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OXYGEN LEVEL CONTROL ON FORAMINIFERAL DISTRIBUTION IN EFFINGHAM INLET, VANCOUVER ISLAND, BRITISH COLUMBIA, CANADA

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ABSTRACT

Samples were analyzed from Effingham Inlet, southwestern Vancouver Island, British Columbia, to assess the oceanographic controls on benthic foraminiferal distribution. The resultant proxy data will be used to interpret cores collected throughout the basin, and assess the causes of periodic variation in fish populations over time.

Seven foraminiferal assemblages were recognized with the primary controlling factors being oxygen content, and proportion of organic matter in the sediment. The estuarine *Buliminella* Assemblage characterizes well-oxygenated environments with high levels of terrestrial plant matter. This assemblage disappears when oxygen levels fall beneath suboxic levels of 40 μM/kg. The *Buccella* Assemblage, dominated in part by attached forms and islandiellids, is typical of well-oxygenated bank environments in the region. The *Psammosphaera* Assemblage is related to the lower salinity and variable conditions present in the shallow water where it occurs. The *Stainforthia-Nonionella* Assemblage characterizes one well-oxygenated environment outside the inlet. The *Stainforthia-Bolivinellina* Assemblage is typical of suboxic/dysoxic conditions (10–40 μM/kg) in the outer basin. The *Stainforthia* Assemblage is identified from dysoxic environments of deepest parts of the outer basin. A gradation between the *Stainforthia-Bolivinellina* Assemblage and the *Stainforthia* Assemblage is significant as a whole range of suboxic/dysoxic/anoxic conditions are detectable, potentially permitting recognition of even subtle variations in paleoceanographic/atmospheric circulation. The *Stainforthia-Buccella* Assemblage was recovered from the least oxygenated area of Effingham Inlet under fully anoxic (with H_2S) conditions, and provides evidence that even the most isolated portions of Effingham Inlet are periodically oxygenated.

INTRODUCTION

Considerable research has been dedicated to assessing the ability of foraminifera to adapt to low levels of dissolved oxygen in seawater, both in natural settings (Lutze, 1964; Phleger and Soutar, 1973; Douglas and Heitman, 1979; Douglas and others, 1979; Douglas and others, 1980; Douglas, 1981; Pujos-Lamy, 1973; Alve, 1990; Schafer and others, 1991; Moodley and Hess, 1992; Alve, 1995; Bernhard and Alve, 1996; Sen Gupta and others, 1996; Bernhard and others, 1997) and under controlled laboratory conditions (Bernhard, 1993; Kitazato, 1994, 1995; Alve and Bernhard, 1995; Moodley and others, 1997). Results of these studies indicate that foraminifera can live where O_2 concentration is low (<40 μM/kg of seawater) and even under anoxic conditions. Not only can foraminifera survive extended periods of anoxia (Alve and Bernhard, 1995; Moodley and others, 1997) but some species actively metabolize during that time as well (Bernhard, 1993). These observations have greatly broadened the potential utility of foraminifera as paleoecologic indicators in low oxygen environments.

The relationship between foraminiferal faunas and oxygen content has been particularly well studied in the Santa Barbara basin of the California Borderland (Douglas and others, 1976; Douglas, 1981; Douglas and others, 1979; Douglas and Heitman, 1979; Douglas and others, 1980; Bernhard and others, 1997). The dysoxic and anoxic conditions there, and in the nearby Gulf of California, have greatly suppressed bioturbation and have resulted in the preservation of annual varves containing abundant pelagic fish scales that allow year-to-year reconstruction of pelagic fish productivity in the region for the past 2000 years (Soutar and Isaacs, 1969; Baumgartner and others, 1992; Holmgren-Urbá and Baumgartner, 1993).

To extend the fishery investigation beyond Santa Barbara basin, additional anoxic and suboxic sites were looked for along the west coast of North America. Even though fjords are quite different oceanographically from Santa Barbara basin, some of these exhibit bottom anoxia that permit preservation of organic matter in the form of annual varves. Effingham Inlet, a deep-silled fjord on the west coast of Vancouver Island, characterized by a dysoxic outer basin and usually anoxic inner basin, is such a basin (Fig. 1).

During several cruises of the CCGS *John P. Tully* to Effingham Inlet (1995, 1997 and 1999), piston cores and Kasten cores were taken from the bottom of the fjord for the purpose of pelagic fish productivity reconstruction. In addition, physical oceanographic parameters (e.g. oxygen and salinity profiles) were measured during each cruise.

During the 1997 cruise, gravity core samples representing the upper 10 cm of the sediment column were collected at various places and depths in the fjord, to document the modern distribution of benthic foraminifera in relation to well-oxygenated, reduced oxygenation and anoxic conditions. The purpose of the present paper is to investigate relationships between modern foraminiferal assemblages (living+dead material) and levels of aeration (oxic, suboxic, dysoxic, and anoxic). For this research we follow the general oxygenation level classification index developed by Kaiho (1994). Under this scheme, five levels of oxygenation are recognized: high oxic (3–6 ml/l [133–266 μM/kg]); low oxic (1.5–3 ml/l [67–133 μM/kg]); suboxic (0.3–1.5 ml/l [13.3–67 μM/kg]); dysoxic (0.1–0.3 ml/l [4.4–13.3 μM/kg]); and anoxic (0–0.1 ml/l [0–4.4 μM/kg]. Although this system provides a useful guide to oxygenation, we recog-

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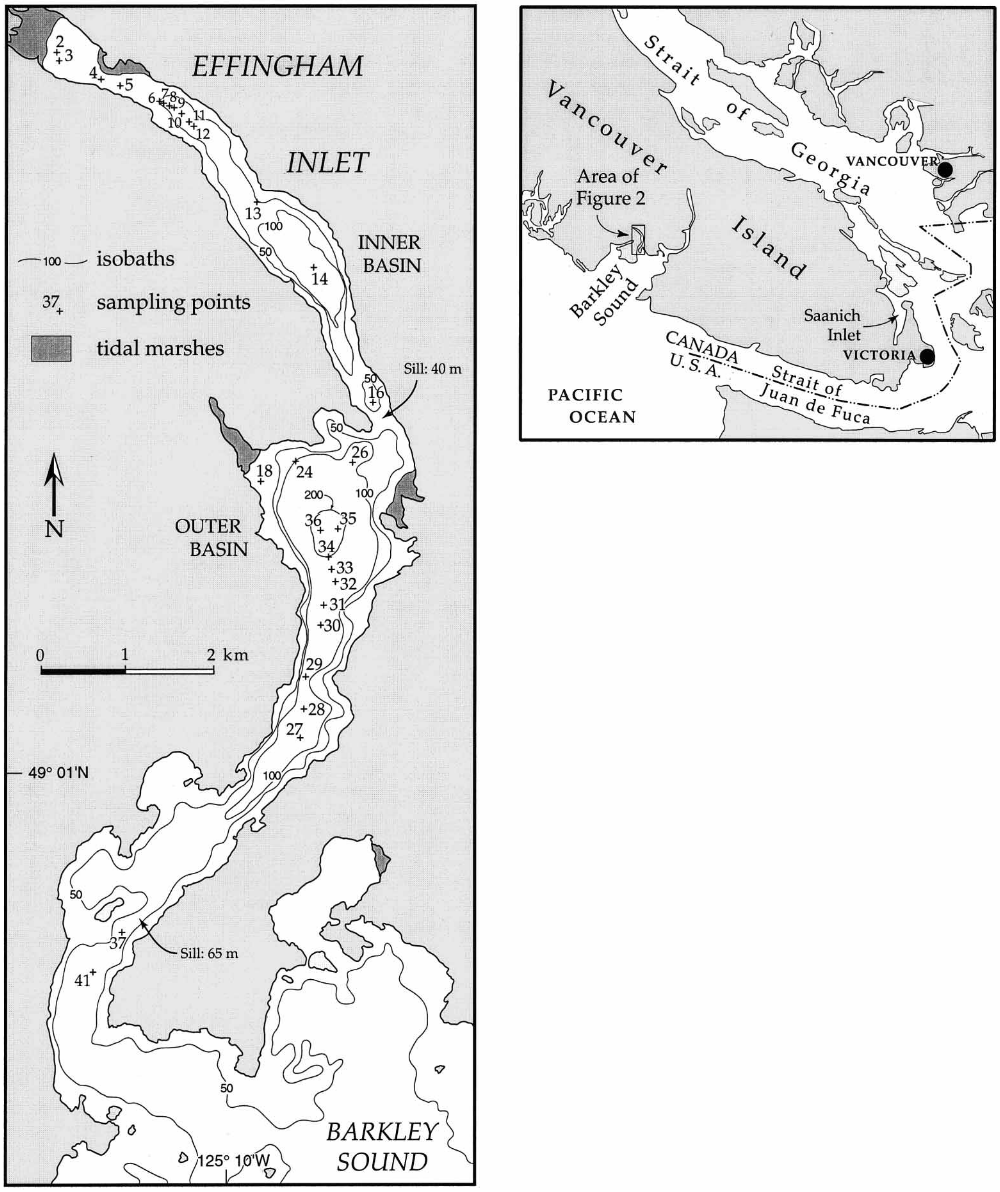

FIGURE 1. Location map of Effingham Inlet showing position of inlet, sample locations, and depth contours in meters.

nize that it does not permit differentiation within the severely dysoxic 0–4.4 μM/kg oxygen concentration range, a level sufficient to maintain significant foraminiferal populations (Bernhard and others, 1997). However, it is still very useful for providing a general assessment of oxygenation. The results of this research will be used as proxies to assess oxic, reduced oxygen (suboxic/dysoxic) and anoxic intervals downcore, important parameters as we unravel the paleoceanographic history of the region.

