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HORIZONS

Phytoplankton blooms: a 'loophole' in microzooplankton grazing impact?

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Phytoplankton size and relations between phytoplankton and microzooplankton (ciliates and heterotrophic dinoflagellates) biomass are analysed in 12 globally distributed areas. In view of the results, a hypothesis is posed where blooming species are those able to escape control by microzooplankton through a combination of predation avoidance mechanisms (e.g. larger size, colonies, spines, and toxic compounds) at the beginning of the bloom. Factors that help to enhance subsequent bloom development include positive feedback from the poor nutritional status of the phototrophic prey which adversely affects predation, inter-microzooplankton grazing and top–down grazing by mesozooplankton on microzooplankton. Blooming conditions are interpreted as physical or chemical perturbations disrupting the predator–prey controls that normally operate at the level of the microbial loop, opening 'loopholes' into which some phytoplankton species populations can explode.

INTRODUCTION

Phytoplankton blooms are unique events in nature where photoautotrophic biomass may increase by up to 3 orders of magnitude over a time scale of days by a combination of growth, accumulation and physical advection exceeding loss processes such as lysis, sinking and predation. The species composition of these blooms plays an important ecological role. Blooms dominated by fast-growing species such as diatoms contribute substantially to global biogeochemical cycles (Smetacek, 1998), those dominated by haptophytes like *Phaeocystis* sp. or *Emiliania huxleyi* are, in addition, important sources of dimethyl sulphide (DMS), a biogenic gas affecting cloud formation and albedo (Malin, 1997). Others, notably Raphidophytes and dinoflagellates, may form harmful algal blooms adversely affecting shell and finfish production (Hallegraef, 1993).

The predator–prey link is critical for the control of primary production; this is in part a classic match–mismatch issue (Cushing, 1990), but is in fact more complex. Although the relative predation impact is still a subject of debate (Dolan and McKeon, 2004), microzooplankton grazing is generally accepted as being the main predatory pressure on planktonic primary production, consuming 60–70% (Calbet and Landry, 2004), whereas mesozooplankton, and in particular copepods, consume in general 10–40% of the primary production (Calbet, 2001). The trophic pathway through microzooplankton results in a decrease in the export of primary production both in terms of sinking and/or consumption by higher trophic levels. It also, through rapid regeneration and cycling of nutrients, acts to maintain high phototroph nutrient status and thence growth rates (e.g. Flynn and Fielder, 1989). Ultimately, then, microbial loop primary production is limited, biotically, by predatory pressure; directly through grazing, or indirectly through a lack of nutrient regeneration (Flynn, 1989). Blooms may thus be considered as events generated principally by a failure of the microzooplankton grazers to contain phytoplankton production. Through the analysis of phytoplankton composition, phytoplankton biomass and microheterotroph (ciliates and

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heterotrophic dinoflagellates) biomass data, one may search for and speculate upon the possible link between the particular characteristics of the bloom forming phytoplankton taxa and microzooplankton predation pressure.

Bakun and Broad (Bakun and Broad, 2003) proposed the idea that 'loopholes' in the fields of biological control organisms resulting from disruptive environmental perturbations may in fact lead to remarkable recruitment success. Success lies in exploiting loopholes in the established biological controls. In this study, we use 'loophole' in the sense of Bakun and Broad, loophole in the fields of biological controls on recruitment success.

METHOD

Samples were taken from 12 different areas, in the Norwegian Sea (NWS), North Atlantic (NA), Iceland Basin (ICB), Irminger Sea (IRS), Long Island Sound (LIS), North Sea (NS), English Channel (EC), the Benguela upwelling (BU), the Oregon upwelling (OU), Indian Ocean (IO), mesocosms in the Bergen fjord (BM) and in a meridional transect in the Atlantic (AMT) (Fig. 1). The database has already been partially (only surface data) used for a global biodiversity analysis and details of the sampling can be found in Irigoien *et al.* (Irigoien *et al.*, 2004, see also additional material in that reference for sampling station details).

