

Regime shifts in marine ecosystems: detection, prediction and management

Brad deYoung¹, Manuel Barange², Gregory Beaugrand³, Roger Harris², R. Ian Perry⁴, Marten Scheffer⁵ and Francisco Werner⁶

¹ Department of Physics and Physical Oceanography, Memorial University, St John's, NL A1B 3X7, Canada

² Plymouth Marine Laboratory, Prospect Place, Plymouth, PL1 3DH, UK

³ Station Marine, Université des Sciences et Technologies de Lille 1, 28 Avenue Foch, BP 80, 62930 Wimereux, France

⁴ Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, BC V9T 6N7, Canada

⁵ Aquatic Ecology and Water Quality Management Group, Department of Environmental Sciences, Wageningen University, PO Box 8080, 6700 DD Wageningen, The Netherlands

⁶ Marine Sciences Department, University of North Carolina, Chapel Hill, NC 27599-3300, USA

Regime shifts are abrupt changes between contrasting, persistent states of any complex system. The potential for their prediction in the ocean and possible management depends upon the characteristics of the regime shifts: their drivers (from anthropogenic to natural), scale (from the local to the basin) and potential for management action (from adaptation to mitigation). We present a conceptual framework that will enhance our ability to detect, predict and manage regime shifts in the ocean, illustrating our approach with three well-documented examples: the North Pacific, the North Sea and Caribbean coral reefs. We conclude that the ability to adapt to, or manage, regime shifts depends upon their uniqueness, our understanding of their causes and linkages among ecosystem components and our observational capabilities.

Developing understanding of regime shifts

Regime shifts, defined here as relatively sudden changes between contrasting, persistent states of a system, have been observed in earth system dynamics [1], terrestrial ecology [2] and freshwater systems [2]. By sudden, we mean short relative to the time in the different states, which can represent different structures of the system. Such shifts have been identified in all the major ocean basins [3]; however, the dynamics underlying the observed changes remain largely unknown. Marine ecosystems show relatively sudden and dramatic changes in form and function, called regime shifts, that have surprised researchers and managers [1,4,5]. Greater consideration of ocean regime shifts is timely as we move toward developing ecosystem-based approaches to managing marine systems.

Debate continues about the dynamics, characteristics and even the classification of marine regime shifts. There is now, however, clear acceptance that dramatic variability at periods of decades and longer, potentially spanning ocean basins, might be quite common in the ocean. Here we follow a pragmatic definition [3] considering regime shifts from an empirical perspective. We examine the responses of the marine ecosystem, considering primarily

the biological components of the ecosystem, to drivers such as changes in the sea surface temperature or the depth of the surface, well-mixed, layer of the ocean. Shifts can be driven by natural forcing [6], by human activities [7] or more commonly by some combination of the two. The differing states need not be distinct in a nonlinear mathematical sense [2]; they might simply be different representations of a complex system. Recent work [8] suggests that regime shifts are the nonlinear amplification of stochastic physical forcing, hence supporting an analysis that explores the physical drivers and the biological response. Unfortunately, our limited knowledge of the drivers, the causative agents for change and the internal dynamics of ecosystems remain an impediment to improving understanding of regime shifts and developing management responses to them. We present a new approach to regime shifts and suggest strategies for consideration of regime shifts in ocean management. We focus on three well-known examples in the literature: the North Pacific, the Northwest Atlantic and Caribbean coral reefs.

Drivers of oceanic regime shifts

Three key drivers of oceanic regime shifts are abiotic processes (e.g. changes in ocean stratification), biotic processes (e.g. internal foodweb dynamics) and changes to structural habitat (e.g. bottom type). These drivers can include natural and anthropogenic components that operate synergistically and whose influences are difficult to separate (e.g. climate). Abiotic factors, such as global warming or large-scale oscillations in the atmosphere and ocean, are generally the most easily identified [9]. Biotic drivers can include restructuring of foodwebs resulting from overfishing [10] and internal population dynamics of key species, an example of the latter being the alternation of sardine and anchovy populations in upwelling systems [11]. Destruction of structural habitat can be the result of natural abiotic events such as hurricanes [7] or of anthropogenic effects such as dynamite fishing in coral reefs or clearing and destruction of mangrove forests with the subsequent loss of nursery areas for reef fishes [12]. Another anthropogenic example is the introduction of exotic species [13]. In general these drivers act

Corresponding author: deYoung, B. (bdeyoung@physics.mun.ca).

together, so our separation of them here is just for the purpose of discussion.

The spatial scales of the drivers and the response can differ. The scale for the shift might range from a few kilometers (e.g. a coral reef) to a few hundred kilometers as on the Scotian Shelf in the Northwest Atlantic [14] to basin scales of thousands of kilometers, as for the North Pacific [6] or perhaps even globally [15]. Not all organisms of an ecosystem are necessarily involved in, or influenced by, the shift.

The three types of drivers operate at different scales depending upon their dynamics and the ecosystem in question. At small spatial scales, on Caribbean coral reefs, for example, a species-specific pathogen caused mass mortalities of the sea urchin *Diadema antillarum* during the early 1980s. Urchin densities crashed to 1% of their original level, triggering a regime shift in the community as the reefs became overgrown with brown fleshy algae (Figure 1) that were released from grazing [16]. The timescale of the altered state is long, with the new state having persisted now in some areas for over 20 years. However, the timescale over which the shift occurred was short: within 1–2 years for both the trigger (the pathogen) and the shift to algal dominance. The shift was preceded by a pre-conditioning stage, during which changes in land-use practices (which increased nutrient loading) combined with intensive fishing reduced the numbers of herbivorous fish. Operating over a period of several decades before the shift, these two effects eroded the resilience of the system (Figure 2) thereby making the system more vulnerable to

external forcing [2]. Ecosystem resilience is defined as the ability of an ecosystem to rebound from a disturbance [17]. Environmental forcing, such as fishing or changes in temperature, can also directly force a regime shift [18], or reduce the resilience of the current state of an ecosystem. Such marine ecosystems are then more vulnerable to other changes causing them to shift, or tip, from one state to another.

