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Inter-regional comparison of climate effects on marine fish populations facilitated through classification of mechanisms

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ABSTRACT

Variations in climate strongly affect the structure and function of marine ecosystems, but a number of different mechanisms are at play and their relative importance varies between regions and with time. There are obvious semi-permanent regional differences in how marine populations respond to climate, but there may also be long-term trends either in climate itself or in the response pattern. In some cases single strong climate events may shift an ecosystem from one state to another (e.g., El Niño). To facilitate comparison between different large marine ecosystems we here give an overview of some of the manners in which one can classify how marine fish populations are affected by climate. Responses to climate fluctuations may be bottom-up, top-down or middle-out, immediate or temporally delayed, direct or via an intermediate population of predators, prey or competitors. Climate may invoke a linear or non-linear effect at the population or community level. Ecological effects of the NAO have been classified according to the four major classes: direct effects, indirect effects, integrated effects and translations, which also may be applied to other climate patterns and regions. By using classification schemes a more precise description of the particular properties of the various ecosystems may be possible. This approach enhances the possibility to compare between regions that may differ not only with regards to the relative importance of different climate factors for ecology, but also through dissimilarities in scientific tradition and terminology.

Keywords: Climate, fish, population dynamics, mechanism, comparative approach

Marine fish populations fluctuate at a multitude of time-scales, due to variations in the dynamics internal to the population, interactions with predator, prey and competitive species and variable impacts of climate (Lehodey et al., 2006). The multitude of forcing and pathways through which climate may impact marine populations (e.g., Ottersen al., 2004a) can often make it difficult to establish unequivocal connections between climate and the ecological response. However, many climate effects are indisputable and it is important to understand the main patterns in how physics affects ecology as well as the actual mechanisms and processes involved.

When linking climate to ecology, climatic features are often represented by specific indices. Climate indices aggregate complex temporal and spatial patterns into simple measures. Such indexes might properly be seen as ‘weather packages’. Still, it is important to realize that climate operates mechanistically on ecological systems through local (ocean) weather variations. Stenseth et al. (2003) point to the relationships between climate indices, representing large scale climate patterns, and local weather not always being straight forward and underline the following complications:

(i) *Spatial variation*. Local weather (or oceanographic) response to a given climate situation typically depends on the geographical location.

(ii) *Seasonality*. In the extratropics most months or seasons are not dominated by any particular climate pattern.

(iii) *Non-stationarity*. Truly stationary periodic behaviour in the atmosphere is unusual. The relationship between climate and local weather/oceanography, and consequently also between climate and ecological responses, may vary over time.

(iv) Nonlinearity. Often one assumes that the ecological response to climate is linear or perhaps log-linear, but nonlinear (and even non-monotonic) relationships may exist both between large-scale climate and local weather/oceanography, as well as between local abiotic conditions and ecological processes.

The North Atlantic Oscillation (NAO) is one such climate pattern. It quantifies large-scale atmospheric fluctuations between the subtropical and sub-polar regions of the North Atlantic, determining the speed and direction of the prevailing westerly winds. It is the dominant mode of atmospheric behaviour in the North Atlantic throughout the year, although it is most pronounced during winter, the season of strongest pressure gradients and interannual variability. A positive NAO phase is associated with strong wind circulation in the North Atlantic, high atmospheric and sea temperatures in western Europe and low temperatures on the east coast of Canada (Fig. 1, Fig. 2). Thus there are pronounced spatial differences in the effects of the NAO on local weather and oceanography, which again will affect the ecology of, e.g., cod. Furthermore, the atmospheric pattern represented by the NAO is not stationary in time. During 1950-1975 the NAO was associated with a meridional pattern with the northern, low pressure, centre of action located to the west of Iceland. In the latter 25 years, the "Icelandic low" is, on average, no longer close to Iceland, but near the opening to the Barents Sea, and the pattern is much more zonal (Fig. 3).