In these areas, water samples, for nano and microplankton (>2 μm, nanoplankton + microplankton) species identification and carbon biomass estimation, were generally collected and preserved in 1% final concentration Lugol's iodine solution (Holligan and Harbour, 1977). The data set includes all data collected, comprising those obtained at different depths at the same station (North Atlantic, Indian Ocean and Atlantic meridional transect). Subsamples (100 ml) were settled (Utermöhl technique) and counted with an inverted microscope. Phytoplankton carbon biomass was estimated from cell volume (Strathmann, 1967) using a factor of 0.21 pg C μm^{-3} (Ohman and Runge, 1994) for ciliates. Heterotrophic dinoflagellates were separated from autotrophic forms according to taxonomic considerations (Lessard and Swift, 1986). In chains and colonies, cell carbon estimates refer to single cells within colonial species. The total number of data points in the global database is 1083. All the biomass data are available in the additional information provided on-line. Curves were fit to data using the S-plus 2000 software spline smoother routine (cubic spline). The English Channel seasonal cycle has been further analysed based on phytoplankton biomass and composition samples and temperature profiles collected weekly from 1992 to 2003 (Data available at www.pml.ac.uk\L4), and nutrient data were collected weekly from 2000 to 2004.

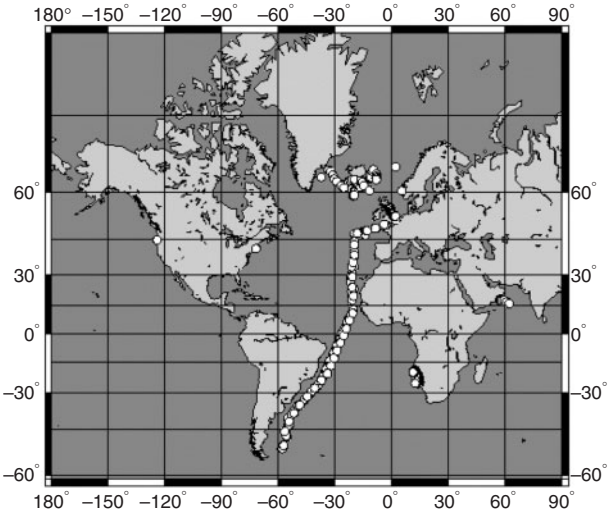

Fig. 1. Map of the sampled stations.

RESULTS

At low total phytoplankton concentrations small flagellates (<5 μm) generally represent from 70 to almost 100% of the total autotroph biomass (Fig. 2a). However, at concentrations higher than 20 mg C m^{-3} there is a rapid decrease in the contribution of small flagellates to the total phytoplankton biomass, as their contribution relative to the total levels off (Fig. 2b). These small cells are unable to capitalise on improved conditions that occur from time to time. The positive relation between average cell size and total phytoplankton biomass (Fig. 2c) is associated instead with blooms of diatoms (BU, OU and LIS), dinoflagellates (EC), coccolithophorids (BM) or the haptophyte *Phaeocystis* spp. (NS and IRS). The biomass of microzooplankton, namely ciliates and heterotrophic dinoflagellates, increases with total phytoplankton concentration but plateaus at around 50 mg C m^{-3} (Fig. 2d and e), coincident with the pattern for small flagellates (Cf. Fig. 2a). Hence, there is a positive relationship between microheterotrophs biomass and small flagellates biomass (Figs 2f and g). There is also a positive relation between heterotrophic dinoflagellates biomass and ciliates biomass (Fig. 2h).

The English Channel data show an increase in both total phytoplankton biomass and small flagellates biomass coinciding with the warming and stratification period (Fig. 3a, b, d and e). However, and accordingly with other data sets, the percentage of the small flagellates on the total phytoplankton decreases during this period (Figs 2 and 3),

