

Maximal feeding with active prey-switching: A kill-the-winner functional response and its effect on global diversity and biogeography



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ABSTRACT

Predators' switching towards the most abundant prey is a mechanism that stabilizes population dynamics and helps overcome competitive exclusion of species in food webs. Current formulations of active prey-switching, however, display non-maximal feeding in which the predators' total ingestion decays exponentially with the number prey species (i.e. the diet breadth) even though the total prey biomass stays constant. We analyse three previously published multi-species functional responses which have either active switching or maximal feeding, but not both. We identify the cause of this apparent incompatibility and describe a kill-the-winner formulation that combines active switching with maximal feeding. Active switching is shown to be a community response in which some predators become prey-selective and the formulations with maximal or non-maximal feeding are implicitly assuming different food web configurations. Global simulations using a marine ecosystem model with 64 phytoplankton species belonging to 4 major functional groups show that the species richness and biogeography of phytoplankton are very sensitive to the choice of the functional response for grazing. The phytoplankton biogeography reflects the balance between the competitive abilities for nutrient uptake and the degree of apparent competition which occurs indirectly between species that share a common predator species. The phytoplankton diversity significantly increases when active switching is combined with maximal feeding through predator-mediated coexistence.

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1. Introduction

Active prey-switching is a predatory behavior that has been documented in natural ecosystems (Murdoch, 1969, 1975; Hughes and Croy, 1993; Kiørboe et al., 1996; Gismervik and Andersen, 1997; Elliott, 2006; Kempf et al., 2008; Kiørboe, 2008; Kalinkat et al., 2011) and is known to stabilize ecosystem dynamics (Murdoch and Oaten, 1975; Haydon, 1994; Armstrong, 1999; Morozov, 2010). Active switching differs from passive switching in that the predators' switching is variable and based on relative prey density (i.e. frequency-dependent predation), rather than being fixed and based on constant prey preferences (see Gentleman et al. (2003) for a review). Thus, active switching represents a behavioral change of the predator (Gentleman et al., 2003), either in terms of feeding strategy (e.g. from passive suspension feeding to active ambush feeding) (Kiørboe et al., 1996; Gismervik and Andersen, 1997; Wirtz, 2012b) or learning how to increase the efficiency of capturing and handling certain prey types (Murdoch,

1973). Active switching makes the proportion of a given prey attacked to change from less than expected to more than expected as the relative abundance of that prey increases (Hassell, 2000).

From an ecosystem modeling perspective, active switching is an interesting property because it allows for a greater degree of species co-existence in competitive food webs (Vallina and Le Quééré, 2011; Prowe et al., 2012a,b). Multi-species ecosystem models can overcome the competitive exclusion principle (Hardin, 1960; Hutchinson, 1961; Armstrong and McGehee, 1980) by including some form of active switching (Adjou et al., 2012). In a broad sense, selective predation can be argued to fit within the “killing the winner” theory, which is sometimes invoked to explain the high diversity we observe in microbial communities (Thingstad and Lignell, 1997; Thingstad, 2000). The basic idea is that the most abundant bacteria types will be killed preferentially by host-selective viral lysis. Therefore, the coexistence of competing bacterial species is ensured by the presence of viruses that kill-the-winner, whereas the differences in substrate affinity between the coexisting bacterial species determine viral abundance (Thingstad, 2000). Active switching follows conceptually the same principle but for predator–prey selectivity.

However, current formulations of active prey-switching show anomalous dynamics, like *antagonistic* feeding and *sub-optimal* feeding in which predators are unable to maximize the ingestion

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of the total food available when it becomes divided among several prey (Tilman, 1982; Holt, 1983; Gentleman et al., 2003). In antagonistic feeding, if total food abundance is evenly distributed among many prey, it will give a smaller total ingestion than if the same total food is concentrated in one prey species (Tilman, 1982). In other words, for a given total food availability, the most even distribution of prey biomass will give the lowest total ingestion. Sub-optimal feeding occurs when an increase in the abundance of one prey can also result in a decrease of ingestion, despite that total food is actually increasing. Sub-optimal feeding is an extreme form of antagonistic feeding (Gentleman et al., 2003). When taken to the limit where each prey contributes to an infinitesimal fraction of the total prey abundance, these two modes of non-maximal feeding imply that the total ingestion by the predators will tend towards zero, even if the combined biomass of all their prey is high.

These formulation inconsistencies are conceptually problematic and have been used to warn against the use of active switching functional responses in ecosystem models (Gentleman et al., 2003). Here we argue that the problem does not lie with the use of active switching *per-se* but with the fact that current formulations are not completely satisfactory representations of switching behavior (Holt, 1983; Mitra and Flynn, 2006; Anderson et al., 2010). Total ingestion should ideally depend on the total food amount and its quality but not necessarily on the biomass distribution of the prey. In such a functional response all the prey would be perfectly substitutable for equal fixed preferences (Tilman, 1982) and feeding will always be maximal. The original Holling Type II functional response is probably the best known example (Holling, 1959; Gentleman et al., 2003). However, it does not allow for active prey-switching and therefore the competitive exclusion among the prey is very difficult to prevent and the ecosystem stability is drastically reduced (Gismervik and Andersen, 1997). Ward et al. (2012) suggests an equation for the switching between herbivory and carnivory. We use a similar approach for the switching between individual prey.

The first objective of this work is to identify the origin of the observed incompatibility between active switching and maximal ingestion in current formulations of predation on multiple prey (Gentleman et al., 2003). We evaluate three classical formulations of predation: two that exhibit switching but non-maximal ingestion (one sub-optimal, one antagonistic); and one that exhibits maximal ingestion but no-switching. We also describe a kill-the-winner (KTW) functional response that combines active switching with maximal ingestion (see Appendix A). Maximal and non-maximal ingestion are shown to arise from the implicit assumptions of the food web configuration inherent to each functional response (see Appendix B).

The second objective of this work is to evaluate how grazing functional responses affect the simulated global distributions of marine phytoplankton diversity and biogeography. The choice of the grazing response has already been shown to drastically change the simulated distributions of phytoplankton biogeography (Anderson et al., 2010) and diversity (Prowse et al., 2012a). However, these results were obtained from comparing “passive-switching with maximal feeding” formulations (i.e. Real’s) against “active-switching with non-maximal feeding” formulations (i.e. Fasham’s and Ryabchenko’s). Following a similar approach here we also evaluate the effect of the new KTW formulation that combines active-switching with maximal feeding. Thus we implemented the four functional responses under study (i.e. Fasham, Ryabchenko, Real, KTW) in a global marine ecosystem model with 64 phytoplankton species belonging to 4 functional groups which are differentiated by their dependence of growth on external nutrients. We show that active switching is a mechanism that allows higher levels of species co-existence, specially when combined with strong top-down control (i.e. maximal feeding). We use the

term “species” in a very broad and general sense, simply denoting variability of the phytoplankton traits for nutrient uptake. An alternative term could be phytoplankton ecotypes (Dutkiewicz et al., 2009).

2. Functional responses

The functional response describes how the ingestion rate of a predator changes with prey density. That is, it gives the function that relates the amount of prey ingested per predator and unit of time to the density of the prey in the environment (Murdoch, 1973). Although there are many functional responses described in the literature (Gentleman et al., 2003), the most common are the Holling Type I, II, III (Holling, 1959) and the Ivlev (Ivlev, 1961) functions for single prey type ingestion (see Fig. 1). A predator can theoretically change mode between functional responses (Real, 1977, 1979; Wirtz, 2012a). This work will only focus on transitions between the Type II (hyperbolic) and Type III (sigmoidal) responses. The Type II response gives a decelerating ingestion rate with increasing prey density, and thus provides prey safety only at high abundances. This leads to a lower per capita risk of being eaten at high prey densities and to a higher per capita risk of being eaten at low prey densities, which tends to destabilize predator-prey interactions. The Type III response, on the other hand, also provides prey safety at low abundances, which tends to stabilize predator-prey interactions. Type III responses can be explained in terms of optimal foraging theory as a way to optimize the energy intake from feeding with respect to the energy cost of foraging (MacArthur and Pianka, 1966; Pahlow and Prowse, 2010).

Most multi-species functional responses for predation are simply variations of the original Holling Type II/III formulations for one prey (Holling, 1959) but extended to consider many prey (Murdoch, 1973), and can be found in the literature as several mathematically equivalent equations. The general expression common to all four functional responses in this study is:

$$G_j = g_{max} Z \delta_j Q = V_{max} \delta_j Q \quad (1)$$

$$G = \sum G_j = V_{max} Q \sum \delta_j = V_{max} Q \quad (2)$$

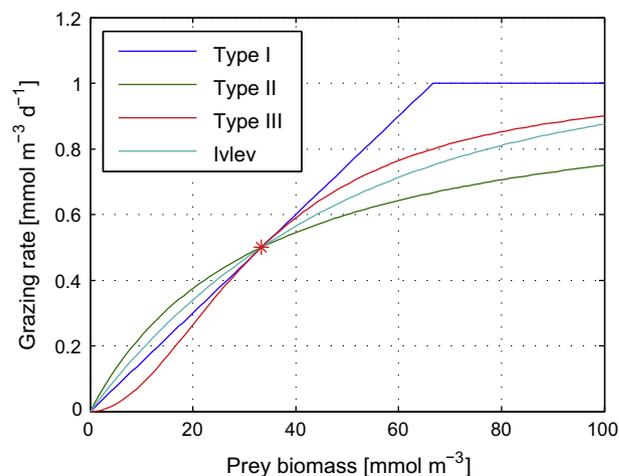


Fig. 1. Shape of the classical Holling Type (I, II, III) and Ivlev functional responses for ingestion [$\text{mmol m}^{-3} \text{d}^{-1}$] upon a single prey type [mmol m^{-3}] with a maximum grazing rate of 1.0 [$\text{mmol m}^{-3} \text{d}^{-1}$] and a half-saturation biomass of 33.33 [mmol m^{-3}].

where g_{max} [d^{-1}] is the maximum biomass-specific ingestion rate of a community of predator species Z [mmol m^{-3}]; $V_{max} = g_{max} Z$ is the maximum ingestion rate [$\text{mmol m}^{-3} \text{d}^{-1}$]; δ_j [n.d.] dictates switching towards prey p_j ; Q [n.d.] gives the predators' probability of

feeding as a saturating function of the available (i.e. palatable) prey biomass; G_j [mmol m⁻³ d⁻¹] is the ingestion rate upon prey p_j ; and G [mmol m⁻³ d⁻¹] is the total ingestion rate from all prey. Both δ_j and Q are non-dimensional terms that vary between 0 and 1. The sum of their multiplication across all prey gives the total food limitation for the predator, which will also be between 0 and 1. The total ingestion rate will be controlled by Q (see Eq. (2)) while the fraction of each prey in the diet will be determined by δ_j (see Eq. (1)).

The differences between functional responses come from how they characterize the prey-switching δ_j and feeding-probability Q terms. When the relative frequency of prey eaten is their relative density in the environment, the switching is passive; otherwise the switching is active. When the total ingestion is a function of total food and independent of the prey biomass distribution, the feeding is maximal; otherwise the feeding is non-maximal. The term δ_j is only different for the one passive-switching functional response (Real's formulation), while the other three active prey-switching functional responses (Fasham, Ryabchenko, and KTW formulations) share the same δ_j but differ in their Q (see Tables 1 and 2).

