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Phytoplankton ecology of Sechelt Inlet, a fjord system on the British Columbia coast. II. Potentially harmful species

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ABSTRACT: Many temperate phytoplankton species considered harmful occur in the Sechelt Inlet system, Britsh Columbia, Canada. Some of the harmful species (*Chaetoceros concavicornis, Nitzschia* (*Pseudonitzschia*) *pungens*, and *Dinophysis fortii*) were predictable spatially and/or temporally on an annual basis. Other species (*Alexandrium catenella* and *Heterosigma carterae*) exhibited greater interannual variability and are probably influenced by cyclical events (e.g El Niño Southern Oscillation) longer than the period of this study. The ecology of *C. concavicornis* suggested a physiological adaptation to low light, enabling this diatom to live along the pycnocline in stratified water away from turbulence. Fall blooms of *C. concavicornis* appear to be a function of lower temperatures and decreasing light levels characteristic of the summer-autumn transition. *N. pungens* was found to occur regularly in summer and autumn; populations during the latter period were chiefly composed of f. *pungens* but f. *multiseries*, which has been linked to domoic acid production, also occurred. One large bloom of *A. catenella* occurred in late September 1989, which appeared to originate from outside the inlet complex. This PSP (paralytic shellfish poison)-producing dinoflagellate was advected into the system where it found conditions favourable to form an extensive bloom, with cell concentrations well in excess of those considered harmful (1000 cells l^{-1}) down to 10 m throughout. This led to the highest toxicity ever recorded in British Columbia (31 000 µg per 100 g shellfish). *Dinophysis*, which produces okadaic acid, formed subsurface concentrations exceeding the reportedly harmful level of 200 cells l^{-1}. *D. acuminata* was the predominant *Dinophysis* species and was often abundant at 10 to 15 m in summer near the region of tidal turbulence. In autumn there was a regular increase in the *D. fortii* population at 5 to 10 m in waters of the sheltered southern end. The fish killer *H. carterae* appeared as early as March in the relatively shallow waters of the southern end. The predominant pattern, however, was summer advection of *H. carterae* into the inlet complex from outside. Further stimulation of growth occurred at the confluence of 2 inlets where nutrient flux from tidal jets was possibly augmented by the chemical conditioning from waters overlying an anoxic bottom.

KEY WORDS: Harmful phytoplankton · *Chaetoceros concavicornis* · *Nitzschia pungens* · *Alexandrium catanella* · *Dinophysis* · *Heterosigma carterae* · Sechelt Inlet PSP

INTRODUCTION

The impact of phytoplankton on aquaculture is obvious in the case of shellfish since it constitutes the primary food source for the stock. Optimum locations for shellfish farms should therefore be in areas of high phytoplankton productivity, particularly where diatom blooms are dense and prolonged. However, the product may become contaminated by toxic substances (produced by certain species of phytoplankton) which do not harm the shellfish but become concentrated in their tissues. This leads to outbreaks of various types of shellfish poisoning (paralytic, diarrheic, amnesic, neurotoxic, hepatotoxic, etc.; see recent reviews by Shumway 1990 and Taylor 1990). Since the shellfish depurate after a period of months without further exposure to toxic blooms, there is no loss of the product if the toxicity is detected before harvesting. It is obvious that plankton monitoring can provide an early warning of impending toxicity if the harmful species

are known. For example, domoic acid-producing diatoms have been found to cause Prince Edward Island (Canada) mussels to be toxic on a seasonal basis. A plankton monitoring program is used to detect the start of the blooms, at which time testing for the presence of domoic acid in the mussels begins, with closure as appropriate (Todd 1990). Currently in British Columbia (B.C.), Canada, shellfish are tested by the Department of Fisheries and Oceans (DFO) for the presence of saxitoxins and domoic acid. In 1989 DFO reported a record high level of saxitoxin in Sechelt Inlet (31 000 µg per 100 g shellfish; Anon. 1989). The diatom initially implicated in domoic acid production, *Nitzschia pungens*, is common and periodically abundant in B.C. waters and so are members of the dinoflagellate genus *Dinophysis*, implicated elsewhere as sources of okadaic acid, leading to diarrheic shellfish poisoning. Both occur in Sechelt Inlet.

In recent years blooms of certain phytoplankton species have negatively affected farmed fish. These harmful effects ranged from direct physical damage to fish gills caused by the barbed spines of certain species of the diatom genus *Chaetoceros*, first seen in B.C. in 1961 (reviewed by Gaines & Taylor 1986), to death associated with gill rupture and edema in response to substances released in the water by certain species of flagellates of the group known as chloromonads (Raphidophyceae) and dinoflagellates (Dinophyceae). The earliest record of the latter type in our region was a fish kill at the Lummi Island aquaculture project in Washington State (USA) in 1976 caused by the chloromonad *Heterosigma carterae* (Harrison et al. 1983, Gaines & Taylor 1986). In 1986 the same organism led to a CA$2.5 million loss in Sechelt Inlet. In 1989 a single bloom that covered 7000 km^2 of the Strait of Georgia and Barkley Sound (observed from flights over the region) resulted in a $12 million combined loss in B.C. and Washington State (E. A. Black pers. comm.). *Heterosigma* has also killed farmed fish in other temperate regions such as New Zealand (Chang et al. 1990). Other potential fish killers presently include a non-skeletal variant of the silicoflagellate *Dictyocha* (Thomsen & Moestrup 1985) and a new, undescribed chloromonad flagellate which has killed fish elsewhere in B.C. (our unpubl. obs.).

Given the potential economic impact of harmful phytoplankton blooms, detailed knowledge of phytoplankton species composition and seasonal abundance should be an important consideration in determining the suitability of a particular water body for finfish aquaculture. Because of interannual variability, studies should span periods of years. Short-term variability, particularly during the spring and summer, requires that sampling should be at least every 2 wk. The level of analysis and equipment need not be very sophisticated although identification must be to species level. Partly because of lack of awareness and a shortage of appropriately trained personnel, this has not been the case in most aquaculture regions of the world, with what little analysis that is performed being confined to the farm sites after their establishment.

In this paper we have tried to show the utility of such analyses, both in site selection and in the understanding of bloom ecology. We selected Sechelt Inlet because (1) it is a clearly delimited body of water with distinct inputs and outputs, (2) it has received some limited oceanographic study in the past and will continue to in the future, (3) it was an area of considerable aquaculture activities (there were 15 active fish farm sites plus 12 oyster leases at the start of our study), and (4) it has been the location of both high shellfish poison and fish kills in the past.

MATERIALS AND METHODS

Field samples were collected from 6 stations in Sechelt Inlet (49° 40' N, 123° 45' W) between May 1988 and September 1990 (Fig. 1). Samples were collected at least once a month, and twice a month from June to September. Samples were taken using the Segmented Integrated Pipe Sampler (SIPS; Sutherland et al. 1992). The 2 surface tubes were 1.5 m in length and the remaining 6 tubes were 3.0 m; when the 8 were connected they reached a depth of 21 m. Each segment's content was released into a mixing chamber for sampling aboard the boat. A sample was also taken from 30 m with a closing bottle attached to the winch line.

