

## PART I

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# Background to climate variation and its effects on marine ecology

This part of the book summarizes the climate background together with the more conceptual framework for the climate–ecology link—a general introduction regarding responses of marine ecosystems to climate fluctuations, describing climate variability over the North Atlantic and introducing us to the modelling of marine ecosystems. In this part, we also provide a chapter summarising the modelling of climate fluctuations and their effects on large-scale ecological processes. One main objective of this part is to give a background for applications throughout the various chapters to come.

We, as book-editors, outline in Chapter 1 the main currents and hydrography of the North Atlantic including a brief account of the Atlantic as a whole and how it is linked to other oceans. A short summarizing account of some of the main circulation patterns in the world's oceans and the role of large-scale climate variability is also included. This is followed by an overview of oceanographic processes that affect marine life in the North Atlantic. Much of the chapter is, through examples, devoted to broadening the understanding of how diverse the responses of ecology are to atmospheric and ocean climate variability. As part of this introductory chapter, we also provide a summary account of how climate may affect ecological processes—linearly versus non-linearly, direct versus delayed, etc. (See also discussion in Chapter 10.) That chapter is closed by a synoptic account of how climate effects on ecological processes and patterns may be studied through methods within the field of time series analyses—methods discussed in several subsequent chapters (e.g. 6, 15, and 16).

The patterns and processes involved in climate variability—the topic of Chapter 2—are not easy to

summarize: the issue is on the one side broad, on the other side rather complex making a full in-depth description difficult within limited space. Here, we try to strike a balance between breadth of coverage and depth of detail. To accomplish this some issues had to be left out to allow for coverage of others. Thus, Hurrell and Dickson focus Chapter 2 on a thorough presentation of the North Atlantic Oscillation (NAO), a north–south alternation in atmospheric mass between the subtropical atmospheric high-pressure centre over the Azores and the atmospheric sub-polar low-pressure centre over Iceland. Special attention is paid to the forcing of the North Atlantic Ocean by the NAO, both directly at the atmosphere–ocean interface, as well as gradually more indirect effects towards intermediate and abyssal ocean depths (several authors will, in later parts, cover responses of various parts of North Atlantic ecosystems to the NAO, in particular Chapter 5 dealing with effects on zooplankton and Chapter 13 with a freshwater point of view). Hurrell and Dickson also provide important background information relating to the mean state and variability of both the ocean and atmosphere.

A chapter on modelling the marine ecosystem and how it is affected by climate variability closes this Part. In Chapter 3, Werner and co-workers provide an outline of some of the models developed to increase the understanding of how marine ecosystems “work”. The chapter deals both with lower trophic levels, with a focus on carbon fluxes, and higher levels, with a focus on pelagic fish (fluxes of carbon and other key elements is a main topic in Chapter 14, which takes a limnological point of view; population dynamics of fish will be covered in Chapter 6, Community ecology in Chapter 10

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and in Chapter 11 a population dynamics model including environmental effects for large pelagics, Pacific tuna, is described). Overviews of existing physical–biological models and biological transport models are given with classification by geographical region, dimension, spatial and temporal scale, and other criteria. Moreover, paradigms explaining patterns, abundance, and variability in fish populations are described (in Chapter 12 complexity in fisheries dynamics and climate interactions is studied). Chapter 3 also covers the topic of data assimilation, the integration of models

with data to improve the estimation of a system's state. The data assimilation system consists of three elements: a set of observations (i.e. a model linking data to the model), a dynamical model, and a data assimilation scheme. While data assimilation techniques have been used actively for some time in connection with purely physical numerical models, applications in North Atlantic marine ecosystem models are still rare. Looking ahead, as assimilation procedures progress, Werner and co-workers anticipate the greatest limitation to be scarcity of data.

## CHAPTER 1

# Climatic fluctuations and marine systems: a general introduction to the ecological effects

Geir Ottersen, Nils Chr. Stenseth, and James W. Hurrell

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Climate profoundly influences a variety of ecological processes and, consequently temporal and spatial patterns of population and species abundance. Responses to climate fluctuations are reflected in the productivity of marine ecosystems from phytoplankton to the dynamics of fish populations (Cushing 1982). These effects operate through variations in local weather and climate phenomena, such as temperature, wind, and residual currents as well as interactions among these. In the extra-tropics, local variations in weather are often coupled over large geographic areas through the transient behaviour of atmospheric planetary-scale waves. These large-scale variations drive temporally and spatially averaged exchanges of heat, momentum, and water vapour (Namias and Cayan 1981), which ultimately determines growth, recruitment, and migration patterns.

There is a tendency in all of ecology to believe that measurement of one or a few environmental variables (often those most easily measured) can serve to characterize all of environment. One way to, at least partially, take care of this is to include indices on large-scale climate patterns instead of focusing entirely on a few local weather descriptors such as temperature and wind. By applying the latter approach, an important dimension is missed; namely, the holistic nature of the climate system. Large-scale patterns of climate variability can be seen as a composed function involving a variety of climatic parameters over time and space. Indeed, they may be said to represent 'a package of weather' (see Stenseth *et al.* 2003).

To set the scene for what is to come, we will in this introductory chapter, first provide a brief account of the Atlantic as a whole and how it is linked to other oceans, before we focus on the main currents and hydrography of the North Atlantic. This is followed by a brief summarizing account of some of the main circulation patterns in the worlds oceans and the role of large-scale climate variability. We continue by providing an overview of oceanographic processes that are believed to be of particular importance to marine ecology. Finally, we present examples on the basis of which we provide an account of how diverse the responses of ecology are to atmospheric and ocean climate variability. Throughout we link our discussion to the chapters ahead.

### 1.1 The North Atlantic

The Atlantic is, after the Pacific, the world's second largest ocean. Several topographic features distinguish the Atlantic from other oceans such as the Pacific and Indian Oceans. First of all, the Atlantic Ocean extends both into the Arctic and Antarctic, giving it a total meridional extent (when including the Atlantic part of the southern ocean) of over 21,000 km from the Bering Strait through the Arctic mediterranean Sea to the Antarctic continent. In comparison, the largest zonal distance, between the Gulf of Mexico and the coast of northwest Africa, spans only a little more than 8300 km (Tomczak and Godfrey 1994).

