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1 FINAL PUBLISHABLE SUMMARY

• Executive summary

Article 1: In the face of stochastic climatic perturbations, the overall stability of an ecosystem will be determined by the balance between its resilience and its resistance, but their relative importance is still unknown. Using aquatic food web models we study ecosystem stability as a function of food web complexity. We measured three dynamical stability properties: resilience, resistance, and variability. Specifically, we evaluate how a decrease in the strength of predator-prey interactions with food web complexity, reflecting a decrease in predation efficiency with the number of prey per predator, affects the overall stability of the ecosystem. We find that in mass conservative ecosystems, a lower interaction strength slows down the mass cycling rate in the system and this increases its resistance to perturbations of the growth rate of primary producers. Furthermore, we show that the overall stability of the food webs is mostly given by their resistance, and not by their resilience. Resilience and resistance display opposite trends, although they are shown not to be simply opposite concepts but rather independent properties. The ecological implication is that weaker predator-prey interactions in closed ecosystems can stabilize food web dynamics by increasing its resistance to climatic perturbations.

Article 2: Predators' switching towards the most abundant prey is a behaviour that allows for a higher degree of species co-existence in food webs. Active prey-switching is a mechanism that can stabilize population dynamics and overcome competitive exclusion. However, current parametrizations of prey-switching suffer from the problems known as antagonistic and sub-optimal feeding, in which predators are unable to maximize the ingestion of the total food available. We analyse three previously published multi-species functional responses which have either active prey-switching or maximal feeding, but not both. We identify the cause of this apparent incompatibility and describe a kill-the-winner (KTW) parametrization that reconciles active prey-switching with maximal feeding. 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 combination of active prey-switching with maximal feeding results in the highest level of diversity as well as the most plausible phytoplankton functional-group biogeography of the four functional responses evaluated.

Article 3: There is an ongoing debate about what should be the shape (if any) of the relationship between productivity and diversity or about the mechanisms behind it. Does productivity control diversity? Does diversity control productivity? Or do productivity and diversity affect each other in a convoluted way? Our global ocean simulations using killing-the-winner predation give support to a well stablished hypothesis which suggests that diversity should respond to primary production following a "hump-shaped" relationship, with diversity peaking at intermediate levels of productivity. The theory supporting the "hump-shaped" relationship is essentially based on the idea that a moderate increase in the nutrient supply will help sustain more diversity by allowing more species to exploit a fraction of the total potential production of the system. We show that diversity increases with the nutrient supply because KTW selective grazing helps down-regulate the most dominant species, which allows other species to invade and persist.

- **Summary description of the project context and objetives**

The project seeks to explore the relationships between food web complexity and stability for marine ecosystems in the face of environmental or climatic perturbations. The relationship between food web complexity and stability in marine ecosystem is not well understood in the oceans. Specifically, we are interested on how environmental or climatic variability fluctuations can impact the overall stability of marine ecosystems and how stability is affected by plankton diversity.

Marine ecosystems are believed to be very sensitive to environmental perturbations (e.g. nutrients, solar radiation levels, temperature) but quantifying the impact of climate on natural ocean ecosystems is hindered by the difficulty of performing experimental work at such broad scales. Therefore we make use of mathematical models of complex food web networks coupled to the ocean general circulation (i.e. MIT-darwin ecosystem model). Ecosystem functioning (e.g. productivity, efficiency) and stability (e.g. resilience, resistance, variability) is linked to food web structure through complex feedbacks. Changes in ocean temperature or nutrient supply can imply changes in the strength of interactions between the species present in a food web. This can alter the self-organization of the community itself as well as the speed of mass cycling through the food web, and therefore affect the ecosystem sensitivity to the temperature fluctuations, closing the feedback.

Ecosystem stability is given by the balance between its resilience and resilience to external perturbations and can be measured by simple metrics like the variability of the time-series of plankton populations. Computing ecosystem stability as the plankton populations' variability is currently our preferred approach. A more mathematically formal metric of ecosystem resilience is the dominant eigenvalue of the Jacobian matrix. In order to compute this metric the ecosystem needs to be in a steady-state equilibrium. However, in the ocean, ecosystems are always in a non-equilibrium state due to the ocean currents (i.e. advection and turbulent mixing) and the seasonal forcings (i.e. solar radiation, temperature). A potential way to overcome this difficulty is by using annual averages of the state variables at every pixel (latitude, longitude) and assume that the annually averaged ecosystem is in steady-state, which is a strong assumption. We are still in the process of evaluating the validity of this approach to estimate ecosystem resilience from local non-equilibrium conditions.

The main objective of the project is to obtain global maps of several indices (i.e. plankton diversity, food web connectance and interaction strength, ecosystem complexity/stability/productivity, etc.) and to evaluate the relationships among them and against environmental variables (e.g. nutrients, temperature, solar radiation, turbulence). The ultimate goal is to elucidate the mechanisms behind those relationships. The analyses are being performed both for present and global warming conditions. An important objective of the project is to identify in which ocean regions the ecosystems are potentially more fragile or vulnerable to future global warming.

- **Main scientific and technical results/foregrounds**

Article 1: Stability of complex foodwebs: Resilience, resistance, and the average interaction strength

Introduction

The ability of an ecosystem to return to its reference state after a perturbation stress is given by its resilience (May, 1974; Harwell et al., 1977; Pimm, 1982). A high resilient ecosystem is one that is able to recover fast after inbalances in the populations densities induced by climatic fluctuations. The ability of an ecosystem to resist displacement from its reference state during a perturbation stress is given by its resistance (Webster et al., 1975; Harwell et al., 1977; Harrison, 1979). A high resistant ecosystem is one which is displaced slightly after imbalances in the populations rates induced by climatic fluctuations (Harrison, 1979; Harrison and Fekete, 1980). Both properties will influence how close an ecosystem remains to its reference equilibrium state and the ecosystem's variability in the face of stochastic climatic perturbations. In other words, resilience and resistance are complementary properties that will determine the overall stability of the ecosystem (Ives and Carpenter, 2007).

Ecosystem resilience has been extensively studied and it is probably the most widely used metric for food web stability (May, 1972; Pimm, 1982, 1984; Loreau et al., 2002). The theory of Lyapunov stability predicts that ecosystems of higher complexity should be less stable in the face of perturbations (May, 1974). In this regard, systems are deemed L-stable when the density of all species returns to equilibrium following a perturbation (Pimm, 1982, 1984). Both the probability of displaying L-stable dynamics and the rate of recovering from a perturbation in population densities have been shown to decrease with ecosystem complexity in models (May, 1974; Fussmann and Heber, 2002; Chen and Cohen, 2001b; Ives and Carpenter, 2007).

Despite the importance of resistance for ecosystem stability (Pimm, 1984), theoretical works that address ecosystem resistance are much less abundant than in the case of resilience, probably due to the lack of a unified theory (Harrison, 1979). Therefore, resistance has been a stability property more difficult to quantify (Harwell et al., 1977; Webster et al., 1975; Harrison and Fekete, 1980; Loreau and Behera, 1999). Also, there is not yet a clear picture of how ecosystem resistance may be affected by food web diversity (Loreau and Behera, 1999). Nevertheless, there is some empirical evidence of increased resistance to environmental perturbations (e.g. drought) with biodiversity in natural grasslands (Tilman and Downing, 1994; Tilman, 1996).

It is well know that resilience is a property that characterize the ecosystem as a whole (Loreau and Behera, 1999). However, contrary to previous suggestions that resistance is a property that characterizes each ecosystem component separately (Harrison and Fekete, 1980; Loreau and Behera, 1999), resistance is also a property that characterize the ecosystem as a whole. In a euclidean multi-dimensional space (e.g. multi-species ecosystem), both resilience and resistance can be measured in an analogous way from the time needed to go from one point to another point in that space during the event of single climatic perturbation.

Due to stochastic environmental fluctuations, populations in real ecosystems are almost never able to remain close to their equilibrium densities (Ives, 1995). However, disentangling resilience and resistance individually for stochastic ecosystems can be challenging. Resilience is a measure of the ecosystem stability to fluctuations in the population densities due to environmental perturbations (Harrison, 1979). It does not give, however, any information about how hard might be for the environment to make these populations fluctuate. Resistance, on the other hand, is a measure of the ecosystem stability to fluctuations in the populations rates (e.g. specific growth or mortality) (Harrison, 1979). Thus, it tells how difficult is for the environmental perturbations to make the populations fluctuate.

The main objective of this work is to evaluate whether equilibrium stability properties (i.e. resilience and resistance) can be related to stochastic stability measures (i.e. population variability) and what mechanisms are likely to explain the observed relationship between ecosystem complexity and overall stability.

Ecosystem resilience to perturbations has been shown to depend negatively on the number of species in a food web and the strength of competitive interactions between the species (May, 1972, 1974) and positively on the speed of mass cycling through the system (DeAngelis, 1980; DeAngelis et al., 1989). Equilibrium theory suggest that an increase in species richness and connectance should decrease the resilience of ecosystems because the inter-specific competition between species are destabilizing forces that will tend to push some species to extinction (May, 1974; McCann et al., 1998). However, the presence of weak interactions in complex food webs has been suggested to help sustain high ecosystem diversity (Kokkoris et al., 2002; Neutel et al., 2007).

Natural communities tend to display skewed distributions of the interaction strengths towards weak links, i.e. many weak interactions and few strong ones (Paine, 1992; McCann et al., 1998; Neutel et al., 2002, 2007), although the underlying mechanisms are not completely well understood (Berlow et al., 2004). Among them, the number of prey per predator seems to correlate to the strength of the interactions; polyphages (i.e. predators with many prey) have weaker predator-prey interactions than monophages (McCann et al., 1998; Montoya et al., 2006).

Little is known about the dependence of resistance on ecosystem complexity, species interaction strength and the rate of mass cycling through the food web. Therefore, it is unknown what determines the resistance of ecosystems to climatic perturbations. It is also unknown what is the relative weight of resilience and resistance on the overall stability of stochastic ecosystems.

We address these questions by means of multi-species food web models that are mass-conservative (i.e. closed ecosystems). Specifically, we evaluate how a decrease in the strength of predator-prey interactions with food web complexity will affect ecosystem resilience, resistance and overall stability. We will use as climatic perturbations drastic changes in solar radiation levels (i.e. dark/light pulses). They will therefore affect the specific growth rate of primary producers.

Food web resilience and resistance will be evaluated by applying a single perturbation (i.e. one dark pulse) to the ecosystems. Resistance will be measured as the time needed to reach a given non-equilibrium perturbed state from the reference equilibrium state. Resilience will be measured as the return rate from the non-equilibrium perturbed state back to the reference equilibrium state. Food web overall stability will be evaluated by applying a stochastic perturbation (i.e. many random dark pulses) to the ecosystems. We will define a metric for overall stability that merges both the temporal variability of the system and its average distance to the reference state, and we will compare it to more classical measures of ecosystem variability such as the coefficient of variation of population-level, community-level and ecosystem-level properties.

Methodology

Model description

We constructed a series of food web models that differ in their complexity. Food web complexity here refers to the number of plankton species or plankton functional types (PFT) (Le Quéré et al., 2005). A minimum of 3 and a maximum of 6 trophic levels is considered. Complexity increases along two axis in the model: 3 levels of phytoplankton complexity (p-cmpx) and 4 levels of zooplankton complexity (z-cmpx). Therefore there are 12 food web configurations between the least and most complex ecosystem. The most complex food web is based on the schematic food web described by Duffy et al. (2007). The least complex model is a short linear food web. The topology diagrams for the 12 food web complexities is given in Figure 1. Note that all food web complexities can be generated as substructures of the most complex food web. For phytoplankton we chose to go from large to small when increasing p-cmpx, but we obtain analogous results if we go from small to large phytoplankton. For zooplankton we go from lower trophic to higher trophic levels when increasing z-cmpx.

Primary production is limited by the availability of dissolved inorganic nitrogen (DIN) following Michaelis-Menten nutrient uptake kinetics. Predation is assumed to follow a Holling-Type III (sigmoid) functional response, which is common in filter feeders and marine copepods (Jeschke et al., 2004; Fussmann et al., 2005). Type III functional responses for predation are known to stabilize model dynamics and to promote biodiversity through a relaxation of feeding at low prey densities, allowing for a much greater probability of co-existence of all the species in a food web (Haydon (1994); Gentleman et al. (2003); and references therein). The use of functional relationships including a relaxation of feeding at low prey densities is a way of implicitly taking into account several ecological mechanisms like prey refuge, prey switching and/or predator interference that are difficult to model explicitly. Fish (top carnivore) is used in the model simply as a closure mortality term for zooplankton. All losses (i.e. mortality, non-assimilated food) are assumed to be instantaneously recycled to the nutrients DIN pool, making the ecosystem mass-conservative. The total amount of mass in the system is constant and it is they same for all food web configurations (N_{tot} = 2 mmolN m^{-3}).

The strength of zooplankton predation upon their prey is assumed to decrease with the number of prey per predator (McCann et al., 1998; Montoya et al., 2006). Therefore, the model assumes that pressure on individual prey decreases when predators scavenge multiple prey. This can be understood as a way of implicitly reflecting an increase in the predators difficulty to attack their prey due to an increase in habitat complexity with species diversity (Real, 1977), such as heterogeneities in prey distribution (i.e. patches) or prey defense-strategies, which are not explicitly accounted for in the model. The decrease in predator-prey interaction strength comes from two complementary mechanisms. First, we assume that an increase in the number of prey per predator decreases the predator's efficiency in capturing any of its prey, which is parametrized as an increase in the predator's half-saturation constant for ingestion. This might be seen as a transition from a highly efficient specialist to a low efficiency generalist, or it can reflect an increase in the average transit time spent from going from one prey type patch to another (Oaten, 1977). Second, since each prey has its own implicit grazing refuge in the Type III functional response (or explicit if using Type II with refuge), the presence of more prey types implies a higher overall refuge for the prey as a whole. Both mechanisms will tend to decrease the average interaction strength between predators and prey as food web complexity increases.