Temperature and salinity of the integrated samples were measured using a thermometer and Endeco refractometer or Guildline Autosal salinometer, respectively. Occasionally, a Guildline CTD was used to obtain *in situ* temperature and salinity profiles. Samples of seawater from depth intervals of 0–1.5, 1.5–3, 3–6, 9–12 and 18–21 m were filtered through precombusted 2.5 cm glass fibre filters (GF/F, 0.7 µm) and frozen in 30 ml acid-washed Nalgene polypropylene bottles for nutrient analysis at a later date; no preservatives were added. Nitrate (including nitrite; Wood et al. 1967) and ammonium were later measured on a Technicon AutoAnalyzer. Phosphate was determined using the procedure in Parsons et al. (1984) and measured on a Bausch and Lomb spectrophotometer

Representative microplankton subsamples (125 ml) were preserved with acidic Lugol's solution (final concentration: 1 %) and analysed using the Utermöhl technique (Hasle 1978). Depending on ambient biomass, 2.5 to 10 ml was settled in a counting chamber for at least 12 h. Harmful species, as well as harmless species, were counted in 1 to 6 transect(s) across the

chamber diameter (25 to 26 mm) at 240× or on the entire chamber bottom at 95×.

Contours of cell number with depth along a transect running from the mouth of Sechelt Inlet (Stn 1) to Porpoise Bay (Stn 6) were created for the 5 main harmful phytoplankters (*Chaetoceros concavicornis*, *Nitzschia pungens*, *Alexandrium catenella*, *Dinophysis acuminata*, *D. fortii*, and *Heterosigma carterae*) using the SURFER contouring and graphical package. Potential small-scale patchiness was ignored in order to see large-scale (regional) patterns. Narrows Inlet (Stn 2) and Salmon Inlet (Stn 4) were included in this straight-line transect to represent lateral inputs to the system.

Principal components analysis (PCA) was used to explore the relationships between the harmful species [log (cells l^{-1})] and concomitant environmental variables (chlorophyll, phaeopigments, temperature, salinity, nitrate, ammonium, and phosphate). Multiple regression analysis (Model I) was thought inappropriate for the reasons outlined in Ricker (1973) and Laws & Archie (1981); therefore, we decided to use PCA as a proxy for multiple regression (Model II). PCA is similar to the geometric mean regression for the bivariate case (see Ricker 1984) but allows central trend lines in n dimensions. PCA assumes no dependency and therefore is exploratory rather than predictive. For each species at the times presented herein, the first 3 principal components were calculated (without a secondary rotation) and of the 3 components the one correlating best with the species in question was chosen to explore relationships with environmental variables.

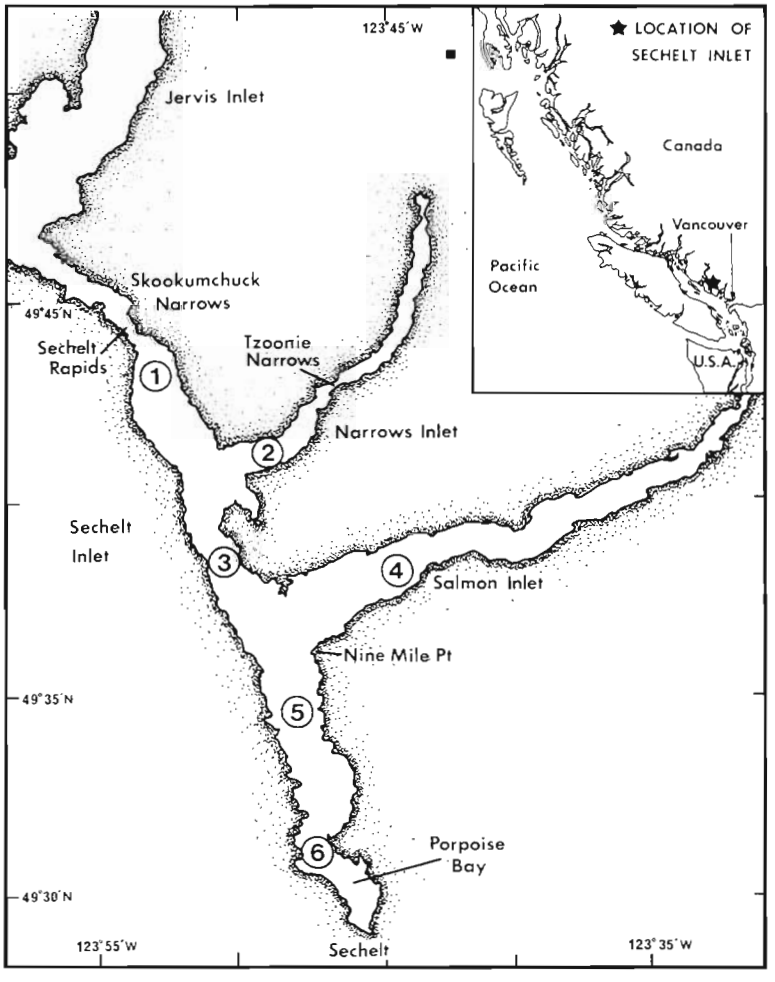

Fig. 1. Sechelt Inlet Complex, British Columbia, Canada, with station locations

RESULTS

The physically harmful diatom *Chaetoceros concavicornis* usually bloomed in late September (e.g. see Fig. 3B; based on raw cell counts ranging from 1 to 101 cells, excluding samples which did not contain this species), concurrent with the fall bloom of *Chaetoceros* species including *C. convolutus* (Fig. 2A). There was an unusual bloom of *C. concavicornis* during late June 1989 in lower Sechelt Inlet (Fig. 3A; based on raw counts of 2 to 186 cells) which occurred during a period of high temperature stratification (Fig. 2B) following bad weather, characterized by lower sunshine hours (Fig. 2C). Typically *C. concavicornis* formed subsurface maxima (Fig. 3) at 5 to 10 m. Harmful levels (>5000 cells l^{-1}; Bell et al. 1974) were exceeded during the 1989 fall bloom and killed farmed salmon (Stockner 1991).

In Sechelt Inlet *Nitzschia pungens* exhibited maximum concentrations in fall with a smaller peak in summer (Fig. 4). It was most abundant in the upper 10 m of the outer region of Narrows Inlet in summer (Fig. 5A; based on raw counts of 1 to 146 cells) and in the upper 10 m of Porpoise Bay in early fall (Fig. 5B; based on raw counts of 1 to 199 cells). From samples of the latter period we observed a few cells of the potentially toxic f. *multiseries*. These summer-fall patterns were consistent for each year of the study.