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Second, the Atlantic has the largest number of adjacent seas, including mediterranean seas influencing the characteristics of its waters. This is particularly true for the Arctic Mediterranean Sea, which plays a crucial role in the formation of Deep Water not only for the Atlantic but for all the oceans in the world. The remaining adjacent seas can be divided on geographical arguments into four groups. The first group contains the waters connected to the Atlantic Ocean proper through the Labrador Sea and consists of the Davis Strait, Baffin Bay, the northwest Passage, and Hudson Bay. The second group is located between Europe, Africa, and Asia and contains the Eurafrian Mediterranean Sea (which includes the Black Sea). The third group is found near the junction of North and South America and contains the American Mediterranean Sea with its subdivisions the Caribbean Sea and the Gulf of Mexico. The shallow European seas make up the fourth and last group, which contains the Irish and North Seas and the Baltic Sea with its approaches.

Third and finally, the Atlantic Ocean is divided rather equally into a series of eastern and western basins by the Mid-Atlantic ridge, which in many parts rises to less than 1000 m depth, reaches the 2000-m depth contour nearly everywhere, and consequently has a strong impact on the circulation of the deeper layers (Tomczak and Godfrey 1994).

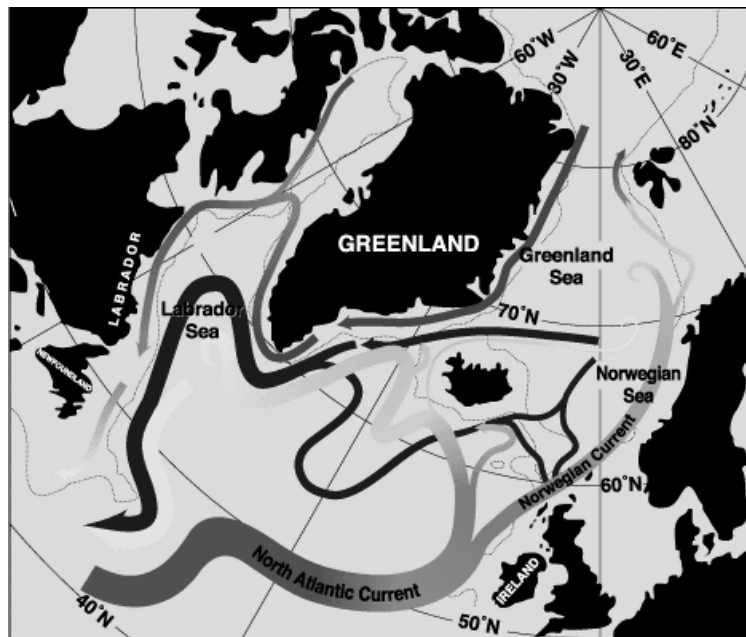
When all adjacent seas are included, the Atlantic covers an area of  $107 \times 10^6$  km<sup>2</sup>. Without the Arctic Mediterranean and the Atlantic part of the southern ocean, its size amounts to  $74 \times 10^6$  km<sup>2</sup>. Although its abyssal basins are deeper than 5000 m and most extend beyond 6000 m, the average depth of the Atlantic Ocean is, due to the fact that shelf seas, including its adjacent and mediterranean seas, account for over 13% of the surface area, 3300 m, less than the mean depth of both the Pacific and Indian Oceans (Tomczak and Godfrey 1994).

The upper water circulation of the Atlantic Ocean consists in its gross features of two great anticyclonic circulations or gyres, a counterclockwise one in the South Atlantic and a clockwise one in the North Atlantic (Fig. 1.1). The two gyres are driven separately, each by the trade winds in its own hemisphere, and they are separated over part of the equatorial zone by the eastward flowing Counter Current (Pickard and Emery 1990). The main features of the circulation of the North Atlantic were described already by Iselin (1936) and Sverdrup *et al.* (1946). The clockwise gyre may be considered to start with

the North Equatorial Current driven by the northeast trade winds. This current flows to the west and is joined from the south by that part of the South Equatorial Current, which has turned across the equator into the North Atlantic. Part of this combined current flows towards northwest as the Antilles Current, the other part into the Gulf of Mexico. From here it escapes between Florida and Cuba into the North Atlantic as the Florida Current. This current joins up with the Antilles Current off the coast of Florida and from about Cape Hatteras, where the joint current breaks away from the North American shore, it is called the Gulf Stream. The Gulf Stream flows northeast to the Grand Banks of Newfoundland at about 40°N, 50°W, after which it continues east and north as the North Atlantic Current. This divides and partly turns south past Spain and North Africa to complete the North Atlantic Gyre and feed into the North Equatorial Current (Pickard and Emery 1990).

The remainder of the North Atlantic Current flows northeast between Scotland and Iceland and enters the Nordic Seas, where the Faroe Islands separate the two main inflowing branches. The major part of the Atlantic Water (AW) continues as a Norwegian Atlantic Current (NWAC) north along the coast of Norway, which branches into the North Sea and also to the more central parts of the Nordic Seas. At the western boundary of the Barents Sea, the NWAC further bifurcates into the North Cape Current flowing eastwards into the Barents Sea, and the West Spitsbergen Current flowing northwards into the Fram Strait (Furevik 2001).

At the western side of the Nordic Seas, there is a cold and fresh flow of Polar Water originating in the Arctic Ocean. The major part of this water leaves the Nordic Seas as the East Greenland Current (EGC) through the Denmark Strait. The remaining part flows into the central areas of the Nordic Seas as the Jan Mayen Current and the East Icelandic Current. Here it gradually mixes with the AW, and modified by atmospheric forcing, it is an important factor in the ventilation of the intermediate and deep waters of the Nordic Seas, and to the thermohaline circulation of the North Atlantic (Furevik 2001). The EGC flows round the southern tip of Greenland into the Labrador Sea and continues up the west coast. The inflow to this area is balanced by the southward flow, along the west side of Baffin Bay, which continues south as the Labrador Current down the west side of the



**Figure 1.1** The main northward flowing warm-water routes and the cold deep southward return flows that form the North Atlantic thermohaline circulation (McCartney *et al.* 1996). Downloaded from the CLIVAR home page, [www.clivar.org](http://www.clivar.org).

