

Subtidal invertebrate fouling communities of the British Columbian coast

by

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BSc, University of Victoria, 2007

A Thesis Submitted in Partial Fulfillment  
of the Requirements for the Degree of

MASTER OF SCIENCE

in the Department of Biology

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University of Victoria

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## **Supervisory Committee**

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**Supervisor**

Dr. John Dower (Department of Biology and School of Earth and Ocean Sciences)  
**Departmental Member**

Dr. Glen Jamieson (Department of Geography)  
**Outside Member**

Dr. Thomas Therriault (Department of Fisheries and Oceans)  
**Additional Member**

## Abstract

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The British Columbian (BC) coast spans a 1000 km range of complex coastal geographic and oceanographic conditions that include thousands of islands, glacial carved fjords, exposed rocky coastline, and warm inland seas. Very little is known about invertebrate fouling communities along the BC coast as studies are usually localised, focused in ports, or are conducted in the intertidal environment. This study provides the first high resolution study of invertebrate fouling communities of the BC coast by describing the identity, richness, diversity, and community composition of invertebrate fouling communities. Studying fouling communities on artificial surfaces was useful because the limiting resource (space) was defined, the researcher could control the timeframe, the samples were easily transported long distances, and the system can be easily replicated. Settlement structures were deployed in the spring of 2007 from the floating structures of marinas, docks, and aquaculture facilities. The deployment sites spanned a range of coastal environments from the Alaskan border to the southern tip of Vancouver Island, and included the Queen Charlotte Islands and Vancouver Island. The settlement arrays were collected roughly five months following deployment. Samples were transported back to the laboratory where all organisms present on the settlement arrays were identified to the lowest taxonomic level possible and their relative abundance recorded.

The invertebrate fouling community was very species rich with 171 species identified and an additional 34 categories of unresolved taxa. This high richness may be attributed to the fact that the settlement arrays sampled the community as a whole, including motile and rare species. The richness per sample ranged from 1 to 29 species with the average being 12 species, of which more than one (1.25) was introduced to the BC coast. This invertebrate fouling community was dominated by relatively few species. Only 20% of

the sessile species had an average cover over 1% and only 13% of the motile species had an average count over 0.5 individuals per sample. Of the sessile species, the *Mytilus* sp. complex was the most common with an average coverage of 35%. The *Mytilus* sp. complex was also found in 78% (126/162) of all samples.

There were eleven introduced and twelve cryptogenic species identified in this study. Introduced species represented 30% of the dominant (=most abundant) sessile species and 20% of the dominant motile species study. The introduced and cryptogenic species were more abundant than native species when comparing abundance based on their distributions in the samples. The prominence and abundance of the introduced species in these communities may be an artefact of studying anthropogenic sites. However, it underscores the fact that the establishment and spread of non-native species are continuing along our coast, and that the strong competitive ability of a number of these species may have negative ecological and economic impacts.

There were strong similarities in community composition across all geographic areas of the BC (Strait of Georgia-SOG, Juan de Fuca Strait- JFS, west coast of Vancouver Island-WCVI, Johnstone Strait-JS, and the north coast of the mainland-NC). The most common species assemblage was the *Mytilus* sp. complex and its associated species. The species assemblages observed across numerous geographic areas included species that were strong space competitors, had ranges that included the length of our study area, had key reproductive periods during the sampling period, and were able to recruit to artificial substrates. Anthropogenic structures may also be partially responsible for the strong similarities in community composition along the coast as we may be sampling species that are best adapted to these environments. Additionally, anthropogenic structures and activities may serve as vectors of species dispersal. Pairwise comparisons showed that the WCVI differed from the JFS and QCI in community composition in that the WCVI was strongly influenced by the *Mytilus* sp. community but the JFS and QCI were influenced by introduced and cryptogenic species.

This study is the first to examine fouling communities that span the length of the BC coast. The data collected can be used as a baseline of comparison for future studies on subjects such as climate change, human mediated species introductions, and anthropogenic disasters.

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Johnstone Strait (JS)- open circles, and West coast of Vancouver Island (WCVI)- crosses. Square blocks with numbering emphasise the clusters at the designated similarity level.92

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# Chapter 1

## Species identity, richness, and diversity of the invertebrate fouling community of the British Columbian coast

### Introduction

Most shallow subtidal marine hard substratum habitats are populated by invertebrate communities that consist primarily of sessile suspension feeders and the motile organisms that are associated with the structural habitat they provide (Nydam and Stachowicz 2007). The composition of these communities is highly variable and is influenced by the successes of individual species in the community. The success of each species is determined by the ability of larvae to survive in the water column and settle in the appropriate habitat, juveniles to recruit (survive) to a community, and adults to compete for resources during the successional stages of the community. Throughout each of these life history stages invertebrates are influenced by a myriad of biotic and abiotic factors.

Invertebrates have complex life histories where reproduction produces larvae that may be planktotrophic (free-swimming and feeding larvae), lecithotrophic (free-swimming but provisioned larvae), or brooded (larvae are not freely released and are provisioned within parental care) (Brusca and Brusca 2002). The spawning of gametes and release of larvae are complex processes that are timed to maximize survival. Particularly for planktotrophic larvae, this means timing reproduction around optimal temperature and food availability (Starr *et al.* 1990, Reitzal *et al.* 2004). For most species along the British Columbia (BC) coast, this means there is a peak reproductive season in late spring to early summer for both lecithotrophic and planktotrophic species. Brooding species may reproduce throughout the year but also show slight timing peaks in the release of larvae in the spring and summer (Reitzal *et al.* 2004).

Larvae that reach suitable habitats settle and metamorphose into juvenile species. The supply of larvae (propagules) to a habitat is an important determining factor in shaping the population and community dynamics (Connolly *et al.* 2001). The survival of the larvae in the water column is influenced by abiotic factors, such as temperature, salinity, and currents, as well as by biotic factors such as predation (*e.g.* Rodriguez *et al.* 1993,

Connolly *et al.* 2001). Once the larvae reach a suitable habitat, the next step in development is to settle and undergo metamorphosis to become juvenile organisms. Settlement rate has been described as one of the most important factors in structuring intertidal communities (Gaines and Roughgarden 1985, Roughgarden *et al.* 1985). Again, the settlement and metamorphosis process is influenced by a number of factors as the larvae respond to environmental cues that induce settling behaviour. The larvae also have some ability to select an appropriate substrate based on physical, chemical, and biological information in the immediate environment (Brusca and Brusca 2002).

The actual recruitment of juveniles into the community, and their survival as adults, is still determined by both abiotic (temperature, salinity, disturbance) and biotic (competition and predation) factors. In the space limited environment of hard substratum communities, the succession and development of the community continues over time as factors, such as natural death, disturbance, and predation, create new space that is open for the recruitment and competition of species (Dayton 1971, Mook 1981). Therefore, the formation, structure and dynamics of these marine epibenthic invertebrate communities are stochastic and remain under constant flux as the abiotic and biotic factors of pre-settlement, settlement, and post-settlement processes vary both spatially and temporally (Todd 1998).

The species recruiting into an epibenthic community in this study can be classified as native, introduced, or cryptogenic. In this study a native species is defined as a species whose natural distribution includes the BC coast. Introduced species are those organisms whose native ranges do not include BC waters and have been introduced to our coast by human activities. Cryptogenic species are species that have such a cosmopolitan distribution that we are unsure of their native range (Carlton 1996).

The British Columbian (BC) coast spans a 1000 km range of complex coastal geography and oceanography that includes thousands of islands, glacial carved fjords, exposed rocky coastlines, and warm inland seas (Thomson 1981). At either end of our coastal range BC is bordered by the US, and though there are many marine invertebrate studies that occur in the northeast Pacific, very little is known about the BC coastline. Studies of invertebrate communities along the Pacific coast of North America often only include minimal locales in BC (*e.g.* Sagarin and Gaines 2002) or bypass the region

entirely. Studies of epibenthic communities actually conducted within BC water are usually localised (*e.g.* Richoux *et al.* 2006), focused in ports (*e.g.* Lu *et al.* 2007), or are conducted in the intertidal environment (Zacharias and Roff 2001). There have been no studies of subtidal epibenthic communities for the entire BC coast. Therefore, my goal was to provide the first high resolution description of invertebrate fouling communities of the BC coast. Fouling communities are an ideal system to study because: i) the limiting resource (space) is defined, ii) we can control the timeframe, iii) it can be easily replicated, and iv) the samples can be transported long distances. By identifying the species and communities that develop on settlement structures, I am providing a baseline survey of BC for comparison for future in response to climate change, natural disasters, large scale pollution (*e.g.* oils spills), and species introductions. A secondary focus of the study was to determine the presence of introduced species in fouling communities of the BC coast. Though there have been numerous reports of introduced species along the BC coast, this will be the first large scale survey to provide insight into the current presence, abundance and distribution of these species along our coast.

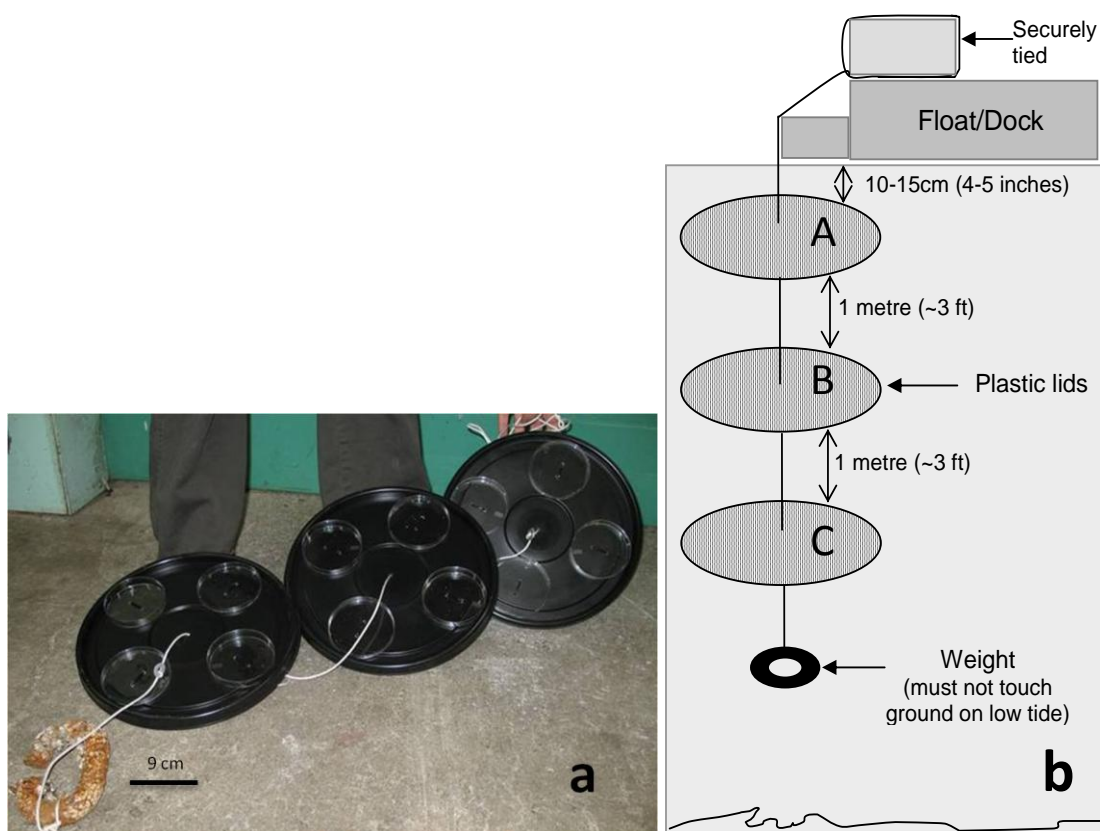
The basic concepts in community ecology focus on understanding and examining the identity of the species present, the number of species (species richness), and the relative abundance of the species (species diversity) in communities (Southwood 1995). In this first chapter of the study, I will focus on describing the species identity, richness, and diversity of subtidal invertebrate fouling communities of the BC coast. The identity of species will be considered in context of their status as native, cryptogenic, or introduced species.

## **Methods**

### **Settlement arrays**

We constructed settlement arrays from large, black, plastic buckets lids that were drilled to securely attach four Petri dishes (9 cm diameter) to the underside with Zap-Straps (Figure 1a). Each settlement array consisted of three of these large plastic lids strung along a length of rope at one meter intervals. We tied metal washers underneath each lid for support. A weight of 0.9-2.3 kg was tied to the end of the length of rope to ensure that the array was always fully submerged and maintained in its orientation. The settlement arrays were tied to a floating structure with enough rope so that the top lid

would hang approximately 15 cm below the water surface. Once the length of rope was secured we lowered the settlement arrays into the water, weight first. Each lid was lowered into the water vertically to prevent trapping bubbles under the Petri dishes. The lids hung horizontally in the water column with the Petri dishes on the underside (Figure 1b). We hung two settlement arrays at each deployment site to minimize the chance of losing a sampling site due to damage or loss of an array.

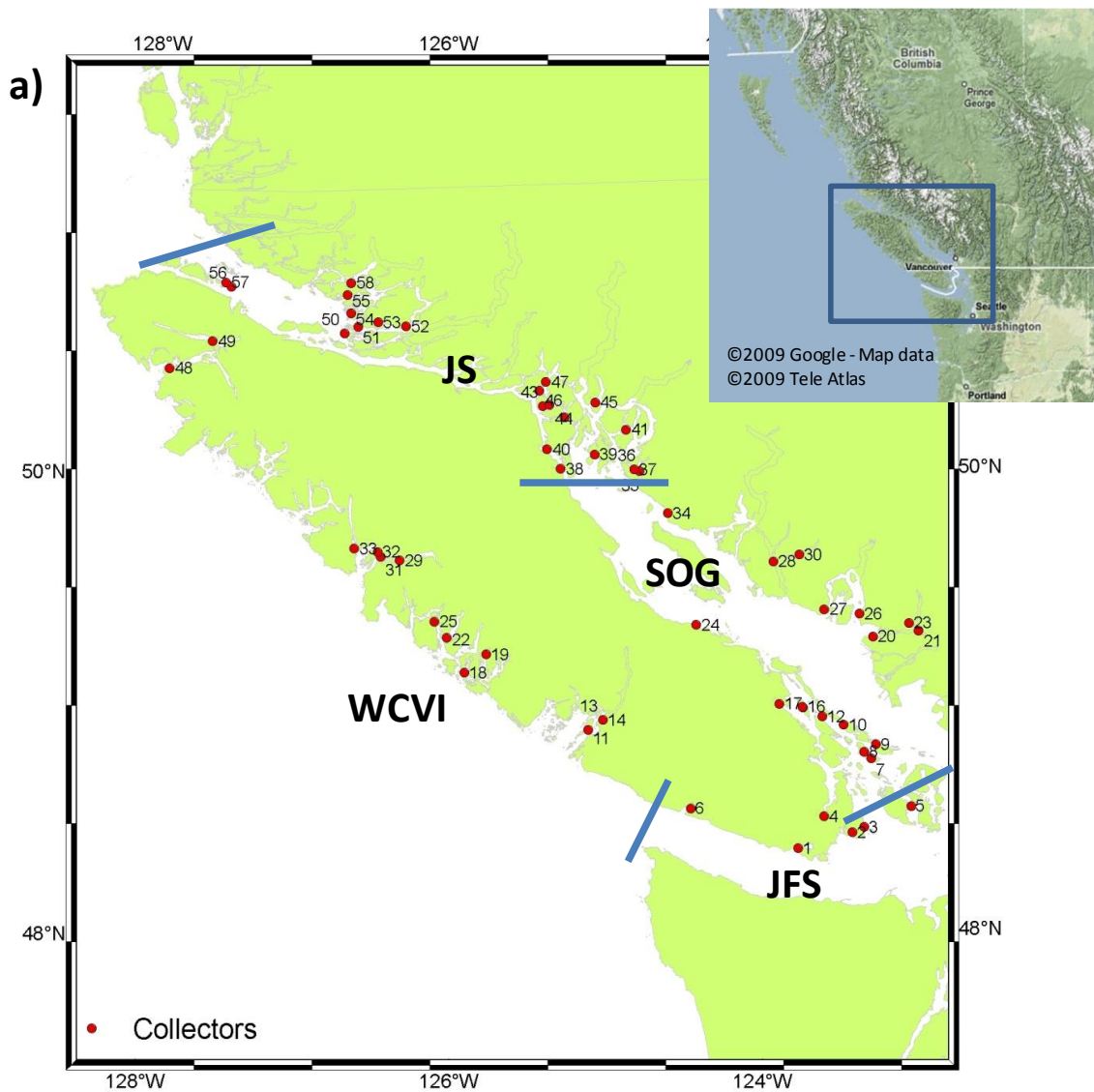


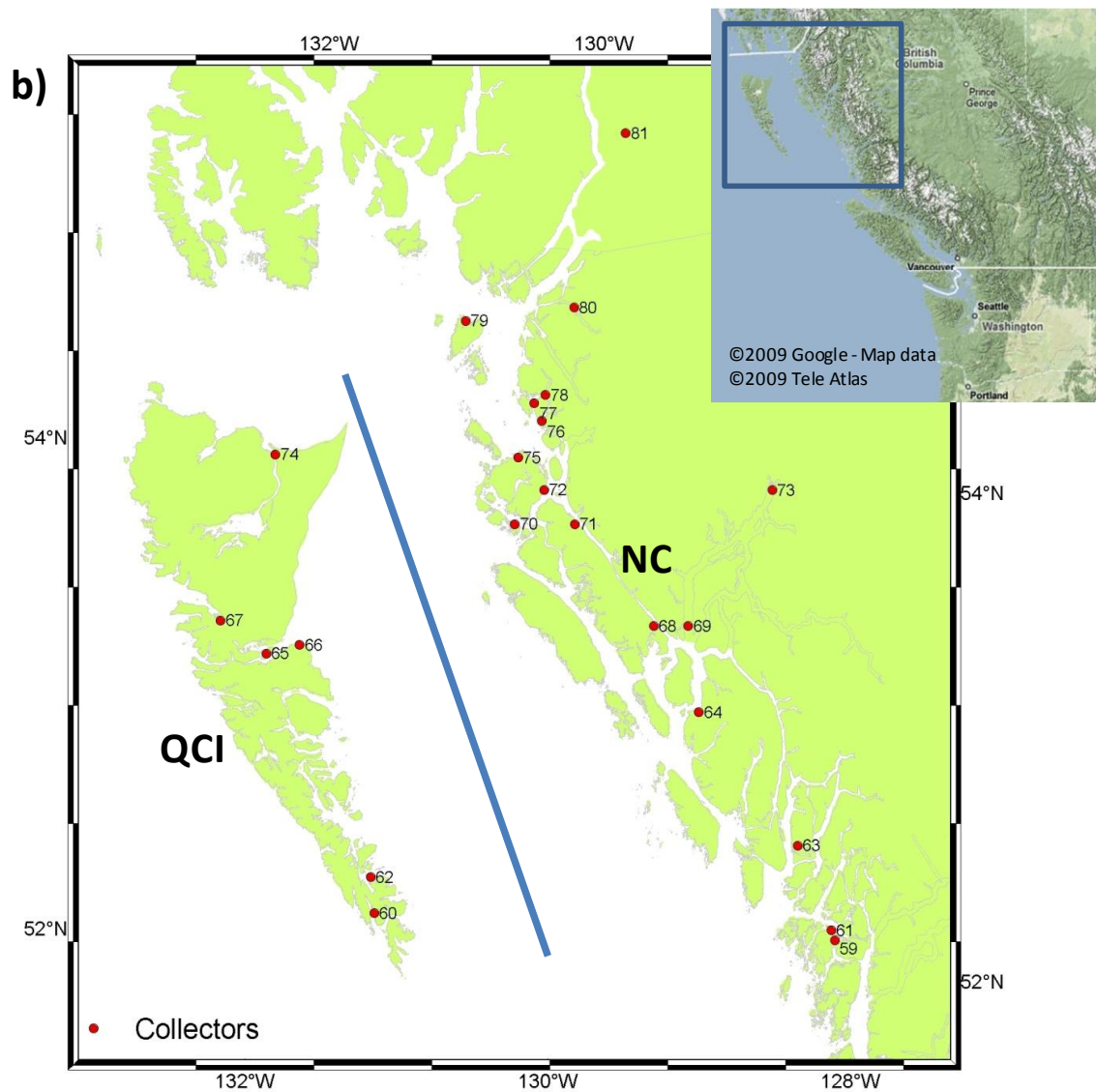
**Figure 1. Settlement array a) A newly constructed settlement array showing arrangement of Petri dishes on the underside of each plastic lid. b) Depiction of a deployed settlement structure. Note the A designation assigned to the lid at 15 cm below the water surface, B to the lid at 1m 15 cm below the surface, and C to the lid 2m 15cm below the surface.**

### **Sampling sites and project set-up**

The settlement arrays were deployed in the spring of 2007. We deployed the settlement arrays in early spring so as to maximize on the seasonality of larval recruitment. Through a large collaborative effort involving marinas, members of the aquaculture industry, and the Canadian Coast Guard, we deployed settlement arrays at

over 160 sites along the BC coast. The deployment sites spanned a range of coastal environments from the Alaskan border to the tip of Vancouver Island, and included both the Queen Charlotte Islands and Vancouver Island. We hung the settlement arrays from man-made floating structures at marinas, shellfish aquaculture farms, and salmon aquaculture farms. We collected the settlement arrays in the fall of 2007, roughly five to six months after deployment. Many of the settlement arrays were lost or damaged over the sampling period and as a result settlement arrays were collected from a total of 101 sites. Eighty one of these sites were processed (Figure 2, Table 1).