Ecological effects of the NAO have been classified according to the four major classes: *direct effects*, *indirect effects*, *integrated effects* and *translations* (Ottersen et al., 2001; Pershing et al., 2004; Ottersen et al., 2004a). A similar categorization may be made for other climate patterns (C). *Direct effects* of C are mechanisms that involve a direct ecological response to one of the environmental phenomena synchronized with C. The effect of C on metabolic rates via temperature is of this type (see, e.g., Fig. 4). *Indirect effects* of C are non-trivial mechanisms that either involve several physical or biological intermediary steps between C and the ecological trait and/or have no direct impact on the biology of the population. An example is the alteration in the competition balance between the two copepod species *Calanus finmarchicus* and *Calanus helgolandicus* in the North Sea by NAO-induced changes in sea surface temperature and phytoplankton production (Fromentin and Planque, 1996). *Integrated effects* of C involve simple ecological responses that can occur during and after the year of an extreme C. This is the case when a population has to be continually affected by particular environmental conditions before the ecological change can be detected (biological inertia) or when the environmental phenomenon affecting the population is itself modulated over a number of years (physical inertia). An example may be the gradual, over several years, exchange of water masses in an area. *Translations* involve movements of organisms from one place to another such as the advection of *Calanus finmarchicus* from the continental slope on to the shelf (Pershing et al., 2004). These alterations are based entirely on the physical changes produced by climate variability.

Ecosystems and populations are typically categorised as being controlled by top-down or bottom-up mechanisms, implying that predation and prey resources respectively are important in regulating population growth rate (Cury et al., 2000). Bottom-up systems may be driven by climate fluctuations working their way through the food web. On a global scale the biomasses of fish are greatest in regions with high primary production, typically sub-Arctic seas and upwelling areas of continental shelves (Hunt and McKinnell, 2006). Thus, the main patterns of distribution are controlled bottom-up, not by absence of predators (who often are abundant in the same regions). However, on a more regional scale predation may be a major controlling mechanism.

Closely linked to the bottom-up and top-down concepts is the principle of trophic cascading. Trophic cascades result in inverse patterns in abundance or biomass across more than one trophic link in a food web. For a three-level food chain, abundant top predators result in lower abundances of mid-level consumers and higher abundance of basal producers. Removing a top predator should, in this case, result in a greater abundance of mid-level consumers and fewer producers (Pace et al., 1999).

Some pelagic ecosystems contain few but abundant species of small pelagic fishes. These fishes can have key roles in the ecosystem, making a substantial impact on the energy flow through the mid-trophic levels. The planktivorous fishes perform what is referred to as wasp-waist (or middle-out) control, both having a top-down control of their zooplankton prey as well as providing bottom-up control on the their piscivorous predators (Rice, 1995; Cury et al., 2000; Hunt and McKinnell, 2006). The “wasp-waist” dual role of small planktivorous fishes has mainly been explored in coastal highly productive upwelling areas such as the Benguela and Humboldt ecosystems (Cury et al., 2000). However, capelin (*Mallotus villosus*) occupies a similar role in several sub-Arctic ecosystems and can have a major impact on its zooplankton resources (Hassel et al.,

1991) as well as controlling the growth of piscivores such as cod (Rose and O'Driscoll, 2002; Yaragina and Marshall, 2000).

A population may react immediately to a climate signal or have a temporally delayed (lagged) response. The atmosphere responds quickly to external forcing, but the response also dissipates quickly. On the other hand, the ocean responds slowly to external forcing but the response persists: it has a long “memory”. As a parallel to these physical properties, it appears that ecosystem responses to bottom-up forcing include both quick and short term responses at low trophic levels and slower and more persistent responses at high trophic levels. Thus ecosystems may exhibit both short and long term memories, and long memory or lagged responses can be utilized for predictive purposes (Ottersen et al. in press).

Predators may typically be effected by both *direct* (on physiology) and *indirect* (through prey) effects of climate (Fig. 4). The classification of responses to climate signals as either direct or indirect is meaningful also at the community level (Lekve and Stenseth, 2004). Changes in temperature that influence, e.g., growth, may lead to a *direct* response in fish species in the community, with the abundances of individual species changing in a predictable manner according to each species’ optimum for growth and reproduction. On the other hand, climate shifts may lead to, for example, variability in oceanic circulation patterns inducing changes in prey abundance and thus affecting fish communities *indirectly* (Lekve and Stenseth, 2004).

