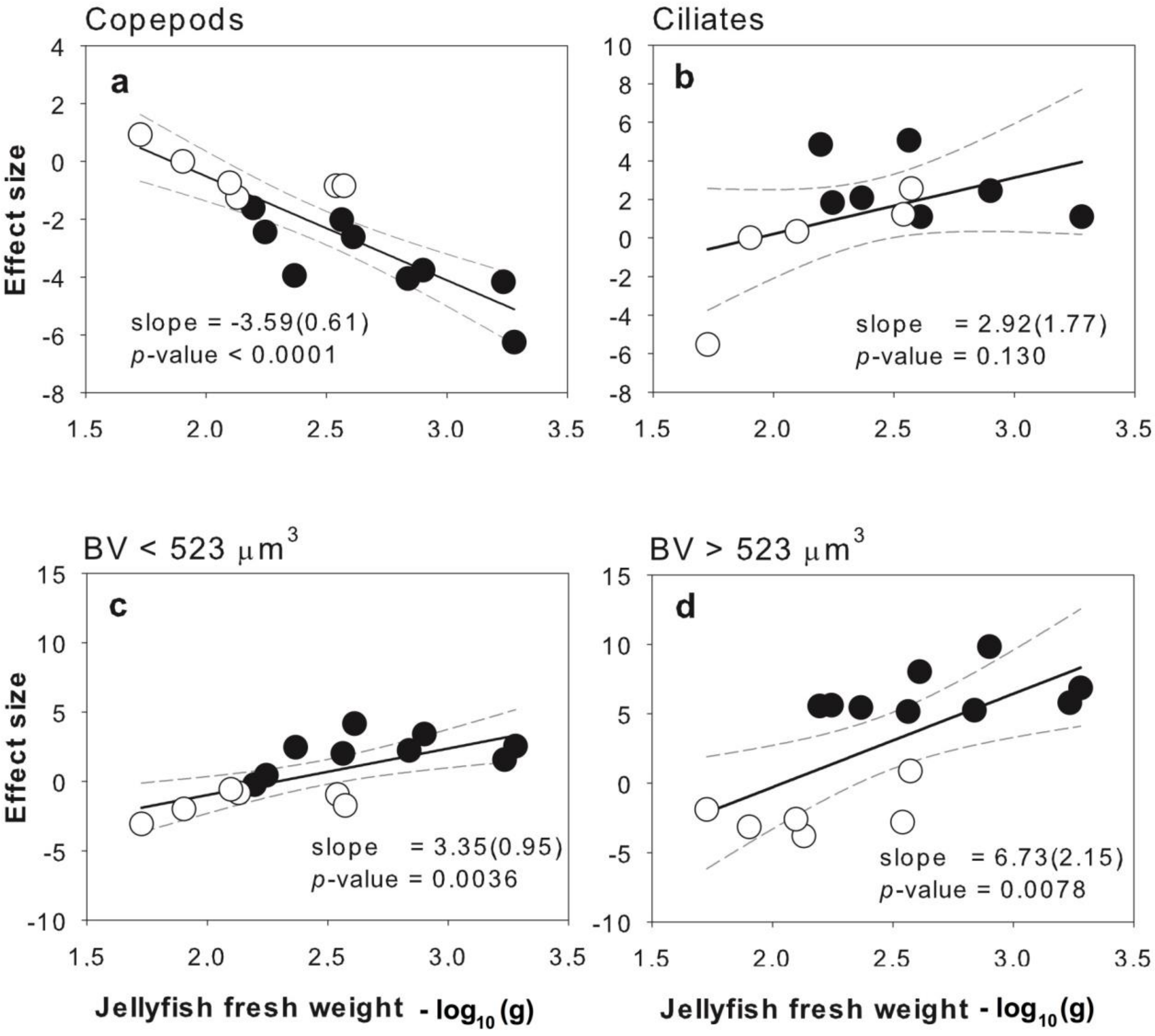

size class
L
S
size class
L
S
a
Jellyfish
b
Jellyfish
c
No jellyfish
d
No jellyfish
Absolute biovolume - $\log_{10}$ (μm^3 L^{-1})
Relative biovolume - logit
Absolute biovolume - $\log_{10}$ (μm^3 L^{-1})
Relative biovolume - logit
r = 0.41, p = 0.0038
r = 0.57, p = 0.00011
r = -0.02, p = 0.89
r = 0.065, p = 0.66
r = 0.099, p = 0.55
r = 0.38, p = 0.023
r = -0.39, p = 0.019
r = 0.3, p = 0.074
10
8
6
4
5
0
-5
-10
0.0
0.5
1.0
1.5
2.0
Total phosphorus - $\log_{10}$(μg L^{-1})
Total phosphorus - $\log_{10}$(μg L^{-1})