**Figure 2. The location of deployment sites for settlement arrays along a) southern coast and b) northern coast of British Columbia. See Table 1 for site names and information.**

**Table 1. The site location (No), latitude (GPS N), longitude (GPS S), geographic area, date of deployment (Date In), date of collection (Date Out), and total number of days submerged (No days) for sites where settlement arrays were retrieved. Also indicated are whether or not a site was processed and the reasoning behind a negative decision. Geographic areas are represented as follows: SOG- Strait of Georgia, JFS-Juan de Fuca Strait, JS- Johnson Strait, WCVI- West Coast Vancouver Island, QCI- Queen Charlotte Islands, and NC- North Coast of BC mainland.**

No	Site	GPS N	GPS S	Area	Date In	Date Out	No days	Proces sed	Reasoning behind not processing
1	Sooke	48.370	-123.726	JFS	23-Mar-07	18-Oct-07	209	Yes	
2	Canoe Club	48.430	-123.371	JFS	27-Apr-07	29-Oct-07	185	Yes	
3	RVicYC	48.451	-123.295	JFS	27-Apr-07	08-Oct-07	164	Yes	
4	Goldstream	48.503	-123.553	SOG	23-Mar-07	18-Oct-07	209	Yes	
5	Friday Harbor	48.533	-122.983	JFS	30-Apr-07	23-Dec-07	237	Yes	
6	Port Renfrew	48.555	-124.420	JFS	5-Jun-07	10-Sep-07	97	Yes	
7	Poets Cove	48.748	-123.229	SOG	11-May-07	22-Nov-07	195	Yes	
8	North Pender	48.777	-123.274	SOG	11-May-07	22-Nov-07	195	Yes	
9	Winter Harbour	48.808	-123.195	SOG	11-May-07	22-Nov-07	195	Yes	
10	Montague	48.897	-123.403	SOG	11-May-07	22-Nov-07	195	Yes	
11	Sarita	48.902	-125.082	WCVI	25-May-07	14-Jan-08	234	Yes	
12	Wallace	48.937	-123.543	SOG	11-May-07	23-Nov-07	196	Yes	
13	Barkley	48.944	-124.986	WCVI	17-Apr-07	30-Oct-07	196	Yes	
14	San Mateo	48.944	-124.986	WCVI	17-Apr-07	30-Oct-07	196	Yes	
15	Thetis	48.978	-123.669	SOG	17-May-07	17-Oct-07	153	Yes	
16	Telegraph	48.982	-123.671	SOG	17-May-07	17-Oct-07	153	Yes	
17	Ladysmith	48.998	-123.820	SOG	12-Jul-07	02-Dec-07	143	Yes	
18	Tofino	49.154	-125.894	WCVI	5-Apr-07	09-Oct-07	187	Yes	
19	Fortune	49.233	-125.752	WCVI	4-Apr-07	23-Oct-07	202	Yes	
	Mussel Rock	49.259	-125.870	WCVI	14-Apr-07	23-Oct-07	192	No	levels A had fallen along rope on top of B lids (limits growth on A)
	Rant Point	49.259	-125.846	WCVI	18-Apr-07	23-Oct-07	188	No	levels A had fallen along rope on top of B lids (limits growth on A)
20	RVYC Jericho	49.275	-123.188	SOG	25-Apr-07	19-Sep-07	147	Yes	
	Coal Harbour	49.291	-123.127	SOG	25-Apr-07	19-Sep-07	147	No	area densely sampled
21	Reed Point	49.291	-122.884	SOG	25-Apr-07	19-Sep-07	147	Yes	

No	Site	GPS N	GPS S	Area	Date In	Date Out	No days	Processed	Reasoning behind not processing
22	Bawden	49.307	-126.011	WCVI	5-Apr-07	23-Oct-07	201	Yes	
	Mosquito Creek	49.314	-123.090	SOG	25-Apr-07	19-Sep-07	147	No	area densely sampled
	Ross Pass	49.323	-126.048	WCVI	5-Apr-07	23-Oct-07	201	No	settlement arrays hung too deep
23	Deep Cove	49.328	-122.947	SOG	25-Apr-07	19-Sep-07	147	Yes	
24	French Creek	49.349	-124.356	SOG	15-May-07	10-Oct-07	148	Yes	
25	Millar Channel	49.375	-126.092	WCVI	4-Apr-07	23-Oct-07	202	Yes	
26	Horseshoe Bay	49.375	-123.273	SOG	25-Apr-07	19-Sep-07	147	Yes	
27	Gibson's	49.401	-123.505	SOG	10-May-07	12-Oct-07	155	Yes	
	Dixon Bay	49.403	-126.151	WCVI	1-May-07	23-Oct-07	175	No	settlement arrays hung incorrectly
28	Salten	49.615	-123.833	SOG	1-May-07	12-Oct-07	164	Yes	
29	Muchalat	49.640	-126.325	WCVI	1-May-07	16-Oct-07	168	Yes	
30	Newcomb Pt	49.641	-123.659	SOG	1-May-07	12-Oct-07	164	Yes	
	Salmon Inlet	49.645	-123.724	SOG	1-May-07	12-Oct-07	164	No	levels B and C missing
31	Atrevida	49.655	-126.454	WCVI	1-May-07	16-Oct-07	168	Yes	
	Williamson Passage	49.656	-126.428	WCVI	1-May-07	16-Oct-07	168	No	settlement arrays hung incorrectly
32	Hanna	49.676	-126.474	WCVI	19-Apr-07	26-Oct-07	190	Yes	
33	Plumber Harbour	49.690	-126.629	WCVI	22-Apr-07	12-Nov-07	204	Yes	
34	Powell River	49.835	-124.530	SOG	23-May-07	11-Oct-07	141	Yes	
35	Okeover Inlet	50.018	-124.713	JS	19-Apr-07	11-Oct-07	175	Yes	
36	Trevennen Inlet 1	50.027	-124.749	JS	19-Apr-07	11-Oct-07	175	Yes	
	Trevennen Inlet 3	50.027	-124.749	JS	19-Apr-07	11-Oct-07	175	No	settlement arrays hung too deep
37	Trevennen Inlet 2	50.027	-124.749	JS	19-Apr-07	11-Oct-07	175	Yes	
38	CR	50.034	-125.245	JS	22-May-07	10-Oct-07	141	Yes	
	Thors cove	50.060	-124.709	JS	19-Apr-07	11-Oct-07	175	No	settlement arrays hung too deep
39	Cortes Island	50.094	-125.014	JS	13-May-07	20-Sep-07	130	Yes	
40	Brent Island	50.119	-125.334	JS	5-May-07	24-Oct-07	172	Yes	
	Church Point	50.183	-124.767	JS	19-Apr-07	11-Oct-07	175	No	levels A and B damaged and most Petri dishes gone
41	Allies Isl	50.200	-124.800	JS	19-Apr-07	11-Oct-07	175	Yes	

No	Site	GPS N	GPS S	Area	Date In	Date Out	No days	Processed	Reasoning behind not processing
42	Cyrus Rks	50.256	-125.213	JS	9-Apr-07	02-Oct-07	176	Yes	
43	Venture Pt	50.305	-125.360	JS	2-May-07	24-Oct-07	175	Yes	
44	Sonora Isl	50.312	-125.315	JS	9-Apr-07	02-Oct-07	176	Yes	
45	Raza	50.320	-125.005	JS	27-Apr-07	24-Oct-07	180	Yes	
46	Broughton Pt	50.373	-125.382	JS	9-Apr-07	02-Oct-07	176	Yes	
47	Thurlow Pt	50.411	-125.339	JS	9-Apr-07	02-Oct-07	176	Yes	
48	Koskimo	50.457	-127.894	WCVI	14-Mar-07	10-Oct-07	210	Yes	
	Farside	50.489	-125.273	JS	9-Apr-07	02-Oct-07	176	No	settlement arrays hung too deep
49	Thorpe	50.577	-127.606	WCVI	11-Apr-07	10-Oct-07	182	Yes	
50	Swanson	50.619	-126.708	JS	17-Apr-07	03-Oct-07	169	Yes	
51	Potts Bay	50.649	-126.617	JS	17-Apr-07	03-Oct-07	169	Yes	
52	Doctor Isl	50.652	-126.289	JS	17-Apr-07	03-Oct-07	169	Yes	
53	Port Eliz	50.669	-126.478	JS	17-Apr-07	03-Oct-07	169	Yes	
54	Arrow Passage	50.708	-126.666	JS	17-Apr-07	03-Oct-07	169	Yes	
55	Wicklow	50.787	-126.690	JS	17-Apr-07	03-Oct-07	169	Yes	
	Burdwood	50.799	-126.496	JS	22-Apr-07	01-Nov-07	193	No	area densely sampled
56	Doyle	50.815	-127.485	JS	25-Apr-07	11-Oct-07	169	Yes	
	Sir Edmund Bay	50.830	-126.594	JS	18-Apr-07	01-Nov-07	197	No	levels A damaged
57	Bell Isl	50.833	-127.522	JS	25-Apr-07	11-Oct-07	169	Yes	
	Cliff Bay	50.834	-126.501	JS	25-Apr-07	01-Nov-07	190	No	area densely sampled
58	Cypress H.	50.838	-126.665	JS	22-Apr-07	01-Nov-07	193	Yes	
	Maude Island	50.855	-126.755	JS	24-Apr-07	01-Nov-07	191	No	area densely sampled
59	Bella Bella 1	52.154	128.124	NC	10-May-07	19-Dec-07	223	Yes	
60	Louscoone Inlet	52.167	-131.216	QCI	13-Jun-07	28-Sep-07	107	Yes	
61	Bella Bella 2	52.194	-128.150	NC	10-May-07	19-Dec-07	223	Yes	
62	Skincuttle Inlet	52.312	-131.258	QCI	12-Jun-07	27-Sep-07	107	Yes	
63	Jackson Pass	52.537	-128.395	NC	15-Mar-07	21-Oct-07	220	Yes	
	Cumshewa Inlet	53.025	-131.912	QCI	10-Jun-07	26-Sep-07	108	No	levels B and C missing
64	Barnard Harbour	53.067	-129.100	NC	18-May-07	15-Sep-07	120	Yes	
	Skidegate Landing	53.079	-132.011	QCI	4-May-07	27-Sep-07	146	No	settlement arrays hung incorrectly
	Queen Charlotte	53.085	-132.071	QCI	4-May-07	27-Sep-07	146	No	settlement arrays hung incorrectly

No	Site	GPS N	GPS S	Area	Date In	Date Out	No days	Processed	Reasoning behind not processing
65	Skidegate Channel	53.191	-132.087	QCI	9-Jun-07	24-Sep-07	107	Yes	
66	Sandspit	53.238	-131.862	QCI	9-Jun-07	24-Sep-07	107	Yes	
67	Shields Bay	53.309	-132.419	QCI	14-Jun-07	04-Oct-07	112	Yes	
	Kiltuish Inlet	53.383	-128.492	NC	12-Jun-07	25-Oct-07	135	No	levels A damaged
68	Union Pssg	53.410	-129.438	NC	12-Jun-07	25-Oct-07	135	Yes	
69	Hartley Bay	53.417	-129.200	NC	19-May-07	14-Sep-07	118	Yes	
70	Kitkatla	53.795	-130.439	NC	28-May-07	13-Oct-07	138	Yes	
71	Captain Cove	53.811	-130.023	NC	28-May-07	18-Oct-07	143	Yes	
72	Oona River	53.943	-130.249	NC	7-Jun-07	18-Oct-07	133	Yes	
73	Kitimat	53.987	-128.656	NC	12-Jun-07	25-Oct-07	135	Yes	
74	Masset Slough	54.007	-132.141	QCI	1-Jun-07	14-Oct-07	135	Yes	
75	Hunt Inlet	54.069	-130.445	NC	29-May-07	19-Oct-07	143	Yes	
76	Port Edward	54.225	-130.293	NC	6-Jun-07	20-Oct-07	136	Yes	
77	Fairview/Pt Henry	54.294	-130.354	NC	6-Jun-07	19-Oct-07	135	Yes	
78	Seal Cove 'N'	54.331	-130.279	NC	4-Jun-07	09-Oct-07	127	Yes	
79	Dundas	54.613	-130.879	NC	26-May-07	24-Oct-07	151	Yes	
80	Palmerville	54.696	-130.114	NC	22-May-07	18-Sep-07	119	Yes	
81	Anyox	55.419	-129.814	NC	23-May-07	30-Sep-07	130	Yes	

## Collection

At each site the settlement arrays were pulled slowly out of the water and laid down with the Petri dish side of each lid facing up. Notes were made on large motile species present, the number of arrays still present at each site, and any damage to each lid and/or Petri dish. Each settlement array had three lid depths; an A level at 15 cm below the surface, then B and C levels at 1 and 2 meter intervals below A respectively (Figure 1.1b). Photographs of the entire lid and each of the four individual Petri dishes were taken for all three depths of each settlement array. All four Petri dishes were then cut away from the lid and placed in a large Ziploc bag with corresponding line and depth labels. The Ziploc bags were then filled with 3.7% formaldehyde (in filtered seawater) solution, placed in large buckets, and transported to the laboratory for further processing.

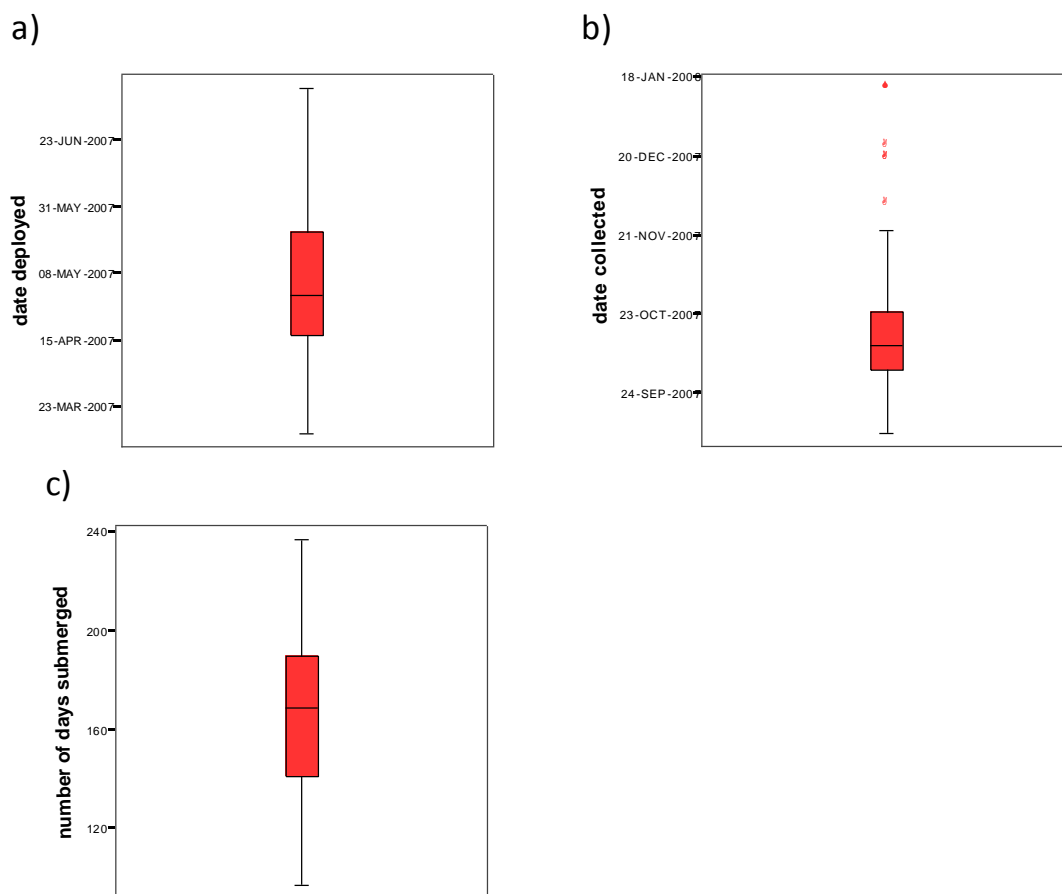
## Timing

There were many individuals and organizations involved with this project. As a result there was some variability in deployment and collection dates for each site, and consequently, the number of days each settlement array remained submerged (Table 1).

The settlement arrays were deployed between March 14, 2007 and July 12, 2007. The mean date of deployment was May 3, 2007 and the median date was April 30, 2007. There was almost a four month spread of the dates of deployment, though none of these dates were outliers (Figure 3a). The Ladysmith location was not deployed until July 12, 2007 and the next closest date was for Shields Bay on June 14, 2007 (Table 1). The Ladysmith site alone added almost an extra month to the spread of deployment dates.

The settlement arrays were collected between September 10, 2007 and January 14, 2008. The mean date of collection was October 16, 2007 and the median was October 12, 2007. There was a span of almost four months during which settlement structures were collected. This time, however, a box and whisker plot of the data indicated five (two sites with the same date) outliers (Figure 3b). These outliers are for the sites Sarita (collected January 14, 2008), Friday Harbor (December 23, 2007), Bella Bella #1 and 2 (December 19, 2009) and Ladysmith (December 2, 2007) (Table 1).

The number of days the arrays remained submerged in the water column ranged from 92 to 237 days. The mean number of days submerged was 166 and the median was 169. Though the number of days submerged spans a range of 137 days, there are no outliers (Figure 3c). Port Renfrew was the only sites submerged for less than 100 days (97). Sarita and Friday Harbor (234 and 237 respectively) were the sites left submerged the longest. In contrast to the data for the deployment and collection dates, the Ladysmith site does not fall out at either end of the spectrum for the number of days submerged (143 days) (Table 1).



**Figure 3. Box and whisker plot of a) the dates of deployment, b) the date of collection, and c) the number of days submerged for the settlement arrays. The top, bottom, and line through the middle of the box correspond to the 75th percentile (top quartile), 25th percentile (bottom quartile), and 50th percentile (median), respectively. The whiskers indicate the upper and lower values not classified as statistical outliers. Points indicate outliers (more than 1.5 times the interquartile range away the bottom or top quartile).**

### **Sample selection**

Eighty-one settlement array sites were processed. Some of the arrays were not processed because at that site, either the arrays were not hung properly or they became damaged. Time constraints were also an additional factor and areas that had a dense number of sampling sites (*e.g.* Johnstone Strait- Figure 1.2a) were sampled haphazardly (dependent on order encountered in each bucket). Though we deployed two settlement arrays at each site, often only one was collected. Therefore, only one settlement array

was processed for each site. If two settlement arrays were collected from a site, I would consult my notes to choose the array that had been hung properly and was not damaged. If both arrays were clear on both points, I processed the first line encountered with all three levels when going through the buckets. I noted during the collection where it was probable that not all arrays had been hung in sufficiently deep water, allowing the C level lid to possibly contact the benthos at low tides. This factor, again coupled with time constraints, lead to the decision to only process the top two levels.