Most studies on links between climate and marine ecology—by assumption—only consider *linear* relations, while challenges related to *nonlinearity* (i.e. that episodic events may be more important than mean conditions), are neglected. While the relation between climate and ecology indeed may be linear, non-linear responses may be introduced in several ways (Fig. 5). The relationship between large-scale and local climatic variables may change over time (i.e. non-stationarity, e.g. Fig. 3), and hence limit the time period for which effects on ecosystems can be predicted from known relationship with climate patterns.

The concept of linearity also makes sense at the community level. It is then to be understood as linear among species, that is, most species are affected in a similar fashion, without changes in interaction effects between them. Even if responses at the species level are linear, the aggregated linear responses of a community may be highly non-linear. For example, each fish species in a community may change its range of latitudinal distribution in a linear manner. If the tolerance limits of the species are wide, the consequences of climate change need not be very dramatic. However, if changes in climate render the environment uninhabitable for key species in the community, large (non-linear) community effects may be observed leading to regime shifts.

The Norwegian pioneer within fisheries biology Johan Hjort realized almost a century ago that most fish populations consist of several year classes, and their abundance was by and large determined early in life (Hjort 1914). Differences in the sizes of year classes were further considered responsible for most variations in abundance of fish populations. Climate may affect the critical early development of entire cohorts and thus give rise to delayed effects. Good climate conditions during reproduction and early life may produce larger cohorts with larger individuals, which in turn may survive at a higher rate, reach maturity earlier, and reproduce at a higher rate during their entire life-span (Fig. 6).

The match-mismatch hypothesis, coined by David Cushing (Cushing 1982), seeks to explain the variation in recruitment at higher trophic levels in the food chain to its phenology in relation to the phenology of species at lower levels. The hypothesis states that if the most energy expensive part of the breeding phenology of the predator) matches the peak availability of the prey), recruitment will be high: the requirement of the predator *matches* the availability of resources provided by the prey species. If there is a *mismatch* between food requirement and food availability, effective recruitment will be low. Recent work has expanded the match-mismatch hypothesis to also include overall food abundance and availability (Durant et al. 2007; Fig. 7).

There is no doubt that interannual and interdecadal variations in atmosphere-ocean climate strongly affect the structure and function of marine ecosystems (McGowan et al., 1998). However, a number of different mechanisms are at play and their relative importance varies between regions and with time. There are obvious semi-permanent regional differences in how marine populations respond to climate, but there may also be long-term trends either in climate itself or in the response pattern. Furthermore, in some cases single strong climate events may shift an ecosystem from one state to another (Fig. 5).

Here we have given an overview of some of the manners in which marine fish populations are affected by climate. The examples highlight both the strengths (regarding the existence of clear patterns) and the limitations (regarding the uncertainty of underlying mechanisms) of trying to explain ecological effects through climate variations. However, we do believe that using classification schemes, as those described and applied above, facilitates comparison between different regions.

