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Bottom-up behaviourally mediated trophic cascades in plankton food webs

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Our traditional view of the interactions between marine organisms is conceptualized as food webs where species interact with one another mainly via direct consumption. However, recent research suggests that understudied non-consumptive interactions, such as behaviourally mediated indirect interactions (BMIs), can influence marine ecosystems as much as consumptive effects. Here, we show, to our knowledge, the first experimental evidence and quantification of bottom-up BMIs in plankton food webs. We used observational, modelling and experimental approaches to investigate how behavioural responses to resource availability influence predation mortality on grazers with different foraging strategies (ambushing versus active foraging). A three-level food chain was used: phytoplankton as resource, copepod nauplii as grazers of phytoplankton and a large copepod as a predator. Ambushers showed little change in foraging activity with resource availability, whereas active foragers decreased their foraging activity with increasing resources, which led to a decrease (24–50%) in predation mortality. Therefore, an increase in resources ('initiator') causes behavioural changes in active grazers ('transmitter'), which ultimately negatively affects predator ('receiver') consumption rates. Consequently, increase in resource abundance may result in decreasing energy transfer to higher trophic levels. These results indicate that behaviourally mediated interactions drive marine food web dynamics differently from that predicted by only density-mediated or consumptive interactions.

1. Introduction

Ecological studies on species interactions have traditionally focused on interactions where one species changes the abundance of another species directly by consumption or indirectly by density-mediated trophic cascades [1,2]. However, it has now been generally recognized that predators not only affect prey density but also may induce changes in prey traits that can propagate to species elsewhere in the ecosystem, i.e. trait-mediated indirect interactions [1–4]. A specific type of such interaction is behaviourally mediated indirect interaction (BMI), which occurs when changes in the property of one species ('initiator') alter the behaviour of a second species ('transmitter'), and these behavioural changes, in turn, influence a third species ('receiver') [2,5]. A clear example of top-down BMI is the influence of fear or predation risk from large carnivores ('fear factor') on the foraging behaviour of herbivores or mesocarnivores, which may benefit plants or mesocarnivores' prey [6,7]. These top-down BMIs are independent of the number of prey directly consumed by the top predator. Resource availability can also affect foraging behaviour [8–11], and probably affects forager's predation risk. This suggests that bottom-up BMIs can also substantially affect ecosystem dynamics. Although there is some empirical evidence of bottom-up BMIs [12,13], these interactions have received less attention than top-down BMIs [3,5].

The trade-off between food intake and predation risk is probably one of the main mechanisms that drive BMI. In most animals, feeding is dangerous owing to the increase in predation risk associated with foraging activity [14–17]. Thus, many animals face the fundamental dilemma of obtaining enough food without being eaten [8,18,19]. From an evolutionary perspective,

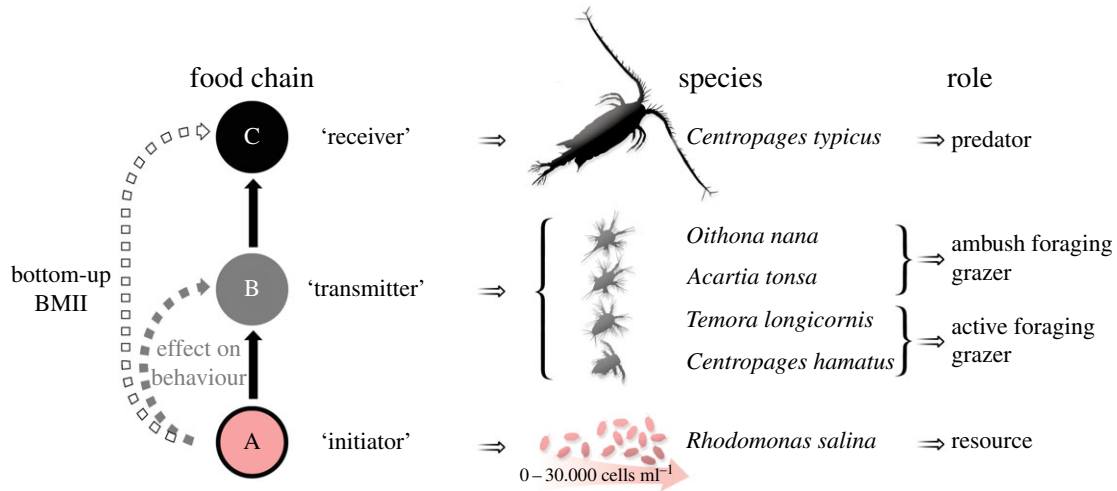


Figure 1. Scheme of the behaviourally mediated indirect interaction (BMII) investigated in this study: resource availability ('initiator', A) causes behavioural changes on grazers ('transmitter', B), which, in turn, affects predator ('receiver', C) consumption rates. Experimental organisms and their role in the interactions in the model food chain are indicated in the scheme. Solid arrows indicate the direction of energy transfer owing to consumption. The grey dashed arrow indicates an effect of species A on the behaviour of species B, and the open dashed arrow indicates the BMII (from the initiator to the receiver). (Online version in colour.)

adaptive behaviours should balance the conflicting demands for food (effective foraging) and safety (predation avoidance) to maximize the energy gain over mortality cost [20,21]. Behavioural responses to variability in resource availability or predation pressure may thus strongly affect an organism's fitness as well as species' interactions and trophic transfer of energy in natural communities [22,23], but empirical demonstration and quantification of these interactions in marine plankton food webs are still limited.

