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HORIZONS

Cascading migrations and implications for vertical fluxes in pelagic ecosystems

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Diel vertical migration is widespread across diverse taxa in the world's lakes and seas, yet its biogeochemical consequences are still poorly understood. The biologically mediated vertical flux of material in the ocean (also known as the "biological pump") is a matter of major interest and concern, as it is thought to play an important role in regulating ocean carbon storage, and by extension, the global carbon cycle. Recent studies spanning multiple trophic levels from fish to dinoflagellates have led us to a concept of coupled vertical migrations that we refer to as "*cascading migrations*". That is, migrations that occur at one trophic level can affect the vertical migration of the next lower trophic level, and so on throughout the food web (e.g. carnivores affect the migrations of herbivores, which in turn affect the migrations of motile phytoplankton). Here we hypothesize that greater trophic complexity in the water column leads to enhanced cascading vertical migrations that in turn increase the vertical fluxes of materials and energy through the water column, both upwards and downwards. We recommend that a combination of observational, experimental and modeling approaches be employed to explicitly test this hypothesis.

KEYWORDS: cascading; plankton; diel; vertical; migration

INTRODUCTION

Diel vertical migration (DVM) is amongst the most common and conspicuous migrations on Earth. While this behavior is thought to have a variety of both proximate and ultimate causes (i.e. immediate cues and adaptive significances, respectively), for mesozooplankton such as copepods and cladocerans, it is now widely held that predator evasion often plays a critical role (Bollens and Frost, 1989a,b; Lampert, 1989; Hays, 2003), although non-biological factors such as light and transparency can also have important effects (Forward, 1988; Ringelberg, 2010; C.E. Williamson, in preparation). Dinoflagellate DVM has also been well documented (Eppley *et al.*, 1968; Blasco, 1978; Cullen and Horrigan, 1981; Schofield *et al.*, 2006; Jephson and Carlsson, 2009), although in a pattern that is usually

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opposite or reverse that of most zooplankton, namely, near the surface during the day and at depth during night. We have recently observed that the vertical distribution and migration pattern of the phototrophic dinoflagellate *Akashiwo sanguinea* (previously *Gymnodinium sanguineum* and a well-studied vertical migrator) are altered by the presence of their copepod predators (Quenette, 2010).

These and other studies have led us to put forward the concept of "*cascading migrations*", whereby zooplanktivores such as fish or large invertebrates trigger DVM in mesozooplankton such as copepods, which in turn affect the opposite (or reverse) migrations in their dinoflagellate prey. Again, abiotic factors (e.g. light, nutrients) will also play a role in vertical migrations, but predator–prey interactions primarily drive the mesozooplankton (copepod) migrations, which cascade into effects on dinoflagellate migrations.

What is far less clear, however, is the importance of vertical migrations to the vertical fluxes of material through the water column. The biologically mediated vertical flux of material in the ocean (also known as the "biological pump") is a matter of major interest and concern, as it is thought to play an important role in regulating ocean carbon storage, and by extension, the global carbon cycle. The biological pump has primarily been understood to affect the downward flux of material; however, the involvement of vertical migrators opens the possibility for a bidirectional flux. Quantifying and predicting vertical fluxes becomes even more important in an era of continued global climate change, which is expected to result in both increased CO_2 entering the ocean and increased stratification (vertical heterogeneity) as a result of global warming (Palacios *et al.*, 2004). Thus knowing how vertical migrations and vertical fluxes interact is of broad oceanographic relevance and importance.

Our concept of "cascading migrations", combined with the brief review below of the role of DVM in modulating vertical fluxes, leads us to the following specific and testable hypothesis. Namely, that greater trophic complexity (i.e. an increase in the number of trophic levels) in the water column leads to enhanced (i.e. more numerous) cascading vertical migrations that in turn repackage and redistribute materials and energy through the water column. As a result, vertical fluxes of materials and energy are increased, both downwards and upwards. (An alternative hypothesis is that greater trophic complexity would lead to weaker trophic interactions, and thus weaker vertical migrations and reduced vertical fluxes.) Near the end of this paper, we make specific recommendations for how this and related topics might be most fruitfully investigated.

The specific objectives of this paper are to: (i) present the concept of "cascading migrations", (ii) briefly review the role of DVM in modulating vertical fluxes in pelagic ecosystems and (iii) suggest some directions for future research.

