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Perspective

The biological carbon pump, diel vertical migration, and carbon dioxide removal

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SUMMARY

Carbon dioxide is increasing in the atmosphere promoting the faster environmental change of the Earth's recent history. Several marine carbon dioxide removal (mCDR) technologies were proposed to slow down CO_2 in the atmosphere. Technologies now under experimentation are related to the increase in gravitational flux. Other mechanisms such as active flux, the transport performed by diel vertical migrants (DVMs) were not considered. We review the effect of DVMs in the epipelagic realm and the top-down promoted by these organisms upon zooplankton and microzooplankton, and their variability due to lunar cycles. A night source of weak light will increase epipelagic zooplankton biomass due to DVMs avoidance from the upper layers to escape predation, promoting DVMs to export this biomass by active flux once the illumination ceases. This mCDR method should be tested in the field as it will increase the efficiency of the biological carbon pump in the ocean.

INTRODUCTION

Climate change is the major problem facing the humankind and the planet. The massive emission of carbon dioxide and other greenhouse gases into the atmosphere after the industrial revolution is promoting the faster environmental and societal changes of the recent history of the Earth. Important and urgent changes in our economy and the way we are using resources are required to face the problem of reversing a drastic shift in the global climate. The use of renewable energies is the immediate ''vaccine'' to stabilize the global temperature. However, this takes time and requires an enormous economic effort which is unaffordable at the short term. Although countries with large economies could promote these changes at a reasonable time schedule, most of the population living in developing countries will be unable to cope with them. Moreover, it would not be fair to make these countries bear the cost of the problem, which they did not create, but instead their inhabitants are suffering. Thus, urgent actions must be taken to slow down the global change.

After a long period of discussion, scientists are now aware that artificial carbon dioxide removal (CDR) should be promoted to generate negative emissions. These technologies are the immediate ''anti-viral'' which, jointly to the increase in renewable energies, should conduct our planet and society to a sustainable environment. There exist several CDR proposals[1] with the potentiality to considerably slow down CO_2 levels. The summatory of all these actions could promote the desired global CDR but at a relatively high economical cost (afforestation, ocean fertilization, artificial upwelling, enhanced weathering, CO_2 capture, etc.).

The oceans have the largest potentiality to store carbon as they are 70% of the Earth's surface but also because carbon could be exported and sequestered (*sensu* Lampitt et al.[2]), retaining large quantities of CO_2 during hundreds of years. In fact, the first marine carbon dioxide removal (mCDR) proposal of providing phytoplankton with iron in high nutrient–low chlorophyll (HNLC) areas of the oceans seeks to fertilize large areas to promote carbon export.[3] Biogeochemical secondary effects such as oxygen consumption and/or increase in other greenhouse gases (N_2O, CH_4, …) were promptly raised, suggesting potential problems.[4,5] Relatively low export of carbon into deeper waters[6] and potentially stimulating the growth of toxigenic diatom species[7] were also raised. Several experiments provided conflicting results[8] and, finally, environmentalists and some scientists were against this negative emission technology as the change to renewable energies was a priority. However, unfortunately, a proper evaluation of this method was never done.

Other mCDR technologies such as artificial upwelling or enhancing ocean alkalinity among others were recently proposed and reviewed.[9] mCDR technologies are mainly related to the increase of primary production to promote higher sinking of particulate organic carbon (POC flux; e.g., iron fertilization and artificial upwelling) or artificial ocean alkalinization using mineral weathering processes to induce pCO_2 decline in surface waters. These methods are mostly based on the use of external compounds to the natural environment to promote mCDR. They are now under research in order to know if these actions interfere with the ocean life.

Most of the technologies now under debate and experimentation in mCDR are related to the gravitational flux, the transport of POC to deep waters, as a major component of the biological carbon pump (about 70% of total flux) in the ocean.[10] Other mechanisms of downward

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carbon transport are the physical mixing of particles and dissolved organic carbon (POC and DOC, respectively) transporting about 20% of the total flux.[10] Active flux is the transport of carbon performed by zooplankton and micronekton diel vertical migrants (DVMs) by feeding in the upper layers of the ocean and respiring, excreting, egesting carbon, and dying in deep waters. Their downward carbon transfer was also recently estimated to be about 10% of total transport.[10] However, these organisms perform the largest migration on Earth[11] roughly moving 10^{15} $gC \cdot d^{-1}$ and consuming epipelagic zooplankton,[12–14] thus affecting their biomass. Mesopelagic fishes and decapods daily consumption also accounted for 25–30% of zooplankton daily production in the Gulf of Mexico.[11–14] Thus, the impact of these migrants on epipelagic zooplankton is significant and the latter prey upon smaller organisms, thus affecting the structure of epipelagic communities. The effect of migrants in the fate of carbon flux in the euphotic zone has been scarcely studied.