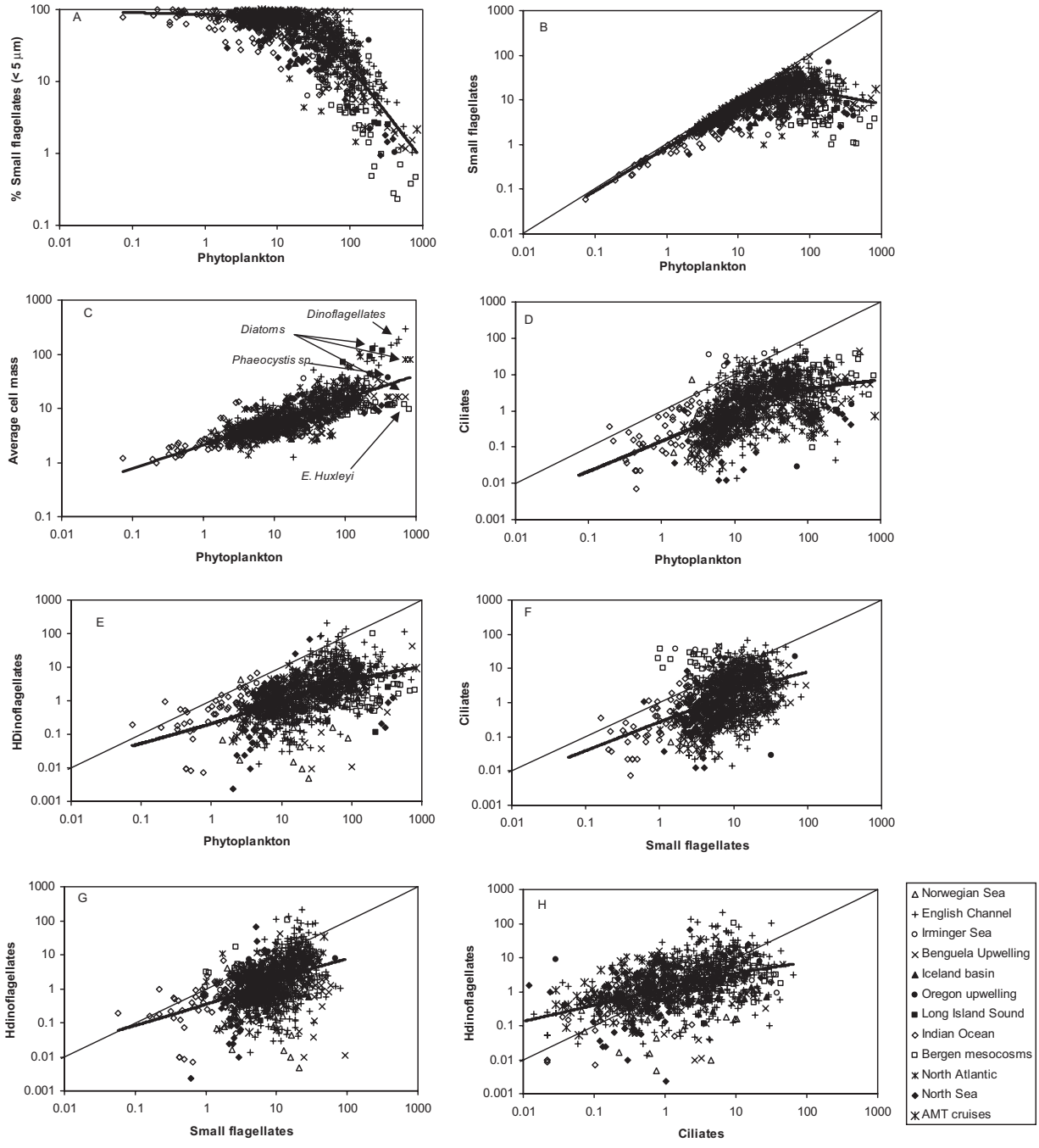

Fig. 2. (**A**) Small flagellate biomass versus total phytoplankton biomass. (**B**) Percentage of small flagellates in the total phytoplankton biomass versus the total phytoplankton biomass. (**C**) Average cell mass (pg C cell^{-1}) versus total phytoplankton biomass (modified from Irigoien *et al.*, 2004). (**D**) Ciliates biomass versus total phytoplankton biomass. (**E**) Heterotrophic dinoflagellates biomass versus total phytoplankton biomass (**F**) Ciliates biomass versus small flagellates biomass. (**G**) Heterotrophic dinoflagellates biomass versus small flagellates biomass. (**H**) Heterotrophic dinoflagellates biomass versus ciliates biomass. The thin line in panels A, D, E, F, G and H indicate the 1:1 line. The bold line is the trend obtained through spline smoothing. All biomass data in mg C m^{-3}.

resulting in an increase of the average cell size (Fig. 3g). This increase of the average cell size coincides with the summer nutrient depletion in the water column (Fig. 3c).