2.1. Fasham's formulation

Based on the work by Hutson (1984), Fasham et al. (1990) suggested the following formulation to account for predators' switching towards the most abundant prey species. Note that here a predator means a community of predators belonging to a given species instead of a single individual organism:

$$G_j = V_{max} \delta_j Q \tag{3}$$

$$= V_{max} \frac{\phi_j p_j}{F_\phi} \frac{F_\phi}{K + F_\phi} \tag{4}$$

$$= V_{max} \frac{\phi_j p_j}{k_{sat} + \sum \phi_i p_i} \tag{5}$$

$$= V_{max} \frac{\rho_j p_j^2}{(k_{sat} \sum \rho_i p_i) + \sum \rho_i p_i^2} \tag{6}$$

where k_{sat} is the half-saturation constant for ingestion [mmol m⁻³]; ρ_j is the constant preference (i.e. not density dependent) for prey p_j [n.d.]; and ϕ_j is the variable preference (i.e. density dependent) for prey p_j [n.d.]. The parameter K is related to the half-saturation for ingestion k_{sat} and in Fasham's formulation is assumed to be constant (see Tables 1 and 2). The predators' active prey-switching is controlled by the variable parameter ϕ_j , which gives the relative abundance of each prey measured with respect to the total food available (see Table 2).

The constant preference (ρ_j) can reflect a given prey palatability, the matchup between attack-survival strategies, or be related to predator-prey size ratios. The variable preference (ϕ_j) is a way to characterize how predators may select preferentially the most abundant prey, reflecting an increase in efficiency at capturing or handling a given prey type as its biomass increases relative to the others. Switching can be interpreted as a way of reflecting a change in the activity or composition of a heterogeneous community of predators that is not explicitly resolved in the model (Fasham et al., 1990). That is, having one generalist predator with active prey-switching is implicitly accounting for having many specialist predators that attack their preferred prey when they become available (see Section 4).

2.2. Ryabchenko's formulation

This formulation has been derived independently by many authors (Ryabchenko et al., 1997; Gismervik and Andersen, 1997; Koen-Alonso, 2007; Smout et al., 2010) and is often referred to as

Table 1

Functional responses. k_{sat} is the half-saturation constant for ingestion [mmol m⁻³]; ρ_j is the constant preference (i.e. not density dependent) [n.d.] for prey p_j ; and ϕ_j is the variable preference (i.e. density dependent) [n.d.] for prey p_j . Note that after substitution of the K parameter, the feeding probability Q for the Real and KTW formulations becomes identical, and that the only difference between Fasham and Ryabchenko formulations is their K parameter.

	Real	Fasham	Ryabchenko	KTW
δ_j	$\frac{\rho_j p_j}{F_\rho}$	$\frac{\phi_j p_j}{F_\phi}$	$\frac{\phi_j p_j}{F_\phi}$	$\frac{\phi_j p_j}{F_\phi}$
Q	$\frac{F_\rho^\beta}{K^\beta + F_\rho^\beta}$	$\frac{F_\phi}{K + F_\phi}$	$\frac{F_\phi}{K + F_\phi}$	$\frac{F_\phi^\beta}{K^\beta + F_\phi^\beta}$
K	k_{sat}	k_{sat}	$k_{sat} \frac{k_{sat}}{F_\rho}$	$k_{sat} \frac{F_\phi}{F_\rho}$

Table 2

Functional responses (cont.).

$F_\phi = \sum \phi_j p_j$	Total food using variable prey preference
$F_\rho = \sum \rho_j p_j$	Total food using constant prey preference
$\phi_j = \frac{\rho_j p_j}{\sum \rho_j p_j}$	Variable prey preference parameter
$\rho_j = [0 - 1]$	Constant prey preference parameter

basic multi-species Holling Type III functional response (Gentleman et al., 2003; Koen-Alonso, 2007; Prowe et al., 2012b):

$$G_j = V_{max} \delta_j Q \tag{7}$$

$$= V_{max} \frac{\phi_j p_j}{F_\phi} \frac{F_\phi}{K + F_\phi} \tag{8}$$

$$= V_{max} \frac{\phi_j p_j}{\left(k_{sat}^2 / \sum \rho_i p_i\right) + \sum \phi_i p_i} \tag{9}$$

$$= V_{max} \frac{\rho_j p_j^2}{k_{sat}^2 + \sum \rho_i p_i^2} \tag{10}$$

The only difference between the Ryabchenko and Fasham formulations is the parameter K of the Q term (see Table 1). In Ryabchenko's, K is made variable by scaling the half-saturation constant k_{sat} with the ratio between k_{sat} and the total prey abundance F_ρ (see Tables 1 and 2). In common with Fasham, a switching predator following Ryabchenko's formulation will concentrate its feeding on the relatively most abundant prey (Gismervik and Andersen, 1997).

2.3. Real's formulation

Derived from an analogy between feeding and enzyme reactions (Real, 1977, 1979), this formulation is equivalent to the general (Type II or III) Holling functional response. Extended to account for multiple prey, it takes the following form:

$$G_j = V_{max} \delta_j Q \tag{11}$$

$$= V_{max} \frac{\rho_j p_j}{F_\rho} \frac{F_\rho^\beta}{K^\beta + F_\rho^\beta} \tag{12}$$

$$= V_{max} \frac{\rho_j p_j}{F_\rho} \frac{F_\rho^\beta}{k_{sat}^\beta + F_\rho^\beta} \tag{13}$$

$$= V_{max} \frac{\rho_j p_j}{\sum \rho_i p_i} \frac{(\sum \rho_i p_i)^\beta}{k_{sat}^\beta + (\sum \rho_i p_i)^\beta} \tag{14}$$

The main differences with the two previous functional responses are that Real's formulation does not account for active prey-switching and that it always gives maximal feeding (e.g. see Michaelis-Menten of Class 1 multiple resource functional

responses in Gentleman et al. (2003)). The power β or “Hill” coefficient (Mittra and Flynn, 2006) is a parameter that determines if the shape of feeding probability Q is Type II or Type III. For comparison with the previous Ryabchenko sigmoidal response, we have chosen $\beta = 2$. Therefore, we can also call this formulation a multi-species Holling Type III functional response for total food.

2.4. Kill-the-winner (KTW) formulation

Maximal feeding with active prey-switching can be achieved if we use a new scaling factor for the half-saturation constant k_{sat} in order to obtain a parameter K (see Table 2) that will make the feeding probability Q to be solely a function of the total food F_ρ and thus independent of the prey biomass distribution:

$$G_j = V_{max} \delta_j Q \quad (15)$$

$$= V_{max} \frac{\phi_j p_j}{F_\phi} \frac{F_\phi^\beta}{K^\beta + F_\phi^\beta} \quad (16)$$

$$= V_{max} \frac{\phi_j p_j}{F_\phi} \frac{F_\rho^\beta}{k_{sat}^\beta + F_\rho^\beta} \quad (17)$$

$$= V_{max} \frac{\phi_j p_j}{\sum \phi_i p_i} \frac{(\sum \rho_i p_i)^\beta}{k_{sat}^\beta + (\sum \rho_i p_i)^\beta} \quad (18)$$

$$= V_{max} \frac{\rho_j p_j^2}{\sum \rho_i p_i^2} \frac{(\sum \rho_i p_i)^\beta}{k_{sat}^\beta + (\sum \rho_i p_i)^\beta} \quad (19)$$

The parameter K is now defined as k_{sat} times the ratio between the total prey abundance computed using the variable preference parameter F_ϕ and the total prey abundance computed using the constant preference parameter F_ρ (see Tables 1 and 2). The new scaling makes K to be dynamic and decrease when F_ϕ becomes smaller than F_ρ (e.g. when the food becomes evenly distributed among all prey) and simply reflects differential patterns in the attack rates upon each prey species (see Appendix A). Basically, this scaling removes the dependence of the feeding probability on F_ϕ , and thus its dependence on the particular distribution of food among the prey. Therefore, the feeding probability will only change as a function of total available food F_ρ and with a constant half-saturation for ingestion k_{sat} (see Eq. (17)). The ecological assumption is that all prey are perfectly substitutable for equal fixed preferences (Tilman, 1982). Note that the KTW formulation combines the same δ_j as in the Fasham/Ryabchenko formulations with the same Q as in the Real formulation. As before, the power β will determine if the shape of Q is Type II or Type III for total food. In order to obtain the same feeding probability as Real's formulations we chose it to be $\beta = 2$. We give a formal derivation of the KTW formulation in Appendix A where we make an explicit link between active switching to fundamental properties like the attack rate upon different prey species.

3. Feeding mode: maximal and non-maximal

Fig. 2 show ingestion upon each prey G_j as a function of the prey biomass p_j for an idealized ecosystem consisting of one predator species feeding upon two prey species with the four functional responses evaluated in this study. Fig. 3 gives both the feeding probability Q and the total ingestion G from the two prey as a function of p_j . The total ingestion is $G = V_{max} Q$ and we assume $V_{max} = 1.0$ [mmol m⁻³ d⁻¹] for simplicity. In common to all four functional responses, the total ingestion increases at low prey abundance and then starts to saturate at higher prey abundance (see Fig. 3). Also, the feeding on a given prey (e.g. Prey 1) is relaxed as the biomass of the alternative prey (i.e. Prey 2) increases (Fig. 2).

The first two functional responses (Fasham, Ryabchenko) account for active switching but while doing so they decrease the feeding probability as the total available food becomes evenly

distributed among the prey (see Fig. 3a and b), which leads to the non-maximal feeding of these formulations (see Fig. 4). This decrease in feeding probability does not occur for the other two functional responses (Real, KTW) for which the feeding is therefore always maximal (see Figs. 3c and 3d and 4). In both sub-optimal (Fasham) and antagonistic (Ryabchenko) feeding, moving along an isocline of equal total food available (e.g. the dotted line connecting the points Prey 1 = Prey 2 = k_{sat} [mmol m⁻³] in Fig. 3) gives different values of feeding probability. Furthermore, with sub-optimal feeding even an increase in the abundance of one prey, while keeping the abundance of the other prey constant (e.g. moving left-to-right along an horizontal line at any Prey 2 biomass), can sometimes lead to a decrease in the feeding probability despite the fact that the total food is actually increasing (see Fig. 3a).

The third formulation (Real) does not consider active prey-switching. Thus, the feeding probability now depends on total food available but not on how biomass is distributed among the prey. This means that if the constant prey preferences ρ_j were all the same (e.g. say equal to 1.0), all prey would become perfectly substitutable from the point of view of the predator. In this situation the feeding is always maximal because the presence of other prey does not interfere antagonistically with the predators' feeding probability (see Fig. 3c). Finally, the fourth formulation (i.e. KTW) behaves as a combination of the other three formulations: it accounts for active switching while giving maximal feeding (see Fig. 3d). We will next give more details about the differences of each of these four functional responses and elaborate on the reasons behind their particular behavior.

3.1. Fasham's formulation

In this formulation and in common to the other two functional responses with switching, the term δ_j is a non-linear function of the prey relative biomass and rapidly increases when the abundance of a given prey is high relative to the total food, which rapidly changes the relative fraction of alternative prey in the diet of the predator (see Fig. 2a). Therefore, the predation pressure is disproportionately large on relatively more abundant prey and disproportionately small on relatively less abundant prey (Murdoch, 1969). That is because the non-linear (i.e. quadratic) increase of the switching term δ_j with prey p_j biomass happens faster than if it were simply a linear function of prey p_j biomass. This implies that relatively low abundant prey are granted implicitly a prey refuge through a relaxation of feeding at low relative prey densities (Vallina and Le Quéré, 2011; Prowse et al., 2012a). That is, when alternative prey are present the functional response becomes sigmoidal (see the shaded area in Fig. 2a). Thus, the functional response on Prey 1 goes from being Type II when Prey 2 abundance is zero to being Type III when Prey 2 abundance is highest (see Fig. 2a).