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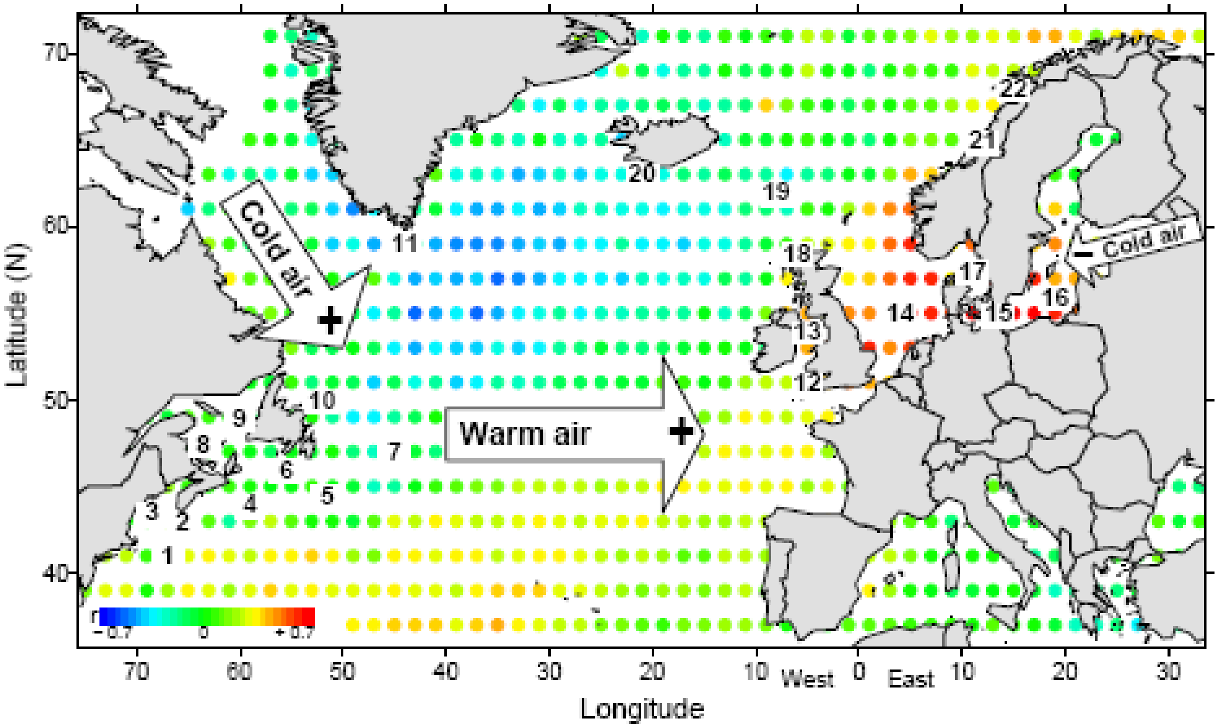


Figure 1. Spawning locations of cod stocks and a schematic diagram of the NAO. During a positive NAO phase, westerly winds increase in strength (+), while easterly winds decrease (–). A negative NAO phase has the opposite effect. The coloured dots indicate Pearson’s coefficients of correlation between the NAO index and sea surface temperatures January to June 1946–2004 on a 2° × 2° grid. From Stige et al. (2006).

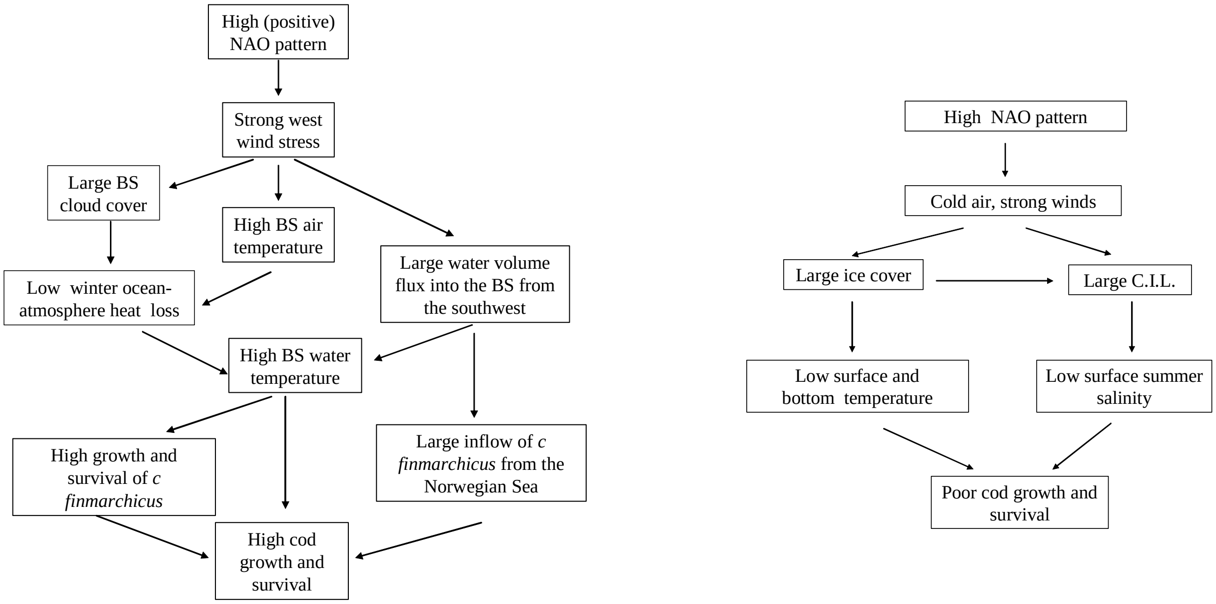


Figure 2. Mechanisms connecting the NAO to cod recruitment for (left panel) The Barents Sea and (right panel) Canadian Northern cod. Modified from Ottersen et al. (2004b).

