P. Mudie

Palynological records of red tide-producing species in Canada: past trends and implications for the future

Peta J. Mudie [a,*], André Rochon [a], Elisabeth Levac [b]

[a] *Geological Survey of Canada-Atlantic, P.O. Box 1006, Dartmouth, NS, Canada B2Y 4A2*
[b] *Centre for Marine Geology, Dalhousie University, Halifax, NS, Canada B3H 3J5*

Abstract

Increases in 'red tides' and other harmful algal blooms (HABs) during the past 50 yr on both the Atlantic and Pacific coasts of Canada suggest that global-scale factors, such as climate change and increased international shipping trade, are the driving forces. Because the historical record is too short to understand the long-term dynamics of HABs, the Holocene history of harmful phytoplankton species was examined using ultra-high resolution studies (annual to decadal scale) of dinoflagellate cysts as a proxy for 'red tide' production. Paleoecological transfer functions were then applied to the cyst assemblage data to determine correlations with changes in sea surface temperature and salinity.

Pacific records were obtained from varved marine sediments in Saanich Inlet, British Columbia, and in the Santa Barbara Basin off California. Comparison of annual cyst production and historical plankton data provides cyst:theca ratios from which the magnitude of past bloom size can be evaluated. The 10 500-yr Pacific record clearly shows that the largest blooms correspond to cysts of *Protoceratium reticulatum* and *Gonyaulax spinifera* during the early Holocene. Sporadic blooms of potentially toxic *Alexandrium* spp., *Lingulodinium polyedrum* and *Gymnodinium* spp. also occurred from ca. 7000 to 5000 yr BP and more frequently from ca. 2000 to 3000 yr BP. Individual Holocene blooms were up to 10 times larger than in the historical record but they almost always occurred sequentially, without overlap of 'red tide' species. In pre-historical times, the bloom cycles started and stopped abruptly in 10 yr or less, and they persisted for about 100–1000 yr. In contrast, the variability and near-concurrence of species blooms in the modern (past 60 yr) record is unmatched in the past, and suggests disequilibrium of the natural ecosystem structure.

Atlantic records from La Have and Emerald basins on the Scotian Shelf are less precise because bioturbation limits time resolution to ca. 25 yr. However, cyst abundances of cf. *Alexandrium*, *Protoceratium reticulatum*, *Gonyaulax spinifera* and *Lingulodinium polyedrum* were also an order of magnitude larger in the early Holocene, where they correspond to a summer sea surface warming of 2–5°C. Lesser peaks also appear during the past 2000 yr where they apparently correspond to a slight increase in winter temperature. There is no evidence of much lower salinity that would support stronger stratification.

The similarity of pre-industrial age cyst records of 'red tide' histories in the oceanographically different Pacific and Atlantic regions of Canada indicates that climate change (including surface temperature and storminess) is the main driving force stimulating blooms. This implies that HABs will reoccur regardless of efforts to limit spreading. However, reduced pollution may decrease the HAB diversity, thereby stabilizing the population dynamics and increasing the predictability of bloom occurrences. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: red tides; harmful algae; dinoflagellate cysts; Holocene; marine varves

---

* Corresponding author. Fax: +1-902-426-4104.   *E-mail address:* mudie@agc.bio.ns.ca (P.J. Mudie).

1. Introduction

'Red tides' is the name commonly used for occurrences or blooms of harmful algae (HABs) that result from local or regional accumulations of a single phytoplankton species which have a negative affect on the environment (Anderson, 1994; Smayda, 1997). During a classical 'red tide' outbreak, the plankton cells divide faster than they are consumed or die and they accumulate near the surface so that the water takes on the color of the algal pigments. The actual color of a so-called 'red tide' therefore depends on the pigment composition of the algal species causing the bloom. The colors range from the classical blood red color of biblical times (Anonymous, in Exodus 7:20–21) produced by the dinophycin pigment of thecate dinoflagellates, e.g. *Alexandrium tamarense* and *Pyrodinium bahamense*, through reddish brown, green and yellow colors produced by athecate dinoflagellates, e.g. *Karenia mikimotoi* Dauberg et al. (2000), and chain-forming diatoms, e.g.

Table 1
Species listed as producing red tides or HABs, showing corresponding theca- and cyst-stage names and the associated toxic effect

Motile name	Cyst name	Type of toxicity
Akashiwo sanguinea	No cyst	Non toxic
Gonyaulax digitale	*Bitectatodinium tepikiense*	Non-toxic
Gonyaulax spinifera group	*Spiniferites elongatus, S. membranaceus, S. mirabilis, S. ramosus*	Non-toxic
Gymnodinium nolleri	*Gymnodinium nolleri* cyst	Non-toxic
Gymnodinium veneficum	No cyst	Non-toxic
Gambierdiscus toxicus	No cyst	CFP
Dinophysis fortii	No cyst	DSP
Prorocentrum concavum	No cyst	DSP
Prorocentrum hoffmanianum	No cyst	DSP
Prorocentrum lima	Possibly	DSP
Prorocentrum maculosum	No cyst	DSP
Prorocentrum micans	Possibly	DSP
Prorocentrum minimum	No cyst	DSP
Prorocentrum minimum var. *mariaelebouriae*	No cyst	DSP
Prorocentrum mexicanum	No cyst	DSP
Amphidinium carterae	No cyst	Ichthyotoxic
Amphidinium klebsii	No cyst	Ichthyotoxic
Gonyaulax monilata	No cyst	Ichthyotoxic
Karenia mikimotoi	No cyst	Ichthyotoxic
Noctiluca scintillans	No cyst	Ichthyotoxic
Ostreopsis ovata	No cyst	Ichthyotoxic
Peridinium polonicum	No cyst	Ichthyotoxic
Pfiesteria piscicida	*Pfiesteria piscicida* resting cyst	Ichthyotoxic
Gymnodinum breve	No cyst	Neurotoxic shellfish poisoning
Ostreopsis siamensis	No cyst	Palytoxin poisoning
Alexandrium catenella	*Alexandrium tamarense*-type cyst	PSP
Alexandrium excavatum	*Alexandrium tamarense*-type cyst	PSP
Alexandrium fundyense	*Alexandrium tamarense*-type cyst	PSP
Alexandrium ostenfeldii	*Alexandrium tamarense*-type cyst	PSP
Alexandrium tamarense	*Alexandrium tamarense*-type cyst	PSP
Gymnodinium brevisulcatum	No cyst	PSP
Gymnodinium catenatum	*Gymnodinium catenatum* cyst	PSP
Pyrodinium bahamense (var. *compressa*)	*Polysphaeridium zoharii*	PSP
Pyrodinium phoneus	No cyst	PSP
Protoceratium reticulatum	*Operculodinium centrocarpum*	Yessotoxin
Lingulodinium polyedrum	*Lingulodinium machaerophorum*	Uncertain

Chaetoceros convolutus, to the milky-white color of coccoliths, e.g. *Emiliania huxleyi*. Some 'red tide' outbreaks are not actually visible as discolored water but are nonetheless manifest as shellfish poisoning or other harmful events.

Most 'red tides' are harmful because oxygen is removed from the water at night and during decay of the plankton, and because the blooms are unsightly and/or odorous (e.g. Hallegraeff, 1993). The most widespread and important 'red tides' (Table 1), however, are the result of toxic dinoflagellates which cause illness in humans by paralytic shellfish poisoning (PSP), diarrhetic shellfish poisoning (DSP), and ciguatera fish poisoning (CFP). There is no known cure for PSP and consumption of large amounts in shellfish or lobster is fatal to humans. PSP-causing dinoflagellates and other toxic species may disrupt food webs by harming zooplankton, larval fish and their predators such as fish, marine birds and mammals (Turner et al., 1998). Plankton species that can avoid the toxins may be harmed by starvation and induction of copious mucilage production may lead to asphyxia in fish (Smayda, 1997; Turner et al., 1998).

Dinoflagellates that cause 'red tides', human illness and loss of marine life are a major concern to shellfish and fish farming industries throughout the world (e.g. Dale et al., 1978; Steidinger and Baden, 1984; Hallegraeff, 1993; Burkholder, 1998). In the Phillipines (Abuso et al. (1999), blooms of *Pyrodinium bahamense* var. *compressum* result in up to 21 human deaths per year (115 from 1983 to 1993) and CFP from *Gambierdiscus* blooms has caused illness in over 1000 people per year, including 24 deaths (Wu, 1999). On a global basis, there are about 2000 reported cases of shellfish or fish poisoning and 300 deaths per year, with losses to Asian aquaculture industries being as high as US$0.5 billion per year (Hallegraeff, 1993). In Canada alone, PSP 'red tides' caused losses of about CAN$4 million per outbreak for coastal fish and shellfish industries during the 1970s, early 1980s and 1990s (e.g. Taylor, 1993; Forbes, 1994), and this number is likely to increase with the rapid expansion of shellfish and fish farming following the collapse of the traditional cod and salmon fisheries. Furthermore,

there is an apparent increase in the number of HABs that are of economic and/or societal importance: for example, the raphidophyte *Heterosigma akashiwo* first appeared in fish pens of British Columbia in 1976 (Taylor, 1993), with intense blooms beginning in 1986; by 1996, financial losses were estimated at CAN$10–20 million (Whyte, 1998) or US$1.5–8 million per event (Horner, 1998). The Canadian government therefore presently spends ~$4 million per year on monitoring programs to prevent public consumption of shellfish contaminated by PSP and to stop discharge of ballast water that may spread HABs to new areas.

In North America, historical records show increases of HABs during the past 50 yr on both the Atlantic and Pacific coasts (e.g. White, 1987; Martin and Richard, 1996; Taylor, 1993). This widespread pattern suggests that global-scale factors, such as climate change and/or increased international shipping trade, are the driving factors in addition to increased use of the coastal zone. Laboratory and field observations over the past 20 yr indicate that blooms of some of the most common PSP dinoflagellates (*Alexandrium* and *Gonyaulax* spp.) are triggered by warm sea surface temperature (SST), high runoff and storm resuspension of their resting cysts (hypnozygotes). However, results of laboratory experiments are variable (cf. Cembella, 1998), and there are very few long-term (more than 10–50 yr) records for any single location (Hallegraeff, 1993).

The hypnozygotes of some 'red tide' dinoflagellates (Table 1) have sporopollenin-like cell walls that are resistant to decay and can therefore be used to trace the history of red tides from their distribution on a geological time scale (e.g. Mudie, 1992; Emslie et al., 1996). Detailed Holocene histories were described for *Gymnodinium catenatum*-like cysts (Fjellsa and Norberg, 1996; Thorsen and Dale, 1998) and cf. *Alexandrium tamarense* cysts (Miller et al., 1982). Thorsen and Dale (1998) showed that peaks of *G. catenatum*-like cysts correspond to intervals of climate warming during the past 2000 yr, but the resolution of most records is too low (100 yr or more) to be useful for comparison with the past 50 yr of climate change and increased HAB occurrences.

Furthermore, it has recently been shown that these *G. catenatum*-like cysts are cysts of *Gymnodinium nolleri*, a non-toxic species that does not always cause 'red tides' (Ellegard and Moestrup, 1999). More studies of high resolution (annual to decadal scale) records from pre-industrial age sediments are therefore needed to understand the long-term dynamics of 'red tide'-producing species and changes in their geographic distribution.

The primary purpose of this paper is to document the Holocene history of HABs in high sedimentation rate cores from Pacific and Atlantic regions of Canada as determined from ultra-high resolution studies (annual to decadal scale) of dinoflagellate cysts associated with 'red tide' production. First, however, resting cyst abundances in varved sediments are compared with plankton sample data for corresponding years to provide a means of estimating the magnitude of 'red tide' plankton populations from the cyst proxy-data. Where possible, paleoecological transfer functions (Guiot, 1990; Rochon et al., 1999) were then applied to the dinoflagellate cyst (= dinocyst) assemblage data to determine the relationship between proxy-red tide occurrences and variations in SST and/or salinity. Comparison of the geological records from different oceans then provides a means of evaluating the relative importance of regional oceanographic regimes and global climate conditions on cyst production of 'red tide' dinoflagellates. Finally, the magnitude and frequency of 'red tide'-producing dinoflagellates in the pre-historic records from each region is compared with the modern records to evaluate the seriousness of the recent increase in HABs.

2. Methods

In 1977, 1987 and 1994, cores of organic-rich (ca. 1% total organic carbon (TOC)), fine-grained mud were taken from Emerald (cores 77-030-20; 87-003-004) and La Have basins (core 95-030-24) on the Scotian Shelf, Atlantic Canada (Fig. 1, site 3), using Benthos-type piston corers (Scott et al., 1984; Gipp and Piper, 1989; Levac, 2001). In 1994, the core site was chosen using high resolu-

tion seismic reflection profiles to select areas of maximum Holocene sediment thickness and absence of gravity flow deposits; seismostratigraphic correlation with lines across the 1977 site also shows that this area is free from turbidites (Gipp and Piper, 1989). All the cores were stored at 4°C and were subsampled (5 cm³ volume) for palynological studies within 1–12 yr after shipboard recovery. The age of the cores was determined by radiocarbon ages on shells or benthic foraminifera. Subsequently, comparison of the dinocyst assemblages in the time-equivalent 3000–7000-yr BP sections of the 1977 and 1987 cores from Emerald Basin showed no differential loss of mid-Holocene cysts during storage over a 17-yr period, although rapid loss of cyst viability has been found in modern sediments stored for 13 yr (Lewis et al., 1999).

The Scotian Shelf cores were processed for palynology using standard methods for extraction of marine palynomorphs (Rochon et al., 1999). In brief, the method uses wet sieving with screen meshes of 125 and 10 microns to remove sands, fine silt (9–4 microns) and clays, followed by digestion of inorganic material by 10% cold hydrochloric acid and 52% hot hydrofluoric acid applied in sequence. This method was selected after tests using two other methods: acetolysis (Faegri and Iverson, 1975) and the Schulze method (Barss and Williams, 1973), both of which resulted in larger losses of dinoflagellate cysts. Marret (1993) also reported large losses of thin-walled cysts from acetolysis in pelagic sediments. A known number of exotic spores were added to each sample in order to estimate the concentrations of cysts per cm³ of wet sediment.

