HORIZONS

Mismatch revisited: what is trophic mismatching from the perspective of the plankton?

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Long-term changes in the seasonal timing of phytoplankton and zooplankton population development (i.e. phenological changes) have been widely reported in freshwater and marine ecosystems, and have been interpreted as a biological response to ongoing climate change. Observed among-species variations in the rates and patterns of these changes have led to concerns that seasonal trophic interactions may become de-synchronized in plankton communities, following the logic of the match–mismatch hypothesis. Herein, the current evidence for long-term mismatching within plankton communities is evaluated and the meaning of this concept for the plankton is explored. Despite the large number of studies documenting phenological change in plankton communities, very few explicitly quantify mismatching among trophic levels within the same study system, and quantify its ecological impacts. There is a clear need to build the evidence base for the mismatching phenomenon. In this endeavour, we must carefully define the seasonality of resource availability based on prior ecological knowledge, and embrace the challenges posed by organisms with more complex life cycles and the ecological network context within which plankton interact. In addition, we must acknowledge that, while mismatching in the plankton and in non-planktonic systems relates to synchrony between resource supply and consumer demand, there are conceptual differences in the phenomenon between these two broad classes of systems. For planktonic systems, mismatching is best visualized as an alteration of the rates and lags of the interaction between dynamically linked consumers and resources, rather than simple and independent phase shifts of seasonal abundance peaks at each trophic level.

KEYWORDS: cladocera; climate; copepoda; phenology; phytoplankton; resource threshold

INTRODUCTION

Ongoing climate change has had discernible impacts upon species' ranges and seasonality, and on the structure of ecological communities (Walther et al., 2002; Parmesan and Yohe, 2003; Root et al., 2003; Rosenzweig et al., 2008). Among the immense diversity of species that may be impacted, planktonic organisms are likely to be sensitive "barometers" of long-term climatic change due to the direct dependence of their growth, development and feeding rates on temperature and temperature-related changes to water column mixing processes, and short generation times that permit rapid demographic responses to environmental changes (Taylor et al., 2002; Hays et al., 2005; Richardson, 2008; Adrian et al., 2009).

For planktonic organisms, as for many other organism groups, one of the most widely reported ecological responses to ongoing climate change has been shifts in the seasonal timing of recurrent events such as blooms/population maxima, phenological changes (Weyhenmeyer et al., 1999; Edwards and Richardson, 2004; Winder and Schindler, 2004a; Adrian et al., 2006; Thackeray et al., 2008; Meis et al., 2009; Schlüter et al., 2010). Long-term changes in the seasonal timing of phyto- and zooplankton population growth have been linked to co-incident changes in water temperature (Edwards and Richardson, 2004; Adrian et al., 2006; Thackeray et al., 2008, 2012; Berger et al., 2010; Schlüter et al., 2010) and correlated changes in patterns of turbulent mixing and thermal stratification (Winder and Schindler, 2004a; Peeters et al., 2007; Thackeray et al., 2008; Berger et al., 2010). However, for phytoplankton, it is important to note that these changes can, at least in part, be attributed to changes in nutrient loading (Huber et al., 2008; Thackeray et al., 2008; Feuchtmayr et al., 2010, 2012).

Multi-species studies have shown that rates and patterns of phenological change are highly variable among co-existing, and interacting, planktonic taxa from the same aquatic ecosystem (Edwards and Richardson, 2004; Winder and Schindler, 2004a; Adrian et al., 2006; Costello et al., 2006; Thackeray et al., 2008; Feuchtmayr et al., 2012). This has led to concerns that key seasonal species interactions may become de-synchronized within planktonic systems (George and Harris, 1985; Winder and Schindler, 2004a,b; George, 2012), with consequences for wider ecosystem functioning. Such reasoning has followed the logic of Cushing's match–mismatch hypothesis [MMH, (Cushing, 1990)]. Based upon data from marine fish (predators) and plankton (prey), the MMH suggests that shifts in the relative seasonal timing of the most energy-demanding stage of the predator life cycle and peaks in prey availability may

compromise the productivity/recruitment success of the former. This reasoning has now been applied much more widely to understand climate impacts on a variety of other systems (Visser and Both, 2005), e.g. insectivorous birds and their prey (Visser et al., 2006), herbivorous mammals and their forage plants (Post and Forchhammer, 2008).

