NOTE

Increased blooms of a dinoflagellate in the NW Atlantic

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ABSTRACT: Sampling by the Continuous Plankton Recorder (CPR) over the NW Atlantic from 1960 to 2000 has enabled long-term studies of the larger components of the phytoplankton community, highlighting various changes, particularly during the 1990s. Analysis of an index of phytoplankton biomass, the Phytoplankton Colour Index (PCI) has revealed an increase over the past decade, most marked during the winter (December to February) months. Examination of the structure of the community using multiple linear-regression models indicates that the winter phytoplankton community composition has changed markedly in the 1990s compared to the 1960s. One phytoplankter, the dinoflagellate *Ceratium arcticum* (Cleve), has undergone dramatic changes in abundance during this period, with pronounced large winter blooms and decreased autumnal levels, and its contribution to the Phytoplankton Colour index values has increased significantly. Other dominant species in the phytoplankton community, both diatoms and dinoflagellates, did not show the same variations over the examined time period. It is suggested that the response of *C. arcticum* is probably a result of previously reported changes in stratification in the NW Atlantic, due to dynamic hydro-climatic (freshening and cooling) events.

KEY WORDS: Phytoplankton · Long-term changes · Blooms · NW Atlantic · *Ceratium arcticum* · Continuous Plankton Recorder

INTRODUCTION

Phytoplankton community structure in the NW Atlantic has received less attention than the higher trophic levels such as fish (Nakashima 1994, Carscadden et al. 2001). Any fundamental changes, however, in the abundance or species composition of autotrophs may impact higher trophic levels. This is especially true in a hydrographically complex area such as the NW Atlantic, with a series of thermohaline and wind-driven currents forming cold–warm water, surface–deepwater interactions (Pickart et al. 1999) and supporting historically rich fisheries in the shelf area (i.e. Grand Banks).

Over the last decade, the well-documented decline of the ground fisheries of the Grand Banks has been attributed to overfishing (Hutchings 1996) as well as environmental pressures (Morgan et al. 2002). The presumption that the cod collapse was solely due to overfishing does not take into account the changes in capelin, a major food source for cod in the area (Lilly 1994), and other environmental factors. During the 1990s, many aspects of capelin biology and distribution changed (DFO 2000a), as well as increases in abundance and extension of distribution of the arctic boreal calanoid *Calanus hyperboreus* (Johns et al. 2001). Changes that may have occurred in phytoplankton abundance and community composition need to be described.

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The composition of the larger components of the phytoplankton community of the North Atlantic is commonly thought to follow an annual succession that begins with the spring diatom bloom and leads to the dominance of flagellates and dinoflagellates in summer. Diatom blooms are normally initiated by the shallowing of the mixed layer and an increase in light intensity in spring (Backhaus et al. 1999). Dinoflagellate communities are associated with post-spring bloom conditions, when surface waters are limited by the amount of nutrients remaining after the initial diatom bloom (Williams & Lindley 1980). In addition, blooms in winter can occur as a response to halostratification following freshwater run-off (Labry et al. 2001).

The Continuous Plankton Recorder (CPR) survey has sampled the phytoplankton and zooplankton community of the NW Atlantic for almost 40 yr (for full methodology see Warner & Hays 1994). Due to the mesh size of the CPR silks, larger phytoplankton species are sampled more quantitatively than smaller species, although small phytoplankton down to 10 μm such as *Scripsiella* and *Prorocentrum* spp. are captured. Robinson (1970) found that the proportion of the population that is retained by the CPR silks reflects the major changes in abundance, distribution and specific composition of phytoplankton. As well as species information, the CPR survey has an index of chlorophyll *a* (chl *a*), the Phytoplankton Colour Index (PCI, Hays & Lindley 1994). Over the last decade the PCI on the Scotian Shelf ecosystem has increased over all seasons, along with an extension of the productive period during winter (DFO 2000b, Sameoto 2001). It is not known

whether this increase is typical of other areas in the NW Atlantic, or whether all members of the phytoplankton community are contributing to the changes observed. In this study, the area of investigation is the neighbouring Grand Banks and northeast Newfoundland Shelf (53–45° W, 45–50° N, Fig. 1), an area of considerable commercial fisheries importance and consistent CPR sampling (n = 5574). Here we aim to show that the changes in PCI, particularly during the winter months, are linked to hydro-climatic variables, and that these may be propagating to higher trophic levels.