Cores from the Pacific region (Fig. 1, sites 1 and 2) were taken from anoxic basins in Saanich Inlet (cores 93-10,-11; ODP Leg 169S, Hole 1034B) and off Santa Barbara (Core SB-262), respectively. In these basins, organic-rich marine varves have been deposited almost continuously during the past 6000–8000 yr (Nederbragt and Thurow, 2001; Hendy and Kennett, 2000). Dating of cores by Pb-210, Cs-137 and C-14 methods shows that in both study areas, each well-defined laminated couplet represents 1 yr of deposition, including a light-colored layer of biogenic materi-
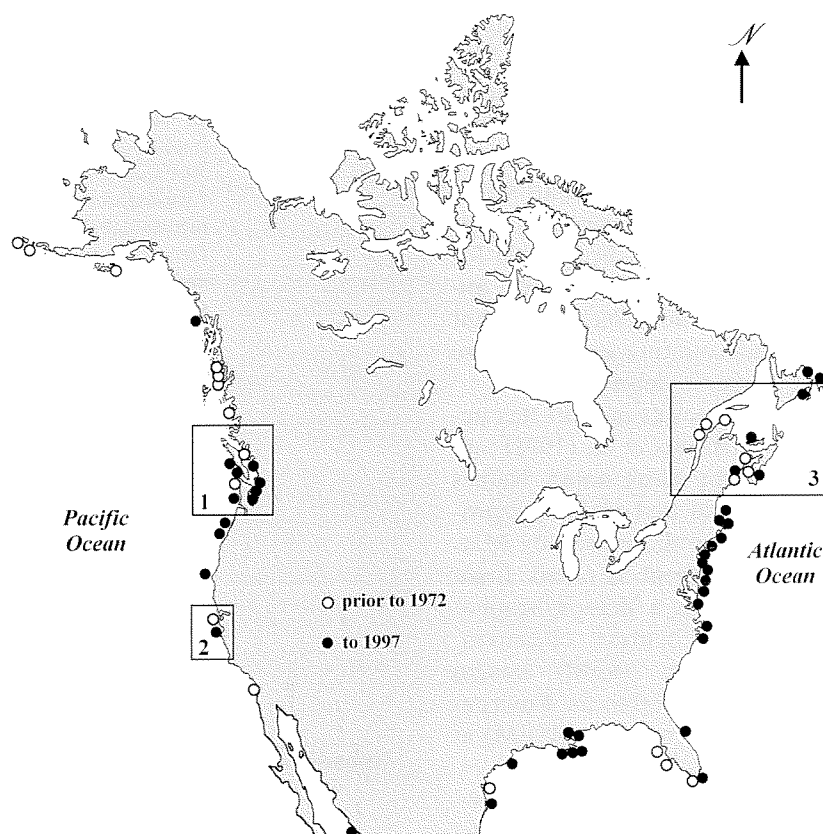
Fig. 1. Map of North America showing the change in number and distribution of reported toxic red tides since 1972. Rectangles delineate the study areas in this report. Data sources are: Quayle, 1969; Prakash et al., 1971; White and White, 1985; Mlot, 1998.

al in spring–early summer and a dark-colored mixed biogenic and clastic sediment in late summer–winter (see Dean et al., 2001 for details). The Saanich varves, however, are much thicker (5–10 mm) than in Santa Barbara Basin (ca. 3 mm). Box cores (75–150 cm length) from both study areas were used to calibrate modern cyst, plankton and climate records for the past century. The Saanich box cores were taken in 1993, using a 'frozen finger' box corer filled with dry ice (e.g. O'Connell and Tunnicliffe, 2001). The Santa Barbara core was taken in 1972 with a Soutar box corer (Soutar et al., 1977). The long Holocene record, however, was only studied in Saanich Inlet, using samples from the hydraulic piston core taken in 1996 on ODP Leg 169S at Site 1034B.

Most subsamples from the annual varves were very small (1–3.5 cm³, 98% water) and the resi-dues had to be used for both pollen–spore studies and dinocysts. Sieving, HCl and HF digestion, and marker spore procedures were the same as for the Atlantic samples. However, acetolysis di-gestion is the standard method for extraction of pollen and this method had previously been used for a pollen study in Saanich Inlet by Heusser (1983) who also reported the presence of intervals very rich in dinoflagellate cysts. Tests were there-fore made on duplicate samples from eight lami-nae in order to determine the effect of a 1-min acetolysis treatment on the extremely organic-rich (ca. 5% TOC) varved sediments. No differ-ences in species composition were found among the treated and standard assemblages which were dominated by thin-walled protoperidinioid species and included gymnodinioids and *Polykrikos* (Ta-ble 2; Fig. 2.4), although the latter is known as a

cyst-type easily destroyed by acetolysis in pelagic marine sediments (Marret, 1993). For the Saanich samples, it was further noted that some cellulose-walled rhizopods and thecate cells (Fig. 2.6, 2.5) had survived the acetolysis treatment, and recovery of exotic spores was much higher than in the non-acetolysed samples. It was therefore concluded that acetolysis treatment is acceptable for these extremely organic-rich, well-preserved anoxic sediments: in fact, this additional treatment makes identification and counting easier because of greater removal of organic debris.

Taxonomic names of dinocysts used in this paper are those given by Williams et al. (1998) and Rochon et al. (1999), except where noted. Names of theca-stage dinoflagellates and other cyst-producing HABs mentioned are those used by Matsuoka and Fukuyo (1995) except as noted. Light photographs were taken with a Zeiss Ultraphot microscope and interference contrast objectives; scanning electron microscopy (SEM) images were obtained using an E3 Electroscan Environmental Scanning Electron Microscope (ESEM) at the Geological Survey of Canada-Atlantic.

Quantitative reconstruction of sea surface parameters was performed with the paleobioclimatic analogs method (Guiot, 1990), based on calibration of modern dinoflagellate cyst assemblages and sea surface parameters (Rochon et al., 1999). A reference database containing 646 surface samples from the North Atlantic and adjacent basins, and from the North Pacific is used for the reconstruction of sea surface parameters, including the temperature and salinity of the coldest (February) and warmest (August) months of the year, and the seasonal duration of the sea ice cover. Temperature and salinity data are from the 1994 World Ocean Atlas; ice data are from the National Sea Ice Data Center. For SST and salinity, the average of all measurements within a 30 nautical mile radius of each reference surface sample was used. For the sea ice, we used the average value of all available measurements within a $1° \times 1°$ grid. To obtain the transfer function, core-top taxa were first clustered to minimize the amount of data by grouping species with close associations and similar ecological requirements. The modern reference database was then searched

Table 2
List of dinoflagellate cysts recorded from ODP Leg 169S, Core 1035B in Saanich Inlet

|	
Gonyaulacoids:	cf. *Alexandrium tamarense*-type cyst (rare–abundant)
	Ataxiodinium choane (rare)
	Lingulodinium machaerophorum (occasional–common)
	Operculodinium centrocarpum sensu Wall and Dale, 1966 (common–abundant)
	Operculodinium centrocarpum f. *truncatum* sensu Mudie, 1992 (occasional)
	Impagidinium pallidum (rare)
	Nematosphaeropsis labyrinthus (rare)
	Spiniferites spp. (occasional)
	Spiniferites bentorii (rare)
	Spiniferites belerius (occasional)
	Spiniferites bulloideus (common)
	Spiniferites delicatus (occasional)
	Spiniferites dentatus (common)
	Spiniferites elongatus (rare)
	Spiniferites frigidus (rare)
	Spiniferites lazus (occasional)
	Spiniferites membranaceus (rare)
	Spiniferites ramosus (common–abundant)
	Pyxidinopsis reticulata (occasional)
	Pentapharsodinium dalei (rare)
Gymnodinioids:	*Gymnodinium catenatum* (rare–common)
	Phaeopolykrikos hartmanii (occasional)
	Polykrikos kofoidii (common)
	Polykrikos sp. (occasional)
Diplopsaloids:	*Dubridinium caperatum* (occasional)
	Zygabikodinium lenticulatum (common)
Protoperidinioids:	*Algidasphaeridium? minutum* var. *minutum* (occasional)
	Algidasphaeridium? minutum var. *cezare* (rare)
	Brigantedinium spp. (common–abundant)
	Brigantedinium auranteum (common)
	Brigantedinium cariacoense (common)
	Brigantedinium grande (common)
	Brigantedinium simplex (common–abundant)
	Lejeunecysta oliva (occasional)
	Lejeunecyst sabrina (occasional)
	Protoperidinium americanum (common)
	Protoperidinium nudum (common)
	Protoperidinium stellatum (rare)
	Quinquecuspis concreta (common–abundant)
	Selenopemphix nephroides (common)
	Selenopemphix quanta (common)
	Trinovantedinium applanatum (occasional)
	Xandarodinium xanthum (occasional)
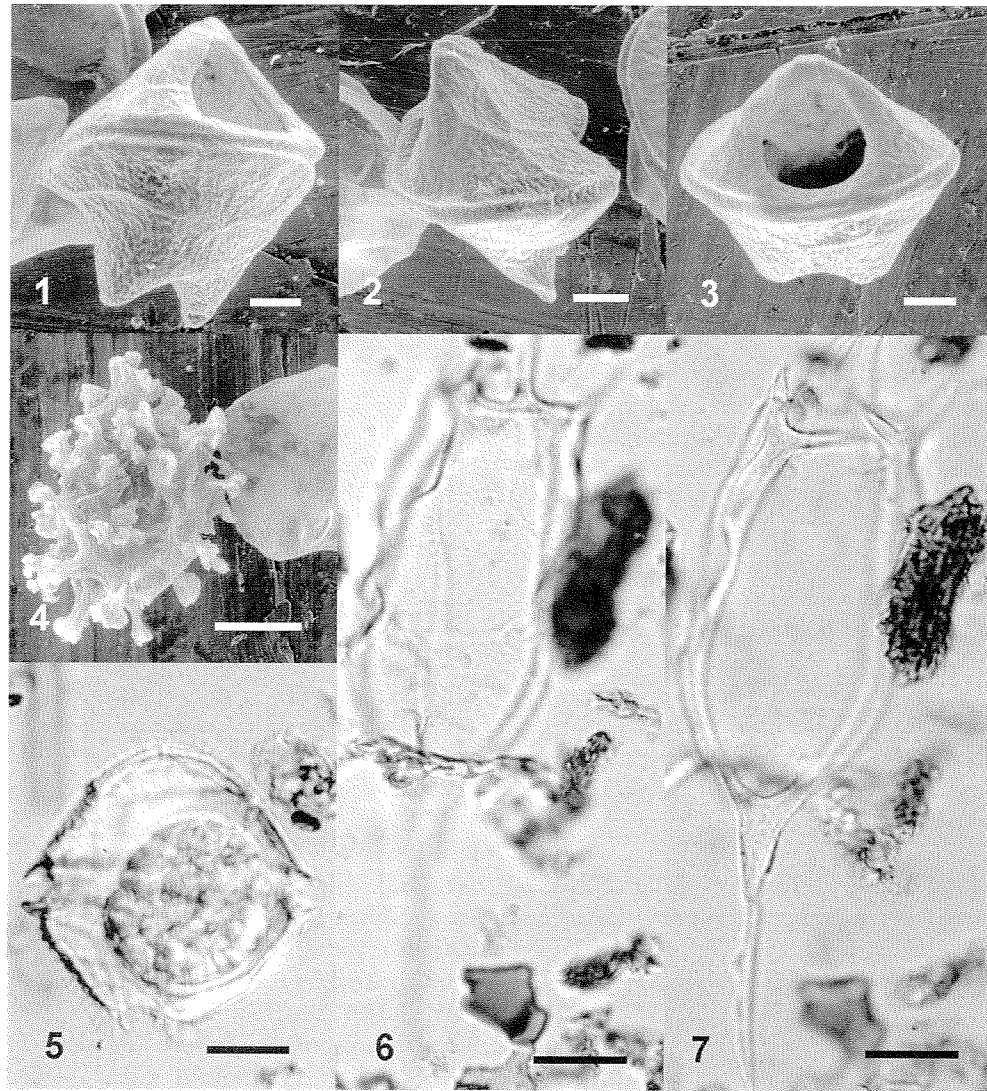
Fig. 2. Thin-walled dinoflagellate cysts and cellulose-walled phytoplankton from Saanich varved sediments, showing excellent preservation despite use of acetolysis (scale bar = 10 microns). 1–4 are ESEM images. 5–7 are from an interference light microscope. (1–3) *Quinquecuspis concreta*. ODP Hole 1034B, section 11-5, 20 cm. (1) Left lateral view showing intercalary archeopyle, paraplate sutures and wall ornamentation; (2) right side of a different specimen showing paraplate sutures on the epicyst; (3) dorsal view of a different specimen showing intercalary archeopyle and wall ornamentation. (4) *Polykrikos kofoidii*, orientation unknown. ODP Hole 1034B, section 11-5, 20 cm. (5–7) ODP Hole 1034B, section 9-5, 20 cm; 80 m sub-bottom. (5) *Protoperidinium* sp. theca with cellulose walls and cell content; optical section. (6 and 7) Fresh water rhizopod with cellulose walls. (6) High focus showing surface details; (7) optical section of the same specimen.

for the 10 best analogs clustered on log-transformed data, using equal weighting of taxa.

The logarithmic transformation diminishes the representation of ubiquitous taxa, and enhances that of secondary taxa. During the search for analogs, the analyzed spectrum is compared to those in the reference database, using a similarity index. The output is expressed as a 'distance' between 0 and 999 that is calculated for each analog based on its similarity with the analyzed spectrum. This

'distance' also allows identification of no-analog situations. The reconstruction of sea surface parameters is based on the 10 best analogs found in the reference database. The weighted average of the environmental parameters is then calculated, taking into account the respective distances between the analyzed spectrum and the 10 modern analogs. This weighted average is considered as the most probable true value and it is included within a confidence interval that corresponds to minimum and maximum values possible according to the set of analogs. The precision of the reconstructions varies from $R = 0.915$ for sea ice cover duration to $R = 0.964$ for February temperatures (cf. Rochon et al., 1999). Reconstruction of temperatures in February and August is accurate to $\pm 1.18°C$ and $\pm 1.57°C$, respectively, the salinities in February and August are accurate to ± 0.66 and ± 1.00 psu, respectively, and the sea ice reconstructions are accurate to ± 1.1 months/yr.