Although Sechelt has some of the highest recorded levels of PSP (paralytic shellfish poison) on the B.C. coast, concentrations of *Alexandrium catenella* were low for most of our study period. The exception was a bloom in late September of 1989 (Fig. 4). Highest concentrations occurred at either end of Sechelt Inlet,

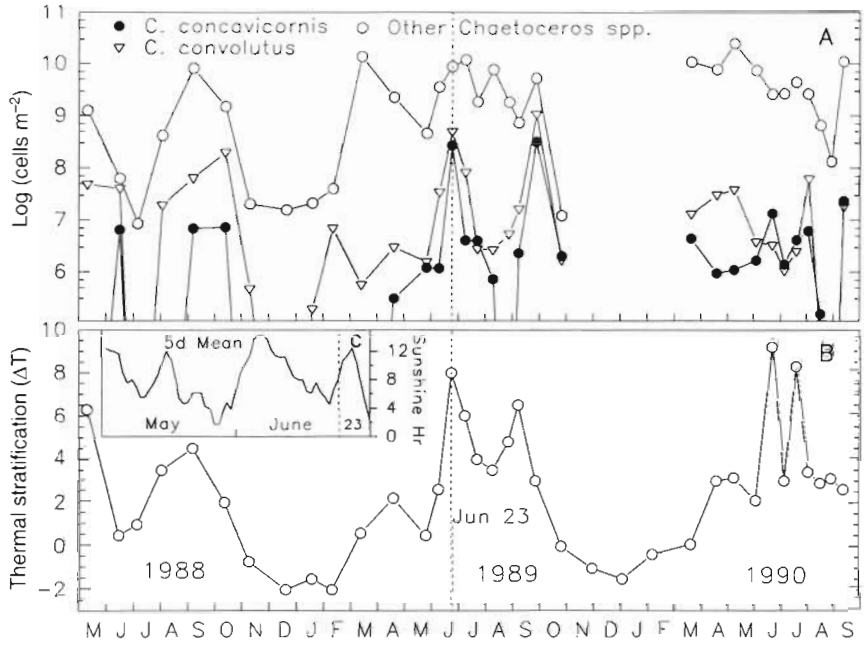

Fig. 2. (A) Successional trend of *Chaetoceros concavicornis*, *C. convolutus*, and the other *Chaetoceros* spp. from May 1988 to September 1990. For each station the cell concentration was integrated over 21 m; the integrated values were averaged and expressed as the common log (note: 10^6 cells m^{-2} ≈ 48 cells l^{-1}, averaged over 21 m). (B) Thermal stratification, calculated as the difference in temperature between the surface and 21 m, at Stn 5 from May 1988 to September 1990. The vertical dashed line indicates the time of the anomalous *C. concavicornis* bloom. (C) Running 5 d mean of sunshine hours recorded at the closest weather station to southern Sechelt Inlet for May and June 1989

though values in excess of 5000 cells l^{-1} were found throughout the system in the top 5 m (Fig. 6; based on raw counts of 2 to 179 cells). At the mouth of the inlet *A. catenella* appeared to be introduced through Skookumchuck Narrows.

Dinophysis was found in Sechelt Inlet from January to October, although its main growing season began in April. *Dinophysis acuminata* concentrations peaked in midsummer whereas those of *D. fortii* peaked later in fall (Fig. 7A). Integrated concentrations of these 2 species exceeded 1 million cells m^{-2} (≈ 48 cells l^{-1}, averaged over 21 m) within the system when thermal stratification exceeded 2 °C (Fig. 7B). Concentrations of *Dinophysis* spp. greater than 200 cells l^{-1}, thought to

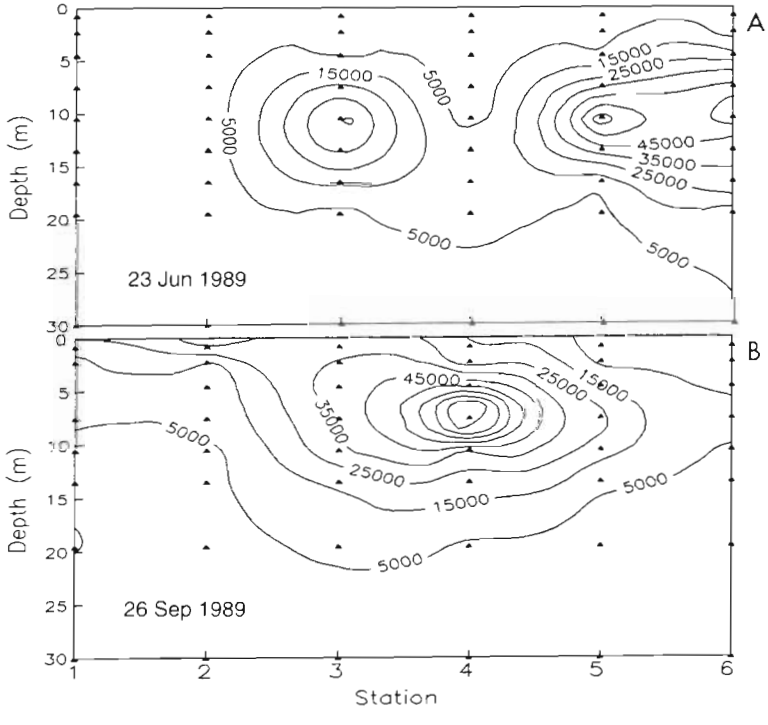

Fig. 3. *Chaetoceros concavicornis*. Depth profiles of abundance (cells l^{-1}) along a transect from Skookumchuck Narrows (Stn 1) to Porpoise Bay (Stn 6), assuming no small-scale patchiness. Sample depths are indicated by ▲. (A) Anomalous summer bloom of 1989; contours based on concentrations calculated from raw counts ranging from 0 to 186 cells. (B) Typical fall bloom in Salmon Inlet (Stn 4), 1989; raw counts ranged from 0 to 101 cells

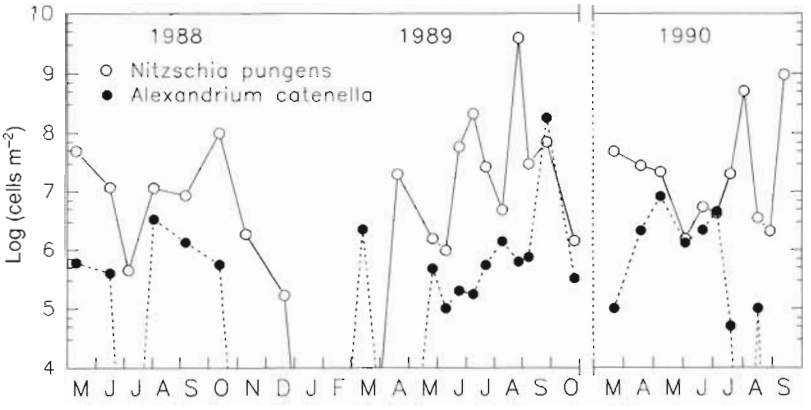

Fig. 4. Successional trend of *Nitzschia pungens* and *Alexandrium catenella* from May 1988 to September 1990. For each station the cell concentration was integrated over 21 m; the integrated values were averaged and expressed as the common log (note: 10^6 cells m^{-2} ≈ 48 cells l^{-1}, averaged over 21 m)

