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Dinoflagellate cyst assemblages from Effingham Inlet, Vancouver Island, British Columbia, Canada

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Abstract

A palynological study of surface samples from Effingham Inlet, southwestern Vancouver Island, British Columbia, was carried out to assess environmental and oceanographic controls on the distribution of dinoflagellate cyst species. Generally dinoflagellate cyst assemblages from all samples are dominated by *Operculodinium centrocarpum* sensu Wall and Dale, 1966, *Spiniferites* spp. and round brown (protoperidinioid) cysts. The differences among the assemblages are mainly in relative and absolute abundance of various taxa, presence and absence of various protoperidinioid taxa, species diversity (Shannon Diversity Index), dinoflagellate cyst concentration in the samples, and ratio of terrestrial to marine palynomorphs. Dinoflagellate cyst assemblages in the two sub-basins of this inlet are quite distinct, with the inner basin characterized by lower diversity and the outer basin being characterized by higher diversity due to the occurrence of several protoperidiniacean species. Primary productivity in this inlet is enhanced by periodic incursion of nutrient-rich surface water from the Pacific Ocean which is related to coastal upwelling. Primary productivity is higher in the outer basin than the inner basin. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: fjord; palynomorphs; dinoflagellate cysts; salinity; oceanography

1. Introduction

The object of this study was to explore the relationship between dinoflagellate cyst assemblages found in the modern sediments of Effingham Inlet, Vancouver Island, British Columbia, and various environmental and oceanographic factors that might control their distribution.

Like diatoms, dinoflagellates are important primary producers. Their relative abundance varies according to season, geographical location and water depth, with greatest concentrations at shallower depths between 18 and 90 m (Taylor, 1987). Regions of highest dinoflagellate productivity are often areas of upwelling, which provide increased nutrients. Dinoflagellate 'blooms' also cause 'red tides', which may be highly toxic and are often responsible for high fish mortality, thus directly affecting the fishing industry (Tappan, 1980; Taylor, 1987; Okaichi et al., 1989). Fossil dinoflagellate cyst assemblages have been related to the

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movement of oceanic currents, upwelling, climate change, winter and summer sea-surface temperature and depth and paleoceanography (Head and Wrenn, 1992; Powell et al., 1990; Aksu et al., 1989).

Fjords such as Effingham Inlet are essentially large sediment traps with relatively high sedimentation rates. There is also little exchange between bottom waters in Effingham Inlet and the open ocean because of the presence of two sills (Figs. 1 and 3). For this reason conditions within the sub-basins of Effingham Inlet generally vary from suboxic to anoxic, resulting in deposition of annual varved layers that can provide a very high-resolution record of paleoenvironmental events.

Since flushing of inlets like Effingham Inlet is relatively infrequent, the dinoflagellate cysts falling through the water column are of primarily local origin rather than transported from the open ocean (Dale, 1976). This characteristic is advantageous, as the sedimentary record preserved in these inlets document significant local oceanographic events with the proxy signal not being lost through bioturbation as often occurs in the open ocean.

The baseline proxy data presented here will eventually be used to interpret late Holocene changes in climatic and oceanographic conditions based on dinoflagellate cyst floras preserved in cores collected from the inlet. This research is part of a large multidisciplinary research project whose aim is to relate variations in climatic, environmental and oceanographic conditions in Effingham Inlet to changes in fish populations through the Holocene. This information is of strategic economic importance, as it will help fisheries managers to better allocate resources in the region. The study of dinoflagellate cysts from both the recent and fossil sediments from Effingham Inlet promises to enhance our ability to derive a high-resolution paleoclimatic and paleoceanographic history of the region.

2. Geology

Effingham Inlet is 15 km long, located on the

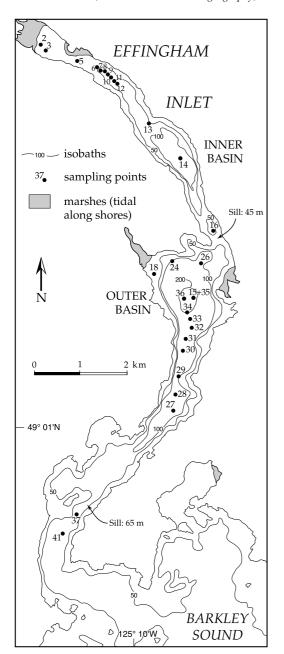
southwest coast of Vancouver Island. It is connected to the Pacific Ocean through a wide bay called Barkley Sound (Fig. 1). This inlet has two sub-basins, the inner and outer, divided by a 45-mdeep sill (inner sill) located in a narrow channel. Another 65-m-deep sill (outer sill) separates the outer basin from Barkley Sound (Fig. 3). The maximum recorded depth in the inner basin is 120 m and 210 m in the outer basin. Tidal marshes are present on both sides of the outer basin and two other large marshes are present near the head of the inlet. Effingham River flows into the head of this inlet, and a small creek also flows into the outer basin. The high level of annual rainfall received in this area results in numerous additional smaller streams flowing into the inlet. The entire region is mountainous and covered with coniferous forests although the western part of the outer basin has recently been logged.

The inlet is surrounded by Mesozoic volcanic rocks, which form a steep and rocky coastline. The underwater slopes of the inlet are steep, and coring in shallower depths was unsuccessful, yielding little sediment. This suggests that margins of the inlet are either made of Mesozoic volcanic rocks or Quaternary glacial gravel.

The sampled sediment consisted of soft, soupy brown mud with organic matter (essentially plant fragments) ranging from 10% in shallow areas to 90% in the deeper parts of the basins (Patterson et al., 2000). A distinct layer of coarse, black and loose organic matter a few centimeters thick, consisting primarily of decomposed vegetation, was present at the sediment surface in the outer basin. At shallower depths (<72 m) in the outer basin and at the mouth of the inlet, the sediment was a firm gray marine mud with a lower organic content. Based on preliminary analysis of laminae recorded in freeze cores collected in October, 1999, the rate of sedimentation varies between 0.5 and 1 cm/yr (Patterson et al., 2000).