PHYSICAL SETTING

Effingham Inlet is a fjord 15 km long, situated on the southwest coast of Vancouver Island (Fig. 1) in an uninhabited area. It is connected to the open Pacific Ocean through Barkley Sound, a wide bay with an irregular bathymetry. At the mouth of Effingham Inlet, there is a narrow neck associated with a 65 m deep sill that opens into a basin (the outer basin) with a maximum depth of 210 m. Further up the inlet, there is a second narrow channel with an associated sill at a depth of 40 m. This channel in turn opens into another smaller basin (the inner basin) with a maximum depth of 120 m. A narrow channel extends from this basin to the head of the inlet.

Nine hundred to 1200 m mountains, comprised primarily of Mesozoic volcanic rocks, surround Effingham Inlet. The shores of the inlet are predominantly steep and rocky, and covered with barnacles and mussels. The slopes of the mountains are also steep and covered with conifer forests. Some logging takes place, especially west of the outer basin, but not near the shoreline. Tidal marshes are present on both sides of the outer basin but the largest marsh is found at the head of the inlet. Effingham River flows into the head of the inlet and is the most important source of freshwater, although a sizable creek also flows into the outer basin. The streams flowing into the inlet are large and supplied by an overall watershed of only 56 km^2, an indication of the high level of precipitation.

SEDIMENTOLOGY

The underwater slopes of the inlet are also steep and rocky. Apart from the deep parts of the basins, which are filled by sediment, coring attempts in sloped areas usually yielded little material. This result suggests that the margins of the inlet are floored either by outcropping Mesozoic rock, or Quaternary glacial gravel.

The sediment at most sampled locations consisted of soft, soupy brown mud. Both the fine sediment fraction (<63 μm) and the fraction from which the foraminiferal content was assessed (63–1000 μm) contained considerable proportions of organic matter, from as little as 10% in shallow areas to as high as 90% in the deeper basins (A. Dallimore, written communication, 1999) (essentially plant fragments). A distinct layer of coarse, black and loose organic matter a few cm thick, consisting primarily of rotted vegetation, was present at the sediment surface in the outer basin. At shallower depths (72 m and less) in the outer basin and at the mouth of the inlet, the sediment was a firm gray marine mud with a lower organic content. In contrast to other areas of the basin examined, these samples contained relatively high numbers of large (>63 μm) diatoms (Hay and Pienitz, written communication, 1999). Near the head of the inlet, the organic matter represented a large proportion of the >63 μm residue but it was coarser than at the bottom of the basins. In general, the rate of sedimentation in the basins is relatively high. 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.

OCEANOGRAPHY

The climate of western Vancouver Island is cool temperate and very wet. 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 and others, 1995). Over the Vancouver Island continental margin, currents are seasonally dependent, reversing from the southeastward-flowing shelf-break current (SBC) in summer to the northwestward-flowing Northeast Pacific Coastal Current (NEPCC) in winter (Thomson and Gower, 1998). The SBC is driven equatorward over the continental slope by the prevailing clockwise circulating winds of the North Pacific atmospheric gyre while the NEPCC is driven poleward over the continental margin by the prevailing counterclockwise winds of the Aleutian Low gyre (Thomson and Gower, 1998). Of particular significance to this study is the upwelling onto the continental shelf of deep (>150 m) slope water. Generated in response to seaward wind-forced Ekman transport in the surface layer, upwelling is most prevalent from May through August when it brings deep nutrient-rich water to the upper layer, leading to a dramatic increase in productivity. This nutrient-rich water is known to spread into the adjoining coastal inlets where it contributes to increased productivity.

During a December 1995 reconnaissance cruise of the CCGS *J. P. Tully* to Effingham Inlet, temperature, salinity, oxygen, and transmissivity profiles were measured at 11 stations throughout the basin. In March 1997, data from an additional 20 stations were measured. These results are compiled in Figure 2. Although not presented here, data from 20 more stations were collected in October 1999. Vertical salinity profiles measured throughout the basin during the 1997 cruise indicated well-developed estuarine-type stratification. Bottom salinity at the outer sill was 31.9 to 32‰ whereas in the outer basin it was 32.8‰. At the inner basin sill, bottom salinity was 30.9 to 31.2‰ (interpolations from closest stations) and in the deepest part of the inner basin, salinity values of 32.5‰ were measured (Fig. 2). The higher salinities at the bottom of the basins than at sill depth leads to stagnant water in the basins and to suboxia and anoxia.

The salinity-induced stratification in combination with the influx of high levels of organic matter from the land and probably local marine productivity results in the formation of anoxic and dysoxic bottom conditions in the inner and outer basins, respectively. In the outer basin, oxygen content is low oxic (more than 100 μM/kg) to a depth of 70–80 m but decreases rapidly to suboxic levels of less than 40 μM/kg below depths of 90–100 m (Fig. 2). Oxygen concentration decreases very slowly below this level down to less than 10 μM/kg near the bottom. The suboxic/dysoxic water (dissolved $O_2 < 40$ μM/kg) is approximately uniform in salinity and temperature, while the overlying water column has step-like temperature variations marking the transition from the actively mixing upper layer and the underlying stagnant layer.

In the inner basin, the water is well-oxygenated to around 50 m depth but then the oxygen content decreases rapidly. At 60 and 70 m depth, oxygen values of zero or near zero are reached and H_2S appears. As in the outer basin, the water properties of the anoxic/dysoxic/suboxic layers are highly uniform, indicative of diffusive processes in stagnant, quiescent water.

The fact that the bottom-water salinity in the outer basin is higher than at the outer sill implies that higher salinity oceanic water occasionally crosses over the sill and spills into the outer basin. In the absence of periodic infusions of salty bottom water, salinity in the typically dysoxic outer basin would eventually diminish through heat and salt diffusion. Intermittent salinity incursions presumably only take place in the winter, under the influence of strong northerly winds at the time of Arctic outbreak conditions, or during the early summer upwelling season during a combination of weak tidal currents in the inlet, significant rainfall and strong (>10 m/s) northwesterly winds (Thomson, 1981; Griffin and LeBlond, 1989). This influx will have the effect of periodically reaerating the bottom of the fjord, leading to an alternation of variably oxygenated and anoxic conditions. An influx of water during the upwelling season also has the effect of bringing in nutrients, which amplify marine productivity and therefore the influx of organic matter on the bottom. Reaeration was observed during the June 1999 survey of the inlet when low oxic levels (>2 ml/l [90 μM/kg]) were observed at the bottom of both basins. By October, 1999, the near-bottom oxygen levels had decreased significantly, suggesting that more characteristic suboxic/dysoxic and anoxic conditions were returning to the deep waters of the inlet.

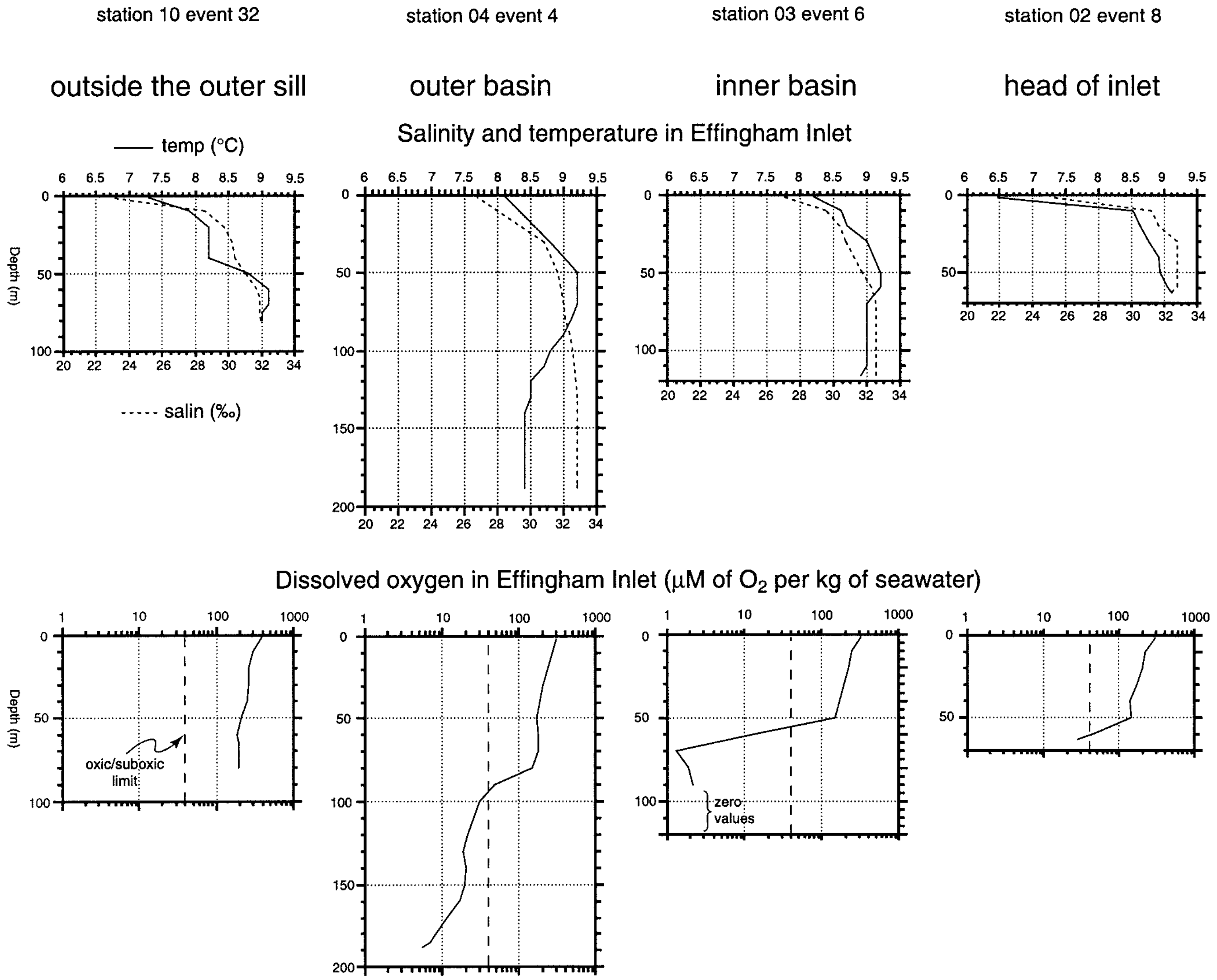

FIGURE 2. Oxygen and salinity profiles for selected stations at the head of Effingham inlet, the inner basin, the outer basin, and outside the outer sill.