CASCADING MIGRATIONS

For zooplankton such as copepods and cladocerans, there are now literally hundreds of well-documented cases of DVM (see reviews by Cushing, 1951; Lampert, 1989; Hays, 2003; Pearre, 2003; Ringelberg, 2010; C.E. Williamson, in preparation). These migrations usually manifest themselves as organisms residing at the surface at night and at depth during the day, although the "reverse" pattern is also sometimes possible for smaller zooplankton (e.g. Ohman *et al.*, 1983; Frost and Bollens, 1992). Rather than always being "hard wired" and inflexible, DVM sometimes reflects individual behavioral flexibility (e.g. Bollens and Frost, 1991a, b) and variable body condition (Hays *et al.*, 2001), including the possibility of making multiple, short-term vertical forays and feeding bouts into and out of vertical layers of food (Bochdansky and Bollens, 2004; Leising *et al.*, 2005; Pierson *et al.*, 2009). While different zooplankton species, and even individuals within a given species, can exhibit enormous variability in the timing and magnitude of their migrations, depending on the exact environmental conditions at the time, there is broad consensus that avoidance of predators such as visually orienting planktivorous fish and/or carnivorous invertebrates is the primary driver of DVM in zooplankton (Lampert, 1989; Bollens and Frost, 1989a,b; Hays, 2003).

Many species of dinoflagellates have also been observed to undertake vertical migration in a wide range of coastal and open ocean habitats, often residing at the surface during the day and residing at depth at night (Eppley *et al.*, 1968; Blasco, 1978; Villarino *et al.*, 1995; Kamykowski *et al.*, 1998; Ault, 2000; Park *et al.*, 2001; Merzouk *et al.*, 2004; Lee *et al.*, 2005; Moorthi *et al.*, 2006; Schofield *et al.*, 2006; Ryan *et al.*, 2009). Some of these taxa are considered toxic or otherwise harmful, and are therefore of particular interest and concern. Both light (from the surface) and nutrients (often at depth, in stratified waters) have been shown to play central roles as drivers of dinoflagellate DVM in laboratory studies (Heaney and Furnass, 1980; Cullen and Horrigan, 1981; Kamykowski, 1981; MacIntyre *et al.*, 1997; Kamykowski *et al.*, 1999; Erga *et al.*, 2003; Doblin *et al.*, 2006; Jephson and Carlsson, 2009; Schaeffer *et al.*, 2009).

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However, our recent experiments have shown that for one common coastal dinoflagellate, *A. sanguinea*, vertical distribution and migration is influenced not only by light and nutrients, but also by copepod grazers (Quenette, 2010). This is similar but different to the now well-known phenomenon of carnivorous predators inducing vertical migrations in zooplankton (Bollens and Frost, 1989a, 1991a, b; Lampert, 1989; Bollens *et al.*, 1993; Hays, 2003), where the strength of the migration can increase with intensity of exposure to the carnivore (Bollens and Frost, 1989b; Bollens *et al.*, 1992b; Frost and Bollens, 1992). While we are still investigating the mechanisms underlying this dinoflagellate–copepod interaction, in terms of both predator cues and prey responses, it is already clear that *A. sanguinea* and its copepod predator [*Acartia* (*Acartiura*) sp.] exhibit opposite (or out of phase) migration patterns; the copepod undertakes a normal DVM (up at night, down during the day), whereas the dinoflagellate undertakes a reverse DVM (down at night, up during the day). More specifically, in the presence of the copepod predator (grazer), *A. sanguinea* seems to move to a depth with fewer predators (Quenette, 2010). Again, while light and nutrients play critical roles in DVM in dinoflagellates (see references above), the role of predators such as copepods must now be considered as well.

These recent findings have led us to a broader concept of coupled vertical migrations that we refer to as "*cascading migrations*". That is, migrations that occur at one trophic level can affect the vertical migration of the next lower trophic level, and so on throughout the food web (e.g. carnivores affect the migration of herbivores, which in turn affect the migrations of motile phytoplankton). We have coined the phrase "cascading migrations" after the well-known concept of "trophic cascades" developed within aquatic ecology (e.g. Carpenter *et al.*, 1985; Carpenter and Kitchell, 1989; Persson, 1999). Our concept of "cascading migrations" should not be confused with Vinogradov's (Vinogradov, 1962) concept of a "ladder of migrations" (or simply "Vinogradov's ladder") consisting of a series of spatially separated but slightly overlapping migrations extending from the epipelagia downward through the mesopelagia.