Among marine food web components, zooplankton holds a key position as both major grazers of phytoplankton (primary producers) and as main prey of higher level consumers [24–26]. Zooplankton foraging behaviours can be classified into two main strategies in terms of motility: 'sit-and-wait' (ambushing) versus 'searching' (active foraging). These contrasting foraging strategies have different cost-benefits in terms of predation mortality-feeding efficiency: active foraging is a more efficient strategy to obtain non-motile prey, but it is also a more risky strategy in terms of predation than ambushing [27–29]. We hypothesize that while in most zooplankton the foraging strategy (active foraging or ambushing) is fixed, the trade-off between food intake and predation mortality may be further shaped by an adaptive behavioural response depending on the foraging behaviour and resources availability. Models of optimal foraging predict that ambushers have an invariant foraging behaviour in relation to resource concentration [21,30], and hence we could expect an invariant predation mortality with food availability. By contrast, foraging activity, and hence mortality risk, in active foragers is expected to vary with resource availability: (i) it is low at low resource concentrations where feeding may not be warranted altogether owing to a negative energy balance, (ii) increases with resource availability, and (iii) decreases at high (saturation) food concentrations in the presence of predators or predator cues [9,21,30–32]. Thus, we could expect a bottom-up BMII where changes in foraging behaviour of active foraging zooplankton (transmitters) in response to resource availability (initiator) would cause effects at higher trophic levels (receivers) in marine food webs. Given the pronounced temporal variability in phytoplankton availability in the pelagic environment [33,34], the proposed bottom-up

BMII would significantly shape trophic interactions and energy transfer in marine plankton food webs, yet empirical studies are non-existing [5].

In this study, we experimentally examine bottom-up BMII in plankton food webs. Specifically, we investigate how behavioural responses of zooplankton to resource availability influence predation risk in zooplankton with different foraging strategies (ambushing versus active foraging) (figure 1). We used a linear three-species food chain, as a model, with phytoplankton as resource (initiator), copepod nauplii as grazers of phytoplankton (transmitters) and a large rheotactic copepod as a predator (receiver) (figure 1). Our specific hypotheses are that: (i) foraging behaviour is independent of resource availability for ambushers but decreases at low and high resource concentrations for active foragers, and (ii) changes in resource-dependent foraging behaviour significantly affect predation risk in active foragers; (iii) consequently, predator's consumption rates are indirectly reduced when there is an increase in resources owing to BMII. Our result will help to understand how BMII can affect trophic transfer in plankton food webs depending on grazer's foraging strategy and resource availability.

2. Methods

(a) Experimental organisms

We used the autotrophic flagellate *Rhodomonas salina* as resource (figure 1). We used, as grazers of *R. salina*, similarly sized nauplii (table 1) of the copepods *Temora longicornis* and *Centropages hamatus* as active feeders and nauplii of *Acartia tonsa* and *Oithona nana* as ambush feeders (figure 1). We used the planktonic copepod *Centropages typicus* (figure 1) as a predator of nauplii. The organisms used in this study were obtained from continuous stock cultures at DTU Aqua. *Rhodomonas salina* was kept in exponential growth in B1 medium [35] at 18°C. All copepod species were kept in culture at 15–18°C and fed with a mixture of cultured plankton as described in Almeda *et al.* [36]. We obtained cohorts of similarly sized naupliar stages by separating adults from the stock culture with 100–200 µm mesh-sieves and placing them in a new tank. After 24–48 h, eggs or early nauplii were isolated. Copepod nauplii were fed with *R. salina* ad libitum and grown at 15°C in the dark until the desired size was reached.

Table 1. Overview of experimental conditions in: (i) the behavioural study to determine the resource (initiator, *Rhodomonas salina*) density-dependent behaviour of copepod nauplii (transmitters, *Temora longicornis*, *Centropages hamatus*, *Oithona nana* and *Acartia tonsa*) with different foraging strategies, and (ii) the predation experiments conducted to measure predation mortality of copepod nauplii (transmitters) with different foraging strategies from *Centropages typicus* (receiver) with variation in resource density.

foraging strategy	grazer species	behavioural observations				predation experiments						
		grazer size (prosome length, $\mu\text{m} \pm \text{s.d.}$)	grazer density (n ml^{-1})	resource size (ESD, $\mu\text{m} \pm \text{s.d.}$)	resource density (cells ml^{-1})	grazer size (prosome length, $\mu\text{m} \pm \text{s.d.}$)	grazer density (n l^{-1})	predator size (prosome length, $\mu\text{m} \pm \text{s.d.}$)	resource size (ESD, $\mu\text{m} \pm \text{s.d.}$)	resource density (cells ml^{-1})		
active (feeding-current)	<i>T. longicornis</i>	178.7 \pm 9.3	1.9	7.9 \pm 1.2	0	187.5 \pm 18.8	50	1100 \pm 45	7.9 \pm 1.2	0		
				945						3780		
				3780						30 000		
active (breast strokes)	<i>C. hamatus</i>	160.9 \pm 17.3	1.3	8.1 \pm 1.2	0	176.9 \pm 17.7	50	1040 \pm 57	7.8 \pm 1.0	0		
				338						1354		
				1354						30 000		
ambush	<i>O. nana</i>	118.2 \pm 12.6	1.9	8.0 \pm 1.2	0	151.1 \pm 16.4	50	984 \pm 11	7.5 \pm 0.9	0		
				321						1285		
				1285						30 000		
ambush	<i>A. tonsa</i>	118.8 \pm 10.9	1.5	8.1 \pm 1.1	0	126.2 \pm 67.2	50	1065 \pm 49	7.6 \pm 1.0	0		
				500						2000		
				2000						30 000		