Non-stationarity: eastward shift in the NAO

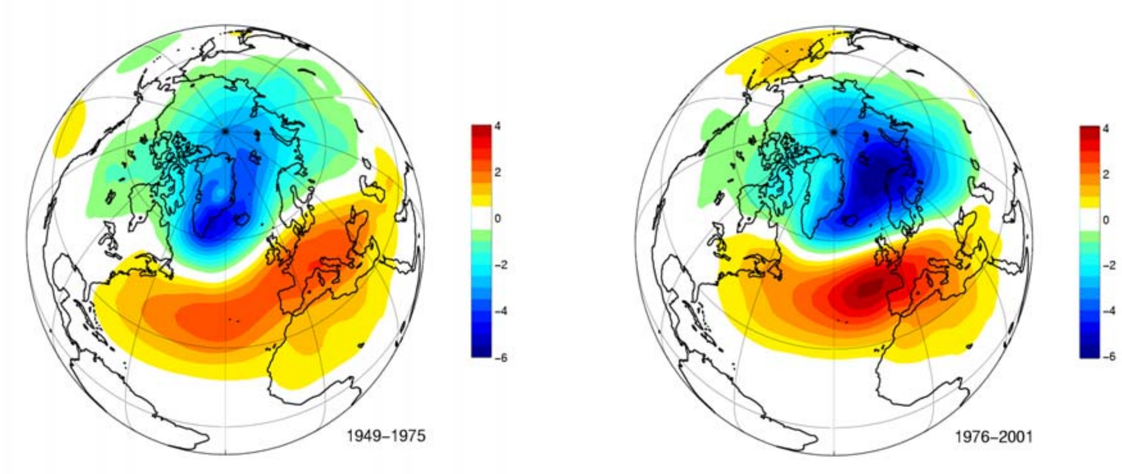
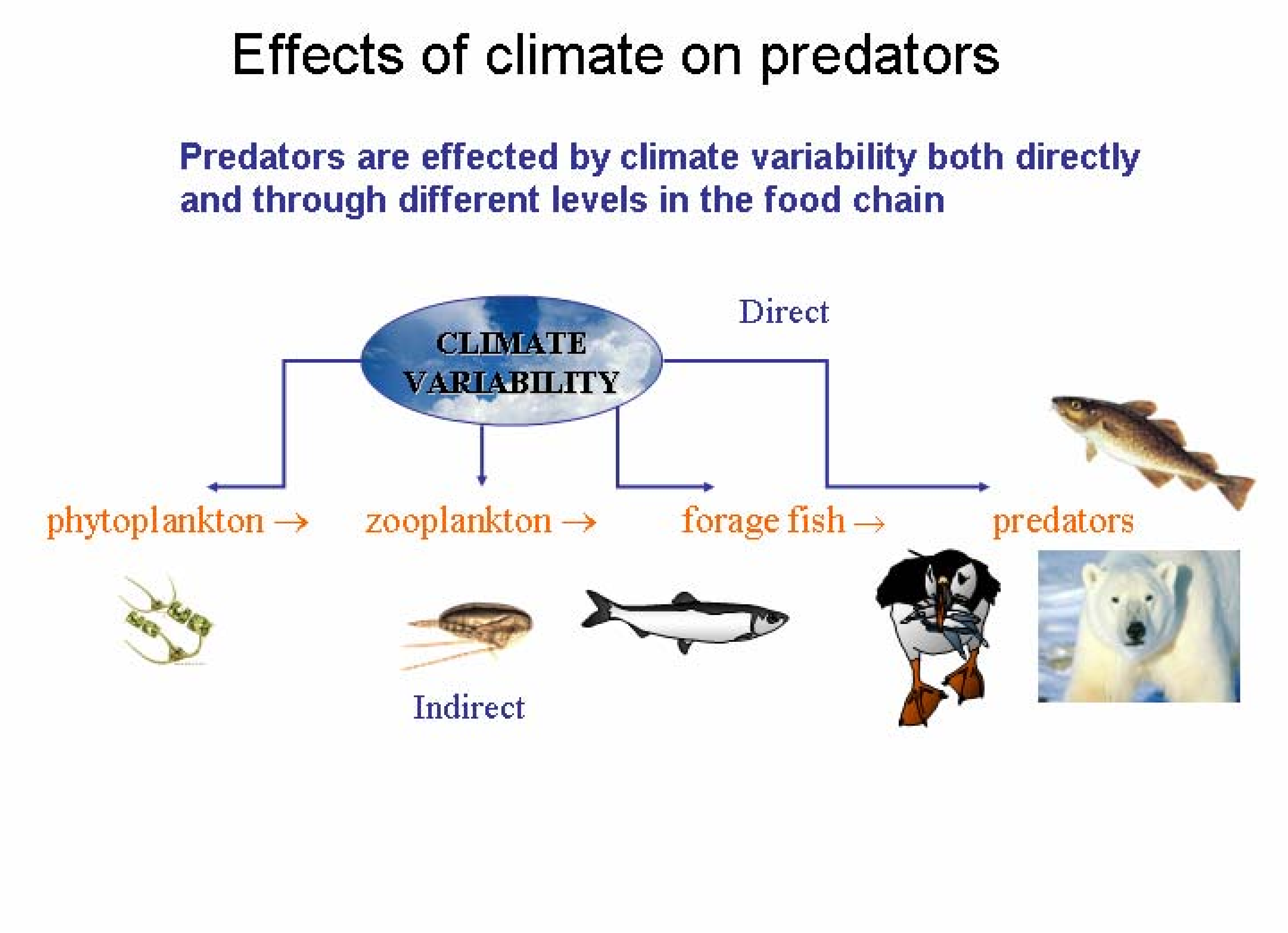


