Coupling low and high trophic levels models: Towards a pathways-orientated approach for end-to-end models

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Abstract :

Existing models of marine ecosystems address specific issues related to the bottom-up forcing of production or to the top-down effects of fishing on a limited range of the trophic spectrum. Very few existing models explicitly incorporate the dynamics from one end of the ecosystem to the other and thus allowing the exploration of interplay between exploitation and climate effects. The shift to an ecosystem approach to fisheries and concerns about the ecological effects of climate change require the assemblage of knowledge assembled from the respective marine disciplines with the view to build end-to-end models of marine ecosystems.

Here, with a focus on plankton and fish models, we present some issues and recommendations for the integration of models between trophic levels (vertical integration) and within functional groups (horizontal integration within trophic levels). At present, vertical coupling of plankton and fish models is mainly realized through predation processes, generally represented as a functional response. In the absence of empirical evidence and quantification, the choice of the functional response term is often made by default, and is reduced to a parameterization problem. A strategy is proposed to overcome this arbitrary choice.

In addition to the vertical coupling of trophic models, the structure of end-to-end models incorporates biodiversity via horizontal integration of trophic levels. For guiding the selection of key components to be included in end-to-end models, the idea that marine food webs are structured as alternative trophic pathways is highlighted and related to observed dynamics. We suggest that an important early step in model development is the identification of major trophic pathways and bottlenecks in an ecosystem using a historical perspective.

1. Introduction

One of the challenges of contemporary research aiming to implement the ecosystem approach to fisheries is the identification of the major trophic controls operating on marine ecosystems and how exploitation combined with climate change can affect their dynamics (Cury et al. 2008). Hence, models should progressively integrate food web dynamics with environmental forcing of marine ecosystems to improve our capacity to understand the contribution of climate or/and fishing effects on observed and future changes (deYoung et al. 2004). To develop so-called 'end-to-end' modelling approaches (Travers et al. 2007) requires the coupling of physical models, with models describing lower trophic levels (i.e. plankton) and higher trophic levels (i.e. fishes, marine birds, marine mammals) that are different in structure and resolution. When focusing on the living components of end-to-end models, two main issues are raised:

1) Vertical integration between trophic levels, or how to couple existing models of different trophic levels? Biomass flux and particularly predation is the main coupling link for building end-to-end models. The way this process is formulated and parameterized is therefore critical. Huse and Fiksen (this volume) propose a detailed model of fish predation behaviour at high resolution. Here, their work will be placed in the broader context of the formulation of predation process in marine ecosystem models;

2) Horizontal integration within a trophic level, or what are the key components that should be explicitly modelled to reproduce and anticipate ecosystem changes? The vertical integration of food webs must be accompanied by a horizontal integration to take into account ecosystem biodiversity (Duffy et al. 2007), and to be able to understand the potential occurrence of regime shifts.

Both issues are presented in this paper, based on discussions raised during the international symposium on "Parameterisation of Trophic Interactions in Ecosystem Modelling" (Cadiz, 20-23 March 2007, Eur-Oceans/Globec/Imber). Ideas and discussions are focused on the zooplankton-fish coupling with an emphasis on fish components.

2. Vertical integration: how to couple existing trophic models?

For decades and until recently, the modelling of marine ecosystems was addressed by two distinct scientific communities. Physical and biogeochemical modellers focused on the forcing and dynamics of the oceans and their impact on primary production, nutrient and carbon fluxes. Fisheries modellers used to focus primarily on the impact of fishing on exploited fish stocks, starting from a purely single species approach (from the foundations in Beverton and Holt 1957 to the modern stock assessment models such as MultifanCL-Fournier 1998) to progressively consider multispecies interactions (e.g. MSVPA – Pope 1979, EwE - Pauly et al. 2000- , Osmose – Shin and Cury 2004) and the effect of climate on particular life stages or processes affecting fish populations (e.g. fish growth, recruitment, migration – Huse and Fiksen this volume, Maury this volume). Because the objectives and the expertise are different in each field, there are differences in the formulation, the diversity and the spatio-temporal resolution of the models which results in conceptual and technical difficulties when trying to couple them.