Only one of the four Petri dishes from each depth was processed. The Petri dish selected was not determined randomly. Damaged or broken Petri dishes were not used. I inspected the undamaged Petri dishes to select which one best represented the community. This does not mean that the Petri dish with the highest diversity was chosen. I did a quick assessment of the species present, their rough coverage, and the percent free space available and I selected the Petri dish that seemed to best represent the average of all three characteristics. If Petri dishes seemed equivalent based on these characteristics then I also looked for the presence of non-native organisms as determining non-native species distributions along the coast was a secondary focus of the survey. With all of these factors taken into account I selected what I determined to be the best representative sample for this study. If all of the Petri dishes looked the same after the quick visual inspection I would select one randomly.

### **Sample processing**

The Petri dish was transferred to a large glass bowl containing filtered seawater to dilute any residual formaldehyde solution. Prior to processing the Petri dish was lifted from the glass bowl and photographed.

Processing involved indentifying all macrofauna (> 1mm) present on the Petri dish to the lowest taxonomic level possible and calculating their relative abundances. I used a grid overlay to estimate percent space coverage for each sessile organism and individual counts were used to calculate motile species abundance. The grid overlay was printed on a transparency sheet and I counted the number of grid squares occupied by all sessile species, to the nearest 0.5. This number was divided by the total number of grid space to give a rough percent cover (rounded to the nearest 0.5%) of the Petri dish. Overgrowing species were removed if needed, thus the total coverage could exceed 100%. Any motile

species encountered were identified and counted. The processed Petri dish and organisms were placed in a Whirl pack and preserved with 75% ethanol. The filtered seawater, now containing suspended organisms, was then passed through a 500  $\mu\text{m}$  sieve. Any motile organisms collected in the sieve were identified and counted. Meiofauna taxa such as nematodes, harpacticoid copepods, and ostracods were not included because they were inadequately sampled by the 500  $\mu\text{m}$  mesh screen and therefore were not considered part of the macrofauna.

Several sources were used to identify the invertebrate species; the two main identification keys used were Marine Invertebrates of the Pacific Northwest (Kozloff 1996) and the Light and Smith Manual: Intertidal Invertebrates from Central California to Oregon (Carlton 2007). Organisms that I was unable to identify to species level were placed in small glass vials in 75% ethanol to be identified at a later date. Further identification and confirmation came from Biologica (small macrofauna), Will Duguid (crustaceans), Dave Denning (bryozoans), Henry Reiswig (sponges), and Lisa Kirkendale (bivalves). Large motile species noted in the field, or through reviewing the photographs, were only considered during any presence/absence analysis of species. Some species identifications and abundances were confirmed or adjusted by reviewing the original field photos (*e.g.* sponge colouration).

There are no data on algae included in this study. Algae were not common in the communities growing on the Petri dishes. If present, the algae were usually microalgae in the form of a slight film consisting primarily of diatoms and their identity and abundances were not calculated. At two sites (Sonora and Friday Harbor) red filamentous algae and thin red blade algae were present. Their abundances were less than five percent coverage. I decided to omit them from any analysis and focus this study on examining only the invertebrate community.

## **Data**

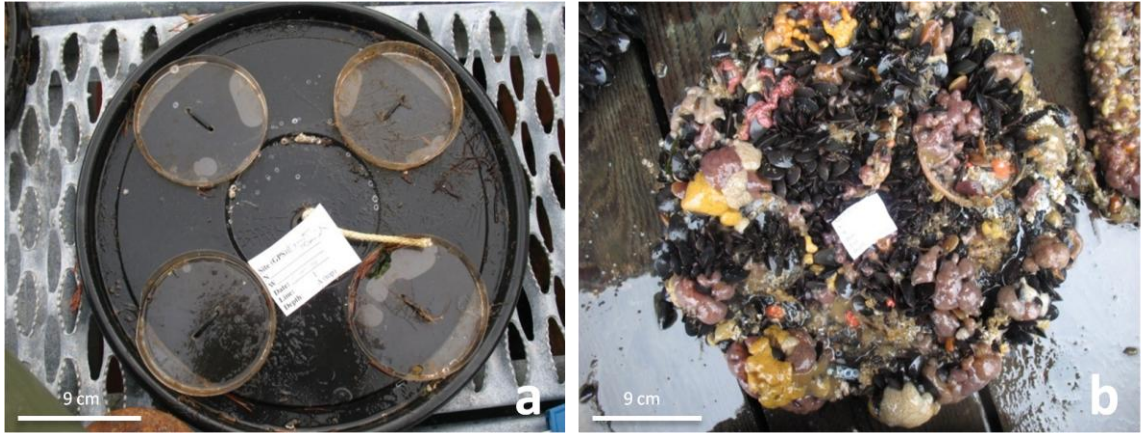
Each organism present in a sample was identified to the lowest taxonomic level possible, usually to the species level. There were, however, some exceptions that should be noted. Some organisms were only resolved to the genus level but were treated as a separate species. In the flatworm and amphipod taxa there were occasionally two species that were difficult to distinguish from each other and which were thus designated as a

species complex. For describing the species present on the BC coast, these species were acknowledged separately, but for all other analyses the complex were considered as one species unit. Additionally, some organisms were damaged and/or were small juveniles that we were unable to resolve to the genus and species level. These unresolved organisms were classified into higher taxonomic levels that may contain more than one species, but were treated as a single unit in all analyses.

## **Results**

### **General description of settlement arrays**

Mussels, barnacles, hydroids, bryozoans, tunicates, and sponges were well represented sessile organisms in these fouling communities. However, the abundances of these taxa varied from site to site, and often from depth to depth. Some lines had almost no growth or settlement of species visible while others had organisms forming several overgrowing tiers (Figure 4). Sometimes there was a complete dominance by one species (often mussels) covering an entire lid or array while at other times there would be a whole cornucopia of organisms (Figure 5). Even within a single settlement array, there was no consistent description of what I saw. At many sites, levels A, B, and C looked like replicas of each other with all levels having similar species composition and abundances (Figure 6). At other sites, all levels could be visually different from each other in terms of species composition, their abundance, and the percent free space visible (Figure 7).



**Figure 4. Coverage of invertebrate growth on settlement arrays. a) Brent Island (Johnstone Strait-JS) showing minimal growth of some barnacles and hydroids. b) Sooke (Juan de Fuca Strait) showing the growth of numerous invertebrate species, some growing on top of one another. The initial bryozoans and barnacles are being overgrown by mussels, which are in turn being overgrown by tunicate species.**



**Figure 5. Variety of invertebrate growth on settlement arrays. a) Deep Cove (Strait of Georgia-SOG) showing a monopoly growth of mussels. b) Burdwood (JS) showing the growth of numerous invertebrate species (and classes). Some of organisms visible on the array include serpulids, barnacles, mussels, hydroids, bryozoans, juvenile seastars, and urchins.**



**Figure 6. Similarity of invertebrate growth on settlement arrays. Arrow Passage (JS) is shown here depicting how similar each of the a) surface (A), b) one meter depth (B), and c) two meter depth (C) can be. The *Ulva* sp. algae viewed in c) are actually attached to the top of the settlement array lid.**



**Figure 7. Differences in invertebrate growth on settlement arrays. French Creek (SOG) is shown here depicting the variation seen among the a) surface (A), b) one meter depth (B), and c) two meter depth (C).**

Despite the variation observed, I identified one general community assemblage that appeared the most frequently along most of the coast: the mussel community. Frequently barnacles and bryozoans had recruited to the settlement arrays first and were found underneath the mussels covering the Petri dishes. Hydroids, sponges, and tunicates also frequently grew amongst or on the mussels. A few motile species, such as caprellids and polychaetes, were associated with this community but were harder to see and identify in the field and were subsequently identified back at the laboratory.

Although algae often grew on the tops of the lids of the settlement arrays, they were almost never seen growing attached to the undersides of the lids. Sediment occasionally accumulated on the tops of the lids, smothering some of the organisms, but did not appear to affect the community growing on the underside of the lids.

## Species recruiting to settlement arrays

### Taxonomic distribution of the identified species

A total of 171 species representing 90 families and 10 phyla were identified from the settlement arrays at 81 sites along the BC coast (Table 2). Annelid polychaetes represented the most species: 30.2% of all the species identified. Motile malacostracan arthropods and the sessile bryozoans were the next best represented classes accounting for 21.5% and 13.4% of the species identified respectively. Ascidians were also prominent in this study and represented 7.6% of all species identified. The calcareous sponge, anoplanid nemertean, oligochaete, pycnogonid, and echinoid classes were each represented by a single species. Table 1.2 contains information only on the organisms that we were able to resolve to at least the family level.

### Species list

In examining newly settled invertebrate fouling communities along the BC coast, two components of the community were considered: the sessile organisms that use and compete for available space, as well as the motile species that inhabit them. As such, the list of species is divided into two groups, sessile and motile, reflecting the two lifestyles.

### Sessile species

Of the sessile invertebrates identified, there were 66 resolved species and an additional seven categories of unresolved higher taxonomic categories (Table 3). The sessile species were primarily represented by bryozoans and tunicates (23 and 13 species respectively). Eleven of the 66 identified sessile species, or 16.7%, were introduced or cryptogenic species to BC. Introduced and cryptogenic sessile species were prevalent in the sponge (50%), tunicate (31%), and bryozoa (17%) phyla.

It was difficult to identify the sponges to species level in this study. The formalin used to fix the communities removed most of the colour from the sponges and the transport often squished the organisms' structure. Both the colour and the structure of a sponge are important characters used in biological keys (Carlton 2007, Kozloff 1996). The species complex *Halichondria* spp. identified in this study likely includes the cryptogenic sponge *H. bowerbanki*. *H. bowerbanki* was likely transported from the Atlantic coast and has a similar form to the native species but a different larval type (Kozloff 1996). *H.*

*bowerbanki* is commonly found on floating docks and pilings (Carlton 2007, Lamb and Hanby 2005) and was found by Lu *et al.* (2007) during their survey of five BC ports.

The *Metridium* sp. in this study is likely *M. senile* which prefers shallower habitats than that of its sibling *M. giganteum* (Lamb and Hanby 2005). *M. senile* is also common on docks, pilings, and rock jetties (Carlton 2007) and has been identified by Nydam and Stachowicz (2007), Greene *et al.* (1983) and Greene and Schoener (1982) in the epibenthic communities of their studies.

In BC we have a *Mytilus* complex that consists of the native mussel *M. trossulus*, two introduced species *M. edulis* and *M. galloprovincialis*, and hybrids these species. These *Mytilus* sibling species and their hybrids can no longer be reliably distinguished based on morphological features and must be analysed genetically to determine their identity and origin (Wonham 2004). For this study we did not have the time or resources to analyse each site genetically so I simply refer to mussels as the *Mytilus* sp., though the complex likely includes the two introduced species.

#### Motile species

Of the motile invertebrates identified, there were 105 resolved species and an additional 27 unresolved higher taxonomic categories (Table 3). The motile species were primarily represented by annelids and arthropods (41 and 38 species respectively). There were a disproportionately high number of unresolved categories for the motile molluscs (six species identified, seven unresolved categories). Twelve of the 105 motile species identified, or 11%, were introduced and cryptogenic species. Motile non-native species were the most prevalent in the annelid (17%) and arthropod (13%) phyla. In total, introduced and cryptogenic species account for 13.5 % of all the species identified from the settlement arrays.

There were a lot of juvenile organisms on the settlement arrays. Because many of these species were small and/or many of their defining characteristics had not yet developed I was unable to resolve them to species level. This was particularly evident for the mollusc and echinoderm phyla. As a result there may be a slight under representation of the diversity possible for those phyla. Organisms were sent out for identification to experts and occasionally these were still not resolved to species level. I believe that most

of the juvenile sea stars were *Pisaster ochraceus* but there was no consensus from the multiple experts.

**Table 2. The taxonomic composition of the identified invertebrate species living on settlement arrays along the BC coast in 2007.**

<b>Phylum and Class</b>	<b>No of Families</b>	<b>No of Species</b>
<b>Porifera</b>		
Demospongiae	3	3
Calcarea	1	1
<b>Cnidaria</b>		
Hydrozoa	2	4
Anthozoa	2	2
<b>Platyhelminthes</b>		
Turbellaria	6	8
<b>Nemertea</b>		
Enopla	3	5
Anoplana	1	1
<b>Mollusca</b>		
Bivalvia	4	4
Gastropoda	6	6
<b>Annelida</b>		
Polychaeta	14	52
Oligochaeta	1	1
<b>Arthropoda</b>		
Crustacea (subclass Cirripedia)	3	4
Crustacea (subclass Malacostraca)	20	37
Pycnogonida	1	1
<b>Bryozoa</b>		
Gymnolaemata	11	23
<b>Echinodermata</b>		
Asterioidea	1	3
Echinoidea	1	1
Holothuroidea	2	2
<b>Chordata (subphylum Tunicata)</b>		
Ascidiacea	8	13
<b>Total</b>	<b>90</b>	<b>171</b>

**Table 3. Invertebrate organisms identified from the settlement arrays deployed along the BC coast. Represented beside each phylum name is the number of introduced and cryptogenic species/total number of species for the phylum. Unresolved taxa are described to the lowest taxonomic level and accompanied by and INDET (indetermined) designation.**

SESSILE SPECIES			
PORIFERA(2/4)			
<i>Halichondria</i> spp. <sup>4</sup>	<i>Cliona</i> spp. <sup>1</sup>	<i>Haliclona</i> sp. <sup>4</sup>	<i>Leucosolenia nautilia</i> <sup>3</sup>
Demospongiae INDET			
CNIDARIA (1/6)			
<i>Clytia</i> sp.	<i>Orthopyxis</i> spp.	<i>Obelia dichotoma</i> <sup>3</sup>	<i>Plumularia</i> sp.
Hydrozoa INDET	<i>Metridium</i> sp.	<i>Anthopleura artemisia</i>	Actiniidae INDET
ANNELIDA (0/12)			
<i>Schizobranchia insignis</i>	<i>Eudistylia vancouveri</i>	<i>Chone infundibuliformis</i>	<i>Pseudopotamilla nr. intermedia</i>
Sabellidae INDET	<i>Serpula columbiana</i>	<i>Crucigera irregularis</i>	<i>Crucigera zygophora</i>
<i>Pseudochitinopoma occidentalis</i>	<i>Circeis armoricana</i>	<i>Paralaeospira malardi</i>	<i>Pileolaria (Simplicaria) potswaldi</i>
<i>Jugaria quadrangularis</i>	Spirorbinae INDET		
ARTHROPODA (0/4)			
<i>Balanus crenatus</i>	<i>Balanus</i> sp.	<i>Semibalanus cariosus</i>	<i>Chthamalus dalli</i>
MOLLUSCA (0/4)			
<i>Mytilus</i> sp. <sup>2</sup>	<i>Hiatella arctica</i>	<i>Pododesmus macrochisma</i>	<i>Kellia suborbicularis</i>
BRYOZOA (4/23)			
<i>Schizoporella japonica</i> <sup>1</sup>	<i>Porella concinna</i>	<i>Alcyonidium polyoum</i> <sup>1</sup>	<i>Bowerbankia gracilis</i> <sup>3</sup>
<i>Cryptosula pallasiana</i> <sup>3</sup>	<i>Callopora horrida</i>	<i>Callopora armanata</i>	<i>Ellisina levata</i>
<i>Tegella armifera</i>	<i>Lichenopora</i> sp.	<i>Disporella fimbriata</i>	<i>Membranipora membranacea</i>
<i>Conopeum reticulum</i>	<i>Scrupocellaria varians</i>	<i>Bugula californica</i>	<i>Bugula pugeti</i>
<i>Bugula pacifica</i>	<i>Bugula</i> sp. (juv)	<i>Caulibugula californica</i>	<i>Dendrobeatia lichenoides</i>
<i>Tubulipora pacifica</i>	<i>Cheilopora praelonga</i>	<i>Cheilopora annulata</i>	Gymnolaemata INDET
TUNICATA (4/13)			
<i>Botrylloides violaceus</i> <sup>1</sup>	<i>Botryllus schlosseri</i> <sup>1</sup>	<i>Styela clava</i> <sup>1</sup>	<i>Styela</i> sp. (juv)
<i>Cnemidocarpa finmarkiensis</i>	<i>Molgula manhattensis</i> <sup>1</sup>	<i>Ascidia</i> sp.	<i>Corella inflata</i>
<i>Chelyosoma productum</i>	<i>Aplidium californicum</i>	<i>Halocynthia igaboja</i>	<i>Diplosoma listerianum</i>
<i>Distaplia occidentalis</i>	Asciacea INDET		
MOTILE SPECIES			
NEMERTEA (0/6)			
<i>Emplectonema gracile</i>	<i>Paranemertes peregrina</i>	<i>Tetrastemma candidum</i>	<i>Tetrastemma</i> sp.
<i>Amphiporus imparispinosus</i>	<i>Cerebratulus californiensis</i>	Nemertea INDET	

PLATYHELMINTHES (0/8)			
<i>Pseudoceros canadensis</i>	<i>Notoplana sanguinea</i>	<i>Leptoplana chloranota</i>	<i>Stylochus exiguus</i>
<i>Acerotisa</i> sp.	<i>Triplana viridis</i>	<i>Triplana</i> sp.	<i>Notocomplana</i> sp.
Leptoplanidae INDET	Plehniidae INDET	Polycladida INDET	
ANNELIDA (7/41)			
<i>Syllis (Syllis)elongata</i>	<i>Typosyllis adamanteus</i>	<i>Typosyllis nr. fasciata</i>	<i>Typosyllis hyalina</i>
<i>Typosyllis alternata</i> <sup>3</sup>	<i>Eusyllis blomstrandii</i>	<i>Eusyllis habeii</i>	<i>Proceraea cornutus</i>
<i>Odontosyllis phosphorea</i>	<i>Exogone dwisula</i>	<i>Typosyllis</i> sp.	Syllidae INDET
<i>Eulalia quadrioculata</i>	<i>Mystides borealis</i>	<i>Clavadoce</i> sp.	<i>Eteone</i> sp.
Phyllodocidae INDET	<i>Harmothoe imbricata</i>	<i>Harmothoe</i> sp.	<i>Halosydna brevisetosa</i>
<i>Lepidonotus squamatus</i>	<i>Lepidonotus</i> sp.	Polynoidae INDET	<i>Chrysopetalum occidentale</i>
<i>Palaenotus bellis</i>	<i>Nereis vexillosa</i>	<i>Nereis procera</i>	<i>Platynereis bicanaliculata</i> <sup>3</sup>
<i>Nainereis quadricupsida</i>	<i>Nereis</i> sp.	<i>Capitella</i> sp. <sup>3</sup>	<i>Armandia brevis</i>
<i>Ophelina</i> sp.	Opheliidae INDET	<i>Boccardia columbiana</i> <sup>3</sup>	<i>Polydora cornuta</i> <sup>1</sup>
<i>Polydora nr. limicola</i> <sup>3</sup>	<i>Polydora websteri</i> <sup>3</sup>	<i>Polydora</i> sp.	<i>Prionospio lighti</i>
<i>Ophiobromus pugettensis</i>	<i>Ophiobromus pugettensis</i>	<i>Micropodarke dubia</i>	Hesionidae INDET
Spionidae INDET	<i>Dorvillea annulata</i>	Terebellidae INDET	Polychaeta INDET
<i>Glycera nana</i>	<i>Dorvillea annulata</i>		
<i>Paranais litoralis</i>	Oligochaeta INDET		
ARTHROPODA (5/38)			
<i>Photis</i> sp.	<i>Podocerus cristatus</i>	<i>Locustogammarus levingsi</i>	<i>Jassa staudei</i>
<i>Jassa</i> sp.	<i>Americorophium brevis</i>	<i>Monocorophium acherusicum</i> <sup>1</sup>	<i>Monocorophium</i> sp.
Corophiidae INDET	<i>Ischyrocerus pelagops</i>	Ischyroceridae INDET	<i>Melita nitida</i> <sup>1</sup>
<i>Desdimelita californica</i>	<i>Gnathopleustes pugettensis</i>	<i>Eogammarus oclairi</i>	<i>Paramoera columbiana</i>
<i>Aoroides columbiana</i>	<i>Aoroides</i> sp.	Pleustidae INDET	Gammaridea INDET
<i>Caprella alaskana</i>	<i>Caprella penantis</i> <sup>3</sup>	<i>Caprella laeviuscula</i>	<i>Caprella anomala</i>
<i>Caprella mutica</i> <sup>1</sup>	<i>Caprella</i> sp. (juv)	<i>Zeuxo normani</i>	<i>Leptocheilia savignyi</i> <sup>3</sup>
<i>Ianiropsis analoga</i>	<i>Gnorimosphaeroma oregonense</i>	<i>Munna fernaldi</i>	<i>Munna</i> sp.
<i>Idotea</i> sp.	<i>Heptacarpus brevirostris</i>	<i>Eualus lineatus</i>	<i>Pandalus danae</i>
Caridea INDET	<i>Hemigrapsus oregonensis</i>	<i>Cancer magister</i>	<i>Cancer gracilis</i>
<i>Cancer productus</i>	<i>Cancer</i> sp.	<i>Anoplodactylus viridintestinalis</i>	Arthropoda INDET
MOLLUSCA (0/6)			
Mopaliidae INDET	<i>Lirularia</i> sp.	<i>Alia tuberosa</i>	Pyramidellidae INDET
Gastropoda INDET	<i>Onchidoris bilamellata</i>	<i>Hermisenda crassicornis</i>	<i>Aeolidia papillosa</i>
Dendronotacea INDET	Doridacea INDET	Aeolidacea INDET	Nudibranchia INDET
<i>Lottia</i> sp.			