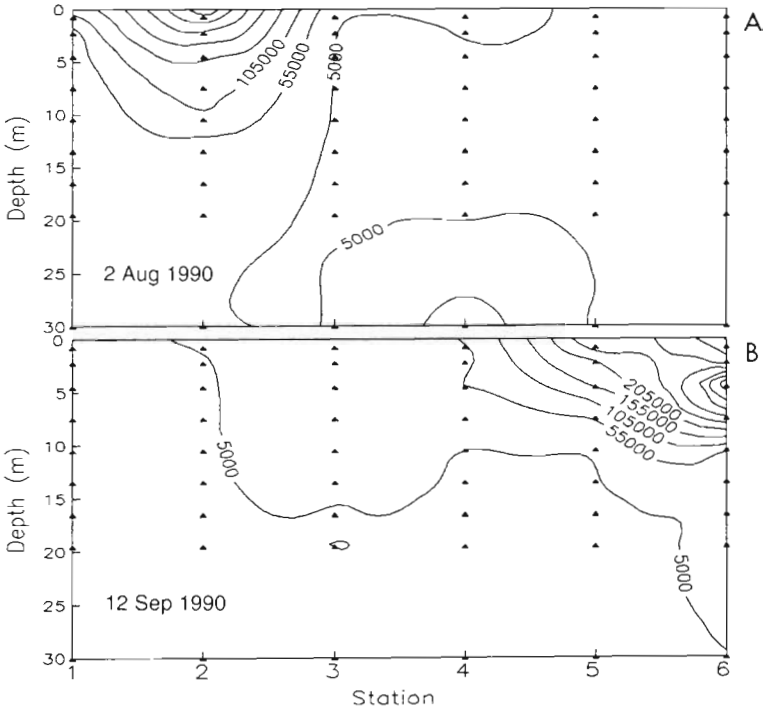

Fig. 5. *Nitzschia pungens*. Depth profiles of abundance (cells l^{-1}) along a transect from Skookumchuck Narrows (Stn 1) to Porpoise Bay (Stn 6), assuming no small-scale patchiness. Sample depths are indicated by ▲. (A) Summer concentration, outer Narrows Inlet (Stn 2), 1990; contours based on concentrations calculated from raw counts ranging from 0 to 149 cells. (B) Fall concentration, Porpoise Bay (Stn 6), 1990; raw counts ranged from 0 to 199 cells

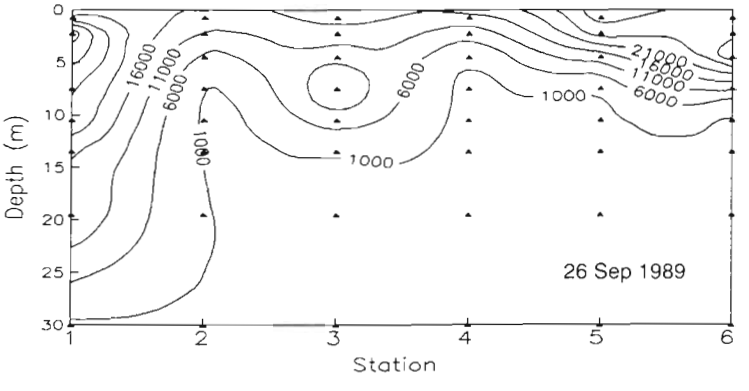

Fig. 6. *Alexandrium catenella*. Depth profiles of abundance (cells l^{-1}) along a transect from Skookumchuck Narrows (Stn 1) to Porpoise Bay (Stn 6), assuming no small-scale patchiness, during the extensive toxic bloom of late September 1989; contours based on concentrations calculated from raw counts ranging from 0 to 179 cells. Sample depths are indicated by ▲

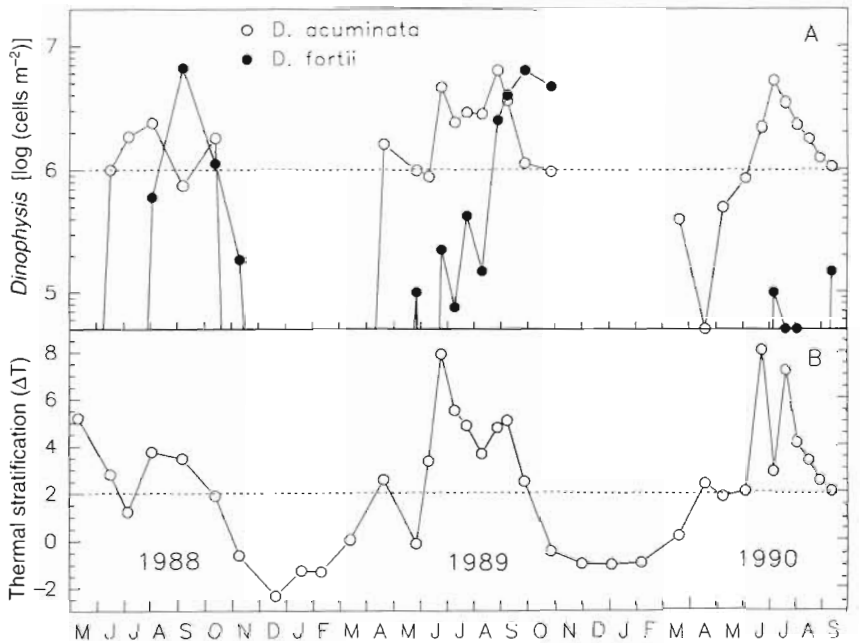

Fig. 7. (A) Successional trend of *Dinophysis acuminata* and *D. fortii* from May 1988 to September 1990. For each station the cell concentration was integrated over 21 m; the integrated values were averaged and expressed as the common log (note: 10^6 cells $m^{-2} \approx 48$ cells l^{-1}, averaged over 21 m). Horizontal dashed line indicates cell concentration of 10^6 m^{-2}. (B) Thermal stratification, calculated as the difference in temperature between the surface and 21 m, for the Sechelt Inlet system (average of 6 stations) from May 1988 to September 1990. Horizontal dashed line indicates $\Delta T = 2°C$

cause shellfish intoxication leading to DSP (Diarrheic Shellfish Poisoning; Yasumoto et al. 1980, Lassus et al. 1985), could be found throughout the system with loci at various stations. The species most prevalent in the inlet complex were *D. acuminata*, *D. norvegica*, and *D. fortii*. During most of the summer *D. acuminata* dominated and formed subsurface maxima in outer Narrows Inlet (Fig. 8A; based on raw counts of 1 to 15 cells). By the fall a subsurface population of *D. fortii* occurred in Porpoise Bay (Fig. 8B; based on raw counts of 1 to 21 cells).

Heterosigma carterae was most abundant in Sechelt Inlet from July to October (Fig. 9) but did make an appearance as early as March, in 1990, at Porpoise Bay,

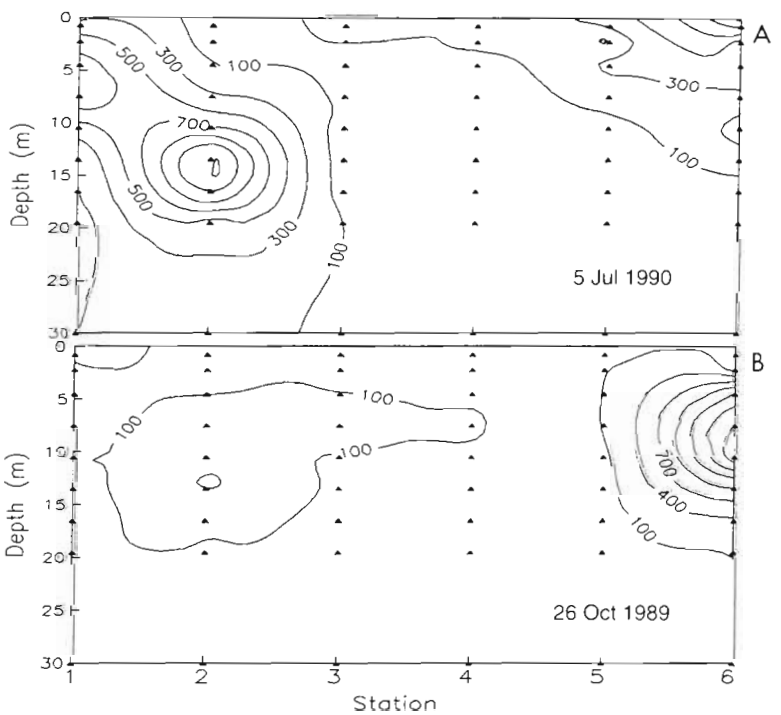

Fig. 8. *Dinophysis* spp. Depth profiles of abundance (cells l^{-1}) along a transect from Skookumchuck Narrows (Stn 1) to Porpoise Bay (Stn 6), assuming no small-scale patchiness. Sample depths are indicated by ▲. (A) Summer subsurface concentration of *D. acuminata* in outer Narrows Inlet, 1990; contours based on concentrations calculated from raw counts ranging from 0 to 15 cells. (B) *D. fortii* subsurface concentration in Porpoise Bay, late fall 1990; raw counts ranged from 0 to 21 cells