However, active flux was observed to vary in a large proportion in relation to productivity in the Atlantic Ocean accounting for only 25% of the passive plus active flux in the oligotrophic ocean but reaching values of 80% in productive waters.[15] This high importance of DVMs in total flux was also observed in the productive waters of the Costa Rica Dome in which most of the downward transport was performed by DVMs.[16] Global models approaching the importance of gravitational, physical, and migrant pumps[10,17,18] found the lower magnitudes in active flux, supporting the results observed at a basin-scale in the Atlantic Ocean[15] as most of the oceans are oligotrophic. However, downward flux is mostly driven by migrants in productive waters[15,16] and, as recently observed, zooplankton biomass increases in the meso- and bathypelagic layers below areas of higher primary production,[19] suggesting an outstanding role of these communities in transporting carbon downward in productive areas of the ocean.

Thus, the migrant pump is relatively unknown and the effect of these communities to transport carbon downward is relatively unexplored. Besides, studies relating active flux and mCDR are also lacking. Here, we perform a first approach to relate the mechanisms of carbon transport promoted by this pelagic fauna and the top-down effects promoted by these organisms by feeding in the upper layers of the ocean. Then, we ask whether this migrant pump could be used in the future to drawdown carbon from the atmosphere.

DIEL VERTICAL MIGRATION AND EPIPELAGIC ZOOPLANKTON VARIABILITY

Non-migrant zooplankton as food for the diel vertical migrants

Epipelagic zooplankton, those species remaining in the shallower layers during day and nighttime, are the main prey of most DVMs.[20] These epipelagic species show a wide body size spectrum from small species such as those belonging to the microzooplankton (e.g., dinoflagellates, ciliates, copepod nauplii, etc), to mesozooplankton such as the genus Oithona and Oncaea, and the typical calanoids such as Calanus, Paracalanus, and Clausocalanus among others. The variability of these organisms is mostly related to primary production but also to the predatory activity of other zooplankton such as chaetognaths and most DVMs such as euphausiids, mesopelagic fishes, and decapods. Daily consumption by these migrants accounted for 25-30% of zooplankton daily production as stated above.[12–14] Despite the impact of these migrants on the epipelagic zooplankton biomass, they were scarcely studied as an important component of the ocean food web until the seminal paper by Longhurst et al.[21] about active flux in the ocean. This downward migration transports a significant portion of carbon produced in the upper layers[15,16,21] to the meso- and bathypelagic zones.[22,23]

Effect of migrants on epipelagic zooplankton

Besides the estimations made by Hopkins and Gartner[12] and Hopkins et al.[14] about daily predation by migrants upon epipelagic zooplankton, there is rather poor information about this predatory impact. This is due to the inherent difficulty to assess this effect in laboratory and field studies. However, another way to study the impact of DVMs upon epipelagic zooplankton is to monitor and model the short-term variability of zooplankton biomass in the upper productive layer of subtropical waters. Scenarios of relatively high and low zooplankton biomass were commonly observed in these waters in relation to lunar cycles.[24] This variability of different species of copepods in relation to the lunar cycle was observed long ago in African lakes.[25] Here, zooplankton increased around the full moon as the effect of the lack of predation by small planktotrophic fishes upon the different species of zooplankton. These small fishes avoided predation by large fishes remaining near the bottom of the lake during the illuminated period of the lunar cycle. In this way, zooplankton was free from predation during that illuminated period, growing and increasing their abundance and biomass. After the full moon, dark periods increase during nights allowing planktotrophic fishes to prey upon the zooplankton crop.

Similarly, the lunar cycles observed in subtropical waters[24] were explained as the effect of DVMs predation upon epipelagic zooplankton, as migrants do not reach the upper shallow waters during the illuminated period of the lunar cycle to avoid predation (Figure 1). This deeper distribution of DVMs during the full moon was observed from field data,[26–28] and using acoustics,[29,30] even at a global scale.[31] DVM is not suppressed but organisms remain deeper, below 80–100 m depth. The absence of DVMs in the upper 80–100 m of the ocean during the full moon allows epipelagic zooplankton to grow and increase their biomass as observed several times in subtropical waters.[24,32–35] This effect was mainly observed during the productive period in subtropical waters, the so-called late winter bloom (LWB). During winter, the lower atmospheric temperature promotes the deepening of the mixed layer due to convection, increasing nutrients in the euphotic layer. The increase in primary production led to the growth of epipelagic zooplankton biomass. However, it was observed to increase around the full moon during the winter productive period, decreasing thereafter as the effect of predation by DVMs (Figure 2). The biogeochemical effect of this cycle was evident as zooplankton and micronekton migrants depleted and transported the epipelagic zooplankton bloom to deep waters as they defecate, excrete, and respire this organic carbon there.[33–36] This effect of moonlight on DVMs was also later described in polar waters.[37]