ECHINODERMATA (0/6)			
	<i>Pycnopodia</i>		<i>Strongylocentrotus</i>
<i>Pisaster ochraceus</i>	<i>helianthoides</i>	<i>Evasterias troschelii</i>	<i>droebachiensis</i>
	<i>Parastichopus</i>		
<i>Cucumaria miniata</i>	<i>californicus</i>	Juvenile seastars	Holothuriodea INDET

<sup>1</sup>Introduced species, <sup>2</sup>Complex likely includes introduced, <sup>3</sup>Cryptogenic species, <sup>4</sup>Complex likely includes cryptogenic.

### Richness per sample

Species richness ranged from one to 29 species present, with the average being roughly 12 species per sample (Table 4). The Kitimat (north coast mainland-NC) samples had the lowest richness while the Koskismo (WCVI) and Jackson Pass (NC) surface samples (A) had the highest. The sessile and motile groups were each represented by roughly six species per sample, though the number of sessile species observed ranged from 1 to 15 per sample, and the motile species from 0 to 16. Cryptogenic species accounted for anywhere from zero to four of these species with an average of less than one (0.7) species per sample. Introduced species ranged from zero to six species with an average of more than one (1.25) introduced species per sample. Thetis A and Telegraph B had strongest representation of introduced species.

**Table 4. The average, standard deviation (Std Dev), and range (Max and Min) for the number of sessile, motile, invasive, and total number of species per sample.**

	All Sessile	All Motile	Total	Cryptogenic	Introduced
<b>Average</b>	5.83	6.01	11.83	0.69	1.25
<b>Std Dev</b>	3.41	3.74	5.99	0.84	1.26
<b>Max</b>	15	16	29	4	6
<b>Min</b>	1	0	1	0	0

### Relative abundances of species

#### Community homogeneity

Evenness is considered an important dimension of species diversity and is simply a measure of how similar species are in their abundances (Magurran 2004). I looked at the evenness of the community using rank abundance plots where each sessile and motile species was ranked separately based on their average abundances (percent cover for sessile and number of individuals for motile) across all samples.

The curve produced by the rank abundance plot for the sessile invertebrates begins with a steep slope that shallows out to produce a long tail comprised of numerous species with a relatively low abundance (Figure 8). The steepness of the slope can be largely attributed to the *Mytilus* sp. complex which has a significantly higher abundance than the next two most abundant species, *Balanus crenatus* and *Obelia dichotoma*. When averaged across all samples most species show little variability. The largest variability is seen for the first few rank species. *Mytilus* sp. has the largest variability with a standard error range of 3.3%. *B. crenatus*, *O. dichotoma*, *Alcyonidium polyoum*, and *Clytia* sp. are the only remaining species with standard error ranges of over 1%.

The abundance distribution for motile species was similar to that produced for sessile organisms (Figure 9). The steepness of the slope of the rank abundance plot can be largely attributed to the Amphipod complex 2 (*Gnathopleustes pugettensis* and *Eogammarus oclairi*). Though there was little variability observed in the tail of the curve, all other organisms displayed a relatively larger degree of variation than their sessile counter parts. The organisms with the largest variability are Amphipod complex 2 and *Caprella laeviscula* with standard error ranges of 1.7 and 1.4 respectively.

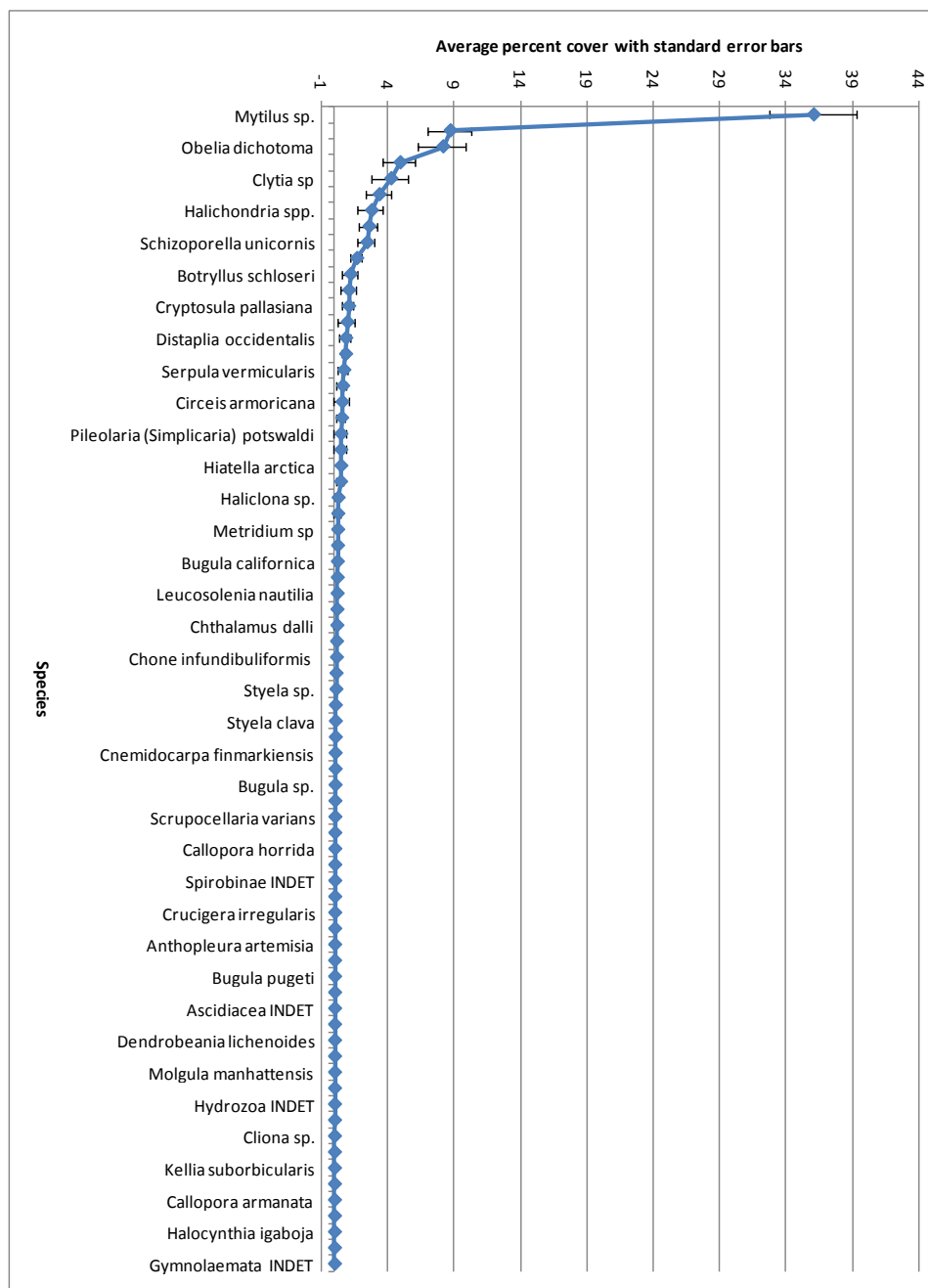
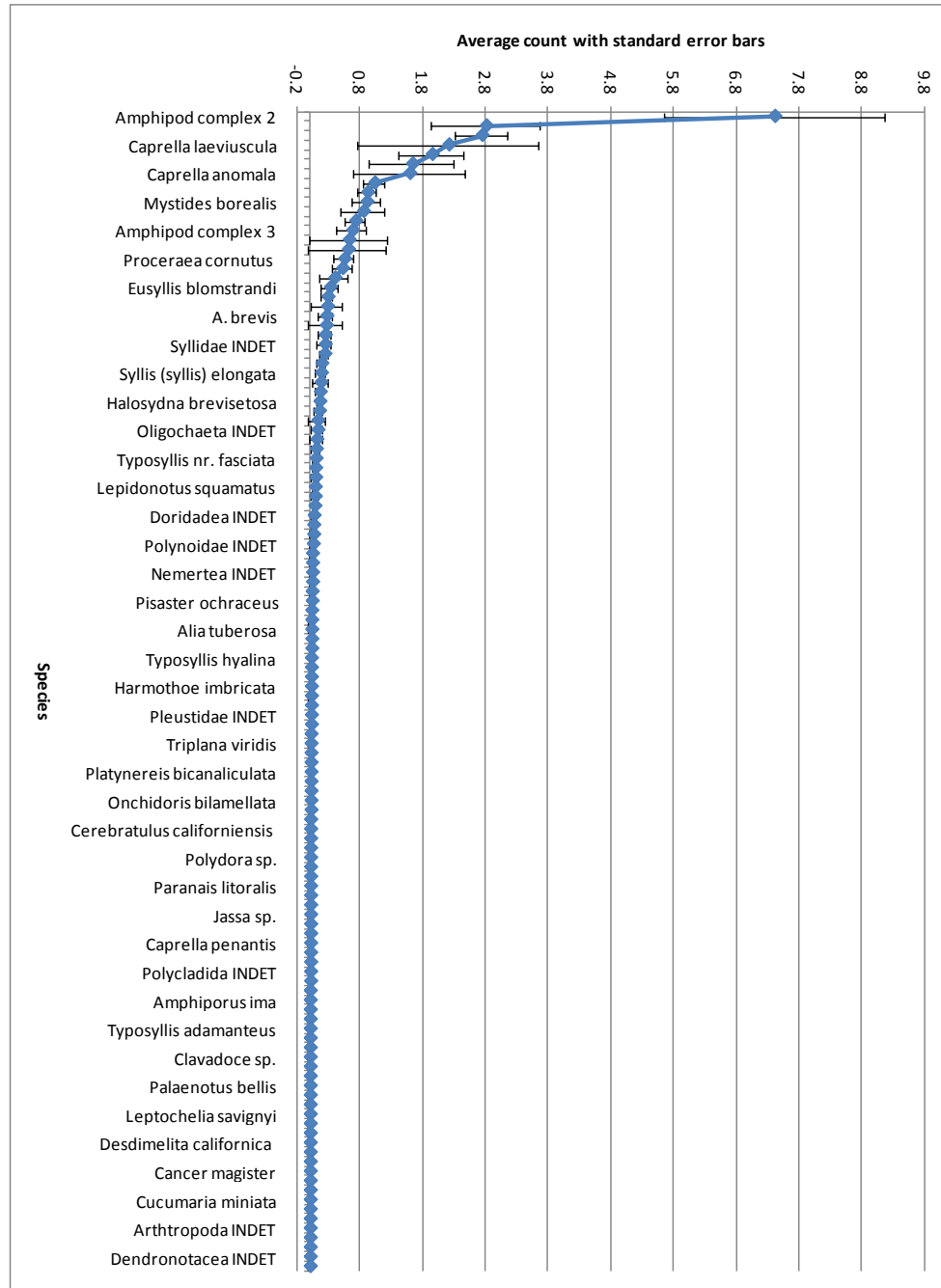


Figure 8. Rank abundance plot for all sessile organisms.



**Figure 9. Rank abundance plot for all motile organisms.**

#### Dominant species

The dominant species in this study were described both in terms of abundance within the community and in terms of distribution (number) in the samples. The dominant species were the top ten ranked species in both categories (abundance and distribution). Consequently, in the abundance data these are the species that comprise the slope of the

rank abundance curve. Additionally, for the abundance data, any species whose average abundance was not statistically different (standard errors of the means overlap) from the previous top ten species abundance was also considered dominant.

The top ten dominant sessile species, in terms of abundance, were the only species with average abundances per sample greater than one percent (Figure 8 and Table 5). They represent roughly 20.5% (15/73) of all the sessile species. The most dominant species was *Mytilus* sp. which had an average abundance of 36.4% across all samples and largely contributed to the steepness of the rank abundance plot.

When ranked based on distribution in the samples, the top ten dominant species were not the same as when ranked based on relative abundance (Table 5). Again, *Mytilus* sp. was the most dominant species in this study being found in 126 of the samples. *Halichondria* spp. and *Clytia* sp. were no longer in the top ten ranking and were replaced by *Hiatella arctica* and *Pseudochitinopoma occidentalis*. The order of the previously ranked top ten also became a bit reorganized, with the biggest change occurring for *Lichenopora* sp. which moved to the third most dominant species based on its occurrence in 82 of the samples.

**Table 5. The ‘top ten’ dominant sessile invertebrate species determined by their relative abundance and their presence in samples.**

Relative Abundance			Presence in samples	
Species	Avg %	SE	Species	No (/162)
<i>Mytilus</i> sp.	36.1	3.3	<i>Mytilus</i> sp.	126
<i>Balanus crenatus</i>	8.7	1.6	<i>Balanus crenatus</i>	82
<i>Obelia dichotoma</i> <sup>3</sup>	8.2	1.8	<i>Lichenopora</i> sp.	61
<i>Alcyonidium polyoum</i> <sup>1</sup>	4.9	1.2	<i>Hiatella arctica</i>	51
<i>Clytia</i> sp.	4.3	1.3	<i>Obelia dichotoma</i> <sup>3</sup>	48
<i>Corella inflata</i>	3.4	0.9	<i>Pseudochitinopoma occidentalis</i>	45
<i>Halichondria</i> spp.	2.8	1.0	<i>Alcyonidium polyoum</i> <sup>1</sup>	44
<i>Botrylloides violaceus</i> <sup>1</sup>	2.6	0.7	<i>Schizoporella japonica</i> <sup>1</sup>	37
<i>Schizoporella japonica</i> <sup>1</sup>	2.5	0.6	<i>Botrylloides violaceus</i> <sup>1</sup>	28
<i>Lichenopora</i> sp.	1.7	0.4	<i>Corella inflata</i>	27
<i>Botryllus schlosseri</i> <sup>1</sup>	1.2	0.6		
<i>Membranipora membranacea</i>	1.1	0.6		
<i>Cryptosula pallasiana</i> <sup>3</sup>	1.1	0.4		
<i>Conopeum reticulum</i>	1.0	0.7		
<i>Distaplia occidentalis</i>	0.9	0.4		

<sup>1</sup>Introduced species, <sup>2</sup>Complex likely includes introduced, <sup>3</sup>Cryptogenic species, <sup>4</sup>Complex likely includes cryptogenic.

The top ten dominant motile species, in terms of abundance, were the only species with average abundances greater than 0.5 individuals per sample (Figure 9 and Table 6). They represent roughly 13% (17/132) of all the motile species. The most dominant species was Amphipod complex 2 (*Gnathopleustes pugettensis* and *Eogammarus oclairi*) which had an average abundance of 7.4 individuals per sample and largely contributed to the steepness of the rank abundance plot.

When considering the number of samples in which each species was found, there was again a bit of reorganization of the top ten most dominant species (Table 6). *Nereis procera* moved to the top of this list by occupying 81 of the samples. The next closest species were *Eulalia quadrioculata* and Amphipod complex 2 (*G. pugettensis* and *E. oclairi*) in 65 and 64 sites respectively. When ranked according to sites *Caprella laeviscula* and *Caprella anomala* were no longer ranked in the top ten most dominant species.

**Table 6. The ‘top ten’ dominant motile invertebrate species determined by their relative abundance and their presence in samples.**

Relative Abundance			Presence in samples	
Species	Avg no	SE	Species	No (/162)
Amphipod complex 2	7.4	1.8	<i>Nereis procera</i>	81
<i>Jassa staudei</i>	2.8	0.9	<i>Eulalia quadrioculata</i>	65
<i>Nereis procera</i>	2.8	0.4	Amphipod complex 2	64
<i>Caprella laeviuscula</i>	2.2	1.4	<i>Chrysopetalum occidentale</i>	62
Amphipod complex 1 <sup>1</sup>	2.0	0.5	Amphipod complex 1 <sup>1</sup>	39
<i>Caprella mutica</i> <sup>1</sup>	1.6	0.7	<i>Nereis vexillosa</i>	30
<i>Caprella anomala</i>	1.6	0.9	<i>Caprella mutica</i> <sup>1</sup>	30
<i>Eulalia quadrioculata</i>	1.0	0.2	<i>Mystides borealis</i>	29
<i>Chrysopetalum occidentale</i>	0.9	0.2	<i>Proceraea cornutus</i>	28
<i>Mystides borealis</i>	0.9	0.2	<i>Jassa staudei</i>	27
<i>Caprella</i> sp. (juv)	0.9	0.4		
<i>Nereis vexillosa</i>	0.7	0.2		
Amphipod complex 3	0.7	0.2		
<i>Polydora cornuta</i> <sup>1</sup>	0.6	0.6		
<i>Ophelina</i> sp.	0.6	0.6		
<i>Proceraea cornutus</i>	0.6	0.2		
<i>Gnorimosphaeroma oregonense</i>	0.5	0.2		

<sup>1</sup>Introduced species.

### Rare species

Rarity is a relative concept that can be determined a number of ways based on the prerogative of the researcher (Magurran, 2004). In this study I will consider all species that fell out in the tail of the rank abundance curves, or that were found at only one site, as rare species.

For the sessile species rank abundance plot the rare species in the tail of the curve were all species with an average percent coverage (with standard error range) that was less than 1% coverage. Therefore, there were 58 (79.5% of total) species classified as rare sessile species based on their relative abundance in this study. Of these 58 species, 22 (30% of total) of them were also deemed rare species because they were only found at one site (Table 7).