Models of plankton communities with low trophic levels (LTL) are dominated by biogeochemical NPZD type models which, in their simplest and initial form, consist of four boxes: a nutrient pool (N), phytoplankton (P), zooplankton (Z) and a detritus compartment

(D). Many variants of this basic structure exist, with explicit modelling of nitrate, ammonium and dissolved organic nitrogen pools like in the well-known Fasham et al. (1990) model, with a size-based structure of the plankton compartments (Moloney and Field 1991, Kishi et al. 2004), with consideration of limitations by various nutrients such as Fe, P and Si and incorporation of several organic matter pools (Aumont and Bopp 2006) or by incorporating 1D to 3D dynamics (e.g. Allen et al. 2001). Recently, attempts have been made to increase the number of planktonic functional types to allow for physiological peculiarities to be taken into account (Le Quéré et al. 2005) or to represent emergent biogeography of explicit microbial communities (Follows et al. 2007). The applications and the target processes may be different, but the structures used are comparable. The hydrodynamic forcing of these biogeochemical type models occurs via the diffusion and advection terms, which means that the approach is formally similar to that used in physical modelling (Dippner 2006). In contrast, it is difficult to group under the same umbrella the different models developed in fisheries science. They strongly differ in the formalisms adopted (continuous or discrete models, eulerian or lagrangian models, differential equations, individual-based models, matrix population models), in their structure, and in the target processes (recruitment, somatic growth, predation mortality, migration). Depending on the approach and underlying hypotheses, the emphasis is placed on species-, flux-, and/or size-based processes. This apparent diversity may reflect either a more comprehensive knowledge of the larger, more easily handled organisms or an inherent gradient of complexity across higher trophic levels which can be related to the duration of life cycles (deYoung et al. 2004).

Practically, coupling models consists of coupling state variables using explicit processes. The key process to link LTL models to HTL models is predation, which affects the growth rate of predators (individual or population growth requiring the formalisation of energy allocation or numerical response respectively) and causes explicit mortality on prey (specification of functional responses, fixed or variable diets, size-based or species-based predation). Predation induced mortality is modelled through the functional response, i.e. the per capita feeding rate. The way it is formulated in predator-prey models has generated a long history of debates (Berryman 1992, Yodzis 1994, Abrams and Ginzburg 2000). Various functional responses have been proposed as alternatives to the linear unsaturated term used in the pioneer Lotka-Volterra model. According to Holling (1966), a predators functional response depends generically on two terms: handling time (which is generally considered to be constant) and the attack rate which is a function of prey or/and predators density. The latter can depend on various factors, either biotic (e.g., morphology of prey and/or predator), behavioural (e.g. schooling behaviour, Cury et al. 2005) or abiotic factors such as the optical properties of the water (Huse and Fiksen, this volume).

Two classes of functional responses are commonly distinguished depending on whether predators interfere in one another's feeding activities (Yodzis 1994; Skalski and Gilliam 2001). The first one assumes no interference between predators. The classical Holling type I, II and type III functional responses belong to this category, which means that the attack rate only depends on prey density. The second class of models assumes predatory interference, i.e. the attack rate of predators on prey tends to decrease when predators density increases. Many theoretical debates have occurred on the importance of predatory interference, but very little empirical evidence has been produced in terrestrial or marine ecosystems (Abrams and Ginzburg 2000).

