Plankton biodiversity of the North Atlantic: changing patterns revealed by the Continuous Plankton Recorder Survey.

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Abstract
The Continuous Plankton Recorder Survey operates across northern ocean basins where it has generated definitive datasets on decadal scale changes in plankton biodiversity. The survey has shown biological, environmental and climatic indicators that relate to global change impacts within marine ecosystems. In the last decade, the survey has demonstrated major alteration within Atlantic plankton communities including the northerly displacement of communities by ~1,000 km. Regime shifts have been identified with sensitivity to a 10°C isotherm with similar responses across multiple trophic levels. Such behaviour of plankton ecosystems offers a method of prediction the locations of future communities. The survey has also shown transfer of Pacific phytoplankton in to the Atlantic for the first time in 800,000 years with unknown consequences for the native ecosystem. Understanding global issues requires a global approach and a future cooperative commonwealth of regional plankton biodiversity surveys is proposed that links current surveys with proposed new surveys.

1. INTRODUCTION
The Continuous Plankton Recorder Survey is the longest (starting in 1931), most geographically extensive (pan Atlantic and other ocean basins) marine biological survey in the world with a unique dataset of marine biodiversity (500 taxa). It has generated over 1,000 peer reviewed papers on various aspects of biological, environmental and climatic indicators particularly on impacts of global anthropogenic change on marine ecosystems.

This paper outlines some of the scientific discoveries achieved by the Continuous Plankton Recorder (CPR) Survey operated by the Sir Alister Hardy Foundation for Ocean Science (www.sahfos.ac.uk) in Plymouth, UK. Although the CPR Survey operates in all the major ocean basins except the Indian Ocean, it severely under-samples the plankton in all basins compared say to the global coverage achieved for ocean color or even ARGO. An exception is the North Atlantic where the CPR Survey has operated since 1931. For this reason, the success stories focus on the North Atlantic. At the end of the paper, we advocate that a global survey needs to be generated and the first steps that are being taken to achieve this.

1.1. Why study plankton biodiversity?
Understanding plankton biodiversity in our oceans is essential for three main reasons.

Firstly, life originated in the ocean some four thousand million year ago and today all but one of the major taxonomic phyla currently live there. The evolutionarily simplest, and indeed the most numerous, life forms in the oceans are the plankton, a taxonomically heterogeneous group of microscopic plants (phytoplankton), animals (zooplankton) and microbes (bacteria, archaea and viruses). Plankton are found throughout the 1.5 x109 km3 living space of the world’s ocean making them the most ubiquitous life form on Earth. An understanding of plankton is a key component to understanding of life on our planet.

Secondly, the ocean’s foodweb depends crucially upon plankton, since these simple primary and secondary producers form the functional base of all marine ecosystems. The totality of the ocean’s primary production estimated to be some 48 x 1015 tonnes C annually [1]. This activity carried out by microscopic phytoplankton is transferred via zooplankton to fuel the global production of 240 million metric tonnes of fish. Of this some 80 million metric tonnes of fish is harvested annually by fishing activity.

Third, but by no means least, plankton play a crucial role with their interaction with our climate. This interaction is a two-way process. On the one hand, plankton are responsible for some 46% of the planetary photosynthesis. This process, which involves the assimilation of CO2 and its transformation into organic material, results in the reduction of ambient CO2. This is the first step in a series of complex biogeochemical transformations, termed the biological pump, that involves the export of carbon and other elements from atmosphere and surface waters into the oceans interior. The waters of the ocean’s interior are out of contact with the atmosphere and therefore the carbon is in a
transient sink so far as climate is concerned. The typical
time scale of the turnover of this transient sink is in the
order of a few thousands of years. However, the role of
plankton in climate control extends much further than
the reduction of atmospheric carbon dioxide. Some
common plankton taxa, typically coccolithophores and
dinoflagellates, produce dimethyl sulfonioproprionate
(DMSP). DMSP is converted to dimethyl sulphide
(DMS) a volatile compound that is important in cloud
formation over the ocean, via biogeochemical
transformations involving viruses, bacteria, archaea,
protozoa and metazoa in the surface ocean. This
remains an active and controversial research field of
how plankton communities may be able to create their
own atmospheric weather.

On the other hand, plankton are also strongly influenced
by climatic, and other environmental, forcing processes.
These include changes in temperature, pH, sunlight,
current speed and direction, water-mixing as well as
innate changes in the properties of the marine foodweb.