For a fixed amount of total food, the feeding probability Q decreases with the evenness of the prey biomass distribution (see Fig. 3a). This happens because Q was calculated using F_ϕ as the measure of total food, which includes the variable preference ϕ_j (i.e. the relative abundance of each prey respect to total food; see Tables 1 and 2). The feeding probability can even decrease with total food for moderate increases of one prey biomass, leading to the sub-optimal feeding observed for this formulation (see Fig. 3a). The main issue with using F_ϕ to calculate Q is that for mass conservative ecosystems having many co-existing species could imply that each of them represents just a small fraction of the total prey abundance. Thus, the parameter ϕ_j will become small because the fraction of each prey p_j abundance respect to a constant total prey abundance decreases with the number of prey. Smaller ϕ_j will make both F_ϕ and Q small as well. Taken to the limit where the relative fraction of each prey is infinitesimally small this will lead to

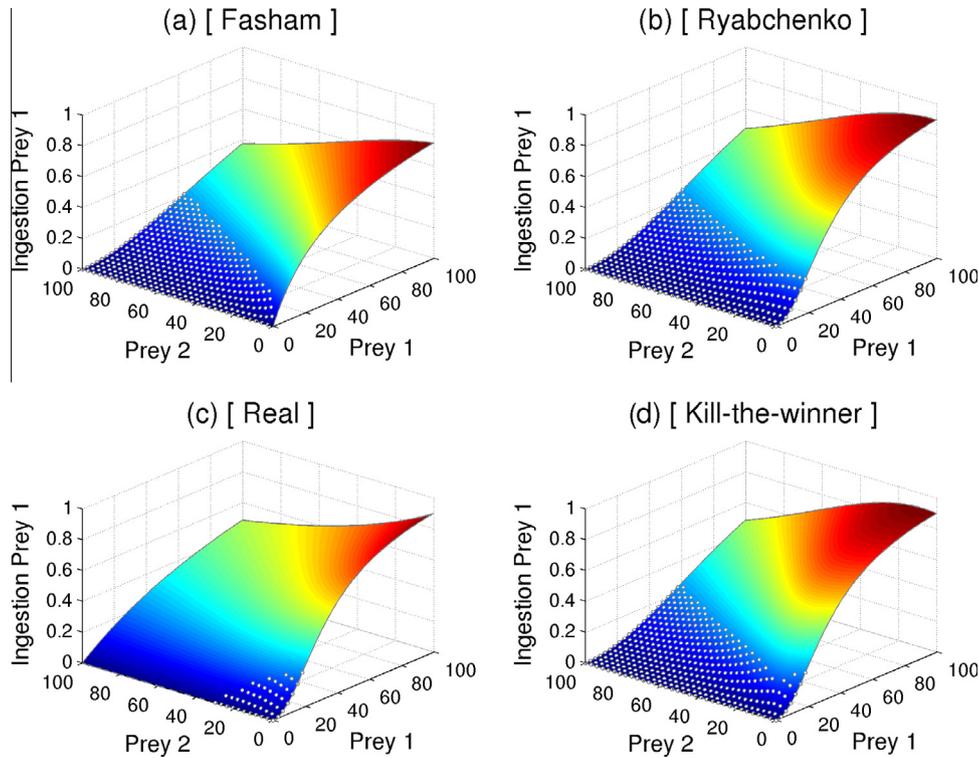


Fig. 2. Shape of the four functional responses (Fasham, Ryabchenko, Real, KTW) for the ingestion G_{p_1} [$\text{mmol m}^{-3} \text{d}^{-1}$] upon Prey 1. Constant parameters: maximum grazing rate $V_{max} = 1.0$ [$\text{mmol m}^{-3} \text{d}^{-1}$], half saturation for ingestion $k_{sat} = 33.33$ [mmol m^{-3}], prey preferences $\rho_j = 1.0$ [n.d.]. The shaded areas depict the region where the functional response is sigmoidal (i.e. Type III). The non-shaded areas depict the region where the functional response is hyperbolic (i.e. Type II).

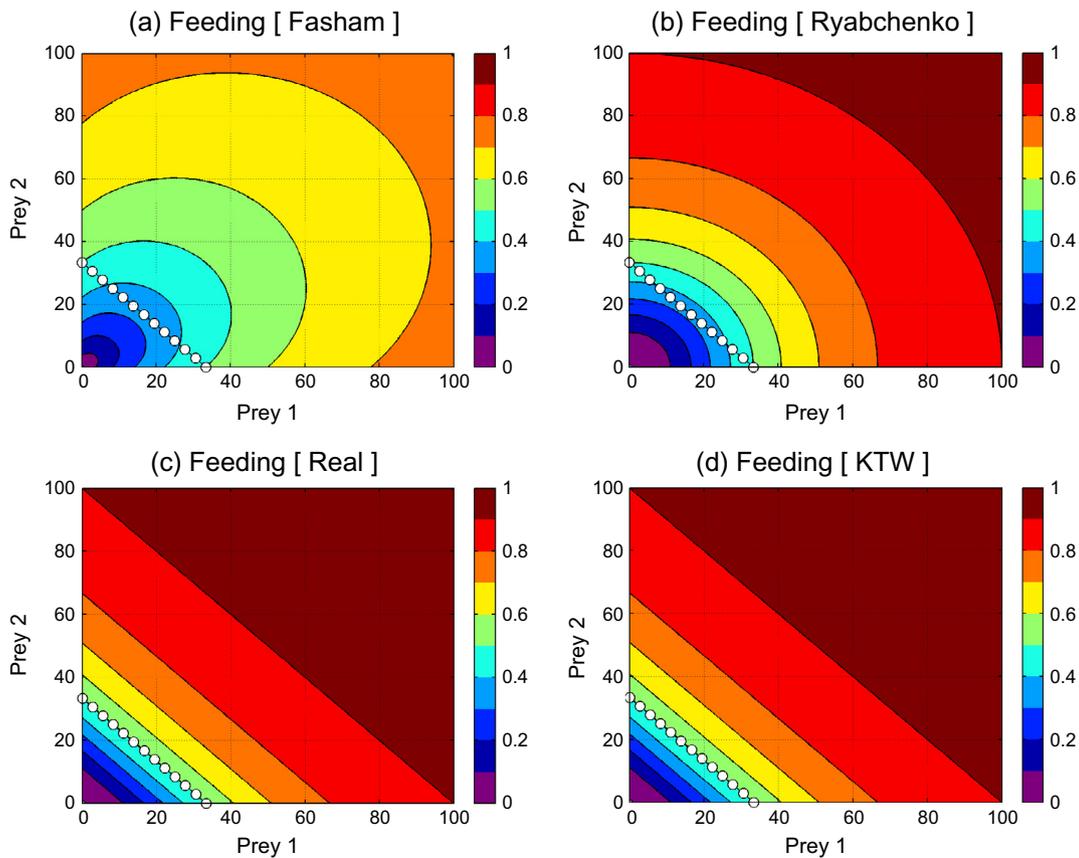


Fig. 3. Countour plots of the feeding probability Q [n.d.] and total ingestion $G = V_{max}Q$ [$\text{mmol m}^{-3} \text{d}^{-1}$] from Prey 1 and Prey 2 for the four functional responses (Fasham, Ryabchenko, Real, KTW) as a function of prey abundance [mmol m^{-3}]. The dotted line gives an isocline of equal total food available ($F_p = \sum \rho_j p_j = 33.33$ [mmol m^{-3}]). Constant parameters: maximum grazing rate $V_{max} = 1.0$ [$\text{mmol m}^{-3} \text{d}^{-1}$], half saturation for ingestion $k_{sat} = 33.33$ [mmol m^{-3}], prey preferences $\rho_j = 1.0$ [n.d.].

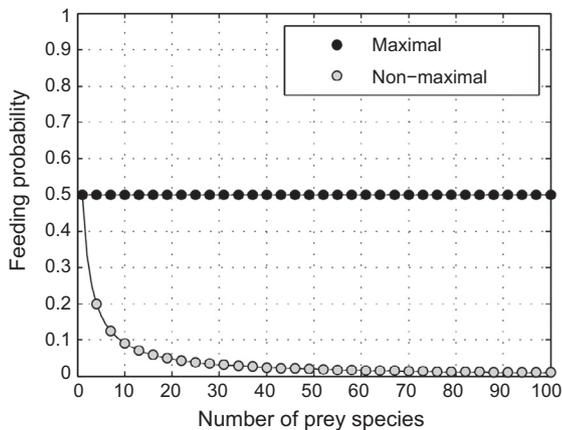


Fig. 4. Feeding probability Q [n.d.] and total ingestion $G = V_{max}Q$ [$\text{mmol m}^{-3} \text{d}^{-1}$] for a constant total food available of 100 [mmol m^{-3}] as a function of the number of equally abundant prey species (i.e. $100/N$) [mmol m^{-3}] in an idealized ecosystem composed of one predator species feeding upon N prey species with: maximal ingestion (Real and KTW formulations; black dotted line) and non-maximal ingestion (Fasham and Ryabchenko formulations; gray dotted line). Constant parameters: maximum grazing rate $V_{max} = 1.0$ [$\text{mmol m}^{-3} \text{d}^{-1}$], half saturation for ingestion $k_{sat} = 100$ [mmol m^{-3}], prey preferences $\rho_j = 1.0$ [n.d.]. (Note that Fasham and Ryabchenko formulations will give slightly different curves if $k_{sat} \neq 100$).

the feeding probability tending to zero, regardless of total prey abundance (see the non-maximal feeding case in Fig. 4).

3.2. Ryabchenko's formulation

One feature of Ryabchenko's formulation is that the shape of the functional response for predation upon any particular prey p_j is always sigmoidal, even if there is only one prey present (Gismervik and Andersen, 1997). Also, and in common to Fasham's formulation, as the biomass of alternative prey increases, the sigmoidal shape of the functional response for any given p_j becomes stronger (see the shaded area in Fig. 2b). Secondly, the feeding probability Q shows lower dependence on prey abundance distribution than the Fasham formulation and always increases with total food (i.e. it does not cause sub-optimal feeding). Yet and in common with Fasham, the feeding probability Q leads to antagonistic feeding because it decreases with the evenness of the prey biomass distribution (see Fig. 3b).

In Ryabchenko's formulation the feeding probability Q is also computed using F_ϕ (see Tables 1 and 2). However, the scaling of the half-saturation constant in the Ryabchenko formulation (i.e. k_{sat} is first squared and then scaled by the total prey abundance; see Table 1) eliminates the sub-optimal feeding of Fasham's formulation (see Fig. 3a and b). Nevertheless, the feature of the feeding probability tending to zero as the relative fraction of biomass in each prey becomes infinitely small still persists in Ryabchenko's formulation (see the non-maximal feeding case in Fig. 4). To avoid these conceptually problematic issues, the solution we suggest is to remove the variable preference ϕ_j from the calculation of the feeding probability Q and use ϕ_j only to compute the switching term δ_j (see Section 3.4).

3.3. Real's formulation

This formulation does not include active switching. For moderate to high total prey abundance (i.e. values above k_{sat}) the predation on a given p_j will still decrease if the abundance of alternative prey increases but this only reflects that p_j becomes a smaller proportion of the total prey abundance in the environment. The term δ_j is now a linear function of the prey biomass and their constant prey preferences ρ_j . The switching is thus passive: for equal fixed

preferences, the fraction of each prey in the diet will simply reflect their fraction in the environment.

Passive switching does not provide a refuge to relatively less abundant prey. In fact, the prey lose their refuge when the biomass of alternative prey increases: there is a transition from a Type III response to a Type II response (see the non-shaded area in Fig. 2c). This differs from the behavior of the Ryabchenko formulation, in which the predation upon each individual prey is always sigmoidal. Furthermore, it is exactly the opposite behavior from the Fasham formulation, in which the transition went from Type II to Type III. With passive switching any increase in either prey will lead to higher predation on both species, especially at low total prey abundance (i.e. values below k_{sat} , before the term Q starts to saturate).