The spectrum of the functional responses which are commonly used for modelling fish and plankton interactions is rather narrow. Except in experimental cases (e.g. Taylor and Collie 2003) or for well-documented predator-prey interactions with few species involved (e.g. Essington and Hansson 2004), the choice of the functional response is mainly constrained by parameterization problems in most models applied to natural marine communities. The simplest reasonable choice is that of the classical Holling II functional response (Table 1) which presents the same kinetics as the Michaelis-Menten equation (Real 1977). This Holling

II functional response is used in the marine ecosystem models Nemuro (Megrey et al. 2007), Atlantis (Fulton et al. 2004) and Apecosm (Maury, this volume; Maury et al. 2007) with the half saturation constant serving as a tuning parameter. Walters et al. (1997) have developed their own formulation of predator functional response in Ecosim by assuming that a predator can only feed on the vulnerable component of a prey population, and that the functional response between predators and the vulnerable part of their prey is unsaturated (Lotka-Volterra predation mortality). The resulting functional response is saturated and depends on both predator and prey densities. Except for the vulnerability setting which determines whether the system is bottom-up or top-down controlled, all parameter values are inherited from a calibration of the associated mass-balance model Ecopath (Christensen and Pauly 1992) to the same ecosystem.

In the absence of *in situ* observations, it is difficult to select one specific functional response among the possible ones. There are two ways to tackle the issue without requiring a precise ecological knowledge of feeding behaviour. The first way to proceed is to test the sensitivity of the model behaviour to the use of different functional responses (Fulton et al. 2003, Koen-Alonso and Yodzis 2005, Piana et al. 2006). The second way consists of considering the simple mathematical properties of the functional responses. For example, the difference between Holling type II and type III functions lies in the behaviour of predators when prey density is low: the Holling type III formulation assumes that predators are inefficient at finding prey when prey abundance is low or that there is a threshold level below which the predator does not respond. Therefore, without making any ecological assumption, if the prey population is highly productive and is steadily at a high density, it is sensible to keep the simplest Holling II formulation. In the category of functional responses with predatory interference, there is a flaw in the behaviour the well-known Hassel-Varley (1969) functional response and the ratio-dependent one (Arditi and Ginzburg 1989): if predator density tends to zero, then the attack rate tends to infinity. In consequence, these formulations should not be used in the case of collapsed predator populations.

Another modelling approach consists of focusing on individual-based processes and letting the functional response emerge (Table 1). The individual-based model of Huse and Fiksen (this volume) proposes a high resolution representation of predator-prey interactions, by making explicit the effects of predators foraging behaviour (swimming velocity, reactive distance, visual range) and environmental conditions (light irradiance, optical properties of the water) on the clearance rate of the predator. Although the local consumption of predators is similar to an environmentally dependent Holling II function, the functional response at the population level emerges from all the local interactions occurring in encounters between prey and predator individuals. This approach certainly leads to an improvement of our knowledge on the nature of predation between fish and zooplankton, but it is data demanding and therefore would be difficult to parameterise for systems more complex than two-species. Less refined in predation behaviour but less data demanding, the Osmose individual-based model assumes that predation is constrained by a minimal and a maximal predator to prey size ratio, a maximum ingestion rate and by the spatial overlap between predators and prey (Shin and Cury 2004, Travers and Shin, this volume). Comparisons between the different modelling approaches should be performed, in order to gain insights into the effects of predation parameterisation in the vertical coupling of plankton and fish models. For example, it would be challenging to provide a more mechanistic basis to functional responses using aggregation methods for scale transfer between models, from models with detailed individual predation behaviour (Huse and Fiksen this volume, Duboz et al. 2003) to the choice and the parameterization of the functional responses in more aggregated population models.

In addition to predation, further processes require attention when coupling HTL and LTL models depending on the issue that is addressed and on the structure of the submodels (Fig. 1). When explicit in HTL models, fish excretion and egestion should supply the ammonium and the organic nitrogen pools of NPZD models (Megrey et al. 2007). The loss of biomass

due to natural mortality of HTL organisms can be coupled to the dynamics of detritus and bacterial pool of LTL models. It is also necessary to clearly determine whether the ichtyoplankton should be considered in the LTL or in the HTL model (or in both models), and to carefully specify linking processes such as individual growth (transfer of biomass from LTL to HTL models) or fish reproduction (transfer of biomass from HTL to LTL models). The spatial distribution of LTL organisms can also determine the spatial dynamics of HTL organisms (e.g. Lehodey et al. 2003) and reciprocally (Huse and Fiksen, this volume).

