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Upward phosphorus transport by *Daphnia* diel vertical migration

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Abstract

In many lakes, zooplankton show a distinct diel vertical migration (DVM) behavior, especially during periods of stratification. Excretion products of these zooplankton could potentially cause an upward nutrient transport and consequent nutrient enrichment for phytoplankton in the epilimnion. We quantified the upward transport of phosphorus by the cladoceran *Daphnia* DVM experimentally by adding a radioactive tracer (^{33}P) to the hypolimnion of large indoor mesocosms and measuring tracer accumulation in the epilimnion over time. During the daytime, when all *Daphnia* were found in the hypolimnion, no phosphorus transport from the hypolimnion into the epilimnion took place. As soon as the *Daphnia* started their upward migration, around dusk, we observed a continuous increase in phosphorus concentration in the epilimnion. The amount of phosphorus transported was in a biologically meaningful range. Our results strongly suggest that *Daphnia* vertical migration presents a continuous nutrient supply for the epilimnion.

Diel vertical migration (DVM) of zooplankton is one of the world's largest synchronized movements of animals (Hays 2003). It is a daily habitat shift of zooplankton from deeper water regions during the day to surface waters at night. DVM is a well-investigated phenomenon and both the ultimate and proximate reasons for this behavior have been elucidated (Ringelberg 1991; Lampert 1993; Loose et al. 1993). Previous DVM research has focused primarily on the ecophysiological consequences for the migrating zooplankton (Loose and Dawidowicz 1994; Reichwaldt et al. 2005), since environmental factors such as temperature or feeding conditions vary in different water layers. In contrast, there have been very few studies on the consequences of DVM for the dynamics of the pelagic ecosystem as a whole (Reichwaldt and Stibor 2005; Haupt et al. 2009). This is surprising since, considering the ecosystem-scale amount of biomass involved in DVM, it is likely that DVM also influences ecosystem dynamics.

Implications of DVM for ecosystem dynamics can be manyfold. DVM can influence phytoplankton dynamics by altering grazing patterns, by influencing zooplankton population growth (and thereby grazing pressure on phytoplankton), and by nutrient redistribution due to excretion of migrating zooplankton. DVM results in a discontinuous grazing pattern of zooplankton on phytoplankton in upper pelagic layers during the daytime. Theoretical models and some experimental evidence suggest that such a temporal refuge for algae can promote growth of certain algal species (Lampert et al. 1988; Reichwaldt et al. 2005), and actually increase the diversity of the phytoplankton community (Haupt et al. 2009). DVM also results in a lower growth rate of migrating zooplankton populations (Loose and Dawidowicz 1994), as animals stay in the colder hypolimnion during the daytime. This DVM directly decreases the grazing pressure on phytoplankton communities when lower zooplankton growth rates result in lower population densities. DVM may also result in nutrient transport and redistribution between deeper and upper water layers. This transport may affect the availability of limiting nutrients, such as phosphorus, and thereby influences the temporal and spatial growth dynamics of primary producers.

The interacting mechanisms by which DVM influences phytoplankton dynamics cannot be separated in nature. For example, grazing and release of nutrients are tightly coupled processes. However, to fully understand the consequences of DVM on phytoplankton dynamics, separate estimates are needed for the different mechanisms by which DVM influences pelagic food webs. Hence, detailed studies examining the effects of DVM on nutrients are needed. Although Lampert and Grey (2003) showed that *Daphnia* could transport nitrogen from the hypolimnion into the epilimnion, their study did not include DVM conditions.

Because of the permanent gravity-induced downward nutrient flux caused by sinking organisms and particles, nutrients tend to concentrate in deeper water layers, especially during periods of stratification, thus depleting the epilimnion of nutrients. Hence, especially during those periods, DVM could be a daily source of nutrients for phytoplankton growth. Physical diffusion processes in the water column can hardly compensate these losses because vertical eddy diffusivities are normally two or three orders of magnitude smaller than horizontal ones (Spigel and Imberger 1987). Hence, biological upward nutrient trans-

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port mediated by migrating zooplankton from deeper water layers may be the only regular internal supply during summer stratification when nutrients, especially phosphorus, are severely limiting in upper water layers (Sommer et al. 1986).