Figure 3. Centres of atmospheric action in the north Atlantic. During 1950-1975 a meridional pattern with the northern centre of action situated to the west of Iceland prevailed (left panel). In the latter 25 years, the northern centre of action is near the Barents Sea Opening, and the pattern is much more zonal (right panel). Modified from Furevik and Nilsen (2005).



Effects of climate on predators

Predators are effected by climate variability both directly and through different levels in the food chain

Figure 4. Climate may affect predators through many different pathways. J. Durant, CEES (pers. com).

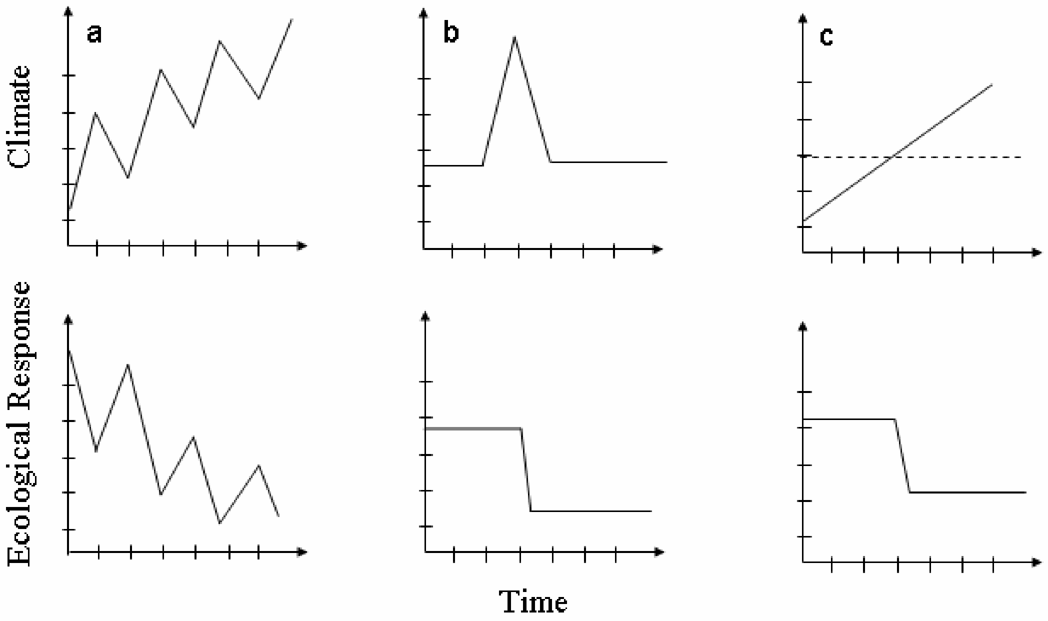


Figure 5. Possible relations between climate signal and ecological response: a) Linear climate signal and linear ecological response. b) Single climate event causes shift in ecological state or regime. c) Linear climate signal that causes shift in ecological state or regime when climate threshold value is passed. From Ottersen et al. (2004a).