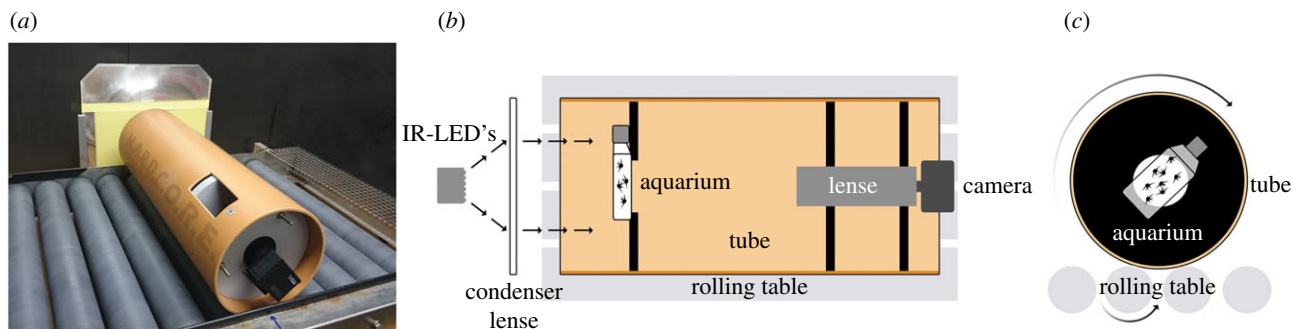


Figure 2. Experimental set-up during the video observations. Picture (a) shows the top/front view of the set-up. The schematic of the top view (b) shows a transect of the set-up: the camera and aquarium (containing copepods (transmitter) and *R. salina* (initiator)) are fixed in the tube and placed on a rolling table. Infrared (IR) illumination is collimated and is provided from the back. (c) The view on the back of the set-up shows the direction of rotation and the position of the aquarium, fixed on a mount in the tube. (Online version in colour.)

(b) Behavioural observations: effect of resource availability on grazer behaviour

Through video-observations, we quantified the behavioural response of copepod nauplii with different foraging strategies to resource concentration. The behavioural response was filmed at 15°C in the dark at 90 frames s⁻¹ and a resolution of 1920 × 1080 pixels. We used a modified infrared (IR) sensitive GoPro Hero4 camera (installed with a Back-Bone Ribcage C-mount and with the IR-cut filter taken out) equipped with a 55 mm lens. A 67.5 ml Nunclon bottle filled to the rim and closed was used as an aquarium. The field of view was 8.5 × 4.8 mm² for *T. longicornis* and *C. hamatus* and 11.7 × 6.6 and 16.6 × 9.4 mm² for *A. tonsa* and *O. nana*. Both the camera and the aquarium were mounted in a tube and placed on a rolling table (figure 2). The rotation velocity was kept low (0.4 rpm⁻¹) to minimize disturbances that may affect copepod behaviour, but high enough to keep the copepods and its resource (*R. salina*) in suspension. The aquarium was illuminated from the back by 25 stationary IR-LEDs and the light was collimated by a condenser lens.

Behaviour of the grazers was filmed at four different resource concentrations, ranging from 0 to 30,000 cells ml⁻¹ (table 1). These concentrations were chosen to include both the concentration where feeding effort is expected to be at a maximum (intermediate resource concentrations) and at satiating concentration based on previous grazing experiments [36]. All animals were picked individually to ensure a consistent body size between individuals. Nauplii were added to the resource suspensions 30 min prior to filming and acclimated under experimental conditions. Three replicates per treatment were prepared and each replicate was filmed during 15 min. After termination of filming, 35 individuals per species were preserved in 1% Lugol's solution to determine their sizes (total body length and maximum width).

We distinguished between the following behaviours: (i) 'swimming' behaviour of active foragers by (a) the generation of a feeding current (feeding bouts) (*T. longicornis*) or by (b) breast stroke swimming (*C. hamatus*), (ii) relocation 'jumps' (*O. nana* and *A. tonsa*), (iii) 'prey capture' events (consisting of consecutive breast-strokes) (*C. hamatus* and *A. tonsa*), and (iv) 'sinking' events. For each species, we analysed the frequency, duration, velocity and time budgets of each type of behaviour for a number of swimming tracks (see below), each lasting between 2 and 116 s. In total, ca 12 000 s of observations were used for the analysis, corresponding to a total of one million frames.

For the ambush foragers *O. nana* and *A. tonsa*, the jump frequency ($n \text{ min}^{-1}$) was determined for 40–60 tracks per food concentration by manual frame-by-frame analysis. Furthermore, the average jump duration (s) and distance (mm) were determined at each concentration from 40 events (from eight animals, five events per animal). For *C. hamatus*, the breast-stroke frequency ($n \text{ min}^{-1}$), the duration (s) and distance (mm) of individual breast

strokes were recorded. For *T. longicornis*, we recorded the frequency ($n \text{ min}^{-1}$) and duration (s) of feeding bouts. For each active forager, we analysed 20–30 tracks per food concentration. For all species, all events of sporadic behaviour ('jumping' for *T. longicornis* and *C. hamatus*, 'prey capture' for *C. hamatus* and *A. tonsa*) were quantified.

Finally, we calculated the speed (mm s⁻¹) and time budget (% of occurrence of total track duration) for swimming, jumping or prey capture events for each track. For *T. longicornis* swimming speed was taken from van Someren Gréve *et al.* [28]. By assuming isotropic swimming directions, we estimated the mean three-dimensional velocities for all behaviours by multiplying the observed two-dimensional average velocities with a conversion factor $4/\pi$ (see the electronic supplementary material, calculation S1 for the mathematical consideration).