Recent evidence showing that zooplankton release phosphorus continuously (DeMott et al. 1998; Anderson et al. 2005; Boersma and Wiltshire 2006) contradicted the traditional view that suggested that excretion of limiting nutrient should approach zero under severe nutrient limitation (Olsen et al. 1986). A physiological explanation for a continuous release is that animals will generally not approach 100% element assimilation efficiency (DeMott et al. 1998), and do not have perfect retention capacity during excretion. Furthermore, there will be some metabolic phosphorus demand, which also results in a net loss (Anderson et al. 2005).

Migrating zooplankton transport nutrients upward as they migrate up at dusk, and transport material downward when they migrate down at dawn. To our knowledge, no direct measurements exist of nutrients transported by *Daphnia* DVM. Dini et al. (1987) estimated the amount of phosphorus transported downward by *Daphnia* DVM to be half of the upward transport. However, the ecological effects of the downward transport are completely different from the effects of upward transport. Downward transport is accompanied by the large gravity-driven sedimentation of particles, and phosphorus is not limiting in deeper water layers. Although upper layers of pelagic ecosystems are often nutrient but not light limited, deeper water layers are usually light limited but have sufficient nutrients. Thus, the input of nutrients into deeper water layers will not enhance primary production. Additionally, the downward migration of zooplankton during DVM also removes phytoplankton from the upper layers and thereby additionally reduces nutrient competition in the upper layers. In contrast, the upward nutrient transport into the nutrient-limited upper layers, where most primary production generally occurs, will immediately result in nutrient uptake by phytoplankton.

The above-mentioned arguments show that the ecosystem-scale consequences of upward and downward nutrient fluxes by DVM are very different. Irrespective of the size of the downward flux, an upward flux will always have direct consequences for phytoplankton primary production. The greater the nutrient limitation of the phytoplankton community in the epilimnion, the larger the effects of upward nutrient import will be. Until now, nutrient transport into upper water layers by migrating zooplankton has not been quantified. Measurements are difficult to perform because it is impossible to distinguish phosphorus originating from upper and lower water layers in natural systems, and also because the amounts of phosphorus involved during migration may be too small to be technically analyzed. The detection limit using photometric methods is far above phosphorus levels that could be important for biological dynamics such as primary production or bacterial growth (Vadstein 2000). The use of radioactive tracers provides an elegant solution to overcome both hindrances.

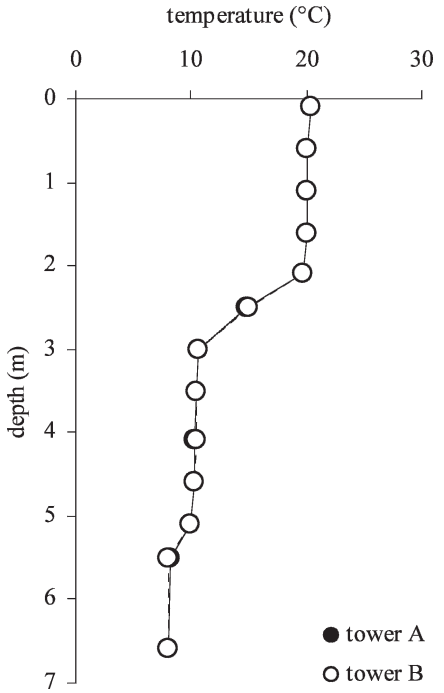

Fig. 1. Vertical temperature gradient in the two plankton towers. The two profiles are nearly identical and the symbols overlay one another.

Methods

We investigated the upward flux of phosphorus using the radioactive phosphorus tracer ^{33}P during *Daphnia* DVM in two large indoor mesocosms, the so-called ''plankton towers'' at the Max Planck Institute for Limnology in Plön, Germany, which have since been removed. The plankton towers were 11.5 m high, had an inner diameter of 0.85 m, and were used in a variety of studies investigating plankton dynamics in controlled large-scale indoor systems. The towers were described in detail elsewhere (Lampert and Loose 1992). We filled the towers with 10 μm of filtered epilimnetic water from mesotrophic Lake Schöhsee, Germany. The experiment was carried out in August 2006, the period of the year when the epilimnion of Lake Schöhsee is largely nutrient depleted. After filling, water was thermally stratified. Temperatures during the experiment were 20°C in the epilimnion (0 to 2.1 m) and 10°C in the hypolimnion (3.0 to 5.1 m), with a steep thermocline between the layers. The maximum hypolimnion depth of 5.1 m was chosen because earlier experiments in the plankton towers showed that *Daphnia* would not easily migrate down the entire plankton tower depth (Reichwaldt 2008). To avoid mixing of the algae into the lower layer of the towers (5.5 to 11.5 m), we adjusted the temperature in this layer to 8°C. Figure 1 shows the temperature profiles in the epi- and hypolimnion in both towers. The light : dark cycle was 12 : 12 h.

