Ecosystem oceanography for global change in fisheries

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Overexploitation and climate change are increasingly causing unanticipated changes in marine ecosystems, such as higher variability in fish recruitment and shifts in species dominance. An ecosystem-based approach to fisheries attempts to address these effects by integrating populations, food webs and fish habitats at different scales. Ecosystem models represent indispensable tools to achieve this objective. However, a balanced research strategy is needed to avoid overly complex models. Ecosystem oceanography represents such a balanced strategy that relates ecosystem components and their interactions to climate change and exploitation. It aims at developing realistic and robust models at different levels of organisation and addressing specific questions in a global change context while systematically exploring the ever-increasing amount of biological and environmental data.

Glossary

Bottom-up control: the food web components are regulated by either primary producers or the input of limited nutrients through changes in the physical environment (i.e. controlled by the environment).

Ecosystem oceanography: a discipline that relates marine living populations and their interactions to environmental fluctuations in order to predict ecosystem responses to global change (e.g. climate change and exploitation). This discipline represents a balanced strategy for developing population, food web and end-to-end ecosystem models. Its name refers to fisheries oceanography, a field of research that was introduced by Hjort's seminal work.

Ecosystem-based fisheries management (EBFM): the overall objective of this new perspective for marine exploitation is to sustain healthy marine ecosystems and the fisheries they support. In EBFM, the overall ecosystem complexity is perceived as critical for sustainable use.

Eddy: circular movement of water formed on the side of a main current. The timescale of these mesoscale events is typically on the order of 10–30 days, whereas the spatial scale is between 10 and 100 km.

Egestion: the process by which undigested food is eliminated by an organism in the form of faeces.

End-to-end model: model of marine ecosystems with representation of the dynamic effects of both the physical environment and human activities on living organisms, ranging from the lowest trophic levels (phytoplankton and zooplankton) to the highest trophic levels (fish, birds and mammals).

ENSO: the El Niño Southern Oscillation is a global event arising from an oscillation in the surface pressure (atmospheric mass) between the southeastern tropical Pacific and the Australian-Indonesian regions. When the waters of the eastern Pacific are abnormally warm (an El Niño event), sea-level pressure drops in the eastern Pacific and rises in the west. The reduction in the pressure gradient is accompanied by a weakening of the low-latitude easterly trade winds.

Fish recruitment: the number of young-of-the-year fish entering a population in a given year and thereby becoming available to the fisheries.

Fisheries oceanography: a discipline that relates marine fish population dynamics to environmental fluctuations to understand variation in fish recruitment in order to predict failure or success in fisheries catches.

Front: oceanic regions where horizontal gradients of temperature and/or salinity are conspicuous. Fronts emerge from various physical processes, such as tides, upwelling and currents, and range from small to large spatial and temporal scales.

Member–vagrant hypothesis: a hypothesis that emphasises that membership in a marine fish population requires being in the appropriate place during the various parts of the life cycle. It implies that animals can be lost from their population, and thus become vagrants.

Mesoscale event: an event that operates at spatial scales between 10 and 100 km and at temporal scales of several days to a few months.

NAO: the North Atlantic Oscillation is the major source of interannual variability in the North Atlantic atmospheric circulation that arises from the oscillation of the subtropical high surface pressures, centred on the Azores, and from the subpolar low surface pressures, centred on Iceland. It controls the strength and direction of westerly winds and storm tracks across the North Atlantic and affects both temperature and precipitation over this area.

Regime shift: a sudden shift in structure and functioning of a marine ecosystem, affecting several living components and resulting in an alternate state.

Top-down control: regulation of ecosystem components at low trophic levels by species at higher trophic levels (i.e. control by predation).

Trophic cascade: reciprocal predator–prey interaction that produces inverse changes in abundance down the food chain. For example, increasing abundance of predators (e.g. cod) in a food chain lowers the abundance of their prey (e.g. herring), thereby releasing the next lower trophic level from predation (e.g. zooplankton).

Upwelling system: large-scale wind-driven areas where dense, cool and nutrient-rich waters are brought toward the ocean surface, replacing the warmer, usually nutrient-depleted surface waters. These systems constitute the most productive marine areas of the world.

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A balanced research strategy for the exploitation of marine resources

Fisheries management is facing unprecedented challenges. Concern regarding global change (i.e. overexploitation and climate change) and its effects on marine ecosystems ranging from coral reefs to coastal ecosystems is growing worldwide [1,2]. Ecological surprises are observed at all levels of organisation. Exploited fish species exhibit higher temporal variability in abundance than unexploited species [3]. Shifts in the diets of predators appear to be exacerbated by the lack of food due to prey overfishing [4,5]. Depletion of top predators can drastically change the functioning of marine ecosystems [6,7].

Consequently, a strong societal demand for managing marine resources from an ecosystem perspective is crystallising around the internationally advocated ecosystem-based fisheries management (EBFM; see Glossary) [8,9]. However, the challenge of integrating both abiotic changes and biological responses in the ocean appears to be substantially more complex than previously expected [10].