(c) Model estimations: effect of resource availability on grazer's predation risk

We used a behaviour-dependent predator encounter model similar to that of van Someren Gréve *et al.* [28] to estimate the predation risk associated with the observed behavioural response of nauplii to resource availability. We used, as input to the encounter model, the parameters quantified in this study from behavioural observations of the studied grazers under four different resource concentrations (table 1). Data on behavioural parameters for the predator were taken from van Someren Gréve *et al.* [28].

Briefly, the encounter model considers the velocity difference between the copepod and its predator as derived from behavioural observations, and encounter sizes based on hydrodynamic disturbances generated by the copepod and the perceptive capabilities of the predator. Different from the directly measured predation mortality, this model does not take into account the capability of the predator to capture copepod nauplii or the actual ingestion of nauplii.

Thus, the predation risk, expressed as the potential predator's clearance rate, β , is then

$$\beta = \beta_{\text{active}} + \beta_{\text{sinking}}, \quad (2.1)$$

$$\begin{aligned} \beta_{\text{active}} = & p_{\text{swim}} \pi (R_1 + R_2)^2 (u^2 + v_{\text{swim}}^2)^{0.5} \\ & + p_{\text{jump}} \pi (R_1 + R_2)^2 (u^2 + v_{\text{jump}}^2)^{0.5} \\ & + p_{\text{prey capture}} \pi (R_1 + R_2)^2 (u^2 + v_{\text{prey capture}}^2)^{0.5} \end{aligned} \quad (2.2)$$

$$\text{and } \beta_{\text{sinking}} = (1 - p_{\text{swim} + \text{jump} + \text{prey capture}}) \pi (R_1 + R_3)^2 u, \quad (2.3)$$

where β is the volumetric encounter rate between the copepod and its predator (\sim predator clearance rate, ml predator⁻¹ d⁻¹), p_{swim} , p_{jump} and $p_{\text{prey capture}}$ are the fractions of the time that the copepod produces a hydrodynamic disturbance owing to

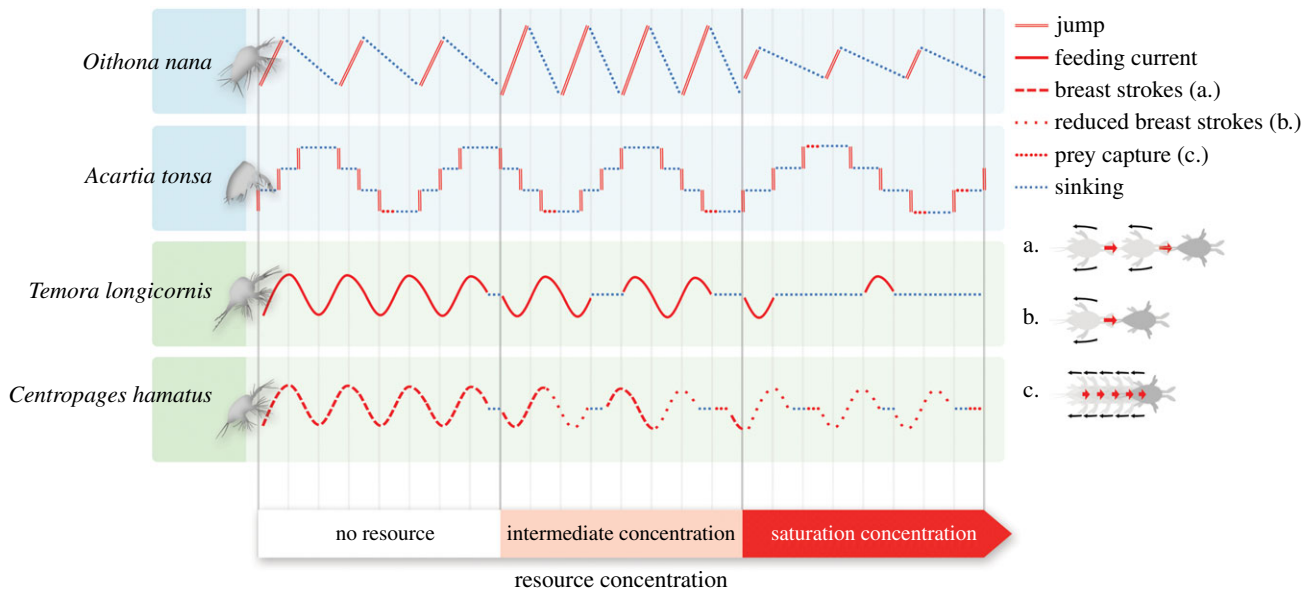


Figure 3. Schematic summary of the observed behavioural response of copepod nauplii (transmitter) with different foraging strategies in response to variation in resource (initiator) concentration. Red indicates activity related to swimming, feeding or relocation, blue indicates sinking. The x -axis represents the relative time, length of each line represents the relative distance. Schematics are based on observed changes in behaviour (electronic supplementary material, tables S1 and S2) for each species. (Online version in colour.)

swimming, jumping or capturing/attacking a prey item, respectively. Furthermore, u is the predator swimming velocity (cm d^{-1}), v is the copepod swimming, jumping or prey capture velocity (cm d^{-1}), R_1 is the predator encounter-radius (cm), R_2 is the spatial extension of the hydrodynamic disturbance that the copepod generates when it swims or jumps ('hydrodynamic radius') (cm) and R_3 is the radius of the copepod when it does not produce a hydrodynamic disturbance ('physical radius') (cm). We further assume a similar threshold fluid velocity as in van Someren Gréve *et al.* [28] for prey detection by a predator, equal to 0.5 mm s^{-1} , to estimate the hydrodynamic radius from experimental observations [14].