After thermal stratification, 0.6 mg C L^{-1} of the chlorophyte *Scenedesmus obliquus* was added into the epilimnion and 0.2 mg C L^{-1} added into the hypolimnion (Fig. 2). *Scenedesmus obliquus* concentrations were deter-

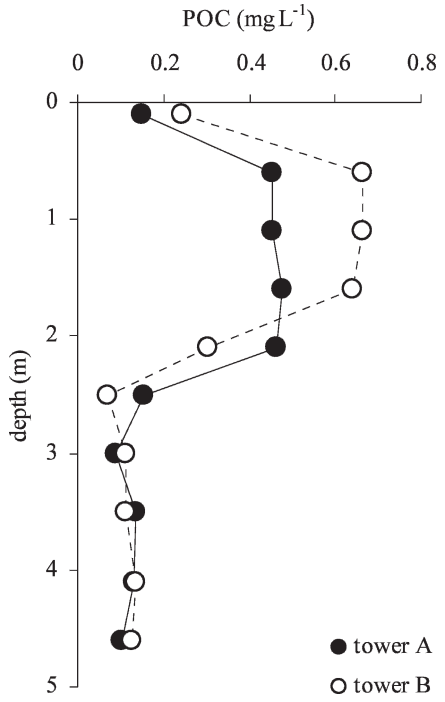

Fig. 2. Vertical gradient of particulate organic carbon (POC) concentrations in the two plankton towers.

mined by measuring fluorescence using a FluroProbe (bbe Moldaenke) and subsequent conversion to particulate organic carbon using a previously established calibration curve. *Scenedesmus obliquus* was cultured in a batch system with Z/4 medium (Zehnder and Gorham 1960) under continuous light conditions. Thereafter, 10,000 to 15,000 *Daphnia magna* were put into each tower. *Daphnia* originated from cultures that had been cultivated at the Max Planck Institute for Limnology for several years, and this clone is known to perform DVM (Loose and Dawidowicz 1994). They were reared in 200-liter containers with 10-μm-filtered water from Lake Schöhsee and *S. obliquus* ($>$ 1 mg C L^{-1}). To induce DVM behavior of *Daphnia*, each tower was stocked with three fish (*Leuciscus idus*) in a cage. The cage was located within the epilimnion of each tower at a depth of 0.5 m and was not moved during the experiment. To estimate *Daphnia* density, vertical hauls with a small plankton net (0.25-m diameter, 150-μm mesh size) were performed in the epilimnion from 2.1 m depth to the surface twice during the light cycle and four times during the dark cycle. We preserved the samples in 4% sucrose–formaldehyde solution (Haney and Hall 1973) and counted all individuals under a dissecting microscope.

To quantify the transport of phosphorus from the hypolimnion into the epilimnion, we incubated 400 mL of a dense culture of *S. obliquus* with the radioactive phosphorus isotope ^{33}P (total activity 185 MBq; specific activity 92.5 TBq $mmol^{-1}$). We added 100 mL of an unlabeled orthophosphate solution (50 μmol L^{-1} P) to the culture to ensure uniform uptake of radioactive phosphorus by *S. obliquus*. After 24 h of incubation, labeled algae were centrifuged and resuspended in Z/4 medium. At the beginning of the light period, the labeled cultures were split into equal amounts and added to the hypolimnion of the two towers by injecting them via ports (for a detailed description of the ports, *see* Lampert and Loose 1992) at a depth of 4.1 m.