While widespread recognition of the *potential* effects of trophic mismatching is beyond doubt, it is imperative to take stock of the current evidence that such a mechanism has actually had a demonstrable impact upon populations of interacting species. Acknowledging this, the aims of this paper are to:

(1) Use published long-term observational studies to critically evaluate the evidence that trophic mismatching has occurred within, and impacted upon, planktonic communities.
(2) Consider what trophic mismatching means for planktonic systems, and how this might differ conceptually between entirely planktonic and non-planktonic systems.
(3) Highlight some key issues that need to be considered in future studies of trophic mismatch in the plankton.

WHAT IS THE CURRENT EVIDENCE BASE FOR TROPHIC MISMATCHING IN THE PLANKTON?

In order to evaluate the volume of field evidence for effects of trophic mismatching upon planktonic taxa, I conducted a literature search in ISI Web of Knowledge version 5.6. The search was for articles (all years in the Sci-Expanded database, conducted 19th June 2012) within which the topic included:

(plankton OR phytoplankton OR zooplankton) AND (mismatch OR match OR synchrony OR phenology)

The search was not intended to yield results for quantitative synthesis, but rather to ensure that key papers on plankton trophic mismatching could be identified. This yielded 572 papers, which were then manually searched to find studies that met the basic criterion of *explicitly comparing long-term (>10 years) changes in phenological metrics across at least two planktonic trophic levels (criterion 1)*. Phenological metrics are indicators of the seasonal timing of plankton population development, such as the day of the year when plankton reach peak abundance or surpass a defined abundance threshold, or the centre of gravity of the seasonal plankton bloom/population maximum. The intention was to retain only

studies of permanent members of the plankton rather than those concerned with species with transient mero-planktonic life-cycle stages, e.g. the larval stages of fish or bivalves. After this process, 12 studies remained (Table I). It is clear that the majority of the current evidence for trophic mismatching in the plankton arises from studies of spring events (see also Ji *et al.*, 2010). Nine of the 12 studies focus on the seasonal interaction between the spring phytoplankton peak and zooplankton grazers. Typically, the former is represented by either the diatoms or estimates of/proxies for total phytoplankton biomass. Six of these nine studies specifically compare phenological changes in spring populations of *Daphnia*, with that of phytoplankton food resources. Three studies compare phenological changes between higher trophic levels (i.e. focussing on the interactions among consumers and not primary producers). These studies all report phenological shifts for Ctenophores (*Mnemiopsis*, *Pleurobrachia*, *Beroe*).

We must of course acknowledge that long-term observational studies can only provide correlative evidence. However, in order for these studies to provide compelling evidence for trophic mismatching they must meet further criteria:

Criterion 2: Rates of phenological change must be significantly different between trophic levels. Rates of phenological change (days or weeks per year) are typically assessed using slope coefficients from linear models of seasonal timing versus year, and may differ among interacting species (Thackeray *et al.*, 2010). However, these rates are based upon estimated parameters and the estimates each have a degree of uncertainty associated with them (the standard error of the slope estimate). It is indeed conceivable that this uncertainty may be rather large, given that plankton may demonstrate high inter-annual variation in phenology about the long-term trend. It is possible to formulate statistical models that (i) assume the same rate of change for each species and (ii) allow different rates of change. These can then be compared to assess which provides a better description of the data. After this, it is possible to make more robust inferences regarding whether the degree of phenological synchrony has decreased or increased over time. At present, many studies adopt a more visual assessment of differences in rates of change (Edwards and Richardson, 2004; Adrian *et al.*, 2006; Costello *et al.*, 2006).