(d) Predation experiments: effect of resource availability on grazer's predation mortality

We experimentally quantified predation mortality on grazers by exposing copepod nauplii (transmitter) to the predatory copepod *C. typicus* (receiver) at different resource (initiator) concentrations. We used nauplii densities well below the food saturation density for the predator *C. typicus* [29], and resource concentrations between 0 and 30 000 *R. salina* cells ml^{-1} , as in the video filming experiments (table 1). Prior to each experiment, *C. typicus* adult females were starved for 24 h. Copepod nauplii were picked individually, rinsed on a $40 \mu\text{m}$ mesh with filtered seawater and added to 1.11 bottles containing the appropriate range of resource concentrations (six bottles per concentration). Two *C. typicus* were added to four of the bottles and two bottles with *R. salina* and nauplii only served as controls. The bottles were mounted on the rolling table (at 0.4 rpm^{-1}) and incubated in the dark for 24 h at 15°C . At termination of the experiment, the contents of each bottle were filtered through a $40 \mu\text{m}$ mesh, checked for mortality of nauplii and predators and preserved in 1% Lugol's solution. Nauplii total length and maximum width were determined for 35 individuals per species. For *C. typicus*, prosome length and width were measured for all experimental individuals.

Predation mortality, expressed as the rate at which the nauplii are cleared from the water (clearance rate) by the

predator (β , $\text{ml predator}^{-1} \text{ d}^{-1}$), was calculated according to Titelman [37]:

$$\beta = \frac{(\ln(n_{\text{start}}) - \ln(n_{\text{end}})) \times V}{n_{\text{pred}} \times \Delta t}, \quad (2.4)$$

where n_{start} and n_{end} are the number of nauplii at start and end of each incubation, respectively, n_{pred} is the number of predators per bottle, Δt is the incubation period (d) and V is the bottle volume (ml).

We conducted an analysis of variance (ANOVA and Tukey post hoc test) to determine the significance level ($p < 0.05$) of differences in motility parameters, predicted predation risk and measured predation mortality between treatments, depending on food concentration.

3. Results

(a) Behavioural response of grazers to resource availability

Copepod nauplii showed different behavioural responses to resource (initiator) availability (figure 3). Among ambush foragers, *O. nana* displayed significant differences in jump frequency, jump duration and jump length between resource concentrations (electronic supplementary material, table S2). The highest jump frequency and the longest jumps were observed at a low resource concentration, and a lower frequency and shorter jumps both in the absence of resource and at higher resource concentrations (figures 3 and 4a; electronic supplementary material, table S2). Nauplii of *A. tonsa* typically moved in a helical pattern by frequent relocation jumps (figures 3 and 4b). We found no consistent variation in jump frequency, jump length or jump duration with variation in resource density (figure 4b; electronic supplementary material, table S2). The active foraging *T. longicornis* swam slowly in meandering paths by creating a feeding current (figure 3). However, it gradually reduced the swimming