The best way to visualize this behavior is by noting that the grazing refuge now applies to the *total* food, instead of to each individual prey. Starting at low total food abundance, as total food increases the refuge will slowly disappear for all prey, regardless of their relative abundances. Prey 1 loses its refuge when Prey 2 increases because Q increases faster than δ_1 decreases. However, the fact that Q is now computed using F_ρ , a measure of total food that does not include the variable preference ϕ_j (see Tables 1 and 2), has the advantage of leading to maximal feeding (see Figs. 3c and 4).

3.4. KTW formulation

This formulation uses the same active switching δ_j as the Fasham and Ryabchenko formulations, in combination with the maximal feeding probability Q of Real's. That is, the variable preference ϕ_j is now only used to compute the switching term but not to compute the feeding probability. The new scaling of the half-saturation constant (i.e. k_{sat} is multiplied by the ratio F_ϕ/F_ρ) makes the feeding probability to essentially depend on F_ρ (see Tables 1 and 2), which eliminates the non-maximal feeding observed for the Fasham and Ryabchenko formulations (see Fig. 3). This results in a multi-species functional response that combines maximal feeding with active switching: more food will always imply higher feeding probability (before saturation) and relatively more abundant prey will contribute a larger fraction of the predators' diet than their fraction in the environment.

Note that the only mathematical difference between the Real formulation and the KTW formulation is the use of quadratic prey abundances in the former to compute the switching term (see Eqs. (14) and (19); see also kill-the-winner coefficient α in Appendix A). Since Real and KTW use the same feeding probability Q , they both give maximal feeding (see Figs. 3 and 4). However, adding active switching leads to important differences in behavior between the two formulations. In particular, we note that now the functional response for each individual prey p_j is always Type III, with the sigmoidal shape becoming stronger as the biomass of alternative prey increases (see the shaded area in Fig. 2d). The prey do not lose their refuge when the biomass of alternative prey increases, contrary to Real's formulation. This is similar to the Ryabchenko formulation but note that if we chose the power to be $\beta = 1$ (instead of $\beta = 2$), it will behave more like the Fasham formulation (transition from Type II to Type III).

4. Food web configuration: explicit and implicit

Fig. 4 shows the feeding probability as a function of the number of equally abundant prey for maximal and non-maximal feeding formulations. Although the total food is constant, the ingestion decreases exponentially with the number of prey in the non-maximal case (Fasham, Ryabchenko) while it is constant when the feeding is

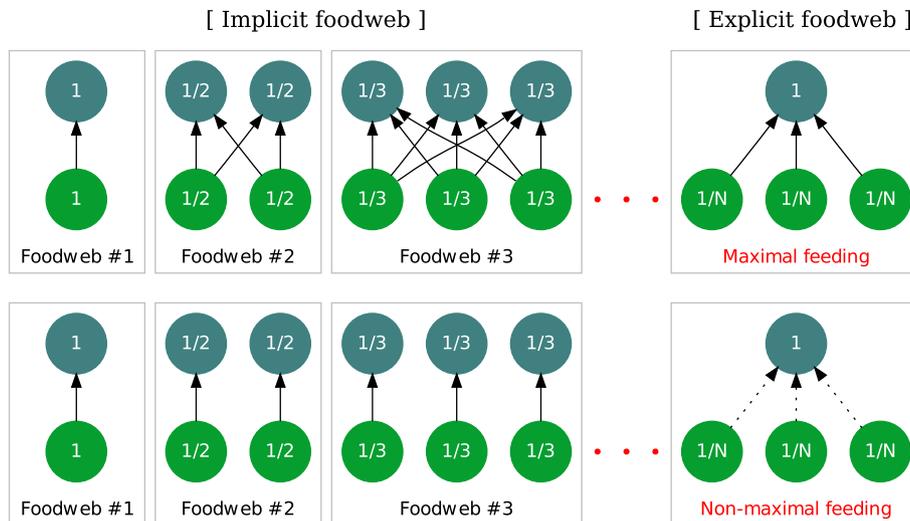


Fig. 5. Food web configurations that are implicit (left-side panels) to an explicit food web (right-side panel) composed of one predator species feeding on N identical prey species using functional responses with maximal feeding (upper panels; i.e. Real and KTW formulations) and non-maximal feeding (bottom panels; i.e. Fasham and Ryabchenko formulations). The dotted lines in the explicit food web reflect that the strength of predator–prey interactions decreases with the number of prey for the non-maximal feeding functional responses. See [Appendix B](#).

maximal (Real, KTW). The root cause of this behavior is that maximal and non-maximal feeding formulations are implicitly assuming different food web configurations: switching is essentially a community response. Food web configuration (either explicit or implicit) has important consequences for the interaction strength between the whole predator and prey communities (see [Appendix B](#)) and for the community assembly process ([Grover, 1994; Loreau, 2010](#)).

Having one explicit predator species with active switching can be seen as a way of implicitly accounting for many predator species feeding preferentially upon different prey ([Fasham et al., 1990](#)). As some prey species become more relatively abundant, this will be followed by an increase in the proportion of their specific predators. Non-maximal feeding formulations with one explicit predator (see lower-right panel in [Fig. 5](#)) are implicitly assuming a food web configuration of *pairwise* predator–prey interactions (i.e. one-to-one) in which a fraction of the community of predators feeds exclusively upon a single prey species (see lower-left panels in [Fig. 5](#)). The fraction of the predator community that becomes fully specialized in a single prey species is given by the fraction of that prey in the environment. Maximal feeding formulations with one explicit predator (see upper-right panel in [Fig. 5](#)) are implicitly assuming a food web configuration of *meshwise* predator–prey interactions (i.e. all-to-all) in which the whole community of predator can feed upon all prey species (see upper-left panels in [Fig. 5](#)).

There is an inverse dependence of total ingestion with the number of prey (N) in the case of explicit pairwise predator–prey interactions that is absent in the case of meshwise predator–prey interactions (see the analytical derivation in the [Appendix B](#)). With fully specialized pairwise interactions adding more prey implies *splitting* the predators' biomass into attacking specific prey species, which decreases the strength of the non-linear interactions between the whole predator and prey communities. With meshwise interactions adding more prey does not affect the interaction strength between the whole predator and prey communities (see [Appendix B](#)). This therefore explains the non-maximal feeding observed for the Fasham's and Ryabchenko's formulations and the maximal feeding observed for Real's and KTW formulations. Both Fasham's and Ryabchenko's formulations are implicitly assuming a food web of pairwise interactions (following Type II and Type III responses,

respectively), whereas for the Real and KTW formulations the total ingestion is independent of N because they are implicitly assuming a food web of meshwise interactions (see [Appendix B](#)).

5. Global ocean simulations

We implemented the four functional responses described above in a global marine ecosystem model ([Follows et al., 2007; Dutkiewicz et al., 2009](#)) in order to evaluate the impact of different modes of predation (i.e. passive/active switching with maximal/non-maximal feeding) on marine phytoplankton diversity and biogeography ([Barton et al., 2010; Prowse et al., 2012a](#)). See [Supp. material \(S1\)](#) for a detailed description of the model. We also performed a sensitivity analysis to the feeding pressure (i.e. low, medium, high) through varying the constant half-saturation constant for ingestion k_{sat} by $\pm 50\%$ respect to the control case. The results are the average of these 3 ensemble runs. The individual runs are given in the [Supp. material \(S2\)](#).

5.1. Species traits

The model was initialized with 64 phytoplankton species belonging to four major phytoplankton functional groups and two size-classes: small phytoplankton (i.e. *Prochlorococcus* and *Synechococcus*) and large phytoplankton (i.e. flagellates and diatoms). The model also resolves two predator size classes that feed preferentially on small and large phytoplankton, respectively: a generic micro-zooplankton and a generic meso-zooplankton. For each phytoplankton group, we generated 16 species by allowing a $\pm 30\%$ variability of the two traits that characterize the groups' ability to take up nutrients: the maximum specific growth rate μ_{max} [d^{-1}] and the half-saturation constant for nutrient uptake ks [$mmol\ m^{-3}$]. Phytoplankton growth will only be limited by nutrients and light levels, without photo-inhibition or temperature dependence. Within each group, the most competitive species will be the one having the highest maximum specific growth rate with the lowest half-saturation constant, which leads to the highest uptake affinity (i.e. μ_{max}/ks). Among groups, there is a trade-off between growth rate and nutrient affinity, which provides each phytoplankton functional group a particular nutrient niche ([Dutkiewicz et al., 2009](#)).

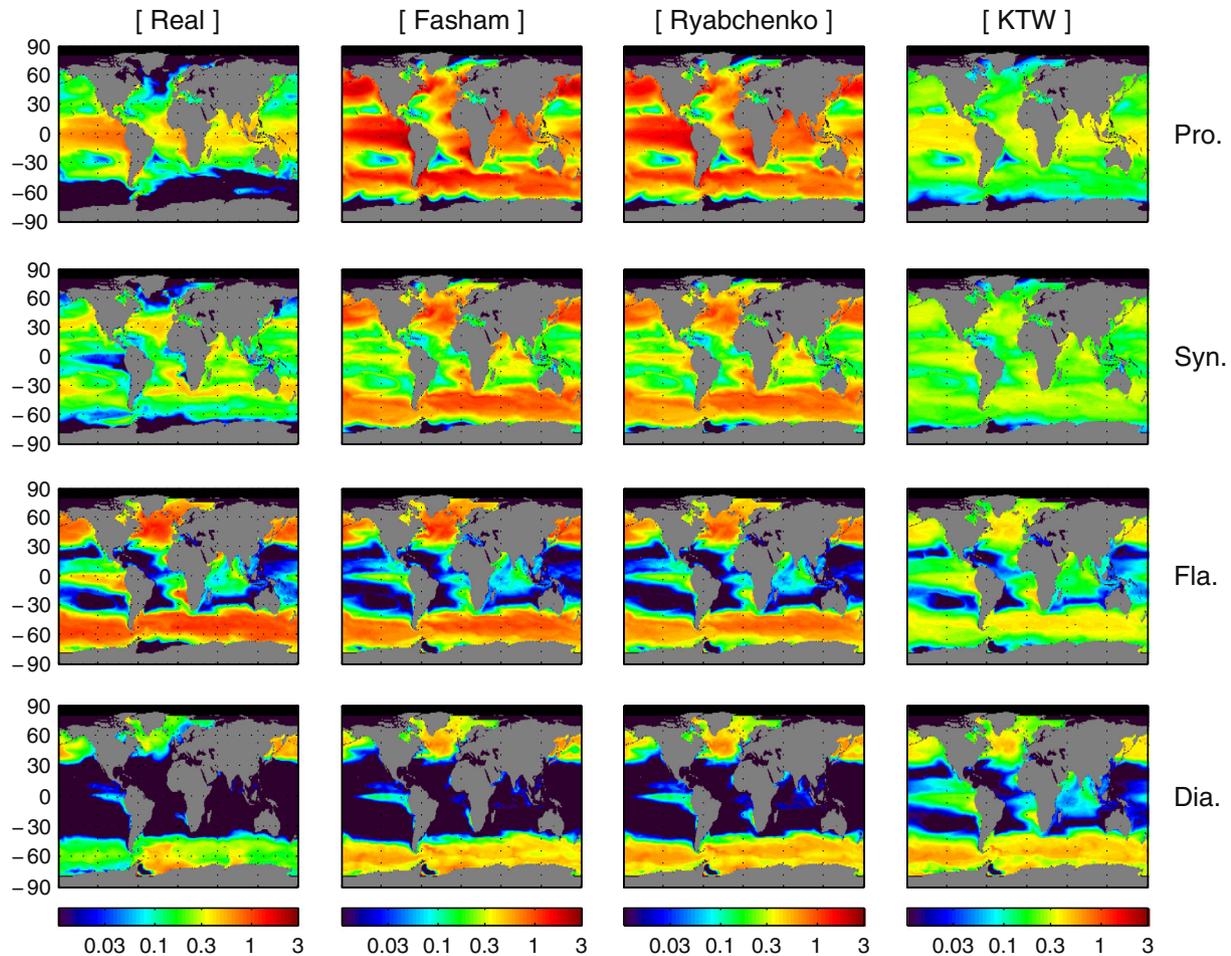


Fig. 6. Phytoplankton biomass [mmolN m^{-3}] by functional group (*Prochlorococcus*, *Synechococcus*, flagellates, diatoms): First column panels: Real formulation, Second column panels: Fasham formulation, Third column panels: Ryabchenko formulation, Fourth column panels: KTW formulation.