DISCUSSION

Although there is considerable scatter (of magnitude dimensions), these results, and in particular the form of

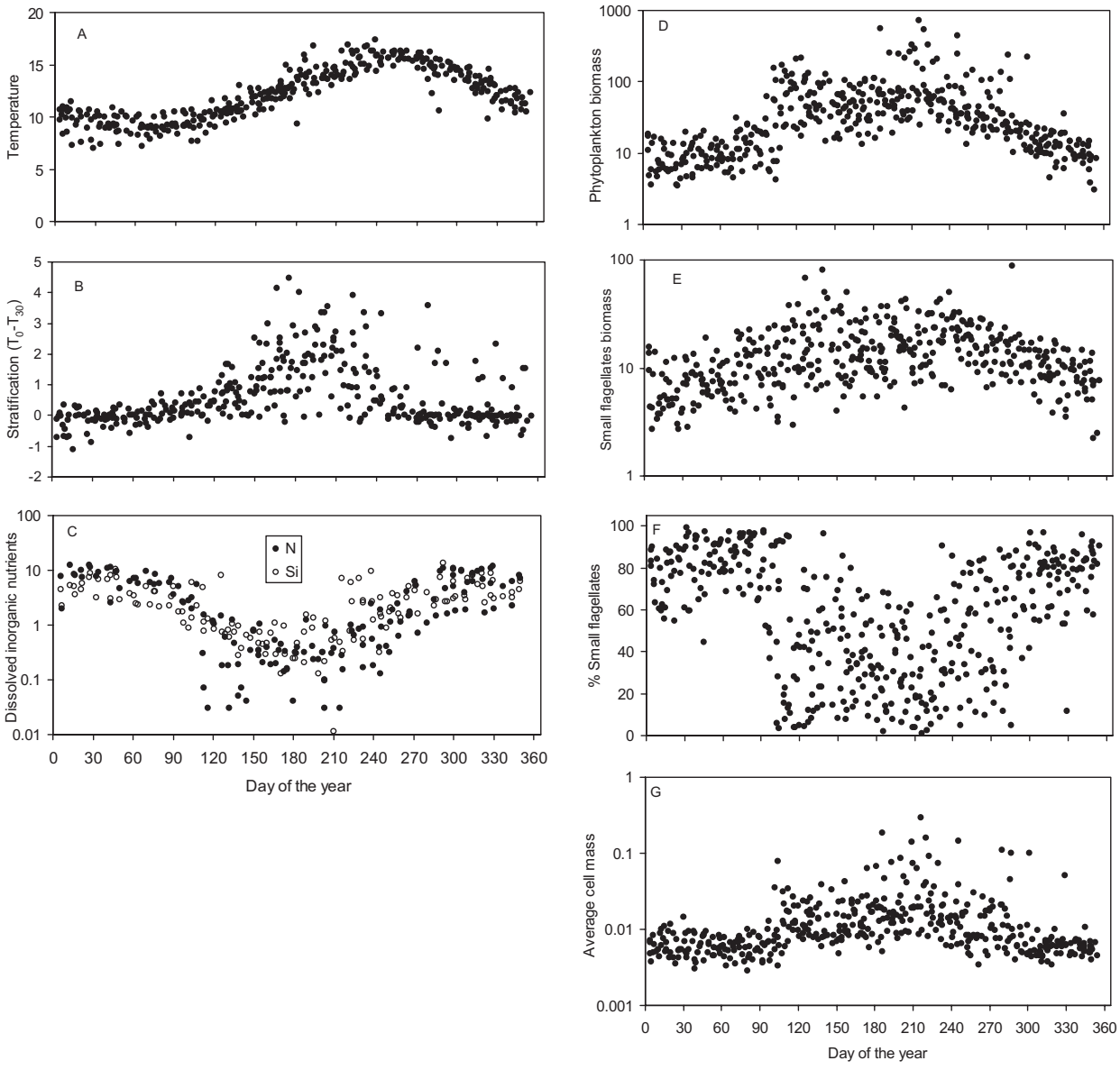

Fig. 3. Seasonal variation at station L4 in the English Channel of (**A**) Sea surface temperature (°C). (**B**) Stratification index, temperature surface to temperature 30 m. (**C**) Total dissolved inorganic N and Silicate concentrations (μmol l^{-1}). (**D**) Total phytoplankton biomass (mg C m^{-3}). (**E**) Small flagellates biomass (mg C m^{-3}). (**F**) Percentage of small flagellates on total phytoplankton. (**G**) Average cell mass (pg C $cell^{-1}$).

the trend lines through the data, pose a number of questions. Why does the contribution of the small flagellates to phytoplankton biomass decline as the total biomass increases above a critical level (Fig. 2a and b), the increase in total biomass being due to larger cells (Fig. 2c)? How is it possible that the biomass of the main consumers of primary production (microzooplankton) saturates in relation to the increase in phytoplankton biomass during the blooms (Fig. 2d and e)? Even if not proportional, an increase may be expected; that is, unless the organisms dominating these blooms are unfavourable prey items, and/or something else limits microzooplankton biomass such as predation by mesozooplankton or inter-microzooplankton grazing. We discuss factors driving the formation and threshold limitation of these blooms below.