**Table 7. Sessile rare species determined by their average percent cover (Avg %) and the confirmation of whether or not they are deemed rare by the number of sites occupied.**

Species	Avg %	SE	Present at only one site
<i>Pseudochitinopoma occidentalis</i>	0.84	0.07	N
<i>Serpula columbiana</i>	0.71	0.06	N
<i>Semibalanus cariosus</i>	0.62	0.05	N
<i>Circeis armoricana</i>	0.57	0.05	N
<i>Bowerbankia gracilis</i>	0.55	0.04	N
<i>Pileolaria (Simplicaria) potswaldi</i>	0.49	0.04	N
<i>Orthopyxis</i> spp.	0.48	0.04	Y
<i>Hiatella arctica</i>	0.48	0.04	N
<i>Cheilopora annulata</i>	0.47	0.04	N
<i>Haliclona</i> sp.	0.28	0.02	N
<i>Paralaeospira malardi</i>	0.25	0.02	N
<i>Metridium</i> sp.	0.25	0.02	N
<i>Tegella armnifera</i>	0.23	0.02	N
<i>Bugula californica</i>	0.22	0.02	N
<i>Cheilopora praelonga</i>	0.22	0.02	N
<i>Leucosolenia nautilia</i>	0.21	0.02	N
<i>Schizobranchia insignis</i>	0.19	0.02	N
<i>Chthalamus dalli</i>	0.19	0.01	Y
<i>Diplosoma listerianum</i>	0.16	0.01	N
<i>Chone infundibuliformis</i>	0.15	0.01	N
<i>Crucigera zygophora</i>	0.12	0.01	N
<i>Styela</i> sp.	0.11	0.01	N
<i>Bugula pacifica</i>	0.07	0.01	N
<i>Styela clava</i>	0.07	0.01	N
<i>Pododesmus macrochisma</i>	0.07	0.01	N
<i>Cnemidocarpa finmarkiensis</i>	0.06	0.00	Y
<i>Alpidium californicum</i>	0.06	0.00	N
<i>Bugula</i> sp.	0.05	0.00	N
<i>Ascidia</i> sp.	0.04	0.00	N
<i>Scrupocellaria varians</i>	0.03	0.00	Y
<i>Balanus</i> sp.	0.03	0.00	N
<i>Callopora horrida</i>	0.03	0.00	Y
Sabellidae INDET	0.02	0.00	N
Spirorbinae INDET	0.02	0.00	N
<i>Plumularia</i> sp.	0.02	0.00	N
<i>Crucigera irregularis</i>	0.02	0.00	N
<i>Chelyosoma productum</i>	0.02	0.00	Y
<i>Anthopleura artemisia</i>	0.02	0.00	Y

Species	Avg %	SE	Present at only one site
<i>Pseudopotamilla nr. intermedia</i>	0.01	0.00	N
<i>Bugula pugeti</i>	0.01	0.00	N
<i>Caulibugula californica</i>	0.01	0.00	N
Ascidiacea INDET	0.01	0.00	N
<i>Eudistylia vancouveri</i>	0.01	0.00	Y
<i>Dendrobeatia lichenoides</i>	0.01	0.00	N
<i>Tubulipora pacifica</i>	0.01	0.00	Y
<i>Molgula manhattensis</i>	0.01	0.00	Y
<i>Ellisina levata</i>	0.01	0.00	Y
Hydrozoa INDET	0.01	0.00	Y
Actiniidae INDET	0.01	0.00	Y
<i>Cliona</i> sp.	0.00	0.00	Y
<i>Jugaria quadrangularis</i>	0.00	0.00	Y
<i>Kellia suborbicularis</i>	0.00	0.00	Y
<i>Porella concinna</i>	0.00	0.00	Y
<i>Callopora armanata</i>	0.00	0.00	Y
<i>Disporella fimbriata</i>	0.00	0.00	Y
<i>Halocynthia igaboja</i>	0.00	0.00	Y
Demospongiae INDET	0.00	0.00	Y
Gymnolaemata INDET	0.00	0.00	Y

For the motile species rank abundance plot the rare species in the tail of the curve are all species whose average percent coverage (with standard error range) is 0.5 individuals or lower. Therefore, there were 115 (87% of total) motile species classified as rare species based on their relative abundance in this study. Of these 105 species, 44 (33% of total) of them were also deemed rare species because they were only found at one site. One additional species, *Ophelina* sp., is listed because it was considered dominant based on its relative abundance but was only present at one site (Table 8).

**Table 8. Rare motile species determined by their average count (Avg No) and the confirmation of whether or not they are also deemed rare by the number of sites occupied. In bold at the bottom of the table is a species that is considered dominant based on average count but rare based on occupying on one site.**

<b>Species</b>	<b>Avg No</b>	<b>SE</b>	<b>Present at only one site</b>
<i>Typosyllis</i> sp.	0.40	0.23	N
<i>Eusyllis blomstrandii</i>	0.33	0.13	N
<i>Emplectonema gracile</i>	0.29	0.09	N
Flatworm complex	0.28	0.25	N
<i>Armandia brevis</i>	0.27	0.11	N
<i>Locustogammarus levingsi</i>	0.27	0.27	<b>Y</b>
<i>Leptoplana chloranota</i>	0.25	0.10	N
Syllidae INDET	0.25	0.11	N
Juvenile seastars	0.24	0.07	N
<i>Ianiropsis analoga</i>	0.19	0.07	N
<i>Syllis (Syllis) elongata</i>	0.19	0.07	N
<i>Anoplodactylus viridintestinalis</i>	0.18	0.12	N
<i>Triplana</i> sp.	0.17	0.05	N
<i>Halosydna brevisetosa</i>	0.16	0.04	N
<i>Nereis</i> sp. (juv)	0.15	0.07	N
<i>Ischyrocerus pelagops</i>	0.13	0.13	<b>Y</b>
Oligochaeta INDET	0.13	0.09	<b>Y</b>
Plehnidae INDET	0.11	0.09	N
Gammaridea INDET	0.10	0.06	N
<i>Typosyllis nr. fasciata</i>	0.10	0.03	N
<i>Eusyllis habei</i>	0.09	0.03	N
<i>Capitella capitata</i> complex	0.09	0.05	N
<i>Lepidonotus squamatus</i>	0.09	0.03	N
<i>Monocorophium</i> sp.	0.09	0.06	N
<i>Pseudoceros canadensis</i>	0.08	0.03	N
Doridacea INDET	0.07	0.02	N
<i>Notocomplana</i> sp.	0.06	0.03	N
Polychaeta INDET	0.06	0.04	N
Polynoidae INDET	0.06	0.04	N
<i>Boccardia columbiana</i>	0.04	0.04	N
<i>Munna fernaldi</i>	0.04	0.03	N
Nemertea INDET	0.04	0.02	N
Spionidae INDET	0.04	0.04	N
<i>Odontosyllis phosphorea</i>	0.04	0.03	N
<i>Pisaster ochraceus</i>	0.04	0.02	N
<i>Ophiodromus pugettensis</i>	0.03	0.02	N
<i>Paramoera columbiana</i>	0.03	0.03	<b>Y</b>
<i>Alia tuberosa</i>	0.03	0.03	<b>Y</b>

<b>Species</b>	<b>Avg No</b>	<b>SE</b>	<b>Present at only one site</b>
Leptoplanidae INDET	0.03	0.03	N
Aeolidacea INDET	0.03	0.02	N
<i>Typosyllis hyalina</i>	0.02	0.02	N
<i>Polydora websteri</i>	0.02	0.02	N
Hesioniidae INDET	0.02	0.02	N
<i>Harmothoe imbricata</i>	0.02	0.01	N
<i>Munna</i> sp.	0.02	0.02	Y
Terebellidae INDET	0.02	0.02	N
Pleustidae INDET	0.02	0.01	N
Nudibranchia INDET	0.02	0.02	N
<i>Tetrastemma candidum</i>	0.02	0.01	N
<i>Triplana viridis</i>	0.02	0.02	Y
<i>Stylochoplana</i> sp.	0.02	0.01	N
<i>Lepidonotus</i> sp.	0.02	0.01	N
<i>Platynereis bicanaliculata</i>	0.02	0.01	N
<i>Aoroides</i> sp.	0.02	0.01	N
<i>Aoroides columbiae</i>	0.02	0.01	N
<i>Onchidoris bilamellata</i>	0.02	0.01	N
Mopaliidae INDET	0.02	0.01	N
<i>Paranemertes peregrina</i>	0.01	0.01	N
<i>Cerebratulus californiensis</i>	0.01	0.01	Y
<i>Acerotisa</i> sp.	0.01	0.01	N
<i>Exogene dwisula</i>	0.01	0.01	N
<i>Polydora</i> sp.	0.01	0.01	N
<i>Polydora nr limicola</i>	0.01	0.01	N
<i>Harmothoe</i> sp.	0.01	0.01	N
<i>Paranais litoralis</i>	0.01	0.01	Y
<i>Zeuxo normani</i>	0.01	0.01	Y
<i>Podocerus cristatus</i>	0.01	0.01	Y
<i>Jassa</i> sp.	0.01	0.01	Y
Ischyroceridae INDET	0.01	0.01	N
<i>Caprella alsakana</i>	0.01	0.01	Y
<i>Caprella penantis</i>	0.01	0.01	Y
<i>Heptacarpus brevirostris</i> (juv)	0.01	0.01	N
<i>Lottia</i> sp.	0.01	0.01	N
Polycladida INDET	0.01	0.01	N
Phyllodocidae INDET	0.01	0.01	N
<i>Tetrastemma</i> sp.	0.01	0.01	Y
<i>Amphiporus ima</i>	0.01	0.01	Y
<i>Notoplana sanguinea</i>	0.01	0.01	Y
<i>Typosyllis alternata</i>	0.01	0.01	Y
<i>Typosyllis adamanteus</i>	0.01	0.01	Y

<b>Species</b>	<b>Avg No</b>	<b>SE</b>	<b>Present at only one site</b>
<i>Prionospio lighti</i>	0.01	0.01	Y
<i>Eteone</i> sp.	0.01	0.01	Y
<i>Clavadoce</i> sp.	0.01	0.01	Y
<i>Glycera nana</i>	0.01	0.01	Y
<i>Microparke dubia</i>	0.01	0.01	Y
<i>Palaenotus bellis</i>	0.01	0.01	Y
<i>Nainereis quadricupsida</i>	0.01	0.01	Y
<i>Dorvillea annulata</i>	0.01	0.01	Y
<i>Leptochelia savignyi</i>	0.01	0.01	Y
<i>Photis</i> sp.	0.01	0.01	Y
Corophiidae INDET	0.01	0.01	Y
<i>Desdimelita californica</i>	0.01	0.01	Y
<i>Melita nitida</i>	0.01	0.01	Y
<i>Eualus lineatus</i>	0.01	0.01	Y
<i>Cancer magister</i>	0.01	0.01	Y
<i>Lirularia</i> sp.	0.01	0.01	Y
<i>Pycnopodia helianthoides</i> (juv)	0.01	0.01	Y
<i>Cucumaria miniata</i>	0.01	0.01	Y
Opheliidae INDET	0.01	0.01	Y
Caridea INDET	0.01	0.01	Y
Arthropoda INDET	0.01	0.01	Y
Pyramidellidae INDET	0.01	0.01	Y
Gastropoda INDET	0.01	0.01	Y
Dendronotacea INDET	0.01	0.01	Y
Holothuriodea INDET	0.01	0.01	Y
<b><i>Ophelina</i> sp.</b>	0.62	0.05	Y

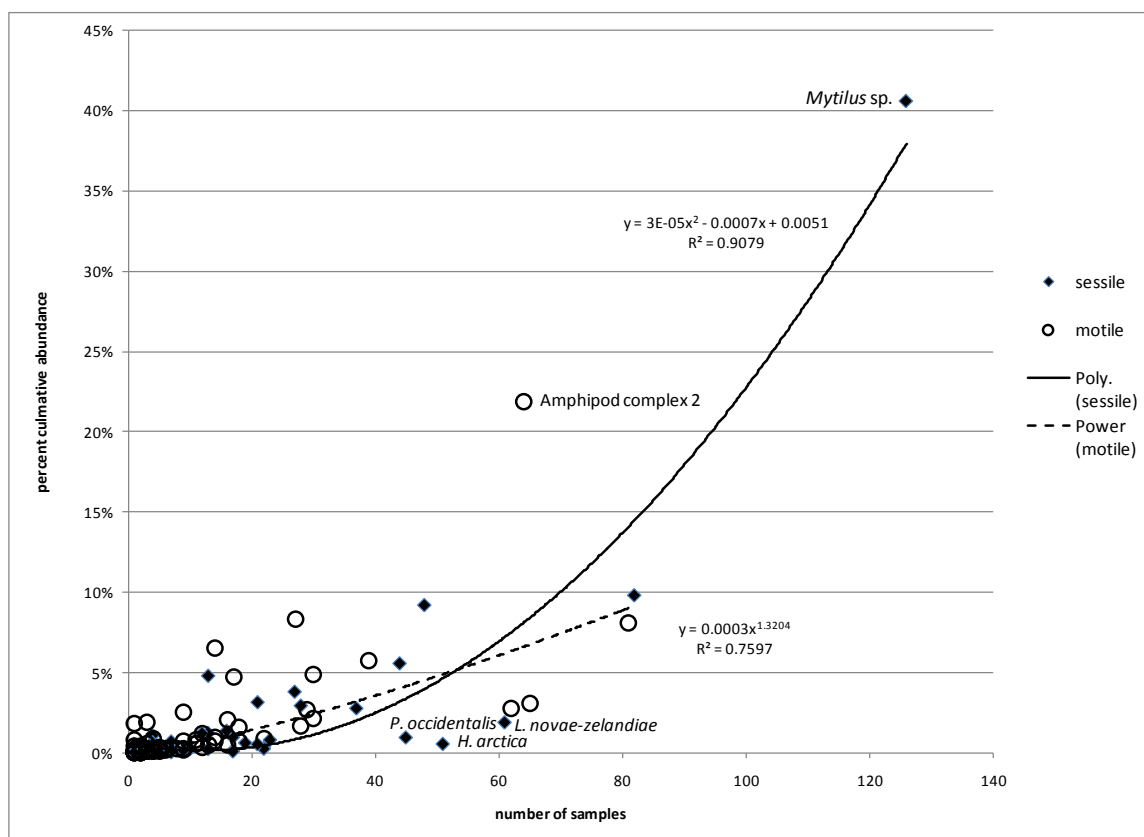
#### Abundance and distribution relationship

Another way to explore the concepts of dominance and rarity in the community is to compare the relationship between the abundance and the distribution of the species in the samples. These relationships are compared in terms of the sessile and motile lifestyles. Both the sessile and motile species roughly follow the trend that species that are found in fewer samples have a low abundance and species found in more samples are more likely to have higher abundances. However, the trend of this relationship can be described differently for each lifestyle (Figure 10).

The relationship between distribution and abundance for the sessile species is best described by polynomial (fluctuating) trend. At low distributions in the samples, between

1 and 20 samples, the species all have very low abundances. However, following the 20-sample mark, the sessile species show a strong relationship where the abundance of the species increases as the number of samples occupied increases. This trend is strongly influenced by *Mytilus* sp. which had a very high relative abundance and occupied a large number of samples (over 40% abundance at 126 sites). There was some variability in the middle section of the trend, where *H. arctica*, *P. occidentalis*, and *Lichenopora* sp., in particular, had relatively low abundances despite appearing at a relatively high number of sites. The polynomial equation describes a lot of the variability in the data ( $R^2=0.9079$ ).

The trend for the motile species is that the percent cumulative abundance increases at a specific rate per number of samples occupied. There was more variability for the motile species, but the power equation is still a pretty good fit ( $R^2=0.7597$ ). Amphipod complex 2 (*G. pugettensis* and *E. oclairi*) stood out from the rest of the motile species in having a very high relative abundance based on the number of samples occupied.



**Figure 10.** The relationships of the cumulative percent abundance and the number of samples occupied for sessile and motile species. See text for comment on the indicated species.

### Introduced and cryptogenic species

A number of introduced and cryptogenic species were observed in this study. There were both dominant and rare introduced species in the fouling community (Table 9).

**Table 9. The introduced species observed in this study. The sessile introduced species are ranked out of 73 species based on percent cover (Avg %) and the number of samples in which they were found (No). The motile introduced species were ranked out of 132 species based on their average count per sample (Avg count) and the number of samples in which they were found (No). In parenthesis before some ranks are the notes on what number of a way tie was observed for that rank (e.g. a three way tie would be 3 w).**

Species	SESSILE				Species	MOTILE			
	Abundance		Sample			Abundance		Sample	
	Avg %	Rank	No	Rank		Avg count	Rank	No	Rank
<i>A. polyoum</i>	4.95	4	44	7	Amphipod complex 1*	1.96	5	39	5
<i>B. violaceus</i>	2.60	8	28	9	<i>C. mutica</i>	1.64	6	30	7
<i>S. japonica</i>	2.46	9	37	8	<i>P. cornuta</i>	0.63	14	3	(14 w) 44
<i>B. schlosseri</i>	1.21	11	16	20	<i>M. nitida</i>	0.01	(30 w) 93	1	(43 w) 80
<i>S. clava</i>	0.07	(2 w) 38	3	(11 w) 38					
<i>M. manhattensis</i>	0.01	(4 w) 58	1	(21 w) 53					
<i>Cliona</i> sp.	0.00	(9 w) 65	1	(21 w) 53					

\*Contains two species; *A. brevis* and *M. acherusicum*, only *M. acherusicum* is non-native.

Three introduced sessile species were consistently ranked in the top ten dominant species based on both abundance and number of sites occupied: *A. polyoum*, *B. violaceus* and *S. japonica*. *B. schlosseri* was only ranked as a dominant species based on overall abundance. Three of the sessile introduced species were rare species that had low abundances (fell out in the tail of the rank abundance plot) and were not found in many samples: *S. clava*, *M. manhattensis*, and *Cliona* sp.

Two motile introduced species were ranked as dominant species based on both relative abundance and number of samples: Amphipod complex 1 containing *M. acherusicum*, and *C. mutica*. *P. cornuta* was considered a dominant introduced motile species based on relative abundance but not the number of samples in which it was found. *M. nitida* was a rare species based on both relative abundance and the number of samples they occupy.

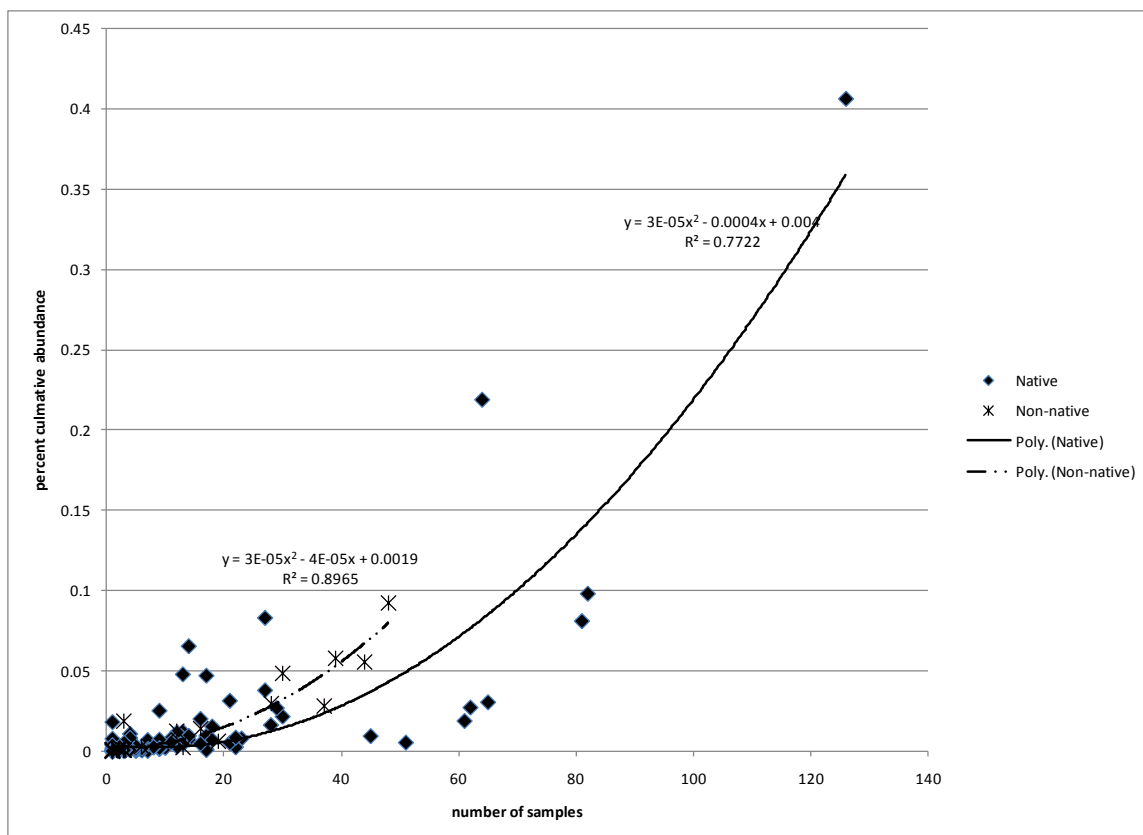
The cryptogenic motile species were mostly rare species in this study (Table 10). *O. dichotoma* was consistently ranked in the top ten most dominant species. The remaining

cryptogenic sessile species (*C. pallasiana*, *B. gracilis*, and *L. nautilia*) were not consistently ranked as dominant species but fell out in the middle of the pack.