3. Oceanography and climate

The climate of western Vancouver Island is cool temperate and wet. Wind patterns along the Pacific coast are controlled by two atmospheric



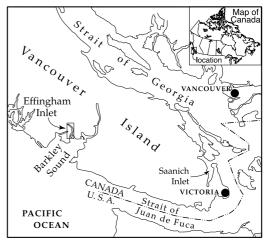


Fig. 1. Geographic location of Effingham Inlet, Vancouver Island, showing sample sites and depth contours (m).

cells: the Aleutian Low (AL) and the North Pacific High (NPH; Fig. 4; Kendrew and Kerr, 1955; Thomson, 1981; Patterson et al., 1995). In the northeast Pacific, there is a seasonal oscillation between the two systems. During the summer when the land is hot and the ocean cool, the re-

gion comes under the influence of the NPH (Fig. 5). NPH winds generate a southward coastal drift and an offshore Ekman transport that triggers coastal upwelling. During the winter the NPH is pushed southward and the area comes under the influence of the AL, centered in the western Gulf

Salinity and Temperature in Effingham Inlet

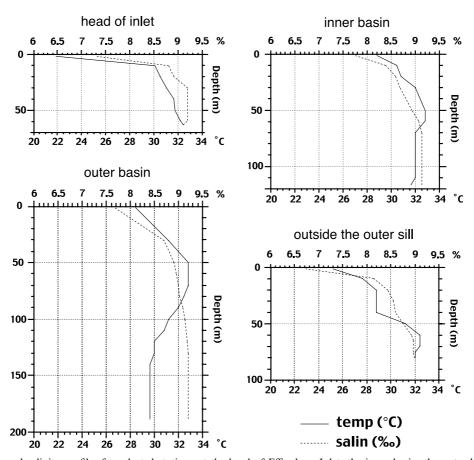


Fig. 2. Oxygen and salinity profiles for selected stations at the head of Effingham Inlet, the inner basin, the outer basin, and outside the outer sill.

of Alaska (Fig. 4), that generates a northward coastal drift and a consequent onshore Ekman transport that prevents upwelling.

The dominant surface currents seaward of the Vancouver Island continental margin are the southward-flowing California Current and northward-flowing Alaska Current (Thomson, 1981; Patterson et al., 1995). In winter, the California Undercurrent is confined to the persistent upwelling regions of California (Thomson, 1981; Patterson et al., 1995). In summer, the relatively warm, high-salinity water of the California Undercurrent flows northward along the continental margin at depths between 250 and 300 m. The upwelling of

this deeper (> 150 m) slope water is of particular interest to this study. It is most prevalent from May through August when it leads to a dramatic increase in productivity. This upwelling is slow, only 1–10 m per day, but it has a profound effect over thousands of square kilometers of the west coast of North America (Thomson, 1981; Patterson et al., 1995). This nutrient-rich water spreads into adjoining coastal inlets such as Effingham Inlet, where it contributes to increased productivity (Patterson et al., 2000). Intermittent high-salinity incursions take place in the winter, under the influence of strong northerly winds, or during the early summer upwelling season as a result of a

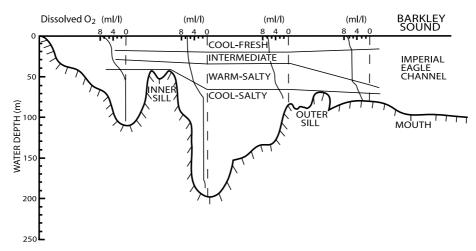


Fig. 3. Water depth, salinity and temperature stratification in the Effingham Inlet showing dissolved oxygen profiles at four different locations.

combination of weak tidal currents, significant rainfall and strong (>10 m/s) northwesterly winds (Thomson, 1981; Griffin and LeBlond, 1989).

During a reconnaissance cruise of the Canadian Coast Guard Ship (CCGS) John P. Tully in December 1995, temperature, salinity, oxygen and transmissivity profiles were measured at 11 stations throughout Effingham Inlet. In March 1997, data from an additional 20 stations were also taken (Fig. 2). Vertical salinity profiles indicate well-developed estuarine-type stratification (Fig. 3). Salinity increases from the surface water toward deeper waters with the top 20-30 m of the water column being less saline, especially in the inner basin and parts of the inlet closer to the river mouth and swamps. The salinity-induced stratification in combination with the influx of high levels of land-derived organic matter and the input of local marine productivity results in the formation of suboxic to anoxic bottom conditions in these basins (Fig. 3; Patterson et al., 2000).

Water is well-oxygenated to around 50 m depth in the inner basin, oxygen content decreases rapidly, and at 60 and 70 m depth, oxygen values of zero or near zero are reached, and H₂S appears. In the outer basin, the water properties of the anoxic/dysoxic/suboxic layers are highly uniform, indicative of diffusive processes in stagnant, quiescent water (Patterson et al., 2000).

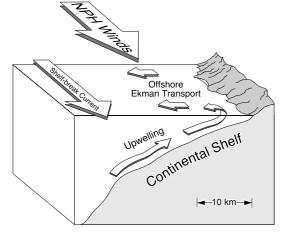
4. Previous work

Few Holocene dinoflagellate cyst studies have been made in the fjords of Vancouver Island and on the British Columbia shelf. Palynological studies of two short cores from Saanich Inlet in southeastern Vancouver Island were published by Heusser (1983), who plotted the relative abundance of dinoflagellate cysts in the overall palynomorph assemblages spanning over the last 12 kyr without identifying any dinoflagellate cyst taxa. Mudie (1998a,b) presented an ultra-high-resolution record of seasonal and decadal climate change indications of paleo El Niños and red tides based on dinoflagellate cyst studies from ODP Site 1034B drilled in Saanich Inlet. Most recently Kumar and Patterson (2000) presented a reconnaissance study on the distribution of dinoflagellate cysts in the bottom sediments of Effingham Inlet.

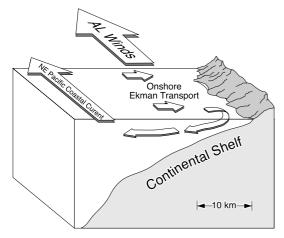
5. Materials and methods

Samples were collected during a cruise of CCGS *John P. Tully* in March, 1997, from the uppermost 10 cm of gravity-cored sediments. Since the rate of sedimentation in this inlet is very high (0.5–1.0 cm/yr; Patterson et al., 2000) the top 10 cm of sediments were considered indicative of present conditions. Sampling depth was

determined by shipboard sonar, and the position of sample stations by using a shipboard Global Positioning System (Fig. 1). Most sediments were muddy, unconsolidated and contained significant



A. Summer: North Pacific High influenced coastal circulation off Vancouver Island.



B. Winter: Aleutian Low influenced coastal circulation off Vancouver Island.

Fig. 4. (A) Atmospheric and oceanographic features of upwelling off the British Columbia coast during the summer: northerly NPH winds generate at the surface, the southward Shelf-Break Current and a consequent offshore Ekman transport-inducing upwelling thus bringing high-salinity deep water closer to the surface. (B) Atmospheric and oceanographic features of downwelling off the coast of Vancouver Island during winter: southerly AL winds generate a northward drift (NE Pacific Coastal Current) and a consequent onshore Ekman transport. This causes accumulation of lowdensity less saline water on the surface, thus restricting the upwelling of deep water (modified after Thomson, 1981).