PREVIOUS FORAMINIFERAL RESEARCH ON THE WEST COAST OF CANADA

Published data concerning the distribution of modern foraminifera from the West Coast of Canada are scarce. Cushman (1925) did a qualitative study of a small collection of samples from shallow water (<50 m) off British Columbia. Cockbain (1963) published a quantitative investigation of the living foraminifera from the Strait of Georgia, a less saline environment than the open ocean. Some research has also been carried out utilizing foraminifera to assess late Quaternary paleoceanographic changes farther north in Queen Charlotte Sound and Dixon Entrance (Patterson, 1993; Patterson and others, 1995; Guilbault and others, 1997). Most pertinent to this paper, Blais (1995) and Blais-Stevens and Patterson (1998) investigated the ecology of benthic foraminifera in Saanich Inlet, another anoxic/dysoxic inlet on the southeastern side of Vancouver Island. The samples analyzed were mostly from the shallower, oxygenated waters of Saanich Inlet but many of the species reported as abundant are also present and abundant in Effingham Inlet. Patterson and others (1998) published an atlas of late Quaternary foraminifers of the British Columbia shelf, which is the most extensive treatment of foraminifera in the region to date.

METHODS

The position of sample stations (Fig. 1) was determined by using a shipboard Global Positioning System, and sampling depths were determined by shipboard sonar. Samples consisting of the uppermost 10 cm of sediment were collected using a one-meter-long, 6.7 cm inner diameter gravity corer. The top 10 cm was collected for foraminiferal analysis for two reasons: 1) the high sedimentation rate in the basins and 2) the infaunal nature of many taxa even under low oxygen conditions. In the shallower portions of the fjord, the corer often hit hard bottom; on three occasions, only bits of mud adhering to the corer could be collected. We wanted to sample the shallower depths in part to see the contrast between the oxic and the suboxic/anoxic settings, but mostly to verify whether some of the specimens found at the bottom of the basins might be interpreted as transported downslope. Despite its soupiness, the sediment in the deep central parts of the inlet was sufficiently cohesive that proper cores were obtained. In the deepest part of the outer basin, the layer of coarse, loose plant matter and the underlying soft mud were clearly separated in the cores, suggesting that the sediment was minimally disturbed by coring. At two stations (31 and 35) the coarse plant matter layer was sampled separately from the underlying mud.

Samples were put in plastic bags and kept in cold storage aboard the ship. Back on shore methanol was added as a preservative. Sieving was done with a 63 μm screen to retain specimens for analysis and a 1 mm screen to remove coarse material. Residues were stained with the biological stain Rose Bengal for one week to detect the presence of protoplasm. Samples were stored wet to prevent the agglutination of plant matter and split to a size manageable for study with a wet sample splitter (Scott and Hermelin, 1993). Analysis was carried out wet under a binocular microscope at a magnification of 50×.

Even though a count of 300–500 or more is most desirable for many micropaleontological analyses (Patterson and Fishbein, 1989) the great quantity of plant debris in some samples made it impossible to practically count more than 40 to 60 foraminifera. However, these samples tended to contain few species, with often one species constituting half or more of the assemblage. Patterson and Fishbein (1989), determined that samples with as few as approximately 50 counts can be considered statistically significant provided that abundant species comprising 50% or more of the total are those considered during interpretation. We consider a count to be significant if the percentage of the species under consideration is 1% greater than the standard error. The standard error for the occurrence of a given species in a given sample is defined by:

$$S_{X_i} = 1.96[X_i(1 - X_i)/N]^{1/2} \qquad (1)$$

where S_{X_i} is the standard error; X_i is the estimated fractional abundance for species i and N is the total number of specimens counted in a sample. In some samples, the dominance was such that even with 40 specimens, the above criterion for significance was met.

Taxonomic Remarks

The most pertinent species in this study is *Stainforthia feylingi* Knudsen and Seidenkrantz, occurring in abundance in the least oxygenated waters. The name *Stainforthia fusiformis* (Williamson) has been widely used in the literature to describe specimens very close to those we report here. Some Scandinavian authors (e.g. Feyling-Hanssen, 1964) have used the name *S. fusiformis* to designate only forms whose aperture moves to a terminal position when fully grown, while employing *Stainforthia schreibersiana* (Czjzek) to describe forms whose aperture remains, at all stages of development, a loop at the base of the base of the final chamber. Knudsen and Seidenkrantz (1994) showed that the name *S. schreibersiana* is a junior synonym of the Miocene species *Fursenkoina acuta* (d'Orbigny) and erected a new species, *Stainforthia feylingi*, to include specimens without the terminal aperture. Individuals of *S. fusiformis* with both apertural characteristics occur down to at least 2000m in the Atlantic (Gooday and Alve, in press), and in Quaternary sediments from the coast of Labrador (A.A.L. Miller, 1998, written communication; Williamson and others, 1984). Comparison of European specimens provided by Elisabeth Alve of the University of Oslo with our own material indicates that those with a lateral or non-terminal aperture ('*feylingi*') are identical in both areas. However, the complete absence of any specimens with a terminal aperture in Recent or Quaternary material off the British Columbia coast suggests to us that there may be a real difference between the Atlantic forms and the northeast Pacific forms, perhaps as a result of neoteny (paedomorphosis). Genetic analysis of living specimens from both regions is required to resolve this problem. Until such a study is carried out, we will continue to use the name *S. feylingi* to designate specimens from the northeast Pacific region. Since both forms seem to thrive in low oxygen environments, we will assume that observations, both in the field and in the laboratory, made on *S. fusiformis* apply also to *S. feylingi.*

Some species of *Trochammina* and *Haplophragmoides* are left in open nomenclature although it is probable that they belong to species previously reported on the North American west coast. However, one of the trochamminids, *Trochammina* sp. 1, is frequent and locally abundant in dysoxic waters of Effingham Inlet, but does not resemble any previously described species. As description of taxa are beyond the scope of this work we will describe this new species in a later publication.

RESULTS

One hundred and forty-six species were observed in 31 samples, including 31 arcellacean species, 6 marsh foraminiferal species, 104 subtidal benthic foraminiferal species, and 5 planktic foraminiferal species (Appendices 1 and 2).

Planktic foraminifera were almost absent from the counted fractions from samples in Effingham Inlet as is typical of restricted access, relatively shallow coastal shelf areas. Arcellaceans dominated the faunas collected from the shallow innermost parts of the inlet, where waters are least saline and foraminifera least abundant. Although arcellaceans could have been washed into the inlet from anywhere above high tide, the species present differ from those found in inland lakes and are mostly typical of tidal marshes, or of areas close to sea level (Guilbault and others, 1996; Patterson and others, 1985; Patterson and others, 1996; Kumar and Dalby, 1998).

Marsh foraminifera represent an important part of the faunal assemblage only in samples from near the salt marsh at the head of the inner basin. The predominant marsh form is *Miliammina fusca* (Brady); although this species can also occur subtidally in hyposaline lagoons (Murray, 1991). The high bottom salinity conditions present at the head of the inlet (>30‰) and the adjacent large tidal marsh there suggest that a large proportion of specimens of *M. fusca* found in inner basin sediments were most likely resedimented from the marsh.

Detection of Living Specimens

Staining with Rose Bengal permits recognition of protoplasm-filled tests but does not distinguish between living and dead protoplasm. In an oxidizing environment, dead protoplasm decays quickly and Rose Bengal staining is sufficient to recognize living material. In a poorly oxygenated setting, where decay is slow, dead protoplasm-filled specimens may be abundant. This phenomenon has been observed in Santa Barbara basin (see Bernhard and others, 1997, and contained citations). For this reason, there were initial doubts concerning claims that foraminifera could live under extremely low oxygen conditions. The development of adenosine triphosphate (ATP) testing eliminated this difficulty (Bernhard and Alve, 1996). Because we only used Rose Bengal stain in this study, we must be cautious of false positive results and thus can only refer to specimens as apparently living, or protoplasm-filled.

Of the 21 species found to have stained specimens, the most commonly stained species in the dysoxic waters of the outer basin are *S. feylingi* and *Bolivinellina pacifica* (Fig. 3). *Stainforthia fusiformis* (closely related to *S. feylingi*) is a typical dweller of dysoxic environments in Norwegian fjords (Alve, 1995) while *B. pacifica* characterizes similar environments of the California Borderland (Douglas, 1981; Douglas and Heitman, 1979).