Regime shifts in the North Pacific and the Northwest Atlantic [3] operating at much larger spatial scales provide contrasting examples of the drivers and the scales of shifts when compared with the Caribbean coral reefs. In the North Pacific there are clear examples of changes in the marine ecosystem, from fish to zooplankton and phytoplankton. Climate-driven regime shifts in the North Pacific (Figure 3) have occurred at least 11 times since 1650, with the average duration of any phase being 23 years [19]. In the Northwest Atlantic a shift running from fish to nutrients has been observed on the Scotian Shelf [14], and is primarily attributed to the indirect effects of fishing. Although the time and space scales of the North Pacific are similar to those of the Northwest Atlantic, that is, years and thousands of kilometers, fishing has a smaller overall role in driving shifts in the Pacific than it does in the Atlantic [20] because fish removals are smaller relative to the scale of the marine ecosystem. Thus, the regimes shifts observed in the North Pacific [20] have been less anthropogenically driven than in the North Atlantic.

A regime shift can exhibit many different timescales. Two timescales to consider are the length of the shift and

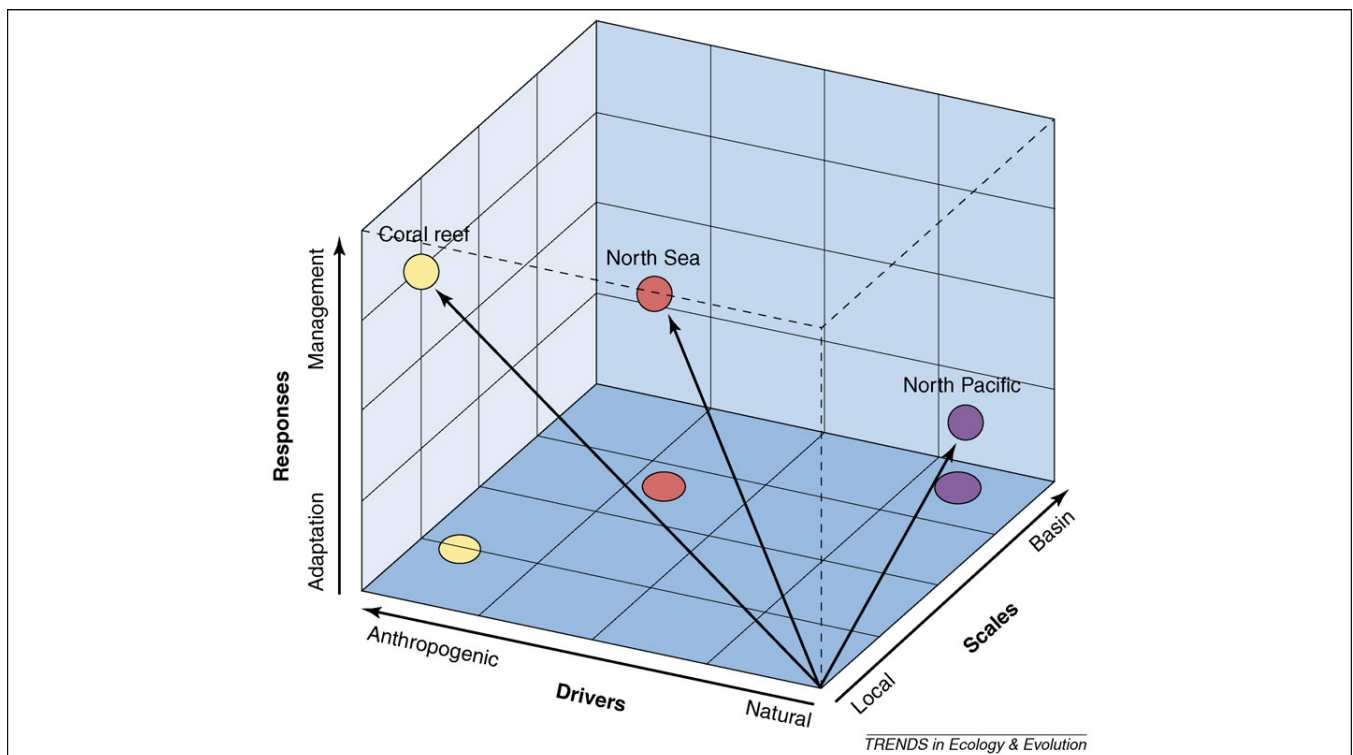


Figure 1. Phase space for drivers and responses of regime shifts. Regime shifts can be differentiated based upon their spatial scales (local or basin), their drivers (natural to anthropogenic) and the potential for human responses (from adaptation to management). The three regime shifts discussed in the text are plotted in this three-axis system. Plotting regime shifts in this phase space differentiates those shifts which are naturally driven and for which there are few management options (the North Pacific) from those which are much more influenced by human activity and for which management options do exist (coral reefs). The North Pacific is an example of a regime shift that is almost exclusively naturally driven, the corals almost exclusively anthropogenically driven and the North Sea a combination of the two drivers.