Labrador Sea back into the Atlantic proper (Pickard and Emery 1990).

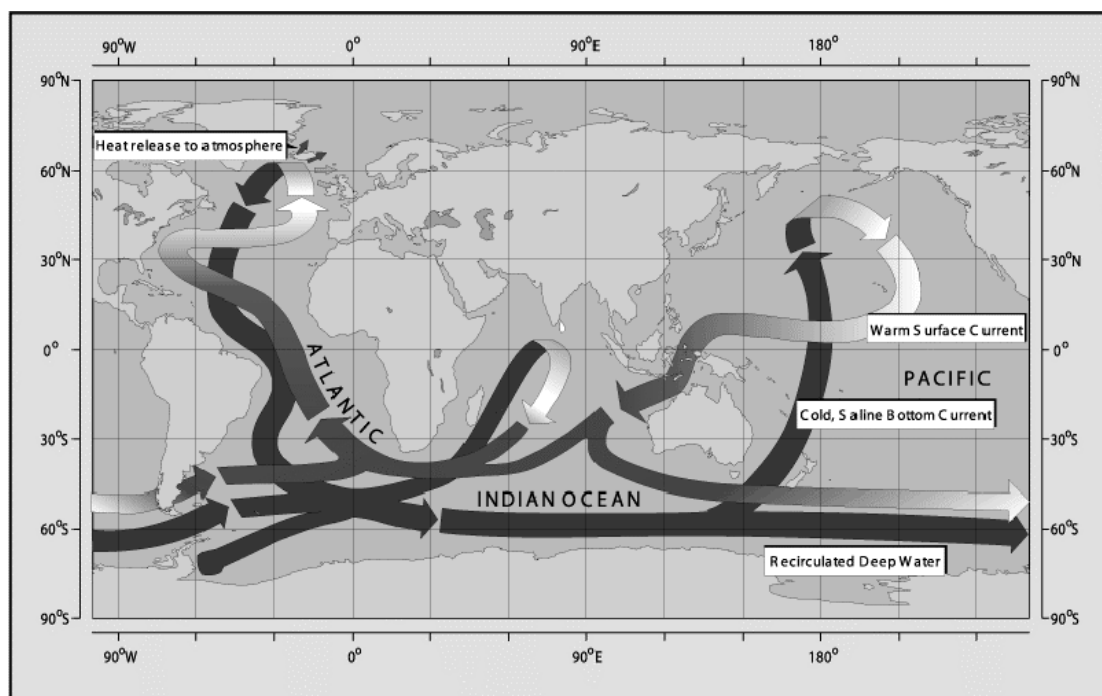
## 1.2 Oceanic circulation and large-scale climate variability

Ocean water circulates in currents that transfer heat from tropical regions to polar regions, influence weather and climate, distribute nutrients, and scatter organisms (Garrison 2002). Coastal regions and the uppermost part of the ocean is the main focus of this book. Here, above the pycnocline, the zone in which density increases rapidly with depth, wind is the primary driving force creating the surface currents. While the effect of wind typically is horizontal movement of water (Fig. 1.1), winds can sometimes induce vertical movement in the surface water, upwelling or downwelling. Wind blowing parallel to shore or offshore can cause coastal upwelling when the removed surface water is replaced by water rising along the shore. Because the new surface water is often rich in nutrients, prolonged wind can result in increased biological productivity. Although we will not directly deal with the ocean interior in this book, it should be noted that most

movements of the oceans water masses are caused not by wind energy, but by differences in density between water masses. This slow *thermohaline* circulation is responsible for most of the vertical movement of ocean water and the circulation of the global ocean as a whole (Garrison 2002).

A schematic account of the global circulation pattern linking the major ocean basins of the planet is shown in Fig. 1.2. The large region of open ocean in the Equatorial Pacific allows significant warming of water as it drifts to the west and past the northern edge of Australia. This warm surface water continues to drift westward through the Indian Ocean and around the southern tip of Africa. From here it turns northward, crossing the Equator (taking a more easterly direction than shown here), and creating the Gulf Stream off eastern North America. The warm surface water continually cools as it moves northward past Great Britain and into the Norwegian Sea. By this time the water is so cold and dense that it sinks to lower depths in the ocean. This creates the start of the global scale return current at low depths that moves southward across the Equator, back around Africa, past the southern edge of Australia and back to the central Pacific Ocean. A smaller branch of the return current splits

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**Figure 1.2** The global ocean circulation pattern 'The Conveyor belt'. Downloaded from the CLIVAR home page, [www.clivar.org](http://www.clivar.org).

off after passing Africa and enters the Indian ocean where sufficient warming augments the warm surface current coming from the central Pacific ([www.meteor.iastate.edu/gccourse/ocean/global.html](http://www.meteor.iastate.edu/gccourse/ocean/global.html)).

The most well known large-scale climate mechanism operating on an inter-annual to decadal timescale is the El Niño-Southern Oscillation (ENSO; see, for example, Philander 1990 or Allan *et al.* 1996). This phenomena originates in the tropical Pacific but has impact worldwide. Ecological effects of ENSO are discussed in Chapters 11, 12, and 16. The first evidence of such patterns of significant simultaneous correlations between weather and climatic anomalies over widely separated regions, teleconnections<sup>1</sup>, emerged from analyses of sea-level pressure and surface-air temperature (Walker and Bliss 1932). Near simultaneous fluctuations of

<sup>1</sup> The actual term 'teleconnections' was first used by Angstrom, A. 1935. Teleconnections of climate changes in present times. *Geographical Annals*, 17, 242–58; and popularized by Bjerknes, J. 1969. Atmospheric teleconnections from the equatorial pacific. *Monthly weather review*, 97, 163–72.

fish stocks in widely separated regions support the view that they are sometimes influenced by climate operating at a global scale (Schwartzlose *et al.* 1999).