3. Environmental background

3.1. Pacific region

Saanich Inlet (ca. 48.75°N, 123.5°W) and Santa Barbara Basin (ca. 34.25°N, 120°W) are located in

Fig. 4. Location map of Santa Barbara Basin (area 2 in Fig. 1), showing bathymetry in meters, California Current (bold arrow) and coastal counter currents. After Hendy and Kennett (2000).
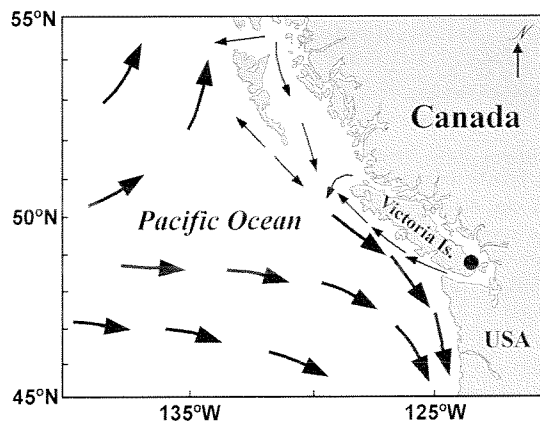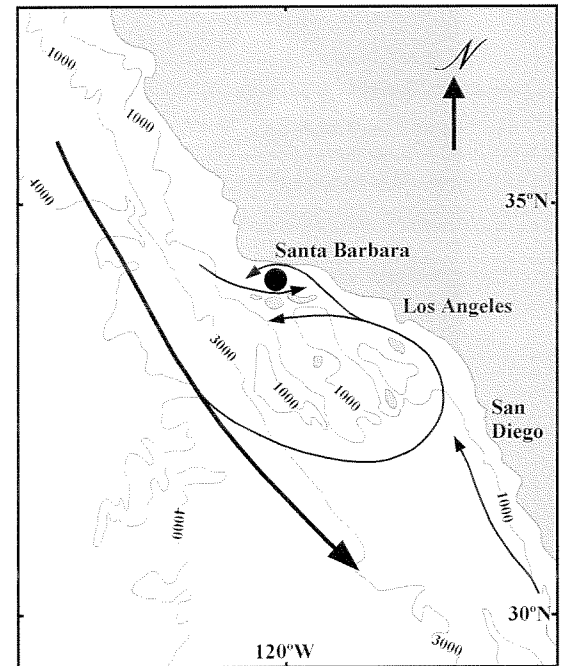

Fig. 3. Location map of Saanich Inlet (large black dot) in the NE North Pacific (area 1 in Fig. 1), showing the major offshore summer surface currents (bold arrows) flowing north (Alaska Current) and south (California Current). Thin arrows are variable coastal currents. After Thompson (1981).

the eastern North Pacific Ocean, near the northern and southern ends of the California Current, respectively (Figs. 3 and 4). The California Current is a southward-flowing eastern boundary current formed by mixing of waters from the temperate, saline North Pacific Drift and the colder, fresher subpolar Aleutian Current. The surface water of the California Current (0–150 m) is underlain by a northward-flowing undercurrent that normally wells up, bringing cold, nutrient-rich water to the surface in winter–spring in the south and in summer in the north. During most El Niño conditions, however, the surface water becomes unusually warm and strongly stratified, so that upwelling is suppressed (Mysak, 1986).

Sediments in both Saanich Inlet and Santa Barbara Basin are varved (Dean et al., 2001; O'Connell and Tunnicliffe, 2001), reflecting the presence of anoxic bottom water in these nutrient-rich, high sedimentation basins. Each annual layer consists of alternating light and dark laminae that represent diatom-rich spring–early summer opa-
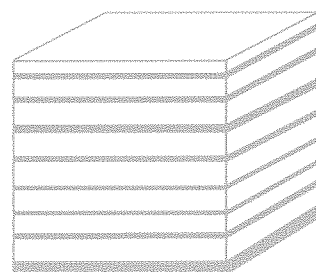
1-Saanich varves:
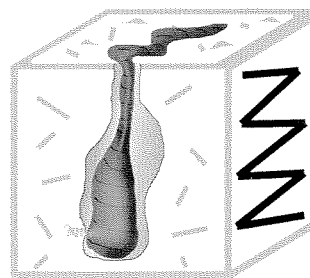**no mixing**

Accumulation rate:

0.5-1 cm per year

2-Scotian shelf:
bioturbated mud

Accumulation rate:

6-12 cm per century
(0.6-1.2 mm per year)

Fig. 5. Block diagrams illustrating the differences between sedimentation rates and appearance in (1) varved Pacific cores and (2) bioturbated Atlantic basins.

line deposits and clay-rich late summer–winter deposits, respectively (Fig. 5.1). Saanich Inlet, on the southeast coast of Vancouver Island, is a narrow coastal fjord about 26 km long and 8 km wide, with a maximum water depth of 236 m (Fig. 3). It is separated by a 70-m-deep bedrock sill from the waters of the southern Strait of Georgia between the Island and mainland British Columbia. Annual SST and salinity are ca. 13°C and 30 psu at the Saanich core site, with a seasonal range from 5 to 22°C and 21 to 32 psu. The history of PSP 'red tides' for this area dates back to 1793 when Captain George Vancouver reported the death of a sailor after eating mussels (Quayle, 1969). Before 1985, 'red tides' occurred at roughly 7–8-yr intervals (Gaines and Taylor, 1985), but subsequently, there has been a large increase of HABs in the fjords of Vancouver Island and the adjacent mainland, and there is concern that increased aquaculture, urban expansion and associated pollution may be causing excessive nutrient enrichment as well as introducing new HAB species (e.g. *Heterosigma akashiwo*) in ballast water from foreign ships or with imported shellfish varieties (see papers in Forbes, 1994).

Santa Barbara Basin is located on the continental shelf north of the Santa Barbara Islands (Fig. 4). It has a maximum depth of 590 m, but it is separated from the main shelf area by a sill of 440–480 m depth which results in the anoxic bottom water layer (Sholkovitz and Soutar, 1975). Annual SST and salinity are slightly warmer (ca. 15°C) and much more saline (35 psu) than in Saanich Inlet. Outbreaks of 'red tides' (mostly *Prorocentrum micans*, *Noctiluca scintillans* and *Lingulodinium polyedrum*) in this area occurred every few years between at least 1901 and 1979 (Sweeney, 1975, 1979) but there has been no clear trend towards increasing recent occurrences (Kahru and Mitchell, 1998).

3.2. Atlantic region

Emerald Basin (ca. 44°N, 63°W) and La Have Basin (ca. 44°N, 64°W) are located on the Scotian Shelf in the northwestern North Atlantic Ocean, near the confluence of the subtropical Gulf Stream and the subpolar Labrador Current (Fig. 6). The Gulf Stream is a northward-flowing western boundary current formed by outflow of

warm, saline water from the tropics, while the Labrador Slope Current is a southward-flowing western boundary current formed by overflow of cold, low salinity water from the Arctic. These two western boundary currents interact to form warm core eddies that periodically cross the Scotian Shelf, transporting unusually warm water to the inner shelf in the vicinity of Emerald Basin (Smith and Schwing, 1991). On the shelf, the surface Scotian Shelf Current is formed by the outflow of low salinity water from the Gulf of St. Lawrence. This cool, low salinity water mostly flows southwest along the coast, but branches near Halifax, with the southern branch skirting the northern edge of Emerald Basin and crossing La Have Basin (Loder et al., 1997). The Scotian Shelf circulation and variability are primarily driven by surface wind stress and buoyancy fluxes. Minor coastal upwelling occasionally occurs along the south coast when strong southwesterly winds prevail (Petrie et al., 1987). More frequent topographically induced upwelling and downwelling occur off western Nova Scotia (Tee and Smith, 1993), but does not extend to the study areas on the central shelf where strong stratification or downwelling during winter cooling normally prevail. Large dinoflagellate 'red

tide' outbreaks in summer and fall are more likely to be associated with storm-induced resuspension of hypnozygotes into a strongly stratified surface layer made buoyant by high runoff.

Sediments in both Emerald and La Have basins are organic-rich, bioturbated olive-gray to black, methane-rich silty clays (Fig. 5.2), reflecting the presence of low oxygen bottom waters and high input of both marine and terrigenous organic matter (Pocklington et al., 1991). Bioturbation to depths of 7 cm means that temporal resolution of events is limited to about 25 yr (J.N. Smith, personal communication, April 2000). Both Emerald and La Have basins are about 75 km long and 50 km wide, with maximum depths of ca. 260–290 m, and separated from the Scotian Slope by relatively shallow (75 m depth) sills. Annual SST and salinity are ca. 13°C and 32.5 psu, with a very large range between winter and summer SST (1.8°C and 17°C, respectively). The recorded history of 'red tides' dates back to 1880 AD and shows that recurring blooms of *Alexandrium tamarense* appear to be endemic to the Gulf of St. Lawrence and Bay of Fundy regions of Nova Scotia (Martin and Richard, 1996). However, there were no 'red tides' on the Scotian Shelf and Newfoundland before ca. 1986 when out-
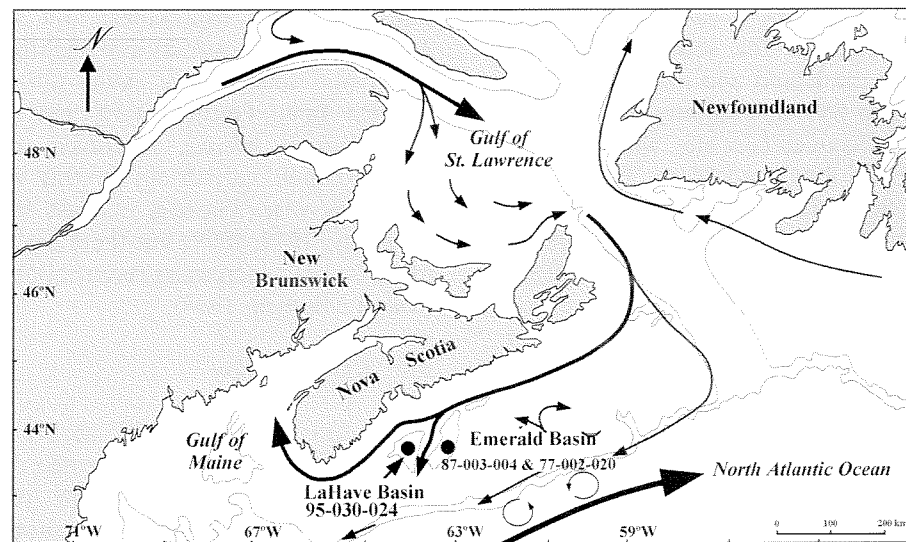

Fig. 6. Location map of Scotian Shelf sites (area 3 in Fig. 1), showing the 200-m and 1000-m bathymetric contours and the main surface currents dominating the shelf, including the westward-flowing Nova Scotia Current, the eastward-flowing Gulf Stream (bold arrows), and the Labrador Slope Water (thin arrows).

breaks of toxic blooms appeared in shellfish farming areas. Most recently, *A. tamarense* and *Prorocentrum lima* have appeared on Georges Bank, forcing periodic closure of the scallop-dredging industry at a cost of CAN$7 million per year.

4. Results of Pacific varved sediment studies

4.1. Box cores

Abundances of 'red tide'-producing cysts were counted in consecutive annual laminae of the box cores to provide geological proxy-records that could be correlated to the motile-stage cell abundances reported for each year during the past half-century of historical records. In Saanich Inlet (Fig. 7), resting cysts of four HAB species were found in Box cores 10 and 11: *Alexandrium* cyst-type (presumed to be a cyst of *Alexandrium catenella*; see Fig. 8.1), *Lingulodinium polyedrum*, *Gonyaulax spinifera* and *Heterosigma* cyst-type (see Fig. 8.3, 8.4) which corresponds closely to the motile-stage occurrences of HABS reported for the region. A few thecate cells of *Akashiwo sanguinea* were also found in varves for 1957 and 1989. The only 'red tide' dinoflagellates not represented in Saanich sediments are *Prorocentrum micans* and *Dinophysis* spp. In Santa Barbara Basin Core 262 (Fig. 7), *L. polyedrum* is the only red tide-producing species with a continuous record; the other HAB species (*A. sanguinea*, *Cochlodinium* spp., *P. micans* and *Noctiluca scintillans*) are not known to produce fossilizable resting cysts and no thecate cells were found in this core.

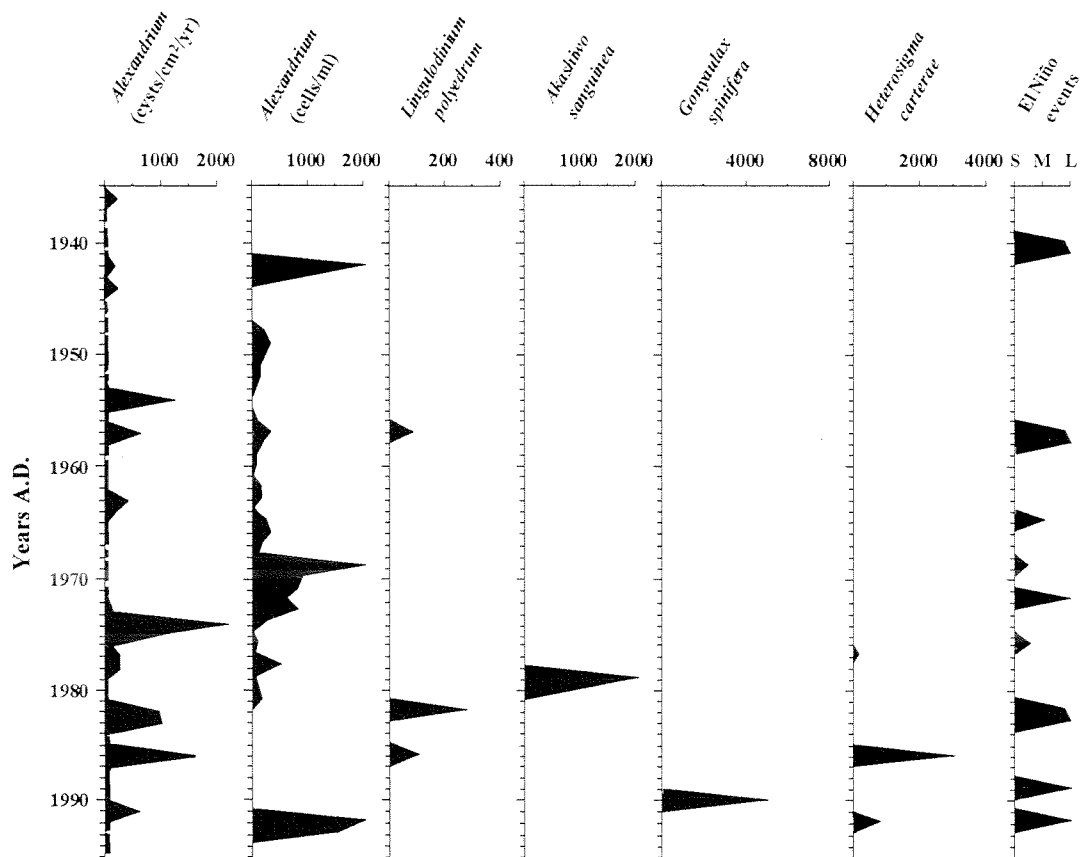Comparison of the proxy-data cyst records with