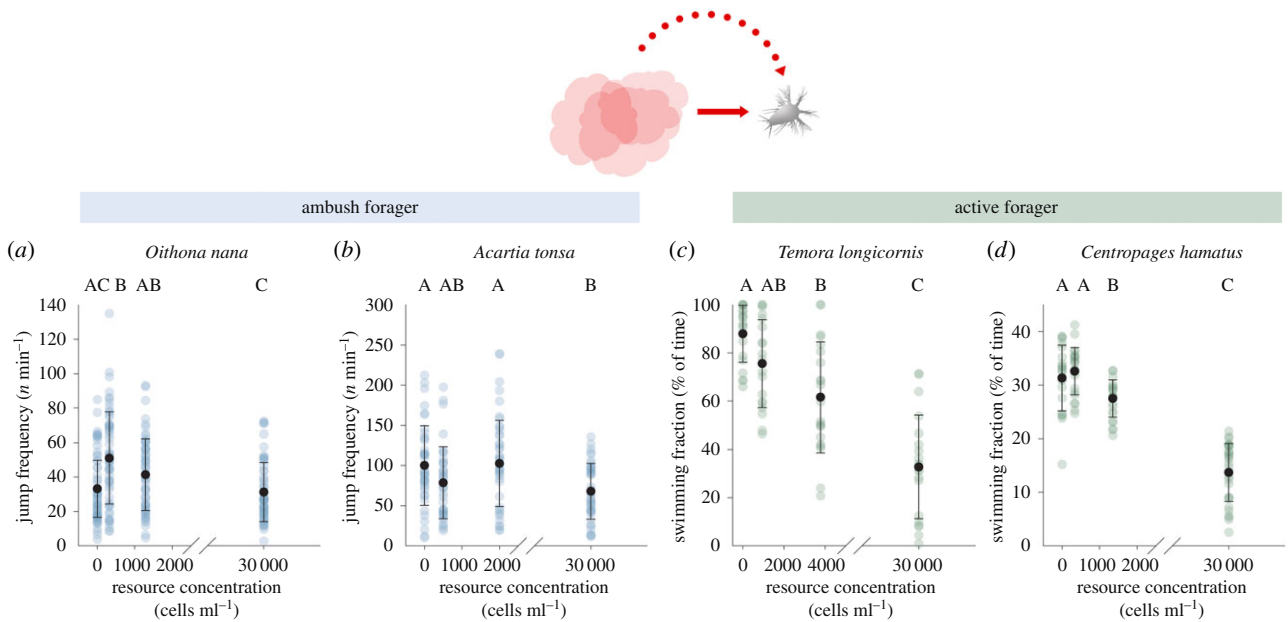


Figure 4. Behavioural response of grazers to resource concentration. The illustration above the panels shows schematically the studied process, where the solid red arrow indicates the direction of energy transfer and the dashed red line indicates the effect of food availability on grazer's behaviour, which is presented in the panels. Panels (a) and (b) show the jump frequency of ambush foragers, panels (c) and (d) the swimming fraction of active foragers in relation to resource availability. Coloured data points correspond to individual track averages, black data points correspond to the average value per resource concentration \pm s.d. Different letters indicate statistically significant difference in behaviour between resource concentrations. (Online version in colour.)

activity by decreasing the fraction of the time it produced a feeding current from 88% in the absence of food to 33% at the saturation concentration (figures 3 and 4c; electronic supplementary material, table S1). This reduction was realized both by decreasing the feeding bout duration and frequency (electronic supplementary material, table S2). *Centropages hamatus* typically swam in helical paths by repeated breast strokes (figure 3). It reduced the fraction of time swimming with increasing resource concentration from 31–33% in the absence of resource and at the lowest concentration to 14% at the saturation concentration (figures 3 and 4d; electronic supplementary material, table S1); this decrease was accomplished by decreasing the breast-stroke frequency and duration (electronic supplementary material, table S2). Prey capture events were most frequently observed at the highest resource concentration (electronic supplementary material, table S2). Despite the different behavioural responses among species, two contrasting behavioural patterns of foraging effort ('activity') to resource density emerged depending on the foraging strategy: (i) small variations in foraging activity in relation to resource density in ambush foragers, and (ii) a clear decrease in foraging activity with increasing resource density in active foragers (figure 4).

(b) The effect of resource density on grazers predicted predation risk and measured predation mortality

Predicted predation risks (figure 5a–d) mimic the food concentration dependency of the foraging activity of the copepods (figure 4) and were largely confirmed by the experimentally determined predation mortality (figure 5c–f). Thus, in the two actively foraging species (*T. longicornis* and *C. hamatus*), both predicted predation risk and measured predation mortality decreased significantly with food concentration by about a factor of two for *T. longicornis* and somewhat less for *C. hamatus*. Among ambush foragers, predation in *O. nana*

was highest at intermediate food concentrations, and lower at both no food and higher food concentrations, both according to the measurements and the predictions (figure 5a,e). For *A. tonsa*, the behaviour-dependent model prediction failed to reproduce the significant increase in predation risk with food concentration determined experimentally (figure 5b,f). Despite the general consistency between food concentration-dependent changes in the measured predation mortality on the one hand, and changes in predation risk predicted from behavioural observations on the other, the model generally underestimated the magnitude of predation mortality (electronic supplementary material, figure S1). Overall, we found two different patterns in terms of variation in both predicted predation risk and observed predation mortality with variation in resource density: (i) no effect or an increase in predation with increasing resource density in ambush foragers, and (ii) a decrease in predation by up to 50% with increasing resource density in active foragers (figure 5).

4. Discussion

There is increasing awareness that prey–predator interactions cannot be simply captured by assuming that population densities are the only dynamic factors that govern the intensity of trophic interactions [2]. Complex interactions between trophic levels may emerge from plasticity in individual traits, in particular modifications of foraging behaviour [3]. Across ecosystems it has been demonstrated that, in the presence of predator cues, a consumer may modify its foraging behaviour to one that is less risk-prone, but less efficient in terms of feeding [8,23,38–40]. As a consequence, the mere presence of predators can have an indirect top-down impact on food web dynamics, or 'top-down' BIII complementary to direct, density-dependent effects on trophic interactions [3,6,41–45]. Also for various zooplankton, both laboratory and *in situ* studies have shown that the presence of predators can directly