The modelled PFTs were allowed to differ in their phenotypic traits for the exploitation of resources. Both the phytoplankton maximum growth rates and nutrient half-saturation constants, as well as the zooplankton maximum ingestion rates and half-saturation constants for ingestion, are assigned randomly from a normal distribution with given mean values given and a standard deviation of 0.2 times the mean value. In practice this means a range for parameter values of approximately ± 50% the mean values. (Using a uniform distribution with a range ± 50% the mean values gave similar results). For each of the 12 food web complexities we performed 400 runs with randomly-assigned phenotypic traits. This amounts to a total of 12 x 400 = 4800 individual runs. For all runs the ecosystems have a single L-stable reference equilibrium under constant light levels, regardless of the initial conditions. Therefore, all food web complexities are globally L-stable (Pimm, 1982; Chen and Cohen, 2001a).

Dynamical Stability Indices

The only external forcing in the model is solar radiation. Therefore, we will use as climatic perturbations dark-pulses in solar radiation levels. The ecosystems will be allowed to be under only two possible environmental conditions: perturbed (full dark) or unperturbed (full light). Three dynamical stability indices (DSI) will be computed numerically: resilience, resistance, and overall stability. Resilience and resistance will be estimated by applying a single perturbation (i.e. one dark pulse) to the ecosystems. Overall stability will be evaluated by applying a stochastic perturbation (i.e. many random dark pulses) to the ecosystems.

Resilience Index

The reference steady-state point (SSP), or unperturbed equilibrium, is the point $\mathbf{X}^*$ with coordinates $(X_1^*, ..., X_n^*)$ in the phase space in which the concentration of the PFTs does not change over time. Since all our model food webs are globally Lyapunov stable, any departure from the reference state caused by a climatic perturbation will decay over time once the perturbation has ceased, and the ecosystems will asymptotically return back to their reference equilibrium. The resilience of the systems will be estimated by measuring the time needed for recovery, and then converting the return times into return rates. This has the advantage of giving a comparable measure to the dominant eigenvalue of the Jacobian matrix (May, 1974).

Resistance Index

The resistance of the ecosystems to the dark-pulse perturbation was measured as the perturbation time (the length of the dark-pulse), i.e. the time needed by the system under the influence of the dark-pulse to reach the selected perturbation distance. Longer perturbation times imply a slower displacement per unit of time and thus a higher resistance to the perturbation (Harrison, 1979).

The ultimate displacement is the distance between the ``all alive'' reference equilibrium state and the ``all died'' equilibrium state that would occur if the disturbance lasted indefinitely (Harrison and Fekete, 1980). Although the ultimate displacement can be different for each ecosystem depending on the coordinates of its reference state, it can be shown that the differences are negligible and all the modelled food webs have similar ultimate displacements that are, in fact, very close to the maximum potential distance (i.e. N_{tot}). Therefore, the measured perturbation time is a dynamical resistance index related to the speed at which the ecosystems depart from the reference state towards its ultimate displacement.

Stability Index

To obtain an estimate of the overall stability of the food webs, we performed a simulation in which the ecosystems were submitted to a stochastic perturbation of light levels (i.e. dark/light pulses) during one year without seasonality. Each day had a probability of 50% to be assigned a zero light level. For those random dark-days, phytoplankton do not grow (perturbed states). For all the other days, phytoplankton growth was not light-limited (unperturbed states). The severity of every perturbation is given by the amount of consecutive dark-days. Prior to the start of the stochastic perturbation each food web was allowed to reach its reference equilibrium state after a year under no light-limited growth.

Ecosystems under stochastic perturbations are always in a non-equilibrium state (Ives, 1995). Every time that a perturbation comes in, the system moves away from its reference equilibrium state; once the perturbation is gone, the system moves back towards its reference equilibrium state. Since there is never enough time to fully recover before another perturbation comes in, the system is unable to reach the steady-state. Under those conditions the equilibrial state can be given by a stationary distribution characterized by its mean and standard deviation (Ives et al., 2003). Specifically we will use the trajectories in the phase space, evaluated with respect to the reference equilibrium (i.e. displacements), as the stationary distribution of the stochastic system. The mean of the stationary distribution measures the average distance to the reference equilibrium. The standard deviation measures the temporal variability of the distances.

Average Interaction Strength

To measure the strength of species interactions we obtained the Interaction matrix from the Jacobian computed at the reference equilibrium (Berlow et al., 2004). The elements c_{ij} in the Interaction matrix give the linear effect of a change in the concentration of species j on the specific (i.e. *per-capita*) rate of change of species i:

$$c_{ij} = \left.\frac{\partial(\dot{X}_i/X_i)}{\partial X_j}\right|_{\mathbf{X}^*} \tag{1}$$

where $\dot{X}_i$ denotes the rate of change of species i and X_i its concentration. The ecosystem average interaction strength (EAIS) was obtained from the absolute value of the off-diagonal elements in the Interaction matrix:

$$\mathbf{EAIS} = \frac{\sum_{i \neq j}^{n} \mid c_{ij} \mid}{n(n-1)} \tag{2}$$

where n is the total number of species in the food web. Note that the interactions with nutrients were not included in the calculations.

Results

In this section we will show the relationship between the ecosystem productivity and stability properties as a function of the food web complexity, which is defined along two axis as the number of phytoplankton and zooplankton species present in each food web (p-cmpx and z-cmpx, respectively; see methods). For each of the 12 food web complexities, we take the average of 400 runs with randomly-assigned phenotypic traits. Figure 2 gives the rate of mass input fluxes between compartments at the reference steady-state as a function of phytoplankton and zooplankton complexity. Between the simplest and most complex food web, primary production decreases by more than 50% (from ≈0.4 to ≈0.2); zooplankton production decreases by more than 60% (from ≈0.12 to ≈0.04); fish production decreases by more than 80% (from ≈0.03 to ≈0.005); and the recycling production of DIN decreases about 70% (from ≈0.9 to ≈0.3). Thus, although the degree of retention of nutrients increases with food web complexity, the rate of instantaneous production in the system decreases (Figure 2) due to the imposed weaker predator-prey interactions when more species are added. Weaker predator-prey interactions means slower recycling of DIN from zooplankton excretion, slowing down the pace of phytoplankton primary production. Thus, assuming that predator-prey interactions are weaker with more prey choices results in a decrease with food web complexity of the speed of mass cycling in the ecosystem.

Figure 3a gives the ecosystems' average interaction strength as a function of phytoplankton and zooplankton complexity. The EAIS decreases strongly along both axes, which is to be expected since the model assumes a general decrease in the predator-prey interactions with food web complexity. The average interaction goes from ≈0.25 to ≈0.1 between the simplest and most complex food web, about a 60% decrease. Figures 3b,c,d give the food webs' DSI: resilience, resistance, and overall stability; respectively. We found that resilience decreases (about 75%) with food web complexity (Figure 3b), with the rate of return (i.e. 99.99% recovery) going from ≈0.2 to ≈0.08 [d^{-1}] between the simplest and most complex food web. On the other hand, resistance increases (about a 200%) with food web complexity (Figure 3c), with the perturbation time going from ≈0.4 to ≈1.2 [d] between the simplest and most complex food web. This means that in order to displace the ecosystems the same perturbation distance (see section 1), the most complex food web can resist the climatic perturbation 3 times longer than the simplest one. The overall stability also increases (about a 200%) with food web complexity, going from ≈3.0 to ≈9.0 [m^3 $mmolN^{-1}$] between the simplest and most complex food web. The similarity between how the resistance index and the stability index change with food web complexity is apparent, which already indicates that the overall stability of the food webs seems more related to their resistance than to their resilience.

Figure 6 shows the dynamics of the stochastic ecosystems just for the simplest and most complex food web. In this case the results are from the single control run (see methods), not the average values from the random runs, since the figure is illustrative only. Figure 6a shows the trajectories in the euclidean phase space of these two stochastic ecosystems (P.Z and PPP.ZZZZ). Figure 6b show the corresponding time-series. The PPP.ZZZZ stochastic ecosystem is clearly more stable than the P.Z stochastic ecosystem; it displays both lower temporal variability and its trajectories remain closer to the reference equilibrium.

Figure 4 shows the relationship between the dominant eigenvalue of the Jacobian matrix versus the average interaction strength and the food webs' DSI. Of these four metrics, only the return rate (i.e. the resilience index) correlates well with the dominant eigenvalue, which is to be expected since in fact they are both measuring the same property (the resilience of the ecosystems). In all other cases, the relationship between the resilience measured by the dominant eigenvalue versus EAIS, resistance, and overall stability, shows negative but not significant trends. One important conclusion is that resilience and resistance are not simply inverse concepts but rather appear to be independent properties, as previously suggested (Harrison, 1979). Likewise, figure 5 shows the relationship between the total primary production in the ecosystem versus the average interaction strength, food webs' DSI resistance and overall stability, and the average rate of mass cycling in the system (excluding primary production). All four metrics correlate strongly with primary production. The correlation is positive, which means that a decrease in primary production is related to a decrease in EAIS, a decrease in the speed of mass cycling, and an increase in resistance and overall stability (note that the plots are against the inverse of these two stability indices).

Conclusion

We have analysed three dynamical stability properties of mass-conservative food web models: resilience, resistance, and variability. The goal was to evaluate what determines the overall stability of complex ecosystems to stochastic climatic perturbations affecting population rates. Although classical theory of ecosystem resilience predicts that the stability of food webs should decrease with its complexity, our results demonstrate that this is not necessarily the case. We do find that resilience decreases with food web complexity. However, resilience only measures measures the speed of recovery from fluctuations in population densities, it does not provide information about how difficult it may be to make the populations fluctuate in the first place. This ecosystem sensitivity to climatic perturbations is given by the stability property resistance. We find that if an increase of food web complexity is combined with a decrease in the strength of predator-prey interactions, the overall stability of the ecosystem does in fact increase with complexity. A lower average interaction strength causes a lower turnover rate of mass in the ecosystem, and this increases its resistance to climatic perturbations. We evaluated the relative weight of resilience and resistance on the overall stability of the food webs and show that resistance dominates. These results suggest that more research should address the resistance of natural ecosystems to climatic perturbations, since this stability property appears to be key for the overall stability of complex food webs and seems to have been overlooked in previous theoretical studies.

Article 2: Maximal feeding with active prey-switching: a kill-the-winner functional response and its effect on global diversity and biogeography

Introduction

Active prey-switching is a predatory behaviour that has been documented in natural ecosystems (Murdoch, 1969, 1975; Hughes and Croy, 1993; Kiorboe et al., 1996; Gismervik and Andersen, 1997; Elliott, 2006; Kempf et al., 2008; Kiorboe, 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 predator's switching is dynamic and based on relative prey density (i.e. frequency-dependent predation), rather than being based on constant prey preferences (see Gentleman et al. (2003) for a review). Thus, active switching represents a behavioural change of the predator (Gentleman et al., 2003), either in terms of feeding strategy (e.g. from passive suspension feeding to active ambush feeding) (Kiorboe 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). For simplicity, through the text we will sometimes refer to active prey-switching as just *switching* and passive prey-switching as *no-switching*.

From an ecosystem modelling 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 Quéré, 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 nature (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 prey-switching follows conceptually the same principle but for predator-prey selectivity.

However, current parametrizations of active prey-switching show anomalous dynamics, like *antagonistic* feeding and *sub-optimal* feeding in which predators are unable to maximize the ingestion 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 parametrizations are not completely satisfactory representations of switching behaviour (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 reconcile the apparent incompatibility between active switching and maximal ingestion in current parametrizations of predation on multiple prey. We identify the origin of this apparent incompatibility and derive a kill-the-winner (KTW) functional response that combines active switching with maximal ingestion. To put our results in context, we first evaluate three classical formulations of predation on multiple prey: two that exhibit switching but non-maximal ingestion (one sub-optimal, one antagonistic); and one that exhibits maximal ingestion but no-switching. All four formulations are variants of the original functional responses defined by Holling (1959).

The second objective of this work is to evaluate how the choice of the functional response for predation can affect the global distribution of phytoplankton diversity and biogeography in a model ocean. We have 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 (analogs of *Prochlorococcus*, *Synechococcus*, flagellates, and diatoms) which are differentiated by their dependence of growth on external nutrients. 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).

Theoretical analysis

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). 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. 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:

$$\mathbf{G_{p_j}} = \mathbf{z} \cdot \mathbf{g_{max}} \cdot \mathbf{Q_{switch}^{p_j}} \cdot \mathbf{Q_{feed}} = \mathbf{V_{max}} \cdot \mathbf{Q_{switch}^{p_j}} \cdot \mathbf{Q_{feed}} \tag{3}$$

$$\mathbf{G} = \sum \mathbf{G_{p_j}} = \mathbf{V_{max}} \cdot \mathbf{Q_{feed}} \cdot \sum \mathbf{Q_{switch}^{p_j}} = \mathbf{V_{max}} \cdot \mathbf{Q_{feed}} \tag{4}$$

where $\mathbf{g_{max}}$ [d^{-1}] is the maximum biomass-specific ingestion rate of a predator $\mathbf{z}$ [mmol m^{-3}]; $\mathbf{V_{max}} = \mathbf{z} \cdot \mathbf{g_{max}}$ is the maximum ingestion rate [mmol m^{-3} d^{-1}]; $\mathbf{Q_{switch}^{p_j}}$ [n.d.] dictates switching towards prey $\mathbf{p_j}$; $\mathbf{Q_{feed}}$ [n.d.] gives the predator's probability of feeding as a saturating function of the available prey biomass; $\mathbf{G_{p_j}}$ [mmol m^{-3} d^{-1}] is the ingestion rate upon prey $\mathbf{p_j}$; and $\mathbf{G}$ [mmol m^{-3} d^{-1}] is the total ingestion rate from all prey. Both $\mathbf{Q_{switch}^{p_j}}$ and $\mathbf{Q_{feed}}$ 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 $\mathbf{Q_{feed}}$ (see equation 4) while the fraction of each prey in the diet will be determined by $\mathbf{Q_{switch}^{p_j}}$ (see equation 3).