The nutrient uptake affinities are related to the species' subsistence nutrient concentration or “R star”, which is defined as $R^* = \frac{m_{phy}}{\mu_{max} - m_{phy}} ks$. This concept was derived by Tilman (1977) and gives the equilibrium requirement of a shared common resource (e.g. phosphate) of a monoculture of each species with constant loss rates (Tilman, 1982). Note that in this restricted definition of R^* the mortality rate m_{phy} is assumed constant. However, including predators adds an extra mortality that varies with top-down pressure, causing m_{phy} (and thus R^*) to increase with the feeding rate. Species with lower maximum growth rate are more sensitive to changes in the mortality rate than species with higher growth rate: if m_{phy} and μ_{max} are of similar magnitude, the R^* will become very high. Therefore, the presence of shared predators adds the potential for *apparent competition* among the prey, which occurs indirectly between the species that share a common predator (Holt, 1977; Grover, 1994; Loreau, 2010).

5.2. Phytoplankton biogeography

The global simulations show that in a non-stationary environment the four phytoplankton groups are able to persist even without active switching (see Real maps in Fig. 6) or even without any grazing at all (see Supp. Material S3). Since among groups there is a trade-off between growth rate and nutrient affinity that gives each phytoplankton group a particular nutrient niche (see Supp. Material S1). Seasonality disturbances provide niches for both low-nutrient adapted groups (i.e. small phytoplankton) and high-nutrient adapted groups (i.e. large phytoplankton) (Dutkiewicz

et al., 2009). However, each group tends to occupy a well defined oceanic region, not being capable of co-existing with other groups due to competitive exclusion. This is more easily noticeable in the individual simulations (see Supp. Material S2) than in the average of the ensemble that significantly blurs these features. Active switching (Fasham, Ryabchenko, KTW) allows for more spatial overlapping of phytoplankton groups; they co-exist over larger regions.

The biogeography of each group is very sensitive to the choice of the functional response. Fasham and Ryabchenko formulations give similar phytoplankton biogeography; Real's gives markedly different distributions; and KTW gives a biogeography that is intermediate. This is similar to the conclusions of an earlier study that tested four functional responses on phytoplankton group biogeography and also found large variations in the extent and magnitude of the simulated distributions of several phytoplankton groups with the grazing formulation (Anderson et al., 2010). With active switching (Fasham, Ryabchenko, KTW) the biogeography of the phytoplankton groups (Fig. 6) matches their species-richness distribution (Fig. 7): the highest diversity in each group is generally observed where it dominates. However, when using active switching with non-maximal feeding (i.e. Fasham and Ryabchenko) there is a probably unrealistic dominance of the small *Prochlorococcus* species over most of the ocean: they display almost global coverage and their biomass concentration is usually the highest of the four groups, even in the Southern Ocean (i.e. 40–60°S) where larger diatoms are known to dominate the phytoplankton biomass (Boyd et al., 2000; Gall et al., 2001; Hoffmann et al., 2006; Hirata et al., 2011).

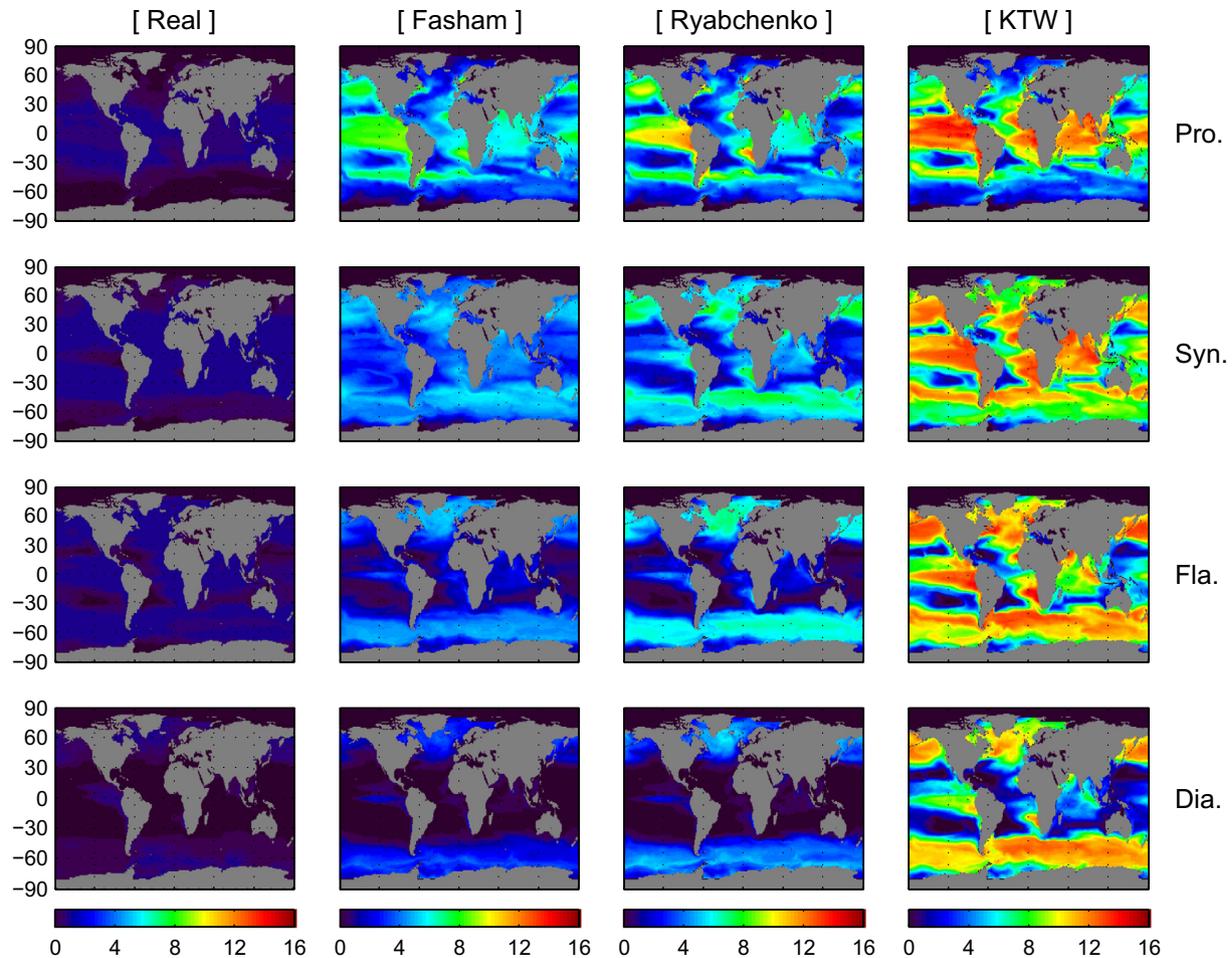


Fig. 7. Species richness by functional group (*Prochlorococcus*, *Synechococcus*, flagellates, diatoms): First column panels: Real formulation, Second column panels: Fasham formulation, Third column panels: Ryabchenko formulation, Fourth column panels: KTW formulation. Species richness is defined as the annual mean of monthly diversity. The monthly diversity is defined as the total number of species comprising greater than 1% of the total biomass at that location and month.

When using passive switching with maximal feeding (i.e. Real), the *Prochlorococcus* distribution appear more realistic since they are known to mostly dominate oligotrophic regions between 40°N and 40°S (Longhurst, 2006; Moore, 2010; Hirata et al., 2011). However, at higher latitudes (e.g. Southern Ocean) the most dominant group should be the diatoms instead of the flagellates (Boyd et al., 2000; Gall et al., 2001; Marañón et al., 2001; Hoffmann et al., 2006; Hirata et al., 2011). The transition between biogeographic regions is also very sharp (see Supp. Material S2). When using active switching with maximal feeding (i.e. KTW) the phytoplankton functional group distributions are more balanced. Each group tends to dominate in some ocean areas with a smooth transition between biogeographic regions. The modeled analogs of *Prochlorococcus* dominate at low latitudes and diatoms dominate at high latitudes; *Synechococcus* analogs are more widely distributed than *Prochlorococcus*; and modeled flagellates are also more widely distributed than diatom analogs. Although diatoms show the highest local biomass, no functional group clearly dominates in terms of global abundance (see Fig. 6).

The feeding probability of zooplankton (see Fig. 8) has a very strong influence on total phytoplankton biomass (see Fig. 9): the Fasham and Ryabchenko formulations lead to much higher biomass concentrations than the Real and KTW formulations (up to a factor of 3×). The lower feeding probability of the non-maximal feeding formulations (i.e. Fasham and Ryabchenko) compared to the maximal feeding formulations (i.e. Real and KTW) means a

weaker predator–prey interaction strength, which allows the total prey biomass to attain higher values.

5.3. Phytoplankton diversity

Regarding the global distribution of species richness obtained with the four functional responses, the two main features are: (i) species co-existence within and among phytoplankton functional groups when using active switching (i.e. Fasham, Ryabchenko, KTW) and (ii) dominance of one species per functional group and competitive exclusion of all the others within each group when using passive switching (i.e. Real) (see Fig. 7). The highest level of species diversity is obtained with the KTW formulation, both per functional group (see Fig. 7) and total (see Fig. 10). Species richness is defined here as the annual mean of monthly diversity, which is measured as the total number of species contributing greater than 1% of the total biomass at that location and month (Barton et al., 2010).

Without active switching (Real) we obtain the lowest level of maximum diversity: 4 species, one per functional group (Fig. 10c); these are the best competitors of each group (see Supp. Material S1) and therefore they outcompete all other species of their group. With active switching plus maximum feeding (KTW) we obtain the highest level of maximum diversity: ≈48 species on an annual average (Fig. 10d); with active switching plus non-maximal feeding (Fasham and Ryabchenko) we obtain intermediate