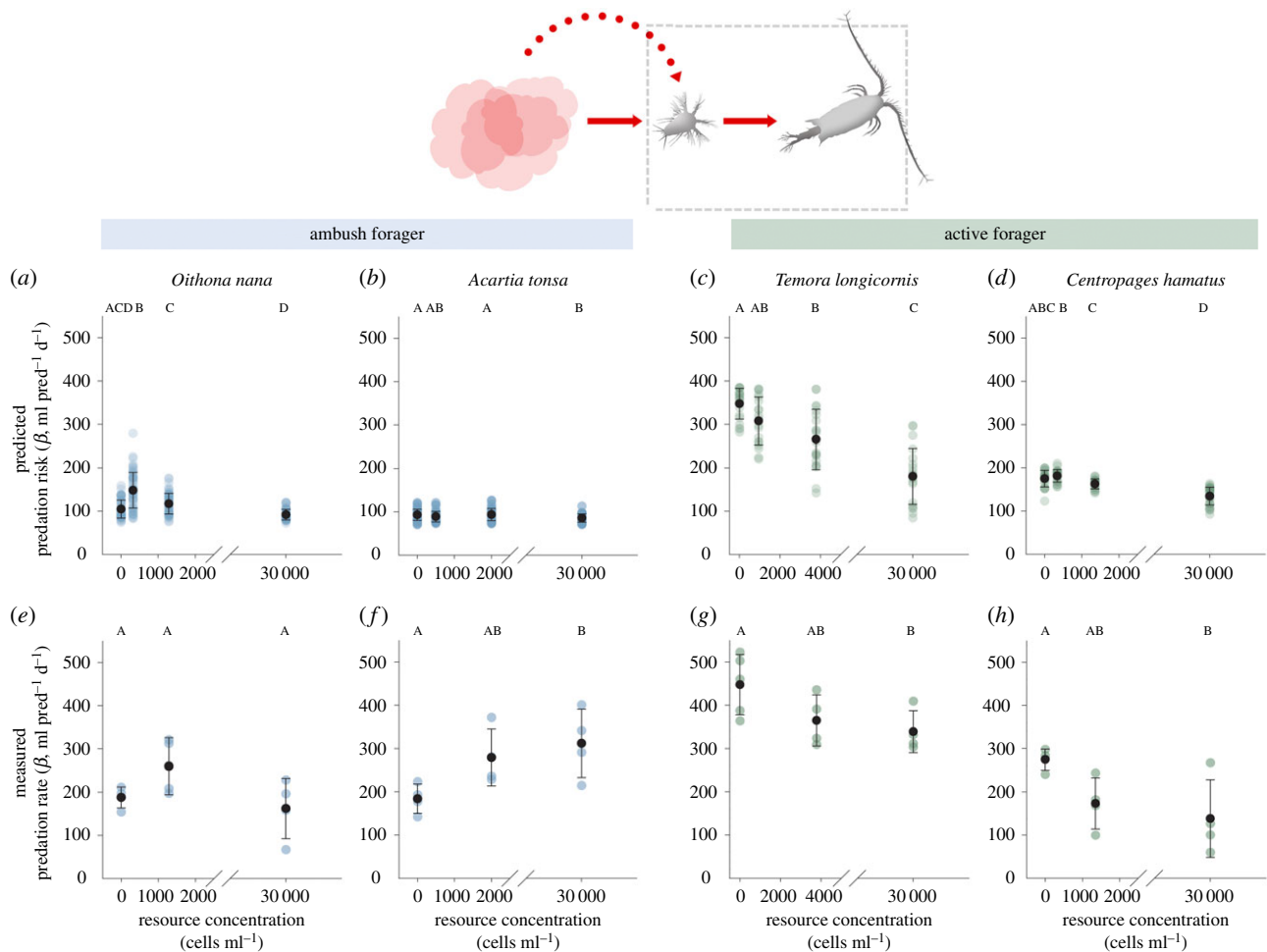


Figure 5. Predation rates depending on the behavioural response of grazers to resource concentration. The illustration above the panels shows schematically the studied process, where the solid red arrow indicates the direction of energy transfer and the dashed red line indicates the effect of resources on grazer's behaviour, which, in turn, affects predation on grazers. Predicted predation risk based on behavioural observations (*a–d*) and measured predation rates from bottle incubation experiments (*e–h*) of ambush and active foraging copepods (transmitter) from a predator (receiver) as function of resource (initiator) concentration. Coloured data points correspond to predicted risk based on individual track averages (*a–d*) or measurements from replicate bottles (*e–h*), black data points give the average value per resource concentration \pm s.d. Different letters indicate a statistically significant difference in predation risk/mortality between resource concentrations. (Online version in colour.)

influence behaviour [46–50] and grazing intensity [42,51], potentially leading to strong indirect top-down effects in the marine food web. Besides altered small scale foraging behaviour of the consumer, predator-induced consumer habitat shifts are often the cause of these top-down BMIs (reviewed by Trussell *et al.* [52]), which has been particularly well documented for zooplankton. Many zooplankton show diurnal vertical migration (DVM): they sacrifice feeding and leave the productive surface layer during the day to seek refuge from visual predators at depth, and the intensity of vertical migration may depend on the susceptibility to predation [53,54] and availability of food [55,56]. Less well studied are the indirect effects of resource availability on behaviourally mediated interactions in food webs, or 'bottom-up BMIs' [3]. These resource controlled multi-trophic cascades, mediated by behavioural plasticity have not, to our knowledge, been previously observed in marine environments, and have been only rarely demonstrated in other aquatic environments [12,13]. In this study we demonstrated that, depending on zooplankton foraging strategy, variation in resource availability can induce a bottom-up BMI by influencing zooplankton behavioural traits and ultimately predation rates of higher trophic level predators (figure 6). Owing to BMI, active grazers are

positively affected by increasing resources (phytoplankton), but predator's consumption rates are reduced and this may result in decreasing energy transfer to higher trophic levels (from grazers to predators) (figure 6).

Zooplankton foraging behaviour may significantly impact susceptibility to predators [28,29,37,57,58], but studies describing the behavioural response of copepods to resource density are rare. Optimal foraging theory considering optimization of net energy gain and applied to free living zooplankton predicts that in active foragers, foraging activity is highest at intermediate resource concentrations, and lower at both higher and lower resource availability, while in ambush foragers, foraging activity is independent of resource availability [30]. We did not observe—contrary to our hypothesis—reduced foraging activity at the lowest resource concentrations in active foragers, but rather a steady decline in foraging effort with increasing resource concentration (figure 3). A similar absence of reduced activity at low resource abundance has been found in other active foraging copepod species (see below), and may simply be because feeding and swimming are closely related processes in actively foraging copepods. A kinetic response with high motility at low food will allow the copepods to search for areas with higher food availability. There is substantial