The anoxic depths of the inner basin yielded only one stained specimen of *S. feylingi* amid many empty tests of the species. This result is expected in an environment that has known a long period of anoxia. However, the dominance of empty tests of this species in that area is difficult to explain by downslope transport because it is not dominant in shallow areas of Effingham Inlet. *Stainforthia feylingi* probably colonizes the area during intervals when oxygenated water is injected into the inner basin, such as we recorded in the basin during the summer and fall of 1999.

Stained specimens recovered from dysoxic waters in the outer basin (108 m and below) include representatives of *S. feylingi, B. pacifica,* and a few *Trochammina* sp. 1. Enigmatically there were no stained *Leptohalysis catella* (Höglund), one of the major species in this area. A few stained *Buccella frigida* (Cushman), *Epistominella vitrea* Parker, and *Lobatula fletcheri* (Galloway and Wissler) may have been transported alive from shallower depths. The consistent occurrence of stained *S. feylingi* and *B. pacifica* in the deepest part of the outer basin suggests that these taxa can thrive in the dysoxic conditions existing there. We found no stained *S. feylingi* in the shallow waters of the outer basin and only one *B. pacifica.*

The number of living specimens counted in a given sample in either the inner or the outer basin never exceeds thirty-three and in most cases is less than ten. These numbers are too small to be statistically significant and we did not attempt clustering or any other statistical treatment. For the same reason, only present/absent data are plotted in Figure 3.

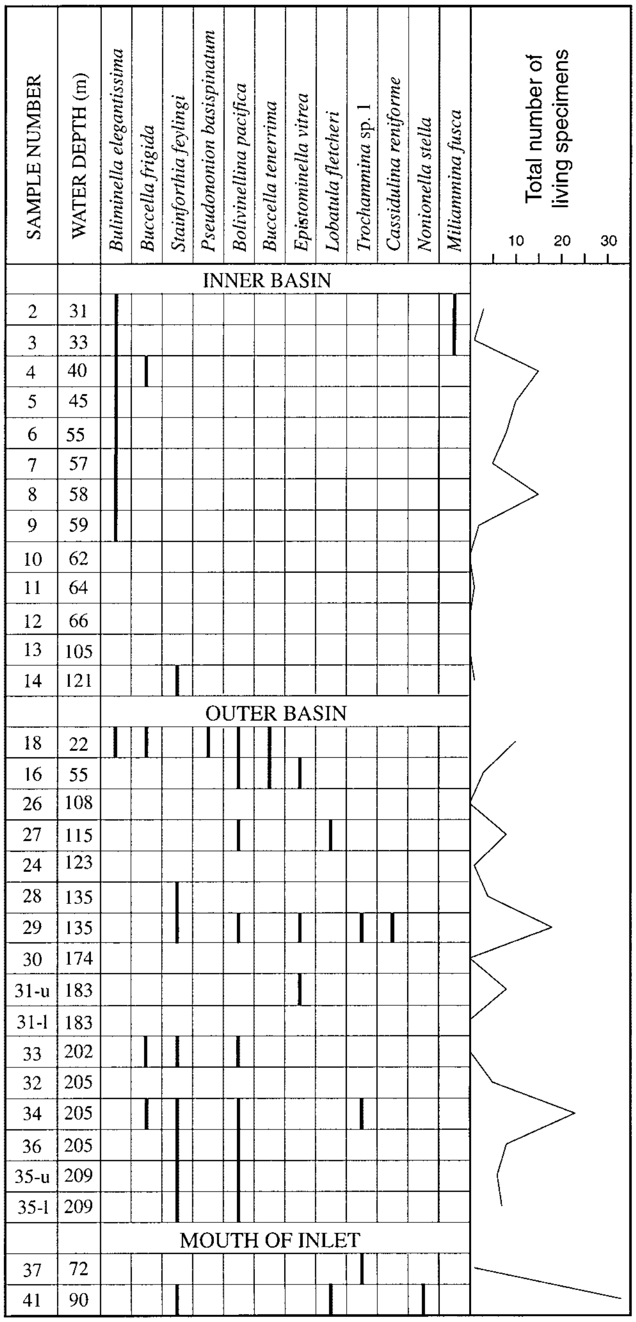

FIGURE 3. Distribution of stained specimens in Effingham Inlet samples. Only species represented by more than one specimen have been retained, and the data are of the present/absence type because numbers are not high enough to be statistically significant. Species have been ranked by order of first appearance except for the marsh species *M. fusca* that was placed at the extreme right.

FORAMINIFERAL ASSEMBLAGES

We defined seven faunal assemblages, or biofacies, based on visual examination of the quantitative results. Four of the recognized assemblages (4 to 7) discussed below show a dominance of *S. feylingi,* three of which (4, 5 and 7) are from depths and areas where, according to our oceanographic profiles, bottom waters are either suboxic/dysoxic or anoxic. Assemblages 1 to 3 are not *S. feylingi*-dominated and were collected in shallow and probably permanently oxic waters. Assemblage 6 from off the fjord sill was not exposed to dysoxic or anoxic conditions. Sample 26 consists essentially of a small number of arenaceous forms and does not fit into any of the assemblages described below. We suspect it may have been subjected to postmortem dissolution and prefer to exclude it from the discussion and from Figure 5.

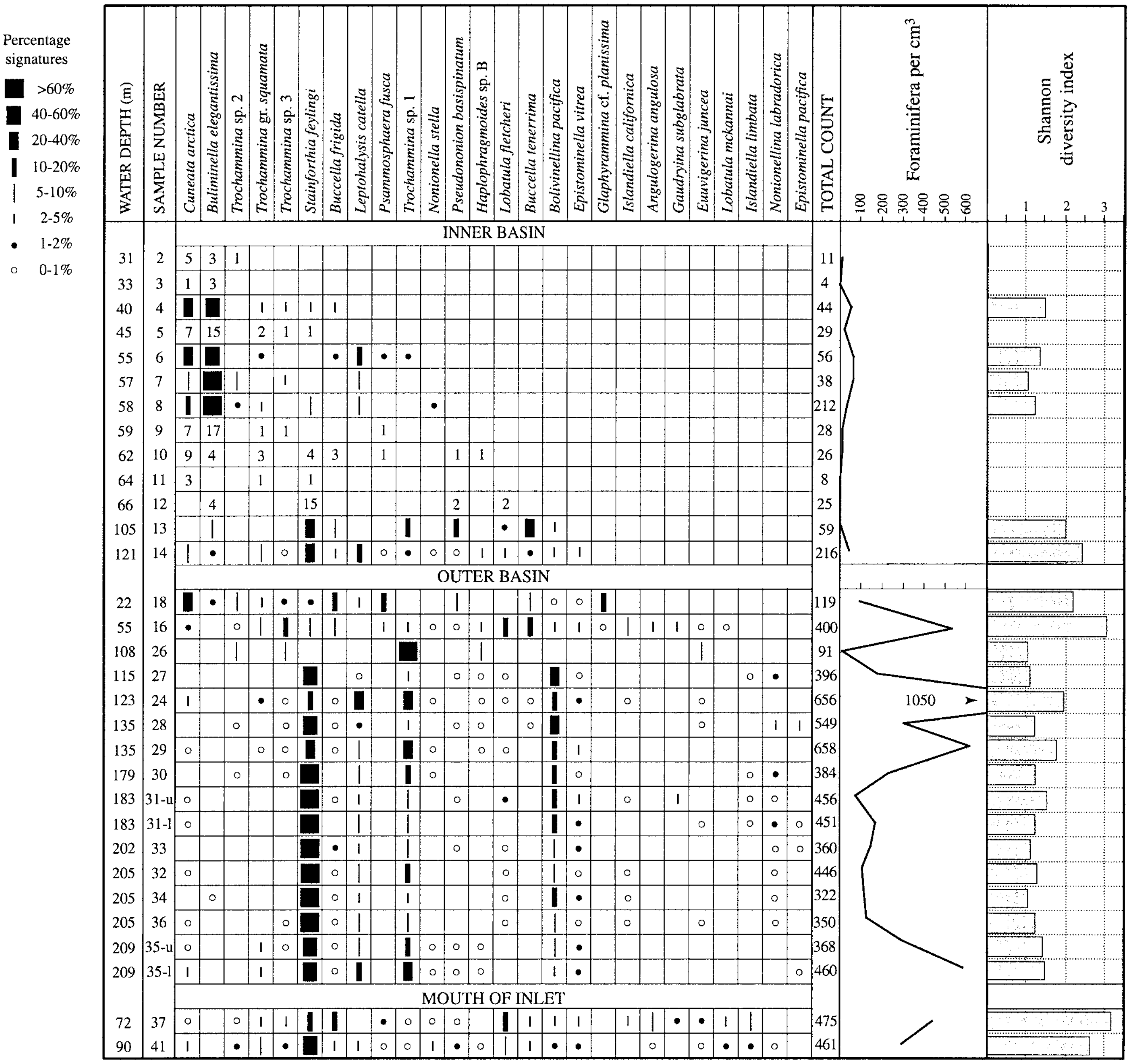

FIGURE 4. The semiquantitative distribution of the most common subtidal foraminifera in Effingham Inlet. Samples have been grouped according to their area of provenance: inner basin, outer basin or mouth of inlet, each area having different oceanographic characteristics especially with respect to dissolved oxygen. Within each category, samples are ranked by increasing depth; species are ranked by order of first appearance starting from the shallowest sample. Only species occurring in statistically significant numbers are considered. In samples with less than 38 specimens, absolute numbers of specimens are given.