The differences between functional responses comes from how they parametrize the prey-switching $\mathbf{Q_{switch}^{p_j}}$ and feeding-probability $\mathbf{Q_{feed}}$ 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 $\mathbf{Q_{switch}^{p_j}}$ is only different for the one passive-switching functional response (Real's parametrization), while the other three active prey-switching functional responses (Fasham, Ryabchenko, and KTW parametrizations) share the same $\mathbf{Q_{switch}^{p_j}}$ but differ in their $\mathbf{Q_{feed}}$ (see Tables 1 and 2).

Feeding mode: maximal, antagonistic and sub-optimal

Figure 7 gives the overall feeding probability $\mathbf{Q_{feed}}$ as a function of $\mathbf{p_j}$ as a function of the prey biomasses $\mathbf{p_j}$ for an idealized ecosystem consisting of one predator feeding upon two prey with the four functional responses evaluated in this study. 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 two prey (see Figures 7a and 7b), which leads to the non-maximal feeding of these formulations (Gentleman et al., 2003). 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 Figures 7c and 7d).

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 = 33.33 in Figure 7) 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 Figure 7a). The third parametrization (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 predator's feeding probability (see Figure 7c). Finally, the fourth parametrization (i.e. KTW) behaves as a combination of the other three formulations: it accounts for active switching while giving maximal feeding (see Figure 7d).

Predator-prey interaction: maximal *vs.* non-maximal

Figure 8 shows the total ingestion rate as a function of the number of equally abundant prey when feeding with maximal and non-maximal feeding. 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 maximal (Real, KTW). This is because maximal and non-maximal feeding are implicitly reflecting two different food web topologies: pairwise predator-prey interactions (non-maximal feeding; see upper panels in Figure 9) and meshwise predator-prey interactions (maximal feeding; see lower panels in Figure 9). The inverse dependence of total ingestion with the number of prey (N) in the case of explicit pairwise interactions can be mathematically derived (not shown). Both Fasham's and Ryabchenko's parametrizations are implicitly assuming a food web of pairwise interactions (following Type II and Type III responses, respectively), whereas for the Real and KTW parametrizations the total ingestion is independent of N because they are implicitly assuming a food web of meshwise interactions. With pairwise interactions adding more prey implies splitting the predators' biomass into attacking different prey, 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.

Numerical analysis

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; Prowe et al., 2012a).

Global ocean simulations

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 Figure 10). Seasonality disturbances provide niches for both low nutrient adapted species and those requiring higher nutrients but displaying high growth rates (Dutkiewicz et al., 2009). However, active switching (Fasham, Ryabchenko, KTW) allows for large spatial overlapping of phytoplankton groups; they co-exist over larger regions. Without switching (Real), although some spatial overlapping is still present, each group tends to occupy a well defined oceanic region, not being capable of co-existing with other groups due to competitive exclusion.

The biogeography of each group is very sensitive to the choice of the functional response. Fasham and Ryabchenko parametrizations give similar phytoplankton biogeography; Real's gives markedly different distributions; and KTW gives a biogeography that is intermediate. This agrees with 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 parametrization (Anderson et al., 2010). With active switching (Fasham, Ryabchenko, KTW) the biogeography of the phytoplankton groups (Figure 10) matches their species-richness distribution (Figure 11): 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°S - 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).

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; Marañon et al., 2001; Hoffmann et al., 2006; Hirata et al., 2011). The transition between biogeographic regions seems also too sharp. 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 modelled analogs of *Prochlorococcus* dominate at low latitudes and diatoms dominate at high latitudes; *Synechococcus* analogs are more widely distributed than *Prochlorococcus*; and modelled flagellates are also more widely distributed than diatom analogs. No one single functional group seems to clearly dominate in terms of global abundance, although it is the diatoms that show the highest local biomass (see Figure 10).

The feeding probability of zooplankton (see Figure 12) has a very strong influence on total phytoplankton biomass (see Figure 13): the Fasham and Ryabchenko parametrizations lead to much higher biomass concentrations than the Real and KTW formulations (up to a factor of x3). 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.

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 Figure 11). The highest level of species diversity is obtained with the KTW parametrization, both per functional group (see Figure 11) and total (see

Figure 14). 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).

These results demonstrate that active predatory switching can increase the diversity of phytoplankton in the oceans, which is in agreement with previous works (Prowe et al., 2012a,b). Without active switching (Real) we obtain the lowest level of maximum diversity: 4 species, one per functional group (Figure 14c); with active switching plus maximum feeding (KTW) we obtain the highest level of maximum diversity: ≈ 48 species on an annual average (Figure 14d); with active switching plus non-maximal feeding (Fasham and Ryabchenko) we obtain intermediate levels of diversity (Figures 14a and 14b). 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 parametrization 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. 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 (Figure 14). 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. $\mathbf{R}^*$).

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).

Conclusions

In order to study the dynamics of complex food webs we need functional responses of predation that introduce the least number of anomalous dynamics while giving stability to the ecosystem models. In particular, the total ingestion of a predator should solely depend on the total food available. Complex food webs models need also mechanisms to overcome the probably unrealistic but common outcome of one or few species outcompeting many others. Using a functional response with maximal feeding and active prey-switching can help achieve these needs. The main problem of non-maximal feeding parametrizations (Fasham, Ryabchenko) is that an increase in the number of modelled prey species implies a decrease of the average predator-prey interaction strength (Vallina and Le Quéré, 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) ecosystems like the global ocean in which the total mass in the system is constant and therefore adding 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 parametrizations (Real, KTW) the average of predator-prey interactions is unaffected by the number of prey species. In this work, we derived a KTW functional response that reconciles active switching with maximal feeding. Global ocean simulations show that active switching combined with maximal feeding are both key elements to sustain higher levels of species diversity while providing realistic phytoplankton functional-group biogeography.

Article 3: Global relationship between phytoplankton diversity and productivity in the ocean

Introduction

There is an ongoing debate about what should be the shape (if any) of the relationship between primary production and diversity or about the mechanisms behind it. Does primary production control diversity? Does diversity control primary production? Or do primary production and diversity affect each other in a convoluted way? (Gross and Cardinale, 2007; Cardinale et al., 2009).

One well stablished hypothesis suggest that diversity should respond to primary production following a "hump-shaped" (i.e. unimodal) relationship, with diversity peaking at intermediate levels of productivity (Mittelbach et al., 2001). This hump-shaped relationship has been documented to occur in many terrestrial plant communities, altough other shapes have been also reported. However, the extra physical dimension of the ocean currents which passively transports planktonic organisms following the laws of classical fluid dynamics has lead to the suggestion that the hump-shaped relationship should not necessary apply to the marine environment. In this alternative view the expected relationship should be "flat" (i.e. no significant relationship). Some works have documented a flat-shaped relationship between phytoplankton diversity and biomass (used as a proxy for primary production) using field data (Cermeno et al., 2013), while others have documented a unimodal relationship (Irigoien et al., 2005).

The theory supporting the "hump-shaped" relationship is essentially based on the idea that a moderate increase in the nutrient supply will help sustain more diversity by allowing more species to exploit a fraction of the total potential production of the system. However, when the nutrient supply becomes too high, this will trigger the uncontrolled blooming of a few very dominant species that will displace many others. Therefore the highest diversity should be found at intermediate levels of nutrient supply and thus primary production. The theory supporting "flat" relationship is based on the idea that processes operating at regional and global scales such as phytoplankton dispersal override the importance of local factors such as competition for resources, flattening the patterns of diversity of eukaryotic microorganisms across the ocean.

Methodology

To address these questions we used a global-ocean ecosystem model (Follows et al., 2007) that includes a total of 64 phytoplankton species belonging to four major functional groups (MIT-darwin model): 16 analogs of *Prochlorococcus*, 16 *Synechococcus*, 16 flagellates, and 16 diatoms. The model also resolves two predator classes: a generic micro-zooplankton and a generic meso-zooplankton. *Prochlorococcus* and *Synechococcus* analogs are small phytoplankton that are grazed preferentially by micro-zooplankton. Flagellates and diatoms are defined in the model as large phytoplankton that are grazed preferentially by meso-zooplankton (Dutkiewicz et al., 2009). The modelled phytoplankton species differ in their ability to take up nutrients. All other functions (e.g. background mortality, exudation, light harvesting, etc.) are common to all. The phytoplankton species compete among them for the nutrients and through this process the community will self-assembly.

The key feature of our model is that phytoplankton are grazed by zooplankton with "killing-the-winner" predatory behaviour. This mechanism is based on the size-specificity of predator-prey interactions. The relatively most abundant species will be killed preferentially by grazing-selective mortality. Thus, the success of one particular prey is held in check by the increased ingestion by the zooplankton that feed preferentially on that prey (Vallina et al., 2013). Predator-prey linkages are not just given by body sizes but also by the consumers' feeding type (Wirtz, 2012b) and the prey nutritional status (Mitra and Flynn, 2005, 2006). High nutrient uptake rates can enhance the competitiveness of the prey but also increase their nutritional quality for the predators. This can lead to a trade-off that enables the coexistence of nutrient exploiters (nutrient uptake winners) and grazing avoiders (nutrient uptake losers) (Branco et al., 2010). According to optimal foraging theory, low quality prey should be ignored because there is an energy cost associated to foraging (Visser and Fiksen, 2013). Kill-the-winner (KTW) predation implicitly simulate these dynamics by using relative abundances as a proxy for prey quality.

Results

Figure 15 shows the annually-averaged global maps of modelled: primary production (FP), total phytoplankton biomass (PHYT), species richness (#spp), and shannon index (H). 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. Visually, there is a clear qualitative agreement between all four variables over large regions of the ocean. Regions with higher primary production and phytoplankton biomass are usually associated to high levels of diversity. Low productive regions contain the lowest levels of species diversity. Figure 16 shows the actual shape of the global relationship between phytoplankton diversity and productivity. The upper panels use annually averaged model outputs and therefore only capture the *spatial* variability between primary production and species diversity. The lower panels use monthly avaraged outputs and therefore they capture both the *spatial* and *temporal* variability of the two variables. There is a strong pattern of increasing diversity with primary production until reaching a peak after which diversity decreases with primary production. Therefore there is a tendency for a "hump-shaped" relationship between modelled diversity and productivity in the global ocean.

This means that moderate levels of production are able to sustain the highest levels of species richness. If productivity is too low, the level of diversity decreases because the system does not produce enough to sustain a larger share of species. If primary production is on the other hand too high, the level of diversity decreases because blooms of a few but very dominant species will tend to displace many others. This is mostly observed when using the monthly maps since they capture some degree of temporal variability. However, most of the data points are contained in the positive side of the relationship where diversity increases with productivity. The drop of diversity at highest levels of production shows a lot of scatter and relatively fewer data points (see colorscale where red means more data points and blue means fewer data). Therefore the most robust pattern is that diversity increases with primary production until reaching a peak at some intermediate level of production. After that point the relationship between diversity and primary production becomes negative and less robust, which can be the result of bloom regimes plus that the role of phytoplankton dispersal is becoming more important.

Discussion

The mechanism that explain the possitive part of the relatioship between diversity and primary production is the "kill-the-winner" selective predation. Selective predation can be argued to fit within the broader "killing the winner" theory of virus-induced mortality of microorganisms, which has been suggested to explain the high diversity of bacteria we observe in the marine environment. The basic idea is that the most abundant species will be killed preferentially by host-selective viral lysis. Therefore, the coexistence of competing species is ensured by the presence of viruses that kill-the-winner, whereas the differences in substrate affinity between the coexisting species determine viral abundance. Kill-the-winner predation uses the same principle for predator-prey selectivity.

Diversity increases with the nutrient supply because KTW selective grazing helps down-regulate the most dominant ones, which allows other species to invade and persist. This mechanism by which stronger feeding pressure increases diversity arises from self-regulatory feedbacks within the ecosystem (i.e. the diagonal elements of the Jacobian matrix of the system at steady-state equilibrium becoming more negative). The kill-the-winner predation introduces a negative feedback in the ecosystem to each prey biomass while increasing the nutrient supply reinforces the self-regulatory feedback and makes it stronger. An increase in the strength of self-regulatory forces will help stabilize the ecosystem, allowing for a higher phytoplankton co-existence and thus diversity (May, 1974; Haydon, 1994).

However, during blooming conditions caused by sustained pulses of high nutrient supply, the predators are not always able to down-regulate the blooming species due to the time lag between any increase in prey biomass and the subsequent increase in predators' biomass. Thus, under conditions of highest productivity usually only a few runaway species will dominate the ecosystem by outcompeting many others, which causes the observed decrease in diversity when primary production is well above intermediate levels. Once the predators biomass starts to increase due to the ingestion of highly productive phytoplankton, the self-regulatory feedback will become stronger reducing the biomass of the dominant species (and thus reducing the primary production) and allowing other species to share the existing supply of nutrients at a more moderate level of total primary production.

Conclusion

Our simulations predict that the global relationship between phytoplankton diversity and productivity in the ocean follows a "hump-shaped" shape. This agrees with a recent global metadata analysis that shows that marine phytoplankton diversity is a unimodal function of phytoplankton biomass, with maximum diversity at intermediate levels of phytoplankton biomass and minimum diversity during massive blooms (Irigoien et al., 2005). We were able to identify "killing-the-winner" predation as a key mechanism that can potentially explain the hump-shaped relationship between diversity and productivity observed in the field data. Selective grazing (i.e. density-dependent mortality) helps modulate phytoplankton dynamics by down-regulating the biomass of intrinsically dominant species, which allows less dominant species to invade and persist in the ecosystem.