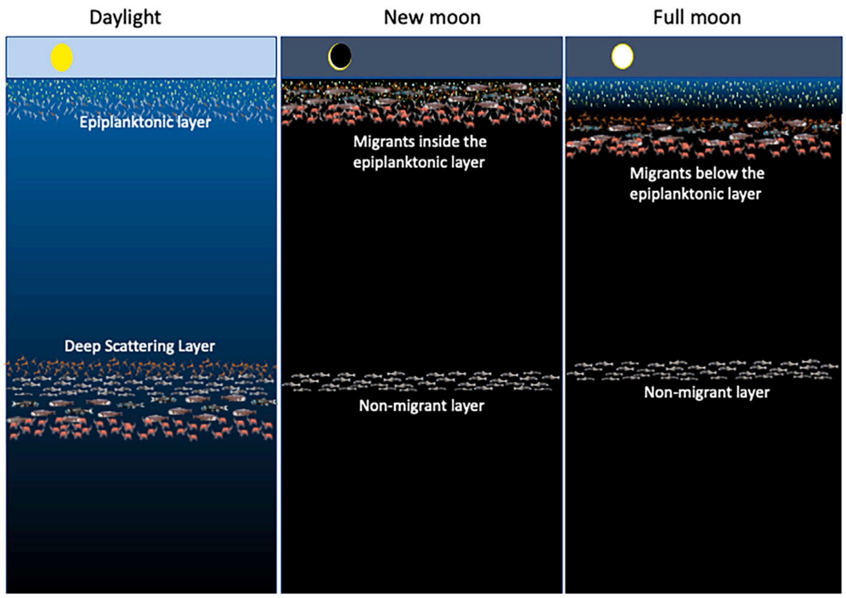

Figure 1. Cartoon showing the distribution of planktonic organisms during daylight and the lunar cycle
The epiplanktonic layer is formed by phytoplankton, microzooplankton, and non-migrant small zooplankton (mainly calanoids and cyclopoids). The Deep Scattering Layer is composed of migrant zooplankton (mainly large copepods and euphausiids), mesopelagic fishes (mainly myctophids and non-migrant stomiids), and others (e.g., decapods and small cephalopods). During the dark phase of the lunar cycle migrants reach the epiplanktonic layer preying upon zooplankton, while during the illuminated phase of the lunar cycle migrants remain deeper because of moonlight makes them visible and vulnerable to predators (e.g., large fishes, cetaceans, …).

Top-down effects promoted by DVMs

Epipelagic zooplankton feeding upon lower trophic levels such a ciliates and dinoflagellates modifies the ocean community structure as predation upon microzooplankton release primary production as these protozoa are the main grazers in the ocean.[38] Increased epipelagic zooplankton biomass (e.g., calanoid copepods) promote a decrease in ciliates and an increase in phytoplankton biomass as observed in mesocosms,[39–41] and field samples in subtropical waters.[42] These top-down effects foster a different food web structure in the euphotic zone of oceanic waters depending on the magnitude of the zooplankton biomass.[43] Low zooplankton biomass releases microzooplankton from predation increasing their biomass and decreasing phytoplankton because of increased grazing (Figure 3A). By opposite, high zooplankton biomass promotes increased feeding upon microzooplankton and, therefore, a decrease of grazing pressure upon phytoplankton (Figure 3B). The consequence is a higher biomass of autotrophs consuming nutrients (new and regenerated production).

This trend was observed by Schmoker et al.[44] studying the planktonic variability during the LWB in the subtropical waters. Epipelagic mesozooplankton, autotrophic picoplankton, and heterotrophic prokaryotes showed similar trends, whereas nano- and microplankton depicted an inverse pattern. The increase in mesozooplankton was parallel to the increase in autotrophic picoeukaryotes because of depletion of microzooplankton and, therefore, grazing. Microplankton was abundant only when mesozooplankton biomass was low. This pattern indicated the effect of DVMs promoting a cascade effect down to prokaryotes by preying upon epipelagic zooplankton, providing an example of the functioning of the pelagic realm in these low latitudes. As previously proposed,[43] the lunar cycle of zooplankton biomass induced by DVMs promoted different top-down effects. High epipelagic zooplankton biomass during the illuminated period of the lunar cycle due to the absence of DVMs in shallow waters favored higher feeding upon microzooplankton and, therefore, an increase in phytoplankton. By opposite, low zooplankton biomass during the dark phase of the lunar cycle allowed microzooplankton to increase due to the absence of their predators, thus grazing upon primary producers (Figure 3).

