Reversing the Match-mismatch relationship: the prey point of view

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ABSTRACT

Climate influences populations through a variety of processes. One mechanism that may be particularly important is the role of climate in disrupting un-equally the phenology of the predator and prey in a food chain. The match-mismatch hypothesis, referring to the development and survival of a predator is affected by the synchrony with its prey is used to describe climate effects on ecological patterns and processes in both terrestrial and marine systems. We expand on the match-mismatch hypothesis by considering the simple statement: "what is bad for the predator should be good for the prey". In other word we reversed the output of the match-mismatch hypothesis, i.e., the increase of the asynchrony lead to a better survival/recruitment for the prey.

We tested the theoretical model using GAM models on marine time series. We showed that the effect of predators on prey in the top-down controlled ecosystems can be modified by the degree of asynchrony. We discuss this result in light of the increase of amplitude of year-to-year variations in phenology linked to climate change.

Keywords: Reverse match-mismatch, Phenology, Recruitment, Trophic interaction

Aquatic food webs have been intensively studied with respect to how trophic interactions between consumer and resource affect species composition and abundance. Different types of control have been suggested (Frank et al., 2007, Cury et al., 2003). First, the regulation of the lowest trophic levels, e.g., the primary producers, can be environmentally controlled (bottom-up control). Second, the regulation of lower food-web components can be made by one or several upper-level predators (top-down control). Finally, in several marine systems there is a mid-trophic level, occupied by a few abundant mid-trophic species, usually pelagic schooling fish; those are dominant populations which vary radically in abundance. They can exert a major control on energy flows channeling energy and nutrients from planktonic primary and secondary producers to top predators. In this case the energy flow is controlled up and down from the middle element (wasp–waist control).

In case of a bottom-up controlled system, a major hypothesis explaining the recruitment variation in the predator population is the match-mismatch hypothesis (MMH, Durant et al., 2007, Cushing, 1969, Cushing, 1990), which focuses on the relation between the predator's phenology - the timing of seasonal activities such as flowering or breeding – and that of the species at the immediate lower level. The MMH states that if the most energy expensive part of the breeding phenology of the higher level (i.e., the predator) occurs at the same time as the peak availability of the lower level (i.e., the prey), recruitment will be high: the requirement of the predator matches the availability of resources provided by the prey species (Fig. 1a). If there is a mismatch between food requirement and food availability, survival and thus recruitment will be low (Durant et al., 2007, Cushing, 1969, Cushing, 1990).

In the case of a top-down control, the match-mismatch hypothesis *sensu stricto* is not applying. Indeed, top-down model postulates that predation controls community organization, and not food abundance as assumed in the match-mismatch hypothesis (Durant et al., 2005, Durant et al., 2007). If top-down control, i.e. predation, is a significant source of mortality, prey populations would be expected to show a timing of their spawning/reproduction that minimizes exposure of the resulting young to predators (Bollens et al., 1992). In other words, in such a system the prey recruitment will be stronger when there is high asynchrony (mismatch) with the predator.

The match-mismatch hypothesis has proved to be a useful hypothesis that can be tested in a range of different settings, and it is a helpful concept for understanding and predicting complex, natural ecosystems. The match/mismatch of predators and prey may be an important structuring mechanism of ecosystems. However, it does not apply to top-down systems and does not describe what happens to prey as a result of predation. In this paper we will look at this particular situation of prey recruitment in a top-down control system, and the mechanisms that can explain its variation. We hypothesize that there is a phenology contest between predators and prey, and in a top-down controlled system the prey can be expected to win the race by creating the highest possible asynchrony between the peak of prey production and the peak of predator requirement. In this "reverse" match-mismatch framework, we predict that the best temporal match between prey and predator is resulting in the lowest yearly recruitment of the prey, and *vice versa* (Durant et al.).

MATERIAL & METHODS

1. The starting hypothesis

Following the classical match-mismatch graphic representation (Cushing, 1990) (Fig 1*a*), we assume that the abundance of the predator and its prey over time (within one season) follows a unimodal bell-shaped distribution. These functions are characterized by mean peak time of food requirement and abundance (m_1 and m_2, respectively; Fig. 1*a*) and the area under the curve (n_1 and n_2, respectively) is a measure of the total predator abundance and the total prey abundance.