At the same time, methodological advances in marine ecology make it possible for the first time to study problems at the ecosystem level. Advances in modelling, such as 3D hydrodynamic high-resolution models coupled with biogeochemical and fish models, together with a vast amount of data collected from, for example, remote sensing and tagging experiments, allow us to integrate our disparate ecological knowledge into ecosystem models ([11] http://www.eur-oceans.org). However, ecosystem models easily become too complex and unfocussed to be useful. Experience shows that complex models trying to represent an ecosystem as realistically as possible, rather than representing the system with regard to a certain purpose, can be of limited use [12]. By contrast, if models focus too much on a certain level of organisation, they might fail to capture the internal structure of the ecosystems.

What we need is a research strategy that puts different types of models, ranging from statistical to dynamical and from simple to complex, in a global change context. We propose a balanced strategy that we name 'ecosystem oceanography' in reference to Hjort's seminal work on fisheries oceanography [13]. Ecosystem oceanography broadens the existing field of fisheries oceanography and relates ecosystem components and their interactions to climate change and exploitation [14,15]. It aims at developing robust approaches for predicting both short- and long-term changes.

Here we consider three levels of organisation (population, food web and ecosystem) and we discuss several ecological processes that are important for studying their dynamics. We start with reviewing the ever-challenging issue of fish recruitment to show that coupling the effects of the environment to fish population dynamics remains an important challenge. We then emphasise the usefulness of combined analyses of environmental and ecological time series in disentangling bottom-up and top-down controls in marine food webs. Finally, we show how recently developed ecosystem models can be coupled with physical oceanographic models to predict long-term ecosystem response to global change.

Populations: from small to large scales

Analysing the strongly fluctuating number of young herring and codfish in the northern Atlantic, Johan Hjort stated in 1914 that "the renewal of the (fish) stock…must depend upon highly variable natural conditions" [13]. A new scientific discipline named 'fisheries oceanography' was born. This approach established the fish population as the focal entity and identified starvation of fish larvae as a central process to be studied. Marine ecosystems were thought to be controlled by planktonic food abundance. Hjort proposed that variations in recruitment mainly stemmed from two factors: changes in the availability of planktonic food for fish larvae, and the influence of wind and current on the potential drift of fish eggs and larvae away from the area of plankton distribution.

Hjort's first hypothesis was further developed by Cushing [16] into the 'match–mismatch' hypothesis (Box 1), under which larval survival is dependent on the exact timing of plankton availability when the resources of the fish larvae in the yolk sack are depleted. The match–mismatch hypothesis has been heavily debated, but some recent examples confirm the importance of food availability and timing on larval survival [17]. In addition to Cushing's concept, Lasker [18] and Cury and Roy [19] suggested that food concentration (not only food availability at a certain time) can be another major controlling factor for fish recruitment. Thus, both the timing and the abundance of planktonic food are important for fish recruitment [20–22].

Sinclair [23] developed the second mechanism proposed by Hjort as the 'member–vagrant' hypothesis, which emphasises the importance of the retention of fish within suitable areas during their early life history. Whereas Cushing's hypothesis is predominantly temporal and trophic, that of Sinclair is primarily spatial and physical, that is, concerned with ocean hydrodynamics.

The fact that temporal and spatial processes simultaneously control recruitment of marine populations requires a balanced view on spatial and temporal aspects. Focussing on temporal processes alone will in many cases be misleading. As an example, the herring population in the North Sea is composed of multiple subpopulations which come together during the feeding season but separate during the spawning season. The survival of early herring life stages has thus to be explored at the level of subpopulations [24], and therefore the spatial component of the population has to be taken into account. By contrast, ignoring seasonal variability in plankton production, concentration or retention will also be misleading because of the match–mismatch mechanism mentioned above [25].

Bakun [25] proposed a unifying framework that integrates the match–mismatch and member–vagrant hypotheses, termed the 'fundamental triad' of production, concentration and retention. A direct implication of Bakun's synthesis for ecosystem oceanography is the importance of resolving both spatial and temporal patterns at the mesoscale, and to do so at the population level as advocated by Hjort [13] (Figure 1a). Mesoscales are important because accumulating evidence shows that the ocean is much richer in mesoscale structures, such as eddies and fronts, than anticipated. In the following, we therefore

Box 1. Potential effects of global change on fish recruitment

The match–mismatch hypothesis [16] postulates that the seasonal timing of fish spawning is essentially fixed (grey curve in Figure I), whereas that of primary production varies from year to year (white curves in Figure I) depending upon fluctuating meteorological conditions (Figure I, Before). The hypothesis can be interpreted as the result of evolution optimising the fitness of the larval fish that is dependent on the primary production (i.e. algae bloom) as a food source. As production usually starts at another time and location than when and where larval predation occurs, adult fish must use environmental cues to synchronise their spawning (and with that