As stated above, the epipelagic zooplankton crop produced during the illuminated period of the lunar cycle is thereafter preyed by DVMs during the dark phase, transporting this carbon to the deep waters by active flux. Energy from the rather small primary producers of subtropical waters (*Prochlorococcus*, *Synechococcus*, picoeukaryotes, etc.) is channeled through microzooplankton and finally packed into large particles such as the mesozooplankton biomass and their molts,[45] carcasses,[46] fecal pellets,[47] and dead eggs.[48] Thereafter, this energy and matter are transferred out of the euphotic zone by active and passive flux (Table 1).

Thus, the old paradigm of a classical food chain in the ocean by which energy from photosynthesis is transferred to zooplankton and fishes[49] evolved to a more comprehensive view of a food web in which viruses, prokaryotes, nano- and dinoflagellates, and ciliates played a central role in energy transfer to upper trophic levels. The so-called microbial loop[50,51] described a more complex energy transfer in the ocean, as previously observed in many studies about the role of these small organisms in the water column. The ocean food web was found to hold a higher diversity and complexity, and relatively poorly known processes were thereafter unveiled. The role of small organisms

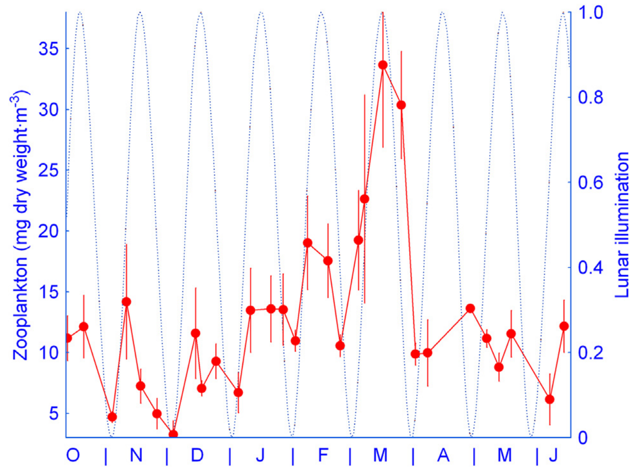

Figure 2. Zooplankton biomass during lunar cycles

Zooplankton biomass (average and error bars) variability in relation to the lunar cyces (dashed line) during the Late Winter Bloom around the Canary Islands (redrawn from Hernández-León et al., 2010). Observe the sharp lunar cycles during the productive season in subtropical waters (January to March).

providing dissolved organic carbon (DOC) to prokaryotes that were consumed by protozoa serving as food for metazoan zooplankton changed our knowledge about the functioning of marine ecosystems. These organisms were afterward accounted for biomass assessments as important components of the ocean food web.[52] However, other organisms remained poorly considered as main components and energy drivers in the ocean. The DVMs composed by macrozooplankton, and especially micronektonic forms such as mesopelagic fishes, decapods, and cephalopods remained almost neglected in energy budgets. This large fauna is not normally sampled on board oceanographic research vessels as the use of large nets or trawls is very costly and time-consuming. As with the components of the microbial loop in the past, these large organisms were underestimated as main components of the ocean food web. In fact, biomass evaluations at a global scale[52] did not consider them, probably because of the lack of biomass data for these large animals.

The export and sequestration of energy and matter through these large organisms was previously called the macrobial pathway.[43] The interplay among the microbial and macrobial pathways promotes a net transport of epipelagic zooplankton biomass by active flux. A rough assessment of this transport simulating the lunar cycle of zooplankton biomass and assuming zooplankton growth and mortality proportional to the lunar illumination[35] showed values higher than gravitational flux measured in the Canary Current.[53]

ECOLOGICAL CONTROLS AND DOWNWARD CARBON TRANSPORT IN THE OCEAN

Trophic controls in ecosystems are one the most fundamental research questions in ecology.[54] Most of the research about bottom-up and top-down effects in aquatic systems were studied in freshwater ecosystems.[55] However, as the latter authors emphasize, the large number of these studies in lakes may pose valuable insights for marine ecosystems. In our finding of the top-down effects induced by the lunar cycle in the ocean, the study in lakes[25] inspired our research about the role of the mesopelagic migrant fauna in driving active carbon flux in the ocean. Research in freshwater ecosystems also provided knowledge scarcely applied in marine ecosystems. In this sense, biomanipulation is used in lakes to restore the aquatic communities and its theory[56–58] predicts changes in ecosystems by adding or suppressing upper trophic levels. These manipulations promote restoring the ecosystem by fostering changes in the presence or not of some components of the food web. Biomanipulation is a concept by which the structure of the community is slightly modified to promote a different pathway of energy without increasing the natural production of the system. Properly designed and tested, it promotes restoration by fostering the presence or not of organisms (e.g., fishes in lakes). Thus, we wonder whether it should be possible to intervene in the natural system at a larger scale in the ocean using the concept of biomanipulation to avoid as much impacts as possible on ocean ecosystems. We speculate if mCDR could be promoted without increasing primary production based on an increase of the biological carbon pump (BCP) efficiency using biomanipulation.