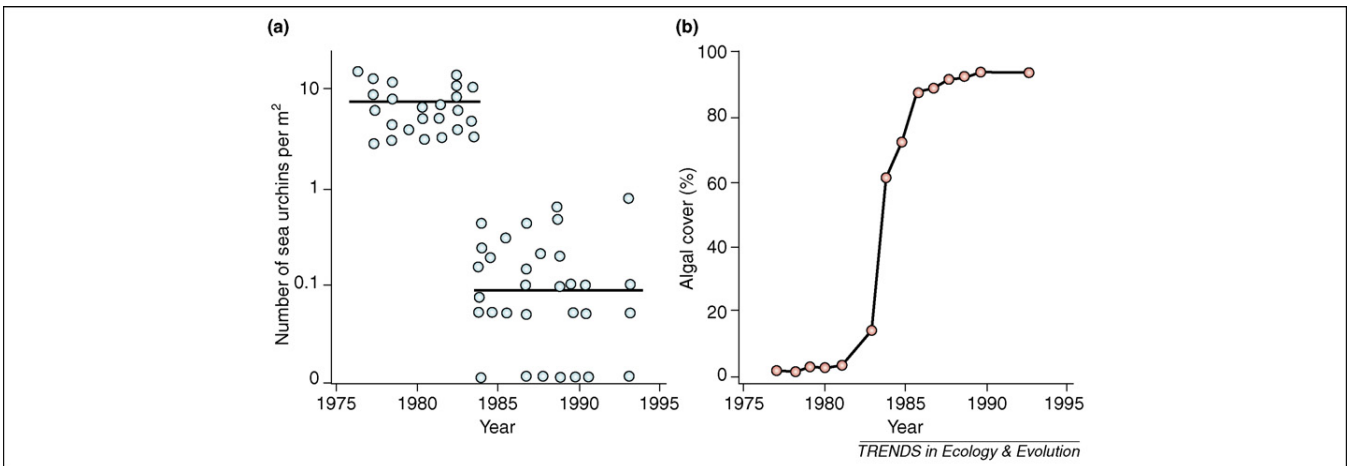


Figure 2. The Caribbean coral regime shift illustrated by changes on Jamaican reefs. **(a)** Collapse of populations of the sea urchin *Diadema antillarum* resulting from a pathogen outbreak. **(b)** Resulting increase in macro-algal cover at 7 m depth. Redrawn with permission from [16].

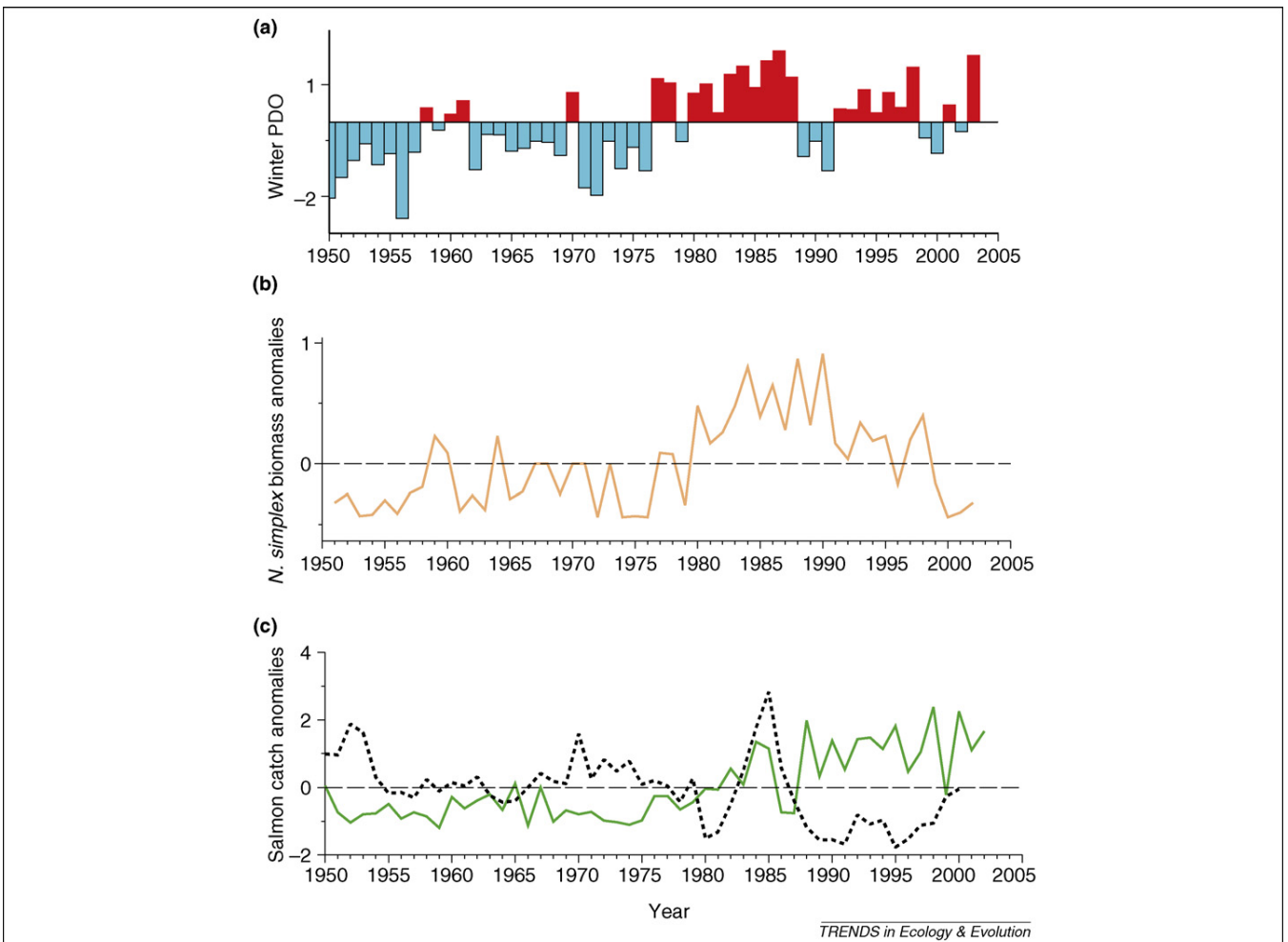


Figure 3. Example of northeast Pacific ecosystem conditions since 1950, illustrating the regime shift of the late 1970s. **(a)** Winter (January-February-March mean) Pacific Decadal Oscillation (PDO) index. **(b)** Biomass anomalies for the euphausiid *Nyctiphanes simplex* in the California Current System as an indicator of plankton biomass. **(c)** Pacific salmon catch anomalies for pink salmon *Oncorhynchus gorbuscha* (solid line) in southeast Alaska (lagged 1 year to match year of entry into the ocean) and Chinook salmon *O. tshawytscha* (dotted line) in Washington, Oregon and California (lagged 3 years to match year of ocean entry). Whereas the PDO shows a series of mostly above-average values since the late 1970s, which includes substantial interannual variability (a), the biological time series clearly show changes from the first half of the record, with the euphausiid biomass index showing negative anomalies until the late 1970s after which the anomalies are positive for more than a decade. The salmon catch data show a somewhat later shift, with a decline in the catches of Chinook by the mid-1980s roughly coincident with an increase for pink salmon. Salmon data are from records compiled by the North Pacific Anadromous Fish Commission, as made available by the North Pacific Marine Science Organization at http://www.pices.int/publications/special_publications/NPESR/2005/npesr_2005.aspx.