Criterion 3: Measures of species performance or abundance (at the lower or upper trophic levels) must have been directly linked to the degree of synchrony between trophic levels. Presently, we can find studies that suggest different rates of phenological change among trophic levels, and studies that note long-term trends in abundance over the same time period that phenological changes have occurred (Sullivan *et al.*, 2007; Schlüter *et al.*, 2010; George, 2012), but very few *directly* link abundance change to a measure of phenological mismatch. Indeed, of the studies in Table I, only Winder and Schindler (Winder and Schindler, 2004a) take this critical step. However, it is precisely this step that is crucial to demonstrating an ecological impact of phenological change. This is of course challenging as numerous factors influence populations of planktonic organisms. Therefore, the potential role of match−mismatch regulation must be assessed within the context of other potentially relevant drivers of change.

Although the previous discussion has focussed upon "real world" observational studies, large-scale experiments offer additional, and valuable, opportunities to assess the evidence for phenological mismatching in response to long-term environmental change. Here too, we find that a number of studies have not generated compelling evidence for trophic mismatching as a result of differential responses of phytoplankton and zooplankton to experimental (warming) treatments (Berger *et al.*, 2010; Feuchtmayr *et al.*, 2010; Nicolle *et al.*, 2012; Winder *et al.*, 2012). Therefore, the emerging picture is that there is currently little robust evidence for phenological mismatching *within* plankton communities. The field evidence that does exist is biased towards spring events (see also Ji *et al.*, 2010) and phytoplankton-grazer (especially *Daphnia*) systems, and few studies directly relate species abundance/performance to a measure of phenological mismatching. Clearly, we need more dedicated research to (i) evaluate the widespread importance of trophic mismatching within the plankton, (ii) identify the environmental/ecological conditions that promote/negate such effects, and (iii) demonstrate a link between mismatching and population/ecosystem effects. However, it is worth pausing to consider what trophic mismatching actually means in these systems.

WHAT DOES TROPHIC MISMATCHING MEAN FOR THE PLANKTON?

Phenological "events" for plankton are conceptually different from those studied for many other organism groups. They are frequently manifestations of population-level processes and not individual life-history events (Winder and Cloern, 2010). For example the timing of peak population size, which is a commonly employed metric (Table I), in fact represents a point of balance between seasonally changing rates of population replication/reproduction on the one hand, and rates of

Table I: Studies making explicit comparisons between long-term changes in the phenology of adjacent planktonic trophic levels.

Trophic levels	Environment type	Season	Study years	Phenological metrics	Source
Total phytoplankton→*Daphnia*	Freshwater	Spring	1979–2003	Peak	Adrian *et al.*, 2006
Acartia→*Mnemiopsis*	Estuarine	Summer	1951–2003	Onset	Costello *et al.*, 2006
Diatoms/dinoflagellates→Copepods	Marine	Spring/ Summer	1958–2002	CofG	Edwards and Richardson, 2004
Asterionella→*Daphnia*	Freshwater	Spring	1956–1991	End/Peak	George, 2012
Total phytoplankton→*Keratella/Bosmina/ Daphnia*	Freshwater	Spring	1979–1998	Peak	Gerten and Adrian, 2000
Pleurobrachia→*Beroe*	Marine	Spring	1975–2004	End/Onset	Schlüter *et al.*, 2010
Total phytoplankton→*Cyclops*	Freshwater	Spring	1971–1994	Onset/Peak	Seebens *et al.*, 2009
Acartia→*Mnemiopsis*	Estuarine	Summer	1950–2004	Onset	Sullivan *et al.*, 2007
Total phytoplankton→*Daphnia*	Freshwater	Spring	1964–2009	Onset/Peak/CofG	Thackeray *et al.*, 2012
Diatoms→Copepods	Marine	Spring	1975–2005	Onset/CofG	Wiltshire *et al.*, 2008
Diatoms→*Keratella/Daphnia/Leptodiaptomus*	Freshwater	Spring	1962–2002	Peak	Winder and Schindler, 2004b
Diatoms→*Keratella/Daphnia*	Freshwater	Spring	1962–2002	Peak	Winder and Schindler, 2004a