Light promoting higher efficiency of the biological carbon pump

The lunar cycle described above promoted higher biomass of epipelagic zooplankton as the effect of moonlight. The predation of DVMs upon epipelagic zooplankton during the dark phase of the lunar cycle transported carbon by active flux as described above. The feeding of the increased epipelagic mesozooplankton upon microzooplankton converts small particles (nanoflagellates, dinoflagellates, ciliates, etc) into large particles with a higher sinking rate as also stated above. In this way, if DVMs remain longer out of the upper productive waters during the lunar cycle as the effect of e.g., the absence of clouds, epipelagic zooplankton biomass can grow during a longer time without predation, also increasing, in turn, their biomass which will be available to DVMs. Our hypothesis here is that this effect could be induced and enhanced by artificially illuminating the ocean surface, thus enhancing the efficiency of the BCP.

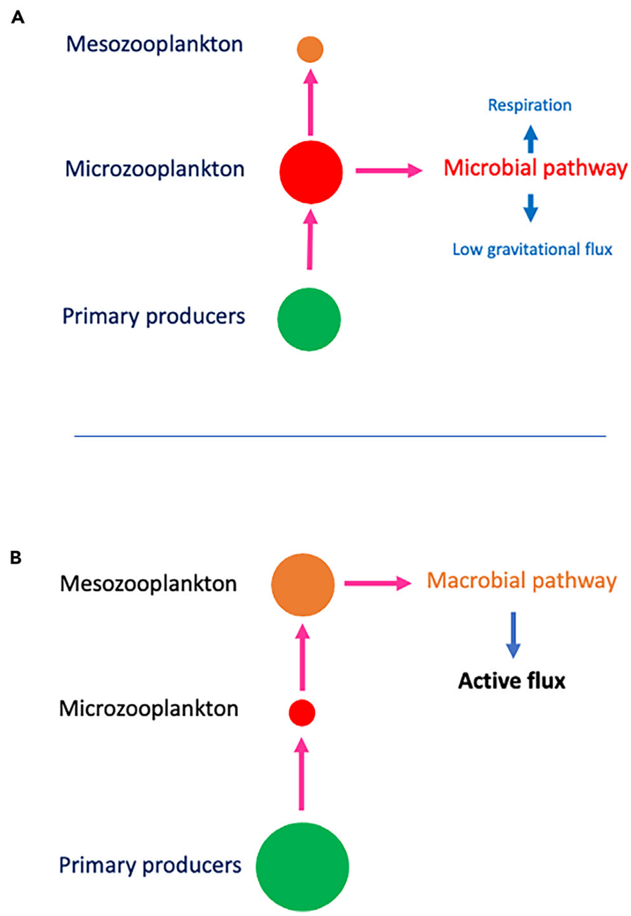

Figure 3. Flux of energy and matter in the epipelagic zone

Conceptual model showing the flux of energy and matter between primary producers, microzooplankton, and mesozooplankton for (A) a typical scenario in subtropical waters of low mesozooplankton biomass and high microzooplankton biomass where energy and matter are recycled in the euphotic zone and mostly respired, and (B) a scenario with enhanced mesozooplankton biomass preying upon microzooplankton. Here, energy and matter are shunted to the mesopelagic zone through active flux (redrawn from Hernández-León[43]). Circles are proportional to relative biomass.

Lunar illumination has a maximum intensity of about 0.3 lux[59] which is a rather low intensity easily affordable for an experiment reinforcing the natural illumination from crescent to waning moon, filling the gaps in moonlighting due to e.g., clouds, lunar timing, lunar angle, phase,… The active flux surplus could be obtained following the evolution of epipelagic zooplankton in the illuminated area. Another area without illumination will be followed as a control (natural active flux). POC flux should be also measured as well as CO_2, nutrients, and phytoplankton and microplankton composition. Although more difficult because of problems related to the assessment of fish biomass,[60] zooplankton and micronekton active flux should be measured and compared to the epipelagic zooplankton decrease due to predation by DVMs. POC flux due to the increase in epipelagic zooplankton biomass and the associated production of fecal pellets, carcasses, molts, and dead eggs should be added to the estimation of active flux. The amount of carbon transported is obtained knowing the variability in epipelagic zooplankton biomass which is simply measured in the illuminated (active flux surplus) and non-illuminated zones (natural active flux) plus the increase in larger particles.