To estimate the transported and released total phosphorus amount, we measured the total phosphorus concentration in the hypolimnion of both towers and related them to radioactive counts. Water samples from the hypolimnion of both towers were taken 3 h after adding the radioactive tracer algae, at which time labeled algae were homogenously distributed. Water samples were taken via ports at 4.1-m depth and filtered through 250-μm gauze to exclude *Daphnia*. Total phosphorus concentrations were measured using standard methods (Wetzel and Likens 1991). Total phosphorus in the hypolimnion was 11.5 μg L^{-1} in tower A and 13 μg L^{-1} in tower B. For radioactivity measurements, 4 mL of the samples were transferred into scintillation vials and 12 mL of scintillation cocktail (Ultima Gold, Packard) were added. The samples were immediately analyzed with a scintillation counter (Packard Tricarb 2900). The addition of the radioactive tracer algae resulted in 10,223 disintegrations per minute (dpm) mL^{-1} on average in tower A, and 20,654 dpm mL^{-1} in tower B within the respective hypolimnion. Therefore, 1 dpm accounted for 1.12 pg P L^{-1} in tower A and 0.63 pg P L^{-1} in tower B.

After adding the radioactive labeled algae, the epilimnion of both towers was sampled continuously (twice during the light phase, once at the start of the dark phase, and three times during the dark phase) for radioactive phosphorus. Water samples were again filtered through a 250-μm plankton net to exclude *Daphnia* and 4 mL of each sample were transferred into scintillation vials to analyze radioactivity as above. Additionally, unpreserved *Daphnia* samples, sampled as described above at the start of the dark cycle in the epilimnion, were used to estimate the amount of labeled algae ingested by *Daphnia* in the hypolimnion. We transferred the *Daphnia* into scintillation vials and added 4 mL of a tissue solubilizer (Soluene-350, Packard). After 24 h, we added 12 mL of scintillation cocktail (Hi-Ionic-Fluor, Packard) and analyzed radioactivity immediately with a scintillation counter (Packard Tricarb 2900).

Results

Daphnia density in the epilimnion during the daytime was 0.02 $\pm$ 0.00 individuals L^{-1} (mean $\pm$ SE). Immediately after switching the lights off, *Daphnia* started to migrate into the warmer and food-richer epilimnion. We found 6.14 $\pm$ 1.02 individuals L^{-1} (mean $\pm$ SE) within the epilimnion during the night. A one-way repeated-measure ANOVA calculated with data from both towers revealed no significant differences in *Daphnia* density in the epilimnion between the time of the dark phase: $F_{1,3} = 0.13$; $p = 0.75$. Hence, the change in light intensity between day and night, together with the presence of fish, caused a strong DVM behavior in *Daphnia*, which was already shown in earlier experiments (Loose et al. 1993).

No radioactive phosphorus was found in the epilimnion during the light period, when *Daphnia* almost exclusively