"CofG" indicates use of a Centre of Gravity phenological metric during the comparison. "Study years" indicates the duration of the analytical time period, although there may be missing years within it.
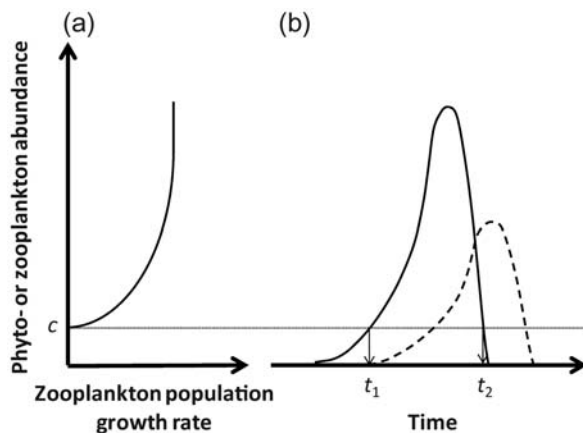

Fig. 1. Spring phytoplankton and zooplankton phenology as a predator–prey interaction. (**a**) The attainable grazer population growth rate depends upon food concentration, and positive population growth cannot be attained at phytoplankton food concentrations below the critical threshold (c, dotted line). (**b**) Grazer populations (dashed line) may be expected to increase when phytoplankton food concentrations (solid line) exceed c (at time t_1), and to collapse after phytoplankton food concentrations fall below this threshold (at time t_2).

population loss/mortality on the other (Thackeray *et al.*, 2008). As a result, any factor that influences rates of population replication or loss affects the balance between these two processes and can thus influence the timing of peak abundance. We must therefore seek demographic explanations for plankton phenological change.

Following on from this, we know that the rates of change in the population size of any given plankton species can be influenced, through species interaction, by changes in the populations of other species. Of most

relevance to the trophic mismatching concept is the interaction between phytoplankton and grazers (which we may consider prey and predators, respectively). A central tenet of current understanding of plankton seasonal succession is that there are feedbacks between phytoplankton and the grazers that consume them (Sommer *et al.*, 1986). If we focus on the spring phytoplankton–cladoceran interaction that forms the basis for many trophic-mismatch studies, current understanding is that spring grazer populations increase rapidly in response to the seasonal "pulse" in phytoplankton food resources and that this response is especially rapid among consumers capable of high rates of population increase (Allan, 1976; Sommer *et al.*, 1986; Reynolds, 1991). Specifically, we would expect grazer population growth to commence when phytoplankton resources exceed the critical threshold that would permit the formation of eggs and thus population growth (c in Fig. 1, Lampert, 1978). In fact, the relevant food threshold would be that which not only permits allocation to reproduction, but that which permits a rate of reproduction that exceeds the cumulative losses acting on the population. Indeed, rapid seasonal increases in the population size/birth rate/fecundity of spring grazers have been observed in response to seasonal increases in the available phytoplankton resource (Herzig, 1987; Müller-Navarra and Lampert, 1996; George and Reynolds, 1997; Winder *et al.*, 2003; Hampton, 2005). This would suggest that, at least to some extent, the seasonal timing of zooplankton population development will be dependent upon that of their food resources. In the extreme case, a population of grazers cannot
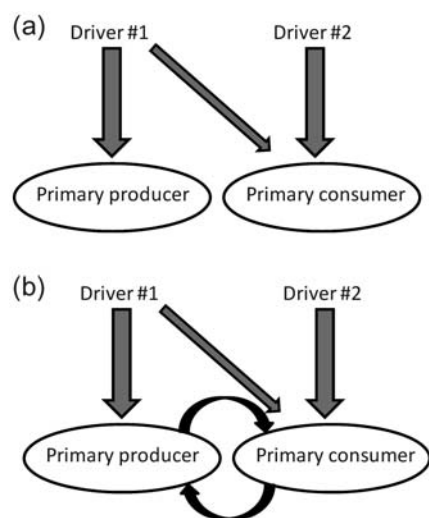
develop if phytoplankton resources do not exceed the critical threshold that would permit the formation of eggs and thus population growth (Lampert, 1978). In turn, resource-driven increases in grazer populations can feed back upon their resources and suppress phytoplankton populations. In the extreme, this can lead to the collapse of the spring phytoplankton bloom, and the maintenance of a clear water phase (Lampert et al., 1986). Indeed, such reasoning is implicit in studies of the latter phenomenon (Müller-Navarra et al., 1997; Straile, 2002). In this way, the seasonal timing of spring phytoplankton population development can be dependent upon that of their grazers. If phytoplankton food resources are suppressed below the critical threshold for grazer population growth, then grazer populations will ultimately collapse due to starvation and reduced fecundity (Fig. 1). Therefore, the spring interaction between phytoplankton and zooplankton grazers is perhaps best visualized as a predator−prey cycle; indeed, numerical models treating it as such are capable of producing realistic seasonal trajectories for abundances at both trophic levels (Scheffer et al., 1997).