**Table 10. The cryptogenic species observed in this study. The sessile non-native species are ranked out of 73 species based on average percent cover (Avg %) and the number of samples in which they were found (No). The motile non-native species were ranked out of 132 species based on their average count per sample (Avg count) and the number of samples in which they were found (No). In parenthesis before some ranks are the notes on what number of a way tie was observed for that rank (e.g. a three way tie would be 3 w).**

Species	SESSILE				Species	MOTILE			
	Abundance		Sample			Abundance		Sample	
	Avg %	Rank	No	Rank		Avg count	Rank	No	Rank
<i>O. dichotoma</i>	8.18	3	48	5	<i>Capitella</i> sp.	0.09	39	6	(2 w) 33
<i>C. pallasiana</i>	1.07	13	12	24	<i>B. columbiana</i>	0.04	49	2	(22 w) 58
<i>B. gracilis</i>	0.55	20	19	16	<i>P. websteri</i>	0.02	(8 w) 58	3	(14 w) 44
<i>L. nautilia</i>	0.21	31	13	(3w) 21	<i>P. bicanaliculata</i>	0.02	(9 w) 66	3	(14 w) 44
					<i>P. nr limicola</i>	0.01	(18 w) 75	2	(22 w) 58
					<i>C. penantis</i>	0.01	(18w) 75	1	(43 w) 80
					<i>T. alternata</i>	0.01	(30 w) 93	2	(22 w) 58
					<i>L. savignyi</i>	0.01	(30 w) 93	1	(43 w) 80

The relationship of the distribution of species in samples with their abundance for both native and non-native (introduced and cryptogenic) species show some variability but are both adequately described ( $R^2 = 0.7772$  and  $R^2 = 0.897$  respectively) by polynomial patterns (Figure 11). However, the polynomial line for the non-native species is slightly offset from the native species, indicating that the relative abundance for a non-native species was higher than that of a native species at the same number of sites occupied.



**Figure 11. The relationships of cumulative percent abundance and the number of samples occupied for native and non-native species.**

## Discussion

### Species recruiting to the settlement arrays

#### Taxonomic distribution and the identity of species

The fouling community recruiting to the settlement arrays along the BC coast is fairly typical of communities living on docks, pilings, and natural rock substrates world-wide. These are composed primarily of sessile and motile invertebrates such as ascidians, bryozoans, hydroids, sponges, and crustaceans (Nydam and Stachowicz 2007).

The bryozoans and ascidians had the highest number of sessile species in this study. Both phyla consist of filter-feeding, benthic organisms that attach to a variety of marine substrata (Brusca and Brusca 2002). These organisms within this phyla have adapted a number of morphologies that allow them to use available space in various ways and occupy different niches. This strong representation by both phyla has been found in other studies of epibenthic communities in the northeast Pacific, although those studies found

that the ascidians had more species than the bryozoans (Nydam and Stachowicz 2007, Lu *et al.* 2007). Greene and Schoener (1982) also found bryozoans and ascidians to be prominent in the fouling community of their sampling site. However the ascidians in their study were primarily solitary species, whereas in my study there was a greater representation of colonial species. The successional studies of Greene and Schoener (1992) and Greene *et al.* (2003) found that the colonial sessile organisms dominated the communities until 20-30 weeks. The settlement arrays in my study were submerged for an average duration of 20 weeks. Therefore, the high proportion of colonial tunicate and bryozoan species may be a result of the early successional stage of this study.

The motile organisms living among the sessile organisms on the settlement arrays were primarily arthropod crustaceans and annelid polychaetes. This is not surprising as both the arthropods and annelids are among the most diverse phyla and inhabit virtually all marine habitats. The success of these phyla is due in part to the plasticity of their segmented body plans which exhibits a range of morphological diversity that allows them to exploit a variety of life history strategies and ecological roles (Brusca and Brusca 2003, Carlton 2007). What was surprising was the strong representation of motile species, as many fouling community studies have low reports of motile species. This may be because the sampling strategies used in a lot of epibenthic studies either use point sampling techniques (*e.g.* Greene and Schoener 1982), digital imaging (*e.g.* Nydam and Stachowicz 2007), or that focus on the 'foundation' species (*e.g.* Sutherland and Karlson 1977). These sampling strategies therefore target large sessile species and little to no information can be collected on the motile and small species occurring in the epibenthic communities. The two studies in the northeast Pacific to report large numbers of motile species were studies of fouling communities by Lu *et al.* (2007) and Richoux *et al.* (2006) where they scraped the sampling surface.

There is a strong overlap with the species identified in this study and those found in other studies of epibenthic invertebrate communities in the northeast Pacific (Lu *et al.* 2007, Richoux *et al.* 2006, Nydam and Stachowicz 2007, Greene *et al.* 1983, Greene and Schoener 1982). However, there was a large proportion of introduced and cryptogenic species found in this study; of the 171 species identified 11 species were introduced and 12 were cryptogenic. Furthermore, these numbers don't include the potential non-native

species discussed previously for the *Halichondria* and *Mytilus* species complexes. Lu *et al.* (2007) did a baseline survey of non-native species in five major ports in BC and found 23 non-native invertebrate species. Similarly, Richoux *et al.* (2006) did a baseline survey for Burrard Inlet in Vancouver and found 12 non-native invertebrate species. Though there is a strong overlap of the non-native species from their lists and the list generated for this study I will not make direct comparison as there are a few discrepancies on which species are deemed native, non-native, and cryptogenic between our three studies. I assigned the designation of introduced and cryptogenic species by compiling information from the lists for non-native species in British Columbia generated by Levings *et al.* (2002) and Gillespie (2007), by identification texts (Lamb and Hanby 2002, Kozloff 1996, Carlton 2007), and made a few amendments following personal communication with Dr. Carlton. Though only 11 introduced species, and 12 cryptogenic species were identified in this study there are definitely more present along the BC coast. A literature review and summary of Levings *et al.* (2002) found that 117 introduced and cryptogenic marine and estuarine species (65 of which are invertebrates) have been reported in the Strait of Georgia. Gillespie (2007) extended the literature review to the entire coast, but only for the intertidal zone, and reported 43 introduced species (38 of which are invertebrates). Though there are local areas in the Northeast Pacific that are more highly invaded (for a summary see Ruiz *et al.* 1999), the high proportion of non-native species present in British Columbia is of major concern as many of these species can have strong impacts on local communities (*e.g.* Dijkstra *et al.* 2007, Ruiz *et al.* 1999, Huxel 1999).

Of the 11 introduced species, one species, *C. mutica*, a caprellid amphipod is previously unknown in BC waters (Frey *et al.* 2009). The native range of *C. mutica* is along the north-east Asian coast and the species has been introduced to western Europe, both coasts of North America, and New Zealand (review in Aston *et al.* 2007). Along the west coast of North America *C. mutica* has not yet been reported in BC, though it has been reported in southern Puget Sound and recently in Alaska (Aston *et al.* 2007, Ashton *et al.* 2008). This first report of the presence in BC waters may be supported by a report by Ashton *et al.* (2007) which indicates that, based on temperature limits, the entire BC coast line provides suitable habitat for *C. mutica*.

### Species Richness

There were 171 species, and an additional 34 categories of unresolved organisms, observed on the settlement arrays. This richness, of at least 205 species, is relatively high in comparison with other studies of epibenthic invertebrate communities (Table 11). The high richness is likely attributed to the large geographic area covered and strong sampling effort. Zacharias and Roff (2001) found 205 species over a similar geographic range and with a similar sampling effort, though their study was conducted in the rocky intertidal and included algae and seaweeds. Lu *et al.* (2007) found a total of 174 invertebrate species from five harbours along the BC coast (Esquimalt, Vancouver, Nanaimo, Port Alberni, and Prince Rupert). This richness may be attributed to the large geographic range of the ports in the study and the high sampling effort, as well as the fact that the researchers were sampling a variety of substrates such as buoys and floating structures that were made of wood, concrete, and steel, that had been submerged anywhere from one to ten years. Richoux *et al.* (2006) found 103 taxa in Burrard Inlet, Vancouver. Though this study was conducted on a small geographic scale a large number of species were found because the researchers also sampled algae and seaweeds in both the intertidal and subtidal zones on a variety of hard substrates. Ardisson and Bourget (1992) sampled the Gulf of Saint Lawrence using navigational buoys and found a total of 68 invertebrate species. Despite the strong sampling effort and long time frame of their study, the authors found lower species richness because their study was conducted over a small geographic range that extended into some very estuarine (low salinity) waters. In the northeast Pacific, Greene and Schoener (1982) found 52 species, Greene *et al.* (1983) found 32 species, and Nydam and Stachowicz (2007) found 24 species. The lower richness may be explained by restricted geographic ranges, sampling techniques, as well as the focus of each of these studies. Generally the researchers were not looking at the entire epibenthic community and were primarily excluding any motile and/or smaller species.

**Table 11. Summary of the authors (Authors), the geographic area they sampled (Area), the typed of substrate/structure sampled (Structure), the sampling effort (No samples), observed richness (Richness) and additional notes (Notes) for epibenthic community surveys.**

Authors	Area	Structure	No Samples	Richness	Notes
Zacharias and Roff (2001)	BC coast	Rocky intertidal	180	205	Includes algae and seaweeds
Lu <i>et al.</i> (2007)	Five major ports in BC	Buoys and docks	125	174	Sampled a variety of substrates types that had been submerged for various amounts of time
Richoux <i>et al.</i> (2006)	Burrard Inlet, Vancouver BC	Low intertidal	34	103	Sampled a variety of substrate types. List includes algae and seaweeds.
Ardisson and Bourget (1992)	Estuary and Gulf of St Lawrence	Buoys	Up to 239 per year	68	Sampled over a twelve year period
Green and Schoener (1982)	Bremerton Harbor Washington	Fouling (Formica panels)	16	52	Sampled only sessile species.
Greene <i>et al.</i> (1983)	Southern Puget Sound Washington	Fouling (Formica panels)	7	32	
Nydam and Stachowicz	Bodge Harbor California	Fouling (PVC panels)	350	24	Included predator exclusion experiments.

A large proportion of the richnesses of my study can be attributed to the strong representation of motile species. One of the few studies to find motile species to sessile species ratio similar to that seen in this study is a study by Davidson *et al.* (2004) in the rocky intertidal of Ireland. Both Davidson *et al.* (2004) and Kerr *et al.* (2002) highlight the positive influence small scale patterns of movement can have on biodiversity and the importance of sampling the entire community in accurate biodiversity measures. I was able to get such a strong representation of motile species, and therefore a more

accurate estimate of richness (biodiversity), because of the sampling gear utilised in the survey. The settlement arrays used in this study were designed so that the Petri dishes, which represent subsamples of the fouling community, were easily removed and transported. Most shallow subtidal sampling involves using large ceramic or PVC (polyvinyl chloride) tiles or plates which are bulky and difficult to transport large distances. The Petri-dish subsamples were easily transported and this design allowed for this study to be conducted on such a large geographic scale. Additionally, because the Petri dishes could be easily removed from the lids, the sampling area did not have to be scraped to gather the organisms. Scraping sampling surfaces often allows researchers to collect more of the motile species present in the community (*e.g.* Lu *et al.* 2007, Ardisson and Bourget 1992) but leads to many of the organisms becoming damaged and difficult to identify (*i.e.* encrusting bryozoans). Processing the samples involved obtaining both percent coverage for sessile species and individual counts of motile species that became visible as each successive sessile species was removed from the community. If, as in many other subtidal epibenthic studies, we had ignored the presence of motile species we would have lost almost two-thirds of the number of species found in this study.

#### Richness per sample

The Petri dishes provided 63.6 cm<sup>2</sup> to be colonized. Within this space, there was a similar average number of six species for both the motile and sessile organisms. Again, the average diversity per sample of both the sessile and the motile species highlights the value in examining the community as whole, as it is obvious that motile species are as much a part of the community as the sessile species.

Each Petri dish always had at least one sessile species (1-15 range) present while occasionally there were no motile species present (0-16 range). Occasionally, there was evidence of motile species present in the past as there were empty tubes and casing. The absence of any motile species suggests at sites may suggest that either the organisms had succumbed to natural mortality or that those sites developed conditions that were unfavourable for the motile species.

The overall richness per Petri dish sample ranged from one to 29 species. Ardisson and Bourget (1992) found anywhere from 0 to 13 species on their buoys. Their lower diversity on the sampling buoys is may partially be explained by low salinity as the only

sites where Ardisson and Bourget (1992) found no species on their buoys were those sites that were located directly in the estuary. The sites in this study that had low species richness, and a lot of free space still available, were also sites with low salinity (*e.g.* Kitimat-NC).

The overall average number of species per sample in this study was almost twelve species (11.8) with more than one (1.25) of these species being introduced to BC. This large representation of introduced species (10.5%) of the average sample reiterates the prevalence of introduced species in the fouling community of the BC coast.

### **Relative abundance of species**

The fact that species abundances differ within a community means that the additional biodiversity dimension of evenness can be used to help define and discriminate ecological communities (Magurran 2004). There are many patterns of evenness observed in communities that are usually best described by the degree of competition in the community. Communities with low evenness (high dominance) are the communities with the strongest inter- and intra-specific competition, with the abundance of each species reflecting its success at competing for the limiting resource (Contgreave and Harvey 1994; Magurran 2004).

In this study the limiting resource is space, and as such, there is low evenness. This low evenness is attributed to a few dominant species that are able to best compete for the limited space of each sample (Petri dish area is 63.6 cm<sup>2</sup>). The concept of dominance in space limited invertebrate communities was first described by Connell (1961) in observing the competitive dominance of an intertidal barnacle over another in the tidal zones of the rocky intertidal. Dominance by relatively few species in resource limited environments have been observed in a number of communities worldwide ranging from algae in the rocky intertidal (Dayton 1975), to plants growing in limited soil nutrients (Wilson *et al.* 1996), and to butterfly species inhabiting Moroccan mountains (Thomas and Malloeri 1985). A marine example of a community with high evenness is for deep sea invertebrate species where resources are ephemeral and patchy in nature (Grassle and Maciolek 1992).

The shape of the rank abundance curves for both the sessile and motile species highlights this dominance by relatively few species with a large proportion of rare species

that are less successful at competing for limited resources, and as such, fill small ecological niches.

### Dominant Species

There is strong overlap of the same species, or east coast equivalents, of the dominant species observed in this study with that of the dominant species association in the east coast survey by Ardisson and Bourget (1992) in the Gulf of St. Lawrence. Ardisson and Bourget (1992) list three traits that are shared by these dominant species that may contribute to their abundance in their study; the species all have planktotrophic larvae, the ability to maintain themselves in the upper layer of the water column, and the capacity to live immersed continuously during the adult phase. The dominant sessile species in this study differ from those on the east coast study by Ardisson and Bourget (1992) in that the reproductive strategies included planktotrophic, lecithotrophic, and brooded larvae. In this study the settlement arrays were suspended from floating structures where the arrays would be in close proximity to established communities. The close proximity facilitated the recruitment of even the short-lived larvae (brooded or lecithotrophic), whereas the sampling structures used by Ardisson and Bourget (1992) were navigational buoys moored further distances from established communities and were likely unreachable by short-lived larvae. Instead of the shared trait of pelagic larvae I suggest another unifying trait of the dominant species in my study; their key reproductive periods are included within the sampling period of this survey. Larval supply is one of the most important factors in determining community composition and by having key reproductive periods that are encompassed in the sampling period (and preferably earlier in the period) species will have a strong competitive advantage (Osman 1977).

Though the traits described above are common to all the dominant species in this study they do not suggest why these species are so dominant. The similarity in the dominant taxa of between my study of the BC coast and Ardisson and Bourget's (1992) is important because it highlights that these species/genera are likely so abundant because they are the organisms that are best adapted to recruiting to fouling communities of artificial substrates. These species may be dominant as they are able to recruit to artificial substrata, survive in the often stressed environments of anthropogenic habitats, and are easily transported by human-mediated vectors. The dominant species are likely the

foundation species of fouling communities. Foundation species will structure a community because they provide locally stable conditions for other species and modulate and stabilize fundamental ecosystem processes (Dayton 1972, Ellison *et al.* 2005 cited in Bangert *et al.* 2006).

#### *Sessile Species*

The most dominant sessile species in this study was the *Mytilus* sp. complex. This is not surprising as members of the *Mytilus* complex ranges span the entire sampling range, are known as the most common bivalves along temperate coastline, and are abundant in various environments such as on pilings, floats, docks, and rocks, even along the outer coast (Carlton 2007). The success of the *Mytilus* sp. complex in this study may be attributed, at least in part to, to its reproductive timing. *Mytilus edulis* had been recorded at spawning primarily in later spring-early summer (April-June) but depending on the location may have either continuous spawning throughout the summer season or have a second spawning season in the late summer (Reitzal *et al.* 2004, Emmett *et al.* 1987). This spawning and recruitment behaviour contributed to the dominance of *Mytilus* sp. in this study as it was recruiting just as the settlement arrays were being deployed in the spring. Also, the species complex could continue recruiting later into the season giving it a strong competitive advantage. There are also a number of features of *Mytilus* sp. that are associated with human-mediated introduction and spread that may have facilitated its dominance in this study: the larvae are planktotrophic and can be passively transported in the ballast water of commercial vessels, the byssal threads allow for transport on hard substrates including ship and boat hulls, and their palatability and relative ease of culture has led to their widespread introduction for aquaculture (summarised in Wonham 2004). *Mytilus* sp. was also considered a dominant species by Nydam and Stachowicz (2007), Greene *et al.* (1983), Greene and Schoener (1982) in their epibenthic studies in the Northeast Pacific.

When the species were then ranked based on the number of samples in which they were found most of the dominant species were simply rearranged within the top ranks. The biggest change in rank occurred for the bryozoan *Lichenopora* sp. This species had a lower abundance relative to the number of sites at which it was present (Figure 1.10). *Lichenopora* sp. is an encrusting bryozoan that I found attached to a variety of substrates

including mussel shell, barnacles, hydroids, other bryozoans, as well as the Petri dish surface. This ability to overgrow a variety of substrates may be the factor that allowed this species to be present at so many sites. I believe its lower rank based on abundance can be attributed to the fact that the small colonies were likely recent recruits. Though the recruitment timing of bryozoan species can be quite broad (April to November), Coe (1932) suggests that in a number of the encrusting species recruitment is delayed to the late spring when their hosts, such as bivalves and barnacles, have had time to grow to a sufficient size. This delay in recruitment may explain why I found that the colonies appeared small and juvenile, particularly when found on shells of mussels.

*Halichondria* spp. and *Clytia* sp. were no longer ranked as the top ten dominant species when based on distribution in samples. *Halichondria* spp. is an encrusting sponge that consists primarily of a loose association of spicule and spongin fibres that shape morphologically according to the shape of the substrate (Carlton 2007). When the sponge was present it was often a quite abundant space competitor as the sponge would spread out across the surface of the Petri dish. This loose aggregation, however, means that the sponge cannot withstand high energy environments and can be easily dislodged from the substrate, which may have contributed to its low presence in terms of number of samples present (Lamb and Hanby 2002). The *Clytia* sp. observed in this study were primarily stolonial colonies; instead of forming tall branching colonies, the colony spreads across a substrate connecting single upright hydranths by stolons (Carlton 2007). Because of this growth pattern it meant that when the *Clytia* sp. was present it would spread across the surface of the Petri dish, thereby accounting for its high abundance despite not being present in very many samples.