Tables and Figures

Article 1:

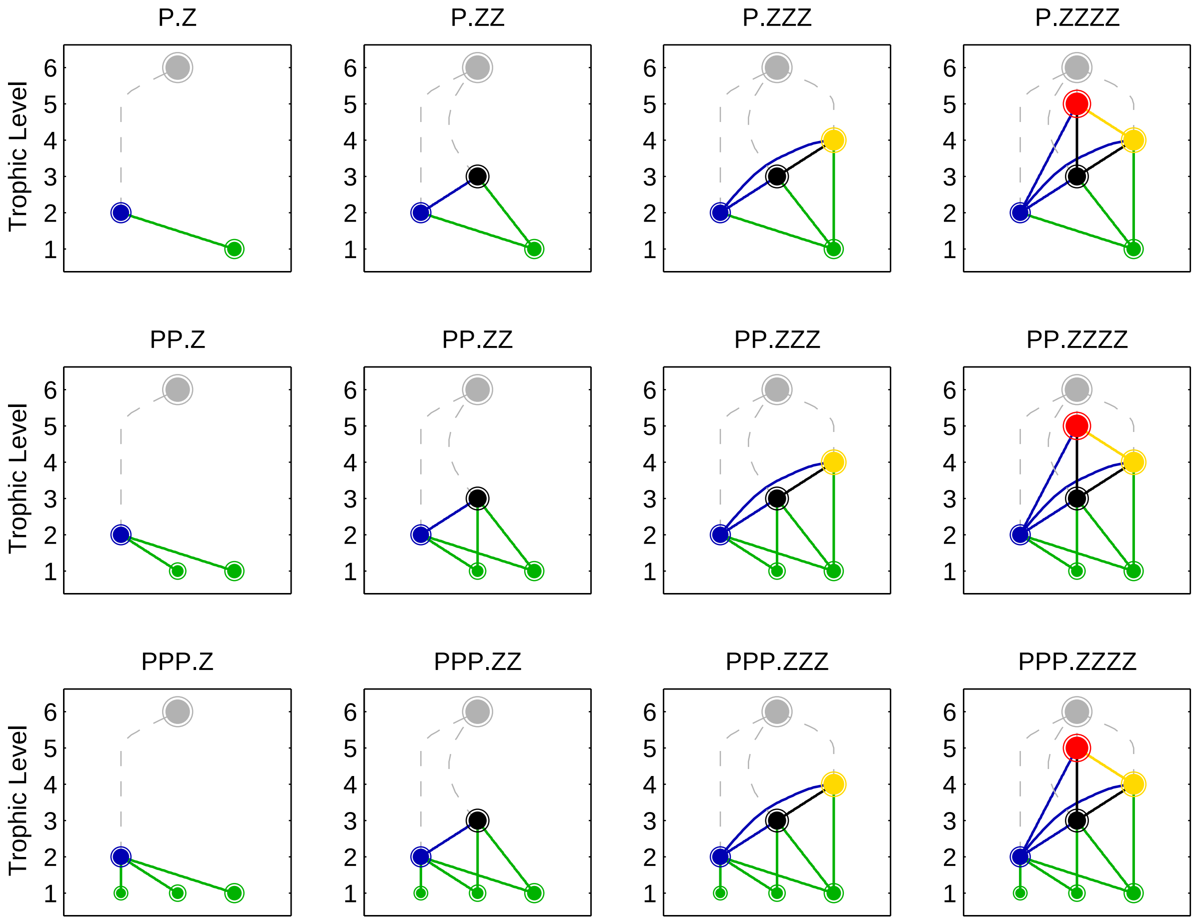

Figure 1: Topology diagrams for the 12 food web complexities. Note that only predator-prey interactions are shown (i.e. nutrients and recycling arrows are not included for simplicity). Color nodes represent food web plankton functional types (PFT): green for phytoplankton (small, medium, large; from left to right); blue for micro-zooplankton; black for meso-zooplankton; yellow for macro-zooplankton; red for mega-zooplankton; and gray for top carnivore fish. The size of the nodes indicates the size of the PFT (not true scale). The color of the lines indicate predation on a given prey, except for gray dashed lines which represent predation by top predator fish on all zooplankton (closure term).

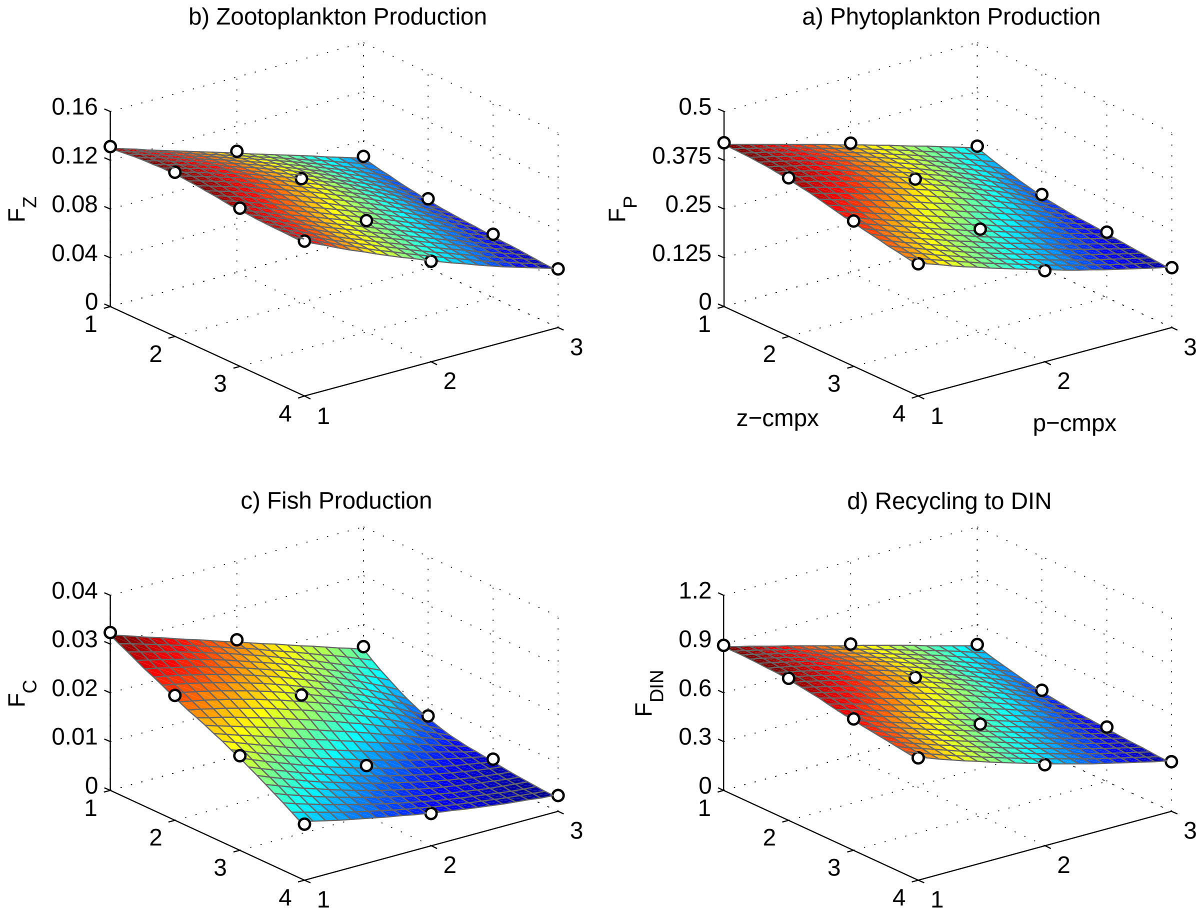

Figure 2: Steady state flux rates under no light-limited conditions as a function of phytoplankton complexity (**p**-cmpx) and zooplankton complexity (**z**-cmpx): a) total phytoplankton production; b) total zooplankton production; c) total top carnivore fish production; d) recycling production of dissolved inorganic nutrients. Units [mmolN m^{-3} d^{-1}].

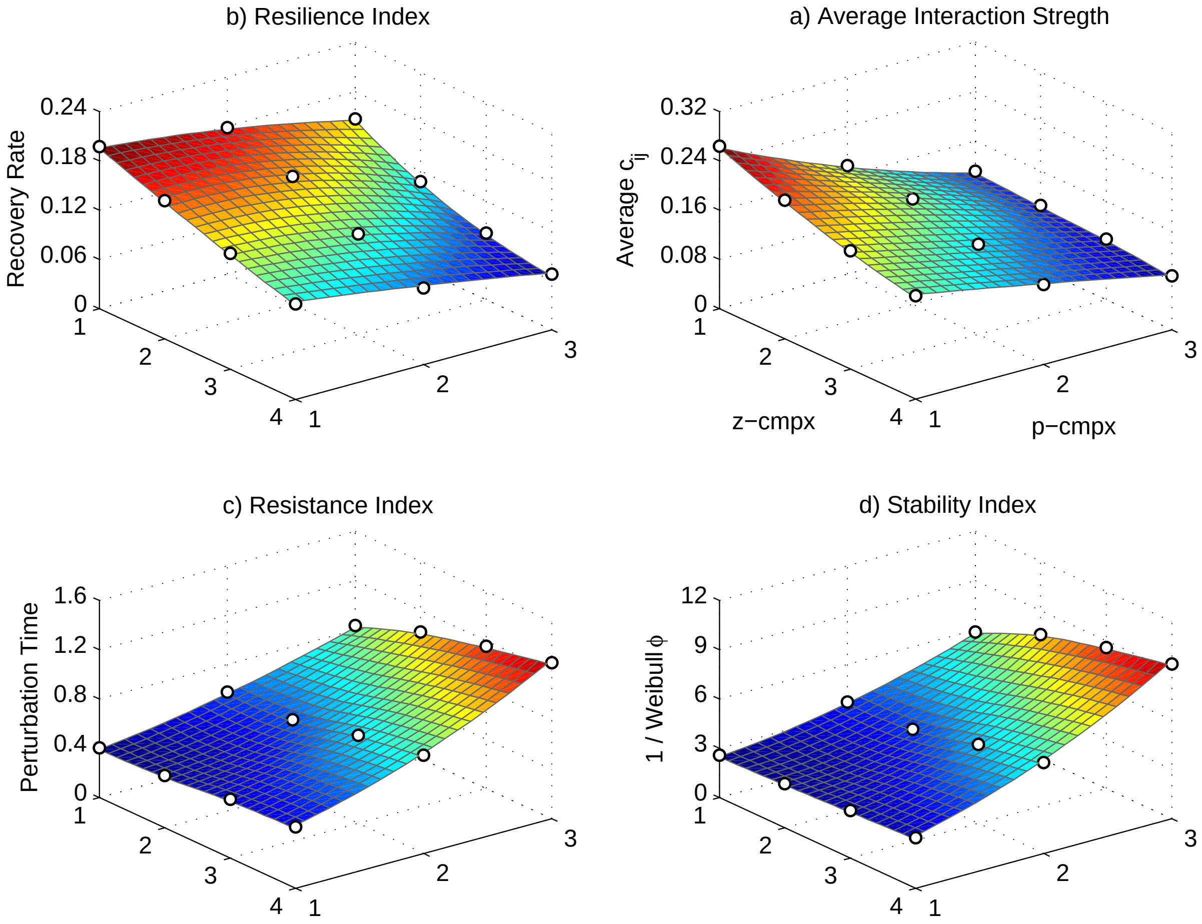

Figure 3: Ecosystem interaction strength and stability indices as a function of phytoplankton complexity (**p**-cmpx) and zooplankton complexity (**z**-cmpx): a) average interaction strength of the Interaction matrix [m^3 mmolN^{-1} d^{-1}]; b) resilience index (99.99% recovery rate for the single perturbation, [d^{-1}]); c) resistance index (perturbation time for the single perturbation, [d]); d) stability index (inverse of the φ parameter of the Weibull distribution of the distances to the steady-state for the stochastic perturbation, 1 / [mmolN m^{-3}]).

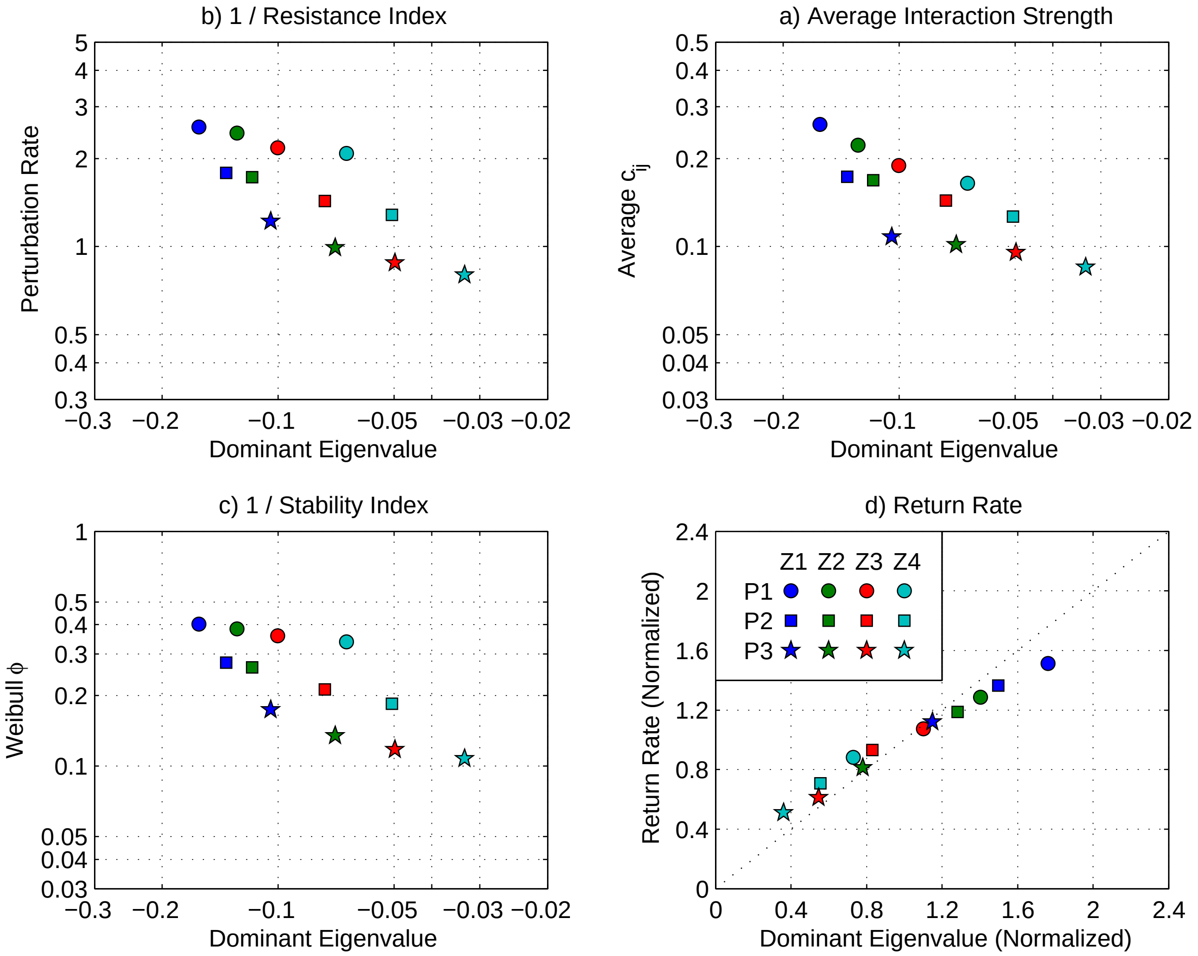

Figure 4: Relationship between the dominant eigenvalue of the Jacobian matrix and: a) average interaction strength between species computed from the elements in the Interaction matrix [m^3 mmolN^{-1} d^{-1}]); b) inverse of the resistance index (perturbation rate [d^{-1}]); c) inverse of the stability index (φ parameter of the Weibull distribution for the distances to the steady-state in the stochastic perturbation [mmolN m^{-3}]); d) return rate [d^{-1}] (dimensionless values obtained by normalizing by the mean).