the hatching of their eggs) with the peak of algae bloom. From this perspective, the effect of climate change will be to weaken the synchrony between food availability and the need for food [63], invariably leading to lower survival of the larvae. Three main effects of climate change can be envisioned: a change in the mean relative timing of prey (as seen for the Baltic Tellin *Macoma baltica* [64]) (Figure Ia), a change in the level of prey abundance [21] (Figure Ib) or a change in the amplitude of year-to-year variations in prey timing in regions where interannual variability in temperature is expected to increase [65] (Figure Ic).
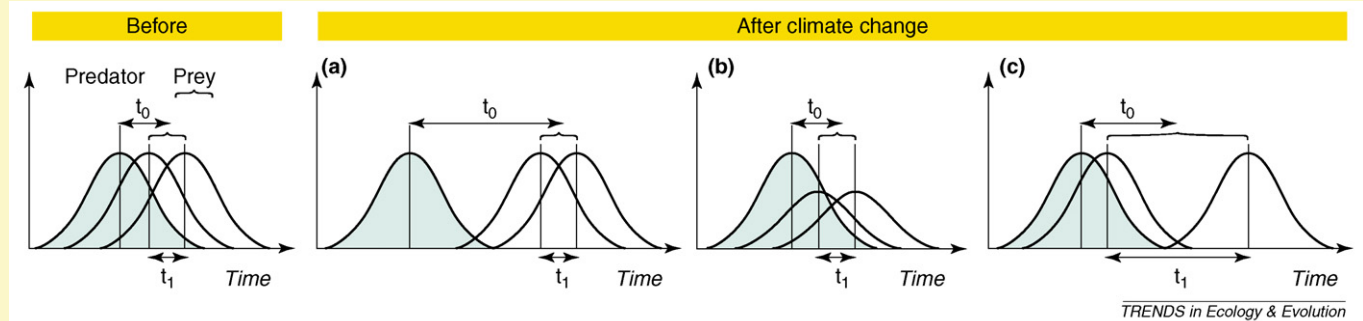
Figure I. The match–mismatch hypothesis and three possible effects of climate change. t_0 is the time lag between the predator and prey populations, that is, the degree of time mismatch; t_1 is the interannual variability in the timing of the prey population.

review the advances that have been made in studying fish recruitment at this intermediate spatial scale.

Mesoscale approaches for studying fish recruitment

The processes determining the distribution and abundance of marine populations are often matched by corresponding oceanic features which develop at the mesoscale, such as fronts related to upwelling, river plumes, eddies or strong flow at the interface between two water masses.

There are two main approaches for addressing mesoscale aspects of fish recruitment (Figure 1b). The first is based on new types of data and involves detecting and characterising mesoscale features of biotic and abiotic elements (e.g. shoals and eddies) rather than large-scale features (climate indices such as the North Atlantic Oscillation; NAO) and studying their potential impact on fish recruitment [26,27]. Mesoscale features are currently accessible from remote sensing (e.g. satellite) observations, field data and hydrodynamic simulations, and new tools required to identify, characterise and track them are constantly being developed, such as spectral and wavelet analyses [28–30].

The second approach is to resolve mesoscale interactions through explicit biophysical models that operate at the mesoscale, such as by coupling high-resolution hydrodynamic models describing ocean currents with simple models of fish eggs and larvae. Such models have already been developed with success in several cases such as haddock in the North Sea [31] and anchovy in the Bay of Biscay [32] and the Benguela current region [33] to define spawning habitats and recruitment dynamics. The challenges in using such models arise from model validation (i.e. assessing whether the models are adequately reproducing observed mesoscale features) and from the level of biological knowledge required to simulate realistic biophysical interactions at the proper scale.

If we are to converge to a consensual approach at the population level, however, we have to be aware that the current theory still neglects processes occurring at a lower level (cohort and individual) and at a higher level (ecosystem). Recruitment success is also known to be affected by density-dependent processes (in contrast to Hjort's mechanisms, which are density independent), such as competition, cannibalism, predation [34] and parental effects [35].

Relating mesoscale events to other scales and climate change

Exploring recruitment at the mesoscale is imperative for achieving the objectives of ecosystem oceanography, but this does not imply that larger and smaller scales can be ignored. Effects of processes operating at the ocean or basin scale, described by indices such as the NAO Index or the Pacific Decadal Oscillation Index, on recruitment have been discussed and synchronies between various fish populations have been depicted, for instance between Californian and Japanese sardines [36]. The details of the connections between large-scale atmospheric and oceanic processes and mesoscale activity in the ocean still need to be resolved, but several patterns are already emerging. One example is the connection between the intensity of the Californian current regime and the development of mesoscale eddies which can constitute suitable retention areas for sardine eggs in the Pacific region; that is, the greater the intensity of the Californian current, the larger the number of mesoscale eddies [36].