When coupling physical and biological models, one must acknowledge that each model focuses on a limited range of processes, related to specific objectives (Fig. 1). The diversity of the models reflects the diversity of the processes that are operative, as also will be the case for end-to-end approaches. A diversity of end-to-end models is necessary for echoing the diversity of ecosystem-specific issues. A diversity of mechanisms also exists in the way climate affects living organisms. Major issues in coupled bio-physical processes concern changes in plankton production (carrying capacity of the system), in the spatial distributions of living organisms (match/mismatch between predators and prey), or in recruitment success (population variability). The extent of the bio-physical processes involved are reflected in the use of diverse physical forcing factors (temperature, light, depth of the mixed layer, salinity, nutrient concentration, wind, currents). By contrast, at the top of the food web, most models consider direct fishing impacts simply through fishing mortality rates (i.e. removal of biomass), which are species, size- or age-structured, with potential information on the spatio-temporal dynamics.

3. Horizontal integration: what are the key components to be modelled?

While monitoring, analysing and modelling marine ecosystems, scientists must often deal with counter intuitive ecosystem responses to climate and fishing changes. Many ecological 'surprises' have been documented worldwide, such as demographic explosions of previously low-abundant populations, e.g. jellyfish and octopus (e.g. Lynam et al. 2006, Gulland and Garcia 1984) or, on the contrary, the non-recovery of collapsed populations after fishing ban (e.g. Canadian northern cod, Bundy and Fanning 2005). We are often bound to assess those events *a posteriori* rather than being able to forecast them. Our capacity to provide reliable predictions is dependent on our capacity to detect, analyse and represent the interplay of controls that structure the dynamics of marine ecosystems and contribute to the emergence of patterns. The difficulties arise from the fact that (i) climate and anthropogenic impacts are not easily disentangled, (ii) changes are due to indirect or combined effects, (iii) the selection of key species is complex and some species may be mistakenly neglected because they are less abundant or less connected to others, (iv) weak interactions prevail in marine ecosystems which make it difficult to identify major pathways and controls. In our effort to improve existing modelling approaches, past failures can be overcome by considering to a certain extent biodiversity within each trophic level in end-to-end models.

Most dynamics observed in marine ecosystems cannot be understood if one considers marine food webs as a single aggregated food chain, with only a vertical integration across trophic levels. By focusing on two species predator-prey systems (herring-copepod or cod-capelin), Huse and Fiksen (this volume) make the strong assumption that the predators are very specialized and that the prey have exclusive predators. This configuration can be observed in a few pelagic ecosystems, but most often pelagic organisms like fish are typical generalists, having multiple prey and multiple predators, and are life-history omnivores (Cury et al. 2003).

Therefore, the number of interactions is high, making food webs of generalists more complex than those of specialists, and the strength of interactions is generally weak (Montoya et al.

2006). This has major consequences in terms of trophic controls operating within marine ecosystems. Contrary to expectations, it has been observed that weak interactions tend to be correlated with high variability in interaction strength so that they can yield strong effects intermittently (McCann 2000) or, reciprocally, are very labile. The net effect of a species on another one results from a suite of direct and indirect interactions that often have effects of opposite sign. If no direct interaction dominates in strength, the net effect displays a large variance because of fluctuations of abundance of all the species mediating the strength of indirect effects (Berlow 1999). On the other hand, Navarrete and Berlow (2006) provide experimental evidence that high spatio-temporal variability in the strength of species interactions can foster the resilience of ecosystems in the face of environmental variation. Predators have potentially multiple prey to feed on, they may act as stabilizing or "noise-dampening" forces because they will tend to target the most abundant species (Bax 1998, Sala 2006).