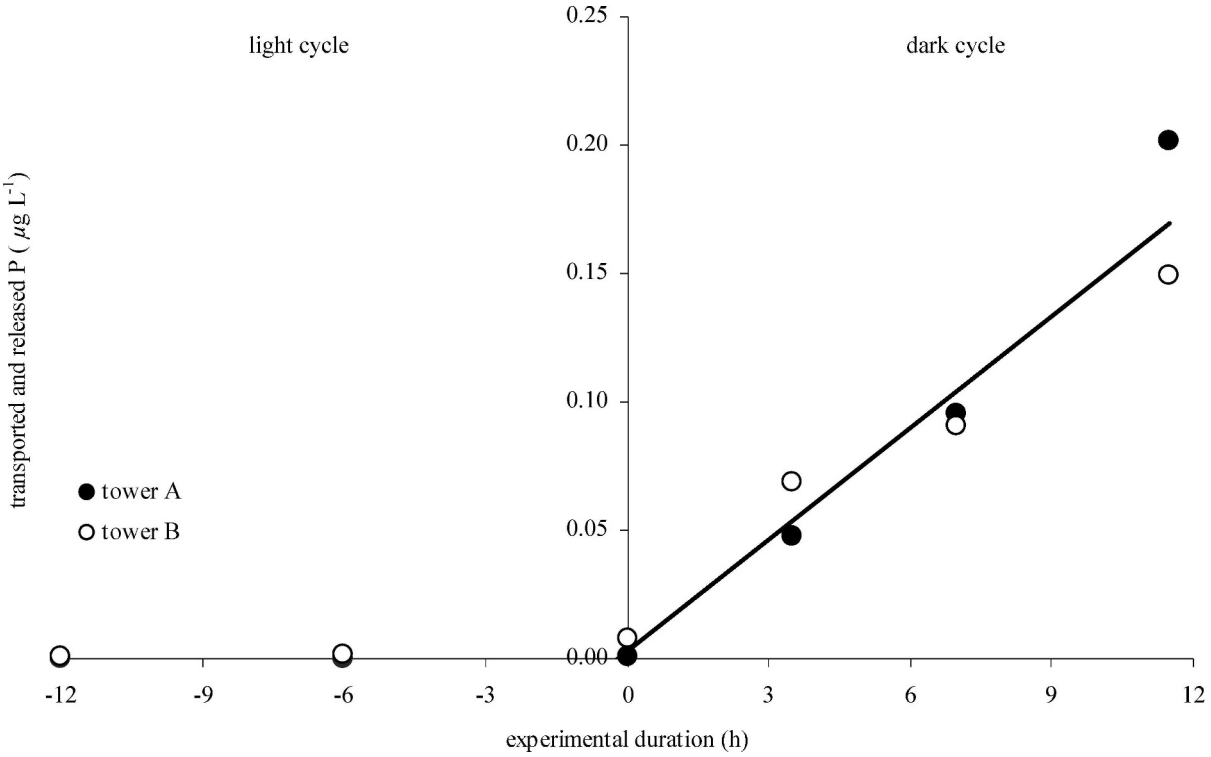

Fig. 3. Phosphorus transported and released from the hypolimnion into the epilimnion by *Daphnia* DVM, shown as changes in phosphorus concentration in the epilimnion in each tower along experimental time (point −12 represents the start of the light cycle and addition of labeled algae to the hypolimnion, point 0 represents the start of the dark cycle and onset of upward migration behavior by *Daphnia*). The line represents the regression between transported and released phosphorus in the epilimnion and time for the dark cycle ($y = 0.015x + 0.003$; $R^2 = 0.94$; $p < 0.001$). Regression was calculated using data from both towers.

remained in the hypolimnion. Immediately after the start of the dark period, *Daphnia* migrated upward and ^{33}P concentrations increased in the epilimnion (Fig. 3). The ^{33}P content of *Daphnia* in the epilimnion shortly after the start of the dark phase accounted for an uptake of 47.4 ± 4.6 ng P *Daphnia*$^{-1}$ (mean ± SE) within the hypolimnion during the 12-h light cycle.

The increase of phosphorus within the epilimnion can be described by a linear function of transported phosphorus vs. time in both towers; the linear regressions were significant (tower A: $y = 0.017x - 0.009$; $R^2 = 0.98$; $F_{1,2} = 84.46$, $p = 0.012$; slope: $t_{(2)} = 9.19$, $p = 0.01$; intercept: $t_{(2)} = 0.66$, $p = 0.58$. Tower B: $y = 0.012x + 0.015$; $R^2 = 0.97$; $F_{1,2} = 75.69$, $p = 0.013$; slope: $t_{(2)} = 8.70$, $p = 0.01$; intercept: $t_{(2)} = 1.57$, $p = 0.26$). An analysis of covariance revealed no statistical difference between the towers at the 5% level (slopes: $F_{1,4} = 5.79$; $p = 0.07$; intercepts: $F_{1,5} = 0.28$; $p = 0.62$.) Therefore, we used data from both towers to calculate a combined regression between phosphorus release in the epilimnion and time (Fig. 3): $y = 0.015x + 0.003$; $R^2 = 0.94$; $F_{1,6} = 91.30$, $p < 0.001$; slope: $t_{(6)} = 9.56$, $p < 0.001$; intercept: $t_{(6)} = 0.29$, $p = 0.79$. On average, the total *Daphnia* community transported and released 15 ng P L^{-1} h^{-1} from the hypolimnion into the epilimnion. This resulted in an overall 180 ng P L^{-1} transported in the 12-h dark phase.

We estimated the released phosphorus as a total phosphorus fraction. Boersma and Wiltshire (2006) showed that *Daphnia* sp. release phosphorus in two fractions: 80% as dissolved phosphorus and 20% as particulate phosphorus. Only the dissolved phosphorus fraction can be used immediately by the phytoplankton community. Hence, in our experiment the amount of transported and released dissolved phosphorus by *Daphnia* from the hypo- into the epilimnion can be estimated as 12 ng L^{-1} h^{-1} and 144 ng L^{-1}, respectively, during the 12-h dark phase.