   The success of the lower trophic level (e.g., survival or reproduction of the prey) is better when the predation is reduced, i.e. lower predator abundance or higher asynchrony. Prey success can then be considered to be inversely proportional to the area of overlap between these curves. This overlap changes as a function of the timing of the peaks of abundance (i.e., the degree of mismatch; $x = m_1 - m_2$) as well as the total prey abundance relative to the total predator abundance ($y = n_2/n_1 =$ relative food abundance).

   Figure 1*b* shows how the prey population may change as a function of the two variables that are predator abundance and degree of time synchrony (mismatch), assuming that the two explanatory variables are interacting. If relative predator abundance (y) is constant, the prey population increases with increasing asynchrony, i.e. increased mismatch (x), following an S-shaped function. If mismatch (x) is constant, the expected prey population decreases with relative predator abundance (y), following a curve shaped function.

2. Data preparation

The copepodites *Acartia tonsa* and *Acartia hudsonica* (individuals m^{-3}) as well as their major predator, the ctenophore *Mnemiopsis leidyi* (individuals m^{-3}), sampled weekly between 2001-2003 in 3 locations in the Narragansett Bay estuary (mouth of the Narragansett Bay estuary (41° 30.6N, 71° 24.0W), the central estuary (41° 30N, 71° 20 W), and a shallow embayment (41° 40N, 71° 24 W)) (for details see Durant et al. submitted, Costello et al., 2006a, Costello et al., 2006b). *A. tonsa and A. hudsonica* were collected with a 64 μm mesh net of ¼ meter diameter mouth opening and *M. leidyi* (>1.0 cm) were collected by two oblique tows with a 0.5 m diameter net (1 mm mesh size) over the entire water column.

i. Copepodites (both sexes)
We did not dissociate sex and concentrated on *Acartia tonsa* (later AT) and *Acartia hudsonica* copepodites (later AH).

For each year, AT and AH abundance (individuals m^{-3}) were estimated by the maximum value recorded. For each year, the timing of the abundance peak (the central tendency, T) was estimated using the time coordinates of the centre of gravity:

$$T = \Sigma M x_m / \Sigma x_m$$

where x_m is the abundance recorded a given year at Julian date *M*.

ii. Ctenophore *Menmiopsis leidyi* (individuals m^{-3})
We focused on the Large *Menmiopsis leidyi* (later *MneL*). Similar to what was done for the Copepodites, *MneL* abundance was estimated by the maximum value recorded. For each year, the timing of the abundance peak (the central tendency, T) was estimated using the time coordinate of the centre of gravity:

$$T = \Sigma M x_m / \Sigma x_m$$

where x_m is the abundance recorded a given year at Julian date M.

iii. Degree of mismatch.
We calculated the degree of mismatch as the time lag between the peak of *MneL* and the peak of *AT* and between the peak of *MneL* and the peak of *AH*.

3. Statistical analysis

Given the prey abundance (y), predator abundance (x_1), and the time lag between the peak predator abundance and the peak prey abundance (x_2, degree of mismatch) we related the change in prey abundance with predator abundance and degree of mismatch using Generalized Additive Model (GAM) formulations, as implemented in the *mgcv* library of R 2.8.1 (Wood and Augustin, 2002, R Development Core Team, 2008). Specifically, let Y_t be the prey abundance at time t. Let X_{it} be a vector of the explanatory variables at time t where i identifies the single components. Let f_i be nonparametric, smoothing functions, specifying the effect of the covariate X_i on the demographic variable Y. The formulation is:

$$Yt = \alpha + \Sigma_i f_i(X_{i,t}) + \varepsilon_t \quad (1)$$

where α is an intercept and ε is a stochastic noise term. The GAM procedure chooses automatically the degrees of freedom of the smooth function f_i (i.e., the wigglyness of the curve) based on the Generalized cross validation (GCV) score, and can also choose it to be linear (i.e., $f_i(X_{i,t}) = b_i \cdot X_{i,t}$). In the final formulation we retained the models that minimized the GCV. We checked for autocorrelation in the residuals of the model.

To model the copepodites *Acartia tonsa* and copepodites *Acartia hudsonica* we used a generalized additive mixed modelling formulation (GAMM in the *mgcv* library) with a quasipoisson error distribution in order to handle overdispersion in Copepodites values. We added to the GAM model (fixed effect) as described above a random effect to take into account the effect of the 3 locations where the data were sampled. Since GCV selection is not applicable for GAMM models we calculated the Small sample unbiased Akaike Information Criterion (AICc, Johnson and Omland, 2004).