Bloom formation drivers

Algal defences against microzooplankton

We propose that perturbations (nutrients and light) open a loophole in the microbial loop where phytoplankton species able to escape predation pressure are those that form dense blooms. Critically, they need to escape

predatory pressure at the potential point of entry into the loophole. This means that microzooplankton should in particular be discouraged from consuming them. Total exclusion from grazing is not required, just a disparity of grazing rates such that some species attain positive net growth whereas other phytoplankton remain under grazing control in the presence of the favourable initiating perturbation. Our data suggest that small flagellates also benefit from the improved growth conditions (see small biomass increases in Figs 1a and 2e) but are not able to translate the improved physiological conditions into a dense bloom.

Blooming species are generally large (diatoms and dinoflagellates), colony forms of small organisms (diatom chains and *Phaeocystis*), armoured (diatoms spines and frustules and coccolithophorids coccoliths), and/or contain chemicals that may adversely affect predators such as toxins (dinoflagellates), DMS (haptophytes) and aldehydes (diatoms). While most of those features have generally been interpreted as a protection against grazing by copepods (e.g. Miralto *et al.*, 1999; Hamm *et al.*, 2003), they actually seem to be a rather ineffective in this capacity. Copepods are able to manipulate chains to eliminate the spines (J. R. Strickler, University of Wisconsin, personal communication.) and to crush the frustules in diatoms. They can also consume *Phaeocystis* colonies (e.g. Hansen *et al.*, 1990; Irigoien *et al.*, 2000) and coccolithophorids (e.g. Harris, 1994). The effect of dinoflagellate toxins on copepods in the field is unclear (see review in Turner and Tester, 1997), but often they do not inhibit ingestion (e.g. Teegarden *et al.*, 2001; Riser *et al.*, 2003) with copepods seeming to act rather as a vector than as a target (e.g. Turner *et al.*, 2000; Durbin *et al.*, 2002). Likewise, chemical compounds such as aldehydes in diatoms, that are only produced after cell damage (Pohnert, 2000) do not inhibit continued predation in the short-term, and hence do not make evolutionary sense as a defence mechanism against mesozooplankton (such as copepods).

On the other hand, one may expect features such as size and spines (increasing apparent volume) to be a more effective defence against microheterotrophs (Fenchel, 1980) and to explain the increase in cell average size with phytoplankton concentration (Fig. 1c). DMS has been shown to inhibit grazing by ciliates (Strom *et al.*, 2003) and production of mutagenic aldehydes after cell damage in diatoms makes more evolutionary sense as defence against unicellular protozoans. Although there is evidence of predation on chains of spiny diatoms by heterotrophic dinoflagellates (Jacobson and Anderson, 1986) certainly an adverse effect, even just a slowing down of predation rate, against a single-celled predator with a short generation time may be expected to be more significant than against mesozooplankters. Such an effect has been shown in field studies where microzooplankton community grazing rates on diatoms and *Emiliania huxleyii* are usually lower than on the other components of the phytoplankton community (Burkill *et al.*, 1987; Verity *et al.*, 1996; Fileman *et al.*, 2002; Merico *et al.*, 2004). The differences we find in the relation between microzooplankton and phytoplankton biomass when considering the whole phytoplankton community (Fig. 1d and e) and when considering only the small flagellates biomass (Fig. 1f and g) seem to confirm the results of previous studies (Burkill *et al.*, 1987; Verity *et al.*, 1996; Fileman *et al.*, 2002).

In the evolutionary arms race between marine phototrophs and their predators, the bulk of the defensive weaponry may be expected to be oriented against the main predator. Accordingly, as microzooplankton seem to be the main source of phytoplankton mortality (Calbet and Landry, 2004), so it is the success or failure of this microbial loop predator–prey relationship, traditionally thought to be well matched, which may govern the initial entry to the loophole state.