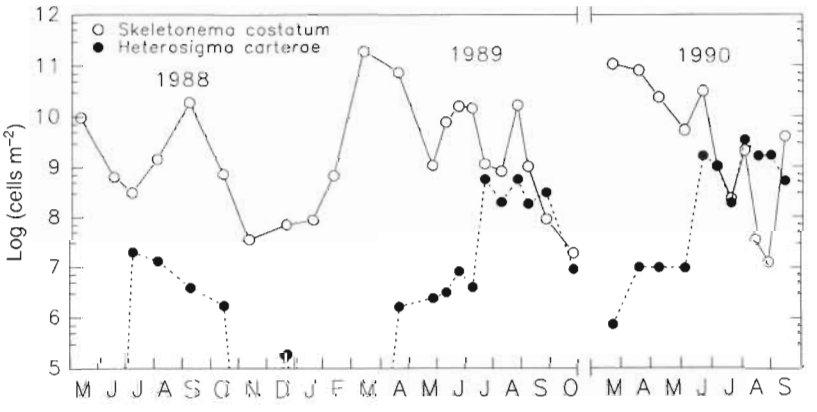

Fig. 9. Successional trend of *Heterosigma carterae* and *Skeletonema costatum* from May 1988 to September 1990. For each station the cell concentration was integrated over 21 m; the integrated values were averaged and expressed as the common log (note: 10^6 cells m^{-2} ≈ 48 cells l^{-1}, averaged over 21 m)

suggesting that some cells may arise from autochthonous benthic 'seed' beds. Over the course of the study highest cell concentrations occurred at the northern end of Sechelt Inlet (Stns 1 & 2). Successively, from 1988 to 1990, the average *H. carterae* concentrations were an order of magnitude higher than those of the previous summer (Fig. 9). In summer there was usually advection of *H. carterae* into Sechelt Inlet through Skookumchuck Narrows (Fig. 10A; based on raw counts of 1 to 249 cells) followed by a local stimulation of this population in outer Narrows Inlet (Fig. 10B; based on raw counts of 1 to 385 cells). There was no obvious exclusion of *Skeletonema costatum* by *H. carterae* (Fig. 9) as suggested by Pratt (1966) until June 1990 when the latter organism reached concentrations on the order of 10^9 cells m^{-2} (≈ 47 600 cells l^{-1}, averaged over 21 m).

The development of *Heterosigma carterae* from a benthic stage in sediments has been shown to be highly temperature dependent (Yamochi 1989). The occurrence of *H. carterae* versus temperature (Fig. 11) shows an increase in abundance until about 18 °C.

The results of the PCA are presented in Table 1. Stratified conditions were correlated with *Chaetoceros concavicornis* (26 Sep 89), *Nitzschia pungens* (2 Aug 1990), and *Heterosigma carterae* (21 Jun 1990 and 2 Aug 1990). The remaining species were more associated with chlorophyll and/or ammonium concentrations: *C. concavicornis* (23 Jun 1989) with high chl *a* and high NH_4; *N. pungens* (12 Sep 1990) with high chl *a* and low NH_4; *Alexandrium catenella* (26 Sep 1989) with high NH_4; *Dinophysis acuminata* (5 Jul 1990) with low chl *a*; and *D. fortii* (26 Oct 1989) with high NH_4.

DISCUSSION

The potentially harmful plankton species in Sechelt Inlet, all photosynthetic, are principally members of 3 groups of phytoplankton: diatoms, dinoflagellates and chloromonads, with some potentially hazardous members of other groups such as the prymnesiomonads and silicoflagellates also present. These species are not unique to B.C. waters, causing similar problems in many other areas with broadly similar water temperature ranges, e.g. eastern Canada, Japan, northern Europe, Chile, New Zealand, Tasmania, as well as the

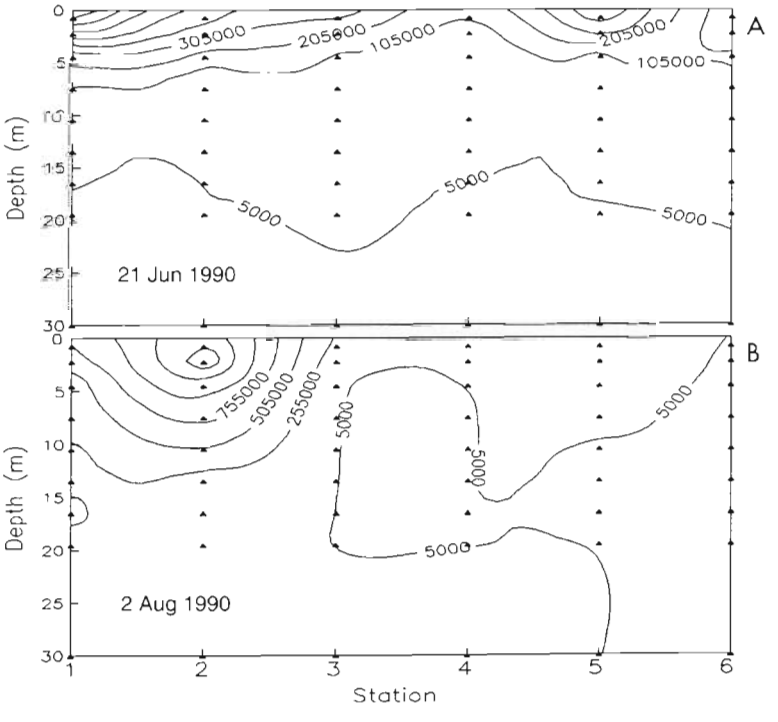

Fig. 10. *Heterosigma carterae*. Depth profiles of abundance (cells l^{-1}) along a transect from Skookumchuck Narrows (Stn 1) to Porpoise Bay (Stn 6), assuming no small-scale patchiness. Sample depths are indicated by ▲. (A) Injection of cells from Jervis Inlet in summer 1990; contours based on concentrations calculated from raw counts ranging from 0 to 249 cells. (B) Stimulation of growth in outer Narrows Inlet of injected populations; raw counts ranged from 0 to 385 cells