the length of the regime following the shift. Precise identification of these timescales can be straightforward, as is the case for the Caribbean coral reefs (Figure 1), where a sudden change in state occurred over a period of 1–2 years. It is more difficult to precisely time regime shifts in large ocean basins. In the North Pacific, the 1970s regime shift which involved clear changes in the dominant zooplankton populations [6] took place between 1975 and 1980 (Figure 2). Of course, not every regime shift is the same and the past is not always a predictor of the future [20]. Additionally, depending upon the trophic level, the organisms involved and the character of the shift, many different time lags can develop. In cases such as the collapse of the Caribbean coral reef system, in which the sea urchins died, there might be little or no lag. If, however, the shift occurs because of removals of fish of a particular age, then lags in the response of the rest of the community might depend on the particular life-history patterns of that fish.

Clearly, marine regime shifts differ widely in scale as well as in drivers, and this has implications for our ability to detect, predict and manage them (Figure 1). We will focus our review on these three approaches, illustrating our points with examples from the regime shifts observed in Caribbean reefs, the North Sea and the Pacific Ocean.

Detection of regime shifts

The observation of some regime shifts, such as the brown algae on Caribbean coral reefs, requires relatively little analysis for detection or determination. The same is not generally true for large, complex systems such as the North Pacific or North Atlantic [9,21,22]. In cases where the shift is neither sudden nor synchronous across all the biotic and abiotic components of the ecosystem, determining its timing and occurrence requires simultaneous analysis of many variables and a decision-making process to interpret conflicting information. Many different approaches have been suggested [6,21–23], each of which has its own conceptual or statistical uncertainties. Whereas identifying changes in variables such as sea surface temperature and elevation in response to atmospheric forcing can be relatively rapid (months), it is the persistence of these ocean responses and their ecological impacts that constitute the new regime. Identifying such persistence takes years, and also requires comparison of the basin's subregions in the case of a basin-scale event which might have different regional expressions. Underlying the uncertainty of detection is our limited understanding of the links between different variables, both biotic and abiotic, in marine ecosystems.

In general, the larger the spatial scale, the greater the complexity and it is therefore unsurprising that detecting a regime shift over, for example, the entire North Pacific basin in a manner that would be helpful to environmental management is difficult. Ecosystems can take on different configurations, or states, and thus shifts can move in different directions. For example, the 1999 shift in the North Pacific [24] exhibited greater north–south structure of the changed populations rather than the east–west variability associated with the 1976 shift [25,26]. Thus, the 1999 shift did not represent a return to the previous regime or state [27,20]. In the North Pacific, detection of a regime shift might best rely on large spatial and short

temporal scale monitoring of physical conditions such as sea surface temperature and height, and lower trophic-level organisms such as zooplankton [20,28].

Data are the key starting point and new observational networks such as the Global Ocean Observing System (GOOS; <http://www.ioc-goos.org>) offer the possibility for more data on the state of our ocean ecosystems. With adequate data, detecting a shift in the North Pacific within 2–3 years of its occurrence is possible. However, although the atmospheric changes that induce a regime shift and the resulting physical oceanographic responses can occur relatively rapidly (within a year), the biological responses to these changes can have different spatial and temporal patterns depending upon the species involved.

Regime shifts can have varying effects on different components of the marine ecosystem. Biological responses to regime shifts in the Pacific are apparent initially through persistent changes in growth and abundance of marine populations (e.g. Refs [6,29]), rather than through large-scale changes in distributions and migration patterns [29], because the large size of the basin makes observations of such changes difficult. Rapid changes in distributions do occur on local and regional scales, for example expansions of Pacific sardine populations along the west coast of North America [30] and Pacific saury in the Northwest Pacific [31], but these are also affected by shorter-scale events such as El Niño–Southern Oscillation (cf. Ref. [15]). Such distributional changes might also represent recoveries of local populations with improved productivity conditions [32]. Estimates from an allometric foodweb model indicate that the time for the fluctuation of phytoplankton biomass to generate a response in the biomass of juvenile fish (e.g. juvenile salmon) is 9 months, and ~21 months for small (1 kg) adult fish [33]. Spatial patterns of the response to atmospheric forcing depend upon whether the dominant influence is on wind patterns and mixing, density (heat and freshwater fluxes) or local scale currents, which can propagate the influence to much larger scales. This sets timescales of 1 year or longer for large fluctuations in phytoplankton to be observable in fish populations, depending on the trophic level at which the fish are feeding.

It can take many years before a shift can be detected. The regime shift in the North Sea at the end of the 1980s was only detected 10 years after it happened [34] by comparing information across several trophic levels. This event coincided with many changes in fish and zooplankton distributions and foodweb structure reported in the literature at that time [34]. For example, the doliolid *Doliolum nationalis*, the dinoflagellate *Ceratium extensum* and the siphonophore *Muggiaea atlantica*, which are usually found in oceanic waters of the Northeast Atlantic, were detected in the central part of the North Sea in 1989 [35,36]. Phytoplankton color, a visual index of chlorophyll derived from the Continuous Plankton Recorder (CPR) survey (http://www.sahfos.ac.uk/cpr_survey.htm), also showed a stepwise increase in intensity and seasonal extent after 1987 [37]. The key zooplankton species, *Calanus finmarchicus*, decreased dramatically after the mid-1980s. Horse mackerel *Trachurus trachurus*, a fish rarely reported from the North Sea during the 1960s and 1970s, showed

a pronounced increase after 1987 [34]. Further changes at the community level were documented by Beaugrand [38] using key attributes of the ecosystem such as diversity, biomass and size. Although originally detected in pelagic ecosystems, the shift might also have occurred in the benthos [39,40]. As in the North Pacific, the biological changes in the North Sea were not spatially uniform, and plankton indicators from different regions give a better understanding of the extent of the changes. Changes in plankton in the southern part of the North Sea have been less evident than changes in the northern stratified regions [41], although a shift in the Wadden Sea has been reported recently [42]. The timing of the plankton change during the 1980s varied from 1984 to 1988 depending on the life history, spatial distribution, seasonal maximum or the particular threshold values of the physiological processes of each species [43]. Species with shifted distributions generally have shorter life cycles and smaller body sizes than do species whose distributions were not affected [44] because of their association with warmer waters.