Figure 4


Copepods
Ciliates
a
b
c
d
BV < 523 μm3
BV > 523 μm3
Effect size
Jellyfish fresh weight - log10(g)
slope = -3.59(0.61)
p-value < 0.0001
slope = 2.92(1.77)
p-value = 0.130
slope = 3.35(0.95)
p-value = 0.0036
slope = 6.73(2.15)
p-value = 0.0078
4
2
0
-2
-4
-6
-8
10
8
6
4
2
0
-2
-4
-6
-8
15
10
5
0
-5
-10
1.5
2.0
2.5
3.0
3.5

481 Table 1. List of all sampling sites.

Year sampled	Name[a]	TP [µg/Liter]	Type	Jellyfish
2010	Mekeald	29.03	lake	No
2010	Ngchas	31.39	lake	No
2010	T Lake	51.23	lake	No
2010	Ngeruktabel	31.93	lake	No
2010	Spooky	136.83	lake	No
2010	Flatworm	29.83	lake	No
2010	Hot Water	20.32	lake	No
2010	Shrimp	87.73	lake	No
2010	Heliofungia	17.60	lake	No
2010	Ngel	19.45	lake	No
2011	Big crocodile	42.19	lake	No
2011	L-shape	51.38	lake	No
2011	Little crocodile	57.08	lake	No
2013	Lipstick	1.9	lake	No
2013	One Shark	4.7	lake	No
2013	Big Fish	12.8	lake	No
2013	Little Mangrove	1.5	lake	No
2013	IRO	1.7	lake	No
2013	Big Mangrove	87	lake	No
2010	Ulebsechel	24.09	Cove/lagoon	Yes
2010	Ongael	39.99	lake	Yes
2010	Ongeim’l Tketau (OTM)	29.32	lake	Yes
2010	Malakal Harbor	22.17	lagoon	Yes
2010	Short Drop-Off	9.76	lagoon	Yes
2010	Uet era Ngermeuangel (NLK).	28.66	lake	Yes

2010	Clear	37.74	lake	yes
2010	Goby	68.21	lake	yes
2010	Bablomekang	13.17	lagoon	yes
2010	German Channel	22.42	lagoon	yes
2010	Jurassic	9.98	Cove/lagoon	yes
2011	Ngelchael	22.34	lagoon	yes
2012	Long Lake/Bassin 1	27.49	lagoon	yes
2012	New 1	18.85	lake	yes
2012	New 2	37.85	lake	yes
2012	Secret	14.72	Cove/lagoon	yes
2012	Jurassic	12.49	Cove/lagoon	yes
2012	Lagoon 1	16.15	lagoon	yes
2012	Lagoon 2	13.87	lagoon	yes
2012	Lagoon 3	14.58	lagoon	yes
2012	Lagoon 3	24.43	lagoon	yes
2012	Lagoon 4	19.75	lagoon	yes
2012	Lagoon 4	16.85	lagoon	yes
2012	Lagoon 5	14.23	lagoon	yes
2013	Tarzan	3.4	lake	yes

[a] Reference: Colin (2009)

Supplemental Material S1

Differences in size distribution of marine phytoplankton in presence versus absence of jellyfish support theoretical predictions on top-down control patterns along alternative energy pathways

Marine Biology

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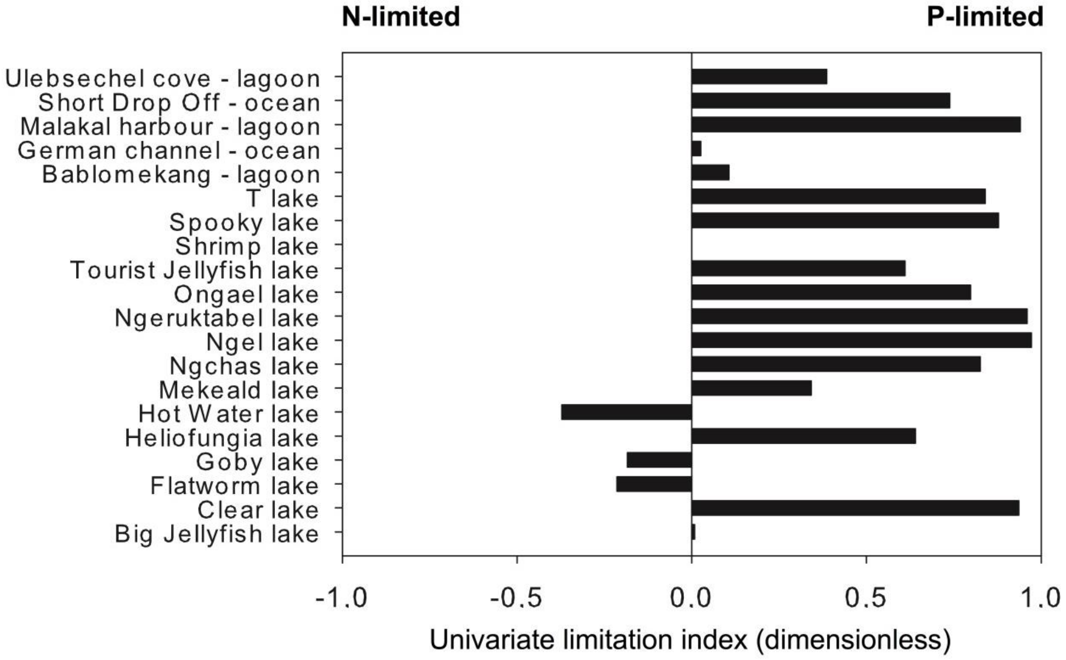