Size and nutrients

The observation of oligotrophic seas phytoplankton dominated by small cells whereas larger cells appear in nutrient rich waters has resulted in the development of theories relating cell size to nutrient concentration. This relation has been attributed to the surface/volume ratio (Raven, 1998) or to geometrical considerations (Jumars, 1993), in both cases interpreting nutrient transport across the membranes in terms of osmotrophy. Our results from the English Channel seasonal study suggest that the cell size—nutrients relation needs to be revisited. The relation appears not to be between cell size and nutrients, but between cell size and growth rates or growing conditions (assuming biomass as growth proxy for a system with a very high turnover). A comparison between marine ecosystems with different nutrient regimes would produce the same result (Fig. 1c), but would be misleading about the underlying mechanism if decreased growth rates in oligotrophic areas are not considered (Marañon, 2005). In the cell size—nutrients relation it has to be also considered that phytoplankton cells are not really osmotrophs, but that nutrients are taken up (in the main) by active transport, by transport proteins synthesised and regulated for that purpose. Cells can often take up nutrients many times faster than maximum steady state requirements. The English Channel data seem to indicate that light limitation may play a more important role than nutrients on the final size structure (Finkel *et al.*, 2004). On the other hand, a relation between cell size and growth rate fits our 'loophole' hypothesis, where large cells will take more benefit of improved growing conditions by their ability to escape high predation rates. In any case, our observations

indicate that further research is necessary on the cell size—nutrient concentration—growth rate relationship.

Diet switching by microzooplankton

Other mechanisms may contribute to limit microzooplankton grazing impact once the initial entry point has been crossed and the bloom is developing. It has long been known that microzooplankton exhibit significant levels of prey selectivity (e.g. Verity, 1991). Microzooplankton, like mesozooplankton, also feed on prey other than phototrophs, including exhibiting cannibalism (Goldman and Caron, 1985). In the presence of unfavourable microalgae, they may thus turn against predation of phototrophic prey. As mentioned above, this has potential for promoting the rapid development of a positive feedback loop. An experimental example is seen in Flynn *et al.* (Flynn *et al.*, 1996), where an otherwise poor competitor (*Isochrysis*) ends up dominating the system when its phototrophic competitor (*Dunaliella*) is grazed out and the microzooplankter (*Oxyrrhis*) then turns against itself as it avoids the by now N-starved *Isochrysis*. Once positive feedback develops the traditional predator–prey interaction can collapse very rapidly.

Enhanced mortality of microzooplankton

The form of Fig. 1d is also consistent with a decrease in grazing on microalgae associated with a decline in phototroph quality as large blooms exhaust nutrients, accumulating excess C and secondary metabolites. It is not possible to set N:C values to these data, though 100 mg C m^{-3} of nutrient-sufficient algal biomass would equate to the use of ~1 μM DIN, so certainly the high biomass blooms may be expected to have been nutrient-stressed. Figure 1d is also consistent with the development of increasing inter-microzooplankton predatory activity as concentrations of these organisms increase. It is likely that the combination of these events could trigger a switch away from predation on the bloom-forming phototroph and that the system may be very sensitive to that state. In addition, it is now known that microzooplankton are prey items by mesozooplankton (Irigoien *et al.*, 1998; Irigoien *et al.*, 2004). Mesozooplankton, especially copepods, benefiting from the general increase in food concentration during the blooms, will also increase predation pressure on microzooplankton. The plateau in Fig. 1(d) may correspond also to the microzooplankton density at which mesozooplankton predation becomes significant. Hansen *et al.* (Hansen *et al.*, 1993) describe how microzooplankton become the dominant food for mesozooplankton during blooms of *Phaeocystis*, the phototroph being deselected by the mesozooplankton. In the early stages of a *Phaeocystis* bloom, the solitary cells are well grazed by the microzooplankton but that control halts when colonies start to form (Verity, 2000), a process that has been associated with the use of nitrate rather than ammonium (Riegman and van Boekel, 1996). These types of events provide the loophole for escape of *Phaeocystis*, enabling it to bloom.