MATERIALS AND METHODS

The CPR survey provides a unique long-term dataset of plankton abundance in the North Atlantic and North Sea, using 'ships of opportunity' on regular routes to tow the CPR at about 10 m depth. Each sample represents 18 km of tow and approximately 3 m^3 of filtered seawater (John et al. 2002). The CPR has been deployed in the study area on an approximately monthly basis from 1960 to 2000, although there was reduced sampling from 1978 to 1991, so this period was omitted from data analysis. Phytoplankton species examined are enumerated as the number of fields of view they were present in for each sample (maximum 20). This number is then extrapolated to a numerical abundance using the method described in Robinson & Hiby (1978). In addition to the identification of phytoplankton abundance on each sample, the PCI is recorded as 1 of 4 categories of colour intensity. This gives an estimate of the density of phytoplankton on the CPR silk (Hays & Lindley 1994).

The most abundant phytoplankton species in the study area were identified (those occurring in >1% of samples). Long-term seasonal trends of the most abundant dinoflagellate and diatom species were examined using monthly means. Missing values were interpolated according to Colebrook (1975) if there were sufficient data available (more than 7 mo sampled in a given year). Due to the paucity of sampling during 1960 and 1961, these periods did not meet the criterion for inclusion and were therefore omitted from seasonal analysis, leaving the periods 1962 to 1978 and 1991 to 2000. To identify phytoplankton species that contributed to the PCIs in each of these periods, multiple linear-regression models were constructed. A forward–backward step-
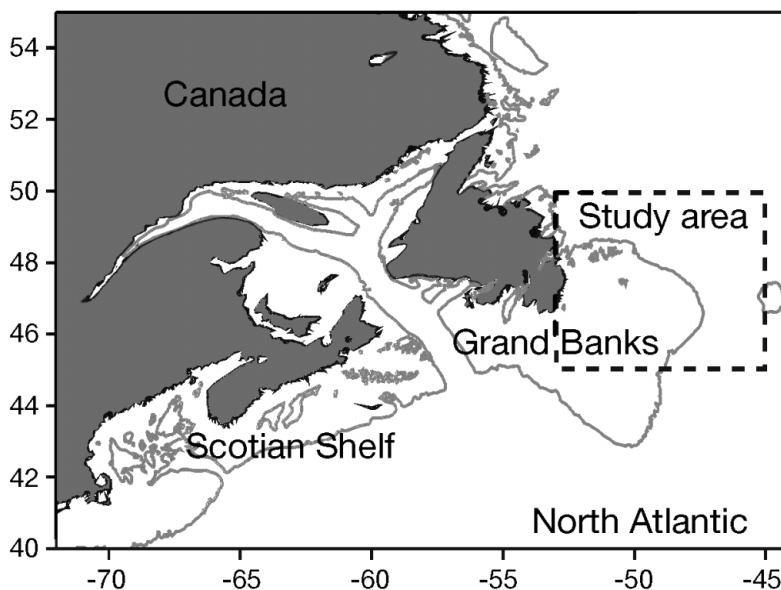

Fig. 1. Map of NW Atlantic. (- - -) indicates study area

wise model-fitting procedure was used based on the Akaike's Information Criterion statistic (Venables & Ripley 2002).