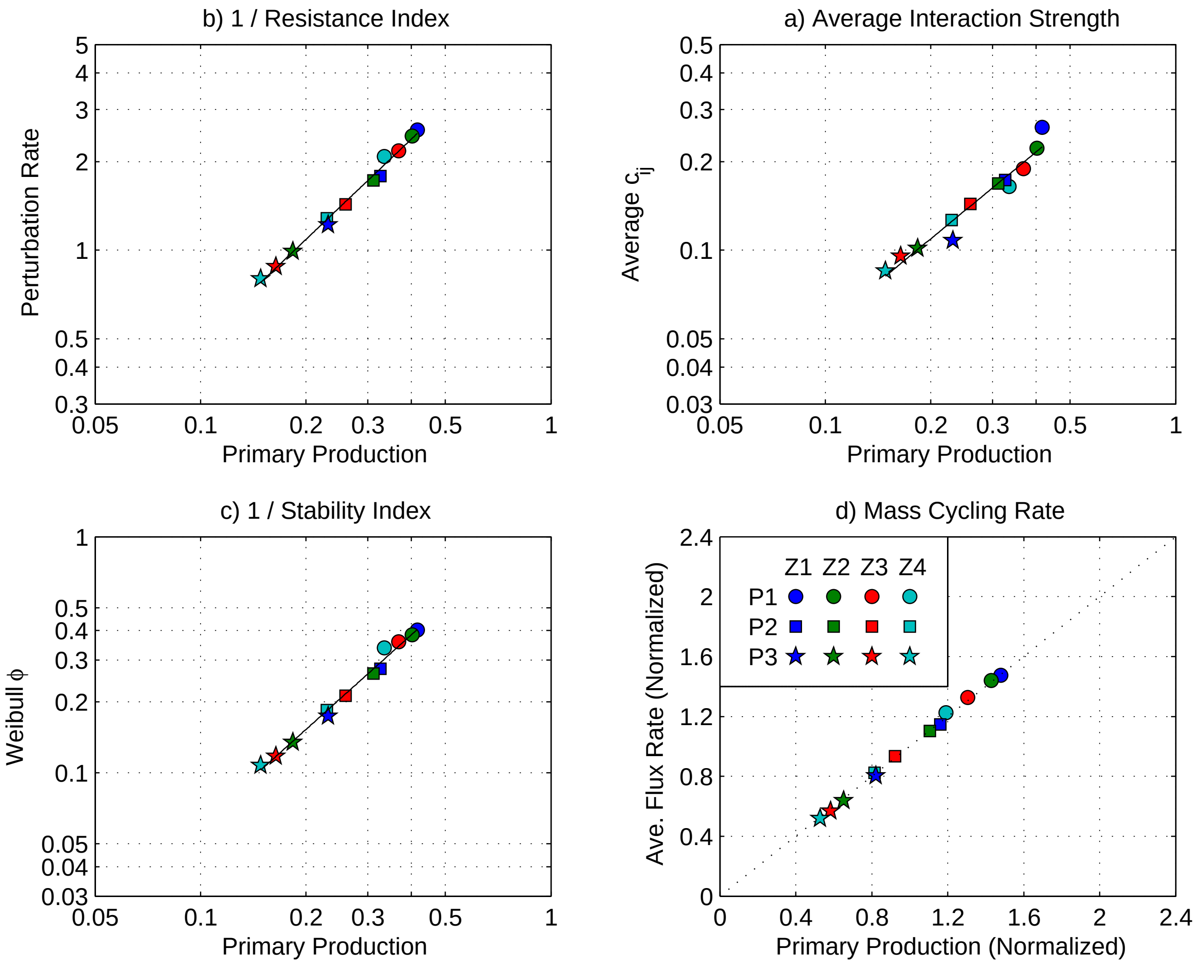

Figure 5: Relationship between total primary production and: a) inverse of the resistance index (perturbation rate [d^{-1}]); b) average interaction strength between species computed from the elements in the Interaction matrix [m^3 mmolN^{-1} d^{-1}]); c) inverse of the stability index (φ parameter of the Weibull distribution for the distances to the steady-state in the stochastic perturbation [mmolN m^{-3}]); d) average flux rate (primary production not included) of mass cycling through the food web [mmolN m^{-3} d^{-1}] (dimensionless values obtained by normalizing by the mean).

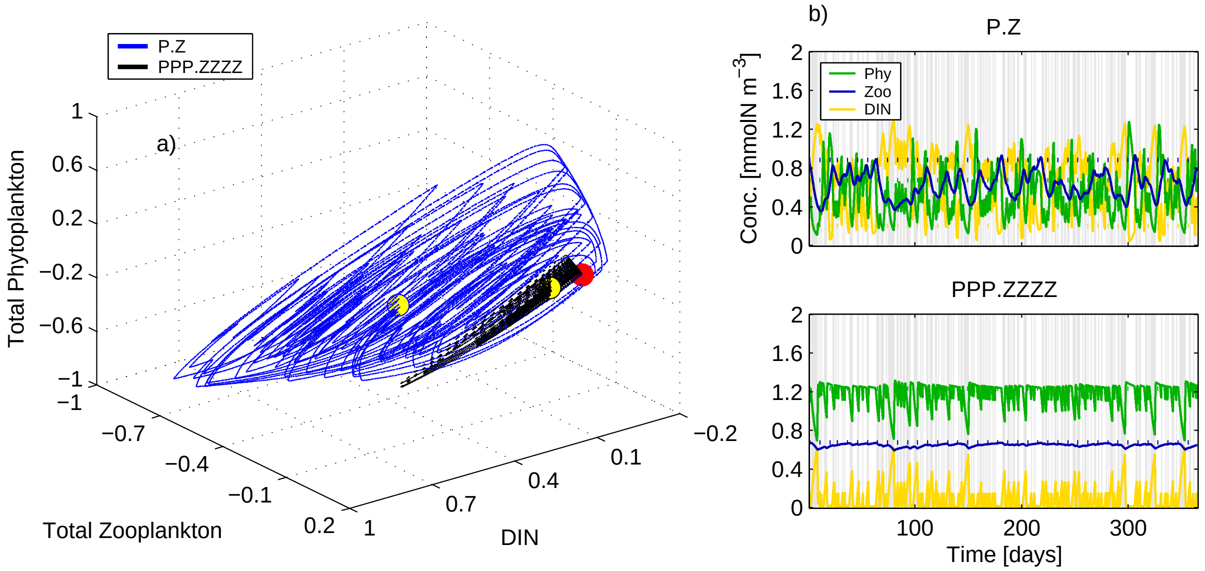

Figure 6: Dynamics of the stochastic ecosystems: a) trajectories in the phase plane for the least (blue lines) and most complex (black lines) food web. The red dot gives the steady-state. The yellow dots gives the mean position of the trajectories. The concentration of total phytoplankton, total zooplankton and dissolved inorganic nutrients have been centered by substracting the steady-state value: $\mathbf{x}(\mathbf{t}) = \mathbf{X}(\mathbf{t}) - \mathbf{X}^*$; b) time-series, for the least (upper panel) and most complex (lower panel) food web, of total phytoplankton (green continuous line), total zooplankton (blue continuous line), and dissolved inorganic nutrients (yellow continuous line). The dotted lines give their steady-state concentration. Random days in which solar radiation is zero are shown as gray vertical bars. Units [mmolN m^{-3}].

Article 2:

	Real	Fasham	Ryabchenko	KTW
$\mathbf{Q^{p_j}_{switch}}$	$\frac{\rho_j \mathbf{p_j}}{\mathbf{F}_\rho}$	$\frac{\phi_j \mathbf{p_j}}{\mathbf{F}_\phi}$	$\frac{\phi_j \mathbf{p_j}}{\mathbf{F}_\phi}$	$\frac{\phi_j \mathbf{p_j}}{\mathbf{F}_\phi}$
$\mathbf{Q_{feed}}$	$\frac{\mathbf{F}_\rho^{\mathbf{m}}}{\mathbf{K}^{\mathbf{m}} + \mathbf{F}_\rho^{\mathbf{m}}}$	$\frac{\mathbf{F}_\phi}{\mathbf{K} + \mathbf{F}_\phi}$	$\frac{\mathbf{F}_\phi}{\mathbf{K} + \mathbf{F}_\phi}$	$\frac{\mathbf{F}_\phi^{\mathbf{m}}}{\mathbf{K}^{\mathbf{m}} + \mathbf{F}_\phi^{\mathbf{m}}}$
$\mathbf{K}$	$\mathbf{k_{sat}}$	$\mathbf{k_{sat}}$	$\mathbf{k_{sat}} \frac{\mathbf{k_{sat}}}{\mathbf{F}_\rho}$	$\mathbf{k_{sat}} \frac{\mathbf{F}_\phi}{\mathbf{F}_\rho}$

Table 1: Functional Responses. $\mathbf{k_{sat}}$ 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 $\mathbf{p_j}$; and ϕ_j is the switching preference (i.e. density dependent) [n.d.] for prey $\mathbf{p_j}$.

$\mathbf{F}_\phi = \sum \phi_j \mathbf{p_j}$	Total food using prey switching preference parameter
$\mathbf{F}_\rho = \sum \rho_j \mathbf{p_j}$	Total food using prey constant preference parameter
$\phi_j = \frac{\rho_j \mathbf{p_j}}{\sum \rho_j \mathbf{p_j}}$	Prey switching preference parameter
$\rho_j = [\mathbf{0} - \mathbf{1}]$	Prey constant preference parameter

Table 2: Functional Responses (cont.)

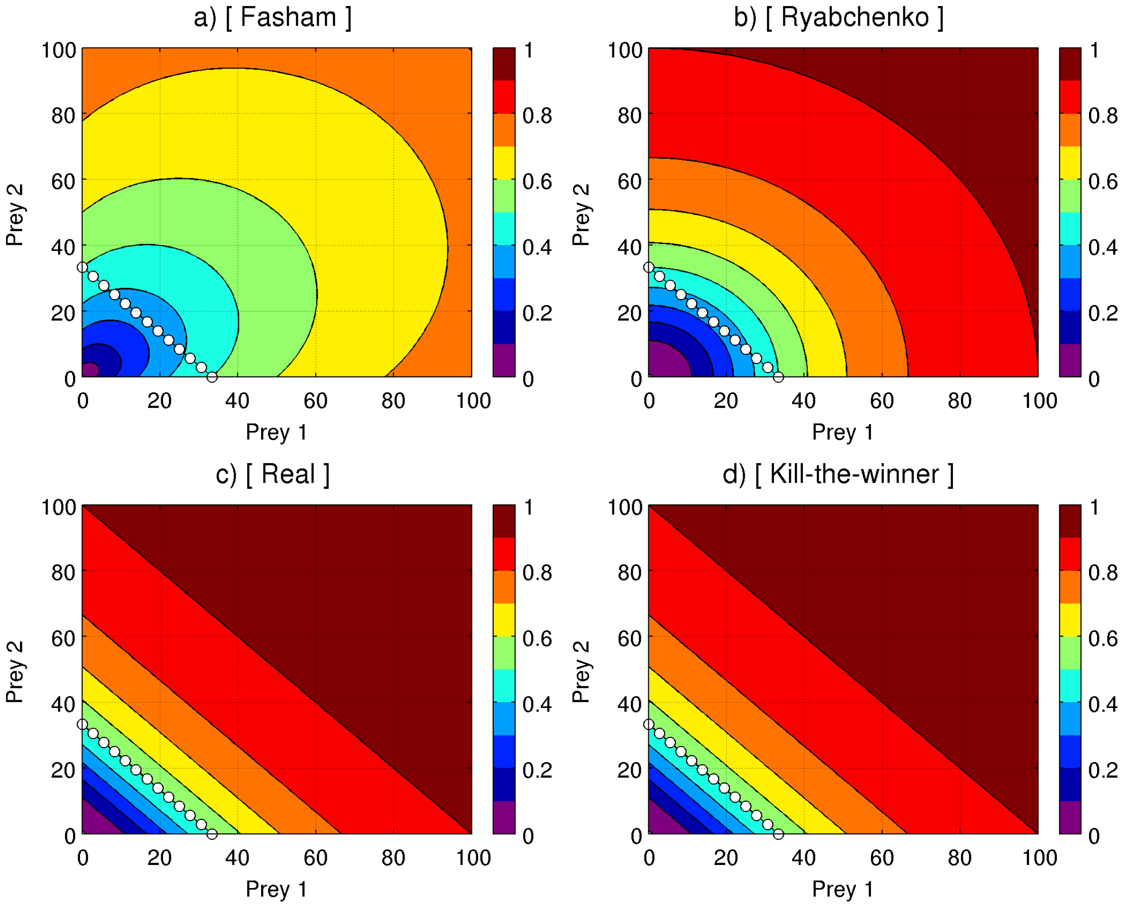

Figure 7: Countour plots of the feeding probability ($\mathbf{Q_{feed}}$) [n.d.] for the four functional responses (Fasham, Ryabchenko, Real, KTW) as a function of prey abundance [mmol m^{-3}]. The dotted line gives an isocline of equal total food available ($\mathbf{F}_\rho = \sum \rho_j p_j$ = 33.33 [mmol m^{-3}]). Constant parameters: half saturation for ingestion $\mathbf{k_{sat}}$ = 33.33 [mmol m^{-3}], prey preferences ρ_j = 1.0 [n.d.]. (Note that in our example the total ingestion is $\mathbf{G} = \mathbf{Q_{feed}}$ [mmol m^{-3} d^{-1}] because $\mathbf{V_{max}}$ = 1.0 [mmol m^{-3} d^{-1}]; see equation 4).