Buliminella Assemblage (1)

This estuarine assemblage includes samples from well-oxygenated waters down to 60 m, and from progressively oxygen-reduced conditions down to 66 m, at the head of the inlet. It is overwhelmingly dominated by *B. elegantissima* (Fig. 4), followed by *Cuneata arctica.* Foraminifer numbers are low in this part of the inlet and many are probably reworked marsh species with only samples 4, 6, 7 and 8 having a statistically significant number of subtidal foraminifera. For these four samples, the Shannon diversity is low with H(S) values of 1.04 to 1.38.

Found between 62 and 66 m in the inner basin are three organic rich, yet depauperate samples containing progressively decreasing quantities of *B. elegantissima* that are also attributable to this assemblage (Fig. 4). The narrow depth range spanned by these samples corresponds to the transition from oxygenated to dysoxic conditions in the inner basin.

B. elegantissima is known to be dependent on high levels of organic matter (Snyder, 1989), provided by the extremely high levels of terrestrial vegetative material present in these samples. This same relationship has been reported in an area

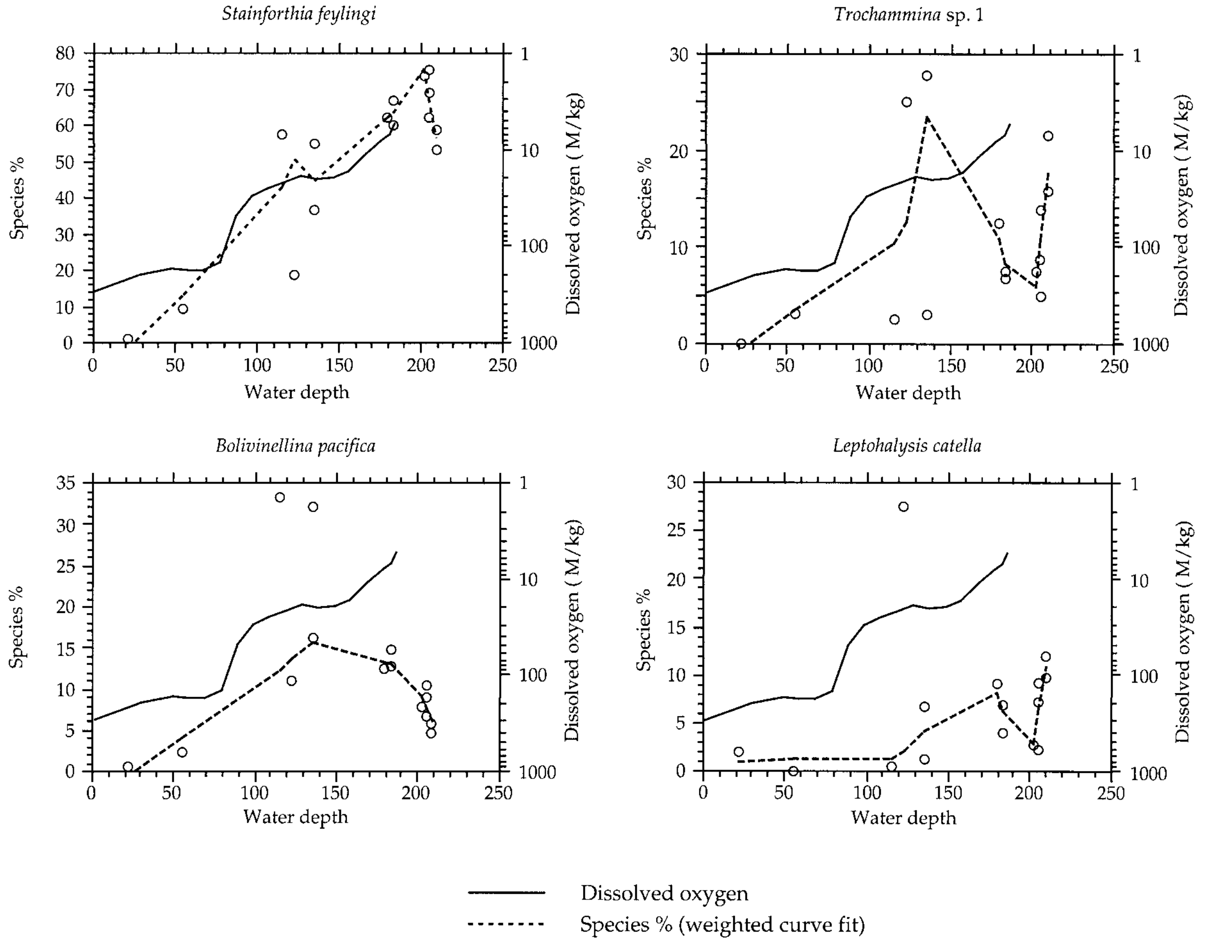

FIGURE 5. Relative abundance vs. depth for *S. feylingi, B. pacifica, Trochammina* sp. 1 and *L. catella* in the outer basin of Effingham Inlet (dashed line). The dashed lines are curve fits for the foraminiferal percentage data, using the locally weighted Least Square error method calculated by the program Kaleidagraph 3.0.5, with a smoothing factor of 50. The solid lines represent the inverse of dissolved oxygen concentrations a function of depth, as measured during the 1997 cruise; this is given for comparison purposes as there are not enough data available to establish a numerical relationship between oxygen and foraminiferal percentages.

centered around the mouth of the Columbia River, where Harmon (1972) correlated maximum abundances of vascular plant debris and *B. elegantissima.* This species does not seem to thrive in suboxic or anoxic settings. Below 60 m in the inner basin, where waters become suboxic, dysoxic and then anoxic, we see *B. elegantissima* rapidly give way to *S. feylingi* (Fig. 4) despite the extreme abundance of plant matter.

Buccella Assemblage (2)

These samples (16 and 37, collected at 55 and 72 m, respectively) are representative of normal shallow marine conditions. The dominant taxa are, in order of decreasing abundance: *Buccella* spp., *B. pacifica*, *Lobatula* spp., and *S. feylingi* (Fig. 4). Species of *Islandiella* are less frequent but their very large size makes them a predominant element of these samples. Shannon diversity values are high (H(S) > 3).

Except for the relatively high proportion of *B. pacifica* and *S. feylingi,* this assemblage is broadly similar to the open middle shelf ''bank'' Gold assemblage of Bergen and O'Neil (1979) and the *Lobatula fletcheri-Bolivina decussata* biofacies of Guilbault and others (1997). The assemblage is also similar to various carbonate bank assemblages described from the California Borderland (Douglas and others, 1976, 1979; Douglas, 1981; Patterson and others, 1990). The *Buccella* Assemblage is characteristic of open shelf, oxic, near-normal salinity conditions. The near absence of stained specimens in the otherwise rich sample 37, along with the poor preservation and the fragmented nature of specimens of *Islandiella* spp. and *Lobatula* spp., suggests that this sample may be comprised largely of relict material.

Psammosphaera Assemblage (3)

This single sample assemblage (sample 18) from a water depth of 22 m is characterized by: *Psammosphaera fusca* (probably includes some *Saccammina atlantica*), *C. arctica*, *Buccella* spp., *Pseudononion basispinatum*, and *Glaphyrammina* cf. *planissima* (Fig. 4). The Shannon diversity is lower than in the *Buccella* biofacies but still fairly high (H(S) = 2.17). The reduced diversity of the *Psammosphaera fusca* assemblage is probably related to the lower salinity and variable conditions present in the shallow water where it occurs.

Stainforthia Assemblage (4) and Stainforthia-Bolivinellina Assemblage (5)

These two assemblages have a broad similarity and are therefore described together. The nine samples (30, 31-u, 31-1, 32, 33, 34, 35-u, 35-1 and 36) comprising the *Stainforthia* Assemblage (4) are very similar to one another. All come from dysoxic environments in the deep part of the outer basin, between 179 and 209 m, the deepest point sampled. The O_2 content measured during the 1997 cruise was less than 10 μM/kg at all of the deepest oceanographic stations in the outer basin. The dominant species is *S. feylingi,* whose most typical frequency is around 60–70%, followed by *Trochammina* sp. 1, *B. pacifica* and *L. catella.* As expected in a very low oxygen environment, Shannon diversity values are low (H(S) = 1.03 to 1.52). There was no meaningful variation in faunal composition whether the substrate was loose, coarse plant matter (31-u, 33, 34, 35-u), fine organic mud (31-1, 35-1) or a mixture of both.

The *Stainforthia-Bolivinellina* Assemblage (5) comprises 4 samples (24, 27, 28 and 29) from between depths of 115 and 135 m in the outer basin (Fig. 4), in suboxic waters with ca. 20 to 30 μM/kg of dissolved O_2 as measured during the 1997 cruise (Fig. 2). It differs from the *Stainforthia* assemblage in that the percentage of *S. feylingi* is generally lower and variable (18 to 57%). Other major species are the same as in the *Stainforthia* biofacies but their percentage is proportionally greater, in particular *B. pacifica* whose occurrence is quite regular. Shannon diversities are low (H(S) = 1.13–1.96).