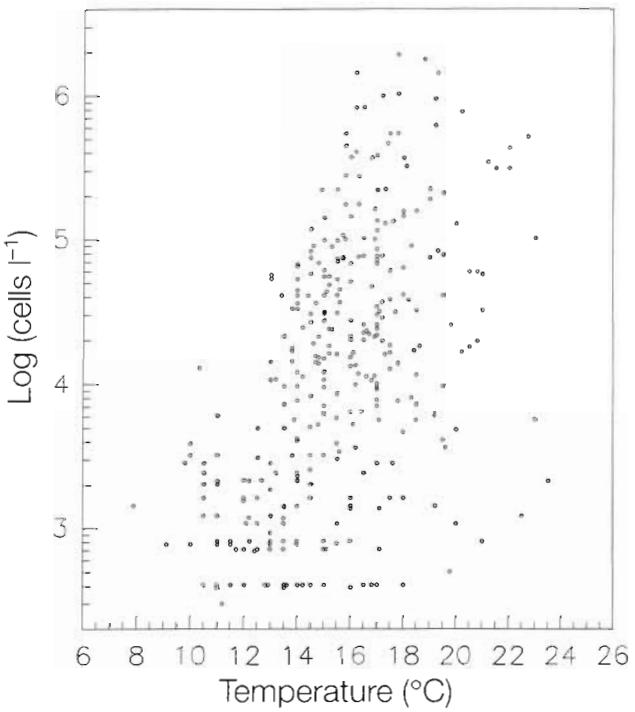

Fig. 11. *Heterosigma carterae.* Abundance plotted against temperature. Samples from all depths and times containing *H. carterae* were used. There is an apparent optimum at 18 °C

adjacent waters of Alaska and Washington State. The species in question have been described in detail (Gaines & Taylor 1986). They have also been included in other regional guides (Larsen & Moestrup 1989, Fukuyo et al. 1990, Hallegraeff 1991).

Chaetoceros concavicornis and *Chaetoceros convolutus*

Chaetoceros concavicornis is a chain-forming diatom which harms fish by penetrating the gill tissues with its barbed setae. Unlike the setae of other *Chaetoceros* species the presence of barbs causes the setae to work into the tissues. The cells are characteristically bullet shaped, 12 to 30 µm wide. The setae are hollow and invaded by plastids, a characteristic of the subgenus *Phaeoceros*. Chains of more than 20 cells can occur but are shorter in winter when single cells also occur. *C. concavicornis* resembles *C. convolutus*, with which it has apparently been confused in earlier British Columbia reports (Bell 1961, Bell et al. 1974, Kennedy et al. 1976). *C. concavicornis* can be recognized under light microscopy by a narrowing of the setae as they approach the body. It also has greater barb development than *C. convolutus* and consequently is more harmful to salmon. *C. convolutus* possesses prehensors on the setae of the rounded valve (Fryxell & Medlin 1981) which are not present on *C. concavicornis* (Evensen & Hasle 1975; also our pers. obs.). No resting spore is known for these species and they appear to be present in the water column year-round, often relatively deep. We view both species to be opportunistic, capable of tolerating lower light levels than other *Chaetoceros* species (Harrison et al. 1993), perhaps due to chloroplasts in the hollow setae.

Chaetoceros concavicornis concentrations considered harmful to fish are 4000 to 5000 cells l^{-1} (Gaines & Taylor 1986); *C. convolutus* has been reported harmful to fish at ca 10^5 chains l^{-1} (Farrington 1988). Fish losses from these species have been reported from neighbouring Washington State (Horner et al. 1990, 1991) and in Sechelt Inlet (E. A. Black pers. comm.). There are indications that salmon species may differ in their sensitivity, with Atlantics being most sensitive (250 000 were lost in Washington State in 1987, worth approximately US$ 0.5 million; Rensel et al. 1989, Horner et al. 1990).

In Sechelt Inlet the peak concentration of *Chaetoceros concavicornis* occurred during the fall bloom of

Table 1 Correlations of original variables with principal component most influenced by the harmful species *Chaetoceros concavicornis, Nitzschia pungens, Alexandrium catenella, Dinophysis acuminata, D. fortii* and *Heterosigma carterae*. Values in **bold** type highlight environmental variables with greatest correlation with principal component

Species:	*C. concavicornis*		*N. pungens*		*A. catenella*	*D. acuminata*	*D. fortii*	*H. carterae*	
Date:	23 Jun 89	26 Sep 89	2 Aug 90	12 Sep 90	26 Sep 89	5 Jul 90	26 Oct 89	21 Jun 90	2 Aug 90
Component:	1	1	1	2	3	3	3	1	1
% Variance:	50.4	52.2	53.5	23.2	14.2	14.0	13.7	57.7	55.9
Log (cells l^{-1})	**0.748**	**0.629**	**0.717**	**0.680**	**0.757**	**0.656**	**0.693**	**0.798**	**0.774**
Chlorophyll *a*	**0.835**	0.641	0.641	**0.557**	0.119	**−0.594**	−0.196	0.650	0.679
Phaeopigment	0.789	0.399	0.371	0.488	−0.134	−0.160	0.064	0.706	0.504
Temperature	−0.726	0.722	**0.850**	−0.476	−0.150	0.369	0.409	**0.853**	**0.846**
Salinity	–	–	**−0.862**	0.501	–	0.041	–	**−0.872**	**−0.836**
Nitrate	0.427	**−0.900**	**−0.856**	0.135	0.227	0.141	0.097	**−0.875**	**−0.863**
Ammonium	**0.815**	0.726	−0.392	**−0.547**	**0.491**	0.343	**0.496**	0.066	−0.347
Phosphate	0.527	**−0.911**	**−0.933**	0.217	0.266	−0.192	−0.101	**−0.894**	**−0.938**

Chaetoceros species. This pattern was also observed in the southern Strait of Georgia (Shim 1976). In the northern Strait of Georgia the maximum abundance of *C. convolutus* occurred in mid-August during 1986 (Haigh & Taylor 1990), and was associated with a diverse bloom of *Chaetoceros* species. The *C. concavicornis* population in Sechelt Inlet on 26 September 1989 was associated with stratified conditions where NH_4 was elevated, perhaps due to high heterotrophic activity (Table 1).

At low temperatures both *Chaetoceros concavicornis* and *C. convolutus* are capable of growing at μ_{max} at very low irradiances (Harrison et al. 1993, grown under constant light). Highest growth rates, however, were achieved at 18 °C when irradiance was > 50 $\mu E\ m^{-2}\ s^{-1}$ (Harrison et al. 1993). High *C. concavicornis* concentrations in Sechelt Inlet (Fig. 3) were associated with a temperature range of 13 to 15 °C at 5 to 10 m. The combination of moderate temperatures and low light levels generally occurs in fall when waters are losing stored heat, and seasonal irradiance decreases rapidly. The anomalous peak in June 1989 is thought to be related to preceding bad weather, which introduced a successional perturbation (Haigh et al. 1992), and to periods of reduced sunshine in June (Fig. 2C). The June peak of *C. concavicornis* in lower Sechelt Inlet (Stns 3 & 5) also coincided with a peak in thermal stratification (at Stn 5: Fig. 2B) and was associated with high biomass and elevated NH_4 concentrations (Table 1).

On the British Columbia coast *Chaetoceros concavicornis* and *C. convolutus* grow best in sheltered waters away from turbulence (Albright et al. 1992). In Sechelt Inlet peak concentrations were usually subsurface (5 to 10 m) in the region of the pycnocline; harmful concentrations rarely formed near the Skookumchuck tidal jet. Harmful *Chaetoceros* in the northern Strait of Georgia were also least abundant near the tidal jet and generally preferred stratified regions (Haigh & Taylor 1990, 1991).