Fig. S1. Nutrient limitation for marine sites as indicated by bioassay experiments performed in Palau in 2010, following the modified procedure by Andersen et al. (2007) following Ptacnik et al. (2010). The x-axis represents the Univariate Limitation Index, ULI, which transforms the probabilities of N, P or the combined limitation of N and P into a one-dimensional scale (Ptacnik et al., 2010); a value of -1 (or +1) indicates that, during a bioassay, the phytoplankton community responded only to N (or P) addition. Conversely, when ULI= 0, this indicates that there is no nutrient limitation (i.e., there are no detectable differences between nutrient addition treatments and the control) or a combined N and P limitation (i.e., only the combined addition of N and P results in an increase in phytoplankton biomass).

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Supplemental material S2

Differences in size distribution of marine phytoplankton in presence versus absence of jellyfish support theoretical predictions on top-down control patterns along alternative energy pathways

Marine Biology

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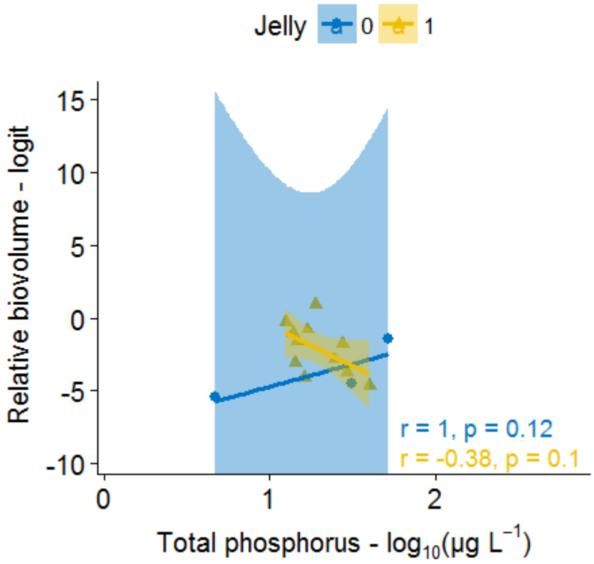

Fig. S2. Logit-transformed relative contribution of very large algae (> 73.000 m³). considered to be inedible. in presence vs. absence of jellyfish.

Supplemental Material S3

Differences in size distribution of marine phytoplankton in presence versus absence of jellyfish support theoretical predictions on top-down control patterns along alternative energy pathways

Marine Biology

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Table S3: Hydrological, physico-chemical, and biological characteristics of the experimental lakes measured during the experimental periods in 2010 (OTM) and 2011 (NLK). Surface temperature and salinity are averages of upper water layers (0-5 meter), the PAR attenuation coefficient is integrated from 0-10m water depth.

	Ongeim'l Tketau (OTM)	Uet era Ngermeuangel (NLK)
Estimated age (years)	10.000	12-15.000
Volume [10^6 m³]	1.087	1.188
Surface area [10³ m²]	62.0	44.6
Mean / max. depth (m)	12.5 / 32.5	20.3 / 38.4
Surface temperature [°C]	31.8	32.5
Salinity [PSU]	28.4	22.2
Mixing regime[a]	Meromictic, chemocline at 15 m depth	Meromictic, chemocline at 17 m depth
Tidal lag time [min]	ca. 136	ca. 190
Total phosphorus [µg L^{-1}]	29.3	28.7 (2010)
PAR attenuation coefficient [m^{-1}]	0.30	0.10
Mastigias abundance [L^{-1}][b]	0.0028-0.025	No data, abundant, but less than in OTM
Aurelia sp. abundance	No data; low	No data; high
Copepod abundance [L^{-1}][c]	0.84	0.41
Chl a [µg L^{-1}]	1.71	1.26

[a] Data from Dawson and Hamner (2003)

[b] Data from CRRF (annual means 2000-2004) and M. N. Dawson (pers. comm.)

[c] Unpublished data from 2010 and 2011 (Stibor, pers. com.)