RESULTS AND DISCUSSION

PCI values have increased over the time period, and are most pronounced during the winter months (December to February, Fig. 2), similar to that noted in the southwest on the Scotian Shelf (Sameoto 2001). The contribution that phytoplankton taxa make towards this increase in PCI during winter for the peri-
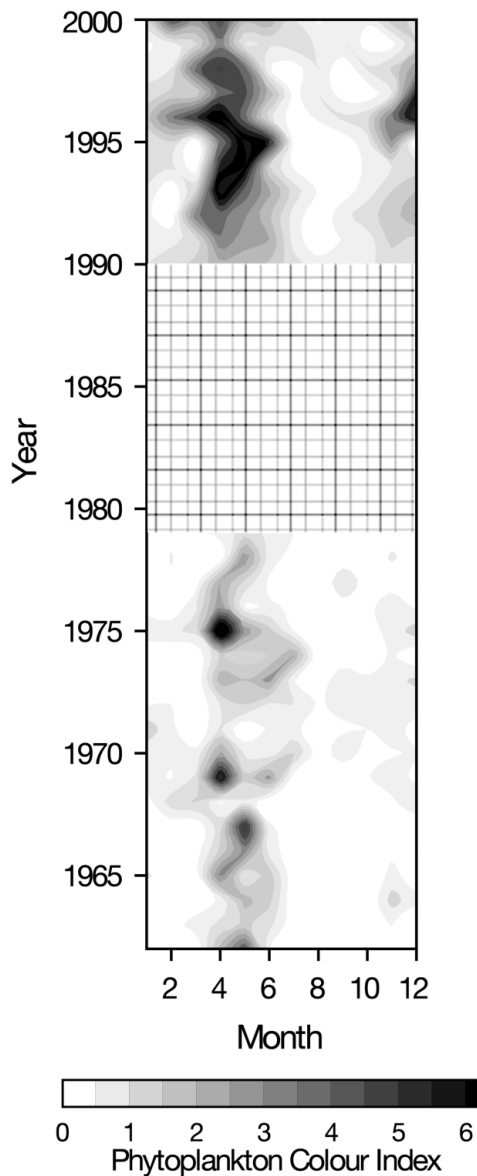
ods 1962 to 1979 and 1991 to 2000 is shown in Table 1. Note that all slopes were positive, indicating that (as expected) increases in abundance of each taxa increased the greenness of the silk. Species are ranked in order from the most important contributors (highest r^2 values) to the least. Viewing both time periods together, it is apparent that significant changes in the phytoplankton community have taken place. The actual number of contributing species to winter PCI has altered, from 14 in the 1962 to 1979 period, to only 9 during the 1991 to 2000 period, indicating that the number of species dominating the phytoplankton community has decreased. In addition, the rank importance of various taxa to PCI values was different in the 2 periods. This was typified by the arctic-boreal dinoflagellate *Ceratium arcticum* (Lebour 1925, Smayda 1958, Okolodkov & Dodge 1996), which did not contribute to the winter PCI in 1962 to 1979, but was the second most important taxon in the 1991 to 2000 period (Fig. 3). This recent strong dependence of PCI on *C. arcticum* abundance is highlighted by the high correlation in the second period ($r^2 = 0.78$, $p < 0.01$, $n = 9$), coupled with the absence of a relationship in the first period. No other dinoflagellate or diatom species were

Fig. 2. Long-term seasonal contour plot of Phytoplankton Colour Index (PCI)

Table 1. Final multiple-regression model for predicting the Phytoplankton Colour Index (PCI) from a suite of 23 phytoplankton taxa for (a) 1962 to 1978 ($r^2 = 53.0\%$) and (b) 1991 to 2000 ($r^2 = 51.8\%$). Phytoplankton taxa are ordered in terms of their relative importance for predicting Phytoplankton Colour (r^2)

| Taxon	Slope	r^2	p
(a) 1962 to 1978			
Thalassiosira spp.	5.7×10^{-6}	36.1	<0.0001
Phaeoceros spp.	6.4×10^{-6}	10.7	<0.0001
Thalassiothrix longissima	4.6×10^{-6}	2.9	<0.0001
Coscinodiscus spp.	1.1×10^{-5}	0.9	<0.0001
Rhizosolenia hebetata semispina	5.8×10^{-6}	0.7	<0.0001
Hyalochaete spp.	1.8×10^{-6}	0.3	<0.0001
Ceratium macrocerus	2.6×10^{-5}	0.3	<0.0001
Rhizosolenia styliformis	7.8×10^{-6}	0.3	<0.0001
Ceratium fusus	2.6×10^{-6}	0.2	<0.0001
Thalassionema nitzschiodes	3.9×10^{-6}	0.1	0.0004
Fragillaria spp.	3.5×10^{-6}	0.1	0.0007
Ceratium tripos	7.7×10^{-6}	0.1	0.0020
Corethron criophilum	5.1×10^{-5}	0.1	0.0103
Pseudo-nitzschia spp.	3.8×10^{-6}	0.1	0.0152
(b) 1991 to 2000			
Thalassiosira spp.	5.2×10^{-6}	26.3	<0.0001
Ceratium arcticum	6.5×10^{-6}	12.1	<0.0001
Thalassiothrix longissima	6.1×10^{-6}	7.1	<0.0001
Phaeoceros spp.	4.2×10^{-6}	3.0	<0.0001
Thalassionema nitzschiodes	1.9×10^{-5}	1.3	<0.0001
Corethron criophilum	3.9×10^{-5}	0.8	<0.0001
Pseudo-nitzschia spp.	3.3×10^{-5}	0.4	0.0003
Ceratium horridum	1.7×10^{-5}	0.4	0.0006
Coscinodiscus spp.	1.3×10^{-5}	0.3	0.0035
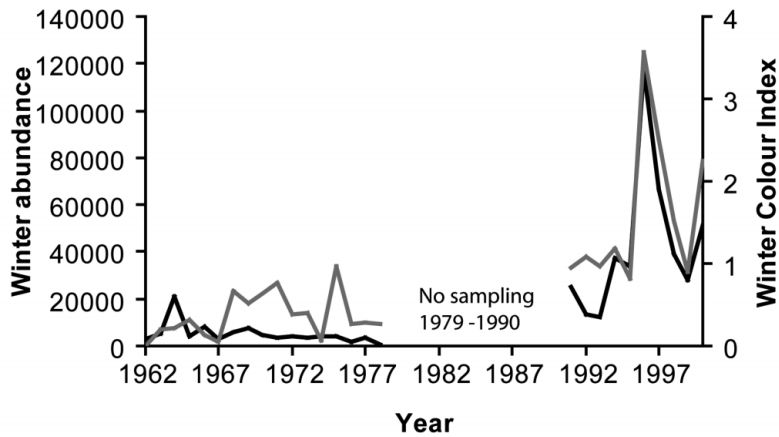
Fig. 3. *Ceratium arcticum.* Long-term winter abundance (black) and long-term winter Phytoplankton Colour values (grey). Density of *C. arcticum* = mean cell count per sample (~3 m^3)