Inlets with surface water salinities below 17‰ are reportedly not conducive to the growth of harmful *Chaetoceros* (Albright et al. 1992). Experimentally, *C. concavicornis* is tolerant of salinities down to 17‰ while *C. convolutus* can only tolerate salinities as low as 25‰ (Harrison et al. 1993). Although Sechelt Inlet experiences freshwater input from the side inlets (Haigh et al. 1992), these species occur at depths which are not directly exposed to low salinity waters.

Nitzschia pungens

Nitzschia (*Pseudonitzschia*) *pungens* is a pennate diatom forming rigid chains. It ranges from 70 to 160 µm in length and 2 to 5 µm in width. The striae and punctae can be seen with light microscopy but confirmation with electron microscopy is required for taxonomic certainty. Blooms of f. *multiseries* off the east coast of Canada have been shown to produce domoic acid (Wright et al. 1989), an amino acid which can be accumulated in great quantities by mussels. The toxin causes intestinal distress and brain damage in humans that eat the mussels (Todd 1990). The syndrome, called Amnesic Shellfish Poisoning (ASP), has occurred on the east coast of Canada (Subba Rao 1988, Bates et al. 1989). No cases of ASP have been recorded from the consumption of B.C. mussels although domoic acid has been found in some B.C. (DFO, Inspection Branch) and Washington State shellfish (Anon. 1991). The latter was produced by the closely related species *Pseudonitzschia australis* (Buck et al. 1992) which was not abundant in Sechelt Inlet.

Nitzschia pungens showed a predictable seasonal trend, blooming in the upper 10 m of outer Narrows Inlet in summer and in the upper 10 m of Porpoise Bay in fall. This spatio-temporal pattern was constant for each year of the study. In Prince Edward Island, where the potentially toxic nature of *N. pungens* was first recognized, the non-toxic f. *pungens* bloomed in summer and the domoic acid-producing f. *multiseries* became more prevalent in fall (Smith et al. 1990). *Nitzschia pungens* produces most domoic acid during stationary phase of growth, especially under nutrient (other than nitrate) limitation (Bates et al. 1991). In the Sechelt Inlet complex the summer populations of *N. pungens* were predominantly f. *pungens* and were associated with stratification (Table 1). The fall populations were also predominantly f. *pungens*; however, our SEM observations found that some cells were definitely f. *multiseries* with 4 to 5 rows of pores between the striae.

Alexandrium catenella

Alexandrium catenella has been reported from many cold-temperate areas including California, Japan, Chile and South Africa, with related forms in eastern Canada, the NE United States and Europe. It was first found in B.C. waters by Wailes (1939) as *Peridinium discoides*. Originally, only *Alexandrium catenella* was known from B.C. but since the 1960s forms corresponding to *A. acatenella* (Prakash & Taylor 1966) and *A. tamarense* (Cembella & Taylor 1986) have also been identified from the more estuarine areas of the Strait of Georgia. The latter authors showed that these 'species' are genetic variants within a single 'species complex'; it is convenient for now to treat them as distinct forms. In Sechelt Inlet the *catenella* form predominated.

Several species of *Alexandrium* are known to produce neurotoxins of the saxitoxin family in B.C. Over the 3 yr study period in Sechelt Inlet, *A. catenella* rarely achieved the cell concentration thought to intoxicate shellfish (1000 cells l^{-1}; Horner et al. 1990). However, the PSP monitoring program (DFO, Inspection Branch) recorded the highest-ever level of saxitoxin (31 000 µg per 100 g shellfish) at Nine Mile Point (between Stns 4 & 5) in October, 1989. This was caused by a bloom of *A. catenella* in late September with maximum concentrations of 35 000 cells l^{-1} being injected by the Skookumchuck tidal jet at 2 to 3 m. The bloom extended throughout the upper 10 m (Fig. 6) of the system and presumably intoxicated shellfish in all areas. Curiously, the bloom was associated with elevated ammonium concentrations (Table 1) which was also found for the *C. concavicornis* population during the same sample time. The higher concentration of this nutrient may be solely coincidental, perhaps generated by greater heterotrophic activity. Data from the previous cruise suggest that the early formation of the bloom involved advection of *A. catenella* into the system from Jervis Inlet. Concentrations from local cyst populations in the shallow southern end of the inlet may have also contributed.

Dinophysis spp.

Many (most?) photosynthetic species of *Dinophysis* seem to be capable of the producing okadaic acid (Murata et al. 1982, Cembella 1989, Yasumoto 1990), a polyether derivative which, when concentrated by mussels, has caused DSP in Europe (principally Spain and The Netherlands, but also France, Ireland etc.). Recently it has been found in B.C. mussels at levels 400× the quarantine level (Boland et al. 1992), as predicted from the presence of *Dinophysis* earlier (Gaines & Taylor 1986) A. D. Cembella (pers. comm.) confirmed that *D. acuminata* in B.C. waters produces okadaic acid. The chief problem species in European coastal waters is *D. acuminata* (Kat 1983, Lassus et al. 1985) and in Japanese waters is *D. fortii* (Osaka & Takabayashi 1985). In our waters these 2 species, along with *D. norvegica*, are the most common.

In Sechelt Inlet *Dinophysis acuminata* was the predominant *Dinophysis* species throughout the system. Concentrations of this species reached 10^6 cells m^{-2} (≈ 48 cells l^{-1}, averaged over 21 m) once the system had stratified to a ΔT_{0-21m} of 2 °C (Fig. 7). Delmas et al. (1992) also showed a correlation between thermal stratification and *Dinophysis* concentrations; however, their offshore stations (France) had populations of 29 to 133 × 10^6 cells m^{-2} over 21 m (≈ 1400 to 6300 cells l^{-1}, averaged over 21 m) once $\Delta T_{thermocline}$ reached 5 °C.

Typically *Dinophysis acuminata* formed subsurface concentrations in Narrows Inlet during summer (e.g. Fig. 8A), exceeding the reportedly harmful level of 200 cells l^{-1} (Lassus et al. 1985). In September the Porpoise Bay region predictably experienced subsurface concentrations (5 to 15 m) of *D. fortii* which exceeded 1000 cells l^{-1} (e.g. Fig. 8B). On 26 October 1989 this dinoflagellate was associated with elevated ammonium levels (Table 1) which probably reflect increased heterotrophic activity. Critical cell concentrations were surpassed for the collective photosynthetic species at various locations and depths throughout the system from May to October. The length of time these levels are maintained is important; for the most part, peaks of *Dinophysis* were sporadic. It was only during late summer at Porpoise Bay (Stn 6) that the extent and duration of a *Dinophysis* population were such that DSP became a real threat. Because of their characteristic subsurface nature, surface monitoring for these species is inadequate.