Both the *Stainforthia* and the *Stainforthia-Bolivinellina* assemblages are clearly associated with low oxygen conditions in the outer basin. The *Stainforthia* assemblage is restricted to water depths of >179 m whereas the *Stainforthia-Bolivinellina* biofacies is found in shallower water (115 to 135 m). The difference in the faunal composition of these assemblages can be directly related to the difference in O_2 content between the waters in which they have been collected (see ''Oceanography'', Fig. 2, and Fig. 5). The absence of data between depths of 135 and 179 m makes it difficult to assert the existence of a continuous gradation between both assemblages but the trend over the whole depth range of the fjord is that of an increase of the *S. feylingi* proportion with depth.

Stainforthia-Nonionella Assemblage (6)

The single sample (41) comprising this assemblage was collected from a well oxygenated environment (>100 μM/kg) in 90 m of water just outside the sill and downslope of sample 37 of the *Buccella* Assemblage, in Barkley Sound (Fig. 4). The assemblage is dominated by *S. feylingi*, but can be distinguished from the *Stainforthia* and the *Stainforthia-Bolivinellina* assemblages by the presence of moderate numbers of *Lobatula* spp., *Buccella* spp. and *Nonionella stella.* By contrast, there are few *L. catella* and even fewer *B. pacifica* and *Trochammina* sp. 1. The Shannon diversity is high: H(S) = 2.61.

An important and diagnostic component of the *Stainforthia-Nonionella* Assemblage is *N. stella.* This species is rare inside the inlet where observed specimens were typically small and the majority of them dead. In contrast, specimens recovered at station 41 were large and stained. Elsewhere, this species has been observed to prefer living under dysoxic/anoxic conditions and has been reported from the most anoxic portions of the Santa Barbara basin (Bernhard and others, 1997). In oxygenated environments, such as found at this site, *N. stella* has been observed to live deep-infaunally, actually within the anoxic sediment layer (Kitazato, 1994). The 10 cm thick sample collected here contains a composite fauna of species inhabiting the surface oxygenated layer and infaunal species abundant near the dysoxic/anoxic boundary. This sort of composite result is useful for comparison with material preserved in cores, because mixed epi-infaunal populations will be preserved.

The only other information that we have on the faunas of

Barkley Sound is from a piston core (97A-04, unpublished data) collected a few kilometers away. In addition to a higher proportion of cosmopolitan arenaceous species, this core yielded, at many levels, assemblages that are rich in *Buccella* spp., *Stainforthia feylingi* and nonionellids. Thus, sample 41 is probably representative of the bottom fauna of Barkley Sound.

Stainforthia-Buccella Assemblage (7)

The *Stainforthia-Buccella* Assemblage was deposited in the least oxygenated area of Effingham Inlet under fully, though not permanently, anoxic (with H_2S) conditions in the inner basin; the assemblage is represented by two samples (13 and 14) from depths of 105 and 121 m, respectively. The assemblage contains the same characteristic species as the suboxic *Stainforthia* Assemblage, but in fewer numbers (Fig. 4). It is distinguished by the presence of species from the *Buccella* assemblage, in particular *Buccella* spp., *Lobatula fletcheri,* and *P. basispinatum,* and by *Trochammina* gr. *squamata,* and *B. elegantissima,* which are common in the shallow water assemblages (1, 2 and 3); these have probably been transported downslope. A similar reworked fauna was recovered from the totally anoxic portions of Saanich Inlet (Blais, 1995; Blais-Stevens and Patterson, 1998). If taxa representative of the shallow water assemblages are removed from the data set, the major indigenous species left in the deep inner basin fauna are the same as in the *Stainforthia* biofacies: *S. feylingi, B. pacifica, Trochammina* sp. 1 and *L. catella.* This seemed to imply that periodically, suboxic conditions develop in the inner basin permitting these four species to thrive as they do in the outer basin. The existence of temporary oxic conditions was confirmed by the summer of 1999 research cruise. However, these oxic periods are too short to provide time for shallow water species to colonize the deep basin.

DISCUSSION

Off the West Coast of North America, anoxic/dysoxic environments have been sampled for foraminifera only in basins of the California Borderland (Lutze, 1964; Phleger and Soutar, 1973; Douglas and others, 1979; Douglas and Heitman, 1979; Douglas, 1981; Bernhard and others, 1997). As an example, the reduced-oxygen deeper part of one California Borderland basin, the Santa Barbara basin, is characterized by a fairly diverse fauna of species such as *Bolivina argentea, N. stella, Bolivina spissa,* and *B. pacifica.* These species, and other taxa typical of the assemblages from which they come, are characterized by delicate slender forms with very thin walls, and no ornamentation.

Direct comparison between the basins of the California Borderland and Effingham Inlet is difficult, though. The California Borderland, including Santa Barbara basin, is in an oceanic environment, in contrast to the very restricted conditions found in Effingham Inlet. The water bathing the California Borderland, whether it originates in the California Current system or from the intermediate depth low-oxygen east tropical Pacific, is little affected by runoff and salinities are at normal marine levels (33.5–34.5‰; Douglas, 1981). Furthermore, organic matter deposited in the California Borderland basin is essentially of marine origin being derived from diatom blooms (Soutar and Isaacs, 1969; Douglas and others, 1976). In Effingham Inlet, our own observations indicate that a large proportion of organic material is derived from terrestrial plant matter, both in the >63 μm and the 63–1000 μm fractions (A. Dallimore, written communication, 1999).

As it is difficult to continuously monitor sea floor conditions to determine the level of anoxia to which foraminifera can be subjected, most research on foraminiferal anaerobiosis has been experimental, under controlled laboratory conditions. Foraminifera seem to be among the organisms most tolerant taxa of anoxic conditions. Under experimental conditions it has been found that all other organisms including larval molluscs, ostracods, copepods and even nematodes, die off rapidly when anoxic conditions develop (Bernhard, 1993; Moodley and others, 1997). On the contrary, most foraminiferal species are anoxia-tolerant and it has been shown that whole assemblages of foraminifera can live though prolonged intervals of anoxia, in some cases reducing with H_2S, for up to a few months. However, for trophic reasons, opportunistic feeders are favored by periodic anoxia (Bernhard, 1993; Alve and Bernhard, 1995) and so are species inhabiting soft sediment, as they normally live within the hypoxic range (Moodley and others, 1997). None of these results indicate that any foraminiferal taxon can live indefinitely under anoxic conditions.

The tolerances of some individual taxa have also been investigated in detail. Kitazato (1995) found that many species actually prefer to live infaunally within the anoxic sediment layer. The rich food resources found at and below the redox potential discontinuity (RPD), the transition from brown, oxidized surficial sediment to gray or black reduced sediment below, offer a potential explanation for a species colonizing this inhospitable habitat. Species like *N. stella* ingest organic detritus and microorganisms attached to sedimentary grains and since microorganism growth is greatest near the RPD this provides a rich food resource for these foraminifera.

Bernhard (1993) found that some assemblages, in particular those dominated by *Globocassidulina biora,* native to anoxic sea bottoms in Antarctica, could be kept alive and metabolically active in the lab for 30 days in an artificial, non oxygenated, H_2S-rich environment. The reason for the prolonged survival of this foraminifer in a hostile H_2S environment may have been related to the presence of bacteria that developed in the foraminifer's protoplasm during anoxia. Bernhard suggested that these bacteria might have been metabolizing the H_2S for the benefit of their foraminiferal host.

Alve and Bernhard (1995) experimented with an assemblage from a cool temperate, brackish Norwegian fjord environment, somewhat similar to Effingham Inlet. The specimens and the substrate for that experiment were collected with a box corer from the inner Oslofjord, an area that may be occasionally suboxic. The water from the experiment was also pumped from the fjord. The minimum O_2 concentration to which the foraminifera were exposed during experiment was a dysoxic 7 μM/kg. The authors found that epifaunal species, especially *Bulimina marginata,* took refuge from low O_2 conditions by moving up polychaete worm tubes before becoming too scarce to show up in counts. They also found that infaunal species migrated toward the sediment surface as oxygen levels declined, before disappearing. The most opportunistic infaunal species, particularly *S. fusiformis*, did not vanish as oxygen concentration declined, but became the dominant form in terms of percentage, albeit in reduced numbers. However scarce other species became though, most taxa must have survived in small numbers because they reappeared and became abundant once again when oxygenated conditions were reestablished.

Moodley and other (1997) carried out a similar experiment on a diverse assemblage from the Adriatic Sea except that in this case, total anoxia was reached. They found that all foraminiferal species could survive and live through at least 78 days of total anoxia even though H_2S appeared after 53 days. However, they found that some opportunistic foraminiferal species fared better than others. Moodley and others (1997, 1998) further reported that 'soft-shelled' foraminifera, that is, the Allogromiina and the genus *Cribrothalammina* of the Textulariina, were less anoxia-tolerant than other, 'hard-shelled' foraminifera.

The *Stainforthia feylingi* -dominated assemblages observed in Effingham Inlet are much more similar to those reported from dysoxic (from pollution) coastal basins in southern Norway (Alve, 1995) than to basins of the California Borderland. The dominant species in the Norwegian basins is *S. fusiformis* a species that, as was discussed earlier, is morphologically similar to *S. feylingi* reported here. Although no *B. pacifica* were reported from that study, the species is common in the Skagerrak-Kattegat region (reported as *Bolivina pseudopunctata* by Höglund, 1947, for example).