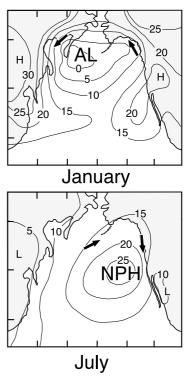


Fig. 5. Air pressure at sea-level in January and July for the northeast Pacific region from 1951 to 1970. During winter, when the land is cold and the ocean relatively warm, a large-scale counter-clockwise low-pressure gyre (AL) develops, dominating the weather over the entire northeastern Pacific. During summer, when land is hot and the ocean relatively cool, a large-scale clockwise high-pressure cell (NPH) moves up from the south and dissipates the AL. Arrows indicate prevailing wind direction. Value on diagram +10000 divided by 10 gives the pressure in millibars (modified after Favorite et al., 1976).

terrestrially derived organic matter. The samples were placed in plastic bags and kept in cold storage aboard the ship, and once back on shore methanol was added as a preservative. Samples were then sieved to remove coarse material and to separate the fine sediment. The fine sediment ($<63 \mu m$) was chemically macerated for preparation of palynological slides at GEOTOP, Université du Québec à Montréal following the method of de Vernal et al. (1999).

Species identification was primarily based on Rochon et al. (1999). Each slide was thoroughly scanned for rare species before counting, and 10

complete transacts were counted at ×400 magnification until at least 500 specimens of palynomorphs (both marine and terrestrial) were counted. Counts obtained from richer samples were often higher than 500 (Table 1). The ratio of terrestrial to marine palynomorphs, the ratio of gonyaulacoid to peridinioid (G:P ratio) dinoflagellate cysts, the percentage of various dinoflagellate cyst species, and the Shannon Diversity Index (SDI) for each sample were also calculated (Table 2) using the method described by Sageman and Bina (1997). In addition, the concentrations (specimens/cc) of total palynomorphs, total dinoflagellate cysts and various dinoflagellate cyst taxa were also calculated (Table 3) using the method of Smith (1998). Distribution patterns are shown for various parameters such as the number of cysts and cyst concentration (Fig. 6a), G:P ratio and SDI (Fig. 6b) and concentration (specimens/cc) of various dinoflagellate cyst taxa (Fig. 6c,d).

6. Results

The palynomorph assemblages identified in Effingham Inlet contain rich and diverse autochthonous (dinoflagellate cysts, foraminiferal remains, copepod eggs and invertebrate remains) and allochthonous (pollen, spores, fungal remains and thecamoebians) flora and fauna (Table 1). Although not directly a part of this study, and thus not included in the counts, several types of fungal spores, hyphae and fruiting bodies also occur commonly in our samples. All the dinoflagellate cysts identified in this study are listed (Appendix 1).

Total palynomorph concentrations vary from as high as 210 473 grains/cc in sample EI 02 (depth 31 m), located close to the marsh at the head of the inlet, to as low as 31 814 grains/cc in sample EI 32 (depth 210 m), located in the outer basin (Table 3). Assemblages are dominated by terrestrial palynomorphs in most samples, especially *Tsuga* spp., bisaccate pollen (Pinaceae) and inaperturate pollen (Cuppressaceae). Inaperturate palynomorphs occur in overwhelmingly large numbers but show a tendency to be broken or damaged, and otherwise poorly preserved.

These specimens were not included in the counts as damage was often so severe that it was difficult to determine whether specimens were inaperturate pollen or leiosphaerid acritarchs. Several types of angiosperm pollen also occur in these samples, most commonly *Alnus* and *Betula*. Fern spores (mainly monolete) occur in significant numbers in almost all samples.

The proportion of marine palynomorphs in our samples varies considerably, ranging from a low of 3.5% of the total assemblage in sample EI 03, located near the head of the inlet, to a high of 70.48% of the total assemblage in sample EI 28, located between the outer basin and Barkley Sound (Table 2). Samples from the outer basin and near the mouth of the inlet have a higher proportion (39.1-70.48%) of marine palynomorphs than from the inner basin and near head of the inlet (3.5–34.3%). The ratio of terrestrial/marine palynomorphs is high in the inner basin (ranging between 26.1:1 in sample EI 03 and 1.8:1 in sample EI 13) and in samples from shallow waters close to the shore and near marshy areas. The ratio significantly decreases (1:1) in the outer basin and toward Barkley Sound (Table 2).

Among the protists, foraminiferal test linings were found in almost all samples, and their number increased significantly in the outer basin where oxygen levels are higher (Fig. 3). Despite strong acid treatment during preparation, three genera of thecamoebians were also noted in samples from the inner basin and from shallow locations close to marshy areas (Table 1). Patterson et al. (2000) reported the occurrence of 31 arcellacean (thecamoebians) species from the same samples studied in this paper.

The numbers of dinoflagellate cysts counted in each sample and the cyst concentration (specimens/cc) varies considerably from one sample to other. However, these numbers are significantly higher in the outer basin and Barkley Sound than for the inner basin (Table 2; Fig. 6a). Both sets of data show a broadly similar pattern. Deeper water (>60 m) locations were found to have higher cyst concentrations than shallow locations, mainly due to sediment focusing at the bottom because sediments deposited along the margins of the basin tended to slip down and re-deposit

Table 1
Raw counts showing distribution of palynomorph taxa in surface sediment samples, Effingham Inlet

Sample	EI 02	EI 03	EI 05	EI 06	EI 07	EI 08	EI 09	EI 10	EI 11	EI 12	EI 13	EI 14	EI 15	El 16
Depth (m)	31	33	45	50	62	63	64	67	69	71	110	126	56	60
Total Counted	545	713	532	752	600	598	787	601	617	617	720	675	597	838
Number of Dinocyst Taxa	3	4	5	9	8	7	9	8	10	8	12	14	11	12
Total Terrestrial Palynomorphs	494	652	403	573	433	415	467	451	384	451	409	411	209	382
Total Pollen	343	494	305	396	301	302	333	375	293	333	346	345	183	322
Total Spores	151	158	98	177	132	113	134	76	91	118	63	66	26	60
Thecamoebians	0	1	1	0	3	0	7	1	4	1	6	2	0	3
Lycopodium clavatum	22	35	55	36	48	40	40	32	43	70	66	38	58	50
Total Marine Palynomorphs	26	25	71	142	114	143	270	114	180	94	227	210	308	377
O. centrocarpum sensu W&D	18	15	61	112	84	109	240	77	122	53	119	89	207	256
Operculodinium - short processes	0	2	2	9	3	6	10	1	4	7	10	7	12	8
Spiniferites ramosus	2	0	4	7	7	5	0	7	3	3	5	4	10	15
S. elongatus	0	0	0	1	1	6	2	5	0	0	2	6	2	5
P. dalei cysts	0	0	0	0	1	1	2	0	2	0	13	13	6	0
Islandinium minutum	0	5	1	1	4	8	5	5	13	1	10	14	9	13
Brigantedinium simplex	0	0	0	0	0	0	0	0	0	1	2	2	0	8
B. cariacoense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brigantedinium spp.	0	0	0	0	0	0	0	0	2	0	0	3	0	0
Protoperidinium spp. indet	0	0	0	0	0	0	0	2	3	3	3	5	3	9
Lejeunecysta oliva	0	0	0	0	0	0	1	0	0	0	0	2	0	4
Selenopemphix nephroides	0	0	0	0	0	0	0	0	0	0	0	0	0	. 2
S. quanta	0	0	0	1	3	0	0	2	2	1	5	5	3	8
Votadinium calvum	0	0	0	0	0	0	1	0	0	0	2	2	2	0
V. spinosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protoperidinium americanum cysts	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Quinquecuspis concreta	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polykrikos spp.	0	0	0	1	0	0	0	0	3	0	3	4	5	9
Total Acritarchs	0	0	3	2	1	0	3	3	4	2	7	11	5	11
Round brown cysts	6	3	0	6	10	8	6	12	22	23	46	43	44	29
Foraminiferal Remains	3	0	2	1	2	0	3	3	6	1	12	14	22	26