Fig. 7. Saanich Core 11: graphs of annual red tide cyst deposition (cysts/cm²/yr) from 1935 to 1993, and concentrations of *Alexandrium catenella* and *Akashiwo sanguineum* motile cells (cells/ml) reported for the study area from 1942 to 1993.
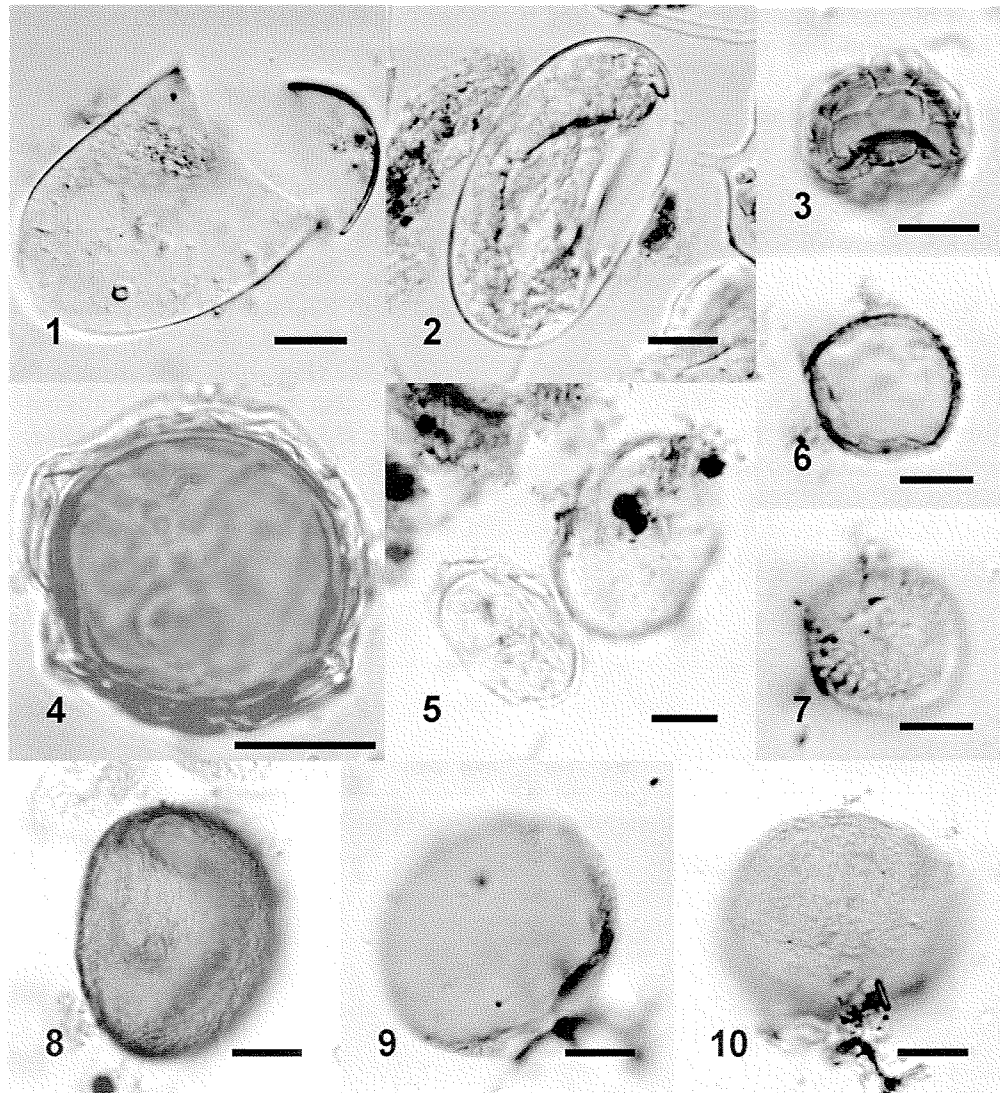
Fig. 8. Interference light microscope photographs of selected HAB species (scale bar = 10 microns). 1, 2 and 5 show oval cysts of cf. *Alexandrium tamarense* with a simple wall structure; 5 also shows the *Alexandrium excavatum* cyst-type of Simard and de Vernal (1998). (1) Sannich Inlet Core 11, 10.1–10.4 cm. (2) Perch Pond sample provided by Don Anderson. (5) Cysts from Core 77-002-20, Emerald Basin, 1050 cm. 3 and 4 are *Heterosigma*-type cysts from varves corresponding to blooms of *Heterosigma akashiwo* in Saanich Inlet. (6 and 7) Cysts of cf. *Gymnodinium nolleri* from Saanich Inlet, ODP Core 1034B, 4H-1, 9–10 cm. (6) high focus on archeopyle margin; (7) low focus on reticulate ornament. (8–10) Cysts of cf. *Gymnodinium catenatum* from Saanich Inlet, ODP Core 1034B, 4H-1, 9–10 cm. (8) High focus on finely reticulate surface; (9 and 10) low and high focus on a germinated cyst.

graphs of the motile cell abundances, as shown for *Alexandrium* and *Lingulodinium polyedrum* in Figs. 7 and 9, indicates that most red tide events (cell abundances > 1000 cells/ml) correspond closely (±2–3 yr) to the presence of peaks of ca.

200–500 cysts/cm^2/yr. However, few of these cyst–theca peaks are concurrent, i.e. appearing in exactly the same year. This apparently anomalous finding is consistent with the calculation of Lewis et al. (1985) which shows that relatively few cysts
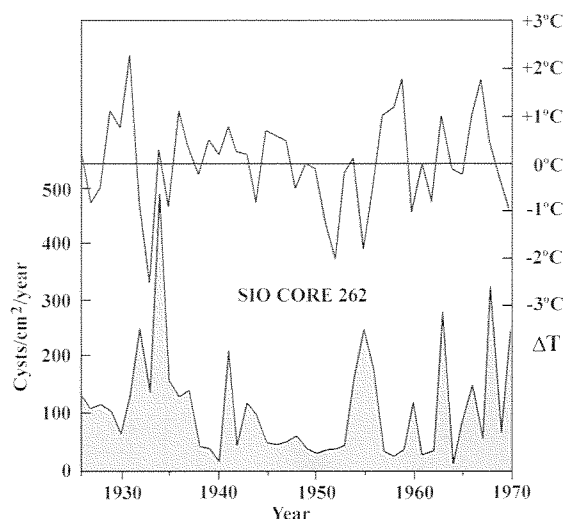
Fig. 9. Santa Barbara Core 262: annual deposition of *Lingulodinium polyedrum* cysts from 1925 to 1970 and recorded SST deviations for corresponding years.

$(10/cm^2)$ are needed to initiate a bloom when growth conditions are favorable. However, these earlier studies were based on short-term (1–2 yr) plankton sample programs and mixed surface sediment cyst populations. Our varved records show that most of the dinocyst peaks precede the motile blooms by 1 or 2 yr. This pattern is in accordance with studies (Franks and Anderson, 1992) that describe the importance of storm resuspension of cysts for 'seeding' of very extensive red tide events: obviously, the larger the viable cyst population, the more likely that blooms will be initiated over a large area. The varve records therefore indicate that the conditions controlling the production of abundant cysts are as important as the cell division-stage conditions for generating red tide outbreaks.

The historical varve records also show that some cyst peaks actually follow the plankton peaks, possibly reflecting the occasional influx of fine sediment as turbidity currents (cf. Sholkovitz and Soutar, 1975) or by offshore transport in density plumes. Furthermore, although some cyst peaks correspond to El Niño events, most lag the events by 1–3 yr, notably even in the years 1942 and 1972–1973 which correspond to very strong El Niños (Mysak, 1986). This irregularity

in the varve record is in accordance with previous work of Gaines and Taylor, 1985) who found that periodic (7–8-yr intervals) large red tide outbreaks in summer and fall may be associated with some but not all El Niño events.

The lack of consistent direct correspondence between annual motile cell and cyst production is not important for low resolution time-series studies because bioturbation results in the mixing of sediment layers deposited over several years (e.g. Anderson et al., 1982). For varved sediment records, however, it must be noted that sampling at multi-annual intervals will allow detection of time intervals when 'red tide' cyst production is very large, with numerous closely spaced peaks, but minimum 'runs' of 5 consecutive yr are necessary for meaningful statistical time-series analysis of recurrence intervals.

4.2. ODP Hole 1043B, Saanich Inlet

At Site 1034B, about 80 m of varved marine sediments was recovered (Fig. 10), representing annual deposition of light diatom-rich laminae in spring–early summer and dark, muddier laminae in late summer–winter (McQuoid and Hobson, 1997; Dean et al., 2001). Eight accelerator (AMS) radiocarbon ages on shells and wood particles provide calibration for the varve-count age scale (Nederbragt and Thurow, 2001) and indicate there is an almost uninterrupted sequence of annual layers covering the past 10 650 yr BP (uncorrected radiocarbon ages).

For this study, the annual layers were sampled every 10–20-cm intervals, where each sample represents the net deposition of cysts in late summer to late winter of 1 yr. Unfortunately, the laminae at the top of the ODP hydraulic piston core were badly disturbed during the coring operation. Consequently, varves for the past ca. 1000 yr could not be sampled in Core 1034B. For comparison of decadal-scale trends for the youngest Holocene, therefore, the decadal-scale record for the past 150 yr in Box Core 11 has been spliced to the top of the ODP record.

Most of the Holocene dinocyst assemblages in Saanich Inlet are dominated by cysts of heterotrophic protoperidinioid species that are non-toxic
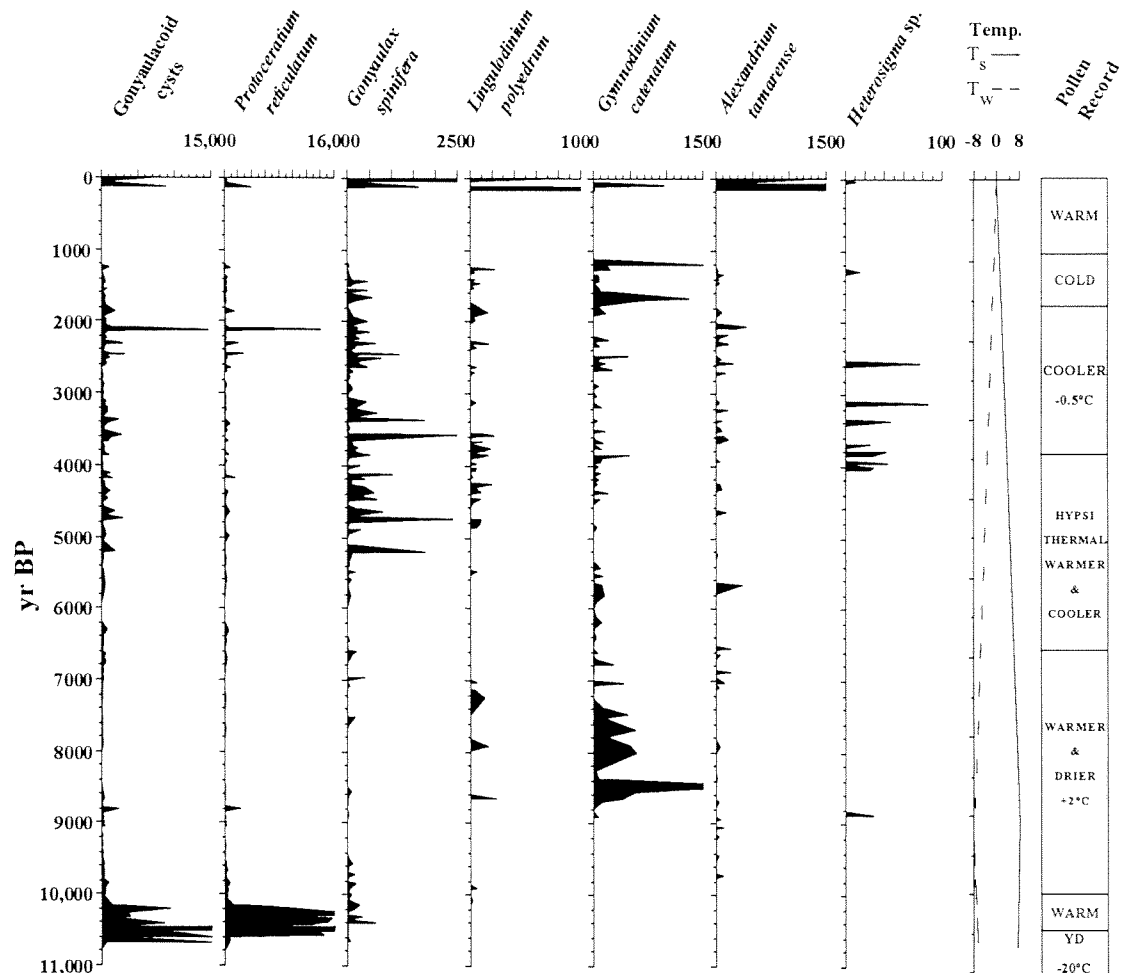
Fig. 10. Geological record from Saanich Inlet at ODP Site 169S, Site 1034B, showing variations in cyst influx (cysts/cm²/yr) for total gonyaulacoids and for cyst-forming red tide species compared to changes in climate according to the pollen record of Pellatt et al. (2001) and % deviations in orbital insolation for summer (S) and winter (W).

and do not produce 'red tides' (see Table 2 for full species list). Here, it is mostly the autotrophic gonyaulacoids that produce 'red tides', although the gymnodinioids *Gymnodinium catenatum* and sometimes the non-toxic *Gymnodinium nolleri* are exceptions to this generalization, and in warmer regions, some *Peridinium* species may produce red tides. Although the protoperidinioids in Saanich Inlet probably do not contribute directly to our understanding of 'red tide' history, the presence at the base of the core of very delicate species such as *Trinovantedinium applanatum* and *Polykrikos kofoidii*, and a few thecate cells with cellulosic

walls (Fig. 2.5–2.7) is important in eliminating the possibility that downcore trends are not simply a function of better preservation of the more resistant gonyaulacoid species. Excellent preservation of cellulose and delicate cysts in the anaerobic sediments probably also accounts for the unusual preservation of *Heterosigma* raphidophyte resting spores in the subsurface sediments (see 6.1. 'Assumptions about bloom sizes' for further taxonomic details).

On a large scale, the Holocene record of 'red tide' production in Saanich Inlet shows the following main features:

(1) All the modern red tide-producing dinoflagellates and *Heterosigma* spores are intermittently represented in the records at least as far back as 8000 yr BP.

(2) During the cool late glacial–earliest Holocene climate interval (ca. 10 600–10 000 yr BP), annual gonyaulacoid cyst deposits were as large or larger (by almost an order of magnitude) than the modern cyst deposits that accompany 'red tide' blooms (ca. 10 000 cysts/cm^2/yr).

(3) In the warm middle Holocene interval, very large annual cyst deposits (i.e. greater than 500 cysts/cm^2/yr) are scattered and rarely exceed 600 cysts although scattered large blooms of *Alexandrium*-type cysts occur during the hypsithermal maximum from 7000 to 5000 yr BP.

(4) Larger annual deposits (1500–3000 cysts/cm^2/yr) are common both at the top of the hyp-

sithermal maximum and during the cooling event about 4000–1000 yr BP.

(5) The very large modern deposits (5000–10 000 cyst/cm^2/yr) associated with recent global warming differ from earlier large blooms in the simultaneous occurrences of two or more HAB species. There is no precise correlation with the pollen climate record for ODP Core 1034B (Pellatt et al., 2001), but the largest blooms occur at the time of greater summer insolation in the early Holocene summer and milder winters in the late Holocene (Fig. 10).