*Halichondria* spp. and *Clytia* sp. were replaced by *H. arctica* and *P. occidentalis* when ranked according to the number of samples in which the species were found. *H. arctica* is known as the 'Arctic nestler' clam whose range spans from the Arctic along the coast down to Chile and is commonly found nestled in algal holdfasts and amid mussel mats (Lamb and Hanby 2005). It is believed that this species may have spread southward from the arctic mediated by human activity, such as boating activity, and is also commonly found on pilings and in fouling communities (Carlton 2007). It is no surprise then that *H. arctica* was found in so many samples when you consider its distribution range, its

preferred ‘nestling’ habitat, the fact that many of the sampling sites were in close proximity to boat activity, and the fact that there may be more than one species within the genus (Carlton 2007). This bivalve however did not have a high overall abundance in this study because of its small size. Though *H. arctica* can have a shell length that extends to 78mm (Carlton 2007), I found that the individuals observed were juveniles that ranged from 5-20mm. *P. occidentalis* is a serpulid (calcareous) tubeworm whose distribution spans the range of our study. Though it was abundant in the samples it had a low overall percent abundance. Again, this may be attributed to the fact that though it is present at many sites it was often in a juvenile state. The small-bored calcified tube of newly settled juveniles of this species only measures 5mm (Carlton 2007). Based on presence in samples, the ‘top ten’ most dominant were rounded out by two solitary species. They replaced two colonial species who when ranked based on abundance preceded the two solitary species. This suggests that though these solitary organisms were able to recruit to more samples, the colonial organisms were strong space competitors once established at a site.

#### *Motile Species*

The dominant motile species based on abundance was the Amphipod complex 2. The high abundance found for this complex may be attributed to the fact that not only does it include two different species but these two species are actually from different families. *G. pugettensis* is from the family Pleustidae which are primarily commensals, egg predators, and microparasites of other invertebrates that are common in fouling communities (Carlton 2007). *E. oclairi* is from the family Anisogammaridae which are free-living, benthic, and epibenthic omnivores and zooplankton predators that inhabit a variety of shallow marine habitats (Carlton 2007). The Anisogammaridae is encompassed within the super family Gammaroidea. The fact that both families inhabit different niches within the community may further contribute to their overall abundance and distribution in this study.

When ranked according to the number of samples in which each motile species was found two polychaetes, *N. procera* and the *E. quadrioculata*, move ahead of Amphipod complex 2 in terms of dominance (Table 5 and Figure 12). *N. procera*, also known as the little pile worm, is a small but fierce predator that secretes and lives in mucous tubes

on/in pilings, mussel beds, eelgrass meadows, or rocky and silty substrates (Lamb and Hanby 2005). The abundance of mussel bed habitat, and the proximity to pilings, made the settlement arrays an ideal home for these nereid worms. Their known distribution also spans the entire length of our study (Lamb and Hanby 2005). Another, but larger, predatory nereid worm was dominant in this study; *N. vexillosa* is a common species on the open coast in association with mussels and barnacles and also on pilings (Carlton 2007). *E. quadrioculata* is another predatory worm which belongs to the Phyllodocidae family as does *M. borealis*. The phyllodocids are among the most common and conspicuous active predators in shallow water habitats, particularly associated with hard substratum (Carlton 2007). *N. procera* and *E. quadrioculata* were also dominant species based on abundance though, because it is based on number of individuals per sample, the larger *E. quadrioculata* was ranked lower.

There were some dominant motile species that were dominant based on abundance but were ranked much lower, or not ranked as dominant, when based on the number of samples in which they were present. These species include *J. staudei*, *C. laeviscula*, *C. anomala*, and *Caprella* sp. (juveniles) (Table 1.6). This can be attributed to the fact that these are predominantly gregarious species; when they are present at a site they were usually quite numerous. *J. staudei* belongs to the family Ischyroceridae which are known for constructing tubes on hard substrates in areas of high water velocity and are among the most common amphipods of fouling communities. Caprellids are clinging organisms that aggregate on any erect substratum, including other invertebrates such as hydroids and bryozoans (Carlton 2007).

One anomaly observed in terms of dominance vs. rarity in this study was for the polychaete *Ophelina* sp. This species was included as part of the 'top ten' most dominant species based on abundance but it is rare based on the fact that it was found in only one sample. In the one sample in which it was found there were 100 individuals. Opheliids are burrowing, infaunal, deposit feeding worms suggesting that the sample site (Reed Point, Vancouver) was particularly silty or sandy (Carlton 2007). Other opheliid species (*A. brevis* and Opheliidae Indetermined) were found in this study but at much lower abundances.

## Rare Species

Eighty-two percent of the species identified in this study were considered rare species. There may be any number of contributing factors that make a species 'rare' in this study (*i.e.* later recruitment period, size distribution based on age, limited distribution within the study limits, speed of motility); but whatever the cause, the take home message here is that rare species were a very large proportion of the species present in this study.

Having rare species was expected as we were studying a very space limited environment that resulted in a very uneven community. However, I did not expect such a large proportion of the overall richness to be accounted for by rare species. One of the few other fouling studies to examine rare species was Ardisson and Bourget's (1992) east coast study of buoy fouling communities and they only found rare species to account 57% of the richness of their communities. The large proportion of rare species significantly contributed to the overall richness observed in the present study. This has very important implications for the methods used to study epibenthic communities, as the sampling methods applied in this study allowed us to examine the community as a whole. Many studies focus on the dominant species, or only the sessile species, and as a result their richness estimates of the community are not as accurate. The large proportion of rare motile species in this study is also important as most biodiversity estimates just get a 'snapshot' of the community, which may be affected by the dispersal, movements and migrations of organisms (Davidson *et al.* 2004).

Accurate representations of richness, along with the concepts of evenness in communities, are important because they are ecological tools that provide insight into communities and are often the proxies establish and maintain protected areas (Ward *et al.* 1999). Conservation practices focused around single species are being replaced in favour of multi-species and ecosystem based management (Simberloff 1998). The goals of many of these newer conservation practices are to maintain total richness as well as populations of rare or threatened species. The primary concept of evenness in a community relates multidimensional niches and the idea that the abundance of each species is determined by combinations of many physical and biological variables that are required for each species survival and reproduction (Brown 1984). Therefore, rare species are organisms that have narrow ecological requirements in the local environment

and are the most susceptible to change. By studying rare species we are therefore not only getting more accurate representation of the richness of the community, but we are gaining insight into the species that are most vulnerable to change (*i.e.* climate change, species introductions) and that are most important for monitoring purposes.

The large proportion of rare species on the settlement arrays also has implications for studies that are attempting to look at succession and the factors that shape communities. Often in these studies the researchers will focus only on the dominant species and may be missing important information (*i.e.* other predators and competitors) than if they looked at the communities as a whole (*e.g.* Greene and Schoener 1982, Greene *et al.* 1983). In this study many of the small grazers and predators were considered to be a rare species. The presence of a small grazer or predator within a community can entirely shift the composition and abundance of species within a community; just as much as large one may (Nydam and Stachowicz 2005). Many of the large motile species were not listed as either dominant or rare because there was not sufficient abundance data for those species. Large motile species are also often predators and grazers that can strongly influence the community dynamics at a site (*e.g.* Nydam and Stachowicz 2007, Roughgarden *et al.* 1988, Connell 1972). An amendment to the procedure utilised in this study would be to include biomass estimates for all species which would reflect population dynamic and energy flow within the community.

The community observed on the settlement arrays is a relatively young one at an early successional stage. It is important to consider that though a species was determined to be rare at this point in time does not imply that the species will remain rare within the community. As an example, *Metridium* sp. individuals were often juveniles that only occupied about 0.5% of the sampling space. However, this solitary species undergoes a significant size increase as it matures to adulthood and can reproduce asexually, by pedal laceration, to form dense clonal colonies (Carlton 2007). Greene and Schoener (1982) found that *M. senile* in a fouling community in Washington did not become an important space occupier until the second year (after about 40 weeks) of succession. The *Metridium* sp. example illustrates that, even though a species is rare, it may still play an important role in shaping the community.

### Abundance and distribution

The ecological pattern of locally abundant species being widespread in distribution and locally rare species being narrowly distributed has been documented and discussed for communities around the world (e.g. Brown 1984; Gaston *et al.* 1997; Gonzalez *et al.* 1998, Gaston *et al.* 2000). The theory that best describes this phenomenon is again based on the concept of multidimensional niches where species that are able acquire sufficient resources to attain a high abundance in on place shoule be able to occur at many other sites (though potentially at lower abundance) over a large area. Whereas, those species that have narrow ecological requirements, and cannot attain high abundances anywhere, will be restricted to the few sites within the geographic area that satisfy their limited needs (Brown 1984). Usually this abundance- distribution relationship is demonstrated by a linear trend. However, the relationship between the abundance and distribution in this study is best depicted by two different equations corresponding to the sessile and motile species data (Figure 10).

The abundance- distribution relationship for the sessile species was best described by a polynomial equation. The trend depicted suggests that species which were found in fewer than 20 samples were weak space competitors that were unable to attain a high abundance. However, at around the 20 sample mark, species that were more prominent in the samples were stronger competitors and had higher abundances. With each increase in the number of samples in which a species was found, the relative abundance increased drastically. This trend suggests to me that, in the space limited environment of the settlement arrays, that there was a threshold abundance for sessile species. If the sessile species were not strong enough competitors to pass this threshold abundance, then they were not likely to be widely distributed.

There were three species that had very low abundances based on the number of samples in which they were found were *H. arctica*, *P. occidentalis*, and *Lichenopora* sp. *H. arctica* and *P. occidentalis* are both solitary organisms that are common in the epibenthic community but do not grow to very large sizes. *Lichenopora* sp. is an encrusting bryozoan that likely had a delayed recruitment period, so the colonies were still young and small (see dominant species section).

In the motile species the abundance distribution trend was best described by a power equation where with every unit increase in the number of samples in which a species was found, it became 1.3 times more abundant. The different equations for the abundance distribution trends for sessile and motile species suggest that there are differences in the way species are able to recruit to the fouling communities based on their lifestyle. The sessile species are more likely affected by the space limitation imposed by fouling communities as the organisms must compete for the primary space available. The motile species are not as strongly affected by the competition for primary space as they are able to utilise the additional dimensions and habitat heterogeneity provided by the sessile species.

#### Introduced Species

In this study we found 11 introduced species and 12 cryptogenic species recruited to the settlement arrays. The overall abundance of each non-native species in this study was variable and abundances ranged from being ranked as among the most dominant species to among the tail end of the rare species.

Five introduced species were ranked among the 'top ten' most dominant for the sessile and motile organisms: *A. polyomm*, *B. violaceus* and *S. japonica* for the sessile, and Amphipod complex 1 and *C. mutica* for the motile. The high representation of introduced species among the dominant species (30% and 20% respectively) indicates that not only are introduced species reaching our coast, but that in these fouling communities they are becoming an integral component of the community. In fact, the average number of introduced species per sample was over one indicating that, in theory, introduced species are so prevalent along the coast that at least one introduced species exists in every fouling community. The abundance and prevalence of non-native species in this study is of strong consideration, as non-natives are known to have negative ecological and economic ramifications.

The strong representation of both *B. violaceus* and *B. schlosseri* may be partly attributed to investigator bias. Identifying the presence and distribution of introduced species along the BC coast was a secondary focus of this study. However, this should not underscore the fact that these species are reaching our coast and are so abundant in fouling communities. Colonial tunicates are very good at competing for space and will

often overgrow and smother existing species, leading to a decrease in local community diversity (Carver *et al.* 2006).

In comparing the abundance-distribution for native with non-native species, we found that they both displayed polynomial trends. However, for the non-native species this increase in abundance per number of samples present increased at a lower number of samples and the slope remained positively offset from the trend for native species. The offset trend indicates that a non-native species had higher abundances than native species that occupied the same number of samples. The non-native species may therefore have a similar distribution to a native species but will be more dominant in the community. This may have important implications for the competitive ability of non-natives relative to native species in space limited environments.

### **Summary**

The invertebrate fouling community observed in this study was very rich, representing a large number of sessile and motile species from a wide range of phyla and classes. Though the community was a very rich one it was dominated by relatively few species. In particular, the sessile species complex *Mytilus* sp. was by far the most abundant and prominent species in the samples. Included in this rich community was a large proportion of rare species, many of which were motile species. The sampling method utilised in this study allowed me to look at the community as a whole, including motile and rare species, and the value gained has important implications for future studies examining biodiversity indices. The abundant sessile and motile species were generally more widespread than species that had low abundances, though this trend was described by different equations for sessile and motile species. The difference in this trend may reflect that the motile and sessile species experienced different degrees of competition in this space limited environment. Introduced and cryptogenic species were found in this study with a few of each being represented as both dominant and rare species. *C. mutica*, a non-native caprellid amphipod was reported for the first time as it was previously unknown in BC waters. Non-native species (introduced and cryptogenic) species had higher abundances than native species that occupied the same number of samples.

## Chapter Two

### Patterns in community composition of subtidal invertebrate fouling communities for the British Columbian coast

#### Introduction

There are many scales at which environmental factors shape the composition of a community. Large scale species distributions are primarily determined by abiotic oceanographic and physiographic features, while at the local scale species distributions are primarily affected by biotic factors such as larval supply, competition, and predations. At regional scales the abiotic and biotic factors together contribute to determine community composition (Zacharias and Roff 2001). In examining community composition for the British Columbia (BC) coast there are six geographic regions where differences in oceanographic and geographic features may contribute to influence the community composition of invertebrate fouling communities. The description of these regions has been compiled from information gathered from Thomson (1981), Zacharias and Roff (2001), Mackas *et al.* (2001), and Gillespie (2007) (Figure 1).

The BC coast spans seven degrees of latitude along the northeast Pacific Ocean and gives way to a complex network of inlets, straits, passes, sounds and narrows. Including the shorelines of the thousands of islands, the BC coastline spans over 27, 000 km.

The Strait of Georgia (SOG) is a relatively warm inland sea that is connected to the Pacific Ocean by the Juan de Fuca Strait at its southern end and the Johnstone Strait at its northern end. It is one of the warmest water masses along the BC coast and in the summer surface water temperatures can reach up to 20°C in certain areas. The major source of freshwater runoff in the SOG is from the Fraser River which has profound effects on the structure and circulation within the SOG and can influence currents as far away as the entrance of Juan de Fuca Strait into Queen Charlotte Sound. The tidal currents in the SOG enter from the Juan de Fuca Strait and most are reflected back at the Northern end of the strait. A major feature of the SOG is that nearly 70% of BC's population lives along the margins. As such, the SOG has the province's largest ports and is a busy waterway for both recreational and commercial traffic.

The Juan de Fuca Strait (JFS) is a long narrow submarine valley that connects the Pacific Ocean to the SOG. Direct exposure to the Pacific Ocean and strong tidal mixing as currents progress along the channel contribute to relatively constant temperature and salinity throughout the year. The JFS is the main route for commercial vessels transporting goods to the major ports in the SOG and Puget Sound in Washington State.

Discovery Passage (DP), Johnstone Strait (JS), and the Queen Charlotte Sound (QCS), together with interconnecting channels, make up the navigational passage between Vancouver Island and the mainland coast of BC. This complex system of waterways connects the SOG to the Pacific Ocean at its northern end. The JS and DP are quite narrow passages that are also characterised as some of the deepest inshore waters in BC. The JS broadens in the shallower QCS basin. The salinity and temperature is relatively uniform along the passage as the area is characterised by rapid tidal streams, constricted passages, and numerous shallow sills that constantly mix the waters. In the summer the surface waters of QCS get a few degrees warmer due to freshwater runoff and solar heat. The area has very few settlements, but relatively high boat traffic due to the protective nature of the channels.

The west coast of Vancouver Island (WCVI) is an exposed, rocky, outer coast. Temperatures off the coast are rarely over 12°C though there are numerous protected and slightly warmer bays and inlets. The low water temperature is due to direct exposure to the Pacific Ocean as well as the upwelling of cold waters along the coast in the summer. The WCVI is in a transition region between the upwelling Northeast Pacific domain caused by the equatorward California Current and the downwelling region generated by the poleward flowing Alaska current. In summer, upwelling conditions generally prevail but the degree to which the coast is influenced by either of the currents fluctuates year by year. The upwelling conditions bring cold, saline, nutrient rich waters to the surface along the coast, stimulating primary productivity. As such, the region is popular for aquaculture and fishing activities.

The north coast of the mainland (NC) is a semi-exposed environment partially protected by the QCI to the west. The coast is a highly broken shoreline of islands, isolated shoals, and countless embayments. The water temperatures of the NC are quite cold as the coast is characterised by complex fjord systems that receive strong freshwater

glacial runoff during the summer months. There are few settlements along the coast, though the Prince Rupert is becoming an increasingly important commercial ship port for the northern coast.

The Queen Charlotte Islands (QCI), or Haida Gwaii, are the most geographically isolated islands in the Northeast Pacific Ocean. However, the basin between the QCI and the NC is relatively shallow and in places only reaches depths of 50 m. On the west coast of the island group the continental shelf drops to over 2500m within only 30m of the shore. The west coast of the QCI is still in this transition zone between the Alaska and California currents but is generally more affected by the downwelling system of the poleward current.

One of the primary aims of community ecology is to examine and explain patterns of natural assemblages of organisms (Ardisson *et al.* 1990). Very little is known about the composition of epibenthic invertebrate communities along the BC coast. In chapter one of this study I identified the species that are recruiting to fouling communities on artificial substrata. In this chapter I will look at patterns in community composition for the BC coast in context of the geographic regions sampled, the timing of sampling, and the depth sampled. I expect to see differences in the six geographic regions outlined based on the oceanographic and geographic features that will influence larval supply, competition, and predation. I will look at the specific assemblages that drive patterns for the coast, with particular attention given to those associated with the dominant *Mytilus* sp. complex. I will also look at patterns in the introduced species community to determine sites of introduction, spread, and potential vectors of transport along the BC coast.

## **Methods**

### **Data analysis**

Three data components were collected for each sample: species presence, sessile species abundances, and motile species abundances. Prior to analysis, the sample data were transformed to presence/absence for the species presence data and were fourth root transformed for the sessile and motile abundance data. The fouling community sampled in this study was very uneven, being dominated by relatively few species. The abundance data was analysed with a fourth root transformation to generate data with a

down-weighting of the dominant species, to allow mid-range and rare species to exert some influence on the calculation of similarity for all the (non-parametric) multivariate representations (Clarke and Warwick 2001).

Depth effects were tested using paired sample T-tests on the species richness and the percent of free space available for the surface (A) and one meter (B) depth at each site. The effects of depth on community composition were then tested using hierarchical agglomerative cluster dendrograms (cluster dendrograms) and analysis of similarity (ANOSIM) generated from Bray-Curtis similarity matrices of the transformed data. Hierarchical agglomerative clusters are generated from similarity matrices, such as Bray-Curtis, and produce dendrogram figures of successive grouping where the y axis indicates the level of similarity between each successive grouping (Clarke and Warwick 2001). ANOSIMs are permutation tests that compute a test statistic to compare the observed difference between groups and within groups. The statistic indicates whether the data reflect the null hypothesis of no difference in community composition between groups ( $R=0$ ) or that all replicates within a group are more similar to each other than the other group(s) ( $R=1$ ). The test statistic is then compared to the permutation distribution and assigned a significance value (Clarke and Warwick 2001).

The date of deployment, the number of days the settlement arrays remained submerged, and the date of collection for each site was highly variable due to the collaborative nature of this study. The date of deployment and the date of collection were transformed to Julian dates. To determine the effects of timing, and to determine which timing components were most influential, regression analyses were run for these three timing components against the percent of free space available and the species richness of the samples. The percent free space available was cube root transformed to meet the assumptions of normality. The date of deployment and the number of days each settlement arrays was submerged were collinear. The trends for these two timing components were similar and only the outcomes for the deployment data will be presented. Two-dimensional (2-d) bubble non-metric multi-dimensional scaling (MDS) ordination plots of the significant timing component(s) were used to determine whether patterns in community composition were determined by the sample timing. MDS ordination plots utilise the same Bray-Curtis similarity matrices as the cluster

dendrograms but instead plot the sites in two dimensional space. The distance between each sample is a representation of their measure of dissimilarity (Clarke and Gorley 2006). Bubbles are then superimposed on these ordination plots with increasing size of the bubble corresponding to the increasing unit of measurement (Clarke and Gorley 2006).