The theoretical and empirical background in trophodynamics reveals that aggregating species into 'boxes' for practical purposes, and imposing a priori trophic controls in models may lead to erroneous projections of ecosystem dynamics. In practice, taking account of the multiplicity of links and species biodiversity in models must be strongly constrained by the operating processes. Clearly, there is a need for simplification; considering the role of biodiversity in models does not imply exhaustiveness. De Young et al. (2004) advocate a "rhomboid" modelling approach, which involves developing details for target species at a specific trophic level and making increasing simplifications with distance both up and down the trophic scale from the target species (Fig. 2). For example, Huse and Fiksen (this volume) represent all the stages of *Calanus finmarchicus*, and describe with high resolution the predation process between herring and copepods, but upper and lower trophic levels are not explicitly represented. The "rhomboid" approach is directed towards practical objectives, i.e., obtaining detailed simulation results on target species. In the same line, as fisheries management is species-based, there is a strong practical concern that end-to-end models should be detailed enough for exploited species.

Generally, the structure of foodweb models is guided by the consideration of the most abundant species and the dominant trophic interactions at a given time and location. But as foodweb dynamics can be highly variable, the snapshot provided by the model does not necessarily reflect the functioning of the ecosystem and may even preclude the use of the model for predictive purposes in a global change context. The analysis of interaction strength should therefore be combined with the identification of potential alternative energy pathways providing an integrative and retrospective view of ecosystem functioning. The importance of those energy pathways would vary depending on the state of the ecosystem.

There is a recent emphasis in the scientific community in trying to explain observed patterns such as regime shifts or alternation of species dominance, blooms or species collapses as resulting from alternation between food chains. For example, Parsons and Lalli (2002) suggest that explosions of jellyfish populations may result indirectly from fish overexploitation considering alternation between the following two basic chains: i) small flagellates → small zooplankton → jellyfish, and ii) large diatoms → large zooplankton → fish. Similar analyses are conducted in upwelling ecosystems for explaining the alternation of sardine and anchovy (Verheye et al. 1998, Van der Lingen et al. 2006). Much progress in understanding and predicting ecosystem responses to fishing and climate change can be achieved if the structure of future end-to-end models allows for the emergence of alternative trophic pathways (Fig. 2). Rooney et al. (2006) emphasize that the stability of complex ecosystems depends critically on the maintenance of the heterogeneity of distinct energy channels and their differential dynamic properties (e.g. productivity and turnover). Often, nutrient loading through bottom-up control can result in complete dominance of the ecosystem by a few energy channels. However, predators through top-down controls can also couple distinct energy channels that differ in productivity, turnover rate and length. By removing larger

species or size classes, fishing can also act to shorten food chains, thereby reducing the resilience of ecosystems (Hutchings 2000). For example, in the northern Benguela, mean path length has been severely reduced and the ecosystem appears less resistant to fishing and environmental perturbations (Heymans et al. 2004). One of the reasons why trophic cascades/top-down controls can be difficult to observe is that the effects often cancel each other out when LTL compartments are aggregated. For example, copepods were shown to act as a switch between alternative trophic chains with counteracting effects on phytoplankton biomass because they would reduce large phytoplankton cells, but simultaneously promote small phytoplankton by feeding on ciliates (Stibor et al. 2004).

The properties of alternative trophic pathways can condition the dynamics of marine ecosystems and the prevalence of types of trophic controls. There is growing evidence that the energy content of alternative food chains is crucial for understanding the reorganization of marine pelagic food webs (Litzow et al. 2006). Parsons and Lalli (2002) support the hypothesis that overexploitation, by targeting large fish, would favour the emergence of low-energy food chains dominated by flagellates, jellyfish and small fish. Wanless et al. (2005) explain the major breeding failure of birds which occurred in 1994 in the North Sea by a switch from a high-energy food chain to a low-energy one, forcing major bird populations to switch prey from sand eels to sprat which has a much lower energy value. Food chains can also be characterized by their turnover rate or production:biomass ratios, so that fast and slow channels can be distinguished within an ecosystem. Rooney et al. (2006) show that, because fast channels would be on average comprised of strong interactions and slow channels of weak interactions, rapid predatory switching capacity may balance the asynchrony between different food chains. Rooney et al. (2006) suggest that a foodweb architecture based on multiple energy channels that are asymmetric in their properties would provide ecosystems with a potent mechanism for responding to large perturbations.