Thus, studying the link between recruitment and environment within the unified framework of ecosystem oceanography requires quantifying and linking processes that occur at different spatial and temporal scales. This implies three challenges. The first one is to use the mesoscale physical activity as the proper scale to relate fish
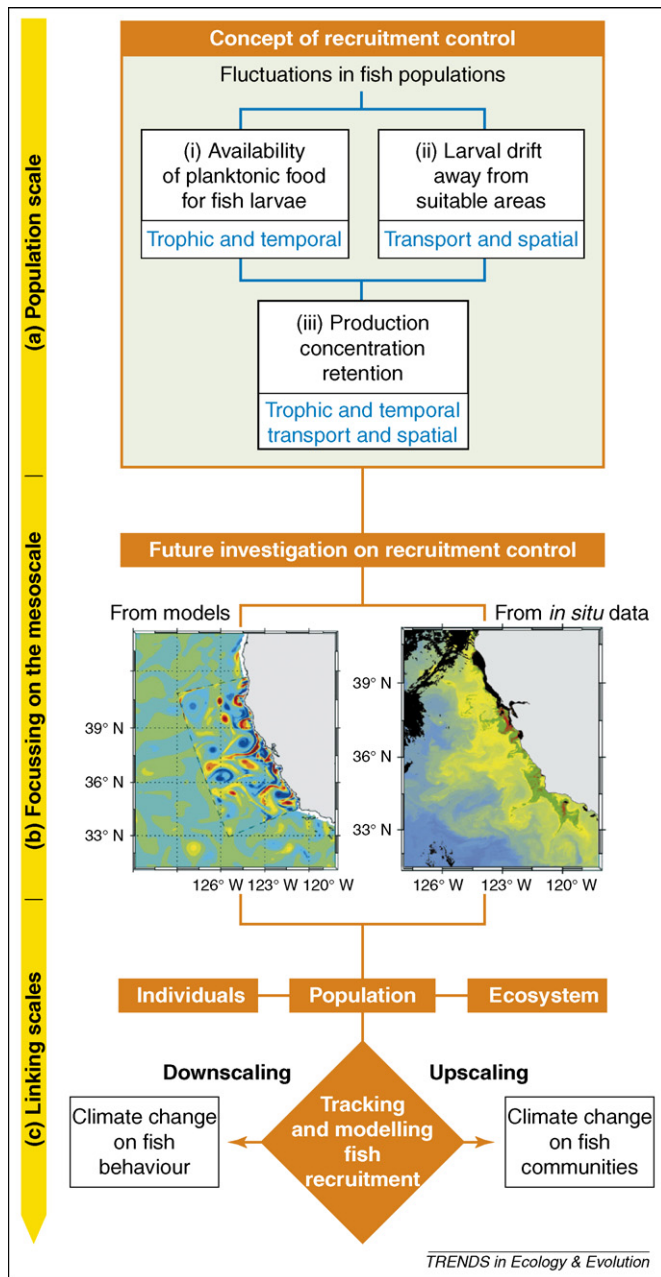
Figure 1. Schematic representation of past and present concepts together with future investigations on recruitment controls in fish populations. **(a)** Population scale: following the two main mechanisms proposed by Hjort [13], fluctuations in fish populations have been mostly explained by (i) a trophic and temporal hypothesis, known as the match–mismatch hypothesis, developed by Cushing [61], completed by Lasker [18] and Cury and Roy [19], among others and (ii) a transport and spatial hypothesis, known as the member–vagrant hypothesis, developed by Sinclair [23]. The fundamental triad of Bakun [25] has reconciled these two approaches in a unifying framework (iii). **(b)** Focussing on mesoscale: future investigations should track and model mesoscale ocean processes that affect fish recruitment, using both *in situ* information (e.g. satellite images) as well as outputs from 3D hydrodynamic models. **(c)** Linking scales: focussing on mesoscale processes should further help in building bridges to larger (e.g. basin scale indicators such as NAO, ENSO and global change indicators) and smaller environmental scales (e.g. turbulence).

recruitment to ocean productivity, and to relate fish recruitment to large-scale environmental indices such as the NAO (Figure 1c). The second challenge is to revisit the fish recruitment issue in the context of global climate change by proposing testable hypotheses, such as the match–mismatch hypothesis (Box 1). The third

challenge is to link recruitment of a given fish species to an integrated view of food web dynamics.

Food webs: integrating views on bottom-up and top-down controls

The general consensus is that controls by the environment (bottom-up, i.e. plankton production) and by predation (top-down) act on populations and communities simultaneously, and sometimes in synergy as stated by Frank *et al.* [37]. Nevertheless, studies of food web dynamics are classically conducted by considering them independently. For example, the trajectories of major resources in the North Sea were recently explained by emphasising the role of environmental forcing (bottom-up [38]), whereas another study focussed on anthropogenic forcing (top-down [39]). However, to explore the susceptibility of marine ecosystems to climate change on the one hand and exploitation on the other, we need to understand their relative impact on food web structure and dynamics [37].

Two recent studies reveal that control in marine food webs is dynamic and can switch between bottom-up and top-down, or be a combination of both. For example, major regime shifts, such as drastic changes of ecosystem functioning and structure, in the Black Sea and the eastern Scotian Shelf in the northwest Atlantic were triggered by both intense fishing (top-down control), resulting in system-wide trophic cascades involving four trophic levels (i.e. piscivore fish, planktivorous fish, zooplankton and phytoplankton), and changes in nutrient production (bottom-up control) [40,41]. In the Black Sea, the relative abundances of consumer versus resource species determined the occurrence of regime shifts that were amplified by eutrophication [42]. In heavily exploited regions of the northwest Atlantic, both primary productivity and fish species diversity at high trophic levels determine whether a trophic cascade ultimately takes place [43]. These examples show that the driving forces shaping ecosystems cannot exclusively be explained by only one of the two control paradigms.

The quantitative analysis of long-term time series can help prevent oversimplified views of how food webs might react to future changes. For instance, the Lofoten-Barents Sea, a relatively simple ecosystem compared to others [44], includes several direct and indirect controls between species and environmental factors that can be disentangled using time-series analysis (Box 2).

Ecosystems: developing integrated and focussed models

Analyses of marine system time series sometimes indicate drastic changes in species composition, such as demographic explosions of previously low-abundant populations (e.g. jellyfish [45]) or, on the contrary, the nonrecovery of collapsed populations after a ban of fishing (e.g. Canadian northern cod [46]). These regime shifts have usually been ascribed to large and irregular changes in oceanic conditions that spread through the food web [47]. Recent findings, however, suggest that overexploitation can also promote such long-term changes in marine ecosystems [7]. How can we predict such changes and understand the role of climate change and exploitation in producing them?