These mCDR experiments will be performed during the LWB in subtropical waters (January to March in the northern hemisphere) when lower atmospheric temperature promotes the deepening of the mixed layer due to convection, increasing nutrients in the illuminated layers of the ocean. In this way, a depletion of nutrients affecting long-term primary production in shallower layers is not promoted, not limiting baseline production over time. Thus, the magnitude of the natural and enhanced blooms will be related to atmospheric temperature promoting mixing. A cold winter will promote a longer natural and enhanced bloom. Similarly, colder temperatures near the temperate zones will promote longer and productive blooms than in areas near the tropical zone. Thus, carbon transport will also vary with latitude.

The effect of lunar illumination on DVMs was observed in other latitudes such as the Arctic Ocean[37] but the effect of moon illumination on DVMs and active flux is unknown in other latitudes such as the quite productive temperate zones of the northern and southern hemispheres. Sharp DVMs were observed in the temperate zone of the North Atlantic Ocean,[61] thus, lunar cycles in epipelagic zooplankton should also be

Table 1. Effects of weak ocean surface illumination upon diel vertical migrants, epipelagic mesozooplankton biomass, direct outcomes, food web impacts, and carbon export effects

Effect of illumination	Direct effects	Direct outcome	Food web impacts	Carbon export effects
Diel vertical migrants forced to stay deeper during lunar illuminated nights and because of artificial illumination	Lower predation by diel vertical migrants upon epipelagic mesozooplankton	Increase in epipelagic mesozooplankton biomass	Higher mesozooplankton feeding upon microzooplankton grazers.	
			Release of primary production from grazing by microzooplankton	
			Increase in larger organisms and particles such as mesozooplankton, fecal pellets, molts, carcasses, and dead eggs	Increase in gravitational flux due large particles such as molts, fecal pellets, carcasses, and dead eggs
Diel vertical migrants allowed to stay in epipelagic waters during non-illuminated nights and because of switching off artificial illumination	Higher predation of diel vertical migrants upon epipelagic mesozooplankton	Decrease in epipelagic mesozooplankton biomass	Lower mesozooplankton biomass and then lower feeding upon microzooplankton grazers	
			Decrease of primary producers due to the increase of microzooplankton and their grazing	
			Decrease of mesozooplankton biomass due to predation by diel vertical migrants	Increase in active flux due to transport of carbon to deep waters and respiration, excretion, defecation, and mortality at depth

expected. Research on this short-term variability of epipelagic zooplankton due to lunar illumination in productive areas needs further research.

In order to provide an account of the potentiality of the mCDR approach, we performed a simple model as those used in previous publications[35] to obtain values of mCDR in relation to days of illumination, different growth values of epipelagic zooplankton obtained in the literature, and ocean surface illuminated (see Supplemental Information). The results of illuminating a small area of the ocean provided a slight active flux surplus in relation to the natural active flux showing that the transport will not promote large amounts of carbon downward, decreasing adverse effects in the meso- and bathypelagic layers. So, the mCDR will depend on the ocean illuminated area. Scaling up the illuminated area for larger mCDR is possible but it is outside the scope of the present study.

ADVANTAGES OF BIOMANIPULATION

The procedure explained above does not need to dump any matter into the ocean, does not increase primary production, nor increase CO_2 in upper layers as it occurs during artificial upwelling. The only intervention is related to reinforcing a natural process avoiding the natural variability of lunar illumination (clouds, lunar timing, angle, phase, etc). Here, the equation relating primary production and respiration plus export is modified. More export promotes less respiration (and less CO_2 flux to atmosphere), diverting export through active flux. This flux is more sensitive to the natural increase in primary production as the slope of the relationship between primary production and POC flux is rather low compared to the regression with the active flux.[15] So, active flux sharply responds to an increase in productivity, while the gravitational flux does not respond in a similar proportion, probably because high epipelagic zooplankton biomass in productive systems attenuates particle flux.[62–64] Thus, a high primary production could not promote a large export or sequestration of particles[15] in quite productive areas of the Atlantic Ocean, explaining at least in part some of the results of iron fertilization experiments.

A new vision of mCDR procedures is also introduced based on the ecological theory such as food web controls rather than modifying the natural environment as most geoengineering procedures propose. In this sense, paraphrasing Poulin and Franks,[65] resources determine how much carbon can be exported and sequestered, whereas consumers determine how much carbon is exported and sequestered. Here, export and sequestration are not dependent on increasing resources (increasing primary production) but on the way carbon is exported or sequestered. Procedures based on natural processes such as biomanipulation should be more environmentally friendly.

Moreover, export time of active flux is on average 150 years[10] but much longer when carbon is sequestered into the thermohaline circulation. In this sense, it was recently observed that an increase in zooplankton biomass in the upper layers of the ocean is propagated downward through the meso- and bathypelagic zones.[19] Thus, a sustained increase of this community during a prolonged illumination should feed deep-sea communities enhancing the downward transport. There is also evidence of DVMs toward the bathypelagic zone as observed from acoustics[66,67] and field data.[68] These poorly known migrations could sequester carbon for centuries, increasing the efficiency of the promoted active flux and relaying carbon to the deep-sea shunting the much slower passive flux.