Knowledge on the existence and the characteristics of alternative trophic pathways appears to be essential to better understand the properties and the dynamics of marine food webs. Alternation between competitive food chains can be in particular proposed as a potential mechanism underlying the occurrence of regime shifts. We propose that the choice of the key components to represent in end-to-end models should not be conditioned by practical constraints only but should also be guided by the identification of a set of alternative food chains. This pathways-oriented modelling approach would benefit from the development and the evaluation of ecosystem indicators for quantifying the properties of distinct food chains, e.g. food chain length and degree of omnivory (Duffy et al. 2007), energy content and turnover rate.

4. Conclusion

We have highlighted major features in the structure and functioning of marine pelagic food webs which should be reflected by end-to-end models: the variability and multiplicity of trophic links, the importance of weak interactions, and the alternation of asymmetric food chains. The vertical coupling of LTL and HTL models allows the combined effects of climate change and over-fishing to be addressed explicitly but it is the minimal requirement. This must be accompanied by a horizontal integration of species diversity within each trophic level to better understand the interplay between different trophic controls operating within marine food webs.

To select the key species or functional groups to be represented in our ecosystem models, not only should the most abundant entities or the main trophic interactions be considered, but we propose to adopt a historical perspective and a comparative framework. A historical perspective would lead to select some species which were abundant in the past because

they are potentially key nodes of alternative trophic pathways. For example, sardine *Sardinops sagax* are presently at very low abundance in the Peruvian ecosystem but depending on the physical forcing, they can potentially alternate with the dominant anchovy *Engraulis ringens* (Chavez et al. 2003). A comparison across similar ecosystems would help identify some species that can dramatically increase in abundance under the influence of global change. For example, the recent explosion of jellyfish in Namibian waters (Northern Benguela ecosystem) can foster the inclusion of this functional group and the associated trophic pathway in the modelling of the South African ecosystem (southern Benguela ecosystem).

In addition, we suggest that the size of organisms is an integrative trait that may help us to elaborate the structure of end-to-end models and reduce the overall complexity of diversified marine food webs. Because size-based opportunistic predation is one key feature of marine food webs (Pope et al. 1994, Jennings et al. 2002, Shin and Cury 2004), the nodes of food chains can be characterized by specific size ranges. Constraints on predator to prey size ratios allow the description of common traits of marine ecosystems such as cannibalism, life-history omnivory, and predator switching behaviour which can even occur across trophic levels, i.e. switching from herbivory to carnivory as was reported for copepods (Saiz and Kiorboe 1995) or small pelagic fish (Van der Lingen et al. 2006). Therefore, considering size-based opportunistic predation in our models would allow for the emergence of alternative trophic pathways depending on environmental conditions, without defining predator diets *a priori.* Size is an indicator that can also help characterizing potential alternative food chains. It is for example a relevant proxy for characterizing species turnover rate. It can also reflect the quantity and the quality of species energy content (Kainz et al. 2004) which can both be determinant for the demography of fish and top predators (Wanless et al. 2005, Litzow et al. 2006). For example, large demersal species are found to contain less essential fatty acids than small pelagic species (Iverson et al. 2002, Litzow et al. 2006), large copepods are characterised as being more lipid-rich than small ones (Hooff and Peterson 2006), large phytoplankton such as diatoms are typically rich in eicosapentaenoic acid and small phytoplankton such as dinoflagellates and coccolithophores are rich in docosahexaenoic acid (Dalsgaard et al. 2003). Many other biological characteristics of organisms such as swimming speed and detection capabilities (Visser 2007), and most metabolic processes (Kooijman 2000, Gillooly et al. 2001, Woodward et al. 2005) are well correlated with body size.