Notes: (1) Foraminiferal linings and thecamoebians are not included among palynomorphs; (2) one *Lycopodium clavatum* tablet (10 679 spores/tablet) was added to each sample; (3) inaperturate palynomorphs and fungal remains were not counted.

Sample
Depth (m)
Total Counted
Number of Dinocyst Taxa
Total Terrestrial Palynomorphs
Total Pollen
Total Spores Protoperidinium americanum cysts O. centrocarpum sensu W&D
Operculodinium – short processe Thecamoebians Lycopodium clavatum Total Marine Palynomorphs Brigantedinium spp. Protoperidinium spp. indel Selenopemphix nephroide: Quinquecuspis concreta P. dalei cysts Islandinium minutum Brigantedinium simplex Spiniferites ramosus S. quanta Votadinium calvum -ejeunecysta oliva cariacoense elongatus spinosum

Round brown cysts Foraminiferal Remains

Polykrikos spp. Total Acritarchs

Fable 1 (Continued)

Table 2 Dinoflagellate cyst percentages and G:P ratios in surface sediment samples, Effingham Inlet

Sample	El 02	EI 03	EI 05			EI 08	EI 09					El 14	El 15	EI 16
Total Dinocysts + Acritarchs	26	25	7.1			143	270					210	308	377
O. centrocaroum sensu W&D	18	15	61			109	240					68	207	256
%	69.23	09	85.91			76.22	88.88					42.38	67.2	67.9
Operculodinium sp. (short processes)	0	2	2			9	10					7	12	80
. %	0	8	2.81			4.19	3.7					3.33	3.89	2.12
Spiniferites ramosus	2	0	4			2	0					4	10	15
. %	7.69	0	5.63			3.49	0					1.9	3.24	3.97
Spiniferites elongatus	0	0	0			9	8					9	2	2
. %	0	0	0			4.19	0.74					2.85	0.64	1.32
Pentapharsodinium dalei cysts	0	0	0			-	2					13	9	0
	0	0	0			4.19	0.74					6.19	1.94	0
Islandinium minutum	0	2	-			80	Ŋ					14	6	13
%	0	20	4.1			5.59	1.85					99.9	4.87	3.44
Brigantedinium simplex	0	0	0			0	0					2	0	80
	0	0	0			0	0					0.95	0	2.12
B. cariacoense	0	0	0			0	0					0	0	0
%	0	0	0			0	0					0	0	0
Brigantedinium spp.	0	0	0			0	0					က	0	0
	0	0	0			0	0					1.42	0	0
Protoperidinium spp. indet	0	0	0			0	0					2	က	6
. %	0	0	0			0	0					2.38	0.97	2.38
Lejeunecysta oliva	0	0	0			0	-					2	0	4
%	0	0	0			0	0.37					0.95	0	1.06
Selenopemphix nephroides	0	0	0			0	0					0	0	7
%	0	0	0			0	0					0	0	0.53
S. quanta	0	0	0			0	0					22	e	œ
%	0	0	0			0	0					2.38	0.97	2.12
Votadinium calvum	0	0	0			0	-					2	7	0
%	0	0	0			0	0.37					0.59	0.64	0
V. spinosum	0	0	0			0	0					0	0	0
%	0	0	0			0	0					0	0	0
Protoperidinium americanum cysts	0 (0 (0 (0 (0 (0 (0 (o 0
%	9 1	0 (0 (0 1	o (> (o (> (
Quinquecuspis concreta	0	0	0			0	0					0 1	Э (0 (
%	0	0	0			0	0					0	0	0
Polykrikos spp.	0	0	0			0	0					4	2	o '
%	0	0	0	0.7	0	0	0	0	2.45	0	1.32	1.9	1.62	2.38
Total Acritarchs	0	0	ო			0	က					=	2	Ξ
%	0	0	4.22			0	1.11					5.23	1.62	2.91
Round brown cysts	9	က	0			œ	9					43	44	59
%	23.07	12	0			5.59	2.22					20.47	14.28	7.69
Terr./Mar. ratio	19	26.08	2.67			5.9	1.72					1.95	0.67	1.01
G:P Ratio	3.33	5.66	22			16.75	31.5					1.7	4.44	4.73
Shannon Diversity Index	0.621	0.628	0.309			0.912	0.391					1.862	1.256	1.468

Table 2 (Continued)