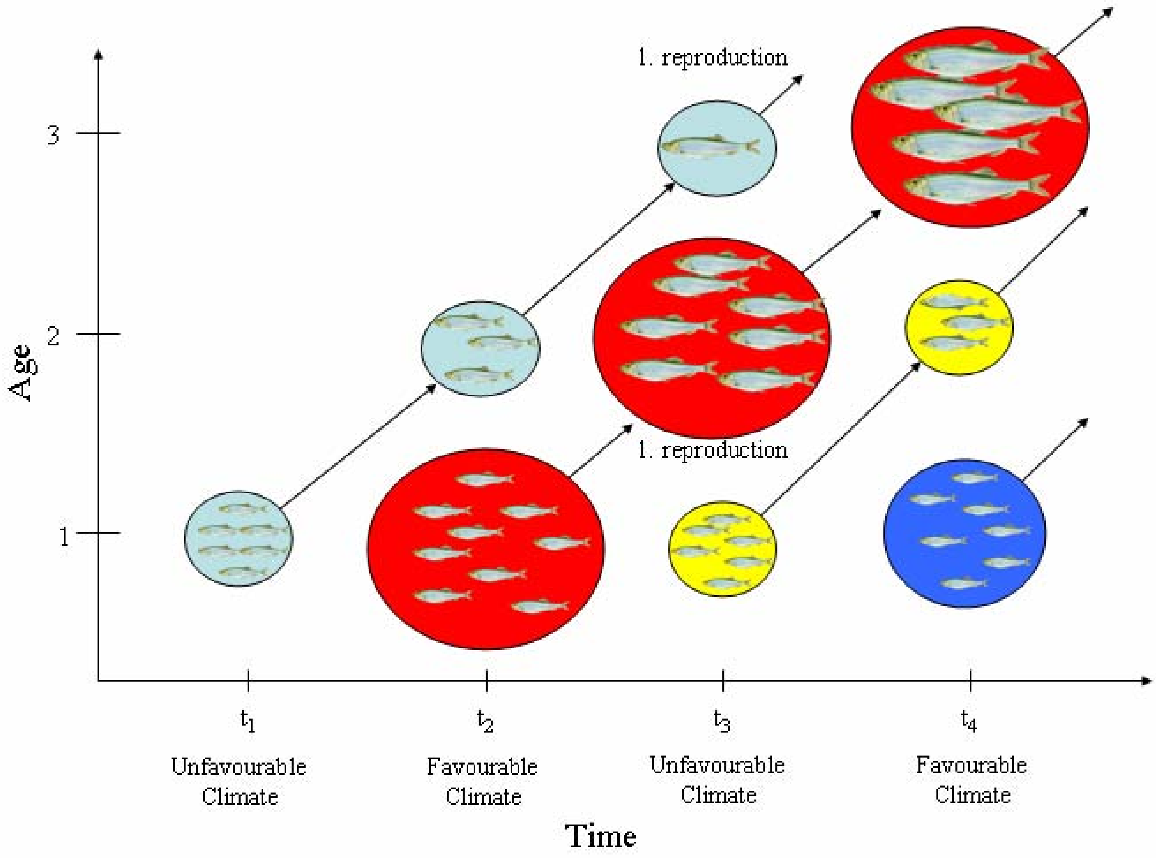


Figure 6. Climate effects during the critical early development may propagate through the entire life span of a cohort. A favourable climate during early life may produce larger cohorts with larger individuals and consequently higher survival rates. Modified from Stenseth et al. (2003).