Ecological regime changes may be linked to global climate variability, which in turn may be associated with an interdecadal cycle of dislocation of the convergence areas in the North Atlantic (Greenland and Labrador Seas) where thermohaline circulation starts (Kawasaki 1994). In the southeastern Atlantic, Benguela El Niño like episodes have been reported (Shannon *et al.* 1986; Gammelsrød *et al.* 1998). Benguela Niños advect warm, more saline water from the north onto the Namibian Shelf. This water may intrude about 600 km further south than in normal years. Off Japan anomalous southward intrusions of the Oyashio Current (ASIOs) have been described by Sekine (1991) and off Tasmania periods of low zonal westerly winds (LZWWs) also may cause a form of Tasmanian 'El Niño' during which temperature rises, nutrients become scarce in surface waters, new production decreases, and the biomass of larger zooplankton is drastically reduced (Harris *et al.* 1992). There is a

correspondence in time between the four Benguela Niños and the four LZWWs between 1949 and 1984. Information on ASIOs is only available since 1955, but the Japanese ASIOs occurred in each subsequent period of Benguela Niños off Namibia and Tasmanian LZWWs (Schwartzlose *et al.* 1999).

Influence on northern NE Atlantic climate by atmospheric teleconnections was suggested already by Izhevskii (1964) who argued for what he called a monophasic form of fluctuation throughout the Gulf Stream system (i.e. no time lag in water temperature fluctuations from the Florida current to the Barents Sea). More recent literature supports the view that atmospheric teleconnections influence marine climate and ecology across the North Atlantic (e.g. Taylor 1995; Rodwell *et al.* 1999; Ottersen *et al.* 2001; Stenseth *et al.* 2003). There is also strong support for much of the decadal variability in the North Atlantic sea surface temperature being explained as a local oceanic response to atmospheric variability (Deser and Blackmon 1993; Battisti *et al.* 1995; Houghton 1996).

### 1.3 Physical processes of importance to marine ecology

A number of physical processes may influence marine life at the individual, population, and community level. Processes that influence the reproductive habitat of many species of fish were, for example, grouped into three main classes by Bakun (1996):

- (i) *Enrichment processes*: upwelling, mixing, cyclonic wind stress curl (Ekman divergence), cyclonic eddy formation;
- (ii) *Concentration processes*: convergent frontal formation, anticyclonic wind stress curl (Ekman convergence), lack of dispersion by turbulent mixing processes, 'encounter-rate' increases/decreases as a result of variability in micro-scale turbulence;
- (iii) *Retention processes*: lack of offshore transport in (1) Ekman field (near-surface and superficial layers), (2) geostrophic current (intermediate layers), and (3) offshore dispersion of eddy-like features (filaments) on the meso-scale; availability of enclosed gyral circulations, stability of current patterns to which life cycles are adapted.

Simplified, *Enrichment processes* make more nutrients available to biological productivity, *Concentration processes* enhance food availability for a predator through increasing the concentration of

food particles and *Retention processes* contribute towards keeping individual members of a population in the appropriate place during the various parts of the life cycle. Examples of many of these mechanisms will be presented in subsequent chapters.

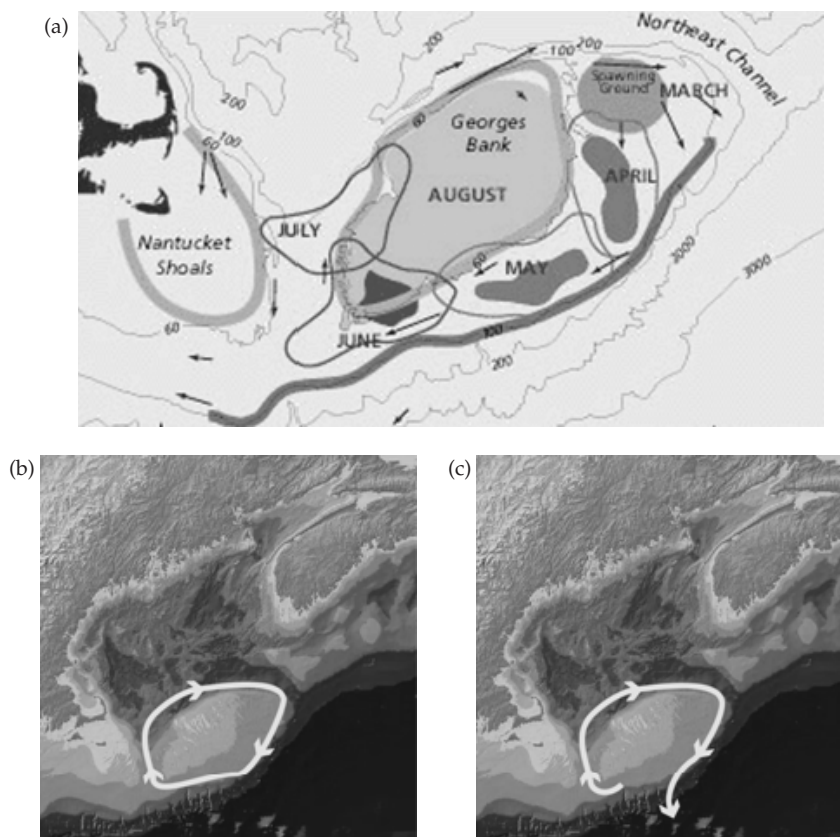
In Chapter 11 Patrick Lehodey points to the importance of upwelling for biological productivity in the Pacific, particularly along the equator and off the west coast of central South America. Since 90% of the world's fisheries traditionally have been in 2–3% of the ocean area, mostly in coastal upwelling areas (Pond and Pickard 1983), we will dwell on this. Upwelling is, simply stated, a result of surface water skimmed away by the wind, being replaced by water masses from below, typically from depths not greater than 200–300 m. For a more thorough description of the processes briefly described here (Ekman transport and divergence) we refer to textbooks in physical oceanography, for example, Pond and Pickard (1983).

When upwelled water of high nutrient content is transported into the photic (light-rich) zone, the production of phytoplankton may increase dramatically, enhancing the production potential upwards throughout the food web. The main regions where large-scale coastal upwelling takes place are in eastern boundary currents off the west coasts of West and South Africa in the South Atlantic and North and South America in the Pacific. However, since subsurface waters do not always have a high content of nutrients, upwelling does not necessarily imply an increase in biological production. In the North Atlantic, northwest Africa and Iberia are major upwelling systems. Chapter 6 exemplifies how interannual variability in upwelling may influence fish recruitment in this region.