It is this two-way dependence of seasonal timing of phenological events among trophic levels that differentiates the nature of plankton trophic mismatch from that

Fig. 2. Simplified path diagram of the impact of environmental drivers on seasonal timing at two adjacent trophic levels. (**a**) Exemplifies the origins of trophic mismatch in a non-planktonic consumer-resource system and (**b**) shows a plankton-based counterpart. In (a), the seasonal timing of activities at two trophic levels may shift independently and to a different extent, creating a mismatch, because (i) each trophic level is strongly responsive to a different environmental driver (e.g. temperature versus photoperiod) or (ii) each trophic level is responsive to the same driver but there are trophic-level differences in sensitivity to that driver (indicated by the width of the grey arrows). These possibilities also exist for plankton systems but, crucially, changes at one trophic level are transmitted to the other via the shared predator−prey interaction.

in other kinds of systems. For example, in mammalian herbivore-vegetation (Post and Forchhammer, 2008) and bird-insect (Visser et al., 2006) systems, we can envisage that seasonal timing at each of the trophic levels may be adjusted independently due to among species differences in the controls on seasonal timing (Fig. 2a). However, in plankton systems, where phenology is at least partially defined by a shared predator−prey dynamic, phenological changes at one trophic level are likely to cascade to the other (Fig. 2b). As a result, phenological shifts at adjacent trophic levels can never occur truly independently of each other. In fact, some studies have reported that interannual variations in the seasonal timing of phytoplankton population growth can partially predict the seasonal timing of zooplankton population growth (Winder and Schindler, 2004b ; Seebens et al., 2009; Thackeray et al., 2012). In both of these broad classes of systems, trophic mismatching relates to the temporal synchrony between resource/prey supply and consumer demand. However, the case of the plankton is distinct in that there are important predator−prey (or consumer-resource) feedbacks that affect the phenological coupling of the trophic levels.

Adopting this predator−prey conceptual model, the seasonal timing of peak phytoplankton abundance may be at least partially defined by the seasonal increase in grazing pressure, which causes total losses to exceed phytoplankton replication and brings about a transition from positive to negative population growth. In turn, the timing of zooplankton peak abundance is defined by the time when phytoplankton populations are suppressed below the critical food concentration, causing a transition from positive to negative zooplankton population growth. In this way, long-term comparisons of the relative seasonal timing of these peaks tell us something about the pace of this predator−prey cycle. It is misleading to interpret an apparent phenological "mismatch", as indicated by the seasonal divergence of phytoplankton and zooplankton phenological metrics, as a product of independent phase shifts in the timing of seasonal abundance peaks at the two trophic levels. Rather, in plankton systems, a long-term divergence in the timing of phenological metrics at different trophic levels indicates a *change in the rate at which the seasonal consumer-resource cycle plays out*. Experimental and modelling studies suggest that the rate of, and time lags in, the consumer-resource cycle may be influenced by changes in temperature, which would alter rates of replication, development and grazing (Beisner et al., 1997; Schalau et al., 2008; Berger et al., 2010; Winder et al., 2012) and mixing depth, which would affect grazer demography via the stoichiometric quality of the phytoplankton food resource in accordance with the "paradox of energy enrichment" (Jäger et al., 2008). Furthermore,

compositional changes in the spring phytoplankton bloom (particularly between morphologically defined "edible" and "inedible" phytoplankton groups) may be expected to affect the rate of the grazer population response, and resulting feedback, by similarly affecting grazer demography via food quality (McCauley *et al.*, 1999; De Senerpont Domis *et al.*, 2007).