RESULTS

In all models tested we found a significant negative effect of predator abundance on the prey abundance. There was also a significant and negative effect of synchrony of the predator on prey on the prey abundance. In other words, more important is the time mismatch between the 2 trophic level better it is for the prey.

The best models selected by reduction of AIC are using only mismatch ($X_{it} = x_{2t}$) as explanatory variable cases although the explanation power was less important than for the full model in *AH* case (Table 1). However, since a mismatch/match situation only occurs when the predator is present, we decided to present on Figure 2 the models containing predator abundance and degree of mismatch and the interaction between the two ($X_{it} = (x_{1t}, x_{2t})$, Table 1). A decrease of the degree of mismatch (i.e., higher synchrony) leads to a decrease of the prey abundance in all cases (Fig. 2). An increase of the predator abundance leads to a decrease of the prey abundance (Fig. 2).

Table 1. Results of the GAM analysis on the relationship between prey abundance (*Y*) and predator abundance and degree of mismatch. Models are ranked by the GCV (generalized cross validation) score. Models can be written $Y_t = \alpha + f_1(X_{1,t}) + f_2(X_{2,t}) + f_3(X_{3,t}) + \varepsilon$, with *f*, a nonparametric smoothing function specifying the effect of the covariates x_i on the dependent variable *y*; **α**, intercept; and **ε**, stochastic noise term. $X_{1,t} =$ (MneL $_t$, Mismatch $_t$) corresponds to an interaction term. *p*-value for each variable (*** $p<0.0001$, ** $p<0.001$, * $p<0.05$, and ˙ $p<0.10$) is shown.

Y	Explanatory variables, X_t	Adjusted R^2	AICc
	X_1		
AT $_t$	Mismatch $_t$**	0.74	11.927
	(MneL $_t$, Mismatch $_t$)**	0.74	24.895
	MneL $_t$	--	24.478
AH $_t$	Mismatch $_t$	0.31	29.800
	(MneL $_t$, Mismatch $_t$)	0.35	42.240
	MneL $_t$	--	33.199

DISCUSSION

There is now evidence for ongoing climate change. The pace of climate change and its impact on populations and biodiversity are thus central issues. Phenology is often the first element affected by climate change (Forchhammer et al., 1998, Visser and Both, 2005, Visser and Holleman, 2001). Increasingly, evidence shows that climate change is leading to differential changes in the occurrence of the predator and the prey (Platt et al., 2003, Visser and Holleman, 2001, Visser et al., 2006). It is clear that the degree of both temporal and spatial overlap between the seasonal peak of predator and prey production is crucial for the recruitment of the predator (see review in Durant et al., 2007). The match-mismatch hypothesis addresses this issue in bottom-up controlled systems. Our results confirmed the importance of temporal synchrony.

Our empirical analysis shows that the main component of the MMH — the predator/prey synchrony or absence of synchrony — can also be used on top-down controlled systems. In a sense our results illustrate the control of predation on population dynamic adding a time component to it (Bollens et al., 1992). Predation has long been discussed as a selective force affecting the reproductive strategies and recruitment

success of marine fishes (Bailey and Houde, 1989). Johan Hjort (1914) led attention to the high mortality during the "critical period" of larval fish: the first few days after the yolk sack is consumed when the fish larvae change from internal to external feeding. While lack of food during this period is detrimental, this period is also a period when the larvae are particularly susceptible to predation because of their small size and relatively undeveloped escape abilities. If this predation is a significant source of mortality, populations would be expected to have better larval survival when their spawning timing is not synchronous to peak of predation (Bollens et al., 1992). This illustrates that top-down and bottom-up controls are not mutually exclusive; both factors can be of importance for larval fish, and survival may depend on the timing of three trophic levels: the timing of both prey and predators relative to the timing of the critical period of fish larvae. Moreover, the two processes interact: food shortage may force fish larvae to spend more time close to the surface ,where prey is more abundant but predation risk is also higher (Fiksen et al., 2007).