Upwelling may also take place in areas remote from physical boundaries, namely, where surface waters diverge along the equator. The prevailing easterly trade winds drag the surface water westward along the equator. The Earth's rotation deflects the westward-flowing current towards the right in the Northern Hemisphere and towards the left in the Southern Hemisphere, driving the surface water away from the equator and bringing up water from below. Chapter 11 illustrates how this system breaks down during El Niño events causing a marked decrease in the productivity of the eastern tropical Pacific.

A specific form of *Concentration process* is that described in the Encounter Rate hypothesis of

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**Figure 1.3** An example of retention versus dispersion of cod eggs and larvae. The characteristic circulation pattern on Georges Bank, northeast United States. (a) Currents, transport eggs, and larvae of cod from the spawning area on the northeastern part of the Bank to the southwest. Main spawning grounds and typical areas of main egg and larval concentration per month are indicated. Variation in the circulation pattern can result in (b) lesser or (c) greater advective losses from the Bank. Downloaded from Dr. Bruce C. Monger at Cornell University (<http://www.eas.Cornell.edu>).

Rothschild and Osborn (1988) dealing with small-scale turbulence and its effect on predator-prey encounter rates during the feeding process. The field study by Sundby and Fossum (1990) confirmed that moderate turbulence was found to enhance contact rates between cod larvae and their prey zooplankton nauplii, and hence increase the effective prey concentration available to larvae. Although, there still is some disagreement with regards to the parametrization, the main findings have later been supported by several modelling studies, recently by Werner *et al.* (2001). This topic is further discussed in Chapters 3 and 6.

*Retention processes* may be illustrated by an example from the waters off northeast United States.

The characteristic circulation pattern on Georges Bank transports eggs and larvae of cod from the spawning area on the northeastern part of the Bank to the southwest. Variation in the circulation pattern can result in greater or lesser advective losses from the Bank (Serchuk *et al.* 1994; see Fig. 1.3). A model study by Werner *et al.* (1993) showed that during the first 60 days circulation had a greater influence on the distribution of eggs and larvae than behaviour. The results of Lough *et al.* (1994) indicate a close connection between egg and larval distribution pattern and year-class strength. They demonstrate that years with good recruitment typically are associated with low losses from the bank due to favourable wind conditions, and vice versa.

Transport-related effects on recruitment are discussed further in Chapter 6. Furthermore, retention processes influencing stability of current patterns to which life cycles are adapted may be seen in the light of the member/vagrant hypothesis of Sinclair and Iles (1989) discussed in Chapter 3.

## 1.4 Ecological responses to climate variability

As we already have touched upon and which will be further demonstrated and discussed in later chapters, there is a great variety in the possible pathways by which climate variability may affect ecological processes. Here, we highlight some of the main topics of general concern. To be able to deal with this, it is, as pointed out by Ottersen *et al.* (2001), often a fruitful exercise to summarize the variety emerged from a number of studies into a restricted number of categories.

### 1.4.1 Direct or indirect response

Climate variability affects animals both directly through physiology, including metabolic and reproductive processes, as well as indirectly through affecting their biological environment (predators, prey, within population interactions, disease). The physical environment also affects feeding rates and competition through favouring one or another species (Fig. 1.4).

Chapter 6 exemplifies this for fish and shellfish, while in Chapter 7 the effect of climate variability on seabirds is described to follow two main lines: directly by physiological effect and indirectly through influence on food. Direct physiological effects include metabolic processes that happen during the life-cycle (e.g. reproduction and moult). Since their feed is composed of organisms with populations that fluctuate in response to climatic

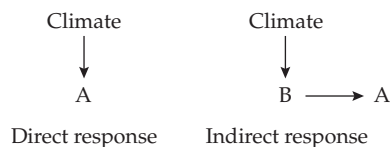
changes, the main indirect influence of climate is for seabirds through regulation of food availability.

Ecological effects of the NAO were classified according to three major types: direct effects, indirect effects, and integrated effects by Ottersen *et al.* (2001). A similar categorization may be made for other climate phenomena.

1. The direct effects of the NAO are mechanisms that involve a direct ecological response to one of the environmental phenomena synchronized with the NAO. The effect of the NAO on metabolic rates via temperature is, for instance, of this type.
2. The indirect effects of the NAO are non-trivial mechanisms that either involve several physical or biological intermediary steps between the NAO and the ecological trait and/or have no direct impact on the biology of the population.
3. The integrated effects of the NAO involve simple ecological responses that can occur during and after the year of an NAO extreme. This is the case when a population has to be repeatedly affected by a particular environmental situation before the ecological change can be perceived (biological inertia) or when the environmental phenomenon affecting the population is itself modulated over a number of years (physical inertia, for example, reduction in the volume of North Sea Deep Water; Heath *et al.* 1999).

A problem with general classification schemes, as that above, is that there always are some cases that do not fit into any of the predefined categories, while sometimes several classes seem to fit. Thus, in Chapter 5 a new class of effects is defined and exemplified, *translations*. 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. These alterations are based entirely on the physical changes produced by climate variability.

The classification of response to change in climate as either direct or indirect makes sense also at the community level (Chapter 10). Changes in temperature that influence, for example, growth and recruitment, 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 and temperature-induced changes in prey abundance. Fish communities may then act



**Figure 1.4** Direct or indirect response. (A and B being biological units of interest.)

indirectly to a change in climate by way of responding to changes in local abiotic or biotic conditions.

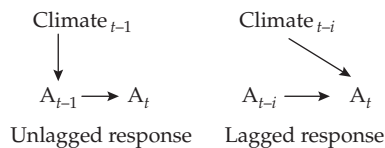
### 1.4.2 Temporally lagged responses

Related to the issue of direct and indirect climate effects is the question of time lags in ecological responses to climatic variation (Fig. 1.5). In Chapter 15, a discussion is provided of how the existence of both immediate and lagged responses to climate introduces conceptual and analytical challenges to the study of ecological consequences of climatic variability.