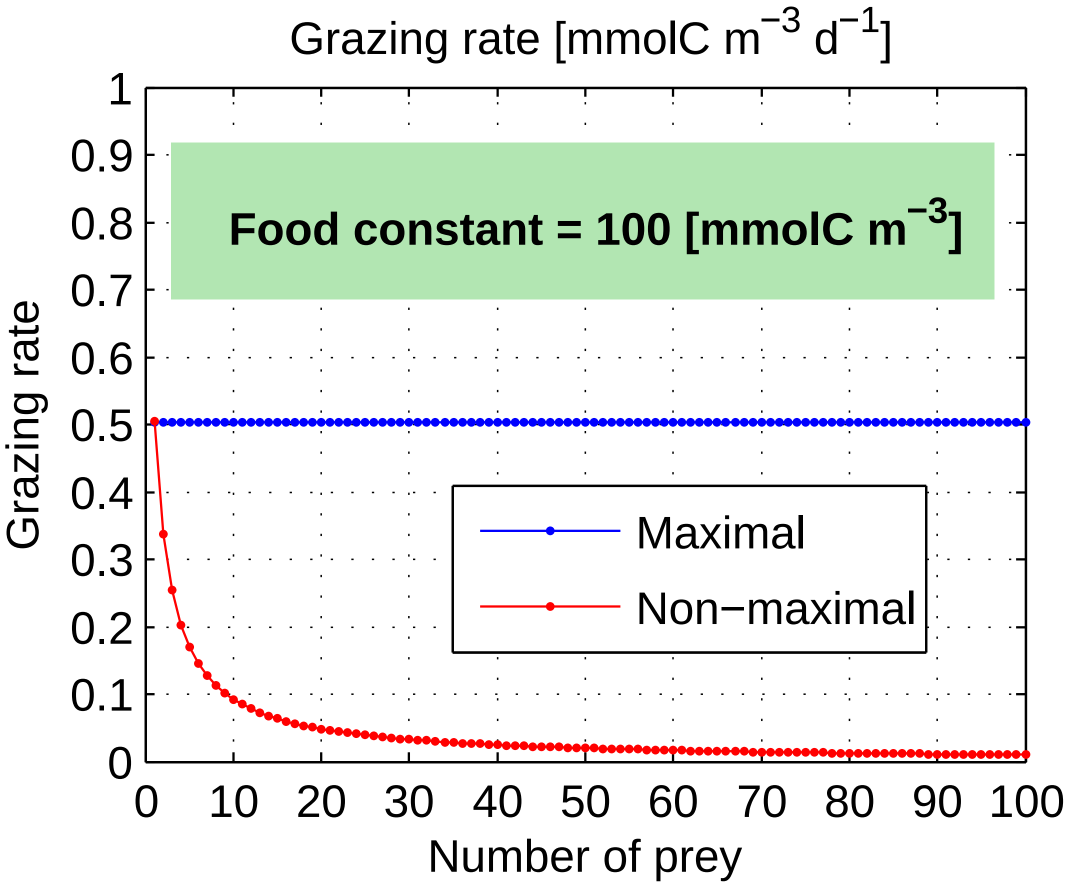

Figure 8: Total ingestion (G) [mmol m^{-3} d^{-1}] for a constant total food available of 100 [mmol m^{-3}] as a function of the number of equally abundant (i.e. 100 / N) [mmol m^{-3}] prey in an idealized ecosystem of N prey and one predator feeding with: maximal ingestion (Real and KTW parametrizations; blue line) and non-maximal ingestion (Fasham and Ryabchenko parametrizations; red line). Constant parameters: maximum grazing rate $\mathbf{V}_{\mathbf{max}}$ = 1.0 [mmol m^{-3} d^{-1}], half saturation for ingestion k_{sat} = 100 [mmol m^{-3}], prey preferences ρ_j = 1.0 [n.d.]. (Note that Fasham and Ryabchenko parametrizations will give slightly different curves if k_{sat} $\neq$ 100).

Figure 9: Implicit food web topologies (left side pannels) under the conditions of constant total prey biomass and all prey being identical in an idealized ecosystem of N prey and one predator (right side panel) feeding with: maximal ingestion (Real and KTW parametrizations; bottom panels) and non-maximal ingestion (Fasham and Ryabchenko parametrizations; upper panels).

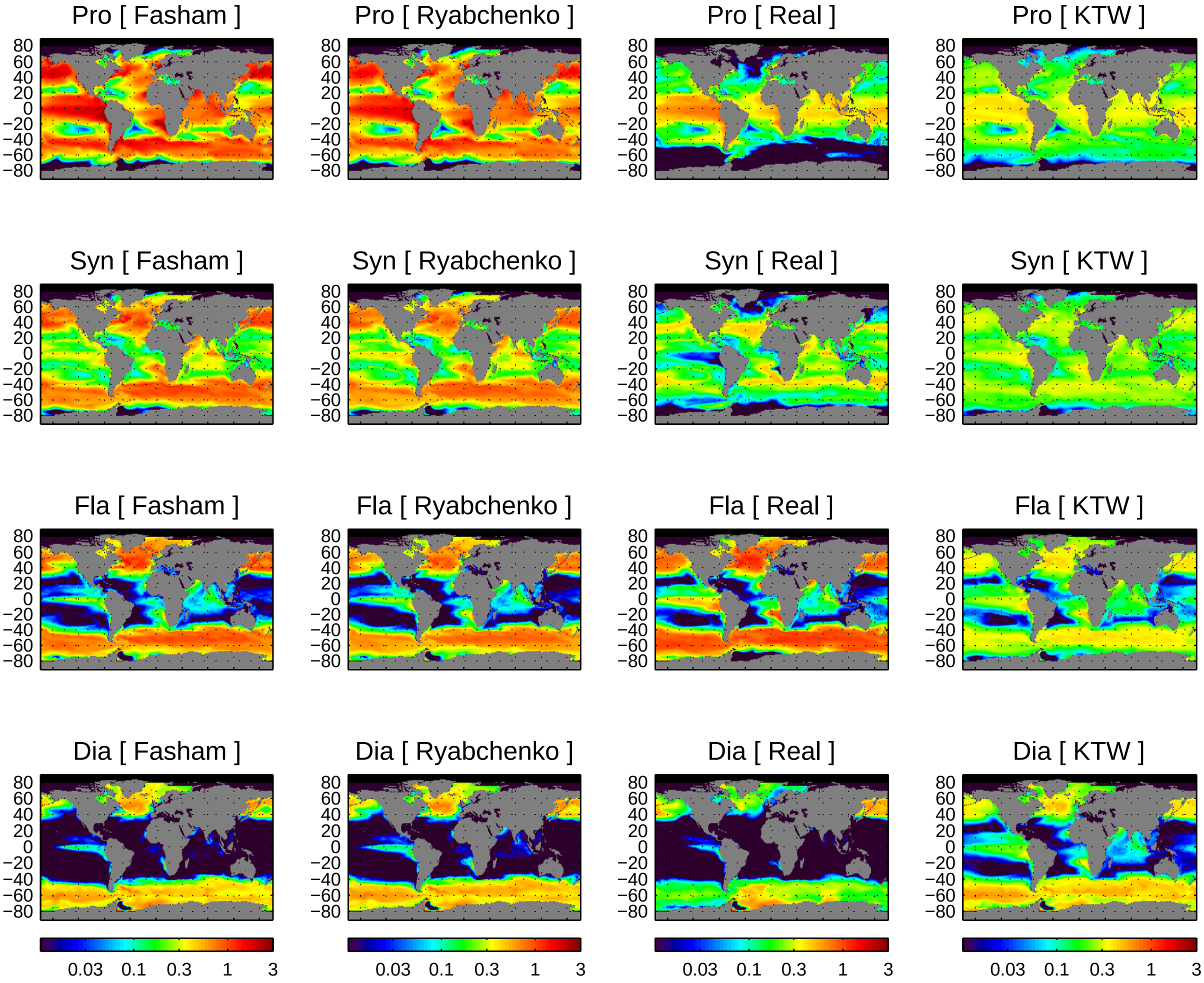

Figure 10: Phytoplankton biomass [mmolN m^{-3}] by functional group (*Prochlorococcus*, *Synechococcus*, flagellates, diatoms): First column panels: Fasham parametrization, Second column panels: Ryabchenko parametrization, Third column panels: Real parametrization, Fourth column panels: KTW parametrization.

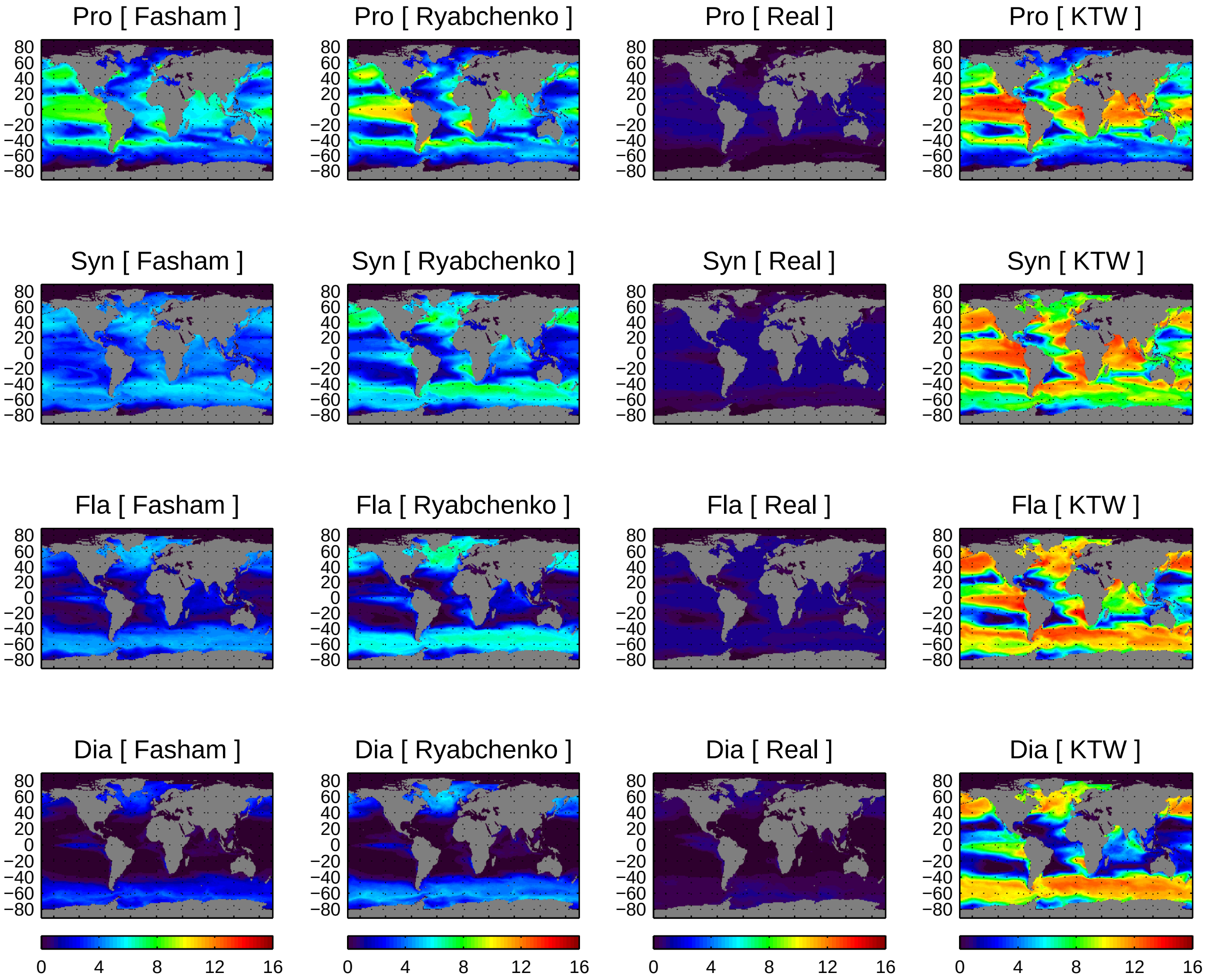

Figure 11: Species richness by functional group (*Prochlorococcus*, *Synechococcus*, flagellates, diatoms): First column panels: Fasham parametrization, Second column panels: Ryabchenko parametrization, Third column panels: Real parametrization, Fourth column panels: KTW parametrization. Species richness 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.