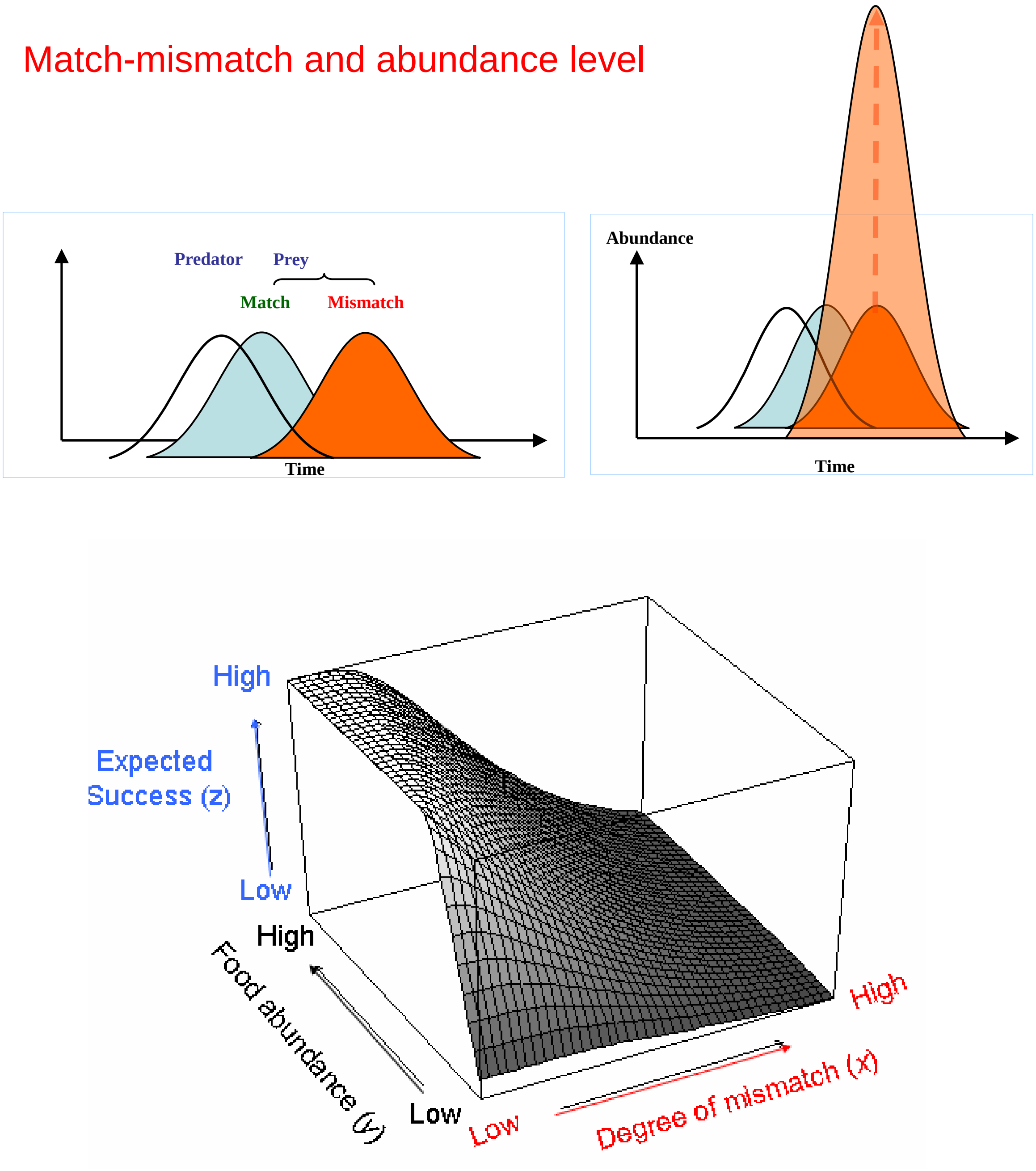


Figure 7. Match-mismatch and the role of abundance. Upper left panel) An increase of the time-lag between the predator and prey populations leads to a low match: a small or non-existent overlap. Upper right) At the same time, a change of the abundance level (here increase) can disrupt or amplify the phenomenon described by the match-mismatch hypothesis. Lower) Effect on the reproductive success (overlap) of degree of mismatch and relative abundance of food for the higher trophic level. Modified from Durant et al. (2007).