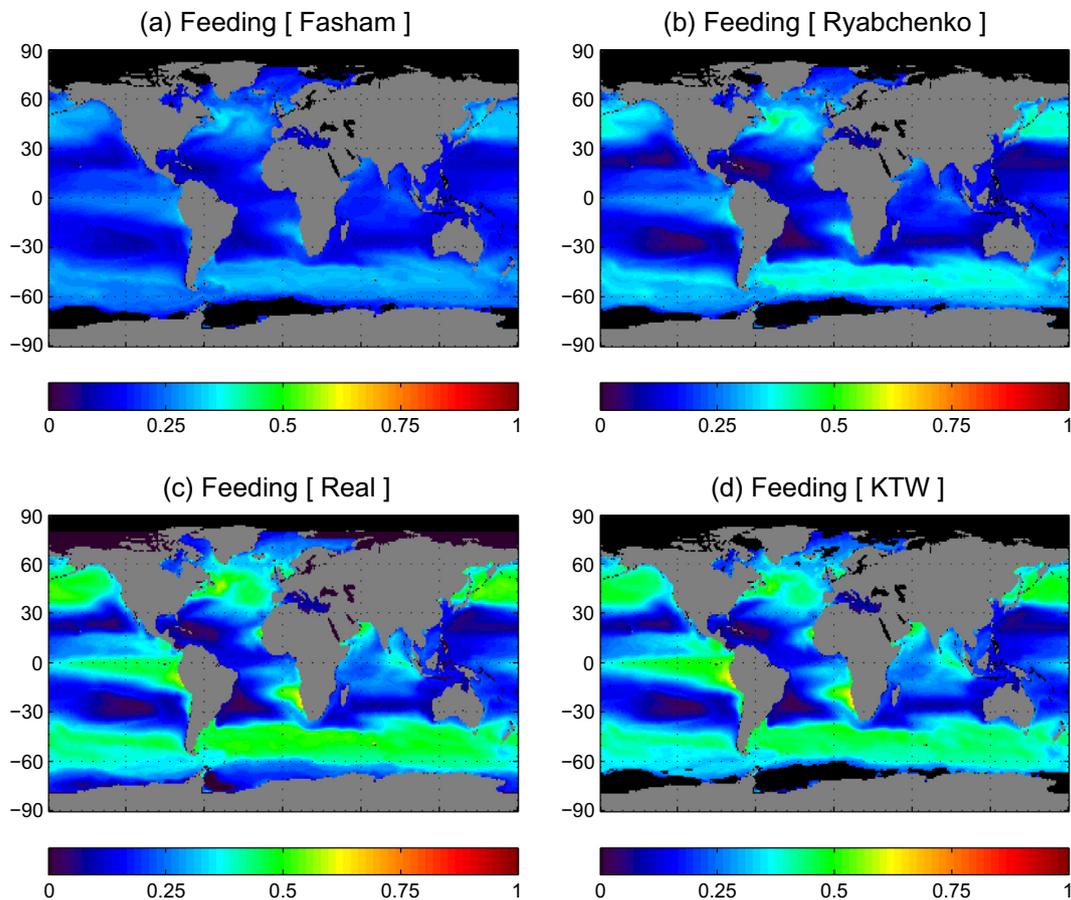


Fig. 8. Average feeding probability [n.d.] from the two generic zooplankton upon phytoplankton for the four functional responses: (a) Fasham formulation, (b) Ryabchenko formulation, (c) Real formulation, and (d) KTW formulation.

levels of diversity (Fig. 10a and b). The Fasham and Ryabchenko formulations support lower diversity than the KTW formulation because their non-maximal feeding decreases the strength of the active switching stabilizing mechanism. Using Fasham's formulation Prowe et al., 2012a showed that increasing the grazing pressure, increased phytoplankton diversity. We performed a sensitivity analysis of the feeding pressure that gives similar results (see Supp. Material S2). When the prey experience less predation pressure, they experience more competition for nutrients (Fuchs and Franks, 2010).

With active switching the lowest diversity is observed in nutrient poor regions like the subtropical gyres, and the highest diversity occurs at nutrient rich regions like the upwelling system off the coast of Peru (Fig. 10). Slightly different patterns of diversity were reported by Barton et al., 2010 and Prowe et al., 2012a but our results are not directly comparable to theirs. These studies included optimal niches of light and temperature that are absent in our simulations. Differences in light and temperature sensitivities affected the species fitness, leading to co-existence at low latitudes of phenotypes with similar subsistence resource concentrations but different light and temperature physiologies. That mechanism is ignored in our simulations for reasons of focus. Grazing induced mortality provides another avenue by which organisms may achieve similar fitness (i.e. R^*).

Contrary to the results with active switching, increasing the grazing pressure with passive switching has been shown to decrease phytoplankton diversity (Prowe et al., 2012a) because non-selective grazing magnifies the competitive abilities for nutrient uptake of the different prey species which results in stronger competitive exclusion. This relates to the early findings of May,

1974 with simple Lotka–Volterra models that an increase in inter-specific competition brings instability to the food web if the intra-specific competition remains constant. That is, when the sum of the inter-specific forces in the ecosystem is higher than the sum of its intra-specific forces, the system becomes unstable (e.g. species extinctions occur). Stronger predation with non-selective feeding falls within this scenario (Haydon, 1994). However, stronger predation with active switching increases intra-specific forces and thus it stabilizes the ecosystem through a negative (i.e. self-regulatory) feedback affecting each prey biomass (Haydon, 1994). That is why active switching combined with maximal feeding gives the higher level of species diversity.

6. Discussion

Selective feeding is known to be an important component underpinning the assembly rules of predator–prey communities (Grover, 1994; Loreau, 2010) and the size-structure of marine communities (Armstrong, 1994; Poulin and Franks, 2010; Banas, 2011). Small phytoplankton types are good competitors for nutrients but are prevented from exhausting all available nutrients by selective top-down control (Ward et al., 2012). Grazing places a limit on the amount of phytoplankton biomass within each size-class, while the nutrient supply dictates the number of size classes and hence the total biomass in the system (Chisholm, 1992; Armstrong, 1994; Ward et al., 2012). This mechanism is based on the size-specificity of predator–prey interactions which makes the assumption that grazing interactions occur preferentially at a certain predator–prey size ratio. The success of one particular prey is held in check by the increased growth of the zooplankton that feed prefer-

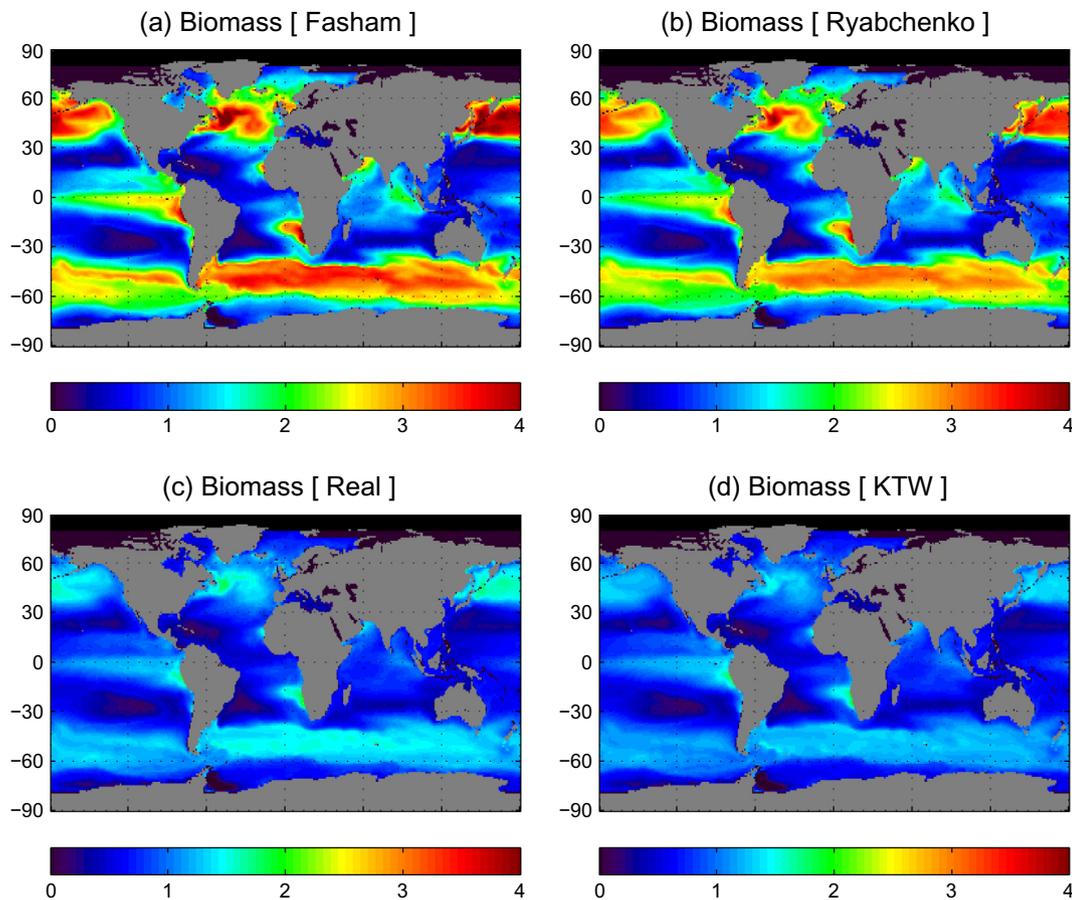


Fig. 9. Total phytoplankton biomass [mmolN m⁻³] for the four functional responses: (a) Fasham formulation, (b) Ryabchenko formulation, (c) Real formulation, and (d) KTW formulation.

entially on that prey. Therefore, size-diversity increases with the amount of nutrients because the selective top-down control of smaller sizes allows larger size classes to invade and persist (Armstrong, 1994; Fuchs and Franks, 2010; Banas, 2011).

However, predator–prey linkages are not just given by body sizes but also by the consumers’ feeding type (Wirtz, 2012b). There is a wide range of prey species at each predator size class (Hansen, 1994; Fuchs and Franks, 2010). Although our global scale simulations are based on just two broad size-classes of plankton (i.e. large and small), combining active switching with more highly resolved size-selective feeding will increase the species diversity within each prey size-class; size preferences alone cannot bring about within size-class diversity. Increasing the number of prey species in our study is thus analogous to increasing selective predator–prey interactions. That is why we find more prey diversity where they are more abundant (i.e. less limited by nutrients) in the global maps with active prey-switching (Fasham, Ryabchenko, KTW). More nutrients are able to sustain more species through selective feeding, which is implicit to active switching formulations (see Section 4). Selective feeding (explicit or implicit) leads to positive niche complementarity among the prey through differentiation of their predators (Loreau, 2010). Prey complementarity arises from avoidance of predator-mediated or “apparent” competition (Holt, 1977; Loreau, 2010).

Previous works have shown that there are large differences in the phytoplankton diversity (Prowe et al., 2012a) and biogeography (Anderson et al., 2010) between selective grazing (e.g. Fasham’s and Ryabchenko’s) versus non-selective grazing (i.e. Real’s) formulations. However, there are also significant differences in

the phytoplankton diversity and biogeography between the Fasham/Ryabchenko versus the KTW formulation. Although the three functional responses with active switching account for selective feeding, the fact that $\sum \phi_j p_j \leq \sum \rho_j p_j$ implies that with non-maximal feeding probability the effective half-saturation for ingestion upon the whole prey community increases with the number of prey (Banas, 2011) (see Appendix B). That means that the ingestion rate of a given predator species decreases with the range of prey species available for consumption (Fuchs and Franks, 2010) which affects the degree of predator-mediated complementarity (Thebault and Loreau, 2003). Here we argue that the feeding probability should not necessarily change with the diet breadth.