We briefly present one other well-known example of such cascading migrations, although this term *per se* has not to our knowledge been used previously. This example concerns the zooplankton assemblage in Dabob Bay, WA, USA, in which several of the larger carnivorous zooplankton taxa undertake normal DVM, such as the copepod *Euchaeta elongata* (Bollens and Frost, 1991b), the euphausiid *Euphausia pacifica* (Bollens *et al.*, 1992a) and the chaetognath *Sagitta elegans* (Fulmer and Bollens, 2005), whereas the smaller, herbivorous copepods *Pseudocalanus* spp., which are preyed upon by the larger carnivorous taxa, often undertake "reverse" DVM (Ohman *et al.*, 1983; Frost and Bollens, 1992). Again, the concept is that DVM that occurs at one trophic level cascades and can cause opposite (or out of phase) migrations at the next lower trophic level.

We strongly suspect that such cascading migrations are common in trophically complex water columns, but rarely are there sufficiently detailed and vertically well-resolved field observations (or experiments) spanning multiple trophic levels to test this hypothesis. We return to this issue below under "Future directions".

IMPLICATIONS FOR VERTICAL FLUXES

Vertically migrating organisms that feed or photosynthesize at one depth and then move to a greater or lesser depth to respire, excrete, defecate or be preyed upon serve to actively transport material and energy through the water column. This has been examined in a range of field and modeling studies, resulting in widely varying estimates of the quantitative importance of DVM to total water-column fluxes. For instance, there have been several major oceanographic field studies that have investigated vertical fluxes generally, and the role of vertical migrants specifically, e.g. JGOFS (Morales, 1999), BATS (Steinberg *et al.*, 2000, 2002), HOTS (Al-Mutairi and Landry, 2001; Hannides *et al.*, 2009), the Arabian Sea (Mincks *et al.*, 2000), E-FLUX III (Landry *et al.*, 2008) and VERTIGO (Kobari *et al.*, 2008).

These field results, which span most of the world's oceans, and are corroborated by several modeling studies (Longhurst and Harrison, 1988; Longhurst and Williams, 1992; Legendre and Rivkin, 2002; Putzeys and Hernández-León, 2005), are in general agreement on two points. First, that the fraction of the total vertical flux of C and N out of the surface layer attributable to DVM is substantial, i.e. up to 10–50% of the total flux. Secondly, that quantifying the absolute magnitude of this DVM-mediated flux in the field is difficult and imprecise (note the 5-fold range in the estimates just mentioned).

Laboratory studies, which offer the potential for much greater control and replication (and thus precision) than field studies, have rarely been applied to this problem. Recently, however, Bochdansky *et al.* (Bochdansky *et al.*, 2010) established tightly controlled environmental conditions and monitored the

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redistribution of particulate organic (POC), dissolved organic (DOC) and inorganic (DIC) carbon from layers of *Isochrysis galbana* in both the presence and absence of two mobile grazers (the protist *Oxyrrhis marina* and the copepod *Acartia tonsa*). These grazers had significant grazing impact on the phytoplankton layers despite the fact that their population maxima were observed outside the layers. Both grazers exported carbon from the phytoplankton layer as body burden (i.e. incorporated into cell tissue) and through release of DOC and DIC into the environment above and below the layers, albeit at different rates. The copepods released larger amounts of DIC and DOC within the phytoplankton layer, while the protist grazer exported more dissolved carbon (in terms of both DOC and DIC) from the phytoplankton layers. In the copepod treatments, a net increase in DIC was observed inside the phytoplankton layer (as a result of increased respiration during feeding) and into the atmosphere above the water column due to their vertical migration between the thin layer and the water surface (i.e. an upward or "reverse" biological pump; see Singler and Villareal 2005 for another, very different example). This study (Bochdansky *et al.*, 2010) points not only to the importance of migration behavior in modulating vertical fluxes, both downwards and upwards, but also to the power of well controlled, replicated experiments.

Vertically migrating organisms can also affect the quality, as well as the quantity, of materials in the water column. Through selective uptake and release, and variable turnover rates among various elements, organisms dictate how elemental nutrients are redistributed relative to each other. Over sufficiently long temporal scales, this leads to a reshuffling of elemental ratios in the environment much in the spirit of Redfield. In addition, the fraction in which carbon appears after passing through an organism, whether inorganic or organic, dissolved or particulate, will have major effects on whether carbon is subsequently available for autotrophic or heterotrophic processes.