There is evidence that marine food web can be controlled via top-down effects (Österblom et al., 2007, Ainley et al., 2006, Worm and Myers, 2003). However, Frank et al. (2006) considered bottom-up controlled food webs, i.e. fundamentally structured by primary productivity, as the normal state, in accordance with the assertion that top-down structuring represents a form of biological instability (Strong, 1992). More recently, top-down systems were suggested to be more common in low-temperature and low-diversity systems (Frank et al., 2007, Petrie et al., 2009). It was also shown that depletion of the apex predator, for instance by overfishing, might induce systems to change from bottom-up to top-down controlled (Frank et al., 2007). Likewise, marine food webs are dynamic and can switch between the bottom-up and top-down state (Hunt et al., 2002), or a combination of both, illustrating that the driving forces shaping ecosystems cannot exclusively be explained by only one of the two control paradigms. Our study suggests that the synchrony between the copepodites and the occurrence of predator as a negative effect on the copepodites. The phenology mismatch may not only change the food chain component but in some cases may modify the structure of the system, for instance by changing the dominant species of the system (e.g., toxic bloom appearance).

Climate changes may affect phenological match/mismatch (Cury et al., 2008, Fréon et al., 2009). The Narragansett Bay system is a good example of this and why this might happen (Costello et al., 2006a). *Acartia tonsa* used to be the dominant secondary producer in this estuary because its main period of production (July) occurred prior to the seasonal appearance of *Mnemiopsis leidyi* in late summer (Durbin and Durbin, 1981). Costello et al. (2006a) have shown that the advance in *M. leidyi*'s seasonal appearance relative to *A. tonsa* has shifted the predator's peak abundance into a time period during which *A. tonsa* has historically enjoyed a temporal refuge from ctenophore predation The ctenophore *M. leidyi* has responded to warmer spring temperatures with earlier seasonal population growth. In contrast, the copepodite *A. tonsa* has retained relatively conservative timing of spring population growth between warm and cold years. The fact that the phenology of *A. tonsa* failed to shift to the same extent as that of the ctenophore results in increased predation. The same is certainly the case for the other copepodite of Narragansett Bay system that is *A. hudsonica*. Of course, climate change may also

decrease the degree of match between predator and prey. Such a situation was described for the Baltic Tellin *Macoma baltica* (Philippart et al., 2003) where climate change created a situation of permanent mismatch.

Our theoretical and empirical analyses have extended the discussion on the match-mismatch hypothesis and of the predator control of the lower trophic level by the upper trophic level in a top-down system: the "reverse Match-mismatch hypothesis". The value of our model rests in its ability to separate a within-season temporal shift of trophic synchrony from an annual component linked to total predator abundance. In the three systems tested, our model helped us showing that the degree of synchrony affects more predator regulation of prey than the predator abundance. On our view, this knowledge will improve our ability to predict the negative effect of predation in a changing environment. One may want to pursue the exploration by extending the model to a spatial overlap/segregation linked to climate change.