The detection of regime shifts caused by fishery collapses would appear straightforward, as there is generally substantial monitoring of the state of the fish resources. However, the potential for geographical shifts in the distribution of such fish stocks makes the precise determination of the trends in population abundance difficult. This problem underlies many of the difficulties associated with fisheries management as illustrated by the collapse of Northern cod *Gadus morhua* on the Newfoundland and Labrador shelves. Although there was evidence of an accelerating population decline during the late 1980s [45], it was discounted in the face of increasing catch per unit effort from the fishery, a result of shifting distributions of cod from north to south, where most of the fishing occurred [46]. The regime shift, from groundfish to shrimp and crab, is apparent now only in hindsight [3], and was not detected at the time of the collapse during the early 1990s. On the Scotian Shelf, the collapse of the groundfish stocks occurred without any expectation of a shift in the ecosystem balance, and the shift has only been determined through retrospective analysis. The trophic cascade on the Scotian Shelf [14], with observed shifts in abundance from groundfish (the primary fishery removals) to planktivorous fish, to invertebrates, including shrimp and snow crab, to zooplankton, phytoplankton and nutrients, provides a dramatic realization of an oceanic regime shift in a fashion that has not yet been detected so clearly elsewhere [18].

Detection is the crucial first step in the practical consideration of regime shifts. First we must have an awareness of the presence or potential for regime shifts. We must then have sufficient data for reasonably timely descriptions of the ecosystem state and the possible progression of regime shifts within that system. Such timeliness is particularly important as we move toward prediction and then management consideration of regime shifts.

Prediction of regime shifts

Given our limited understanding of the dynamics of regime shifts, their successful prediction might seem unrealistic. However, we believe that several different approaches are

possible. The first step is to establish a link between the drivers and the ecosystem response. For at least two of our examples, there are well-stated hypotheses, supported by data, which could be used to develop simulation scenarios of future change: (i) the sudden habitat-driven coral shift in the Caribbean [47] and (ii) the climate- and/or biotic-driven North Sea biogeographical shift [38], both of which are described below. There are situations, however, where it has not been possible to separate the multiple drivers or where different states are occurring in a complex system. Such is the case for the North Pacific [6], where our understanding of the forcing and response is poor, and hence accurate prediction is not possible. Several differing interpretations of the changes have been offered [6,28,30]; however, there is no immediate likelihood that we will have sufficient data to distinguish among possibilities that might allow us to develop empirical forecast models.

Predictions in coral reefs

The simplest model for prediction is the case where we could potentially control a major causal mechanism, for example in coral reef systems, and shelf fisheries. We understand the causal link in the Caribbean coral systems between the removal of reef fish and the ecosystem response. Removal of herbivorous fish, eutrophication through nutrient loading from agricultural runoff, acidification from climate change and bleaching all contributed to making this system increasingly vulnerable to collapse. It is, however, not yet possible to predict stochastic events that trigger the final collapse, such as the disease outbreak in the Caribbean. We might, however, use models in relatively well understood systems to estimate resilience and predict the increased likelihood of a shift, and develop management recommendations to reduce the risk. Predictability is enhanced because there are few stable states in coral reef ecosystems, the key characteristic being the viability of the coral. Thus awareness and control of the drivers makes it possible, with a reasonable degree of confidence, to predict the probable long-term outcome for a particular coral reef system.

Prediction for fishing-dominated systems

At larger spatial scales, although fishing can still be the dominant driver and some of its effects can be anticipated, the consequences of fishing are not predictable without understanding the foodweb dynamics. The Scotian Shelf example, in which fishing has led to a restructuring of the ecosystem [18], is a particularly clear case [14]. Georges Bank [48] and the northeast Newfoundland Shelf provide examples where fishing caused changes in relative species abundance that do not appear to be simply, or easily, reversible. Different fishery collapses have shown that ecosystem restructuring is a common enough outcome that it requires explicit consideration in fisheries management [49,50]. There is no defined fixed point at which the ecosystem becomes susceptible to impact because the scales on the resilience plot (Figure 1) are unknown. Attempts to explore the full historical records for fish abundance [51,52] might help determine the key thresholds at which fish stocks become susceptible to other environmental forcing.

The North Sea provides an example where fishing and environment (biogeographical climate-associated shifts) combine to influence the marine ecosystem. The biogeographical shift was recognized only 10 years after it had occurred. However, now that we are aware of the potential for such shifts in species distributions, it should be possible to predict a reversal to a state similar to the previous one if there is a change in the physical regime, or to predict further development and evolution of the system in response to new conditions. The shift during the late 1980s occurred because of a change in the mean climatic state, a characteristic of the Northeast Atlantic that might be predictable [53]. Thus, although we were unable to predict the 1980s shift, through the understanding that we have gained and with the aid of prognostic atmosphere-ocean-coupled climate models [54], we might be able to forecast future scenarios in the Northwest Atlantic associated with global warming.

Prediction is possible for some systems and should be a goal of new research because of the potential benefits to management. Although such predictions are quite difficult at present, the use and application of predictive models will encourage consideration of the underlying model structures and help us to understand how best to use such predictive models.