Mechanistic insight could be gained by resolving trophic mismatching in plankton systems as more than trophic level differences in the value of a favoured phenological metric. Trophic mismatching in the plankton relates more to the lags between seasonal biomass increase in food resources, and the "transformation" of these resources into grazer biomass. We may consider two distinct types of lag between resource availability and consumer response, in terms of population biomass growth. First, there will be a time lag between resources surpassing the food threshold that permits population growth, and the start of the sustained biomass increase

in the grazer population (Δt in Fig. 3a). We would expect a lag of this sort because of the time needed for adult grazers to assimilate and allocate resources to reproduction and for the resulting eggs to develop, and for juvenile grazers to reach reproductive age (McCauley and Murdoch, 1987; George *et al.*, 1990). This lag may be exacerbated still further if the onset of grazer population growth is limited by photoperiodically constrained hatching of resting eggs, while phytoplankton food resources shift their phenology in response to long-term changes in temperature or mixing regimes (Winder and Schindler, 2004a; De Senerpont Domis *et al.*, 2007). Second, the rate of biomass increase in the grazer population (Fig. 3a, $r_{b, zoo}$) might be expected to be less than, and thus "lag behind", that in the resources that they are responding to [(Reynolds, 1991), Fig. 3a, $r_{b, phyto}$] as some of the assimilated resources would inevitably be committed to immediate maintenance requirements rather than reproduction (Rinke and Vijverberg, 2005). However, we might expect that the relative magnitude of the rates of biomass increase at the two trophic levels would be affected by environmental factors. We could hypothesize that temperature would increase the rate of zooplankton grazing faster than that of phytoplankton replication (Winder *et al.*, 2012, and references therein), increasing $r_{b, zoo}$ relative to $r_{b, phyto}$. We might also hypothesize that reductions in mixing depth might increase the C:P of the resource base and thus limit $r_{b, zoo}$ compared with $r_{b, phyto}$ due to nutritional deficiency in the resources compared with grazer requirements (Jäger *et al.*, 2008). Over the long term, we might expect zooplankton net productivity to be negatively affected by environmental drivers that widen lag Δt or that increase the discrepancy between rates of biomass increase at the two trophic levels. By comparing long-term changes in net zooplankton productivity with these two forms of lag on a response surface (Fig. 3b) and by seeking to relate these lags to environmental drivers, we may be able to further understand the mechanisms behind these aspects of mismatching, and the relevance of these changes for higher trophic levels which depend upon zooplankton production.
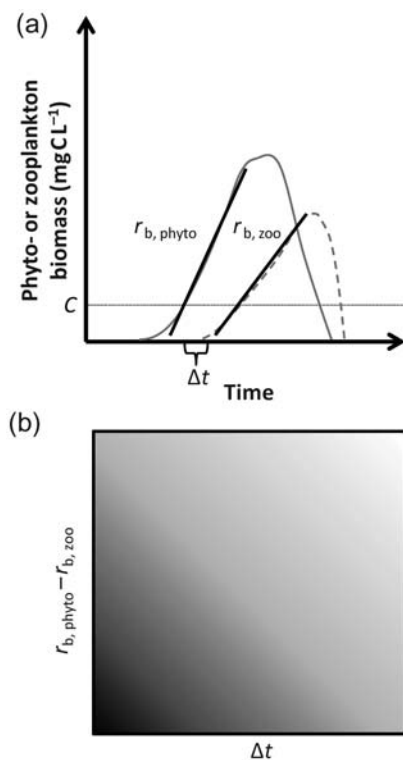
Fig. 3. (**a**) Lags in the spring phytoplankton and zooplankton predator–prey interaction. Both trophic levels are scaled in terms of biomass, e.g. carbon mass per unit volume. Grazer population growth would be expected to initiate, following a time lag Δt, when food concentrations exceed critical threshold c. The rates of increase (here indicated by the slopes of regression lines) of phytoplankton biomass and of zooplankton biomass are indicated by $r_{b, phyto}$ and $r_{b, zoo}$, respectively. (**b**) Response surface in which the abscissa is time lag Δt, the ordinate is the difference in rates of biomass increase at the two trophic levels, and the intensity of shading indicates the net productivity of the zooplankton.