correlated with changes in PCI; and none have exhibited similar seasonal changes as *C. arcticum* has, although there has been an increase in *Thalassiosira* spp., but with no appreciable seasonal changes. The contribution that *Thalassiosira* spp. makes on the winter PCI value has declined.

Dinoflagellates, such as *Ceratium arcticum*, have evolved to exploit nutrient-depleted, well-stratified conditions (Holligan 1987). It is unlikely that the increase in *C. arcticum* is due to eutrophication, as nutrients in the area have varied little over the past 20 yr (P. Pepin, Department of fisheries and oceans; DFO, pers. comm.), and the natural transport of nutrients seasonally onto the Banks would overwhelm any effect of eutrophication (Pepin & Paranjape 1996). Therefore the increase in the PCI as well as *C. arcticum* is likely to be attributable to other factors. The ocean climate of the NW Atlantic is driven by thermohaline mechanisms, and these have an effect on large-scale processes such as the Labrador Current. Changes in the intensity of the Labrador Current have altered the annual structure of haline stratification. Work by Craig et al. (2001, 2002) indicates a change in haline stratification on the inner Newfoundland Shelf, with an index increasing significantly over the past decade. This is because surface waters throughout the 1990s have been fresher in the study area (ICES 2001), creating more persistent stratification. It is likely that this haline stratification plays an important part in *C. arcticum* abundance through a delay in the breakdown or initiation of an earlier stratified layer, although the exact mechanisms are not known. Haline stratification is known to stimulate phytoplankton blooms in coastal environments, even during winter months (Raymont 1963, Kimmerer 2002). The massive abundance of *C. arcticum* in 1996 (Fig. 3), where it contributed almost 47% of the total

recorded phytoplankton community, corresponded to the freshest Labrador seawater event on record (Dickson & Turrell 2000). SST in the area has fluctuated during the period 1960 to 2000, as can be seen from records of St. John's Harbour (DFO 1999). High temperatures were recorded in the 1960s, and declined towards the 1990s (with a minimum during the early 1990s). The exception to this was in 1996, when the 'flip' in the NAO resulted in temperatures well above normal in the area. Although the high NAO value, high temperature and high *C. arcticum* values could suggest a possible linkage, marked changes in the phytoplankton community were apparent from 1991, and SSTs have varied considerably between high and low values over the last decade. In addition, *C. arcticum*, as an arctic species, is present only in waters below 15°C (Dodge & Marshall 1994).

A remaining point to address is how *Ceratium arcticum* has been able to bloom and flourish successfully during winter months over the last decade. It is possible that *C. arcticum* is adapted to flourishing under low-light conditions. For example, the sister species of *C. arcticum*, *C. longipes*, which is a cold water form, has a rate of photosynthesis over 20 times as great as the more cosmopolitan species *C. fusus* (Dodge & Marshall 1994). The increased stratification of the water in the Grand Banks area could suggest reduced turbidity, allowing increased light exposure to marine organisms (IPCC 2001), which is utilised more efficiently by *C. arcticum*.

The Grand Banks has undergone wide-scale, identifiable changes in the marine ecosystem over the last decade, with the fisheries collapse the best documented. Although this has been attributed to anthropogenic influences (overfishing), not all research corroborates this theory. The changes noted in capelin ecology and distribution, forage fish for cod, as well as arctic-boreal zooplankton have been attributed to hydro-climatic variations (DFO 2000a, Johns et al. 2001). It is likely that shifts in the phytoplankton community of the Grand Banks area, due to an increase in stratification and changing hydro-climatic conditions, has had an additional affect on higher trophic levels.

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