Box 2. From quantitative analysis of long-term time series to food web representation

The Lofoten-Barents Sea pelagic ecosystem can be simplified taking into account only the main components of the food web. There are three main prey species in the system (Figure Ia presents the geographical relationships between them): the Norwegian spring spawning herring *Clupea harengus* spawning in the southern Norwegian coast and spending its first 2–3 years of life in the Barents Sea (in red); the northeast Arctic cod *Gadus morhua* spawning along the northern Norwegian coast (in green); and the capelin *Mallotus villosus*, a semelparous fish spawning north of the Norwegian coast in May which follows the zooplankton that is thriving at the ice edge (in blue). Using time series (Figure Ib) of the species abundance (numbers in logarithm) and environmental variables (North Atlantic Oscillation index [NAO]; sea temperature [°C]) and time-series analysis techniques, it is possible to unravel controls and construct a food web diagram for the Barents Sea pelagic ecosystem (Figure Ic).

For instance, the following models describe how the capelin population is controlled by herring and cod, and how the cod is controlled by the capelin, cannibalism on young codfish by older individuals and climate variations:

- Cod + Sea temperature + (Cod/Capelin ratio) → Cod recruitment ($R^2 = 0.72$ [66])
- Cod + Capelin + NAO → Cod population growth ($R^2 = 0.82$ [67])
- Capelin + Herring + NAO + Sea temperature → Capelin population growth ($R^2 = 0.88$ [68])
- Capelin + Cod → Capelin population growth ($R^2 = 0.70$ [68])
- Herring + Sea temperature → Herring recruitment ($R^2 = 0.65$ [66])

The strengths of the trophic relationships between the main components of the food web, including cod cannibalism, are indicated using different arrow thicknesses.
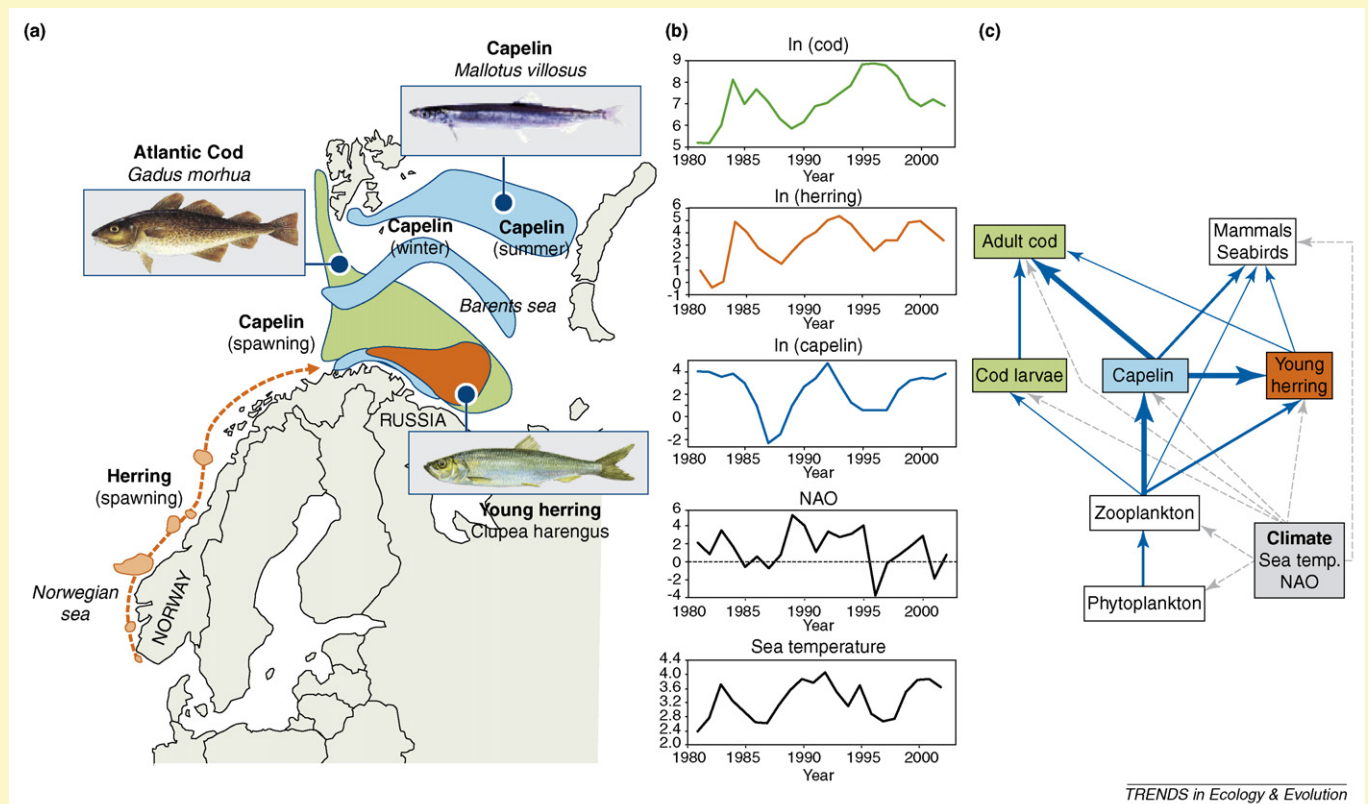

Figure I. The Lofoten-Barents Sea ecosystem description (population distribution, time series and food web).