FOOD FOR THOUGHT? FUTURE PRIORITIES FOR STUDIES OF TROPHIC MISMATCH IN THE PLANKTON

The phenology of resource limitation

In order to meaningfully examine the concept of trophic mismatching, however it is defined, we must make assumptions regarding the food resources that are

available to the focal consumer. Firstly, we must assume that consumer reproduction/population growth is limited by resource availability during some of the year (George *et al.*, 1990; Müller-Navarra and Lampert, 1996). Secondly, we must have enough prior ecological knowledge about the focal consumer to know the critical food threshold concentrations that are required for consumer population growth, so that we can examine long-term changes in the seasonal window of resource sufficiency to which consumer populations will respond (George *et al.*, 1990). It is arguably this threshold-based approach that will reveal more about changes in the matching of consumer population phenology to the seasonal resource supply than studies examining peak resource abundance (Ji *et al.*, 2010). Laboratory studies may reveal the critical resource threshold needed to permit reproduction but in a real ecological system a somewhat higher concentration of food would be needed to not only permit reproduction, but to sustain it at a rate that will offset the losses acting upon the grazer population (Lampert, 1978). The complexity of defining the latter threshold, due to its dependence upon environmental context, may lead us to take the pragmatic approach of estimating it using the former threshold value.

Existing studies of trophic mismatching for the generalist herbivore *Daphnia* have defined food resources as either some measure of total phytoplankton or diatom biomass (Gerten and Adrian, 2000; Winder and Schindler, 2004a,b; Adrian *et al.*, 2006; Thackeray *et al.*, 2012), or have implied the phenology of important microalgal food resources indirectly based upon diatom phenology (George, 2012). However, other field studies normally assume that only phytoplankton below a certain cell/colony size are grazed (Ferguson *et al.*, 1982; George *et al.*, 1990), with larger species/colonies being non-ingestible due to interference with the mechanics of feeding. Furthermore, it has been suggested that *Daphnia* population growth may also be partly supported by grazing on bacteria and allochthonous carbon sources (Nagata and Okamoto, 1988; Grey and Jones, 2001). There are also clear effects of food quality on the life-history parameters of these grazers (Sterner and Schultz, 1998). The definition of the seasonal resource window would be even more challenging for copepods, which are more selective feeders and demonstrate ontogenetic dietary shifts (Paffenhöfer *et al.* 1982; Santer and Lampert, 1995). There is arguably a "mismatch" between the way that food resources have been defined in long-term studies of trophic mismatching, and previous findings on the subset of the total resources most likely to be utilized by consumers and food quality effects. In future studies, it is important to carefully define what food resources are likely to be used, based on prior knowledge, and to assess the seasonality of these resources accordingly. Taking this a step further, attempts could be made to examine long-term changes in the phenology of food quality rather than quantity. This would be a demanding task, and would likely be limited by the available data. Much could be learned from new intensive studies that would attempt to quantify the full resource spectrum and assess seasonal interactions between consumers and these resources, and modifications of these interactions.