Total Dinocysts + Acritarchs	El 24	EI 26	EI 27	EI 28	EI 29				El 33	El 34	El 35	EI 36	El 37	EI 41
sensu W&D	199	207	379	671	368				264	327	177	195	469	386
	114	142	252	532	292				166	246	68	84	223	186
Operculodinium sp. (short processes) 57	57.28	68.57	66.49	79.28	79.34				62.87	75.27	38.41	43.07	47.54	48.18
	4	6	7	23	13				2	10	-	8	16	7
Sns	2.01	4.34	1.84	3.42	3.53				1.89	3.05	0.56	1.02	3.41	0.51
	17	4	18	20	7				2	14	19	18	87	82
gatus	8.54	1.93	4.74	2.98	1.2				1.89	4.28	10.73	9.23	18.55	21.24
	4	0	4	0	0				2	4	2	6	80	2
ım dalei cysts	2.01	0	1.05	0	0				0.75	1.22	2.82	4.61	1.70.9	1.29
	0	0	9	9	9				4	4	6	10	ဗ	4
ntrum	0	0	1.58	0.89	1.63				1.51	1.22	5.08	5.12	0.63	1.03
	7	=	4	6	80				15	10	10	19	23	10
simplex	3.51	5.31	3.69	1.34	2.17				5.68	3.05	5.64	9.74	4.9	2.59
	0	0	-	0	0				ဗ	0	0	9	S	0
	0	0	0.26	0	0				1.13	0	0	3.07	1.06	0
	0	0	0	0	0				0	0	0	0	-	0
Brigantedinium spp.	0	0	0	0	0				0	0	0	0	0.21	0
	0	0	0	0	0				9	4	0	0	0	0
spp. indet	0	0	0	0	0				2.27	1.22	0	0	0	0
	89	9	10	က	က				7	0	5	2	0	6
iva	4.02	2.89	2.63	0.44	0.81	0	1.49	3.44	2.65	0	2.82	1.02	0	2.33
	2	ღ	4	0	-				-	0	0	8	0	0
nephroides	-	1.44	1.05	0	0.27				0.37	0	0	1.02	0	0
	0	0	ო	0	0				2	2	-	2	က	4
	0	0	0.79	0	0				0.75	0.61	0.56	2.56	0.63	1.03
	ω	ß	2	0	-				7	4	0	2	8	80
Ę	2.51	2.41	1.31	0	0.27				2.65	1.22	0	2.56	0.42	2.07
	-	ო	0	0	0				9	0	0	0	0	0
	0.5	1.44	0	0	0				2.27	0	0	0	0	0
	0	0	0	0	0				0	0	0	0	က	0
americanum cysts	0	0	0	0	0				0	0	0	0	0.63	0
	0	0	0	0	0				0	0	0	0	0	0
concreta	0	0	0	0	0				0	0	0	0	0	0
	0	0	0	0	0				0	0	0	0	4	0
	0	0	0	0	0				0	0	0	0	0.85	0
	က	က	၈	0	7				0	8	4	7	7	9
	1.5	1.44	1.05	0	0.54				0	0.61	2.25	3.58	1.49	1.55
	4	0	၈	က	4				0	0	9	4	9	7
sts	7.03	0	1.05	0.56	1.08				0	0	3.38	2.05	1.27	1.81
	20	19	49	7.5	31				35	27	49	22	7.8	63
	10.05	9.17	12.92	11.17	8.42				13.25	8.25	27.68	11.28	16.63	16.32
	1.32	1.26	0.71	0.32	0.44				1.03	99.0	1.8	1.69	0.62	0.87
sity Index	3.86	4.3	3.9	7.37	8.66				2.65	7.4	1.69	5.69	3.47	3.25

Table 3 Concentration (specimens/cc) of selected dinoflagellate cyst taxa in Effingham Inlet

Sample No	EI 02	EI 03	EI 05	EL 06	EI 07	EI 08	EI 09	EI 10	El 11	EI 12	EI 13	EI 14	EI 15	EI 16	
Depth (m)	31	33	50	61	62	63	64	67	69	71	110	126	56	60	
Organic matter (q/cc)	4.89	3.58	3,47	2.73	2.41	2.78	2.72	3.79	2.5	1.59	2.39	4.11	2.43	4.63	
Palynomorph concentration	2,10,473	58.012	37,561	99,143	76,278	70,956	84,043	66,854	76,615	75,302	58,249	54,197	48,853	65,083	
Dinocyst concentration	10.096	2.034	5.626	18,721	14,492	16,967	28,833	12,681	22,351	11,472	18,364	16.861	25,204	29,279	
Operculodinium spp.	6,989	1,383	4,448	15,952	11,060	13,645	26,697	8,676	15,645	7,322	10,436	7,708	17,921	20,503	
Spiniferites spp.	776	?	282	1.054	1,017	1,305	213	1,334	372	366	566	802	981	1,553	
Round brown cysts	2.329	244	?	791	?	949	640	1,334	2,731	2.807	5.654	3,452	3,600	2,252	
Pentapharsodinium dalei cysts	0	0	0	0	127	118	213	0	248	0	1,051	1,043	490	0	
slandinium minutum	0	406	70	131	508	949	533	556	1,614	122	809	1,124	736	1,009	
Brigantedinium spp.	Ō	0	0	0	0	0	0	0	248	122	161	401	0	621	
Protoperidinium spp. indet + L. oliva	0	0	0	263	0	0	106	222	372	366	242	262	245	1,009	
Selenopemphix spp	0	0	0	131	381	0	0	222	248	122	404	401	245	776	
Votadinium spp.	0	0	0	0	0	0	106	0	0	0	161	160	163	0	
Polykrikos spp.	0	0	0	131	0	0	0	0	372	0	242	321	409	698	
Sample No	EI 18	EI 24	EI 26	EI 27	EI 28	EI 29	EI 30	EI 31	EI 32	EI 33	EI 34	EI 35	EI 36	EI 37	EI
Depth (m)	27	128	113	120	140	140	184	105	210	207	210	214	210	77	g
Organic matter (g/cc)	3.87	2.41	2.48	2.89	1.7	2.98	3.1	2.55	2.1	3.54	4.46	2.38	2.12	3.53	3.
Palynomorph concentration	48,586	93,901	76,371	83,815	1,83,178	1,15,536	39,851	58,395	31,814	32,862	49,056	40,350	86,855	46,102	47,
Dinocyst concentration	12,914	36,640	29,771	43,755	1,29,110	74,854	16,042	28,307	11,290	13,619	27,281	11,963	27,765	24,431	22
Operculodinium spp.	11,288	21,726	21,717	29,901	1,06,790	62,039	8,466	22,629	6,841	8,821	21,358	4,663	12,245	12,450	11.
Spiniferites spp.	270	3,866	575	2,539	3,848	1,423	1,145	847	222	361	1,501	1,622	3,844	4,948	5,
Round brown cysts	722	3,682	2,732	5,656	14,431	6,305	3,628	1,949	2,614	1,805	2,252	3,987	3,132	4,063	3,
Pentapharsodinium dalei cysts	180	0	0	692	1,154	1,220	318	678	222	206	333	608	1,423	156	2
slandinium minutum	180	1,288	1,582	1,616	1,731	1,627	891	508	556	773	834	675	2,705	1,198	5
Brigantedinium spp.	0	0	0	115	0	0	381	0	111	464	333	0	854	312	
Protoperidinium spp. indet + L. oliva	90	1,841	1,294	1,616	577	813	0	593	389	412	0	337	569	208	5
Selenopemphix spp	90	920	719	923	0	203	572	254	0	464	500	67	1,423	260	7
Votadinium spp.	90	184	431	0	0	0	0	0	111	309	0	0	0	156	
Polykrikos spp.	0	552	431	346	0	406	254	254	111	0	166	270	996	364	3

Note: Protoperidinium americanum cysts and Quinquecuspis concreta are included among the protoperidinioids.

at the bottom of the basin, enhancing the concentration of palynomorphs.

A low-diversity gonyaulacoid flora dominates the dinoflagellate cyst assemblages, and is represented primarily by Operculodinium centrocarpum sensu Wall and Dale, 1966 (including the variety with short processes), Spiniferites ramosus and a few specimens of Spiniferites elongatus. O. centrocarpum sensu Wall and Dale is the most abundant dinoflagellate cyst forming 38.41-88.88% of the dinoflagellate cyst assemblage (Table 2). The concentration of this species ranges from a low of 1383 specimens/cc in sample EI 03, near head of the inlet, to a high of 106790 specimens/cc in sample EI 28, located between the outer basin and Barkley Sound (Table 3; Fig. 6c). Percentages of Operculodinium spp. significantly decrease in the outer basin and in Barkley Sound (Table 2).