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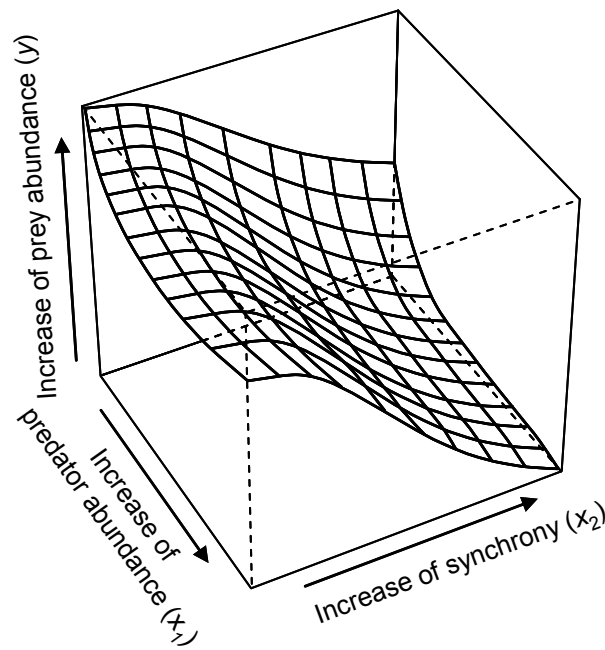
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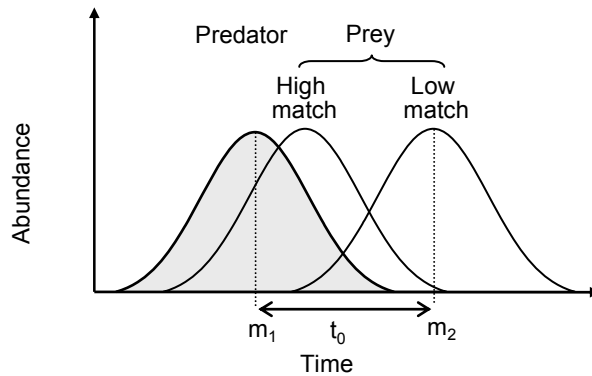
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Figure 1. Interaction between two trophic levels: **a**, Match-mismatch hypothesis (Durant et al., 2007, Cushing, 1969, Cushing, 1990). A high match is represented by a temporal overlap of the predator and its prey. An increase of the time-lag (t_0) between the two populations leads to a low match: a small or non-existent overlap. **b**, Working hypothesis: effect on the prey success (y) of the changes in abundance of predator (x_1) and in degree of mismatch (x_2) assuming an interaction between the 2 explanatory variables. Note that x_1 is always different from 0. If such was the case y would have been independent form x_2.
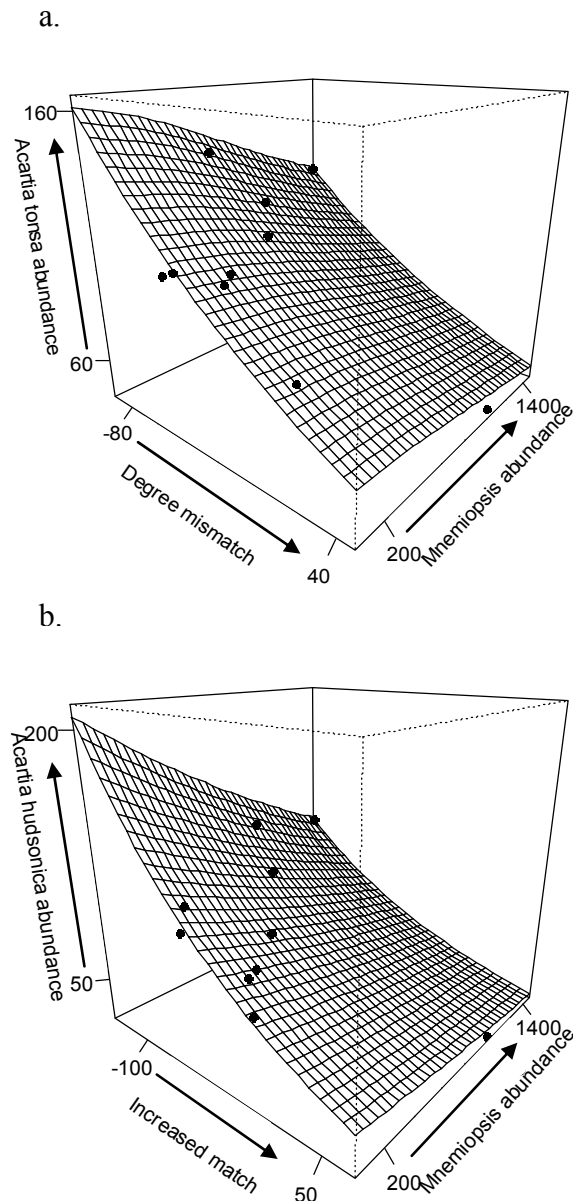
a.

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Figure 2. Results of the Generalized additive modelling (GAM) of effects on prey abundance on 3 different predator/prey pairs: **a**, Copepodite/ctenophore, with predator abundance (x_1) as *Mnemiopsis leidyi* concentration No.m^{-3}, degree of mismatch (x_2) as the difference in days between the peak of abundance of the two trophic levels, and success (*y*) as *Acartia tonsa* concentration No.m^{-3}. **b**, Copepodite/ctenophore, with predator abundance (x_1) as *Mnemiopsis leidyi* concentration No.m^{-3}, degree of mismatch (x_2) as the difference in days between the peak of abundance of the two trophic levels, and success (*y*) as *Acartia hudsonica* concentration No.m^{-3}.