On a detailed scale (Fig. 11), the dinocyst records indicate that there were successive cycles of 'red tide' cyst species dominance, beginning with huge bi-decadal or more frequent occurrences of cysts produced by the yessotoxin-containing species *Protoceratium reticulatum*. At about 10 200 yr
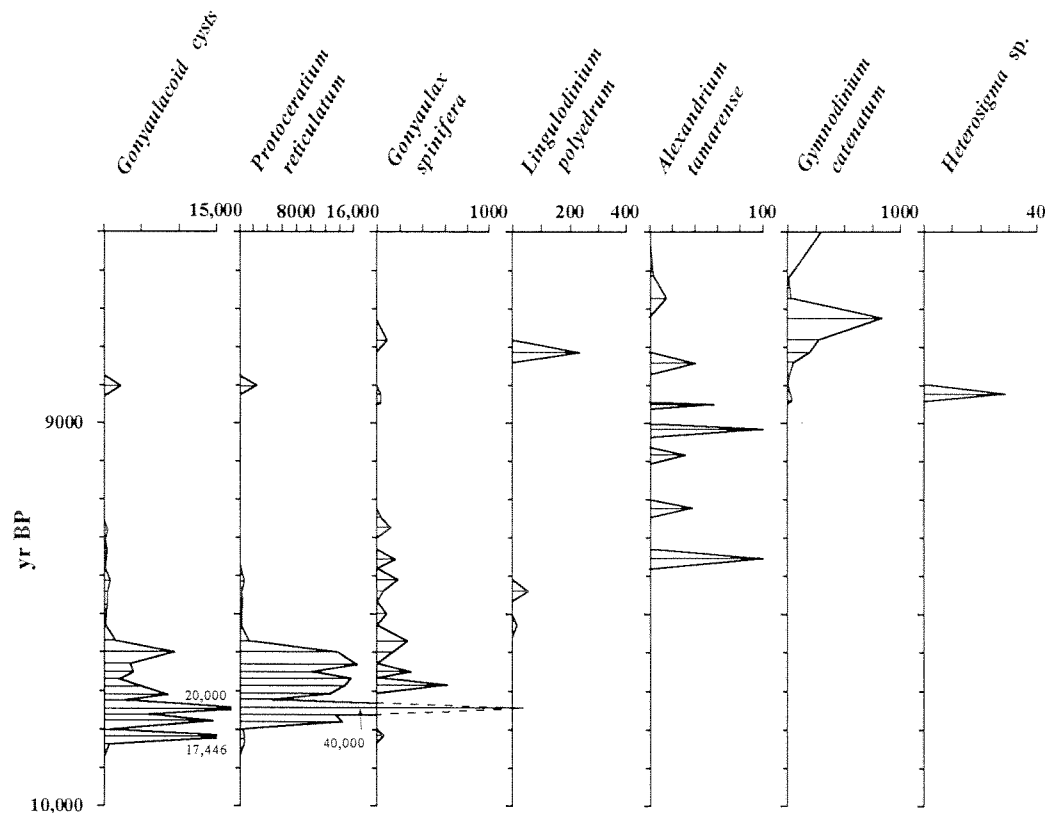

Fig. 11. Expanded late glacial–early Holocene records for Saanich Inlet at ODP Site 169S, Site 1034B, showing the succession of cyst deposits (cysts/cm^2/yr) for 'red tide' species.

BP, a series of alternating smaller (ca. 500 cyst/ cm^2/yr) peaks of the non-toxic 'red tide' cyst-producing species *Gonyaulax spinifera* begin and gradually replace the *P. reticulatum* cyst peaks until about 9500 yr BP. From 9.5 to 9 ka, there is a notable absence of large HAB cyst occurrences, although ellipsoidal cysts of the toxic *Alexandrium*-type make their first appearance and the ichthytoxic species *Heterosigma* appears in large numbers (relative to the modern data) just after 9 ka. Within 25 yr or less, this *Heterosigma* event is followed by the beginning of a succession of *Gymnodinium* (PSP)/*Gymnodinium nolleri* (non-toxic) blooms occasionally alternating with small blooms of the red tide species *Lingulodinium polyedrum*, after which there is an interval of alternating small *Alexandrium* and *Gymnodinium* blooms until ca. 5 ka. From ca. 5 to 2 ka, there is a dominance of non-toxic *G. spinifera* blooms alternating with occasional small blooms of either *Gymnodinium* or *Alexandrium*, and with large peaks of *Heterosigma*-type spores. From ca. 2 to 1 ka, *Gymnodinium* dominates, interspersed with a few peaks of *Lingulodinium* or, rarely, *Protoceratium*.

The modern section (past 150 yr) differs from the older record in showing concurrent major blooms of *Gonyaulax spinifera*, *Lingulodinium polyedrum* and *Alexandrium tamarense*, or at the top (dated 1993), *G. spinifera*, *A. tamarense* and *Heterosigma*. The only other times where blooms overlap, e.g. 3500 yr BP, correspond to sedimentological evidence of major earthquakes (Blais-Stevens et al., 1997) which generated major turbidites and may have seeded short-lived multiple blooms.

On a decadal scale, the ultra-high resolution data from the Saanich varves also show the rates at which sustained bloom cycles start and stop. It is clear that species cycles start very abruptly – in 10 yr or less – and that most persist at intermittent intervals for about 100–1000 yr before returning to background population sizes.

5. Results of NW Atlantic shelf studies

The cores from the Scotian Shelf basins are bioturbated muds with rare silty or fine sand laminae that mark intervals of more frequent storms (Hall and Reed, 1996; Calvin Campbell, personal communication, April 2000). The resolution of these cores is therefore limited to tri-decadal (La Have Basin) or longer time intervals (Levac, 2001).

5.1. La Have Basin

The 10-m-long piston core from La Have Basin has a maximum age of ca. 10.5 ka BP. As in Saanich Inlet, the dinoflagellate cyst record (Fig. 10) is dominated by cysts of heterotrophic proto-peridinioid dinoflagellates (Levac, 2001). Before 10 ka BP, however, cyst concentrations reach their maximum and there are major peaks of *Alexandrium excavatum* cyst-type of Simard and de Vernal (1998), including minor amounts of smooth-walled oval *Alexandrium tamarense*-type cysts (see Fig. 8) and *Protoceratium reticulatum*. Minor peaks of *Gonyaulax spinifera*-group species (including *Gonyaulax digitale*, as *Bitectatodinium tepikiense*) are also present. Most peaks appear to be synchronous but this is probably an artifact of mixing by bioturbation.

From ca. 10 to 7 ka, total cyst influxes decrease by about 50% and cysts of *Protoceratium reticulatum* (*Operculodinium centrocarpum* sensu Wall and Dale, 1966) and *Gonyaulax digitale* become the dominant 'red tide'-producing taxa. *Alexandrium*-type cysts (mostly the *Alexandrium excavatum* cyst-type) are only sporadically present in very small proportions but cysts of the non-toxic species *Gonyaulax spinifera* are still abundant (*Spiniferites elongatus*, *Spiniferites ramosus*, *Spiniferites bulloideus*). The decline in cyst abundance and increase in cold water taxa, e.g. *Algidasphaeridium? minutum*, suggests that conditions were initially favorable to blooms but gradually deteriorated as a result of a decrease in SST.

From 7.2 to 2.5 ka, influxes of all cysts are almost an order of magnitude lower than in the early Holocene, and there are no large peaks of 'red tide' species. The dinocyst assemblages are similar to those at the top of the sequences, except for the warm water oceanic species *Impagidinium aculeatum* between 7.5 and 5.5 ka. These assem-

blages suggest that sea surface conditions were fairly similar to the present day, and possibly slightly warmer in the mid-Holocene.

From 2.5 ka to the top of the core (probably ca. 1850 AD; Levac, 2001), cyst concentrations show a slight increase and there are large peaks of the red tide species *Protoceratium reticulatum*, suggesting a recurrence of blooms but not to levels comparable with the early Holocene. Cysts of *Gonyaulax spinifera* are consistently present but in small numbers.

Paleobioclimatic transfer functions were used to reconstruct quantitative sea surface conditions for the La Have Basin record (Fig. 13). The results show that SST was ca. 5°C higher than present in both summer and winter between the base of the core and 8.5 ka BP. This is consistent with an early Holocene summer insolation maximum predicted by the Milankovich theory. Since 8000 yr BP, August temperature generally remained around today's value, except around 6 ka BP where it appears to have been slightly cooler. Summer SST also decreased in the last 500 yr. Temperature in February is more variable. In general, it has been warmer than present since 7000 yr BP, with recurrent slightly colder episodes. Sea ice cover has been insignificant throughout the Holocene.
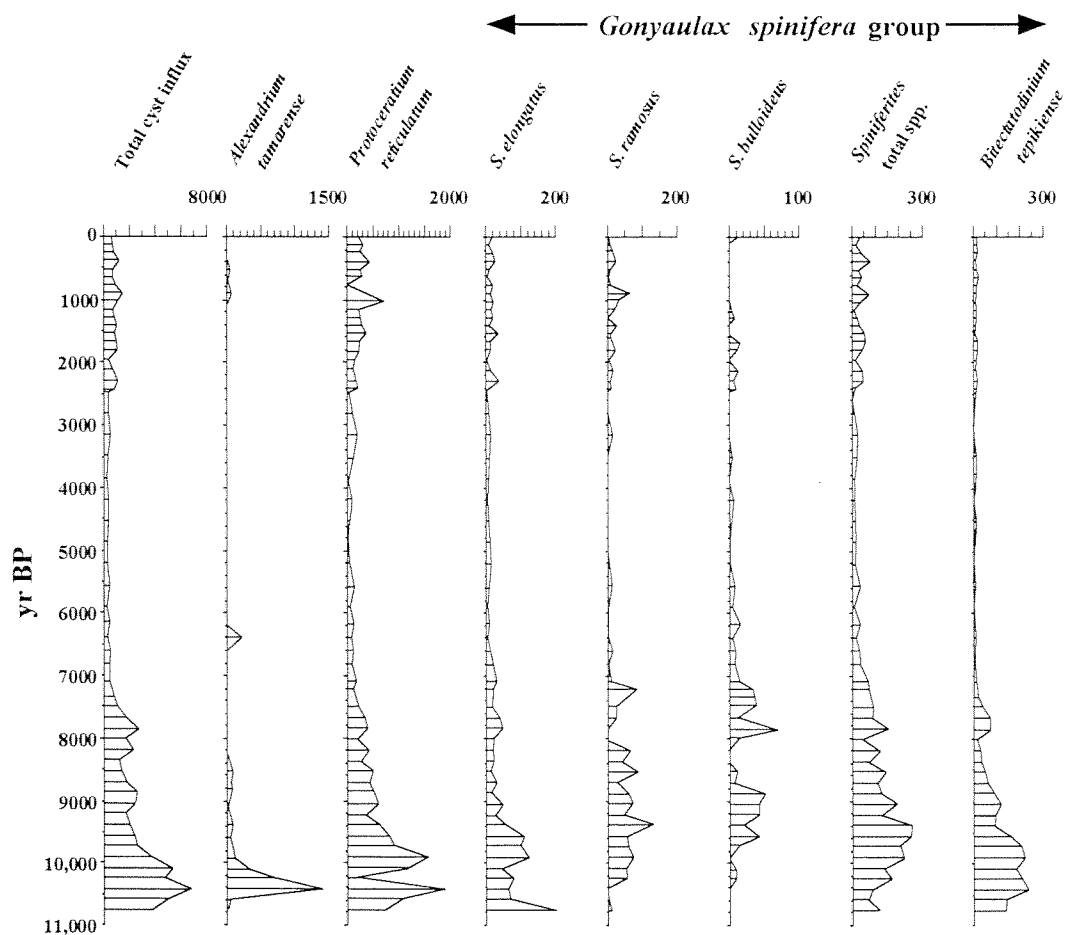

Fig. 12. Geological record for Core 95-030-24 from La Have Basin, showing variations in cyst deposits (cysts/cm^2/yr) for total dinoflagellates and for cyst-forming red tide species.
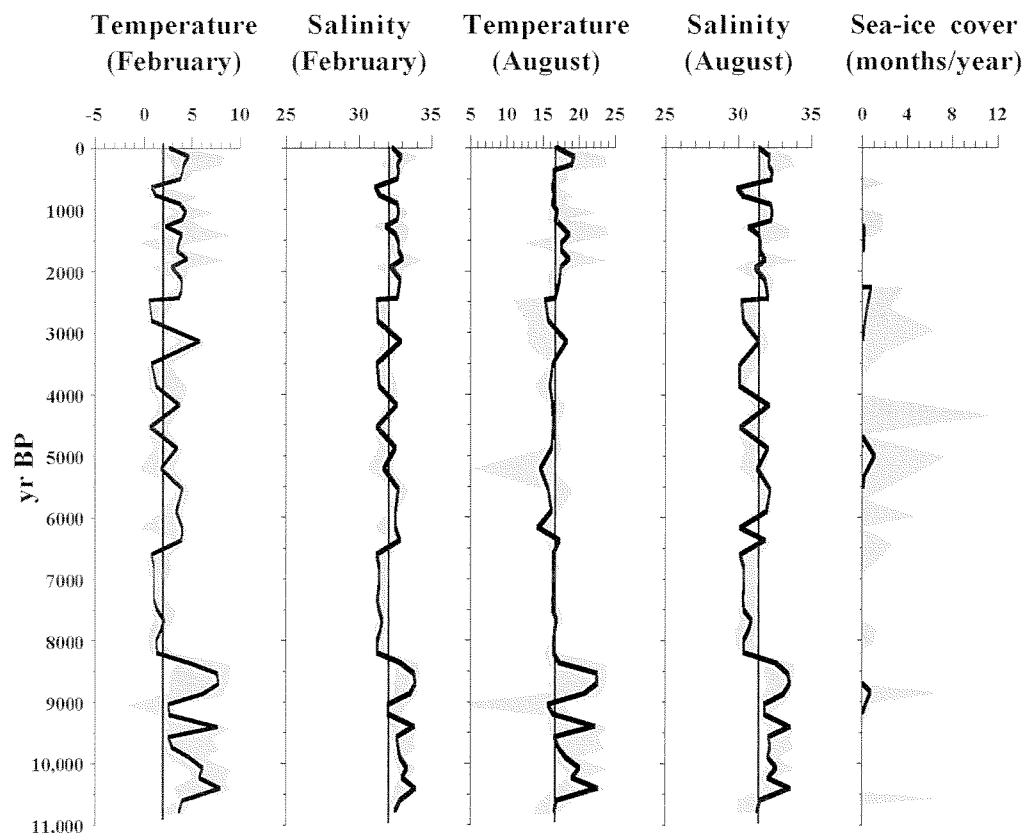
| Temperature (February) | Salinity (February) | Temperature (August) | Salinity (August) | Sea-ice cover (months/year) |

Fig. 13. Reconstruction of seasonal changes in SST (°C), salinity (psu) and duration of sea ice for Core 95-030-24 from La Have Basin (after Levac, 2001).