1.2. The Continuous Plankton Recorder Survey

The Continuous Plankton Recorder (CPR) survey is the
only biological monitoring programme that operates on
an ocean basin scale with monthly sampling over
decadal time scales. Merchant ships voluntarily tow
CPRs, at a depth of ~10 m, on their normal routes of
passage in the Atlantic, Pacific, Arctic and Southern
Oceans. The survey is unique in that the methodology
and plankton analysis procedures for ~500 taxa have
been maintained with little change for more than 70
years [2].

2. DECADAL CHANGES IN PLANKTON
   BIODIVERSITY

The broad temporal and spatial scales upon which the
CPR Survey operates offers an unique insight into how
the plankton communities are changing. Some of recent
scientific discoveries from the north Atlantic survey are
presented below.

2.1. First hints of contemporary climatic forcing of
   phytoplankton at basin scale

Decadal scale changes within phytoplankton
communities in the Atlantic and North Sea were
originally identified by Reid et al [2]. They suggested
that these were climatically driven with the spreading of
unusually cold waters from the Arctic resulting in the
decline in phytoplankton north of 59°N. Further south,
phytoplankton increased in their season length and
abundance. They suggested that changes in the North
Atlantic Oscillation altered the centre of deep-water
convection from the Greenland Sea to the Labrador Sea
after 1988. The likely sources of these colder waters are
stronger westerlies with a larger export of fresh water
from melted ice around the Arctic Sea. These results
provided the first suggestion that phytoplankton may be
responding to climatic forcing on decadal scales. Since
then further analysis of new data obtained showed that
presence of a regime shift in the phytoplankton in the
North Sea with an inflection point in the late 1970’s
(Fig. 1).

![Figure 1: Long term monitoring of phytoplankton in the North Sea demonstrated a clear regime shift in the late 1970s. The new regime was characterised by a higher rate of increase of phytoplankton and extended growth period. The upper panel shows phytoplankton chlorophyll concentration in ug/l. The lower panel shows monthly results over a period of some 60 years. Updated from [2].]
2.2. Continuous change of Atlantic plankton biodiversity

A biogeographical analysis of zooplankton in the eastern North Atlantic revealed that calanoid copepods were distributed as 5 separate communities with distinct taxonomic groupings. Large-scale changes in the distribution of these communities in the eastern North Atlantic Ocean and European shelf seas were shown by Beaugrand et al [3]. Strong biogeographical shifts in all copepod assemblages occurred with a northward extension of more than 10 degrees latitude of warm-water species associated with a decrease in the number of colder-water species. These biogeographical shifts agreed with changes in the spatial distribution and phenology detected for many taxonomic groups in terrestrial European ecosystems. The shifts are related to both the increasing trend in Northern Hemisphere temperature and the North Atlantic Oscillation (Figure 2).

**Figure 2:** Decadal scale changes in the distribution of the warm temperate and sub-arctic communities of plankton in the eastern North Atlantic water. Over the 5 decades both communities have moved northwards by >10° of latitude. Updated from [3].

2.3. New biological coupling of Pacific and Atlantic Oceans

In 1999, the CPR survey revealed large numbers of the Pacific diatom *Neodenticula seminae* in the Labrador Sea [4]. This was the first occurrence of this species in the North Atlantic for more than 800,000 years (Figure 3). The arrival coincided with modifications in Arctic hydrography and circulation, increased flows of Pacific water into the Northwest Atlantic and the exceptional occurrence of extensive ice-free water to the North of Canada in the previous year. These observations suggest that *N. seminae* was carried in a pulse of Pacific water in either 1998 or 1999 via the Canadian Arctic Archipelago. The species occurred previously in the North Atlantic during the Pleistocene from ~1.2 to ~0.8 Ma as recorded in deep sea sediment cores. The reappearance of *N. seminae* in the North Atlantic is an indicator of the scale and speed of changes that are occurring in the Arctic and North Atlantic oceans as a consequence of regional climate warming. Because of the unusual nature of the event, it appears that a threshold has been passed, marking a change in the
circulation between the North Pacific and North Atlantic Oceans via the Arctic. Trans-Arctic migrations from the Pacific into the Atlantic are likely to occur increasingly over the next 100 years if Arctic ice continues to melt. The invasion by a single species is remarkable enough but the real significance of this is that a physical barrier has been breached between the two oceans [5]. If viable pathways through the Arctic result in more Pacific species following, this might pose a threat to native Atlantic species through competition for resources, transformation of the plankton ecosystem and potentially alteration of biogeochemical processes associated with the biological pump. Another phytoplankton *Coscinodiscus wailesii*, previously invaded the North Sea from the Indian and Pacific Oceans. This diatom displaced indigenous species under certain conditions. It was also found to be unpalatable by some phytophagous species suggesting there may be further effects within the marine food web.