An example of a temporally lagged response to a large-scale climate signal, not included in Chapter 15, is provided by Ottersen *et al.* (2001). They show how some of the effects of the NAO may be carried by a biological population over a number of years following a particular NAO situation. The increase in survival through the vulnerable early stages of Barents Sea cod during warm, high NAO years historically results in stronger year classes also at later, catchable, stages (see 'the cohort-effect' discussed by Stenseth *et al.* 2002). When the year class matures, the number of spawners as well as their individual size may be increased, enhancing the potential for high recruitment to the next generation. On the other hand, the year-class strength of cod in the North and Irish Seas is inversely related to a positive NAO phase and high temperature. This is possibly a result of limitation in energy resources necessary to achieve higher metabolic rates during warm years (Planque and Fox 1998). In both cases, the effects of the NAO are perceived in the fisheries with a lag of several years. (See Chapter 6 for more on population dynamics of cod and other fish and Chapter 10 for fish community ecology).

### 1.4.3 Continuous fluctuations versus episodic events: linear and non-linear responses

The environment may undergo slow continuous change, or more rapid, episodic events may transfer



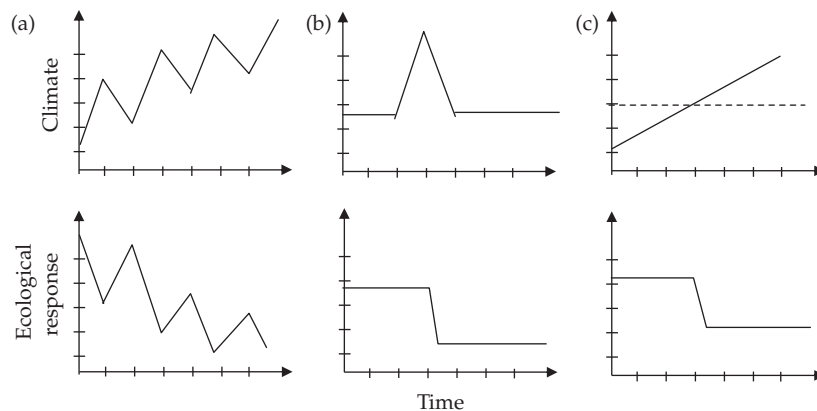
**Figure 1.5** Temporally unlagged or lagged response. ( $t-1$  and  $t$  indicate the immediate past and the present, respectively.)

conditions between different states and regimes. The most well-known example of the latter is the switching between El Niño La Niña and 'normal' conditions in the tropical Pacific, another is the Pacific Decadal Oscillation between a 'warm' and a 'cold' phase (more on this in Chapter 12).

These two categories may be exemplified by the mechanisms that seem to initiate and sustain regimes of sardine and anchovy worldwide. There may be a continuous modification of habitat, for example, a trend to warming that permits an expansion in spawning range and enhanced egg production (Lluch-Belda *et al.* 1992). Alternatively, there may be episodic environmental events that trigger changes in populations and ecosystems in well separated areas. Formation of powerful year-classes could cause a population to expand quickly and, for short-lived species, a few poor year-classes could result in a rapid population decrease. Empirical evidence exists for both these forms of environmental influence at a global scale, and it is quite possible that several factors may operate at any given time (Schwartzlose *et al.* 1999).

By far most studies of links between climate and marine ecology—by assumption—only consider linear relations, while challenges related to non-linearity (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. 1.6). The relationship between large-scale and local climatic variables may change over time (i.e. non-stationarity; Jones *et al.* 2001), and hence limit the time period for which effects on ecosystems can be predicted from known relationships with climate patterns. The relatively clear link between the NAO (as estimated by traditional two-station indices) and regional climate in the Barents Sea that has been observed since around 1970 was, for example, not present during the preceding 50 years (Dickson *et al.* 2000; Ottersen *et al.* 2003).

A study with starting point in terrestrial ecology, but with consequences also for a marine setting by Myrsetrud *et al.* (2003) examines this issue, with special emphasis to the NAO. They point to two different ways in which the effect of the NAO on ecological systems may be expected to be non-linear. First, the NAO may not be linearly related to local climatic variables, and plankton and fish are indeed expected to respond to the climate they experience at a local scale. Second, the plant's or



**Figure 1.6** Differential 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.

animal's response to changes in local climate may not always be linear. It should be emphasized that the issue of non-linear responses may at least in part be an issue of scale, as transforming the predictor and/or the response variable may linearize the relationships. Non-monotonous relationships, as found in Mysterud *et al.* (2001), cannot be linearized, however.

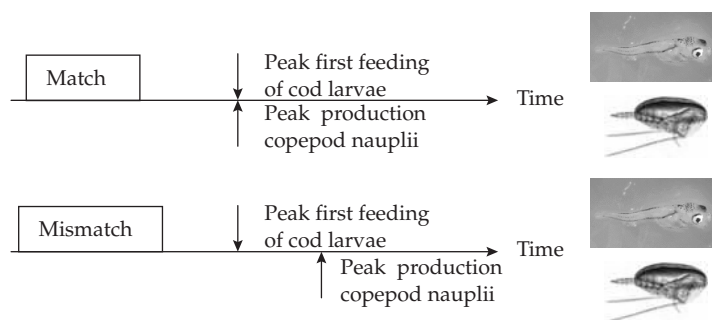
There is evidence that climate change may lead to a higher frequency of more extreme events, as a consequence of increased variance and not just change in average. It is generally regarded that the spatio-temporal distribution of extreme events are often ecologically more significant than seasonal mean values. Increased environmental variance has in general a negative effect on population growth, and non-linear relationships between climate and population processes imply that a change in climatic variability will affect the mean value of a process, even if the mean value of the climatic parameter remains the same (Mysterud *et al.* 2003).

It may further be useful to distinguish between linear and non-linear responses of fish communities to a climate signal (see Chapter 10). The linearity in the former case is understood as linear among species, that is, most species are affected in a similar fashion, without changing interaction effects among species. However, if changes in climate render the environment uninhabitable for key species in the community, large (non-linear) community effects may be observed.