Model structure should therefore account for the whole range of organism size, with sufficient disaggregation to allow for the emergence of distinct energy channels. LTL models such as NPZD models should ideally consist of two or more size classes for phytoplankton and zooplankton, and HTL selected species should cover a representative range of sizes. Considering size as an essential functional trait allows the parsimonious representation of the plasticity and the multiplicity of trophic links and energy pathways within marine ecosystems, and the level of size differentiation within a species component (size or stage structure) will depend on the importance that modellers attach to the recruitment process, to cannibalism and to life-history omnivory.

Aknowledgements

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Tables

Table 1: Functional responses used in marine foodweb models representing plankton and fish components.

Formulation	MODEL (reference)	Functional response *Predation hypotheses*	Parameterization
System of differential equations Deterministic functional response	NEMURO.FISH (Megrey et al. 2007) ATLANTIS (Fulton et al. 2004)	Holling type II *No predator interference, prey preferences*	- vulnerability coefficients - half-saturation constant (or clearance rate), tuned - maximum ingestion rate
	APECOSM (Maury, this volume Maury et al. 2007)	Holling type II *No predator interference, size-based predation, no prey preferences*	- half-saturation constant, tuned - maximum ingestion rate - predator size-based selection function
	ECOSIM (Walters et al. 1997, Christensen et al. 2005)	Foraging arena theory *Natural refuge for prey, prey preferences*	- vulnerability coefficients - effective search rates Most parameters are inherited from prior calibration of Ecopath model
Individual-based model Emerging functional response	Behavioural high-resolution IBM (Huse and Fiksen, this volume)	*Importance of small-scale foraging behaviour, light effects on predator/prey encounter rate, prey preference*	- handling time - clearance rate dependent on prey size, on predator behaviour (swimming velocity, angle of visual field) and on environmental conditions (light irradiance, optical properties of the water)
	OSMOSE (Shin and Cury 2004, Travers and Shin, this volume)	*Size-based opportunistic predation, no prey preferences*	- maximum ingestion rate - minimum and maximum predator/prey size ratio