2.4. What are the consequences of regime shifts?

One of the many questions posed by changes to biodiversity—given that the biological changes are species dependent, are all species within a community equally susceptible to change? Is community reassembly a natural consequence of climatic change? Will community function alter with climate change? Will there be an imbalance in system trophodynamics? In some systems, regime shifts [6], have been documented. These are characterized by large scale abrupt changes in the ecosystem with major ecological modifications. Regime shifts remain poorly understood, and may not be recognised until long after they had actually occurred [6].

2.5. Forecasting future plankton regimes.

Recent studies have shown that plankton in the North Atlantic differ in their sensitivity to temperature change [7]. The Atlantic ecosystem has a critical thermal boundary at ~10°C across which small temperature changes trigger abrupt community shifts. Furthermore, this thermal boundary seems to be a conservative feature of the pelagic ecosystem since it influences phytoplankton, zooplankton and fish (Figure 4).

This is a significant step forward in understanding climatically driven regime shifts at macroscales. Changes in biodiversity and in the ecosystem function are essential to understanding fish stocks that are already under pressure from fishing. Although mechanistic details remain to be determined, the identification of the 10°C isotherm as a critical boundary, offers an approach to project future changes in the North Atlantic ecosystem. This is an important tool for policy makers for regional and basin scale ecosystem management. The study also offers a broader insight to regime shifts since the regions in which a biome boundary shift occurs appear to be the areas most vulnerable to climate change impacts in the North Atlantic. Other regions embedded within a major biome can maintain relatively ecologically stable over long periods. With the speed and magnitude of climate warming is expected to be elevated [8], abrupt ecosystem shifts will probably accelerate with consequences for fishing. Monitoring of rising variance in biodiversity gives an early warning for ecosystem
Figure 4. Climatological annual mean distribution of upper-ocean chlorophyll concentration as measured by SeaWIFS (a, left; 1997–2006); diversity (Gini index; 1958–2005) of calanoid copepods as measured by the CPR survey (b, left); mean size of female calanoid copepods (c, left; 1958–2005), mean probability of cod occurrence (d, left) and the local variance of these biological parameters as a function of sea surface temperature (right). Each point denotes a geographical pixel on the map. High values of local biological variance are mainly detected between 9 and 12°C with a maximum between 9 and 10°C, indicating substantial variability in these functional attributes in regions with a temperature regime of 9–10°C. Red bars, showing the assessment of the (multivariate) variance when all three indicators are combined, confirmed that high values of variance are located between 9 and 10°C. Grey lines denote the isobath 200 m. Redrawn from [7]).
managers of an impending abrupt shift. The study suggests the paradigm of relative stability of marine ecosystems should be abandoned and that a proactive, dynamic and flexible management strategy, based on a large-scale ecosystem approach and regular monitoring of plankton biodiversity, should be adopted.

3) GOING GLOBAL – THE FUTURE EVOLUTION OF CPR SURVEYS.

CPR Surveys address a global challenge – identifying how and why plankton communities are changing as well as what the consequences of such changes are. This challenge requires a global perspective. Fortunately a number of regional CPR surveys (based in USA, Australia, New Zealand as well as UK) are now established and more surveys are starting each year. However each survey currently works independently and it is now timely to build a more cohesive structure. The aim is now to generate a commonwealth of surveys linked with common objectives with the ability to pool knowledge and experience, cemented through common international standards of sampling, analysis, quality control, data processing and sample and data storage. Such an ocean-wide network of CPR surveys should interface with other biological, chemical and physical sampling and analysing technologies as part of regional integrated marine observing programmes. Further details are identified in [9].

Such a step is essential if coordinated plankton monitoring system at basin scale is to be achieved. There are increasing imperatives to achieve this. Within Europe, there is an opportunity to achieve this through the advent of the Marine Strategy Framework Directive which will require all nations to demonstrate “good environmental status” targets for biological diversity, non-indigenous species, status of fish stocks and of the marine food web, eutrophication, marine litter as well as indicators. These need to be developed for each European regional sea by 2012 and a monitoring programme established by 2014 that includes measurements of phytoplankton and zooplankton.

As global fisheries come under increasing pressure there is an urgent need to understand the “natural rules” that underpin fish sustainability. The long overdue recognition of an ecosystem approach to fisheries management requires understanding of the resources that fish require to grow and develop. This includes their food and all utilise fish stocks require plankton at some stage of their lives.

Understanding climate change requires, again at the basin scale, data on key variables that influence climate. Plankton are the biological pump and an understanding of the activity of these complex biogeochemical processes are now needed on the global scale. The impact of climate on marine ecosystems is also paramount and as has been shown above, the results from the CPR survey provided some of the most convincing evidence for this for IPCC Fourth Assessment Report [8].

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