#### 1.4.4 The match–mismatch hypothesis

Climatic fluctuations may affect the relative timing of food requirement and food availability. Survival of a predator depends on its ability to encounter and eat a sufficient quantity of suitable prey in order to avoid starvation and to grow. Differences in the temporal and spatial match between predator and prey may thus generate variability in predator survival rates, including interannual variability. This 'match–mismatch' hypothesis was first presented by D. Cushing some 30 years ago and later updated (Fig. 1.7; Cushing 1990; Cushing 1996).

Match–mismatch type mechanisms have been reported for different regions and at different trophic levels, often in its original context, relating cod larvae to their zooplankton nauplii prey (e.g. Ellertsen *et al.* 1989 for Barents sea cod), but also for other species, for example herring in the St Lawrence estuary (Fortier and Gagne 1990). However, it should be noted that it has been suggested that the survival–food availability coupling may be less precise than proposed in the 'match– mismatch' hypothesis (Leggett and Deblois 1994). Still, recent work by Brander *et al.* (2001) tested the hypothesis by examining the relation between modelled production of chlorophyll and copepod eggs, driven by meteorological forcing, and cod recruitment. They concluded that the interannual variability in *Calanus* egg production did have a significant effect on cod recruitment in the Irish Sea and at Iceland.



**Figure 1.7** The match–mismatch hypothesis.

In polar marine ecosystems variability in biological stocks and productivities is pronounced on all timescales because of the marked variability in the environmental forcing (meteorological and hydrographical) factors on all timescales. Polar pelagic ecosystems are, in fact, notoriously unstable (Sakshaug 1997).

One seasonal feature is, however, quite predictable in regions like the Barents Sea. All parts experience a spring phytoplankton bloom sometime during April–July. This bloom is based on the ‘new’ nutrients admixed to the upper layers during the winter. The timing of the spring bloom depends on the supply of light to the phytoplankton in spring, which in turn critically depends on the mixing characteristics of the upper water masses. Deep mixing causes phytoplankton to spend a major fraction of their life in very low light, causing severe light limitation and thus delays in the onset of a bloom (Sverdrup 1953).

Different processes may generate the stabilization of the upper layers necessary to allow phytoplankton prolonged access to the photic zone. Typically, the earliest blooms (in mid-April) arise in Atlantic waters close to the oceanic Polar Front—this happens in ‘cold years’ when the ice cover reaches that far south. In such situations, a meltwater-generated (salinity dependent) stabilization of the upper layers occurs early because the sea ice starts melting early as a consequence of the warming effects of the Atlantic waters. North of the oceanic Polar Front, stability trails the retreating ice as a consequence of the supply of fresh melt-water. This establishes a 30–50 km wide phytoplankton bloom zone that trails the ice edge. Such an effect is known from all seasonally ice-covered polar seas. South of the Polar Front, that is in the permanently ice-free areas that are characterized by Atlantic surface waters, stability typically depends instead on the formation of

a temperature-dependent thermocline. This thermocline is created fairly late, thus the spring bloom is not triggered until mid-May or early June (Sakshaug 1997).

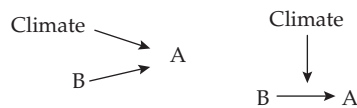
Differences in the timing of spring blooms affect the match between phytoplankton and zooplankton maxima. To maximize grazing and minimize sedimentation (‘match’), phytoplankton blooms should not begin too early and they should be of long duration so that the probability of zooplankton stocks encountering phytoplankton blooms is maximized (Sakshaug and Skjoldal 1989; Hassel *et al.* 1991). The late and protracted phytoplankton blooms in the permanently ice-free Atlantic waters may represent good examples of a ‘match’ whereas the early blooms that arise where sea ice overlies Atlantic water may be textbook examples of a ‘mismatch’ (Sakshaug 1997).

Match or mismatch is a fundamental issue also in several other systems, for instance for sea birds as discussed more comprehensively in Chapter 7. The ambient conditions in the sea (such as water temperature and currents) and large-scale climatic and hydrographic processes that affect these variables, generate variation in the production, distribution, and abundance of organisms on which seabirds feed and hence on the birds themselves. A climate-induced delay in food-production could create a mismatch between the prey production and the predator requirement that might have heavy impact on reproduction success.

In Chapter 3, Werner *et al.* examine several hypotheses providing explanations to how physical processes affect fish recruitment. The match–mismatch hypothesis is here seen in the light of the Hydrographic Containment hypothesis, which is a combination of match–mismatch and the migration triangle hypothesis of Harden–Jones (1968).

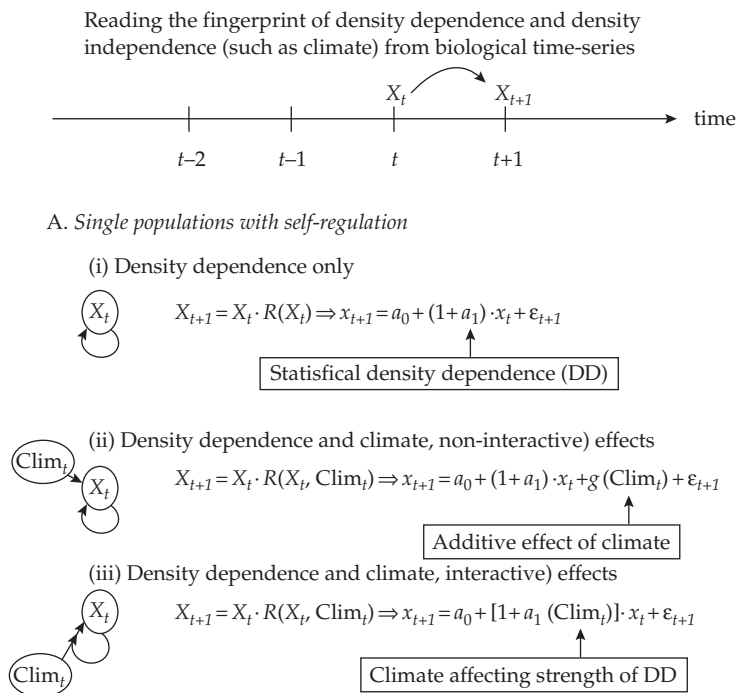
### 1.4.5 Modelling the ecological effects of climate fluctuations: a time series approach

Any ecological impact will depend on a variety of factors affecting the population biology of the particular species in question (Fig. 1.8). It is common when analysing the response of populations, communities, or ecosystems to environmental variables to implicitly or explicitly assume that other factors remain unchanged. However, response to a climate signal will depend on other ecological factors like density-dependence and interactions. It is therefore too simplistic to predict population abundances and demographic rates only based on, for example, the NAO—particularly if the responses are non-linear (Mysterud *et al.* 2003).