Another advantage of the described procedure is that carbon transport is rather easily estimated as it is mainly related to measurements of epipelagic zooplankton biomass, which does not require a sophisticated technology. Moreover, it could be monitored using a new generation of biochemical Argo devices or gliders containing zooplankton and particle image systems. Thus, remote monitoring of the carbon exported could be done in almost real-time.

INDIRECT EFFECTS

Changes in the biomass of the different components of the food web structure due to top-down controls promote indirect effects.[69] The mCDR proposed here is based on the manipulation of ocean predators (DVMs) to promote increased epipelagic zooplankton biomass. Also, there is an intervention on the ocean environment as the natural lunar cycle is artificially enlarged. Therefore, this action should be monitored to identify possible drawbacks due to indirect effects because of the longer illumination effect upon DVMs.

Migrant zooplankton, mesopelagic fishes, decapods, and cephalopods will be forced to stay just below the productive euphotic zone,[31] so slightly lower levels of food could promote indirect effects. It is known that mesopelagic fishes show asynchronous migration by which only a portion of these organisms migrate each night.[70] Fishes remain in deep waters not migrating every day and only part of the population that is hungry undergoes this migration.[71] Moreover, it was observed[72] some individuals move to shallower layers during daylight balancing their risk of predation and feeding. These organisms can remain in a fasting state during some days, predating in deep waters, or making incursions into upper layers in relation to the presence or not of predators. Thus, they could remain out of the epipelagic layer for days.[72]

However, the effect of lunar illumination does not suppress the DVM. It avoids the migrants to reach the upper lunar illuminated layer, mostly the upper 80–100 m layer, but they remain below this depth feeding there. Acoustic data at the global scale[31] clearly showed DVMs reaching the upper 200 m layer and avoiding the upper 100 m layer during full moon nights. Thus, the lunar illumination does not promote severe starvation to harm these populations. Moreover, advection in the upper illuminated layer is much faster than below the seasonal thermocline and, therefore, the artificially illuminated area will drift over the mesopelagic water mass and their communities, diminishing the time affecting these organisms to reaching the upper 100 m depth. This time is related to ocean surface currents, and this will depend on the oceanic area.

It is known that top predators such as dolphins, pilot whales,[73] and fur seals[74] respond to lunar illumination having deeper and longer dives as the effect of having to forage deeper during the full moon as DVMs stay some tens of meters deeper. However, it seems that these larger organisms should be able to resist these slightly deeper dives. In any case, attention should be paid to mammal pups as they could be affected, not only because of possible starvation effects but also because an increase in predator encounters due to longer night illumination (e.g., predation by sharks). Also, tuna fishes could be forced to forage slightly deeper, but as cetaceans, these species can reach the nighttime residence depth of DVMs.[75] Also, their large body mass should not be affected by slightly longer feeding difficulties.

Other indirect effects are those related to fish larvae in the ocean. It is known that moonlight enhances growth in larval fish[76] as these organisms are visual predators and, therefore, they can also feed during illuminated nights. A review about the effect of moonlight on fishes and fisheries[77] showed a positive effect of moonlight as the effect of higher larval growth due to enhanced zooplankton prey, and the lack of predators as DVMs remains deeper during the illuminated period. Thus, longer illumination of the ocean should promote a higher survival of fish larvae and a positive effect on fisheries. Similarly, seabirds are also favored by moon illumination as these organisms take advantage during the full moon to feed also at night.[78] However, if these organisms feed upon mesopelagic organisms[79] they could be affected negatively as migrants stay deeper during illuminated nights.

Finally, attention should be paid to avoid these mCDR technologies in oxygen minimum zones (OMZs) of the oceans[80] as, although this procedure promotes a quite slight increase in downward carbon transport (see Supplemental Information), DVMs could affect these depleted oxygen zones.

These examples (compiled in Table 2) are given to recognize that these indirect effects should be tested at small and medium scales and monitored during the use of this procedure for mCDR. This biomanipulation slightly modifies night lighting in the ocean (filling the gaps in moonlighting from crescent to waning moon), consequently also slightly modifying the structure of marine ecosystems to increase the efficiency of the biological carbon pump. Thus, these indirect effects should be considered when testing these procedures.

OUTLOOK

Nature-based solutions are needed to remove carbon dioxide from the atmosphere. The proposal explained above changed the paradigm of mCDR in the oceans as it advanced a new concept based on biomanipulation. This is based on the application of the ecological theory related to top-down and bottom-up controls in nature. Playing with the components of the food web, mainly with upper trophic levels, it clearly established restoring solutions to rather small environments such as lakes. This concept is now scaled up to marine ecosystems and biomanipulation is suggested to be a next step in mCDR research, even if it is combined with other procedures such as iron fertilization or artificial upwelling.