Spiniferites spp. occur in almost all the samples, but form only 0.74–22.53% of the dinoflagellate cyst assemblage (Table 2). The concentration of Spiniferites spp. ranges from a low of 282 specimens/cc in sample EI 05, near head of the inlet and close to a marsh, to a high of 5161 specimens/cc in sample EI 41, closest to Barkley Sound (Table 3; Fig. 6c). The percentage of Spiniferites spp. significantly increases in the outer basin and in Barkley Sound (Table 2).

Although peridinioid cysts are a minor constituent of the assemblage, they are represented by several species belonging to the genera *Brigante-dinium*, *Lejeunecysta*, *Votadinium* and *Selenopem-phix*, as well as indeterminate round brown protoperidinioid cysts (Tables 2 and 3).

Round brown cysts (RBC) are the second most dominant group of dinoflagellates next only to *Operculodinium* spp. These cysts occur in all samples, except sample EI 05 (Tables 2 and 3). The highest concentration of these cysts was found in samples from the outer basin and deepest locations of the inner basin (Fig. 6d). *Islandinium minutum* occurs in low numbers in almost all samples (Tables 2 and 3). The highest concentration of this species was observed in the samples from outer basin, but one sample, EI 11, from the inner basin also had a very high concentration of *I. minutum* (Fig. 6d).

Cysts of Pentapharsodinium dalei, Polykrikos

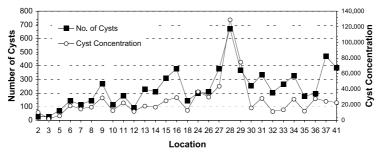
kofoidii and Polykrikos schwartzii occur in low numbers in deeper water locations of the inner basin and in all locations of the outer basin and Barkley Sound (Tables 2 and 3).

The ratio of G:P cysts in the Effingham Inlet is quite variable, although values are significantly higher for the inner basin than the outer basin (Fig. 6b). Lower G:P ratios in the outer basin indicate higher primary productivity than for the inner basin.

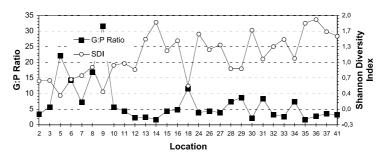
SDI values vary considerably from sample to sample, and range between 0.309 in sample EI 05, located close to marsh near the head of the inlet, to 1.839 in sample EI 35, located in the outer basin (Table 2). SDI values are significantly higher for the outer basin, Barkley Sound, than the inner basin (Fig. 6b). This is mainly due to greater influence of high salinity, oxygenated oceanic waters from Barkley Sound in the outer basin than inner basin.

Dinoflagellate cyst assemblages in the outer basin are thus mixed assemblage of dinoflagellates from the inlet as well as from the open ocean. The concentration of Operculodinium spp. (up to 100 000 specimens/cc) and Spiniferites spp. (up to 4000 specimens/cc) is highest among samples from the outer basin. At locations close to Barkley Sound (EI 37 and EI 41) Operculodinium spp. concentrations decrease from an average of 20 000 specimens/cc to almost 10000 specimens/cc, whereas Spiniferites spp. concentration increase from an average of 1000 specimens/cc to a high of over 5000 specimens/cc (Fig. 6c). This relationship is also reflected in the relative and absolute abundance of these species (Tables 2 and 3). Thus, judging from the modern salinity gradients in our study area, the abundance of Spiniferites spp. is a better indicator of more oceanic conditions than *Operculodinium* spp.

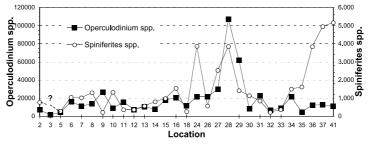
The concentrations of RBC and *Islandinium minutum*, as observed for most other species, varies considerably from sample to sample, but broadly follow similar trends, with both taxa having highest concentrations in samples from the outer basin (Fig. 6d). The average concentration of RBC was around 3000 specimens/cc, but this value reached a high of over 14000 specimens/cc (sample EI 28) in the outer basin. A higher con-



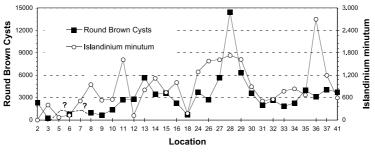
a. Distribution of number of cysts counted and cyst concentration



b. Distribution of G:P Ratio and Shannon Diversity Index (SDI)



c. Distribution of Operculodinium spp. and Spiniferites spp. $\,$



d. Distribution of Round Brown Cysts and Islandinium minutum

Fig. 6. (a) Distribution of cysts counted and cyst concentration. (b) Distribution of G:P ratio and SDI. (c) Distribution of Oper-culodinium spp. and Spiniferites spp. (specimens/cc). (d) Distribution of RBC and Islandinium minutum (specimens/cc).

centration of *I. minutum* was found in deeper locations throughout the inlet (Fig. 6d).

7. Discussion

Dinoflagellate cyst assemblages from Effingham Inlet are dominated by *Operculodinium centrocar-pum* sensu Wall and Dale, *Spiniferites* spp. and round brown protoperidinioid cysts, with differences between samples mainly relating to varying proportions of these taxa. However, significant differences between samples also relate to the presence and absence of various peridiniacean taxa, SDI, dinoflagellate cyst concentrations (specimens/cc) in the samples and the ratio of terrestrial to marine palynomorphs. These differences are closely correlated with salinity variations due to the proximity to marshes, streams, shoreline and open ocean.

Due to variations in temperature, salinity, oxygen level and the influence of the Pacific Ocean in the surface waters of Effingham Inlet, basins and channels are distinct sub-environments within this Inlet. Since these sub-environments have distinct dinoflagellate cyst assemblages, they are discussed separately.

7.1. Inner basin

Nine samples (samples 2 through 12, location 4 had no sample) are from the channel connecting the inner basin with the head of the inlet, and only two samples, 13 and 14, are from the inner basin itself (Fig. 1). The salinity of surface waters in this basin is low, and varies from 25% near the head of the inlet to 27% within the inner basin (Fig. 2). This variation is due to influx of fresh water from Effingham river. The salinity increases to 32.5% at the bottom, resulting in the water column being stratified, and dissolved oxygen levels being depleted at the bottom (Fig. 3).