Recent fish-centered models have improved our understanding of long-term changes occurring in ecosystems by including explicit trophic interactions and addressing trophic controls (e.g. the widely used Ecopath-Ecosim model [48], the Atlantis model [49] and the Osmose model [50]). To anticipate the many ecological surprises that arise in marine ecosystems, however, models have to progressively integrate food web dynamics with dynamic environmental forcing of marine ecosystems.

To support an ecosystem approach to fisheries management, marine ecosystem modelling needs to move toward so-called end-to-end modelling. Models focussing on only one trophic level [51] or interaction are useful but might fail to capture regime shifts at the ecosystem level. End-to-end models are also based on simplifying assumptions, but are developed to represent the entire food web and the associated abiotic environment. This requires

intergrating physical and biological processes at different scales, implementing feedback between ecosystem components and taking into account the dynamic forcing effect of climate and human impacts at multiple trophic levels [11].

In practice, end-to-end models are best achieved by coupling three classes of existing models: physical models of the abiotic environment, biogeochemical models describing nutrient and plankton dynamics, and models describing higher trophic levels (i.e. fishes, marine birds, mammals and fishery). The advantages of coupling existing models are that it can be time and cost effective and that each submodel of the food web (life stages, populations or functional groups) represents key processes at adequate spatio-temporal scales. However, coupling models also requires resolving the conceptual and technical difficulties arising from differences in the

formulation, in the structure and in the spatio-temporal resolution of the models.

Coupling trophic models

Coupling models across trophic levels requires integration across previously separate scientific disciplines that have different objectives and tools. Biogeochemical modellers traditionally focus on the dynamic forcing of the oceans and its impact on primary production and nutrient fluxes, and fisheries modellers focus on the impact of fishing on exploited fish stocks, starting from a purely single-species approach that subsequently is extended to communities. To couple biogeochemical and fisheries models into an end-to-end model, one has to focus on the main processes that link the different components of the ecosystem. The key process linking low trophic level models (LTL) to high trophic level models (HTL) is predation, which affects both the growth rate of predators and the mortality of the prey. At the individual level, modelling growth rates of predators requires formalisation of energy allocation (i.e. how

the food is used in the body of the predator for e.g. maintenance, and somatic and gonadal growth). At the population level, the functional and numerical responses of predators have to be characterised. The functional response of a predator describes the per capita consumption of prey; the numerical response describes how their population growth rate increases with prey consumption. Furthermore, it is also important to specify whether the preferences of the predator are size based or species based.