The precautionary principle is a priority and scaling-up experiments should be carried out in small, illuminated parcels of the ocean. We have to account for the enormous variability of ocean climatology (eddies, fronts, etc), and the life associated with mesoscale structures, as well as to islands, seamounts, etc. In any case, this research should be started as experiments are simple and the technology is ready. To delay

Table 2. Indirect effects of illumination due to changes in community structure due to top-down effects, expected impact, and research

Effect of illumination	Indirect effects	Expected impact	Research
Diel vertical migrants forced to stay deeper during artificial illumination	Lower level of food experienced by diel vertical migrants, thus lower feeding and growth of these organisms	Low expected impact as diel vertical migrants can still feed upon zooplankton just below the illuminated layer Low expected impact as mesopelagic fishes also show asynchronous migrations, not reaching the epipelagic zone every night Low expected impact as advection is faster above the seasonal thermocline and, therefore, the enlighted water mass stay over the diel vertical migrant community for a shorter period, decreasing the time of forced deeper stay	Study of feeding and growth of diel vertical migrants during artificial illumination Investigate asynchronous migrations and feeding at daytime residence depths Measurement of surface current field to estimate the time of forced deeper stay of micronekton
Diel vertical migrants forced to stay deeper during artificial illumination	Feeding of top predators such as large fish (e.g., tuna), cetaceans, and seals could be affected due to deeper nighttime residence of diel vertical migrants	Low expected impact as those large predators are able to easily reach 100–150 m depth for feeding Unknown predation by large top predators such as sharks due to illumination Unknown impact on mammal pups as they are not able to perform deep dives	Study of the feeding of large predators and their migrations during artificial illumination Investigate this effect during moonlight nights Avoid experiments near islands and coastal zones
Feeding of fish larvae	Fish larvae are visual predator, so they can feed during lunar illuminated nights	Positive impact as fish larvae enhances growth during moonlight nights Predation of micronekton upon fish larvae should be lower as larvae inhabits shallow waters and micronekton stay deeper due to illumination	Study of larvae growth during the illuminated period Study of fish larvae motility and their escapement ability at the end of the illuminated period because of their larger size
Feeding of seabirds	Seabirds take advantage of full moon illumination to feed at night	Positive impact as seabirds enhance feeding during illuminated nights Negative impact if these organisms feed upon diel vertical migrants	Study of the feeding of seabirds in the area of mCDR experiments

this science is rather reckless as it will deny the advancement of knowledge about the functioning of the marine trophic web. Ocean iron fertilization moved forward our knowledge of how nature works in the ocean, but unfortunately these field experiments were banished more than 15 years ago. A lot of time was lost since that ban. Now, we should foster this science by applying the precautionary approach. Its actual range will not be known until field tests could be carried out, and this is urgent.

These DVMs can shunt carbon to the meso- and bathypelagic zones in a rather short-time scale where carbon will remain for hundreds of years. This residence time of carbon is relevant as zooplankton biomass in deep layers' mirror epipelagic productivity, showing an energy and matter transport to the bathypelagic zone.[19] Moreover, it is also known that some organisms migrate into the bathypelagic zone,[66–68] also promoting true carbon sequestration. The proposed carbon transport and other CDR procedures such as afforestation, reforestation, and other tested ocean approaches jointly to the slow change toward renewable energies could help to buy time to keep the planet temperature below the 1.5–2°C target.

LIMITATIONS OF THE STUDY

Enhancement of carbon export and sequestration in the ocean is of paramount importance to avoid the accumulation of CO_2 in the atmosphere. In almost a decade, and after an important decrease of net carbon emissions to the atmosphere, the drawdown of residual CO_2 from the atmosphere will be a challenge to stabilize the global temperature. Different technologies were proposed (iron fertilization, alkalinity enhancement, etc.) and they are now under scrutiny. Here, it is proposed a technology based on the concept of biomanipulation with minimum interference with ocean communities and following a natural process. The methodology proposed should be tested in field experiments and its viability as marine carbon dioxide removal (mCDR) proved. Also, indirect effects potentially promoted by this method should be studied in these field experiments before any mCDR could be carried out in the future. Changes in the biomass of the different components of the food web structure due to top-down controls promote indirect effects. There is an intervention on the ocean environment as the natural lunar cycle is artificially enlarged. These indirect effects should be evaluated when testing this biomanipulation procedure.

DATA AND CODE AVAILABILITY

Model data generated during and/or analyzed during the current study will be available upon request.

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2023.107835.

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AUTHOR CONTRIBUTIONS

Concept developed by S.H.L.

DECLARATION OF INTERESTS

The author declares no competing interest.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct research.

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