Management of regime shifts

In recent years, ecosystem resource management has developed increasingly sophisticated ways of accounting for the uncertainty that pervades ecosystem processes. One successful way of doing so has been through management systems robust to uncertainty and capable of handling diverse hypotheses regarding resource dynamics [55]. However, the rapid and perhaps alternate nature of regime shifts challenges a basic principle behind resource management, which aims to develop optimal harvesting strategies for resources that are assumed to be fundamentally stable and subject to random noise (e.g. fish). In addition, there is generally a mismatch between the geographical and temporal scales of management actions and ecosystem change points. Successful management under these circumstances requires flexibility to adapt to novel and unexpected events through new adaptive management strategies [56].

The likelihood of climate-driven regime shifts has been shown to increase when humans reduce ecosystem resilience, for example by removing key functional groups of species, age groups or trophic levels, or adding waste and pollutants [13]. The possibility of a regime shift should encourage management of marine ecosystems that is geared toward developing resilience, understood as the capacity of a system to absorb disturbance and reorganize itself while undergoing change so as to retain essentially the same function, structure, identity and feedback mechanisms [13]. The significant erosion of ecosystem resilience caused by regime shifts has similarly dramatic consequences on social systems which depend on these ecosystem resources [2]. Thus, building resilience into both social and ecological systems through adaptive management should be the ultimate objective of management under regime shifts [47]. Adaptive management is aimed

at integrating existing interdisciplinary information into dynamic models that attempt to make predictions about the impacts of alternative policies [57]. In the case of marine fisheries, various simulation studies have examined what constitutes an optimum adaptive management strategy for resources that undergo regime shifts. One possible approach is through the application of regime-specific harvest rates [20,58]. Simulation work has demonstrated the value of this approach, particularly for short-lived species (species with life spans shorter than the duration of the adverse conditions) [59]. The most effective approach is to set such rates as part of a decision-rule framework, associated with timeframes for a management response that is triggered when there are indications that a regime shift has occurred; hence the importance of identifying a regime shift. A provisional stepwise approach to changing harvest rates could be applied in which, for example, harvest rates decline given the uncertainty of the shifting state of the ecosystem, until the productivity level of a new regime has been verified. Simulation work indicates that improved management results could be achieved even if the switch in harvest rates did not coincide with the regime switch but lagged by the age of recruitment to the fishery of the given resource [59,60]. This is useful because, in addition to delays in recognizing the shift, the implementation of any management action is generally delayed by scientific uncertainty, stakeholder pressure or institutional resistance [61]. Alternatively, assuming that regime shifts are fundamentally decadal to multi-decadal events, a two-level management strategy has been suggested [62] combining a conventional single-species management to deal with short-term fluctuations with a long-term ecosystem management strategy (e.g. driving fishing fleet capacity and investment cycles).

Because the response of long-lived marine species, such as cod, to regime shifts is likely to be slower or lagged compared to the response of short-lived species, such as anchovy, maintaining an appropriate age structure in spawning stock biomass should be a major management goal to develop resilience to regime shifts [20]. Where shifts involve a change in dominance between species, such as the anchovy and sardine fluctuations that are observed in both the Atlantic and the Pacific [11], management procedures designed under the assumption of out-of-phase sinusoidal trends in species abundance are more effective than are traditional modeling approaches [63], particularly if the fisheries interact. Such approaches have not yet been implemented and appear to be strongly sensitive to the amplitude of regime cycles [63].

Regime shifts also have implications for international agreements, such as those dealing with transboundary stocks. At present, such agreements generally assume that the geographic patterns of movement and distribution of the species under consideration are fixed [60]. However, forecasts of climate change [64] suggest that climatically driven biogeographical shifts will become more common and, as a result, fixed management zones defined by the historical geography might no longer be viable. Consideration of the possibility of a regime shift would enable, and require, some consideration of adaptive structures (including changing management zones) in future agree-

ments that would operate if a regime shift were to take place [60,65].

In conclusion, in managing the impacts of regime shifts, attention has in the past focused on preventing perturbations rather than enhancing the stability of the ecosystem. Building and maintaining resilience of desired ecosystem states is likely to be the most pragmatic and effective way to manage ecosystems in the face of increasing environmental change [2], followed by the development of flexible, adaptive management practices applied by governance structures that are capable of interacting at ecological, social and economic levels and at multiple temporal and geographical scales [57,65]. In some cases, such as the North Pacific, there might be few options for management actions in advance of the shift because of our inability to forecast the shift or its trajectory but, once detected, different management options should be considered [66].

Future developments

There is now clear evidence for regime shifts in the ocean. The growing literature shows not only that they do occur but also that they can have substantial impact. More regime shifts are likely, given the growing influence of climate and other anthropogenic impacts on the oceans, which lead to environmental stress and reduced resilience. Our understanding of regime shifts is growing, both in terrestrial [2] and marine [4] ecosystems, but the limited data, systemic complexity and the range of differing structures in marine ecosystems present formidable challenges. What can we do? It might appear, at first glance, that the best response would be to improve our rather incomplete understanding of marine ecosystems dynamics and of regime shifts in particular. We argue, however, that a shift in our approach to the problem is needed and that we must act even given our limited knowledge. The first step would be the development of a more active and flexible management approach, and greater exploration of those situations in which detection and prediction are possible such as in the coral reef systems and some of the fishery systems presented here. For some of these cases, we understand enough about the drivers, and have enough information on the marine ecosystem for management, to respond to minimize the possibility of or the impact of a regime shift. Of course, unambiguous recommendations are unlikely, and uncertainty and probabilistic analyses remain essential in the provision of advice.

Clearly our ability to monitor and model marine ecosystems is improving [67]. There are new tools for observing the ocean (e.g. GOOS) which expand our ability to make measurements that span the physical, biogeochemical and ecological properties of the ocean. Such data are of limited value without process understanding; however, cooperative, multidisciplinary studies (e.g. GLOBEC, SOLAS and IMBER) continue to help fill the gaps in our knowledge of ecosystem function. With such new data, and improved process models, numerical models are attaining greater realism. New approaches to physical climate modeling, such as ensemble techniques to represent uncertainty, are now beginning to have an impact on the ecological modeling community [3].