Bloom threshold drivers

At the peak of the bloom, net algal growth halts. The large, invariably nutrient-limited bloom collapses because of a combination of processes. During that event there will be limited regeneration of inorganic nutrients that are suitable for support of primary production as either biomass sinks, limiting elements are conserved within the predators (as per stoichiometric arguments) or growth efficiency falls and more material is voided either to sink or to be degraded via microbial loop processes. Inorganic nutrients that are liberated will be consumed rapidly; nutrients entering phytoplankton will enhance algal biomass but will be insufficient to improve the nutrient status (and hence food quality) until the bloom size decreases significantly. The loss of nutrients from the surface waters needs physical intervention to replace them, restarting the process with a background population of nutrient-sufficient mixed algal species favouring phytoplanktivory amongst the zooplankton. The microbial loop re-equilibrates itself, whereas the mesozooplankton-dominated 'metazoan loop' (Flynn, 1989) is relegated to a minor role.

When the physical and chemical conditions (light and nutrients) again allow a significant increase in the phytoplankton growth rate, species subjected to lower microzooplankton mortality would be able to enter the loophole because microzooplankton would not be able to consume 100% of that species production. A number of species may be able to enter such a loophole at that point in time and space but the best equipped phytoplankton species starts to bloom, consuming nutrients and perhaps releasing allelopathic chemicals inhibiting the growth of competitors (Fistarol *et al.*, 2003, 2004). Once nutrients stress starts to develop, a positive feedback between poor phytoplankton quality and grazing occurs, limiting subsequent grazing and nutrient regeneration. The bloom develops to its maximum extent, sucking up all nutrients available to it. Although more research is necessary, it is interesting to observe that within diatoms, only a few genera seem to be involved in the really large blooms (additional material within Irigoien *et al.*, 2002). These results suggest that, as for other systems (Worm and Duffy, 2003), in marine phytoplankton blooms the species composition is not simply a consequence of the high productivity, but also a cause.

CONCLUSIONS

At a different scale, the mechanisms proposed here are in general similar to those advanced by Bakun and Broad (Bakun and Broad, 2003) in order to explain the high yield of the Peru-Humboldt current fisheries in comparison with the other Eastern Boundary Current systems (Benguela, Canary and California currents). The idea is that physical or chemical perturbations (El Niño for fisheries and nutrient inputs for phytoplankton) disrupt biological controls opening 'loopholes' into which some species can explode (see a possible example in the Ironex II experiment Landry *et al.*, 2000).

In ecological terms the 'loophole' blooming mechanism can be translated as an ecosystem at maturity, with strong trophic links, where a perturbation loosens some of the trophic links allowing an opportunistic species to colonise (dominate) the ecosystem. The perturbation not only breaks down the equilibrium in the system but also promotes an improvement of the growing conditions (e.g. more nutrients and light). This mechanism links bottom-up (physical perturbation) with top–down (predation) controls, explaining both the increase in biomass (bottom–up improvement of the growth conditions) and the change in species composition (predation avoidance).

For phytoplankton the most immediate perturbation may result most likely from a change in illumination. While relief from nutrient stress, or increases in temperature are also important factors, neither are so immediate as light either in effect on the ecosystem or in response by the organisms. Further, changes in temperature will affect predator activity (indeed they may be more sensitive to temperature changes), and regenerated nutrients are sourced primarily from predators. Changes in mixing depth, atmospheric conditions and associated factors impacting on light and the introduction of new nutrients are thus most likely the factors promoting entry to the loophole.

Models of marine ecosystems generally either lump all phytoplankton together, or separate them along the lines of diatoms and non-diatoms. They also typically fail to take account of changes in zooplankton growth efficiency or prey preference according to prey nutritional status, despite clear evidence of the importance of these events. When included, these factors have highly significant impacts on model output beyond that implicit with pure stoichiometric concerns (Roelke, 2000; Mitra *et al.*, 2003; Mitra and Flynn, submitted for publication). In addition, given the importance of microzooplankton, and that most of these will be predated by other microzooplankton if not by mesozooplankton, one could also argue that the closure term describing the fate of zooplankton (e.g. in NPZ-type models) should also be a function of phytoplankton quality (i.e. N:C) and zooplankton biomass density, rather than the simple linear or quadratic terms commonly employed (Evans and Garçon, 1997). Much field and theoretical research is needed to explore this loophole concept further, but evidence is gathering that some level of re-evaluation of plankton dynamics is warranted, with commensurate modifications required for modelling bloom events.

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