Figures

Fig. 1. : Processes involved when coupling sub-models of high trophic levels (HTL) to low trophic levels (LTL). The black arrows represent the processes used to couple LTL and HTL models (the thick black arrow represents the main process used, i.e. predation). The thinner arrows represent other processes that can be considered. The '+' and '-' signs represent respectively the gain and loss of matter for each process. The particular case of ichthyoplankton possibly included in both sub-models (overlap) is represented by dotted arrows. The physical environment acts directly on the production of phytoplankton, causing potential bottom-up control on the ecosystem. It also affects the spatial distribution and the reproduction timing of living organisms, hence controlling the match/mismatch between predators and prey, and recruitment success. Fishing acts directly on the fish compartment, with potential cascading effects down the foodweb. Depending on the modelling objectives, not all processes are to be considered. Two examples of model structures are provided, addressing two specific issues: 1- Fish predation control on zooplankton production (e.g. Huse and Fiksen, this volume). 2- Ecosystem effects of both fishing and pollution (e.g. Fulton et al. 2004).
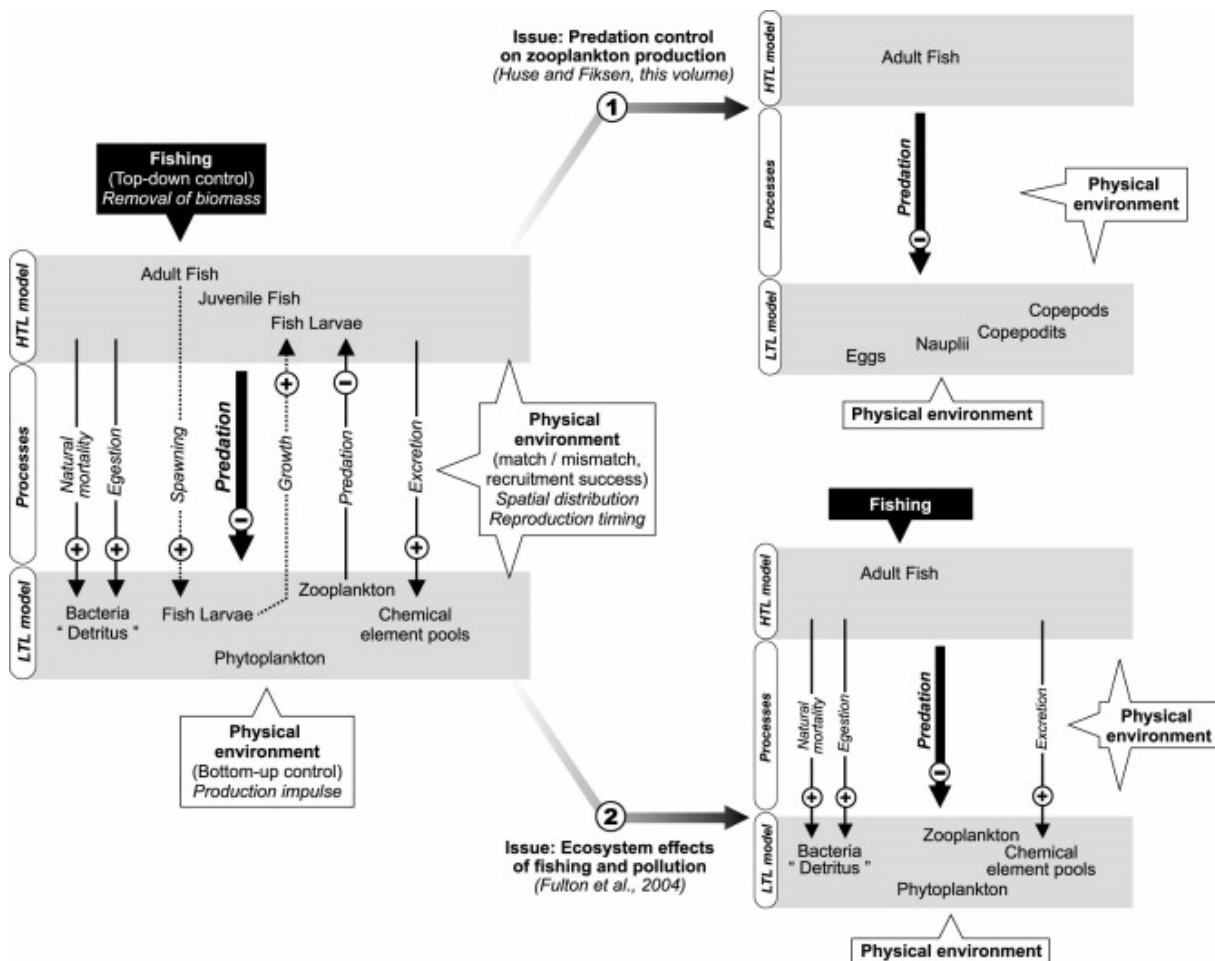
Fig. 2. : Vertical and horizontal integration of end-to-end models. The boxes represent species or groups of species, and the lines the trophic interactions. The "rhomboid approach" consists of developing details in target components of the food webs, either fish-centered models (e.g. Shin and Cury 2004, Walters et al. 1997) or plankton-centered models (e.g. Megrey et al. 2007, Hermann et al. 2001), resulting in simplification at the top or bottom of the foodweb (deYoung et al. 2004). The 'pathways-oriented approach" acknowledges the role of biodiversity in the emergence of alternative trophic pathways. Depending on climate and fishing forcing, the dominance of trophic pathways alternate, e.g. low energy food chains versus high energy food chains (in green) or food chains with slow turnover rate versus food chains with high turnover rate (in red). This pathways-oriented approach could help better understanding and predicting drastic ecosystem responses such as regime shifts to changes in climate and fishing.