Alve (1995) reports that total anoxia in Drammensfjord in the late 1970s and early 1980s led to barren seafloors below 30 m (N.B. Drammensfjord opens into Oslofjord). Gradual reoxygenation during the 1980s led to reestablishment of a foraminiferal fauna with *S. fusiformis* as the dominant species. Similarly, in Effingham Inlet, the anoxic inner basin yielded only one live stained *S. feylingi*, the dead specimens being likely relict from an earlier oxic/suboxic period. The suboxic/dysoxic outer Effingham Inlet basin, on the contrary, contains numerous living specimens, *S. feylingi* being the dominant one. This is also in general agreement with the experimental results of Alve and Bernhard (1995).

There are many environmental similarities between Effingham Inlet and Drammensfjord. Both are silled fjords in cool, wet temperate climates and both receive a large amount of land-derived plant matter. However, in the Norwegian fjords, this material is derived mostly as effluent from pulp and paper mills and sawmills. In addition, there is no urban pollution in Effingham Inlet, whereas the Oslo region is densely populated and provides additional organic pollutants beside wood fibers to Oslofjord. The most significant difference may be that the bottom salinity in Drammensfjord is ca. 30‰ against 32‰ in Effingham Inlet. That might explain the relative abundance of *B. pacifica* and *L. catella* in Effingham Inlet and their absence in Drammensfjord (our *B. pacifica* is probably a synonym of *Bolivinellina pseudopunctata* as reported in the Scandinavian literature).

Elisabeth Alve (written communication, 1999) has recently investigated another fjord in southernmost Norway (Lyngdalsfjord) that will probably be found to be more directly, and favorably, comparable to Effingham Inlet. This fjord is not polluted and, in the same way as Effingham Inlet, receives organic matter from the surrounding forest. *S. fusiformis* is the predominant species in the deeper areas (about 100–250 m; salinity 34‰) where the oxygen concentration is generally less than 0.4 ml/l (18 μM/kg), and is occasionally anoxic. The second most abundant species is *Bolivinellina pseudopunctata* in the deepest area and there are also some specimens of *Leptohalysis.* It thus seems that there is a great similarity between the foraminiferal fauna found in Effingham Inlet and in Lyngdalsfjord, despite them being situated in different oceans.

The results of the present study suggest that it should be possible to determine whether a given core interval (from Effingham Inlet and probably from other fjords) has been deposited under either oxic, suboxic/dysoxic or anoxic conditions. Our research shows the existence of two assemblages that are associated with the deep suboxic waters in the outer basin: the *Stainforthia* and the *Stainforthia-Bolivinellina* assemblages. Since investigations in Norwegian fjords with similar oceanographic characteristics reveal similar assemblages, and since laboratory experiments show that at least *S. feylingi* can take advantage of suboxic/dysoxic conditions, it thus seems likely that there is a causal link between suboxia and the occurrence of the *Stainforthia* and the *Stainforthia-Bolivinellina* assemblages. These two assemblages appear to grade into one another with lower oxygen levels at greater depths leading to a stronger dominance of *S. feylingi.* This relationship is valid when using the oceanographic data of the 1997 cruise. In the above discussion, we assumed that conditions prevailing at that time were representative of the long-term conditions in the fjord and that oxic intervals such as that of the summer of 1999 were only of short duration. Fully quantifying the relationship between oxygen level and foraminiferal assemblages, critical to recognizing regional oceanographic change in cores, is a complex task that will require many years of sampling, through at least one full cycle of development of oxic and anoxic conditions in the inner basin.

CONCLUSIONS

We found that variable suboxic conditions result in characteristic assemblages (e.g. the *Stainforthia* and the *Stainforthia-Bolivinellina* biofacies) in Effingham Inlet that are remarkably similar to faunas observed in some Norwegian fjords under similar conditions. The apparent gradation between the *Stainforthia-Bolivinellina* Assemblage and the *Stainforthia* Assemblage is also significant as it indicates that a whole range of dysoxic/anoxic conditions should be detectable. This result provides considerable promise for the future use of foraminifera as indicators of variable suboxia downcore.

Our results further indicate that reworking of specimens will not complicate interpretation of samples from cores collected in either the inner or outer basins. Few elements of the shallow *Buccella* assemblage are present in the deep water *Stainforthia-Bolivinellina* assemblage of the outer basin, indicating only minor redeposition. In the inner basin redeposited tests are relatively more abundant, the result of the small size of the basin and the relatively small autochtonous population able to withstand the primarily anoxic conditions found there.

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APPENDIX 1. Effingham Inlet foraminifer species list. Species with an asterisk (*) have at least one living occurrence. Species are listed with author name and year of publication only. In cases where the present generic designation differs from the original, or when the species was originally described as a subspecies, the original name is provided in square brackets.

NON-MARSH SPECIES

Ammodiscus sp.
Angulogerina angulosa (Williamson), 1858, [_Uvigerina_]
*_Angulogerina fluens_ Todd in Cushman and Todd, 1947
Astrononion gallowayi Loeblich and Tappan, 1953
Atlantiella sp.
Bathysiphon spp.
Bolivina cf. _acuminata_ Natland in Cushman and Gray, 1946, [_Bolivina subadvena_ var.]
Bolivina cf. _fragilis_ Phleger and Parker, 1951
Bolivina cf. _minuta_ Natland, 1938
*_Bolivina pseudoplicata_ Heron-Allen and Earland, 1930
*_Bolivinellina pacifica_ (Cushman and McCulloch), 1942, [_Bolivina acerosa_ Cushman, var.]
cf. _Botuloides pauciloculus_ Zheng, 1979
*_Buccella frigida_ (Cushman), 1922, [_Pulvinulina_]
*_Buccella tenerrima_ (Bandy), 1950, [_Rotalia_]
Bulimina aculeata d'Orbigny, 1826
Bulimina gibba Fornasini, 1902
*_Buliminella elegantissima_ (d'Orbigny), 1839, [_Bulimina_]
Buliminella subfusiformis Cushman, 1925
Cassidulina bradshawi Uchio, 1960
*_Cassidulina reniforme_ Nørvang, 1945, [_Cassidulina crassa_ d'Orbigny, var.]
*_Cribroelphidium excavatum_ (Terquem), 1876, [_Polystomella_]
Cribroelphidium frigidum (Cushman), 1933, [_Elphidium_]
*_Cribroelphidium hallandense_ (Brotzen), 1943, [_Elphidium_]
Cribroelphidium incertum (Williamson), 1858, [_Polystomella umbilicatula_ var.]
Cribroelphidium microgranulosum (Galloway and Wissler in Thalmann), 1951, [_Elphidium_]
Cribrostomoides crassimargo (Norman), 1892, [_Haplophragmium_]
Cribrostomoides jeffreysii (Williamson), 1858, [_Nonionina_]
Cuneata arctica (Brady), 1881, [_Reophax_]
Cyclogyra involvens (Reuss), 1850, [_Operculina_]
Eggerella advena (Cushman), 1922, [_Verneuilina_]
Eilohedra laevicula (Resig), 1958, [_Epistominella_]
Elphidiella hannai (Cushman and Grant), 1927, [_Elphidium_]
Entolingulina translucida (Heron-Allen and Earland), 1932, [_Lingulina_]
Eoeponidella pulchella (Parker), 1952, [_Pninaella_]
Epistominella pacifica (Cushman), 1927, [_Pulvinulinella_]
*_Epistominella vitrea_ Parker, 1953
Euuvigerina juncea (Cushman and Todd), 1941, [_Uvigerina_]
Favulina melo (d'Orbigny), 1839, [_Oolina_]
*_Fissurina_ cf. _fasciata_ (Egger), 1857, [_Oolina_]
Fissurina laevigata Reuss, 1850
Fissurina cf. _lucida_ (Williamson), 1848, [_Entosolenia marginata_ (Montagu), var.]
*_Fissurina marginata_ (Walker and Boys), 1784, [_Serpula_]
Fissurina subquadrata Parr, 1945
Fissurina vitreola (Buchner), 1940, [_Lagena_]
Gaudryina arenaria Galloway and Wissler, 1927
Gaudryina subglabrata Cushman and McCulloch, 1939
Gavelinopsis campanulata (Galowy and Wissler), 1927, [_Globorotalia_]
Glabratella aff. _californiana_ Lankford in Lankford and Phleger, 1973
Glaphyrammina planissima (Cushman), 1927, [_Haplophragmoides_]
Globobulimina auriculata (Bailey), 1851, [_Bulimina_]
Globocassidulina obtusa (Williamson), 1858, [_Cassidulina_]
Globocassidulina subglobosa (Brady), 1881, [_Cassidulina_]
Glomospira gordialis (Jones and Parker), 1860, [_Trochammina squamata_ var.]
Gyroidinoides altiformis Stewart and Stewart, 1930

APPENDIX 1. Continued.