Apparent competition occurs indirectly between prey that share a common predator species (Holt, 1977). This introduces a new element to the prey community assembly which now depends not only on the nutrient concentration but also on the predators’ concentration (Grover, 1994; Loreau, 2010). *Prochlorococcus* tend to dominate in Fasham’s and Ryabchenko’s formulations because for weak apparent competition among prey they are intrinsically the best competitors (i.e. lowest R^*). Complete suppression of grazing activity (i.e. zooplankton dying out of starvation) to evaluate the effect of removing apparent competition leads to similar phytoplankton biogeography, although now with only one species per phytoplankton group being able to survive due to the lack of active switching (see Supp. Material S3). However, strong apparent competition decreases the relative competitive ability of the species with slower maximum growth rate like *Prochlorococcus*, which benefits the species with faster maximum growth rates like diatoms (see Supp. Material S2). The apparent competition of the Real

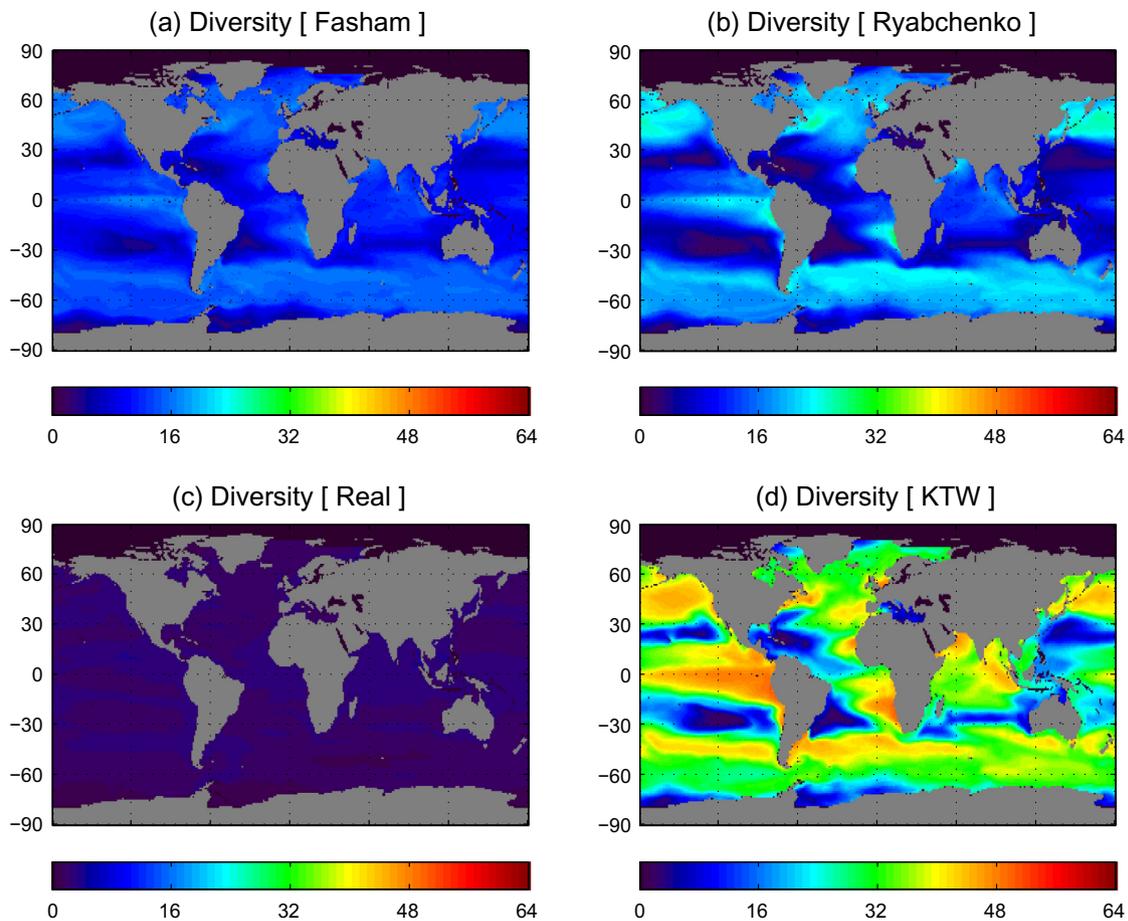


Fig. 10. Total species richness for the four functional responses: (a) Fasham formulation, (b) Ryabchenko formulation, (c) Real formulation, and (d) KTW formulation. Species richness is defined as the annual mean of monthly diversity. The monthly diversity is defined as the total number of species comprising greater than 1% of the total biomass at that location and month.

and KTW formulations is stronger than in Fasham/Ryabchenko formulations due to the maximal feeding.

7. Limitations and generality of this work

This work is essentially a theoretical exercise. No attempt has been made at this stage to formally validate the model simulations with global datasets of phytoplankton diversity and biogeography. The main goal of our analyses was to better understand the assumptions of switching functional responses with regard to the implicit food web configurations of predator–prey communities, and to explore the effect that the different functional responses for predation may have on modeled ecosystem dynamics. This work adds theoretical support to the early suggestion that active switching is a potentially powerful mechanism to sustain high levels of diversity (Oaten and Murdoch, 1975; Murdoch and Oaten, 1975). However, is active switching an important driver of diversity in natural ecosystems? More experimental and field work should be able to better answer this theoretical hypothesis. Although switching towards alternative prey has been documented to occur in the laboratory (Murdoch, 1969, 1975; Hughes and Croy, 1993; Gismervik and Andersen, 1997; Kiørboe et al., 1996; Elliott, 2006; Kiørboe, 2008; Kalinkat et al., 2011), conflicting results based on the analyses of even the same data sets have been also reported (e.g. (Rindorf et al., 2006; Kempf et al., 2008)). Thus, an unambiguous proof of its relevance in the field remains elusive (Hassell, 2000; Elliott, 2006).

Should we expect total ingestion always to be maximal? When the predators must trade off their own predation success against their own risk of predation, maximal feeding may not always be the emergent property (Mariani and Visser, 2010). Also, a decrease in the predation efficiency with the number of prey species could be an emergent property in some complex food webs if there is an increased difficulty for the predators to attack their prey due to an increase in habitat complexity with prey diversity, such as heterogeneities in prey distribution (i.e. patches) or prey-defense strategies (Abrams and Allison, 1982; Duffy et al., 2007). On the other hand, should we expect total ingestion to become infinitely small as prey diversity becomes large? Solutions with negligible total ingestion when prey diversity is high appear unphysical and enforcing a maximal feeding behavior can alleviate this unrealistic response.

Active switching formulations are by design *phenomenological* models, which describe a phenomenon without explicit consideration of the lower-level processes that generate it (Loreau, 2010). Both the Hill coefficient β and the kill-the-winner coefficient α (see Appendix A) impose density-dependent predatory mortalities upon the prey without saying which mechanisms are causing it. They are an abstraction for a wealth of factors that are neither well understood nor explicitly modeled. The focus is thus placed on the consequences that switching has on ecosystem dynamics, rather than on the causes that generate the switching itself. The main strength and the corresponding main weakness of phenomenological models is their simplicity: on the one hand they provide simple

predictions and clear interpretations; on the other hand they do not provide a complete description of reality (Loreau, 2010). The lack of well-defined first-principle rules to model active switching from pure mechanistic grounds can lead to formulation inconsistencies (see Appendix C). Therefore active switching formulations should ideally move towards a more mechanistic approach. Also, it is worth noting that there is a clear mismatch between the scales at which the plankton communities interact and the scales at which global ocean models operate (Siegel, 1998).

8. Conclusions

Complex food web models need mechanisms to overcome the probably unrealistic but common outcome of one or few species outcompeting all others. The use of functional responses with active prey-switching can help alleviate competitive exclusion. However, active switching formulations in which the feeding is non-maximal (Fasham, Ryabchenko) have the problem that an increase in the number of modeled prey species implies a decrease of the average predator–prey interaction strength (Vallina and Le Quééré, 2011). If the strength of predator–prey interactions decreases, the total prey biomass will therefore increase. This mostly applies to closed (i.e. mass conservative) systems like the global ocean in which the total mass (biotic + abiotic) of essential elements is roughly constant at the seasonal scale and therefore more prey species means less biomass per prey, until reaching a point where they all become protected from predation in their own prey refuge and none can be eaten. With maximal feeding formulations (Real, KTW) the average of predator–prey interactions is unaffected by the number of prey species. However, the number of species decreases to very low levels in the absence of active switching due to strong competitive exclusion (Real). We derived a kill-the-winner functional response that combines active switching with maximal feeding (KTW). Global ocean simulations show that both active switching and maximal feeding are key elements to sustain higher levels of species diversity while providing realistic phytoplankton functional-group biogeography.

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Appendix A. Kill-the-winner functional response

The generic functional response for feeding on multiple prey was mathematically derived by Murdoch (1973). The ingestion rate upon a single prey species j is characterized using the following expression:

$$G_j = \frac{a_j \rho_j P_j Z}{1 + \sum_k (a_k/h_k) \rho_k P_k} \quad (20)$$

where Z is the concentration of predators [mmol m^{-3}]; P_j is the concentration of prey species j [mmol m^{-3}]; a_j is the predators' attack rate on prey species j [$\text{m}^3 \text{mmol}^{-1} \text{d}^{-1}$]; h_j is the predators' handling rate of prey species j [d^{-1}]; and ρ_j is a constant prey preference [n.d.]. Assuming that the handling rates are constant and the same for all prey species (i.e. $h_j = h$) implies that any switching towards particular prey species will solely be given by differences in the attack rates:

$$a_j = a \frac{\delta_j}{\phi_j} \quad (21)$$

$$\phi_j = \frac{\rho_j P_j}{\sum_i \rho_i P_i} \quad (22)$$

$$\delta_j = \frac{\rho_j P_j^\alpha}{\sum_i \rho_i P_i^\alpha} \quad (23)$$

$$a = a' \left(\sum_i \rho_i P_i \right)^{\beta-1} \quad (24)$$

where a is a density-dependent attack rate [$(\text{m}^3 \text{mmol}^{-1} \text{d}^{-1})$]; a' is a density-independent (i.e. constant) attack rate [$(\text{m}^3 \text{mmol}^{-1})^\beta \text{d}^{-1}$]; ϕ_j is the relative abundance of prey species j [n.d.]; δ_j regulates the switching towards prey species j [n.d.]; β is the Hill coefficient that measures how the attack rate varies with total prey density [n.d.]; and α is the kill-the-winner coefficient that measures the potential for selective predation: when α is equal to 1.0 we have that $a_j = a$ and the switching is *passive* (i.e. no KTW predation); when α is bigger than 1.0 we have that $a_j \geq a$ and the switching is *active* (i.e. KTW predation). Note that $\sum a_j \rho_j P_j = a \sum \rho_j P_j$ which implies that total feeding is always maximal: if some species are being attacked faster than some others must be being attacked slower.

Substituting Eqs. (21) and (22) into Eq. (20):

$$\begin{aligned} G_j &= \frac{a \delta_j \left(\sum_i \rho_i P_i / \rho_j P_j \right) \rho_j P_j Z}{1 + (a/h) \sum_k \delta_k \left(\sum_i \rho_i P_i / \rho_k P_k \right) \rho_k P_k} \\ &= \frac{a \delta_j \sum_i \rho_i P_i Z}{1 + (a/h) \sum_i \rho_i P_i \sum_k \delta_k} \\ &= \frac{a \delta_j \sum_i \rho_i P_i Z}{1 + (a/h) \sum_i \rho_i P_i} \\ &= \frac{h \delta_j \sum_i \rho_i P_i Z}{(h/a) + \sum_i \rho_i P_i} \end{aligned} \quad (25)$$

Substituting Eq. (24) into Eq. (25):

$$\begin{aligned} G_j &= \frac{h \delta_j \sum_i \rho_i P_i Z}{(h/(a' (\sum_i \rho_i P_i)^{\beta-1})) + \sum_i \rho_i P_i} \\ &= \frac{h \delta_j \sum_i \rho_i P_i (\sum_i \rho_i P_i)^{\beta-1} Z}{(h/a') + \sum_i \rho_i P_i (\sum_i \rho_i P_i)^{\beta-1}} \\ &= \frac{h \delta_j (\sum_i \rho_i P_i)^\beta Z}{(h/a') + (\sum_i \rho_i P_i)^\beta} \end{aligned} \quad (26)$$

We can now define:

$$V_{\max} = hZ \quad (27)$$

$$k_{\text{sat}}^\beta = h/a' \quad (28)$$

where V_{\max} is the maximum ingestion rate [$\text{mmol m}^{-3} \text{d}^{-1}$] and k_{sat} is the half-saturation constant for ingestion [mmol m^{-3}]. Substituting Eqs. (27) and (28) into Eq. (26):

$$\begin{aligned} G_j &= V_{\max} \frac{\rho_j P_j^\alpha}{\sum_i \rho_i P_i^\alpha} \frac{(\sum_i \rho_i P_i)^\beta Z}{k_{\text{sat}}^\beta + (\sum_i \rho_i P_i)^\beta} \\ &= V_{\max} \delta_j \frac{F^\beta}{k_{\text{sat}}^\beta + F^\beta} \\ &= V_{\max} \delta_j Q \end{aligned} \quad (29)$$

where Q gives the overall feeding probability [n.d.]; δ_j dictates the switching towards prey species j [n.d.]; and $F = \sum_i \rho_i P_i$ is the total food available [mmol m^{-3}].