Food chains to food webs

Much of our current understanding of trophic mismatching in the plankton is based upon studies that adopt a linear food chain paradigm. However, if we are to understand the drivers and ecosystem consequences of mismatching, we must widen our approach to adopt a more community based, food web approach (Nakazawa and Doi, 2012). The seasonal timing of the end of the window of time over which food resource availability exceeds that required for population growth (t_2 in Fig. 1) may be affected not only by grazing pressure from the focal organism, but also by that from co-existing competitors that are feeding on the same resources. We may or may not have data on these species. If the focal consumer is the one that contributes most to the total grazing rate, then we might study trophic mismatching in the terms described above: as an alteration of the rates and lags in the studied consumer-resource system. However, if the collapse of the spring resource peak is driven largely by grazing pressure from another species, then the width of the food resource window will be set by ecological interactions outside of the focal consumer-resource dynamic. For example, the seasonal period of abundance of the phytoflagellates consumed by cyclopoid nauplii might be affected by strong grazing pressure from co-existing *Daphnia* (Santer and Lampert, 1995). In these circumstances, the lags between seasonal resource increase and competitor population response might be important predictors of the net productivity of the focal consumer population. Similarly, the net productivity of a focal consumer might be affected not only by trophic mismatching with respect to resources and competitors, but also with respect to potential predators. The lags associated with the population response of predators to the availability of the focal consumers (prey) will affect the predation pressure experienced by those consumer populations and thus, their net productivity (Wagner and Benndorf, 2007).

The complexity of copepods

Though there are studies documenting phenological shifts and alterations in the seasonality of copepod populations (Mackas *et al.*, 1998; Adrian *et al.*, 2006; Winder *et al.*, 2009), there are relatively few that directly examine potential mismatching between copepods and their food resources (Edwards and Richardson, 2004; Winder and Schindler, 2004b; Wiltshire *et al.*, 2008; Seebens *et al.*, 2009). Considering studies of mismatching at the primary producer–consumer interface, we can see that *Daphnia* is a commonly studied consumer organism (Table I). It is therefore apparent that we need to develop our understanding of plankton trophic mismatching by examining interactions involving a wider diversity of consumer organisms (also see Ji *et al.*, 2010 regarding species bias for marine phenological studies).

Studies of copepods present considerable challenges, when compared with studies of cladocerans or rotifers. They have longer and more complex life cycles that necessitate explicit consideration of the whole ontogenetic sequence when studying mismatching (Yang and Rudolf, 2009; Varpe, 2012). Indeed, it is known that critical food threshold concentrations and diet show ontogenetic shifts in copepod species (Santer and Van Den Bosch, 1994; Santer and Lampert, 1995; Søreide *et al.*, 2010). Therefore, to truly understand mismatching in copepods, it would be necessary to define multiple developmental stage-dependent food resource windows and examine shifts in their seasonality over the longer term. In fact, the interpretation of seasonal abundance peaks in copepod life stages is subtly different from that for cladocerans and rotifers: a seasonal increase in the abundance of any particular life stage is not an indication of rates of reproduction at that time, but of rates of recruitment from the previous developmental stage to the one being monitored. Rates of copepod development are food resource dependent (Ban, 1994; Campbell *et al.*, 2001) and are therefore likely to be affected by the seasonal availability of these resources, but we may still fruitfully examine the lags between development to each stage and the initiation of the seasonal window of availability of the resources required by that stage. As a further complexity, the life cycles of copepods may also be interrupted by quiescence and diapause, which may induce lags between resource availability and copepod development (but see Seebens *et al.*, 2009).

CONCLUSIONS

Trophic mismatching has frequently been proposed as a mechanism by which long-term environmental change could impact upon the functioning of ecosystems. In planktonic systems, there is currently a limited evidence base for this phenomenon, and its ecological impacts. Existing evidence is biased towards studies of a small number of organism groups, and interactions between spring populations. Future studies must address these biases, as well as the overall paucity of evidence. However, in future work, we must explicitly recognize the feedbacks that exist between population development at different trophic levels, and the network context within which these changes occur. By recognizing and incorporating these interactions in our studies, we will be more able to evaluate the ecosystem-level consequences of phenological change in aquatic communities.

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