An explicit representation of predation allows for studying the propagation of direct effects of climate change (e.g. on primary production and thus prey biomass) and overfishing (e.g. removal of top predator biomass) both up and down the food web. Further processes require attention when coupling HTL and LTL models into an end-to-end model, depending on the issue that is addressed. For example, when fish excretion and egestion are explicitly represented in HTL models, these processes involve the transfer of matter down to LTL models by contributing to the ammonium and nitrogen pools [52]. Similarly, the loss
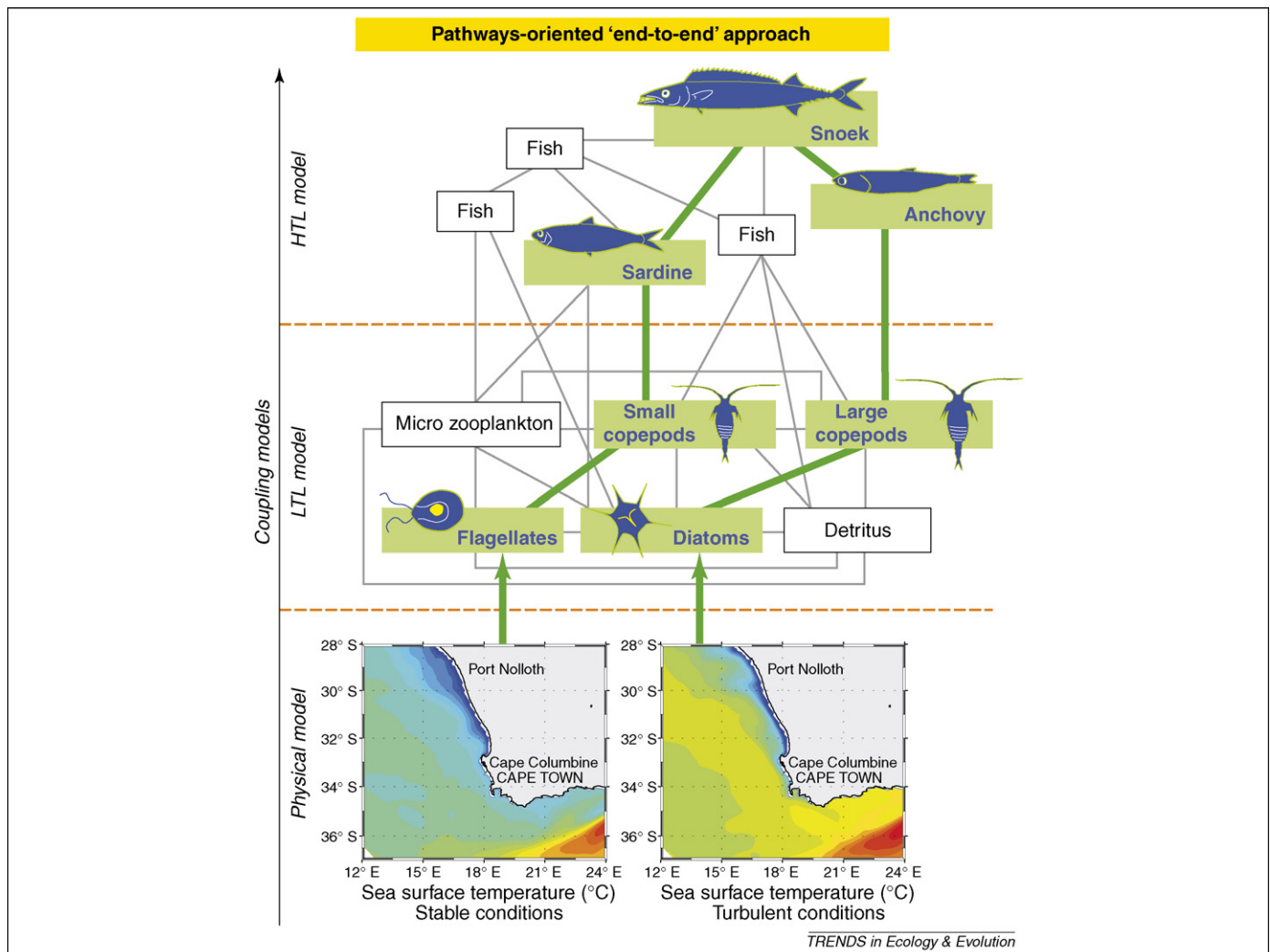
Figure 2. End-to-end models can be built by coupling three types of models: high trophic level (HTL) models, low trophic level (LTL) models and physical models (output of physical model from [62]). The boxes represent key species or groups of species, the lines represent the trophic interactions (pathways) and the arrows represent the forcing of hydrodynamic models on the LTL model. The pathways-oriented approach acknowledges the role of biodiversity in the emergence of alternative trophic pathways. Depending on the climate and fishing forcings, the dominance of trophic pathways alternates, for example, 'sardine' or 'anchovy' regimes can alternate in upwelling ecosystems as illustrated here. By carefully selecting the species to represent using empirical and retrospective analyses, this pathways-oriented approach could help predict drastic ecosystem responses to changes in climate and fishing.

Box 3. Validating ecosystem models using the pattern-oriented modelling approach

The principle of pattern-oriented modelling (POM) [12,60,69] is to use multiple patterns of different scales and hierarchical levels, as observed in real systems, at two steps of the modelling process, that is, during model building and validation (Figure I):

Model building

Figure Ia: end-to-end models easily include too many choices in how to represent coupling processes, species or functional groups. To narrow down this structural uncertainty, in POM field data are scanned for patterns, that is, regularities of any kind that subsequently are interpreted as indicators of the internal organisation of the ecosystem. If, for example, we see major patterns in the body-size structure of the populations, then size-dependent processes, such as trophic interactions, are likely to be key processes. Therefore, body size should explicitly be represented in the model. Observed patterns thus provide hints as to what entities, variables and processes a model should include.

Model validation

Figure Ib: a single pattern, such as a certain size structure, might be relatively easy to reproduce with all kinds of alternative models. However, simultaneously reproducing an entire set of patterns, observed at different scales and hierarchical levels, is much more demanding and requires that the model is 'structurally realistic,' that is, captures the system's key elements and processes of a system. For example, a model that simultaneously reproduces multiple patterns at the individual, population and community level is more likely to be structurally realistic than a model that reproduces only one of these patterns. A strong indicator of structural realism is if the model can be validated by patterns that are predicted by the model but were not used, or even known, while developing the model.

The patterns chosen for model development and validation could be spatially or temporally structured and originate from different data sources (e.g. catch or survey data). At the community level, a set of indicators based on size (e.g. slope of size spectrum), on biodiversity (e.g. species dominance) and on trophic interactions (e.g. trophic level) can also be used, as they are estimated routinely by scientific surveys for an ecosystem approach to fisheries and underlie diverse ecological processes.
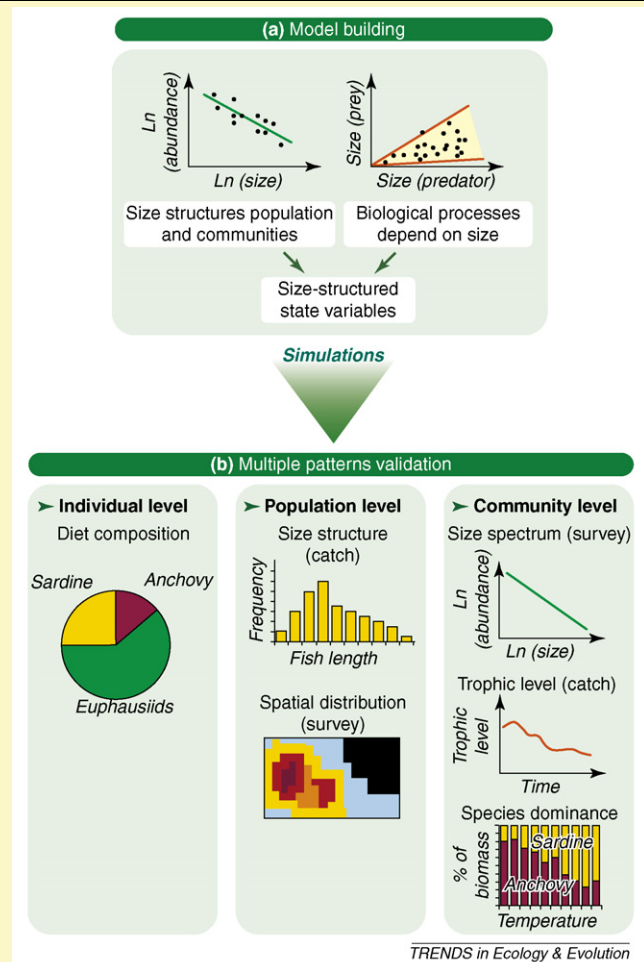