Operculodinium spp., RBC and Spiniferites spp. are the main dinoflagellate cysts in the inner basin, with rare specimens of a few other peridiniacean species (Table 2). Their absolute abundance is low, but relative abundance is high because of fewer dinoflagellate cyst species occurring in the

inner basin than the outer basin. For example, the absolute abundance of *Operculodinium centro-carpum* sensu Wall and Dale, ranges from 15 (EI 03) to 240 (EI 09), but relative abundance ranges between 42.38% (EI 14) and 88.88% (EI 09). This observation is also reflected by the low SDI (0.309–1.862) of the samples from the inner basin. Terrestrial/marine palynomorph ratios are higher, since most samples were close to marshes and river mouth. The inner basin dinoflagellate cyst assemblages typically represent a local dinoflagellate flora with a minimal influence from the open ocean.

The lower salinity, lesser influence of Pacific Ocean water, and the relatively closer proximity to a river mouth, marshes and shore line are major controls on the distribution of dinoflagellate cysts in the inner basin and channel connecting this basin to the mouth of Effingham River. These taxa are almost ubiquitous and tolerate a wide range of salinities (20-36%) and water temperatures (freezing winters to 22°C in summer), and occur both in the neretic and oceanic domains (Rochon et al., 1999). The rarity of protoperidinioids is another distinguishing character of this assemblage. Salinity has been found to control the diversity of dinoflagellate cysts in the waters off Germany, where similar low-diversity dinoflagellate cyst assemblages were reported from the lower-salinity waters of the Keil Bight and higher diversity in the higher-salinity marine waters of the German Bight (Nehring, 1997).

Higher G:P ratios, lower diversity (SDI) and lower proportions of round brown protoperidinioid cysts indicate lower primary productivity in the inner basin than the outer basin.

7.2. Outer basin

Twelve sample locations were sited in this basin and another five stations were located in the channel connecting this basin with Barkley Sound (Fig. 1). Due to the periodic influx of oceanic waters in this basin, dissolved oxygen levels in the top 80 m of water in this basin are higher than the inner basin. This basin is characterized by higher species diversity (SDI 1.256–1.915) as well as higher relative and absolute abundance

of species. The higher species diversity in this basin is due to the occurrence of several peridiniacean species which were not found in the inner basin. *Spiniferites* spp. occur in significantly higher proportions in the outer basin samples and are very high in samples close to Barkley Sound. The outer basin dinoflagellate cyst assemblages are mixed and are assumed to represent both local inlet dinoflagellates and those from the open ocean.

More significant in the assemblage is the presence of *Brigantedinium* spp., an opportunistic taxon that has a widespread distribution under varying temperature and salinity conditions. It has often been associated with upwelling zones, and thus nutrient enrichment. Although heterotrophic, *Brigantedinium* spp. depend on primary production as a food source (Rochon et al., 1999).

Among the important species found in this assemblage Spiniferites elongatus is typically a cool temperate species that has been widely reported from the fjords of Norway (Dale, 1996). Islandinium minutum occurs as a minor constituent (< 2% of the assemblage) but is important as it has been associated with cold to sub-Arctic water masses, and is known to occur in fjords to shelf environments and tolerates a wide range of salinities (about 5-10% to 35%, Head et al., 2002). Brigantedinium simplex is known from estuarine to inner neritic cool temperate regions (Edwards and Andrle, 1992). Votadinium calvum and V. spinosum, as reported, here were grouped together with other taxa as miscellaneous congruentidiacean cysts by Rochon et al. (1999), and their distribution was associated with warm winter and summer conditions (about 16°C and 21°C respectively) and salinities of <36%. Cysts of Pentapharsodinium dalei occur in a wide range of environmental conditions with respect to temperature and salinity and were also reported from Norwegian fjords (Dale, 1976, 1977; Rochon et al., 1999).

Along the southeast continental margins of Canada, high percentages of *Protoperidinium* spp. have been recorded in areas characterized by high nutrient inputs, low-salinity surface waters and high primary productivity, including that of diatoms, thus showing affinities with estu-

arine-type environments (de Vernal et al., 1997). Mudie (1998a) reported the common occurrence of *Protoperidinium leonis* (= *Quinquecuspis concreta*) in Saanich Inlet, a silled fjord in southeastern Vancouver Island.

Dinoflagellate cyst assemblages from the Effingham Inlet are characterized by the presence of fairly high proportions of round brown protoperidinioid cysts in almost all samples (Fig. 6d; Table 2). Dale (1996) found the presence of high proportions of protoperidiniods as the dominant signal for upwelling in southwestern Africa and various other upwelling regions of the world including southern California. Due to coastal upwelling, nutrient-rich surface water of the Pacific Ocean spreads into adjoining coastal fjords, such as Effingham Inlet (see 3. Oceanography and climate), where it stimulates increased productivity. Although there are no published records of any cyst signal for these coastal upwellings off Vancouver Island, it is quite possible that protoperidiniods such as RBC in Effingham Inlet are due to incursions of nutrient-rich surface water from the Pacific Ocean.

Dinoflagellate cyst assemblages from the outer basin are characterized by higher cyst concentrations, lower G:P ratios and higher diversity (SDI) than the inner basin. All these factors indicate that primary productivity is higher in the outer basin than the inner basin. This is also indicated by presence of several protoperidinioid taxa in the outer basin, whose presence in the inner basin is only rare.

Cysts of gymnodinioid *Polykrikos schwartzii* and *P. kofoidii* occur sporadically and in low numbers. They have been previously reported from the temperate regions of the North Atlantic where they are associated with summer temperatures of 12°C and salinities of about 35% (Rochon et al., 1999).

8. Comparison with other dinoflagellate cyst floras

Mudie and Harland (1996) have synthesized all available published and unpublished information on the distribution of dinoflagellate cysts in the Pacific Ocean, and defined five floras that corre-

spond to different sectors of the cool, temperate California Undercurrent. The dinoflagellate cyst assemblage 'WI' is distributed in the offshore regions of Washington–Oregon just south of the Vancouver Island. This is the region where the Kuroshio-North Pacific Current System divides to form the sub-Arctic northward-flowing Alaskan Current and the cool temperate southward-flowing California Undercurrent. *Protoperidinium* spp., *Spiniferites* spp. and *Operculodinium centrocarpum* morphotypes dominate the assemblage, with *Brigantedinium* spp. co-dominant in the northerly San Juan area. This assemblage is closely comparable to the outer basin assemblages of Effingham Inlet.

Since Effingham Inlet is a fjord, it is important to compare the dinoflagellate cyst floras from other fjords. Norwegian fjords have long been studied by Dale and co-workers. Dale (1976) found that cysts behave as fine silt particles in the sedimentary regime, increasing in abundance as the percentage abundance of finer sediment increases, usually with increased water depths. This condition was also observed in Effingham Inlet, where deeper locations had numerically abundant and more diverse dinoflagellate cyst flora.