An awareness of regime shifts needs to be included in the management of marine systems. We suggest a framework in which the drivers, scales and responses of the regime shift are considered as a guide to their consideration by management. Systems in which the drivers are primarily anthropogenic, such as in the North Sea and in the coral reefs of the Caribbean, offer the greatest potential for practical management response. Nonetheless, even very complex systems such as the North Pacific, in which our understanding is more limited, demonstrate the need for the consideration of regime shifts given their dramatic impact on the structure and dynamics of the ocean ecosystems.

Acknowledgements

The authors thank funding support provided by GLOBEC and NOAA (through the Intergovernmental Oceanographic Commission of UNESCO, IOC) and Mark Ohman for access to data for *Nyctiphanes simplex* in the California Current System. We thank Richard Beamish for comments on an earlier draft. This paper is dedicated to the late Ümit Ünlüata, from IOC-UNESCO, who encouraged and supported this contribution.

References

- 1 Rahmstorf, S. (2002) Ocean circulation and climate during the past 120,000 years. *Nature* 419, 207–213
- 2 Scheffer, M. *et al.* (2001) Catastrophic shifts in ecosystems. *Nature* 413, 591–596
- 3 deYoung, B. *et al.* (2004) Detecting regime shifts in the ocean: data considerations. *Prog. Oceanogr.* 60, 143–164
- 4 Steele, J. (2004) Regime shifts in the ocean: reconciling observations and theory. *Prog. Oceanogr.* 60, 135–141
- 5 Lees, K. *et al.* (2006) Characterizing regime shifts in the marine environment. *Fish Fish.* 7, 104–127
- 6 Hare, S.R. and Mantua, N.J. (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Prog. Oceanogr.* 47, 103–145
- 7 Bellwood, D.R. *et al.* (2004) Confronting the coral reef crisis. *Nature* 429, 827–833
- 8 Hsieh, C.H. *et al.* (2005) Distinguishing random environmental fluctuations from ecological catastrophes for the North Pacific Ocean. *Nature* 435, 336–340
- 9 Mantua, N. (2004) Methods for detecting regime shifts in large marine ecosystems: a review with approaches to North Pacific data. *Prog. Oceanogr.* 60, 165–182
- 10 Cury, P. *et al.* (2000) Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES J. Mar. Sci.* 57, 603–618
- 11 Schwartlose, R.A. *et al.* (1999) Worldwide large-scale fluctuations of sardine and anchovy populations. *S. Afr. J. Mar. Sci.* 21, 289–347
- 12 Mumby, P.J. *et al.* (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* 427, 533–536
- 13 Folke, C. *et al.* (2004) Regime shifts, resilience and biodiversity in ecosystem management. *Annu. Rev. Ecol. Evol.* 35, 557–581
- 14 Frank, K.T. *et al.* (2005) Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308, 1621–1623
- 15 Chavez, F.P. *et al.* (2003) From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* 299, 217–221
- 16 Hughes, T.P. (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265, 1547–1551
- 17 Gunderson, L.H. *et al.* (2002) *Resilience and the Behavior of Large-Scale Systems*, SCOPE 60. Island Press
- 18 Scheffer, M. *et al.* (2005) Cascading effects of overfishing marine systems. *Trends Evol. Ecol.* 20, 579–581
- 19 Gedalof, Z. and Smith, D.J. (2001) Interdecadal climate variability and regime-scale shifts in Pacific North America. *Geophys. Res. Lett.* 28, 1515–1518
- 20 King, J.R., ed. (2005) *Report of the Study Group on Fisheries and Ecosystem Responses to Recent Regime Shifts*, PICES Scientific Report no. 28 (http://www.pices.int/publications/scientific_reports/Report28/Rep_28_default.aspx)