Appendix B. Food web configuration and feeding mode

B.1. Explicit food webs

B.1.1. Pairwise interactions

When a food web is composed by specialized predators that can only feed upon one single prey species (see lower-left panels in Fig. 5), increasing the number of prey will decrease the total feeding of the predator community as a whole. Let us call N the number of prey and predators that are present in the food web. If the total biomass P of prey and the total biomass Z of predators is constant, we have that:

$$P = \sum_j^N P_j \quad (30)$$

$$Z = \sum_j^N Z_j \quad (31)$$

In the simplest scenario in which all the prey have equal biomass and all the predators have equal biomass, we have that:

$$P_j = P/N \quad (32)$$

$$Z_j = Z/N \quad (33)$$

The predators' total ingestion rate G will be given by:

$$G = \sum_j^N g_{\max} Z_j \frac{P_j^\beta}{K + P_j^\beta} \quad (34)$$

where the power β will regulate the functional response (Type II when $\beta = 1$ and Type III if $\beta = 2$) and K is a parameter related to the half-saturation constant for ingestion. Substituting Eqs. (32) and (33) into Eq. (34) gives:

$$G = \sum_j^N g_{\max} (Z/N) \frac{(P/N)^\beta}{K + (P/N)^\beta} \quad (35)$$

$$= g_{\max} Z \frac{(P/N)^\beta}{K + (P/N)^\beta} \quad (36)$$

$$= g_{\max} Z \frac{P^\beta}{N^\beta K + P^\beta} \quad (37)$$

If $\beta = 1$ and $K = k_{\text{sat}}$, we have the Type II case:

$$G = g_{\max} Z \frac{P}{N k_{\text{sat}} + P} \quad (38)$$

If $\beta = 2$ and $K = k_{\text{sat}}^2/N$, we have the Type III case:

$$G = g_{\max} Z \frac{P^2}{N k_{\text{sat}}^2 + P^2} \quad (39)$$

In either case, N is multiplying the half-saturation constant for ingestion k_{sat} . Thus, as we increase the number of prey with their own specific predator in the ecosystem, the total ingestion of the whole predator community will decrease exponentially. This simply reflects that increasing N implies splitting the predators' biomass into attacking specific prey. If we have a food web composed of only one prey and one predator ($N = 1$), all the predators' biomass is interacting with all the prey's biomass; whereas if we have a food web composed of two prey and two predators ($N = 2$), now half of all the predators' biomass is interacting with half of all the prey's biomass while the other half biomass are interacting independently. Therefore, the overall predator–prey interaction strength decreases with N . For example, if the total biomass of either predators and prey is 100 [mmolC m⁻³], and assuming for simplicity Lotka–Volterra interactions ($Z \cdot P$), we can see that $100 \times 100 = 10,000$ (one predator–one prey) is bigger than $(50 \times 50) + (50 \times 50) = 5000$

(two predators–two prey). Thus increasing N in the ecosystem will necessarily decrease the predators' total ingestion. This is analogous to the non-maximal feeding formulations (i.e. Fasham's and Ryabchenko's).

B.1.2. Meshwise interactions

When a food web is composed by generalist predators that feed on all prey (see upper-left panels in Fig. 5) and the total biomass of both prey and predators is constant, the feeding of the whole predator community will be independent of the number of prey and predators N in the system. The predators' total ingestion rate G will be given by:

$$G = \sum_j^N g_{\max} Z_j \frac{(\sum_i^N P_i)^\beta}{K + (\sum_i^N P_i)^\beta} \quad (40)$$

where the power β will regulate the functional response (Type II when $\beta = 1$ and Type III if $\beta = 2$) and K is a parameter related to the half-saturation constant for ingestion. Substituting Eqs. (30) and (33) into Eq. (40) gives:

$$G = \sum_j^N g_{\max} (Z/N) \frac{P^\beta}{K + P^\beta} \quad (41)$$

$$= g_{\max} Z \frac{P^\beta}{K + P^\beta} \quad (42)$$

If $\beta = 1$ and $K = k_{\text{sat}}$, we have the Type II case:

$$G = g_{\max} Z \frac{P}{k_{\text{sat}} + P} \quad (43)$$

If $\beta = 2$ and $K = k_{\text{sat}}^2$, we have the Type III case:

$$G = g_{\max} Z \frac{P^2}{k_{\text{sat}}^2 + P^2} \quad (44)$$

In either case, the predators' total ingestion is independent of N . That means that changing the number of prey and predators in the ecosystem will have no effect on the predators' total ingestion as a whole. This reflects that all the predator biomass is always interacting with all the prey biomass, regardless of N . Thus, increasing N in the ecosystem will not affect the overall predator–prey interaction strength. This is analogous to the maximal feeding formulations (i.e. Reals's and KTW).

B.2. Implicit food webs

B.2.1. Non-maximal feeding

For non-maximal feeding formulations, the total ingestion rate G is given by:

$$G = \sum_j^N g_{\max} Z \frac{P_j^2}{\chi + \sum_i^N P_i^2} \quad (45)$$

where N is the number of prey species (note that there is only one predator species) and χ is a parameter related to the half-saturation constant for ingestion. Substituting Eq. (32) into Eq. (45) gives:

$$\begin{aligned} G &= \sum_j^N g_{\max} Z \frac{(P/N)^2}{\chi + \sum_i^N (P/N)^2} = \sum_j^N g_{\max} Z \frac{P^2}{N^2 \chi + N P^2} \\ &= \sum_j^N g_{\max} (Z/N) \frac{P^2}{N \chi + P^2} = g_{\max} Z \frac{P^2}{N \chi + P^2} \end{aligned} \quad (46)$$

If $\chi = k_{\text{sat}} P$, we have the solution for Fasham's formulation:

$$G = g_{\max} Z \frac{P}{N k_{\text{sat}} + P} \quad (47)$$

If $\chi = k_{sat}^2$, we have the solution for Ryabchenko's formulation:

$$G = g_{max} Z \frac{P^2}{Nk_{sat}^2 + P^2} \quad (48)$$

Note that Eq. (47) is equivalent to Eq. (38) and that Eq. (48) is equivalent to Eq. (39). This means that under the condition of constant total prey and predator biomass, and for the simplest scenario in which all prey have equal biomass, the Fasham and Ryabchenko formulations are implicitly resolving a community of specialist predators (not explicitly modeled) that form a food web of pairwise predator–prey interactions in which each predator feeds upon one single prey species (see lower panels in Fig. 5).

B.2.2. Maximal feeding

For maximal feeding formulations, the predators' total ingestion rate G is given by:

$$G = \sum_j^N g_{max} Z \frac{P_j^\alpha}{\sum_i^N P_i^\alpha} \frac{P^\beta}{K + P^\beta} \quad (49)$$

where the power β will regulate the functional response for total food ingestion (Type II when $\beta = 1$ and Type III if $\beta = 2$), and the power α will regulate the prey switching (passive if $\alpha = 1$ and active if $\alpha = 2$; i.e. Real and KTW formulations, respectively). N is the number of prey species (note that there is only one predator species) and K is a parameter related to the half-saturation constant for ingestion (i.e. $K = k_{sat}^\beta$). Substituting Eq. (32) into Eq. (49) gives:

$$G = \sum_j^N g_{max} Z \frac{(P/N)^\alpha}{\sum_i^N (P/N)^\alpha} \frac{P^\beta}{K + P^\beta} \quad (50)$$

$$= \sum_j^N g_{max} Z \frac{(P/N)^\alpha}{N(P/N)^\alpha} \frac{P^\beta}{K + P^\beta} \quad (51)$$

$$= \sum_j^N g_{max} (Z/N) \frac{P^\beta}{K + P^\beta} \quad (52)$$

$$= g_{max} Z \frac{P^\beta}{K + P^\beta} \quad (53)$$

Note that Eq. (53) is equivalent to Eq. (42). This means that under the condition of constant total prey and predator biomass, and for the simplest scenario in which all prey have equal biomass, the Real and KTW formulations are implicitly resolving a community of generalist predators (not explicitly modeled) that form a food web of meshwise predator–prey interactions in which all predators feed upon all prey (see upper panels in Fig. 5).

Appendix C. The common sense criterion

When a given species is divided into two (or more) identical species with a combined density equal to the density of the original species, this should not lead to a difference in the total amount of that species eaten (Arditi and Michalski, 1995; Berryman et al., 1995). Maximal feeding is a necessary, although not sufficient, condition for this common sense criterion to hold. Therefore both Fasham's and Ryabchenko's formulations violate this criterion under all conditions. On the other hand, while Real's formulation always fulfills the common sense criterion under any condition, the KTW formulation fulfills this criterion in the simplest case where one prey species is subdivided into two (or more) identical species. However, it can violate the criterion for more complicated cases where there are several different classes of prey (e.g. several food classes such as phytoplankton and bacteria) one of which is subdivided into two (or more) others that are identical. In that case the total ingestion from the food class being subdivided will decrease with the number of subdivisions (Visser and Fiksen, 2013).

This becomes clearer if we consider the case of an omnivorous predator that feeds on two different food classes, say phytoplankton and bacteria, with only one prey species per food class. If both food classes are present with the same relative abundance (i.e. 50% each), the predator will eat the same amount of phytoplankton and bacteria. If we now subdivide the phytoplankton food class into two identical prey species, each contributing 25% of the total food, while keeping bacteria as one prey species contributing 50% of the total food, the predator will now eat more bacteria than phytoplankton (66.66% versus 33.33%) even though the combined amount of phytoplankton and bacteria has remain unchanged (50–50%). Yet, the predators' total feeding will be maximal and exactly the same for both scenarios; only the proportion of ingestion from each food class has changed.

Subdivision of the prey species present in one food class can thus alter the relative ingestion of the other food classes. This behavior has no ecological basis and should be avoided or at least minimized. The cause is the way the prey-switching term δ_j is computed: the squared biomass of each prey species is compared to the sum of the squared biomass of all prey species, regardless of how closely related they might be. One sensible solution is to group biologically similar prey species into the same category or food class (e.g. primary producers, herbivores, carnivores, etc.), and then compute the prey-switching term for the prey within each food class independently. Switching among food classes can also be included (Ward et al., 2012). The generalized form of the KTW formulation that fulfills the common sense criterion for an indeterminate number of food classes i and prey species j per food class (under the condition that food classes themselves will not be further subdivided) is thus:

$$G_{p_j} = V_{max} \frac{\rho_j P_j^\alpha}{\sum_k \rho_k P_k^\alpha} \frac{F_i^\gamma}{\sum_k F_k^\gamma} \frac{F^\beta}{k_{sat}^\beta + F^\beta} \quad (54)$$

$$= V_{max} \delta_j \delta_i Q \quad (55)$$

where $F = \sum F_k$ gives the total food available from all food classes; $F_i = \sum \rho_k P_k$ gives the food available from all prey within food class i ; and the parameter ρ_j is a constant prey preference. The term δ_j dictates the switching towards prey j within food class i , and the term δ_i dictates the switching towards food class i . The power α will regulate the switching for prey species j : passive when $\alpha = 1$ and active if $\alpha = 2$. The power γ will regulate the switching for food class i : passive when $\gamma = 1$ and active if $\gamma = 2$. The power β will regulate the functional response for total food: Type II when $\beta = 1$ and Type III when $\beta = 2$. In all cases the total food ingestion will be maximal.

Appendix D. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.pocean.2013.08.001>.

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