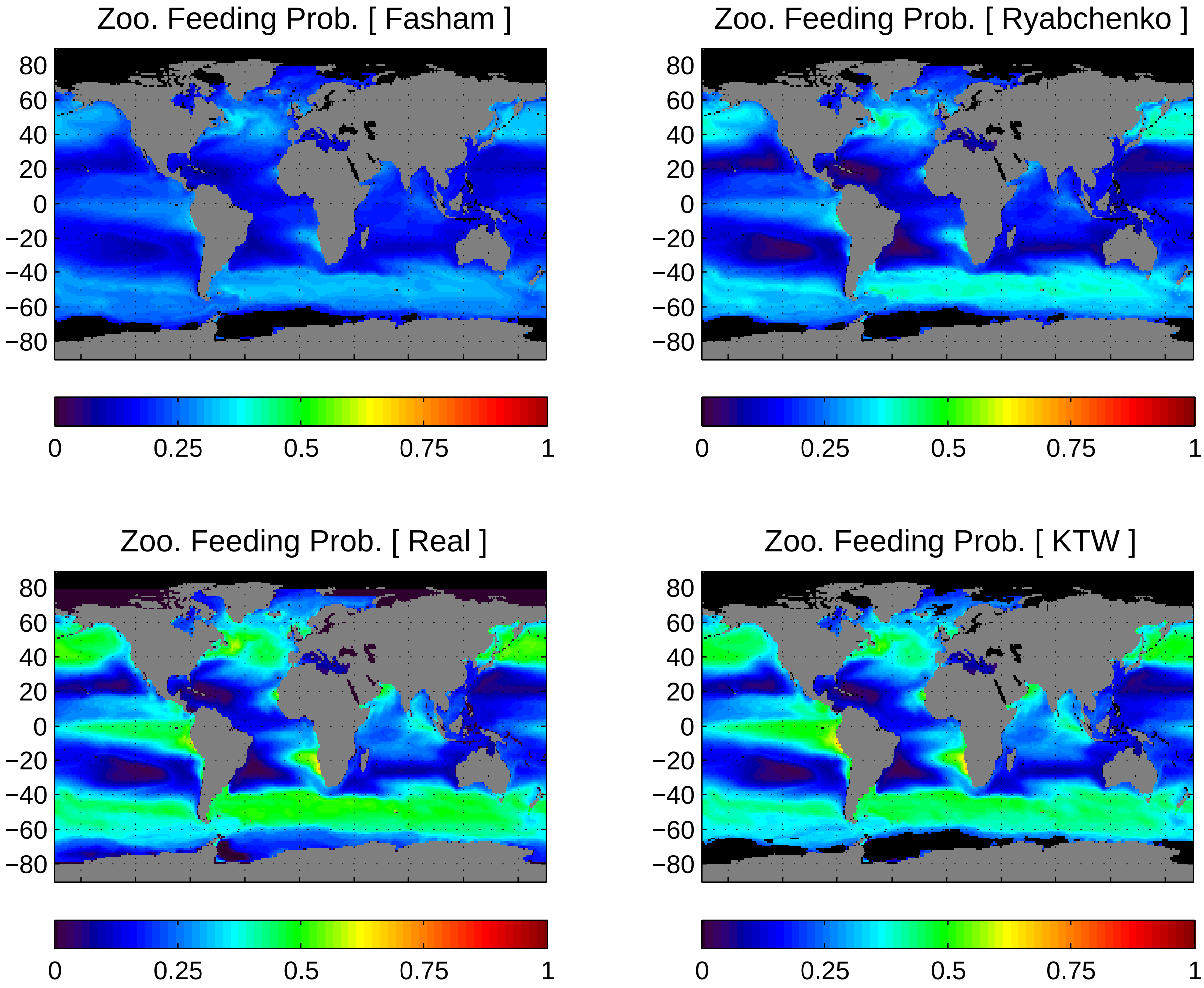

Figure 12: Average feeding probability [n.d.] from the two generic zooplankton upon phytoplankton for the four functional responses: (a) Fasham parametrization, (b) Ryabchenko parametrization, (c) Real parametrization, (d) KTW parametrization.

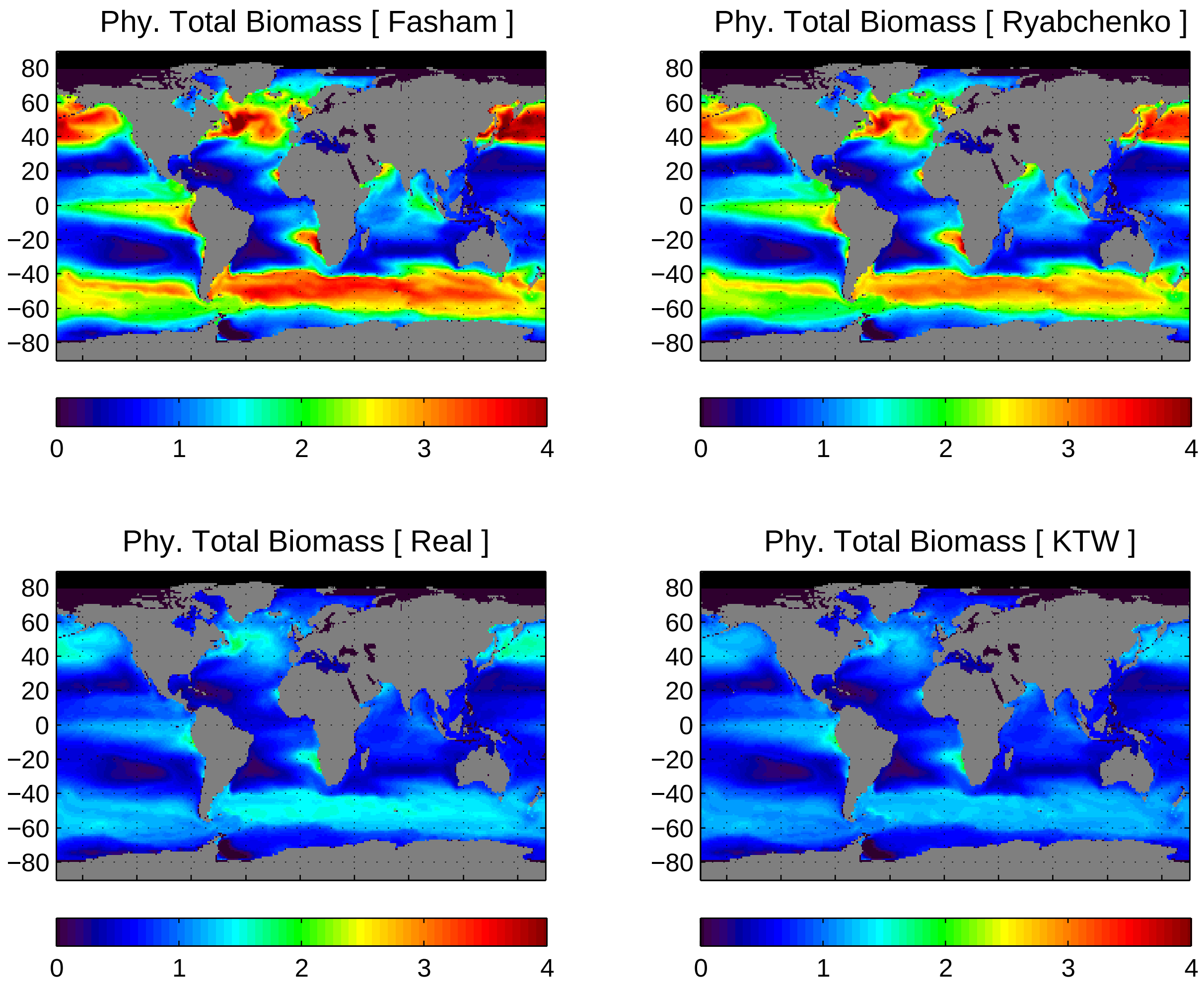

Figure 13: Total phytoplankton biomass [mmolN m^{-3}] for the four functional responses: (a) Fasham parametrization, (b) Ryabchenko parametrization, (c) Real parametrization, (d) KTW parametrization.

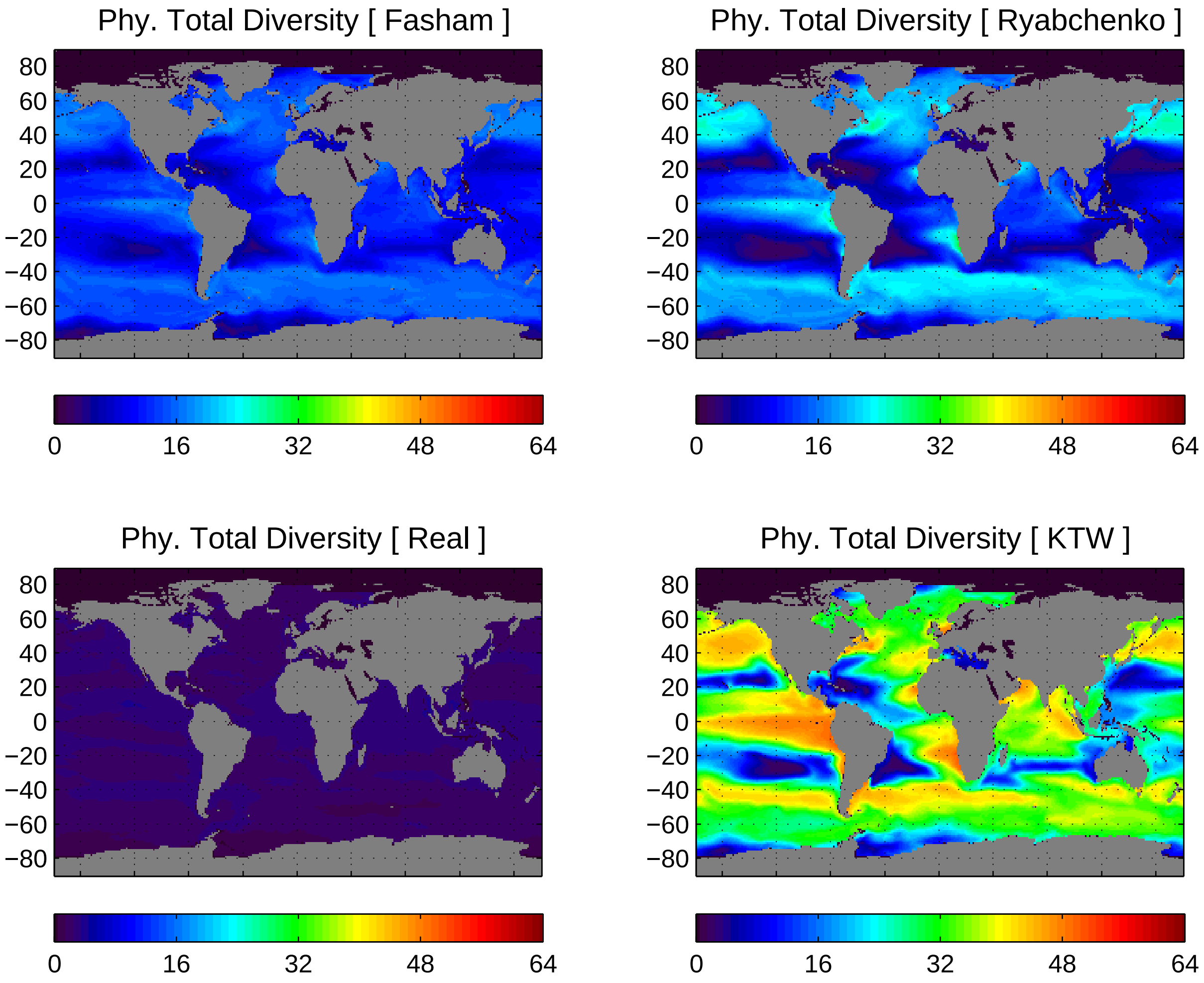

Figure 14: Total species richness for the four functional responses: (a) Fasham parametrization, (b) Ryabchenko parametrization, (c) Real parametrization, (d) KTW parametrization. Species richness is defined as the annual mean of monthly diversity. The monthly diversity is defined as the total number of species comprising greater than 1% of the total biomass at that location and month.