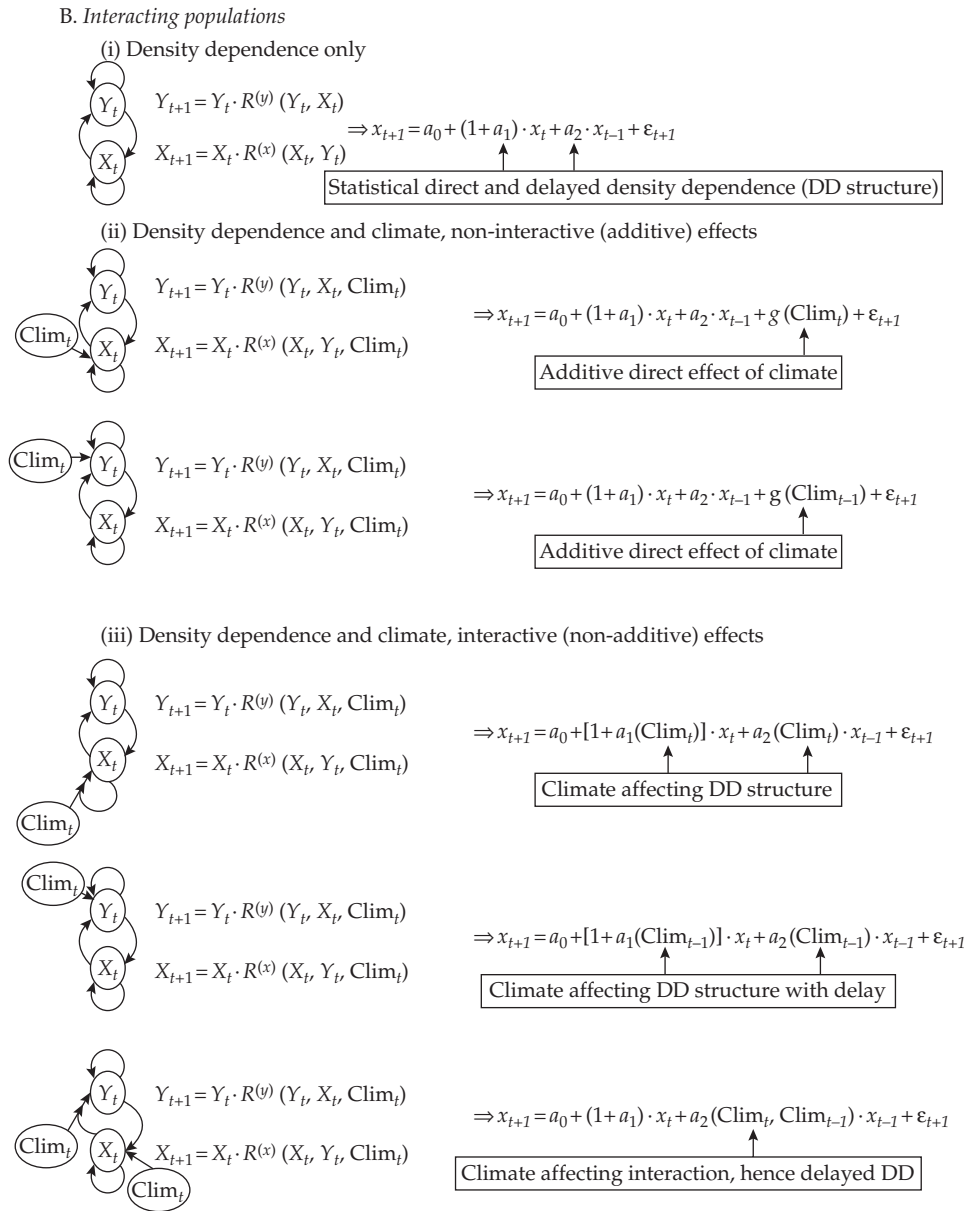


**Figure 1.8** Interaction with other factors.

Recently, it has become rather common to search for signals of climate fluctuations in time-series data (e.g. see Stenseth *et al.* 2002, 2003). Figure 1.9 summarizes various ways climate effects may appear in time-series models—and how this may be interpreted ecologically. Panel A summarizes the (somewhat theoretical) case where only one population lives in an area without any closed feedback interactions with any other part (or species) of that system (this might, for instance, be exemplified by a species not being food-limited and only being exposed to some nomadic generalized predator (e.g. see Stenseth *et al.* 1999). Panel A.i depicts the case where there, within such a system, is no climate effect—that is, what is typically encountered in the non-climate oriented part of the ecological literature. Panels A.ii and A.iii depict two cases where climate affects the population—one (panel A.ii) where the climate effect is non-additive (on log-scale) implying, for instance, that climate affects the food-supply in a non-dynamic manner, whereas the other (panel A.iii) shows the case where climate fluctuations affect the way individuals interact within the population. Among these, the former



**Figure 1.9** Expected signals of various types of climate effects on ecological systems. See text for discussion.  $x_t = \ln(X_t)$ .



**Figure 1.9** (Continued)

(panel A.ii) is fairly commonly treated in the ecological literature, whereas the other is only now being approached (e.g. see Stenseth *et al.* 2002).

Panel B of Fig. 1.9 illustrates time-series models for interacting species, but for which we only are studying one of the species (due to, for example, only data being available on this species

and not the other). Again the distinction between additive and non-additive effect of climate is illustrated—the latter representing quite a bit of methodological challenges to statisticians. Indeed, it is our conviction that bringing specialists within the field of time-series analysis into the field of climate-ecology impacts will be very rewarding.