Dale (1976) recorded a higher diversity of gonyaulacoid cysts in Trondheimsfjord, than we observe in Effingham Inlet. The gonyaulacoid cyst genera *Bitectatodinium*, *Impagidinium*, *Nematosphaeropsis* (*Gonyaulax spinifera* group) and *Lingulodinium* (*G. polyedra*) occur in Trondheimsfjord, but not in Effingham Inlet. Effingham Inlet assemblages, however, have more diverse and abundant protoperidinioid cysts than Trondheimsfjord. These differences are possibly related to a greater influence of oceanic waters in Trondheimsfjord and higher primary productivity in Effingham Inlet.

Ecophenotypic adaptation to sub-normal salinities in some cyst species results in morphological change (Wall et al., 1973), including reduced process length (Dale, 1996). *Operculodinium centrocarpum* sensu Wall and Dale with short processes occur consistently in Effingham Inlet assemblages (Tables 1 and 2), although salinities of the surface waters in Effingham Inlet are relatively higher (22–27‰) than those observed by Dale (1996)

for this morphotype from the low-salinity (10–20%) waters of Oslofjord and the Baltic Sea.

In order to observe the latitudinal distribution of dinoflagellates, Dale (1996) plotted 17 dinoflagellate taxa (both living motile forms and dead cysts) from the Norwegian fjords ranging from south Oslofjord (just under 60°N) to north Varangerfjord (about 70°N). Among them, Operculodinium centrocarpum sensu Wall and Dale, Spiniferites ramosus (as S. bulloideus), S. elongatus, Brigantedinium simplex (as Protoperidinium conicoides) and P. americanum occur in all the fjords except in the northernmost Varangerfjord, and also occur in Effingham Inlet. Selenopemphix quanta (as Protoperidinium conicum) occurs in all the Norwegian fjords as well as Effingham Inlet. There is a possibility that there are even more taxa common to these regions, if we consider that several forms of Spiniferites in Effingham Inlet were grouped as S. ramosus and Spiniferites spp. However, two common dinoflagellate cysts, Bitectatodinium tepikiense and Lingulodinium machaerophorum, occur in the Norwegian fjords but are absent from Effingham Inlet.

Most of the dinoflagellate cyst taxa found in Effingham Inlet also occur in fjords, bays and other restricted bodies of marine waters in cool temperate regions of the Pacific Ocean and northern Europe (Rochon et al., 1999).

9. Conclusions

- (1) Well-preserved and diverse assemblage of palynomorphs were recovered from the surface sediments of Effingham Inlet.
- (2) The palynomorph assemblages are dominated by allochthonous terrestrial palynomorphs, with autochthonous marine palynomorphs constituting a minor proportion.
- (3) Dinoflagellate cyst assemblages are more diverse in the outer basin (a mixed fjord and oceanic assemblage) than the inner basin (fjord assemblage).
- (4) Gonyaulacoid dinoflagellate cysts occur in all samples and are represented in higher proportions than peridinioid dinoflagellate cysts.
 - (5) Operculodinium centrocarpum sensu Wall

and Dale (including short processed variety) is the most common species, and occurs in all samples. Other common gonyaulacoid dinoflagellate cysts are Spiniferites ramosus and S. elongatus.

- (6) Protoperidinioid dinoflagellate cysts are minor constituents of the assemblage but include many more species than the gonyaulacoid cysts. Most peridinioid species belong to the genera Islandinium, Brigantedinium, Lejeunecysta, Quinquecuspis, Selenopemphix and Votadinium. Although Islandinium occurs in most samples, other genera are more prominent in the outer basin.
- (7) Peridinioid dinoflagellate cysts occurs mainly in the outer basin and deeper locations.
- (8) Round brown (protoperidinioid) cysts occur in all samples, but are more common in the deeper samples, probably due to sediment focusing.
- (9) Shallower (<60 m) and low surface-water salinity locations (close to rivers, creeks and marshes) are dominated by terrestrial palynomorphs, and deeper (>60 m) and higher-salinity locations are dominated by marine palynomorphs.
- (10) Remains also of foraminifera occur in almost all the samples, but are common in deeper samples and all the samples in the outer basin and channel connecting Barkley Sound.
- (11) The distribution of dinoflagellate cysts in Effingham Inlet is primarily controlled by the salinity variation of surface waters due to proximity to rivers, creeks, swamps and to the open ocean.
- (12) The dinoflagellate cyst assemblages recorded from Effingham Inlet conform with the known distribution of dinoflagellate cysts in the cool temperate regions of the northern hemisphere, and they also occur in estuarine environ-

ments and low surface salinity environments of fjords.

(13) Primary productivity in Effingham Inlet has been enhanced by the periodic incursions of coastal upwelling-related nutrient-rich surface water from the Pacific Ocean. Primary productivity is higher in the outer basin than the inner basin.

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Appendix 1

The following dinoflagellate cysts, here listed with their thecate counterparts, were identified in Effingham Inlet surface sediments. The nomenclature and cyst-thecal equivalences are from Fensome et al. (1993), Head (1996) and Head et al. (2002).

Paleontological (cyst) name Gonyaulacoid dinoflagellates Operculodinium centrocarpum (Deflandre and Cookson 1955) Wall, Protoceratium reticulatum (Claparéde and Lachmann, 1859) 1967 sensu Wall and Dale, 1966 Spiniferites elongatus Reid, 1974 Spiniferites ramosus (Ehrenberg, 1838) Mantell, 1854 Peridinoid dinoflagellates Islandinium minutum (Harland and Reid in Harland et al., 1980) Head et al., 2002 Brigantedinium cariacoense (Wall, 1967) Lentin and Williams, 1993 P. avellanum (Meunier, 1919) Balech, 1974 B. simplex Wall, 1965 ex Lentin and Williams, 1993 Lejeunecysta oliva (Reid, 1977) Turon and Londeix, 1988

Theca-based Name

Bütschli, 1885 Gonyaulax spinifera complex Gonyaulax scrippsiae Kofoid, 1911

Protoperidinium? sp. indet

Protoperidinium sp. indet Protoperidinium sp. indet. Quinquecuspis concreta (Reid, 1977) Head, 1996 Selenopemphix nephroides Benedek, 1972 emend. Bujak in Bujak et al., 1980 S. quanta (Bradford, 1975) Matsuoka, 1985 Votadinium calvum Reid, 1977 V. spinosum Reid, 1977

Gymnodinioid dinoflagellates

P. leone (Pavillard, 1916) Balech, 1974 P. subinerme (Paulsen, 1904) Loeblich III, 1970

P. conicum (Gran, 1900) Balech, 1974
P. oblongum (Aurivillius, 1898) Parke and Dodge, 1976
P. claudicans (Paulsen, 1907) Balech, 1974
Pentapharsodinium dalei Indelicato and Leoblich III, 1986
emend. Montresor et al., 1993

Polykrikos kofoidii Chatton, 1914 Polykrikos schwartzii Bütschli, 1873

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