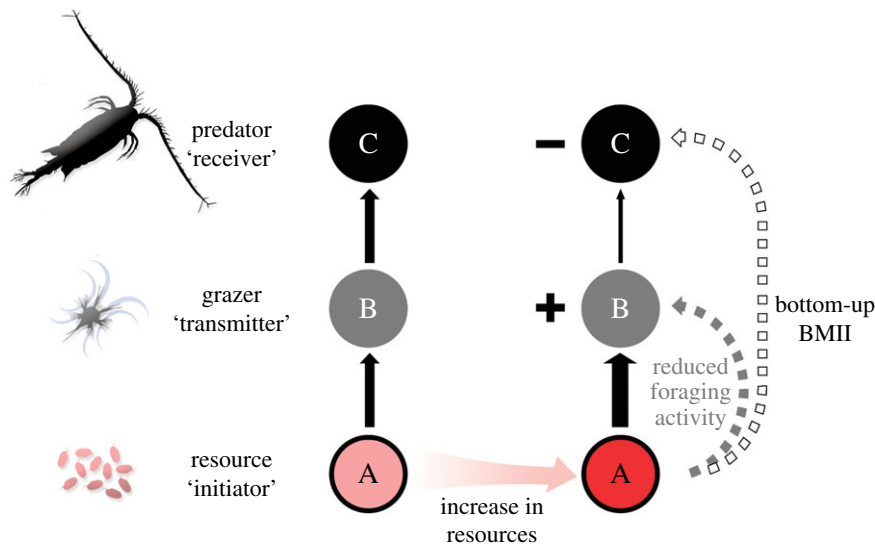


Figure 6. Schematic summary of the observed bottom-up BMI in a plankton food chain and their implications for the transfer of energy up trophic levels. Increases in resources (A) result in a positive effect (+) on grazer (B) with an active foraging strategy (increased resource consumption and reduced predation mortality) but indirectly results in a negative (−) effect (lower consumption rate) on a higher level predator (C). Consequently, the transfer of energy to higher trophic levels (predators) is indirectly reduced when phytoplankton resources increase (bottom-up BMI). Solid arrows indicate the direction of energy transfer owing to consumption and the width of the arrows indicates if the transfer is reduced or decreased. (Online version in colour.)

evidence of a similar behavioural response to low food environments in other organisms that, often induced by a low energetic state of the animal, sacrifice vigilance and increase risk prone foraging behaviour, thus reflecting a trade-off between predation risk and starvation/growth [12,59,60]. Although no behavioural response to food availability is predicted by optimal foraging theory for ambush foragers, *O. nana* nauplii for unknown reasons showed elevated jump activity at intermediate resource concentration, while ambush feeding nauplii of *A. tonsa*, as expected, showed resource-concentration independent activity.

Similar and different behavioural responses to resource availability have been established previously for a limited number of active foraging copepod species and they may reflect different behavioural solutions to minimize the risk of starvation and predation and maximizing growth. Thus, adult *Acartia* spp. can reduce or completely stop the generation of a feeding current below a certain food concentration and switch to a passive, ambush foraging behaviour [30,58,61–63]. Similarly, adult *Centropages* spp. may reduce the time spent swimming at a low resource concentration [30,64,65]. Furthermore, van Duren & Videler [66] observed a small decrease in foraging activity with declining resource abundance in late naupliar stages of *T. longicornis* but no behavioural plasticity in early nauplii or copepodites in contrast to our findings. Paffenhöfer & Lewis [67] reported inconsistent behavioural changes in *Eucalanus pileatus*, where adults decrease while the late copepodites increase their foraging activity with decreasing resource concentration. Finally, for adult stages of *T. longicornis* [66], *Eucalanus elongates* [68] and *A. tonsa* [30], foraging activity is highest at intermediate food concentration and lower at both low and higher food concentrations, as predicted by optimal foraging theory. Thus, multiple studies have demonstrated that foraging and swimming activity in suspension feeding copepods vary with the availability of their resource. However, none of these studies have examined the implications of these changes in copepod foraging behaviour on predation risk.

Prey–predator interactions in traditional food web models are described considering population densities as the only dynamic variable, i.e. the density-dependent direct effects on the intensity of trophic interactions [2]. However, the observed variation in predation risk/mortality implies that variation in predation owing to bottom-up BMI is equally important or may oppose density-dependent direct effects on predation rates on copepods [29]. This nonlinear bottom-up trophic transfer suggests that our current understanding and predictability of food web interactions and bottom-up trophic transfer is insufficient, as indirect effects owing to trait plasticity are currently not considered in models of pelagic food webs.

5. Conclusion

Our results demonstrate that: (i) motile behaviour strongly determines predation risk from rheotactic predators; (ii) behavioural plasticity of active foragers in response to resource availability significantly affects its predation mortality; and (iii) high resource concentrations ('initiator') induce behavioural changes on grazers ('transmitter'), which ultimately reduces predation rates of a higher trophic level planktonic predator ('receiver') by up to 50%. Therefore, an increase in resources does not necessarily result in increased energy transfer to higher trophic levels in plankton food webs. These results emphasize the importance of identifying and quantifying behavioural traits and bottom-up-driven BMIs in plankton food webs to better understand and predict the structure and dynamics of marine ecosystems under varying environmental conditions.

Data accessibility. Supporting tables, figures and calculations have been included in the electronic supplementary material.

Authors' contributions. H.v.S.G. designed the experimental set-up for the behavioural study, conducted the behavioural study and predation experiments and analysed the experimental data. H.v.S.G., R.A. and T.K. contributed equally to the design of the study and data interpretation. All authors contributed to drafting and revising the manuscript.

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