Article 3:

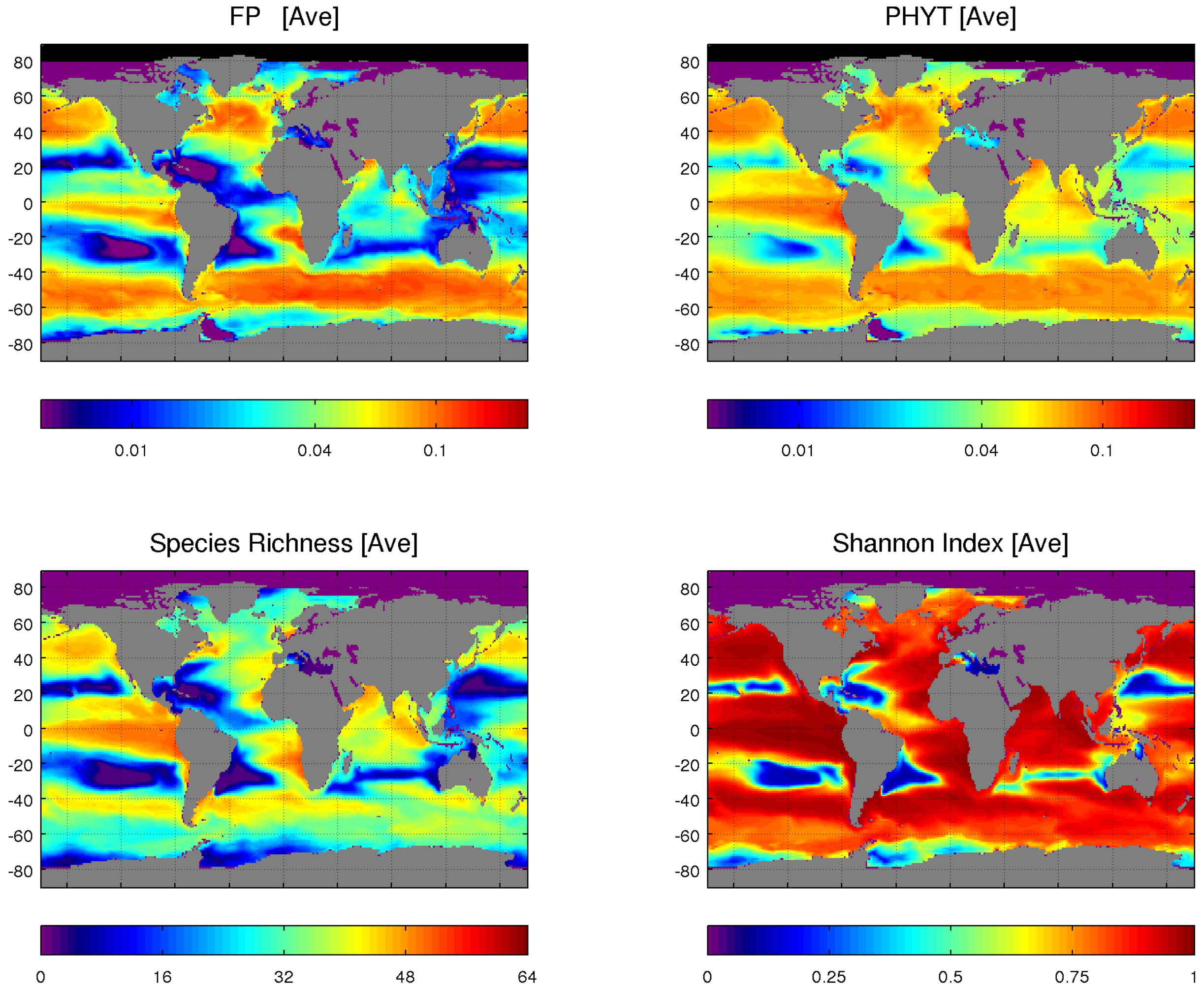

Figure 15: Global maps with annually averaged values of: a) Primary production (FP, units [mmolN m^{-3} d^{-1}]); b) Phytoplankton biomass (PHYT, units [mmolN m^{-3}]); c) Species richess (units [#spp]); d) Shannon index (normalized units [n.d.])

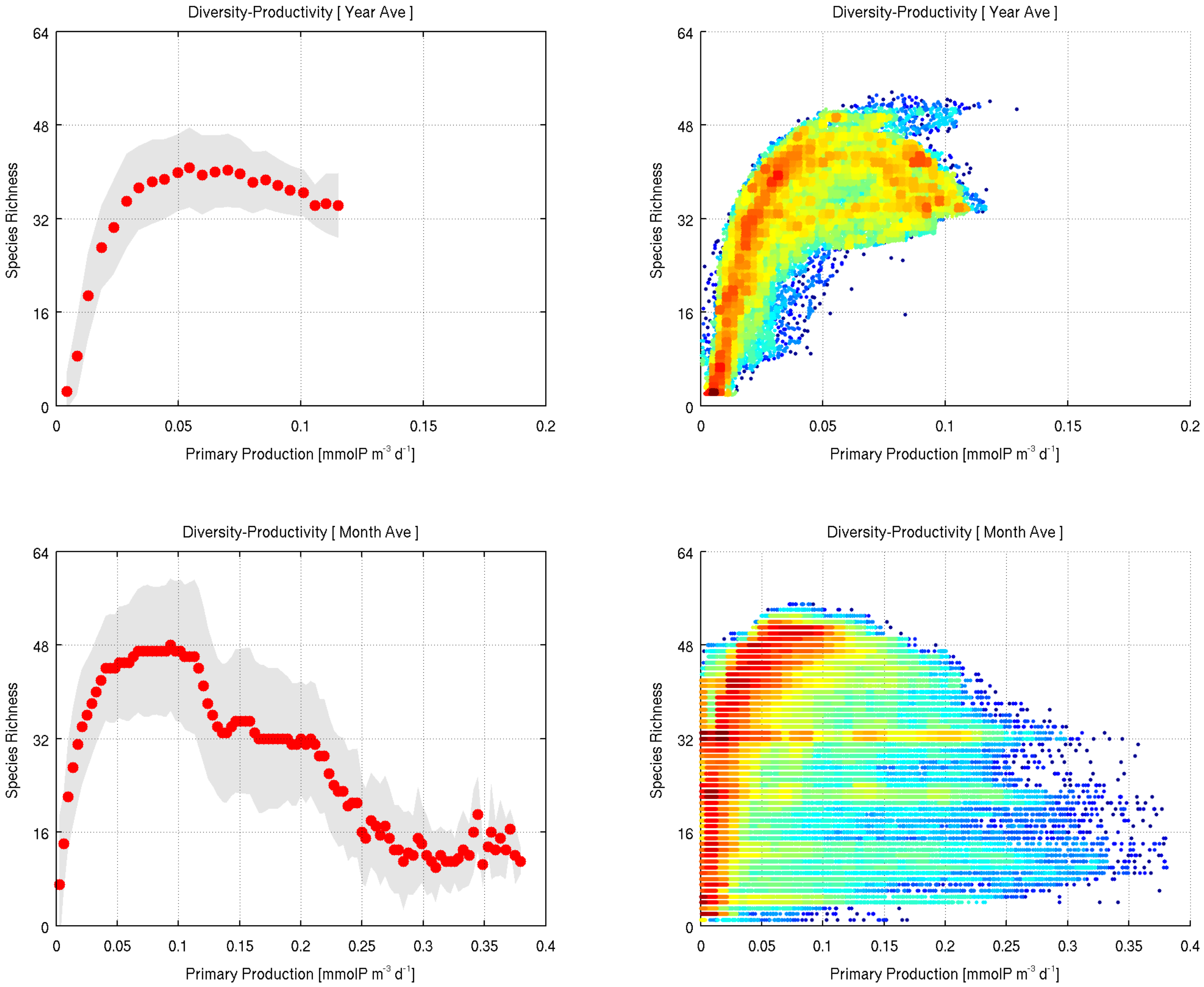

Figure 16: Global relationship between primary production [mmolN m^{-3} d^{-1}] and species richness [#spp] for ocean as a whole. The upper panels correlate annually averaged maps of diversity and productivity. The lower pannels correlate monthly-averaged maps of diversity and productivity. The colorscale of the right-side panels gives a measure of the amount of data points included in each dot (red means more data and blue means fewer data). The left-side panels give the average values and standard deviations by bins of primary production.

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- **Potential impact and main dissemination activities**

The use and application of theoretical ecology to marine ecosystems models is a much less developed field than in the case of their terrestrial counterparts. The ecosystem model I have been used during the project (MIT-darwin; developed by Mick Follows at MIT, the outgoing host), broke with the classical approach to marine ecosystem modelling and is leading the way to the future generation of models. Moreover, historically Spanish marine ecology is mostly based on experimental research. This means that the level of skills and knowledge in Spain on marine ecosystem modelling can not yet compete with that existing in other countries (USA, UK, Australia, France, Germany, The Netherlands, Italy, etc). Therefore, the knowledge I have gained during the duration of the project is currently being transfered at the return host institution to the new generation of MSc and PhD students interested on theoretical ecology and global ecosystem modelling.

The management of marine environments and the harvesting of natural resources with socio-econmic impact, such as global fisheries, can only be sustainable if we can understand the mechanisms and processes that shape the assembly of planktonic communities because they are the beginning of the marine trophic food web. However, many of the most fundamental questions regarding the rules that govern predator-prey interactions in the marine environment and how these interactions can affect community assembly processes, and thus ecosystem stability, are still very poorly understood. For us as a global society it is becoming essential to find ways to test and evaluate the potential fragility of our marine ecosystem food webs we very much rely on. Ecosystem models can help us better understand where and why ecosystems are more robust or more fragile. They are essential tools in modern science, which increasingly deals less with old heuristic descriptions and more with first principle rules and mechanisms.

The results of this project have made an important contribution towards this long term goal of improving our most fundamental knowdlege of how marine ecosystems operate. More knowdlege necessarily implies a better, more sustainable and more efficient management of resources. We modelled and tested different hypothesis in several environmental scenarios in order to obtain theoretical predictions of how marine ecosystems may be operating in nature. We identified key mechanisms that can explain some of the patterns observed in real ecosystems, like the global relationship between marine productivity and diversity. This could potentially help develop policies regarding the conservation of the marine environment along with its ecosystem diversity and functioning.

For example, our results suggest that nutrient fertilization of the ocean, which has been sometimes suggested as way to capture atmospheric CO2 through algae photosynthesis, may have a deleterius side effect on the level of phytoplankton diversity by promoting the uncontrolled blooming of a few dominant species that could outcompete many others. I beleive that before using any bioengineering approach to deal with human induced ecosystem problems we need to be sure we understand what we are doing and what could be the unexpected consequences. This project has hopefully help us gaing some new knowdlege that could be relevant for both scientists and policy makers seeking to undertake the necessary steps and policies to better protect marine ecosystems.

2 USE AND DISSEMINATION OF FOREGROUND

- **Section A**

A1: Scientific publications

N°	Title	Author	Year	Journal	Volume	Publisher	Pages	Open Access?
1	Stability of complex foodwebs: Resilience, resistance and the average interaction strength	S.M. Vallina	2011	Journal of Theoretical Biology	272	Elsevier	160-173	no
2	Maximal feeding with active prey-switching: a kill-the-winner functional response and its effect on global diversity and biogeography	S.M. Vallina	2013	Progress in Oceanography	Under review	Elsevier	?	yes
3	Global relationship between phytoplankton diversity and productivity in the ocean	S.M. Vallina	in prep.	?	?	?	?	?
4	Disconnecting marine phytoplankton diversity from primary productivity	P. Cermeno	2013	Marine Ecology Progress Series	Under review	Inter-Research	?	?

A2: Dissemination activities

N°	Activity	Leader	Title	Date	Place	Audience
1	Conference	S.M. Vallina	AGU Ocean Sciences Meeting	Feb 2010	Portland, Oregon, US	Scientists
2	Conference	S.M. Vallina	ASLO aquatic sciences meeting	Feb 2011	San Juan, Puerto Rico	Scientists
3	Conference	S.M. Vallina	Advances Marine Ecosystem Modelling Research	Jun 2011	Plymouth, UK	Scientists
4	Conference	S.M. Vallina	AGU Ocean Sciences Meeting	Feb 2012	Salt Lake City, US	Scientists
5	Conference	S.M. Vallina	ASLO Aquatic Sciences Meeting	Jul 2012	Lake Biwa, Japan	Scientists

- **Section B**

Not applicable.

3 SOCIETAL IMPLICATIONS

A: General Information	
Grant Agreement number: 236079	
Project title: Complexity, stability and chaos in marine ecosystems	
Name and title of coordinator: Jose M. Montoya - Research Scientist	
B: Ethics	
1. Did your project undergo an Ethics Review?	[NO]
2. Did your project involved any of the following issues?	
Research on humans	
Did the project involve children?	[NO]
Did the project involve patients?	[NO]
Did the project involve persons not able to give consent?	[NO]
Did the project involve adult healthy volunteers?	[NO]
Did the project involve Human genetic material?	[NO]
Did the project involve Human biological samples?	[NO]
Did the project involve Human data collection?	[NO]
Research on human embryo/foetus	
Did the project involve Human Embryos?	[NO]
Did the project involve Human Foetal Tissue / Cells?	[NO]
Did the project involve Human Embryonic Stem Cells (hESCs)?	[NO]
Did the project on hESCs involve cells in culture?	[NO]
Did the project on hESCs involve the derivation of cells from Embryos?	[NO]
Privacy	
Did the project involve processing genetic information or personal data?	[NO]
Did the project involve tracking the location or observation of people?	[NO]
Research on animals	
Did the project involve research on animals?	[NO]
Were those animals transgenic small laboratory animals?	[NO]
Were those animals transgenic farm animals?	[NO]
Were those animals cloned farm animals?	[NO]
Were those animals non-human primates?	[NO]
Research involving developing countries	
Did the project involve the use of local resources?	[NO]
Was the project of benefit to local community?	[NO]
Dual use	
Research having direct military use?	[NO]
Research having the potential for terrorist abuse?	[NO]

C: Workforce Statistics

3. Whats the number of people who worked on the project?

Type of position	Number of Women	Number of Men
Scientific coordinator	0	2
Work package leaders	1	0
Experienced researchers	0	2
PhD students	0	0

4. How many additional researchers were recruited for the project?

Number of people	0	0

D: Gender aspects	
5. Did you carry out gender equality actions under the project?	[NO]
6. Which actions did carry out and how effective where they?	[NONE]
7. Was there a gener dimension associated with your research?	[NO]
E: Synergies with Science Education	
8. Did your project involved working with students?	[NO]
9. Did your project generate any education material?	[NO]
F: Interdisciplinarity	
10. Which disciplines are involved in your project?	
• Natural Sciences	1.0
• Mathematical modelling	1.1
• Earth and environmental sciences	1.4
G: Engaging with civil society and policy makers	
11. Did you engage with societal actors beyond researchers?	[NO]
H: Use and dissemination	
14. How many articles were accepted in peer-review journals?	2
How many of these were published in open access?	1
How many of these were published in open repositories?	0
Reasons for not providing open access?	
• Publisher's licensing agreement would not permit using a repository • No suitable open access journal available	
15. How many new patent application have been made?	0
16. How many Intellectual Property Rights were applied	
• Trademark	0
• Registered	0
• Other	0
17. How many spin-off companies were created?	0
18. Potential impact on employment of your project?	
• Difficult to estimate / not possible to quantify	
19. Employment effect from your participation in FTE?	3
I: Media and communication to the general public	
20. Beneficiaries profesionals in communication or media?	[NO]
21. Beneficiaries received communication or media training?	[NO]
22. What has been used to communicate information?	Website
23. Which languages were used to communicate information?	English