Haplophragmoides canariensis (d'Orbigny), 1839, [_Nonionina_]
Haplophragmoides sp. A
Haplophragmoides sp. B
Heronallenia sp.
Homalohedra apiopleura (Loeblich and Tappan), 1953, [_Lagena_]
Homalohedra borealis (Loeblich and Tappan), 1954, [_Oolina_]
?_Hormosina_ sp.
Hyalonetrion clavatum (d'Orbigny), 1846 [_Oolina_]
Islandiella californica (Cushman and Hughes), 1925, [_Cassidulina_]
Islandiella limbata (Cushman and Hughes), 1925, [_Cassidulina_]
Karrerulina cf. _apicularis_ (Cushman), 1911, [_Gaudryina_]
Lagena cf. _laevis_ (Montagu), 1803, [_Vermiculum_]
Lagena striata (d'Orbigny), 1839, [_Oolina_]
Lagena sulcata (Walker and Jacob), 1798, [_Serpula_ (_Lagena_)]
Leptohalysis catella (Höglund), 1947, [_Reophax_]
*_Lobatula fletcheri_ (Galloway and Wissler), 1927, [_Cibicides_]
Lobatula lobatula (Walker and Jacob), 1798, [_Natuilus_]
Lobatula mckannai (Galloway and Wissler), 1927, [_Cibicides_]
Montfortella bramlettei Loeblich and Tappan, 1963
Nodulina sp. crf. _dentaliniformis_ (Brady), 1881, [_Reophax_]
*_Nonionella stella_ Cushman and Moyer, 1930, [_Nonionella miocenica_ Cushman, var.]
*_Nonionella_ cf. _turgida_ (Williamson), 1858, [_Rotalina_]
Nonionella turgida digitata Nørvang, 1945
Nonionellina labradorica (Dawson), 1960, [_Nonionina_]
Oolina williamsoni (Alcock), 1865, [_Entosolenia_]
Parafissurina himatiostoma Loeblich and Tappan, 1953
Parafissurina tectulostoma Loeblich and Tappan, 1953
Pateoris hauerinoides (Rhumbler), 1936, [_Quinqueloculina subrotunda_ (Montagu) var.]
Procerolagena complurecosta (Patterson), 1990, [_Lagena_]
Procerolagena gracilis (Williamson), 1848, [_Lagena_]
Procerolagena cf. _gracillima_ (Seguenza), 1862, [_Amphorina_]
Procerolagena meridionalis (Wiesner), 1931, [_Lagena_]
*_Procerolagena wiesneri_ (Parr), 1950, [_Lagena_]
Psammosphaera fusca Schultze, 1875
*_Pseudononion basispinatum_ (Cushman and Moyer), 1930, [_Nonion pizarrensis_ Berry, var.]
Quinqueloculina akneriana d'Orbigny, 1846
Quinqueloculina stalkeri Loeblich and Tappan, 1953
*_Quinqueloculina_ sp. A
Recurvoides cf. _turbinatus_ (Brady), 1881, [_Haplophragmium_]
Rosalina columbiensis (Cushman), 1925, [_Discorbis_]
Rudoloculina hooperi Guilbault and Patterson, 1998
Saccammina atlantica (Cushman), 1944, [_Proteonina_]
Seabrookia earlandi (Wright), 1889, [_Milletia_ nom. nud.]
Sigmomorphina spp.
Spiroplectammina biformis (Parker and Jones), 1865, [_Textularia agglutinans_ d'Orbigny var.]
*_Stainforthia feylingi_ Knudsen and Seidenkrantz, 1994
Textularia earlandi Parker, 1952
Tritaxis fusca (Williamson), 1858, [_Rotalina_]
*_Trochammina_ sp. 1
Trochammina sp. 2
*_Trochammina_ sp. 3
Trochammina sp. 5
Trochammina gr. _squamata_ Jones and Parker, 1860
Valvulineria cf. _glabra_ Cushman, 1927, [_Valvulineria vilardeboana_ (d'Orbigny), var.]

MARSH SPECIES

*_Balticammina pseudomacrescens_ Brönniman, Lutze and Whittaker, 1989
Haplophragmoides wilberti Andersen, 1953
Jadammina macrescens (Brady), 1870, [_Trochammina inflata_ Montagu var.]
*_Miliammina fusca_ (Brady), 1870, [_Quinqueloculina fusca_]
Trochammina inflata (Montagu), 1808, [_Nautilus_]
Trochamminita salsa (Cushman and Brönniman), 1948, [_Labrospira_]

Appendix 2. Foraminiferal counts for species occurring in statistically significant numbers in at least one sample. L: living, T: total.

Sample number		2	3	4	5	6	7	8	9	10	11	12	13	14	18	16	26	27	24	28	29	30	31-u	31-l	33	32	34	36	35-u	35-l	37	41
water depth (m)		31	33	40	45	55	57	58	59	62	64	66	105	121	22	55	108	115	123	135	135	179	183	183	202	205	205	205	209	209	72	90
Assemblage		*	*	1	*	1	1	1	*	*	*	*	7	7	3	2	†	5	5	5	5	4	4	4	4	4	4	4	4	4	2	6
total count, subtidal forms		11	4	44	29	56	38	212	28	26	8	25	59	216	119	400	91	396	658	549	656	384	456	451	360	446	322	350	368	460	475	461
fraction counted		0.03	0.02	0.03	0.05	0.03	0.02	0.13	0.05	0.05	0.05	0.33	0.33	0.13	0.03	0.03	0.5	0.06	0.02	0.06	0.03	0.04	0.17	0.06	0.06	0.08	0.06	0.06	0.03	0.02	0.03	0.03
SUBTIDAL SPECIES																																
Angulogerina angulosa	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12	–	–	–	–	–	–	–	–	–	–	–	–	–	–	42	2
Bolivinellina pacifica	L	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	7	–	–	9	–	–	–	1	–	3	1	2	2	–	–
	T	–	–	–	–	–	–	–	–	–	–	–	2	7	1	10	–	132	74	177	106	48	67	57	28	40	34	24	22	21	16	8
Buccella frigida	L	–	–	1	–	–	–	–	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	2	–	1	–	–	–	–	–
	T	–	–	1	–	1	–	–	–	3	–	–	4	5	12	34	–	–	4	1	2	–	1	–	5	2	3	1	2	3	50	19
Buccella tenerrima	L	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	–	–	–	14	4	10	40	–	–	2	1	–	–	–	–	–	–	–	–	–	–	11	22
Buliminella elegantissima	L	3	1	14	10	8	5	15	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	3	3	23	15	27	27	134	17	4	–	4	4	3	2	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Cuneata arctica	L																–	–														
	T	5	1	10	7	17	3	28	7	9	3	–	–	14	27	6	–	–	32	–	5	–	1	1	–	1	–	1	2	10	3	19
Epistominella pacifica	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	13	–	–	–	1	1	–	–	–	–	1	–	–
Epistominella vitrea	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	–	–	–	–	5	1	9	–	1	11	–	17	2	12	6	6	2	6	3	4	5	15	8
Euuvigerina juncea	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	8	–	6	1	–	–	–	1	–	–	–	1	–	–	5	1
Gaudryina subglabrata	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	–	–	–	–	–	–	18	–	–	–	–	–	–	–	6	–
Glaphyrammina cf. *planissima*	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	–	–	–	–	–	12	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Haplophragmoides sp. B	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	1	–	–	–	5	–	15	7	1	1	1	1	–	–	–	–	–	–	–	1	1	–	2
Islandiella californica	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	–	–	–	–	–	–	28	–	–	1	–	–	–	3	–	–	1	1	3	–	–	22	–
Islandiella limbata	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	1	1	–	–	–	–	–	–	32	6
Leptohalysis catella	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	6	3	15	–	–	–	–	–	22	3	–	–	2	184	7	44	35	18	31	10	41	7	25	36	55	–	12
Lobatula fletcheri	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	2
	T	–	–	–	–	–	–	–	–	–	–	2	1	10	–	45	–	2	4	–	3	–	7	–	1	1	1	2	–	–	48	31
Lobatula mckannai	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	21	5
Nonionella stella	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5
	T	–	–	–	–	–	–	4	–	–	–	–	–	2	–	1	–	–	1	–	2	1	–	–	–	–	–	–	3	1	1	21
Nonionellina labradorica	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	17	–	4	2	7	2	3	2	3	–	–	–	2
Psammosphaera fusca	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	1	–	–	1	1	–	–	–	1	17	9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	1
Pseudononion basispinatum	L	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	1	–	2	6	2	11	1	–	1	–	1	–	–	1	–	1	–	–	–	2	1	1	6
Stainforthia feylingi	L	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	4	2	–	6	–	2	–	16	7	4	5	–	22
	T	–	–	1	1	–	–	18	–	4	1	15	16	77	2	38	–	227	125	302	240	239	274	301	265	278	243	245	219	244	67	190
Trochammina gr. *squamata*	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	2	2	1	–	5	1	3	1	–	–	21	3	23	–	–	13	–	4	–	–	–	–	–	–	–	8	10	14	25
Trochammina sp. 1	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	2	–	–	–	1	–
	T	–	–	–	–	1	–	–	–	–	–	–	8	8	–	12	63	10	167	17	182	48	34	31	27	62	16	31	59	99	2	2
Trochammina sp. 2	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	1	–	–	–	–	2	3	–	–	–	–	–	–	7	2	5	–	–	1	–	1	–	–	–	–	–	–	–	–	2	5
Trochammina sp. 3	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
	T	–	–	2	1	–	1	–	1	–	–	–	–	2	2	43	6	–	6	1	3	1	–	–	–	–	–	3	1	–	17	9
MARSH (INTERTIDAL) SPECIES																																
Miliammina fusca	L	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	27	18	3	4	5	–	16	3	4	2	7	–	2	12	2	4	–	5	–	1	–	1	–	–	1	–	1	2	–	1	–
other marsh taxa	L	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	19	15	4	8	4	4	18	10	10	4	3	–	6	16	4	5	–	4	–	1	–	1	–	–	–	–	–	2	–	–	1
ARCELLACEANS	L	2	1	–	–	–	1	2	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	181	142	174	127	157	101	733	283	236	220	82	48	162	31	36	3	–	22	–	6	–	4	–	1	3	2	–	19	11	4	6

* Number of subtidal specimens statistically not significant.

† Unreliable. Calcareous specimens possibly dissolved.