Throughout the sequence, both summer and winter salinity show similar trends to February temperature. Sea surface salinities were higher before 8500 yr BP. Between 8.5 and 6.5 ka, they were below today's values. After 6500 yr BP, the February temperature and salinity remained slightly above today's value, except for short episodes with a recurrence interval of about 1000 yr. There is a slight increase in cyst influxes during the past 2000 yr, but there is no indication in the La Have Basin record of major sea surface cooling during the Neoglacial.

5.2. Emerald Basin

The proxy-'red tide' records for this basin (Fig. 12; Fig. 14) were compiled by splicing together data from cores 77-002-20 and 94-003-004 to provide an expanded sequence with better dating control than provided by a single core. Total dinoflagellate cyst assemblages (Scott et al., 1984) in most of the sequence are dominated by protoperidinioids similar to La Have Basin. Likewise, total dinocyst influx and large peaks of both *Alexandrium tamarense*-type and *Protoceratium reticulatum* cysts are also present in the late glacial interval (10.5–14 ka), along with minor peaks of *Gonyaulax digitale* (*Bitectatodinium tepikiense*) and *Gonyaulax spinifera*. However, relatively large peaks of *Lingulodinium polyedrum* and *Pyrodinium bahamense* succeed these around 10.5 ka, indicating that there were major incursions of Gulf Stream water into this basin at this time, similar to warm water events that periodically cross the
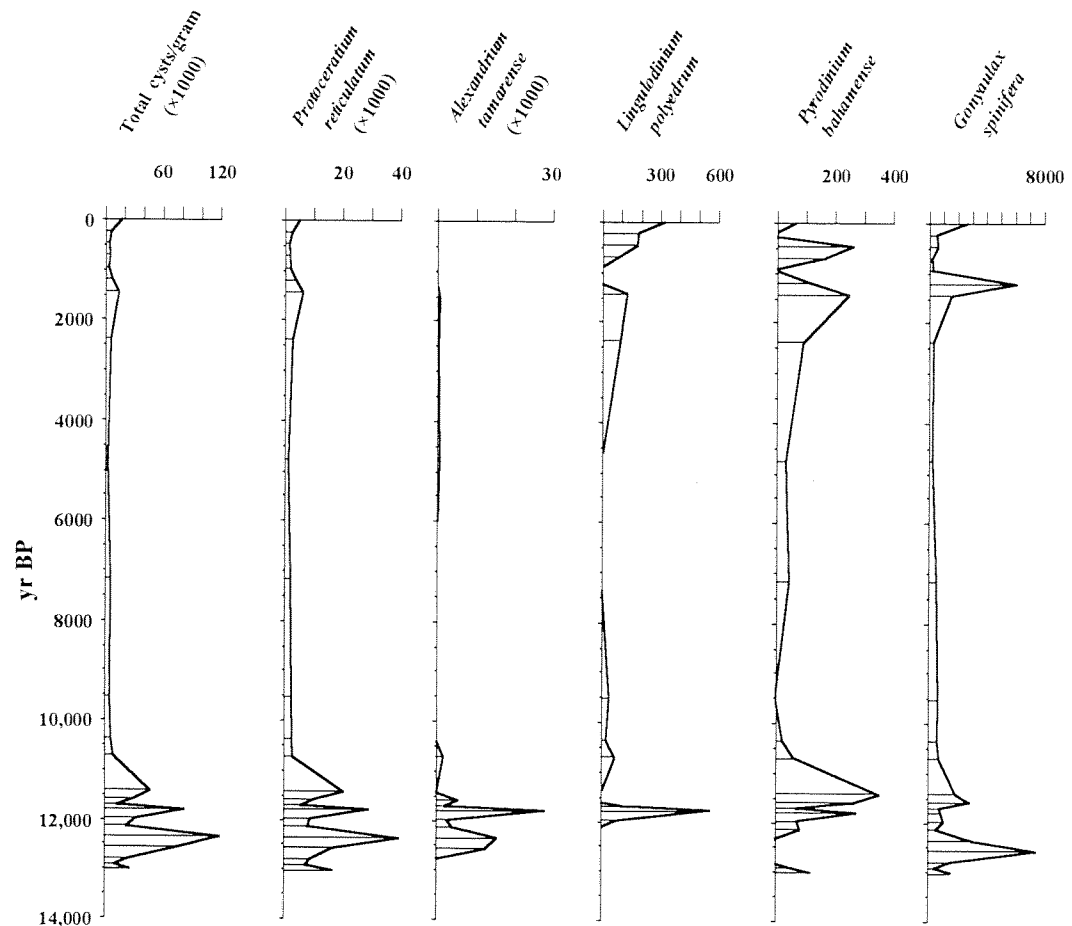
Fig. 14. Geological record for cores 77-002-20 and 87-003-004 from Emerald Basin, showing variations in cyst deposits (cysts/ cm²/yr) for total dinoflagellates and for 'red tide' species.

central Scotian Shelf at present. Migration of these warm boundary current eddies is known to transport dinoflagellate red tide patches from the continental slope into the Sargasso Sea (Balch, 1979) and may possibly account for these excursions into Emerald Basin during late glacial intervals of weaker Labrador Current flow.

As in La Have Basin, there is also a rapid reduction in abundance of red tide-producing cysts during most of the middle Holocene. The Emerald Basin record also shows a recurrence of intermittent 'red tide' cyst production during the past 2000 yr, particularly at the surface (past ca. 300 yr) where there is a peak of *Lingulodinium polyedrum*.

6. Discussion

6.1. Assumptions about bloom sizes

Quantitative reconstruction of the history of dinoflagellate 'red tide' blooms from fossil records requires a good understanding about the relationship between the magnitude of a motile dinoflagellate bloom population and the abundance of fossilizable resting cysts produced by that population. Despite the common use of dinoflagellate cysts to reconstruct phytoplankton productivity (Devilliers and de Vernal, 2000), few studies have investigated the quantitative relationship between the size of motile dinoflagellate blooms and

the abundance of resting cysts. In comparing plankton tow data with surface grab samples from Trondheimsfjord, Dale (1976) found that some cysts appeared over- or under-represented relative to motile cell numbers and he cited earlier work at Woods Hole which showed that motile populations of the gonyaulacoid species *Protoceratium reticulatum* produce relatively large numbers of cysts (1:2 cyst:theca ratio) while *Gonyaulax digitale* and protoperidinioid species are much less prolific cyst producers (1:500 and 1:120, respectively). However, the short plankton record (2 yr) and bioturbated (mixed age) sediments limited the certainty of this interpretation. Similar limits pertain to plankton tow and cyst data from mixed sediments (Lewis, 1988; Anderson and Keafer, 1985) which suggest that *Lingulodinium polyedrum* and *Alexandrium tamarense* produce relatively few cysts (ca. 4:1000). Nonetheless, Keafer et al. (1993) were still able to show that even in bioturbated sediments, 'red tide' bloom years can usually still be discerned as peaks of cysts marking the base of the mixed interval. In contrast, non-bloom years have much lower cyst abundances.

Our ultra-high resolution data from the 50-yr record of annual laminae in Saanich Inlet provide a measure of the number of cysts deposited/cm^3 during a given year which can be compared to the size of the corresponding dinoflagellate or *Heterosigma* species bloom (in cells/ml) recorded for the same year. Our varve record generally confirms these earlier results about cyst:theca ratios and allows us to state that peaks of *Alexandrium* and *Gonyaulax spinifera* comprising at least 500 cysts/ml of wet sediment correspond to recorded 'red tide' events with bloom abundances of > 1000 cells/ml. For the PSP species *Alexandrium tamarense*, 500 cysts/ml would also be equivalent to toxicity levels of about 80 mouse units which is the minimum recommended level at which shellfish harvests must be closed (Quayle, 1969). Likewise, smaller amounts of cysts of *Lingulodinium polyedrum* (250/ml) and *Heterosigma* (200 cysts/ml) correspond to the occurrence of harmful blooms.

In our interpretation of the Saanich Inlet results and their significance to society, we shall assume that these cyst:theca ratios have persisted during the past 10 500 yr, and we also assume that the species have retained the same toxicity during this time. For example, at present we have no precise way of discerning between toxic and non-toxic strains of *Alexandrium tamarense* (see Cembella, 1998). The apparent monospecificity of the proxy-bloom data, however, seems to support our assumption of toxic populations that poisoned or starved their predators, giving the HAB species an advantage over other phytoplankton competitors. Our interpretation of the Atlantic shelf records will also assume monospecificity of the 'red tide' blooms and persistent toxicity.

Likewise, we acknowledge that our interpretations are limited by uncertainty regarding the taxonomy of some cysts. In particular, there is presently some confusion regarding the morphology of cysts produced by the *Alexandrium* (*Gonyaulax*) *excavatum* species complex (including *Alexandrium tamarense, Alexandrium fundyense, Alexandrium ostenfeldii* and possibly *Alexandrium catenella*). Based on study of cysts from laboratory cultures of *A. excavatum* and field samples, Simard and de Vernal (1998) included morphotypes with a loosely attached prominent outer wall and no obvious archeopyle in their taxon *A. excavatum* cyst-type. Other workers (e.g. Cembella, personal communication, June 2001) have also noted the difference in morphology of cysts from laboratory cultures and field samples. In our cores from Bedford and Emerald basins, counts of oval cysts with almost smooth hyaline walls and simple chasmic apical archeopyles (e.g. Fig. 8.2, cf. *A. tamarense* cyst) were listed separately from the *A. excavatum* cyst-type with a loose outer wall (Fig. 8.5). This is the only morphotype that was found in the coastal Bedford Basin and Saanich Inlet cores. It was subsequently noted that in the Scotian Shelf cores, the two morphotypes almost invariably occurred in the same assemblage, and they are probably conspecific, with the *A. excavatum* cyst-form of Simard and de Vernal (1998) being the dominant morphotype in the early Holocene.

It should also be noted that after acid treatment, calcareous cysts of *Scrippsiella lachrymosa*

(Lewis, 1991) could possibly be reduced to an oval cyst resembling our cf. *Alexandrium tamarense* cysts. However, the smooth-walled cyst linings of *Scrippsiella* spp. would differ in having a zig-zagged opening because the theropylic archeopyle includes paraplates 2′–4′ in addition to 1–3a. Furthermore, we have not found any oval calcareous cysts of *Scrippsiella* in any of our untreated core samples despite the fact that *S. trochoidea* is sometimes present in Saanich Inlet (Hobson and McQuoid, 2001). There are only two records of this taxon from continuous plankton records (CPR) off Nova Scotia and the genus is not listed in the CPR for the United States (Doug Sameoto, personal communication, June 2001).

Finally, it must be said that there is presently much uncertainty regarding the recognition of *Heterosigma* cysts in the geological record. Our identification in Saanich Inlet is based on the observation that in this extraordinary depositional environment, the small round cysts that accompany modern plankton blooms of *Heterosigma akashiwo* always retain reddish pigment bodies and some of them are enveloped in a coarsely reticulate outer wall (see Fig. 8.4, 8.5). These criteria were used to identify the presence of *Heterosigma*-type cysts in the ODP Core 1034B samples.

6.2. Regional similarities and differences

Despite the differences in the oceanographic regimes of the eastern Pacific upwelling margin and the Atlantic western boundary current margin, there are several outstanding similarities between these two regions.

In both regions, all the cyst-producing modern 'red tide' species listed in the local historical records have been intermittently present for the past 10 000 yr or more, and, judging from the cyst proxy-record, have attained bloom sizes at various times in the past. This has important implications regarding the idea that some species, e.g. *Heterosigma* and *Gymnodinium catenatum*, are recent introductions in ballast water, although discharge from ballast water may be an important factor accounting for the apparently abnormal

multi-species blooms in the modern record for Saanich Inlet. It is also notable that there are no occurrences of *G. catenatum*-type cysts in the western Atlantic although this species may be present with *Gymnodinium nolleri* in a long record from the eastern North Atlantic coast (e.g. Ellegaard et al., 1993). In the western Atlantic, *G. catenatum* and *G. nolleri* are also absent from the Gulf of St. Lawrence and western Newfoundland fjords (Levac, unpublished data) which may indicate that this species is not able to survive in the Atlantic Canada region even if introduced with ballast discharge.

Both regions show very large late glacial–early Holocene cyst influx peaks, presumably reflecting 'red tide' blooms, with *Protoceratium reticulatum* dominating. At this time, the sizes of the basin and sill depths (ca. 30 m cf. the modern 70-m depth) were probably similar. Possible environmental factors that may account for these extraordinarily large blooms are discussed below.

6.2.1. Seasonal insolation

Large abundances of late glacial and early Holocene dinoflagellate cysts have been observed in records from many regions, and Dale and Fjellsa (1994) and Simard and de Vernal (1998) have suggested a climatic cause related to sea surface warming. In particular, the prevalence of *Alexandrium*-type cysts on the Atlantic margin supports this interpretation: the modern distribution of the *Alexandrium excavatum* cyst-type suggests that this species prefers warmer waters in summer (15°C) and absence or very short duration of winter sea ice cover (Simard and de Vernal, 1998). The coincidence of the largest 'red tides' with the summer insolation maximum of the late glacial–early Holocene (Fig. 13) suggests that the peaks of cyst production were favored by warmer SST conditions than today. The higher salinity on the Atlantic shelf and the presence of temperate red tide-producing species may also reflect more frequent seeding of blooms by cross-shelf transport of warm water eddies from the Gulf Stream. Conversely, on the Scotian Shelf, the generally lower salinity and lower summer temperature of the middle Holocene correspond to a decrease in red tide-producing dinoflagellates. The slight in-

crease of cyst peak size and frequencies in the late Holocene can again be correlated with intervals of higher salinity and winter SST.

6.2.2. Nutrients, eutrophication and competition

The late glacial dinoflagellate assemblages in La Have Basin include a strong representation of several species that have been linked (Devilliers and de Vernal, 2000) with high nutrient concentrations and productivity, including *Selenopemphix quanta*, *Ataxiodinium choane* and *Pentapharsodinium dalei*. While this may account for the higher total cyst influxes, Goodman et al. (1984) have shown that although upwelling and nutrients are the main trigger for spring diatom blooms, the summer dinoflagellate red tide blooms are not associated with either upwelling or with increased nitrogen and phosphate. Likewise, Dale et al. (1999) and Matsuoka (1999) also noted that strong eutrophication tends to increase heterotrophic dinoflagellates over the gonyaulacoid species while mild eutrophication may increase the occurrence of *Lingulodinium polyedrum* but not *Protoceratium reticulatum*, the major late glacial species in both Pacific and Atlantic regions. It is possible that shifts in nutrient availability account for some of the species successions, e.g. the change from dominance of *P. reticulatum* to *L. polyedrum*. In Saanich Inlet, however, diatoms and silicoflagellate assemblages show very little change in abundance or species composition throughout most of the Holocene (McQuoid and Hobson, 2001), apart from a possible slight abundance increase in the early mid-Holocene. The succession of 'red tide' species for Saanich Inlet therefore does not clearly indicate a response to either changes in macronutrients or competition at a community level. By implication, the similar records from the Scotian Shelf must also be attributed to other factors.