Discussion

Phytoplankton compete for released phosphorus within the epilimnion. Phosphorus uptake rates for *Scenedesmus* sp. depend on dissolved phosphorus concentration within the pelagic environment (Rhee 1973). Rhee (1973) suggested a phosphorus uptake range for *Scenedesmus* sp. under laboratory conditions between 1×10^{-11} and 3×10^{-11} μmol cell^{-1} min^{-1}. Applying this value to our *S. obliquus* population (6000 cells mL^{-1}), we can calculate a maximum uptake rate of 110 ng P L^{-1} h^{-1} in our experiment. This value is in good agreement with one of the few estimates of phosphorus uptake in a natural bacterial and phytoplankton community in a eutrophic lake, which suggested a maximum total biologically reactive phosphorus uptake of 120 ng L^{-1} h^{-1} (Lean 1973). The amount of phosphorus transported and released by migrating *Daphnia* in our experiment was at least 10% of the maximum uptake rates given by Rhee (1973) and Lean (1973). A recent study of

phosphorus dynamics in a stratified eutrophic lake revealed a mean daily uptake rate of the primary producers in the epilimnion of 7.83 mg P m^{-2} d^{-1} (Kamarainen et al. 2009). The transported and released phosphorus in our experiment accounted for 0.36 mg m^{-2} in the 12-h dark cycle, and thus the transported phosphorous was about 5% of the daily uptake rate estimated by Kamarainen et al. (2009). Both of the above examples show that the transported and released phosphorus in our experimental pelagic system is certainly biologically relevant and is probably one of the mechanisms fueling primary production in the highly phosphorous-limited epilimnion.

Although the upward flux of phosphorus by zooplankton DVM may be low compared with other processes influencing phosphorus dynamics in the epilimnion, it is a regular nutrient supply during periods of stratification. The phosphorus transported by DVM may comprise a substantial phosphorus source for primary production. During periods of stratification, a constant gravity-driven flux of phosphorus from upper water layers to the sediments often results in limited phytoplankton growth. In this case, new production of phytoplankton biomass relies on direct input of phosphorus from terrestrial sources and nutrient recycling within the epilimnion. Phosphorus concentration is often extremely low within the epilimnion of stratified lakes such that any new input of phosphorus is immediately translated into an increase in primary production. Therefore, even if the nutrient balance resulting from nutrient transport by DVM for the epilimnion is negative, a daily transport of phosphorus into the epilimnion will have consequences for phytoplankton growth. Our results indicate that even at natural *Daphnia* densities (approximately 6 *Daphnia* L^{-1} in our experiment), this transport is within a biologically relevant range.

The phenomenon described here can be considered of real ecological value given that in deeper lakes, during summer stratification, a distinct epilimnion exists with concurrent low exchange rates with deeper water layers and therefore an increasing nutrient depletion in the epilimnion caused by sinking losses. A relatively low mixing depth of the epilimnion would increase the nutrient depletion due to a high light availability for the phytoplankton community, resulting in a higher primary production rate requiring more nutrients (Sommer et al. 1986). The upward-transported nutrients should hence be mainly of interest in oligo- and mesotrophic lakes with a nutrient-rich hypolimnion. Whether *Daphnia* DVM causes a net up- or downward nutrient transport depends on the quantity and quality of food in upper and deeper water layers and the duration spent in these layers. Most likely, the upward transport would be most relevant in lakes with a chlorophyl maximum, ample food, and sufficient amount of phosphorous in deeper water (Lampert and Grey 2003; Winder et al. 2003).

DVM is not confined to freshwater systems. Most marine pelagic environments are also affected by DVM of zooplankton (Hays 2003). Longhurst and Harrison (1989) suggested that DVM is a critical component of the "biological pump" that draws organic carbon and atmospheric CO_2 into the ocean. The present results suggest that zooplankton DVM may also play an important role in the redistribution of other nutrients, such as nitrogen. Further experimental analyses on the role of nutrient transport by migrating marine zooplankton are necessary to fully elucidate the importance of the world's largest synchronized movement of biomass on global carbon and nutrient dynamics.

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