Figure I. Illustration of the pattern-oriented modelling approach applied to a marine ecosystem model.

of biomass from HTL models as a result of natural mortality of fish can be considered as a coupling process, as it will contribute to the detritus and bacterial pool of LTL models. Climate change can have a direct effect on the habitat of species (i.e. habitat loss, fragmentation or shift) causing potential changes in fish spatial distribution; such potential effects can be represented in coupled biophysical models [53].

Selecting key species and alternative pathways

In addition to selecting the processes that couple LTL and HTL models, building end-to-end models also involves choosing the species or functional groups to be represented, which can be challenging. The structure of food web models is classically guided by the consideration of the most abundant species and the dominant trophic interactions at a given time and location. Because these features are highly variable in marine ecosystems, however, this method might produce only a snapshot of the ecosystem that does not necessarily reflect its dynamic functioning. In particular, dominance patterns can be completely reversed when regime shifts occur.

In the context of food webs, regime shifts can be seen as the emergence of dominant food chains to the detriment of

alternative competitive food chains. Thus, to predict possible ecosystem impacts of climate change and overexploitation, the structure of end-to-end models should reflect the existence of major alternative food chains by explicitly representing the corresponding species or functional groups. Alternative food chains can be characterised by specific properties. For example, there is a growing consensus that the energy content of food chains is crucial for understanding how marine pelagic food webs are reorganised [54]. In the North Sea, the replacement of a high-energy food chain by a low-energy one forced the most abundant bird population (common murre *Uria aalge*) to switch its prey from sandeels to sprat, leading to a major breeding failure in 2004 [55]. Similarly, Parsons and Lalli [56] identified large fish as being part of high-energy food chains, so that overexploitation by targeting large fish would favour the emergence of the alternative low-energy food chain where flagellates, jellyfish and small fish dominate. Rooney *et al.* [57] also distinguish fast and slow pathways within the food web, that is, chains with different turnover rates characterised by their production to biomass ratios, which can be important for the stability of the food web. Much progress in understanding and predicting long-term ecosystem responses to fishing and climate

change can be achieved if a pathways-oriented approach guides the structure of future end-to-end models, allowing for the emergence of alternative energetic pathways (Figure 2).

Coping with complexity

Coupling models and including alternative food chains could easily lead to models that are too complex to be properly analysed and parameterised. A first approach to assess the relevance of end-to-end models is to develop null models that do not assume any functional relationship and make minimal assumptions on the processes at stake [58]. Comparing null models with models of increasing complexity can provide a rigorous framework for identifying those key elements and processes of ecosystems that are needed to explain observed patterns [59].

Another strategy for limiting the complexity of end-to-end models is to use the general strategy of pattern-oriented modelling (POM [60]). With POM, data analysis serves as a basis for building models, and eventually our confidence in the model is enhanced by validating the model output with a multiplicity of patterns observed at various levels in the real ecosystem (Box 3).

Toward ecosystem oceanography

Fisheries oceanography traditionally divided the controls of fish stocks into two paradigms, bottom-up (resource-driven) and top-down (consumer-driven) forces, and focussed mostly on single species. By contrast, ecosystem oceanography is the study of interactions among ecosystem components and drivers at the level of the population, the food web and the ecosystem. Ecosystem oceanography does not contrast the two main control paradigms but aims at understanding their contribution and interactions at each level of organisation by confronting model results with the empirical reality expressed in the data.

In terrestrial and aquatic ecology, there is an urgent need both to make complex ecosystem models efficient for solving pending ecological issues and to find ways to rejuvenate existing 'simple' models in the context of global change. The ecosystem remains an uncomfortably large-scale unit for ecological studies. However, it is now viewed as a structural organisation that can be integrated into fisheries management. With global change, new environmental and ecological surprises are challenging our present ecological perception. To acknowledge the complexity of marine ecosystems in a comprehensive manner, the analysis of a limited number of controlling processes at the proper level of organisation will greatly improve the way we understand ecosystem functioning. Consequently, it will provide new avenues for contributing to the ecosystem-based fisheries management. Through the balanced modelling perspective attempted by ecosystem oceanography, we might be able to provide innovative answers to old riddles, but also to new problems that fisheries are going to face in our changing world.

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