Heterosigma carterae

Heterosigma carterae is the name now in use for the major fish-killing species of chloromonad in B.C. waters (formerly *H. akashiwo*; Taylor 1992). Since the 1960s it has been misidentified as *Olisthodiscus luteus* in U.S. publications (e.g. those dealing with Narragansett Bay; Tomas 1978) and has had many experimental observations published under that name. In Scotland a similar organism which has killed fish has been referred to as 'Flagellate X' (Gowen 1984). *H. carterae* cells are small, 8 to 25 µm long, ovoid, and often flattened laterally (*O. luteus* is flattened dorsoventrally). The 2 flagella emerge roughly one-third from the anterior end (see descriptions in Larsen & Moestrup 1989, Fukuyo et al. 1990). The numerous chloroplasts are yellowish-brown to brown. Mucilage may be produced from small peripheral mucocysts (Leadbeater 1969). When preserved in Lugol's Iodine the cells have a raspberry-like appearance in which the chloroplasts are much more apparent. The species does produce a spherical benthic stage, which is difficult to recognize in sediments because of material attached to its mucoid coat. In Japanese sediments it was found that population excystment began at 10 °C and was effectively complete at 15 °C (Yamochi 1989).

The species is extremely halotolerant, surviving a range of 2 to 50‰ (Tomas 1978). Our data suggest a temperature optimum of 18 °C (Fig 11). It migrates vertically, with a swimming speed of roughly 1 m h^{-1}, rising to the surface during the day and descending at night (Wada et al. 1985). Because of its ability to tap higher-nutrient water at depth it does not seem likely

to be regulated by macronutrients in a stable water column. In the Inland Sea its abundance was thought to be regulated by micronutrients (Takahashi & Fukazawa 1982). In the Strait of Georgia blooms can last for 4 mo or more, depending on the weather (Taylor & Haigh 1993).

The pattern of fish death due to *Heterosigma* can resemble that of *Chattonella*, with damage to gill epithelia leading to suffocation and blood changes (Okaichi 1985). There is also evidence of neurological damage (Whyte 1991). However, the nature of the substance(s) liberated is not known. A preliminary study (unpubl. obs.) suggests that fish begin to die at 12 million *Heterosigma* cells l^{-1}, but the harmful level may be much lower depending on the species of fish cultured, their size, and environmental factors.

At no time during the course of the Sechelt study did *Heterosigma carterae* reach cell concentrations high enough to kill fish, the highest recorded level being 1.8×10^6 cells l^{-1}. *Heterosigma* populations in Sechelt Inlet are perhaps influenced by a longer-term cycle such as the ENSO (El Niño Southern Oscillation) event, as suggested for *Alexandrium* by Erickson & Nishitani (1985). In 1986 there was a large loss of fish due to a bloom of *H. carterae* within the Sechelt system, during which concentrations of 200×10^6 cells l^{-1} were observed (Taylor in Dale et al. 1987). Due to aggregations by vertical migration, even higher concentrations can be achieved (e.g. 800×10^6 cells l^{-1}; Whyte 1991). Some farmers of the period thought it prudent to move their farms into the less protected waters of neighbouring Agamemnon Channel but unfortunately were hit by a massive bloom in 1989 which covered ca 7000 km^2 along 750 km of B.C. and Washington coastline. The irony was that the bloom did not enter Sechelt Inlet even though it intruded up Jervis Inlet via Agamemnon Channel.

There is evidence that many grazers avoid *Heterosigma carterae*, especially at higher concentrations (Verity & Stoecker 1982, Egloff 1986, Verity 1987, Taniguchi & Takeda 1988). In a non-bloom situation where *H. carterae* is abundant there is usually a host of other food species from which the grazers can select. This was the situation during August 1990, the period when *H. carterae* was most abundant in our study. The oligotrichous and tintinnine ciliates were potential grazers of *H. carterae* at this time but the incidence of high nanoflagellate concentrations would have presented a more favourable alternative food source.

We found no convincing evidence of an allelopathic interaction between *Heterosigma carterae* and *Skeletonema costatum* as suggested by Pratt (1966) since *S. costatum* was usually present during peaks of *H. carterae*. However, *S. costatum* blooms occurred when *H. carterae* was low, preferring spring bloom rather than stratified conditions. The latter is ideal for flagellates with migrating abilities (e.g. *H. carterae*; Table 1). Tomas (1980) was skeptical that *H. carterae* exerted chemical inhibition and suggested that increased grazing pressure on *S. costatum* by copepods was the underlying factor. However, it is worthy of note that during any large *H. carterae* bloom a few dinoflagellate species co-occur and diatoms are virtually absent. *H. carterae* excretes or exfoliates a polysaccharide-protein complex which suppresses the growth of certain species while enhancing the growth of others (Honjo 1992), including *H. carterae* itself (Honjo 1993). This could be one reason why blooms of this flagellate are so successful, although there is probably a threshold cell concentration required before the allelopathic substance impacts species composition.

The ecology of this flagellate in Sechelt appeared to involve 2 mechanisms. The first was an early excystment of an autochthonous population from a seed bed in the Porpoise Bay region (Stn 6). The second was an introduction from Jervis Inlet of an allochthonous population which, once established within the system, thrived in the favourable environment of outer Narrows Inlet. It is was originally thought that inner Narrows Inlet might act as a seed bed (Sutherland & Taylor 1990). Sutherland's (1991) study suggests that the sediments of inner Narrows Inlet are too anoxic to host *Heterosigma carterae* seed beds. Anoxic sediments, however, release sulphides which stimulate flagellate blooms (Iizuka & Nakashima 1975) and chelate inhibitory metals (Iizuka & Irie 1969). *H. carterae* grew well in outer Narrows Inlet (as did most other plankters; Haigh et al. 1992), perhaps due to the chemical conditioning from inner Narrows Inlet. We found no evidence of local stimulation of *Heterosigma* blooms by fish farms as was the case in the smaller and shallower Big Glory Bay, New Zealand (Pridmore & Rutherford 1992).

No appreciable eutrophication

Many areas of the world have experienced increasing problems with phytoplankton blooms due to elevated nutrient loading (see numerous accounts in Okaichi et al. 1989) from human activity (industrialization, sewage discharge, agricultural fertilizer runoff, aquaculture, etc.). Often the affected water bodies are shallow and/or enclosed so that dilution or flushing is not great enough to maintain the normal ecological balance.

Sechelt Inlet sustained a massive *Heterosigma* bloom in 1986; however, it is a relatively pristine fjord surrounded for the most part by mountains and wilderness. There is no significant nutrient loading by indus-

try or agriculture and probably only small loading from aquaculture and the town of Sechelt. Our nutrient data indicate no obvious eutrophication; the range of macronutrient (NO_3, NH_4, PO_4) concentrations was typical for B.C. waters (Taylor et al. 1991). Occasionally ammonium and phosphate concentrations exceeded those considered normal for upper values (3 µM each). Spikes of ammonium occurred throughout the year but tended to be more numerous in summer and were especially prevalent near Skookumchuck Narrows (Stn 1). High ammonium may have been due to patches created by zooplankton/fish excretion, advection from Jervis Inlet, or simply an artifact of sample freezing and thawing. Phosphate and nitrate regularly reached high values in winter due to seasonal mixing.

Chlorophyll exhibited an inverse correlation with nitrate but the relationship was not linear as found by Gowen et al. (1992) for the Scottish west coast sea lochs. Our system experienced much greater ranges in chlorophyll (0 to 50 vs 0 to 8 µg l^{-1}) and nitrate (0 to 30 vs 0 to 4.5 µM) than the Scottish system. The variance in the data was greatest at low nitrate which occurred just after the spring bloom (high biomass of diatoms) and throughout the summer period (lower biomass of nanoflagellates). Sechelt Inlet production is apparently not solely limited by nitrate; grazing, micronutrient limitation, light limitation, and other factors probably complicate growth dynamics.

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