- 21 Rudnick, D.R. and Davis, R.E. (2003) Red noise and regime shifts. *Deep Sea Res.* 50, 691–699
- 22 Solow, A.R. and Beet, A.R. (2004) A test for a regime shift. *Fish. Oceanogr.* 14, 236–240
- 23 Rodionov, S.N. (2004) A sequential algorithm for testing climate regime shifts. *Geophys. Res. Lett.* 31, L09204
- 24 Peterson, W. and Schwing, F. (2003) A new climate regime in northeast Pacific ecosystems. *Geophys. Res. Lett.* 30, 1–6
- 25 Beamish, R.J. and Bouillon, D. (1993) Pacific salmon production trends in relation to climate. *Can. J. Fish. Aquat. Sci.* 50, 1102–1116
- 26 Trenberth, K. and Hurrell, J. (1994) Decadal atmospheric-ocean variations in the Pacific. *Clim. Dyn.* 9, 303–319
- 27 Bond, N. *et al.* (2003) Recent shifts in the state of the North Pacific. *Geophys. Res. Lett.* 30, 2183–2186
- 28 Wooster, W. and Zhang, C.I. (2004) Regime shifts in the North Pacific: early indications of the 1996–1997 event. *Prog. Oceanogr.* 60, 183–200
- 29 Zhang, C.I. *et al.* (2007) Effects of the 1988/89 climate regime shift on the structure and function of the southwestern Japan/East Sea ecosystem. *J. Mar. Syst.* 67, 225–235
- 30 McFarlane, G.A. *et al.* (2002) Climate variability and Pacific sardine populations and fisheries. *Am. Fish. Soc. Symp.* 32, 195–214
- 31 Zhang, C.I. and Gong, Y. (2005) Effect of ocean climate changes on the Korean stock of Pacific saury, *Cololabis saira* (Brevoort). *J. Oceanogr.* 61, 313–325
- 32 Rodríguez-Sánchez, R. *et al.* (2002) Dynamic geography of small pelagic fish populations in the California Current System on the regime time scale (1931–1997). *Can. J. Fish. Aquat. Sci.* 59, 1980–1988
- 33 Denman, K.L. *et al.* (1989) Comparisons of time scales for biomass transfer up the marine food web and coastal transport processes. In *Effects of Ocean Variability on Recruitment and an Evaluation of Parameters Used in Stock Assessment Models* (Beamish, R.J. and McFarlane, G.A., eds), pp. 255–264, Canadian Special Publication Fisheries and Aquatic Science 108
- 34 Reid, P.C. *et al.* (2001) A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. *Fish. Res.* 50, 163–171
- 35 Lindley, J.A. *et al.* (1990) Doliolids in the German Bight in 1989: evidence for exceptional inflow into the North Sea. *J. Mar. Biol. Assoc. U. K.* 70, 679–682
- 36 Greve, W. (1994) The 1989 German Bight invasion of *Muggiaea atlantica*. *ICES J. Mar. Sci.* 51, 355–358
- 37 Reid, P.C. *et al.* (1998) Phytoplankton change in the North Atlantic. *Nature* 391, 546
- 38 Beaugrand, G. (2004) The North Sea regime shift: evidence, causes, mechanisms and consequences. *Prog. Oceanogr.* 60, 245–262
- 39 Kroncke, I. *et al.* (1998) Long-term changes in macrofaunal communities off Norderney (East Frisia, Germany) in relation to climate variability. *Mar. Ecol. Prog. Ser.* 167, 25–36
- 40 Warwick, R.M. *et al.* (2002) Tapp inter-annual changes in the biodiversity and community structure of the macrobenthos in Tees Bay and the Tees estuary, UK, associated with local and regional environmental events. *Mar. Ecol. Prog. Ser.* 234, 1–13
- 41 Beaugrand, G. and Ibañez, F. (2004) Monitoring marine plankton ecosystems (2): long-term changes in North Sea calanoid copepods in relation to hydro-meteorological variability. *Mar. Ecol. Prog. Ser.* 284, 35–47
- 42 Weijerman, M. *et al.* (2005) Regime shifts in marine ecosystems of the North Sea and Wadden Sea. *Mar. Ecol. Prog. Ser.* 298, 21–39
- 43 Beaugrand, G. and Reid, P.C. (2003) Long-term changes in phytoplankton, zooplankton and salmon linked to climate change. *Glob. Change Biol.* 9, 801–817
- 44 Perry, A.L. *et al.* (2005) Climate change and distribution shifts in marine fishes. *Science* 308, 1912–1915
- 45 Hutchings, J.A. and Myers, R.A. (1994) What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Can. J. Fish. Aquat. Sci.* 51, 2126–2146
- 46 Rose, G.A. *et al.* (2000) Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean. *Can. J. Fish. Aquat. Sci.* 57, 644–663
- 47 Hughes, T.P. *et al.* (2005) New paradigms for supporting the resilience of marine ecosystems. *Trends Ecol. Evol.* 20, 380–386
- 48 Fogarty, M.J. and Murawski, S.A. (1998) Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. *Ecol. Appl.* 8 (Suppl. 1), S6–S22
- 49 Costanza, R. *et al.* (1998) Principles for sustainable governance of the oceans. *Science* 281, 198–199
- 50 Lessard, R.B. *et al.* (2005) Should ecosystem management involve active control of species abundances? *Ecol. Soc.* 10, 1 In: <http://www.ecologyandsociety.org/vol10/iss2/art1>
- 51 Rose, G.A. (2004) Reconciling overfishing and climate change with stock dynamics of Atlantic cod (*Gadus morhua*) over 500 years. *Can. J. Fish. Aquat. Sci.* 61, 1553–1557
- 52 Rosenberg, A.A. *et al.* (2005) The history of ocean resources: modeling cod biomass using historical records. *Front. Ecol. Environ.* 3, 84–90
- 53 Taylor, A.H. (2005) A model of variations in the North Atlantic Oscillation. *Geophys. Res. Lett.* 32, L24713
- 54 Enfield, D.B. and Cid-Serrano, L. (2006) Projecting the risk of future climate shifts. *Int. J. Climatol.* 26, 885–895
- 55 Butterworth, D.S. (2007) Why a management procedure approach? Some positives and negatives. *ICES J. Mar. Sci.* 64, 613–617
- 56 Pikitch, E.K. *et al.* (2004) Ecosystem-based fishery management. *Science* 305, 346–347
- 57 Walters, C.J. (1997) Challenges in adaptive management of riparian and coastal ecosystems. *Conserv. Ecol.* 1, 1
- 58 Polovina, J.J. (2005) Climate variation, regime shifts, and implications for sustainable fisheries. *Bull. Mar. Sci.* 76, 233–244
- 59 MacCall, A.B. (2001) Fishery management and stock rebuilding prospects under conditions of low frequency variability and species interactions. *Bull. Mar. Sci.* 70, 613–628
- 60 Miller, K.A. and Munro, G.R. (2004) Climate and cooperation: a new perspective on the management of shared fish stocks. *Mar. Resour. Econ.* 19, 367–393
- 61 Shertzer, K.W. and Prager, M.H. (2007) Delay in fishery management: diminished yield, longer rebuilding, and increased probability of stock collapse. *ICES J. Mar. Sci.* 64, 149–159
- 62 Fréon, P. *et al.* (2005) Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. *Bull. Mar. Sci.* 76, 385–462
- 63 De Oliveira, J. *et al.* (2005) Long-term harvest strategies for small pelagic fisheries under regime shifts: the South African fishery for pilchard and anchovy. In *Climate Change and the Economics of the World's Fisheries: Examples of Small Pelagic Fish Stocks. New Horizons in Environmental Economics* (Hannesson, R. *et al.*, eds), pp. 151–204, Edward Elgar
- 64 Intergovernmental Panel on Climate Change (2001) *Climate Change 2001: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press
- 65 Wilson, J.A. (2002) Matching social and ecological systems in complex ocean fisheries. *Ecol. Soc.* 11, 9 In: <http://www.ecologyandsociety.org/vol11/iss1/art9>
- 66 King, J.R. and McFarlane, G.A. (2006) A framework for incorporating climate regime shifts into the management of marine resources. *Fish. Manag. Ecol.* 13, 93–102
- 67 deYoung, B. *et al.* (2004) Challenges of modelling decadal variability in ocean basin ecosystems. *Science* 304, 1463–1466