FUTURE DIRECTIONS

We make three specific recommendations for the direction of future research into cascading migrations and variable vertical fluxes. The first concerns the *causes* of cascading migrations. The ultimate causes, or adaptive significances, of DVM for zooplankton (e.g. predator evasion) and dinoflagellates (e.g. maximizing photosynthesis, but with an additional role now suspected for predator evasion) have already been touched upon above. The proximate cause, or the specific cues that trigger migrations, is another area that warrants additional research. For instance, while much has been done in recent years regarding predator-released kairomones or chemical cues (Dodson, 1988; Neill, 1990; Lass and Spaak, 2003; see also the review in C.E. Williamson, in preparation), much less is known about predator-mediated mechanical or visual cues in eliciting migrations (but see Woodson *et al.*, 2007). Additionally, as noted above, there is clearly an important role for non-biological (i.e. physical and chemical) processes in eliciting DVM [e.g. light for zooplankton (Forward, 1988), and light and nutrients for dinoflagellates (see references above)], and these too should continue to be examined, especially in combination with biologically mediated cues (e.g. predator × light interaction effects on prey behavior).

Our second major recommendation is that more attention be paid to investigating the *consequences* of cascading migrations. These include physiological consequences to individual migrators (e.g. the effects of temperature, salinity and pressure changes) as well as the demographic consequences to populations (e.g. variable birth, death and growth rates that are affected by vertical heterogeneity of physicochemical and predator–prey conditions in the water column). However, in particular, we recommend that more attention be paid to the effects of cascading migrations on vertical transport of material (carbon and nutrients) and energy through the water column. Understanding the role of the migration-driven biological pump in carbon cycling is becoming all the more urgent given continuing global climate-induced changes such as increased atmospheric CO_2, surface warming, ocean acidification and enhanced vertical stratification of the oceans.

Finally, we recommend that several *different approaches* be applied to future studies of cascading migrations and variable vertical fluxes, including field observations, laboratory experiments and modeling. Field observations should include concurrent sampling of the vertical distributions and diel migrations of taxa spanning multiple trophic levels (e.g. primary producers, primary consumers, secondary consumers, etc.). Indeed, upper-level predators have recently been documented to undertake DVM (Sims *et al.*, 2005; Hays *et al.*, 2009; Sims *et al.*, 2009). The spatial scales involved will often be different (i.e. generally greater for larger, higher trophic level taxa), but in any event should be sufficiently well resolved to provide the necessary precision and accuracy to confidently determine migration patterns. In addition, more emphasis needs to be paid to actual rates of migration rather than the mere observation of changing population peaks in the environment. This is important because the relative distribution of

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populations in the water column is not necessarily representative of the actual migrations undertaken by individual organisms (e.g. Hays *et al.*, 2008). Experimental manipulation, heretofore underutilized in this context, is recommended because only in this way can the potentially confounding effects of multiple factors present in the field be isolated, controlled and unambiguously evaluated (Hairston, 1989). Moreover, rate processes are often extremely difficult (or impossible) to measure in the field. Laboratory experiments will therefore be essential, either for measuring specific biogeochemical, physiological or demographic processes, or through the use of micro- or mesocosms to examine system-wide dynamics (i.e. multiple trophic levels and their consequences for vertical fluxes, e.g. Bochdansky *et al.*, 2010). Field enclosures (i.e. mesocosms or limnocorrals) might be another fruitful approach to experimental manipulation. Finally, modeling will continue to be an important approach to addressing these research questions, as it is practically impossible to directly and concurrently measure all physical and biological rate processes that affect vertical fluxes. Thus, models will to some degree be necessary to integrate the various observational and experimental results, and to help test specific hypotheses (as well as generate new hypotheses for future testing). Individual-based models of DVM (e.g. Leising *et al.*, 2005; Ji and Franks, 2007; Ralston *et al.*, 2007), perhaps coupled with NPZ models of bulk carbon and nutrient transport (e.g. Batchelder *et al.*, 2002), might be a particularly fruitful modeling approach.

There would appear to be an obvious role for combining these three approaches. Unfortunately, this rarely occurs in practice. Two other recent *Journal of Plankton Research* "Horizons" articles point to the lack of coordination and integration between modelers on the one hand and observationalists and experimentalists on the other hand (Flynn, 2005; Franks, 2009). We concur and add that in biological oceanography, observationalists and experimentalists also do not often collaborate closely enough. We recommend that all three approaches, observation, experimental manipulation and modeling, be applied (preferably in an integrated and coordinated manner) to the complex challenge of understanding and predicting cascading migrations and their role in modulating vertical fluxes in pelagic ecosystems.

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