6.2.3. Stratification

Although there are numerous contradictions concerning the specific cause of dinoflagellate red tides, it is generally agreed that blooms produced by gonyaulacoids dominate in regions of low turbulence and high nutrients (Hallegraef, 1998; Cullen and McIntyre, 1998). Therefore,

although some turbulence or transport in frontal zones is necessary to convey resting cysts from the sediments to the photic zone, stability of the surface water is necessary for the subsequent rapid development of dinoflagellate blooms (e.g. Carreto et al., 1986). Strongly stratified surface water with a shallow pycnocline may also be important in retaining available nutrients within the photic zone. For example, Therriault and Levasseur (1985) have shown that light is the most important factor influencing the phytoplankton growth in the St. Lawrence estuary. The depth of the stable photic zone may also have an important influence on the the dominant red tide species; for example, the chain-forming species of *Alexandrium* and *Gymnodinium* have more buoyancy and greater ability for vertical migration than small compressed species such as *Karenia aureolum* and *Prorocentrum* spp. which must aggregate in a thin surface water layer (see Cullen and McIntyre, 1998).

6.2.4. Sediment resuspension

Lower sea level may partly explain the long interval of large blooms leading to the high cyst influxes during the late glacial and early Holocene. On the Scotian Shelf, relative sea level was about 40 m lower than now at about 10 ka (Scott and Collins, 1996) which means that the basin entrances would be only about 30 m deep. The high influxes of cf. *Alexandrium tamarense*-type cysts and *Bitectatodinium tepikiense* are also indicative of shallower sill depths: these species are most abundant in silled bays along the present coast of Nova Scotia and Maine (cf. Miller et al., 1982). With a shallower sill depth, seeding of surface waters by sediment resuspension during storms may have triggered more frequent red tides. Both stability and seeding of surface waters seem to be necessary conditions for high productivity as shown by Therriault and Levasseur (1985) in the St. Lawrence estuary. Higher frequency of sandy laminae in Emerald Basin (Hall and Reed, 1996) also show that more sediment was swept into the basins from local sources in the early Holocene which suggests that storms may have been more frequent than the present storm-dominated Atlantic shelf, but the lower rel-

ative sea level prevents quantification of this parameter.

On the other hand, Saanich Inlet lies in the protected lee of Vancouver Island and is not directly subject to storm waves, yet it shows a similar abundance of red tide blooms in the late glacial–early Holocene. Unfortunately, the sea level curve for this inlet is poorly constrained (see Mosher and Moran, 2001), and although it has been suggested that the early Holocene sill depth was as low as 25 m, there is no clear evidence from either dinoflagellate or diatom data to support this interpretation. Likewise, there is no microfossil evidence to support the hypothesis that Saanich Inlet was isolated from the Pacific Ocean waters after ca. 11 ka. The only evidence for the possible importance of sediment resuspension in this Pacific region comes from initial results of a spectral analysis of the high frequency signals in the Saanich red tide cyst records. Most of the 'red tide' signals just record statistical noise, suggesting that the sampling interval used in this study is too low. However, the lower frequency *Heterosigma* record shows significant peaks at 112-yr intervals which is very close to the 116-yr cyclicity of gravity flow events reported by Blais-Stevens et al. (1997).

6.3. Species succession

Most of the Holocene cyst record for Saanich Inlet indicates recurrent bloom cycles in which 'red tide'-producing species seem to replace each other throughout the Holocene, so that only one species blooms at a time. The rare exceptions before ca. 1000 yr BP correspond to gravity flow events as discussed above. In contrast to the Holocene succession, the modern record shows simultaneous occurrences of two or more blooms. This concurrence of blooms seems to be exceptional compared to normal phytoplankton population dynamics and historical data on red tide blooms (e.g. Sweeney, 1979; Prezelin and Sweeney, 1979; Smayda, 1997; Matsuoka, 1999). For example, normal phytoplankton bloom responses usually follow a sequence in which nutrient enrichment triggers non-harmful spring diatom blooms during which the water is turbulent and

saturated with silica, followed by a bloom of autotrophic dinoflagellates in the warm stratified summer surface layer, and terminated by predation from blooms of heterotrophic dinoflagellates such as *Polykrikos* and *Noctiluca*. In the Southern California area, which has the best historical data series on red tide bloom successions (Sweeney, 1975), a 61-yr record shows that spring-blooming *Prorocentrum micans* formed the recurrent red tides at ca. 10-yr intervals from 1920 to 1938, then disappeared until 1961–1965. From 1938 to 1978, the summer-blooming *Lingulodinium polyedrum* formed 'red tides' at ca. 4-yr recurrence intervals from 1938 to 1945, then reappeared in 1961 and 1964, finally appearing again in almost consecutive years from 1970 to 1975. The only year in which both species bloomed was 1961 which was an interval of prolonged severe El Niño conditions (see Fig. 4).

The Holocene succession of 'red tide'-producing species in Saanich seems to conform with these normal bloom dynamics on a longer time scale, with monospecific successions prevailing for centuries to a millennium. The late glacial–early Holocene interval of up to 5°C warmer SST in summer was marked by sustained, large, monospecific blooms of the non-chain-forming species *Protoceratium reticulatum*, a cosmopolitan opportunistic species that today only reaches HAB proportions off the coast of Southern Africa (Reinecke, 1966) and New Zealand, and apparently does not have very high nutrient requirements as is shown by its lack of response to eutrophication (Dale et al., 1999; Matsuoka, 1999). On the exposed Atlantic shelf where sediment resuspension was high, the *P. reticulatum* peaks were interspersed with peaks of the highly toxic, chain-forming PSP species *Alexandrium* and the non-toxic species *Gonyaulax spinifera* or *Gonyaulax digitale* which also have relatively low nutrient requirements according to the statistical studies of Devilliers and de Vernal (2000). *Alexandrium* is highly sensitive to light and stable stratification (Therriault and Levasseur, 1985). In Saanich Inlet, the *G. spinifera* blooms precede the *Alexandrium* blooms which are notably short-lived in this area, and do not commence until the onset of continuously varved sediments after ca. 9000 yr

BP, perhaps reflecting less stable summer stratification in the very early Holocene. In Emerald Basin, the non-toxic *G. spinifera* blooms are interspersed with peaks of *Lingulodinium polyedrum*, which has high nutrient requirements and is an indicator of modern eutrophic conditions (Dale et al., 1999; Matsuoka, 1999). This species does not reach bloom size until about 8 ka in Saanich Inlet, at which time diatom production also begins to increase and the chain-forming PSP species *Gymnodinium catenatum* first occurs. This ends the early Holocene sequence in Saanich, while the sustained occurrence of the subtropical species *Pyrodinium bahamense* ends the succession on the Scotian Shelf. Today, *P. bahamense* forms red tides in low salinity bays of southern USA but it is only toxic in tropical Pacific regions as the chain-forming variety *P. bahamense* var. *compressum*.

The factors that account for the species successions therefore probably include a combination of summer SST, 'seeding' conditions, water column stability, nutrients and depth of the photic zone, but there is presently insufficient knowledge regarding individual species tolerances to distinguish among these factors with any certainty. The periodic break-down of the succession in Saanich Inlet, however, strongly suggests the introduction of some new factor(s) – which started well before the modern increase in fish farming and tanker shipping traffic and possibly include the beginning of eutrophication and chemical pollution by logging and paper pulp industries around 1850 (see O'Connell and Tunnicliffe, 2001). Multiple bloom events are often recorded in areas of macronutrient enrichment and may partly account for the post-1980 events in Saanich Inlet which correspond to increased urban development of the western shore.

7. Conclusions

(1) The geological records show that throughout the Holocene, cysts of all the modern red tide-producing species known for the Pacific and Atlantic study areas have been present in abundances that suggest dinoflagellate or *Heterosigma*

bloom proportions). The ultra-high resolution Pacific records show that natural red tide/HAB mega-cycles occur every 100–1000 yr, and that most cycles begin and end abruptly, in less than 20 yr.

(2) Pacific and Atlantic red tide histories show a similar late glacial–early Holocene succession of sustained high production of non-toxic and toxic red tide blooms, with the only obvious common denominator being the warmer (up to 5°C) SST in summer. This finding strongly implicates the importance of global warming for the historical increase in frequency of 'red tides' and other HABs.

(3) In some areas, sediment disturbance by storms may be important for sustained 'seeding' of blooms, but the Saanich record shows that this is not always a pre-requisite. The importance of storms and earthquakes for resuspension and initiation of blooms, however, suggests that sediment disturbance by dredging or tanker turbines should be carefully investigated as a possible contributory cause of modern 'red tide' increases.

(4) Both Pacific and Atlantic study regions show increased 'red tide' occurrences in the past 2000 yr, which is possibly related to the long-term switch towards increased winter insolation as seen in increased winter SST. However, only the nearshore Pacific record shows a chaotic modern signal in which species succession seems to breakdown periodically. This unnatural chaotic signal seems to indicate a disequilibrium in plankton communities that may indicate a limit of tolerance for nutrient enrichment and/or discharge of chemical toxins in coastal fjords.

(5) In Pacific fjords, although efforts to clean up pollution and to stop ballast discharge may reduce the frequency of HABS, it is unlikely that dinoflagellate red tides will be eliminated. Continued studies of the varved geological record on an annual scale, however, may allow refinement of our ability to predict the timing and species composition of 'red tide' blooms following the restoration of equilibrium conditions in the phytoplankton communities.

Acknowledgements

References

Abuso, Z.V., Cabella, L.M.T., Tuazon, L.C., 1999. Red tide monitoring in Maqueda and Villareal bays, Samar, Central Phillipines. In: Watson, I., Vigers, G., Ong, K.-S. (Eds.), ASEAN Marine Environmental Management. Proceedings Fourth ASEAN-CANADA, Technical Conference on Marine Science, Langkawi, October 26–30, pp. 488–498.

Anderson, D.M., 1994. Red Tides. Sci. Am. 271, 62–68.

Anderson, D.M., Aubrey, D.G., Tyler, M.A., Coats, D.W., 1982. Vertical and horizontal distributions of dinoflagellate cysts in sediments. Limnol. Oceanogr. 27, 757–765.

Anderson, D.M., Keafer, B.A., 1985. Dinoflagellate cyst dynamics in coastal and estuarine waters. In: Anderson, D.M., White, A.W., Baden, D.G. (Eds.), Toxic Dinoflagellates. Elsevier Science Publishing, pp. 219–224.

Anonymous, 1100–1200 A.D. Exodus Chapter 7, verses 20–21.

Balch, W.M., 1979. Gulf Stream rings as a mechanism of patch formation. In: Taylor, D.L., Seliger, H.H. (Eds.), Toxic Dinoflagellate Blooms. Proceedings Second International Conference on Toxic Dinoflagellate Blooms, Elsevier, NY, pp. 275–278.

Barss, M.S., Williams, G.L., 1973. Palynology and nannofossil processing techniques. Geol. Surv. Can. Pap. 73-26, 1–25.

Blais-Stevens, A., Clague, J.J., Bobrowsky, P.T., Patterson, R.T., 1997. Late Holocene sedimentation in Saanich Inlet, British Columbia, and its paleoseismic implications. Can. J. Earth Sci. 34, 1345–1357.

Burkholder, J.M., 1998. Implications of harmful microalgae and heterotrophic dinoflagellates in management of sustainable marine fisheries. Ecol. Appl. 8 (Suppl.), S37–S62.

Carreto, J.I., Benavides, H.R., Negri, R.M., Glorioso, P.D., 1986. Toxic red tide in the Argentine Sea. Plankton distribution and survival of the toxic dinoflagellate *Gonyaulax excavata* in a frontal Area. J. Plankton Res. 8, 15–28.

Cembella, A.D., 1998. Ecophysiology and metabolism of paralytic shellfish toxins in marine microalgae. In: Anderson, D.M., Cembella, A.D., Hallegraeff, G.M. (Eds.), Physiological Ecology of Harmful Algal Blooms. NATO Advanced Science Institutes Series G, vol. 41, Springer-Verlag, Berlin, pp. 381–403.

Cullen, J.J., McIntyre, J.G., 1998. Behaviour, physiology and the niche of depth-regulating phytoplankton. In: Anderson, D.M., Cembella, A.D., Hallegraeff, G.M. (Eds.), Physiological Ecology of Harmful Algal Blooms. NATO Advanced Science Institutes Series G, vol. 41, Springer-Verlag, Berlin, pp. 559–579.

Dale, B., 1976. Cyst formation, sedimentation, and preservation: factors affecting dinoflagellate assemblages in recent sediments from Trondheimsfjord, Norway. Rev. Palaeobot. Palynol. 22, 39–60.

Dale, B., Fjellsa, A., 1994. Dinoflagellate cysts as paleoproductivity indicators: state of the art, potential and limits. In: Zahn, R. et al. (Eds.), Carbon Cycling in the Glacial Ocean: Constraints on the Ocean's Role in Global Change. NATO Advanced Science Institutes Series, vol. 117, pp. 521–537.

Dale, B., Yentch, C.M., Hurst, J.W., 1978. Toxicity in resting cysts of the red tide dinoflagellate *Gonyaulax excavata* from deeper water coastal sediments. Science 201, 1223–1225.

Dale, B.D., Thorsen, T.A., Fjellsa, A., 1999. Dinoflagellate cysts as indicators of cultural eutrophication in the Oslofjord, Norway. Estuar. Coast. Shelf Sci. 48, 371–382.

Dauberg, N., Hansen, G., Larsen, J., Moestrup, Ø., 2000. Phylogeny of some of the major genera of dinoflagellates based on ultrastructure and partial LSU rDNA sequence data, including the erection of three new genera of unarmoured dinoflagellates. Phycologia 39, 302–317.

Dean, J.M., Kemp, A.E.S., McQuoid, M.R., 2001. Paleo-flux records from electron microscope studies of Holocene laminated sediments, Saanich Inlet, British Columbia. Mar. Geol. 174, 139–158.

Devilliers, R., de Vernal, A., 2000. Distribution of dinoflagellate cysts in surface sediments of the northern North Atlantic in relation to nutrient content and productivity in surface waters. Mar. Geol. 166, 103–124.

Ellegaard, M., Christensen, S.F., Moestrup, Ø., 1993. Temperature and salinity effects on growth of a non-chain-forming strain of *Gymnodinium catenatum* (Dinophyceae) established from a cyst from recent sediments in the Sound (Øresund), Denmark. J. Phycol. 29, 418–426.

Ellegard, M., Moestrup, Ø., 1999. Fine structure of the flagellar apparatus and morphological details of *Gymnodinium nolleri* sp. nov. (Dinophyceae), an unarmoured dinoflagellate producing a microreticulate cyst. Phycologia 38, 289–300.

Emslie, S.D., Allmon, W.D., Rich, F.J., Wrenn, J.H., de France, S.D., 1996. Integrated taphonomy of an avian death

assemblage in marine sediments from the late Pliocene of Florida. Paleogeogr. Paleoclimatol. Paleoecol. 124, 107–136.

Faegri, K., Iversen, J., 1975. Textbook of Pollen Analysis, 3 edn. Munksgaard, Copenhagen, pp. 101–107.

Fjellsa, A., Norberg, K., 1996. Toxic dinoflagellate 'blooms' in the Kattegat, North Sea, during the Holocene. Paleogeogr. Paleoclimatol. Paleoecol. 124, 87–105.

Forbes, J.R., 1994. Proceedings of the Fourth Canadian Workshop on Harmful Marine Algae. Canadian Technical Report on Fisheries and Aquatic Sciences 2016, 92 pp.

Franks, P.J.S., Anderson, D.M., 1992. Toxic phytoplankton blooms in the southwestern Gulf of Maine: testing hypotheses of physical control using historical data. Mar. Biol. 112, 165–174.

Gaines, G., Taylor, F.J.R., 1985. An exploratory analysis of PSP patterns in British Columbia: 1942–1984. In: Anderson, D.M., White, A.W., Baden, D.G. (Eds.), Toxic Dinoflagellates. Elsevier Science Publishing Company, pp. 439–444.

Gipp, M., Piper, D.J.W., 1989. Chronology of Late Wisconsinan deglaciation, Emerald basin, Scotian Shelf. Can. J. Earth Sci. 26, 333–335.

Goodman, D., Eppley, R.W., Reid, F.M.H., 1984. Summer phytoplankton assemblages and their environmental correlates in the California bight. J. Mar. Res. 42, 1019–1099.

Guiot, J., 1990. Methods and programs of statistics for paleoclimatology and paleoecology. In: Guiot, J., Labeyrie, L. (Eds.), Quantification des changements climatiques: methodes et programmes. Institut National des Sciences de l'Univers (INSU-France), Paris, Monograph Number 1, 253 pp.

Hall, F.R., Reed, S.J., 1996. Rock (mineral)-magnetic properties of post-glacial (16–0.5 ka) sediments from the Emerald basin (Scotian Shelf), Canada. In: Andrews, J.T., Austin, W.E.N., Bergstein, H., Jennings, A.E. (Eds.), Late Quaternary Paleoceanography of the North Atlantic Margins. Geological Society Special Publication 111, pp. 103–116.

Hallegraef, G.M., 1998. Concluding remarks on the autecology of harmful algal blooms. In: Anderson, D.M., Cembella, A.D., Hallegraef, G.M. (Eds.), Physiological Ecology of Harmful Algal Blooms. NATO Advanced Science Institutes Series G, vol. 41, Springer-Verlag, Berlin, pp. 371–378.

Hallegraeff, G.M., 1993. A review of harmful algal blooms and their apparent global increase. Phycol. Rev. 13, 79–99.

Hendy, I.L., Kennett, J.P., 2000. Stable isotope stratigraphy and paleoceanography of the last 170 k.y.: Site 1014, Tanner Basin, California. In: Lyle, M., Koizumi, I., Richter, C., Moore, T.C. (Eds.), Proceedings Ocean Drilling Program Scientific Results 167. College Station, TX (Ocean Drilling Program), pp. 129–150.

Heusser, L.E., 1983. Palynology and paleoecology of postglacial sediments in an anoxic basin, Saanich Inlet, British Columbia. Can. J. Earth Sci. 20, 873–885.

Hobson, L.A., McQuoid, M.R., 2001. Pelagic diatom assemblages are good indicators of mixed water intrusions into Saanich Inlet, a stratified fjord in Vancouver Island. Mar. Geol. 174, 125–138.

Horner, R.A., 1998. Harmful algal blooms in the U.S.: an update. In: GEOHAB: Global Ecology and Oceanography of Harmful Algal Blooms. International Oceanographic Commission/EC-XXXI/15, Item 5.2, p. 10.

Kahru, M., Mitchell, B.G., 1998. Spectral reflectance and absorption of a massive red tide off Southern California. J. Geophys. Res. 103, 21601–21609.

Keafer, B.A., Buesseler, K.O., Anderson, D.M., 1993. Burial of living dinoflagellate cysts in estuarine and nearshore sediments. Mar. Micropaleontol. 20, 147–161.

Levac, E., 2001. High resolution Holocene palynological record from the Scotian Shelf, eastern Canada. Mar. Micropaleontol., in press.

Lewis, J., 1988. Cysts and sediments: *Gonyaulax polyedra* (*Lingulodinium machaerophorum*) in Loch Creran. J. Mar. Biol. Assoc. UK 68, 701–714.

Lewis, J., 1991. Cyst–theca relationships in *Scrippsiella* (Dinophyceae) and related Orthoperidinioid genera. Bot. Mar. 34, 91–106.

Lewis, J., Harris, A.S.D., Jones, K.J., Edmonds, R.L., 1999. Long-term survival of marine planktonic diatoms and dinoflagellates in stored sediment samples. J. Plankton Res. 21, 343–354.

Lewis, J., Tett, P., Dodge, J.D., 1985. The cyst–theca cycle of *Gonyaulax polyedra* (*Lingulodinium machaerophorum*) in Creran, a Scottish west coast loch. In: Anderson, D.M., White, A.W., Baden, D.G. (Eds.), Toxic Dinoflagellates. Elsevier Science Publishing Company, pp. 85–90.

Loder, J.W., Han, G., Hannah, C.G., Greenberg, D.A., Smith, P.C., 1997. Hydrography and baroclinic circulation in the Scotian Shelf region: winter versus summer. Can. J. Fish. Aquat. Sci. 54 (Suppl. 1), 40–56.

Marret, F., 1993. Les effets de l'acetolyse sur les assemblages des kystes de dinoflagellates. Palynosciences 2, 267–272.

Martin, J.L., Richard, D., 1996. Shellfish toxicity from the Bay of Fundy, eastern Canada: 50 years in retrospect. In: Yasumoto, T., Oshima, Y., Fukuyo, Y. (Eds.), Harmful and Toxic Algal Blooms. Intergovernmental Oceanographic Commission of UNESCO, Paris, pp. 3–6.

Matsuoka, K., 1999. Eutrophication process recorded in dinoflagellate cyst assemblages – a case of Yokohama Port, Tokyo Bay, Japan. Sci. Total Environ. 231, 17–35.

Matsuoka, K., Fukuyo, Y., 1995. Taxonomy of cysts. In: Hallegraeff, G.M., Anderson, D.M., Cembella, A.D. (Eds.), International Oceanographic Commission Manuals and Guides No. 33. UNESCO, Paris, pp. 381–401.

McQuoid, M.R., Hobson, L.A., 1997. A 91-year record of seasonal and interannual variability of diatoms from laminated sediments in Saanich Inlet, British Columbia. J. Plankton Res. 19, 173–194.

McQuoid, M.R., Hobson, L.A., 2001. A Holocene record of diatom and silicoflagellate microfossils in sediments of Saanich Inlet, ODP Leg 169S. Mar. Geol. 174, 111–123.

Miller, A.A.L., Mudie, P.J., Scott, D.B., 1982. Holocene history of Bedford Basin, Nova Scotia: foraminifera, dinoflagellate and pollen records. Can. J. Earth Sci. 19, 2342–2367.

Mlot, C., 1998. The rise in toxic tides: What's behind the ocean blooms? Sci. News 152, 1.

Mosher, D.C., Moran, K., 2001. Post-glacial evolution of Saanich Inlet, British Columbia: results of physical property and seismic reflection stratigraphic analysis. Mar. Geol. 174, 59–78.

Mudie, P.J., 1992. Circum-arctic Quaternary and Neogene marine palynofloras: paleoecology and statistical analysis. In: Head, M.J., Wrenn, J.H. (Eds.), Neogene and Quaternary Dinoflagellate Cysts and Acritarchs. American Association Stratigraphic Palynologist Foundation, Dallas, TX, pp. 347–390.

Mysak, L.A., 1986. El Niño, interannual variability and fisheries in the northeast Pacific Ocean. Can. J. Fish. Aquat. Sci. 43, 464–497.

Nederbragt, A.J., Thurow, J.W., 2001. A 6000 yr varve record of Holocene climate in Saanich Inlet, British Columbia, from digital sediment colour analysis of ODP Leg 169S cores. Mar. Geol. 174, 95–110.

O'Connell, J.M., Tunnicliffe, V., 2001. The use of sedimentary fish remains for interpretation of long-term fish population fluctuations. Mar. Geol. 174, 177–195.

Pellatt, M.G., Hebda, R.J., Matthewes, R.W., 2001. High resolution Holocene vegetation history and climate from Core 1034B, ODP Leg 169S, Saanich Inlet, Canada. Mar. Geol. 174, 211–226.

Petrie, B.D., Topliss, B.J., Wright, D.G., 1987. Coastal upwelling and eddy development off Nova Scotia. J. Geophys. Res. 92, 12979–12991.

Pocklington, R., Leonard, J.D., Crewe, N.F., 1991. Sources of organic matter to surficial sediments from the Scotian Shelf and Slope, Canada. Cont. Shelf Res. 11, 1069–1082.

Prakash, A., Medcof, J.C., Tennant, A.D., 1971. Paralytic shellfish poisoning in eastern Canada. Fisheries Research Board of Canada Bulletin 177, Ottawa, 87 pp.

Prezelin, B.B., Sweeney, B.M., 1979. Photoadaptation of photosynthesis in two bloom-forming dinoflagellates. In: Taylor, D.L., Seliger, H.H. (Eds.), Toxic Dinoflagellate Blooms. Proceedings Second International Conference on Toxic Dinoflagellate Blooms, Elsevier, NY, pp. 101–106.

Quayle, D.B., 1969. Paralytic shellfish poisoning in British Columbia. Fisheries Research Board Canada Bulletin 168, 68 pp.

Reinecke, P., 1966. Gonyaulax grindleyi sp. nov.: a dinoflagellate causing a red tide at Elands Bay, Cape Province, in December 1966. J. S. Afr. Bot. 33, 157–160.

Rochon, A., de Vernal, A., Turon, J.L., Matthiessen, J., Head, M.J., 1999. Distribution of recent dinoflagellate cysts in surface sediments from the North Atlantic Ocean and adjacent seas in relation to sea-surface parameters. Contributions Series No. 35, American Association Stratigraphic Palynologists Foundation, 152 pp.

Scott, D.B., Collins, E.S., 1996. Late mid-Holocene sea-level oscillation: a possible cause. Quat. Sci. Rev. 15, 851–856.

Scott, D.B., Mudie, P.J., Vilks, G., Younger, D.C., 1984. Latest Pleistocene–Holocene paleoceanographic trends on the continental margin of Eastern Canada: foraminiferal, dino-

flagellate and pollen evidence. Mar. Micropaleontol. 9, 181–218.

Sholkovitz, E., Soutar, A., 1975. Changes in the composition of the bottom water of the Santa Barbara Basin: effect of turbidity currents. Deep-Sea Res. 22, 13–21.

Simard, A., de Vernal, A., 1998. Distribution des kystes du type *Alexandrium excavatum* dans les sediments recents et postglaciares des marges est-Canadiennes. Geogr. Phys. Quat. 52, 361–371.

Smayda, T.J., 1997. Bloom dynamics: physiology, behaviour, trophic effects. Limnol. Oceanogr. 42, 1132–1136.

Smith, P.C., Schwing, F.B., 1991. Mean circulation and variability of the eastern Canadian continental shelf. Cont. Shelf Res. 11, 977–1012.

Soutar, A., Kling, S.A., Crill, P.A., Duffrin, E., Bruland, K.W., 1977. Monitoring the marine environment through sedimentation. Nature 266, 136–139.

Steidinger, K.A., Baden, D.G., 1984. Toxic marine dinoflagellates. In: Spector, D.L. (Ed.), Dinoflagellates. Academic Press, Orlando, FL, pp. 210–261.

Sweeney, B.M., 1975. Red tides I have known. In: LoCicero, V.R. (Ed.), Proceedings First International Conference on Toxic Dinoflagellate Blooms. Elsevier, NY, pp. 225–235.

Sweeney, B.M., 1979. The organisms, opening remarks. In: Taylor, D.L., Seliger, H.H. (Eds.), Toxic Dinoflagellate Blooms. Proceedings Second International Conference on Toxic Dinoflagellate Blooms, Elsevier, NY, pp. 37–40.

Taylor, F.J.R., 1993. Current problems with harmful phytoplankton blooms in British Columbia waters. In: Smayda, T.J., Shimizu, Y. (Eds.), Toxic Phytoplankton Blooms in the Sea. Elsevier Scientific Publications, Amsterdam, pp. 699–703.

Tee, K.T., Smith, P.C., 1993. Topographic upwelling off Southwest Nova Scotia. J. Phys. Oceanogr. 23, 1703–1725.

Therriault, J.-C., Levasseur, M., 1985. Control of phytoplankton production in the lower St. Lawrence estuary light and freshwater runoff. Nat. Can. 112, 77–96.

Thompson, R.E., 1981. Oceanography of the British Columbia Coast. Canadian Special Publications in Fisheries and Aquatic Sciences 56, p. 231.

Thorsen, T.A., Dale, B., 1998. Dinoflagellate cysts as indicators of pollution and past climate in a Norwegian fjord. Holocene 7, 433–446.

Turner, J.T., Tester, P.A., Hansen, P.J., 1998. Interactions between toxic marine phytoplankton and metazoan and protistan grazers. In: Anderson, D.M., Cembella, A.D., Hallegraeff, G.M. (Eds.), Physiological Ecology of Harmful Algal Blooms. NATO Advanced Science Institutes Series G, vol. 41, Springer-Verlag, Berlin, pp. 454–475.

White, A.W., 1987. Relationship of environmental factors to toxic dinoflagellate blooms in the Bay of Fundy. Rapports P.-v Reunion Consul Internationale Exploration du Mer 187, pp. 38–46.

White, D.R.L., White, A.W., 1985. First report of paralytic shellfish poisoning in Newfoundland. In: Anderson, D.M., White, A.W., Baden, D.G. (Eds.), Toxic Dinoflagellates. Elsevier, New York, pp. 511–516.

Whyte, J.N.C., 1998. Heterosigma carterae, a major killer of pen-reared salmon in British Columbia. In: GEOHAB: Global Ecology and Oceanography of Harmful Algal Blooms. International Oceanographic Commission/EC-XXXI/15, Item 5.2, p. 22.

Williams, G.L., Lentin, J.K., Fensome, R.A., 1998. The Lentin and Williams index of fossil dinoflagellates, 1998 edition. Contributions Series 34, American Association Stratigraphic Palynologists Foundation, 817 pp.

Wu, R.S.S., 1999. Eutrophication, waterborne pathogens and xenobiotic compounds: environmental risks and challenges. Mar. Pollut. Bull. 39, 11–22.