Patterns in community composition were explored using the hierarchical cluster dendrograms of all three data sets. To determine if the geographic area sampled had an effect on the community composition the samples were labelled with corresponding area symbols on the cluster dendrograms and were subsequently tested with ANOSIMs. Similarity levels were selected that represented the first basic level of general clustering of samples and were used in SIMPER (similarity percentages) analysis to determine which species were the most influential (*i.e.* accounted for at least 80% of the similarity) in the grouping of the samples. SIMPER analysis was also utilised to determine the most influential species that contributed to the dissimilarities indicated in community composition for ANOSIM pair-wise comparisons of geographic areas.

*Mytilus* sp. was by far the most prominent and most abundant sessile species in the samples across all geographic areas of this study. *Mytilus* sp. beds and patches are known to increase habitat heterogeneity and harbour other organisms (Tsuchiya 2002). To examine patterns within the *Mytilus* sp. community the datasets were manipulated to only include sites where *Mytilus* sp. was present and hierarchical dendrograms were generated. The effects of geographic area and the influence of species within the groupings were again tested using ANOSIMs and SIMPER analysis respectively.

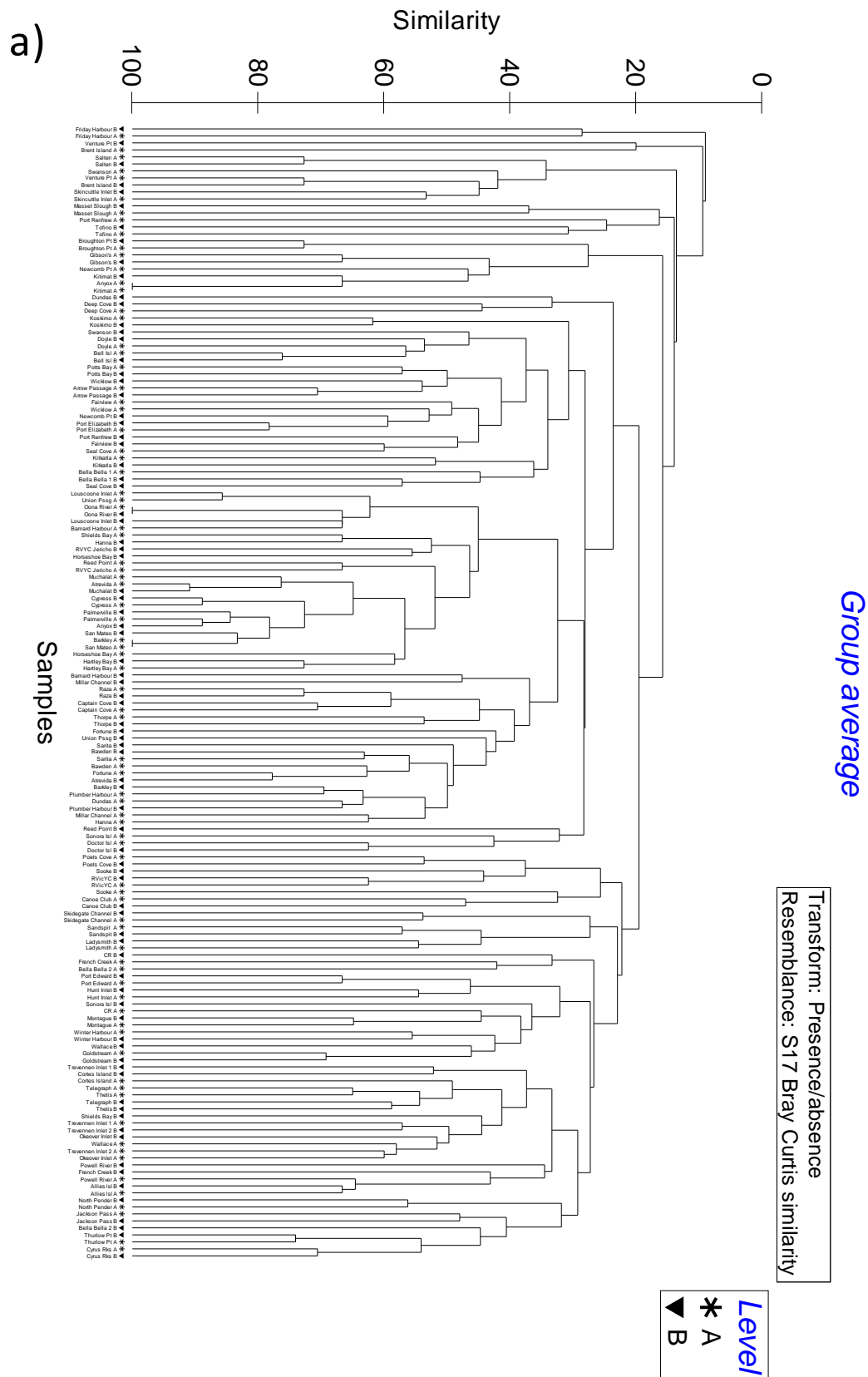
Twelve introduced species were recorded within the fouling community of this study. To examine patterns within the introduced species community the datasets were manipulated to include only introduced species and hierarchical cluster dendrograms were generated from the data. The effects of geographic area, and the type of structure from which the settlement arrays were hung, on community composition was tested using ANOSIMs. SIMPER analysis was again utilised to highlight the influential species within clusters and those that contributed to the dissimilarities observed in any ANOSIM pairwise comparisons.

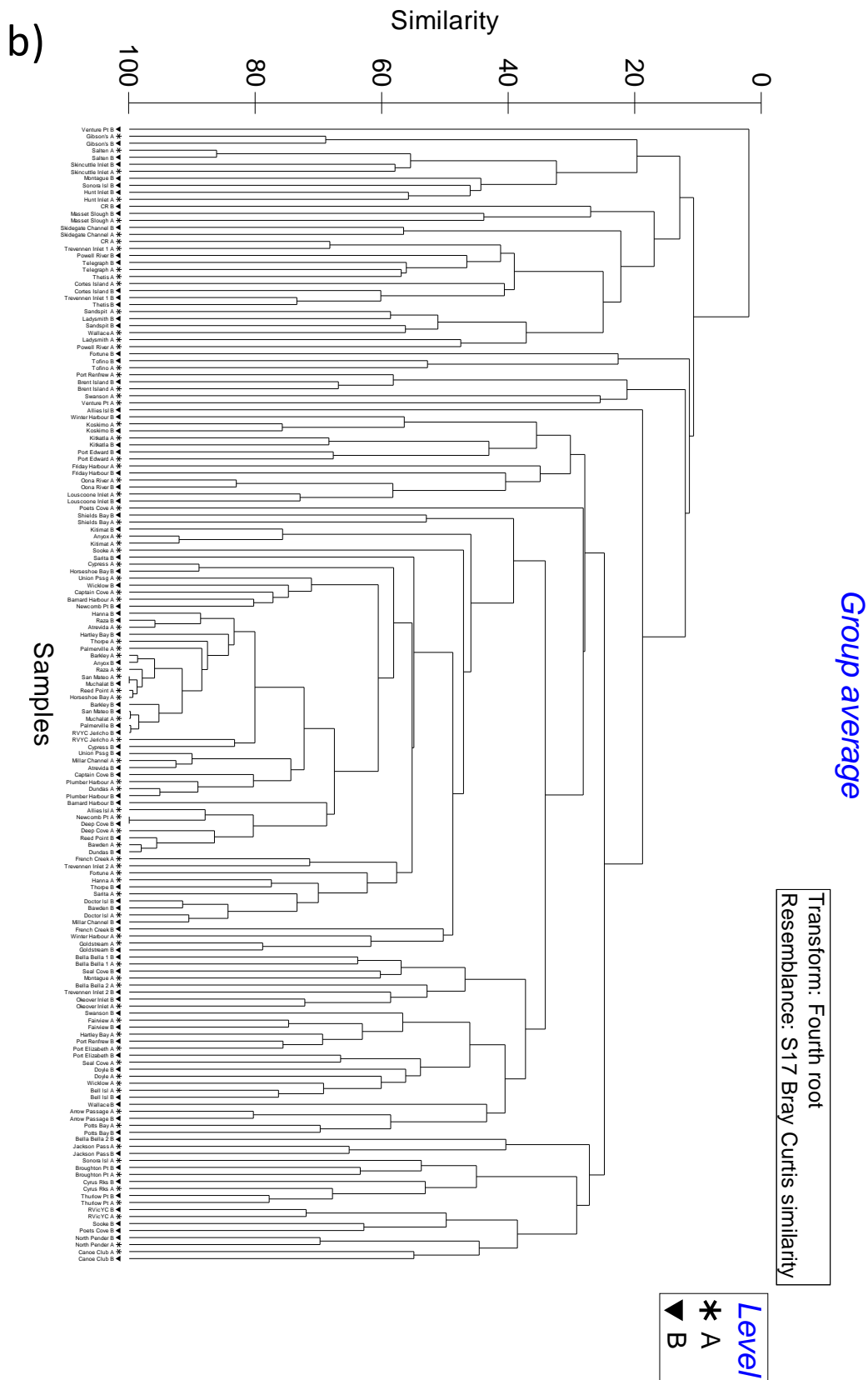
All multivariate analyses were done using multivariate techniques included in the PRIMER program (Plymouth Routines In Multivariate Ecological Research; Clarke, 1993).

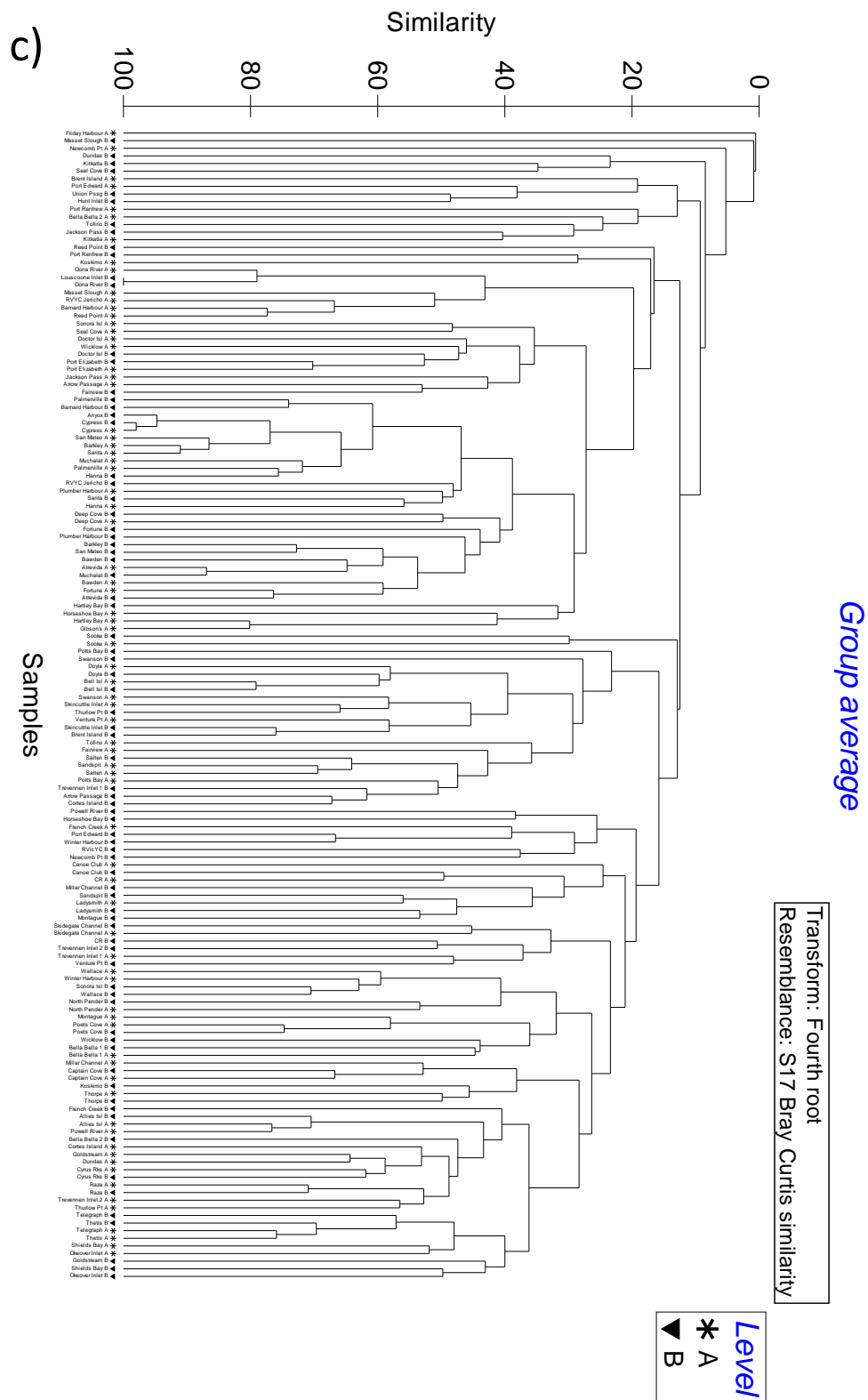
## Results

### Depth Level

The average species richness at the surface (A: 11.3 species +/- 0.7 SE) was significantly lower than the average richness at one meter depth (B: 12.3 species +/- 0.6 SE) (Paired t-test:  $t=2.279$ ,  $df=80$ ,  $0.01 < p < 0.05$ ). However, the average percent free space available at the surface (A: 18.0% +/- 3.0% SE), was not significantly different from that at one meter depth (B: 17.9% +/- 3.2% SE) (Paired t-test:  $t=0.028$ ,  $df=80$ ,  $p=0.978$ ). Across the datasets, there was no difference in the community composition between the two depths (ANOSIMS:  $r \sim 0$ ,  $p \gg 0.05$ ). The two depth levels from one site often shared the highest similarity or were found in the same cluster (Figures 12a, b, c). The similarity levels between the depth levels from one site were lowest for the motile species abundance data (Table 12).







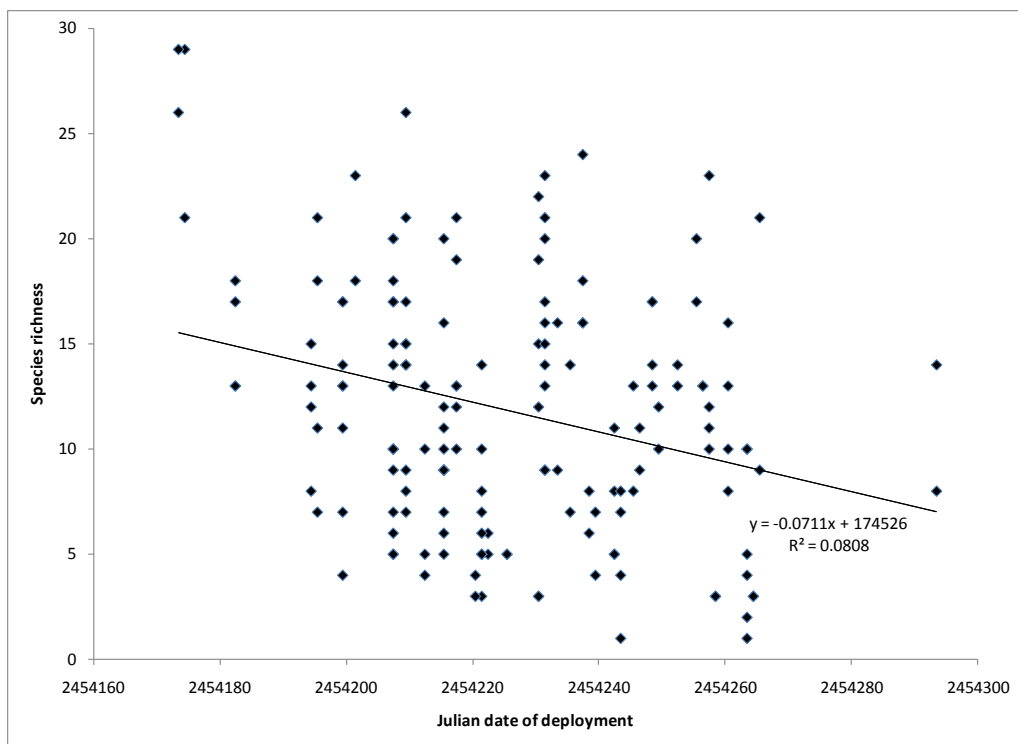
**Figure 12. Hierarchical cluster dendrograms of sample community composition based on a) species presence, b) sessile species abundances, and c) motile species abundances. Surface (A) depth levels are indicated by asterisks and one meter (B) depth levels by solid triangles.**

**Table 12. The number of sites (out of 81) where the surface (A) and one meter (B) depth levels shared the highest similarity in the hierarchical cluster dendrogram.**

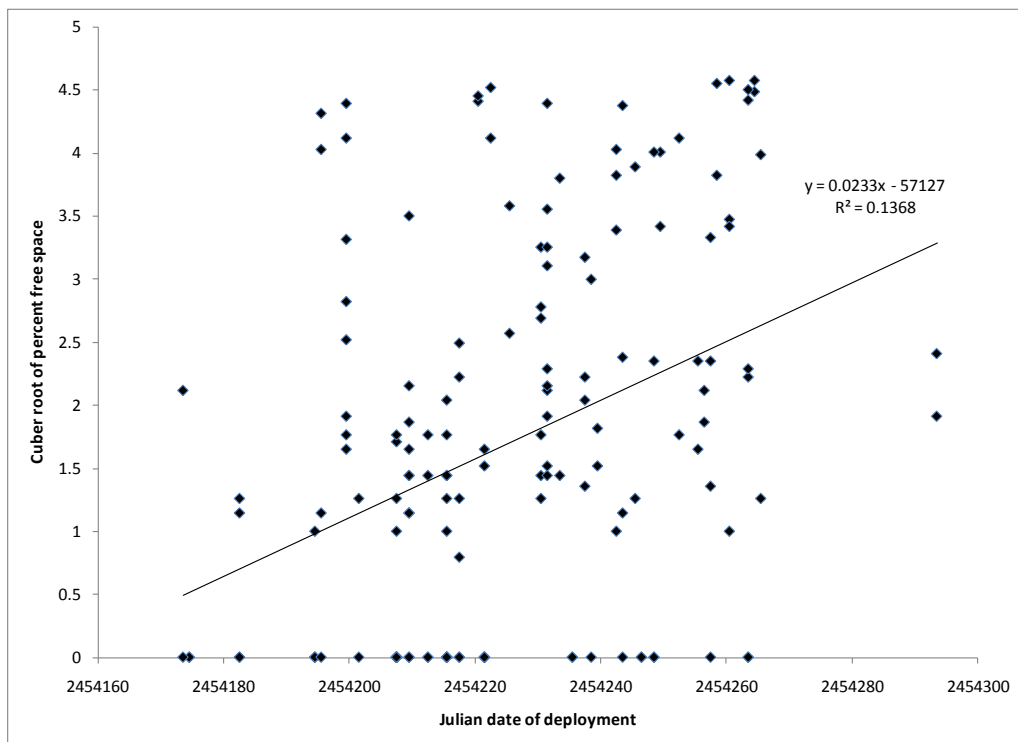
Data set	Number of sites A&B together
Species presence	36
Sessile species abundances	27
Motile species abundances	15

### Timing

The collection date (Julian date of collection) had no significant relationship with the species richness (Regression:  $F_{1,160}=1.405$ ,  $p=0.238$ ) of each sample or the (cuberoot) percent of free space available (Regression:  $F_{1,160}=1.853$ ,  $p=0.175$ ). The species richness of each sample decreased as the settlement arrays were deployed later in the year (Julian date of deployment), though very little of the observed variance across the samples is explained by this timing component (Regression:  $F_{1,160}=14.06$ ,  $p<0.001$ ,  $r^2=0.075$ ; Figure 13). Also, the amount of free space available increased as the settlement arrays were deployed later in the year, though again very little of the observed variance is accounted for (Regression:  $F_{1,160}=25.36$ ,  $p<0.001$ ,  $r^2=0.131$ ; Figure 14). The community composition was not affected by the timing of deployment (Figure 15).

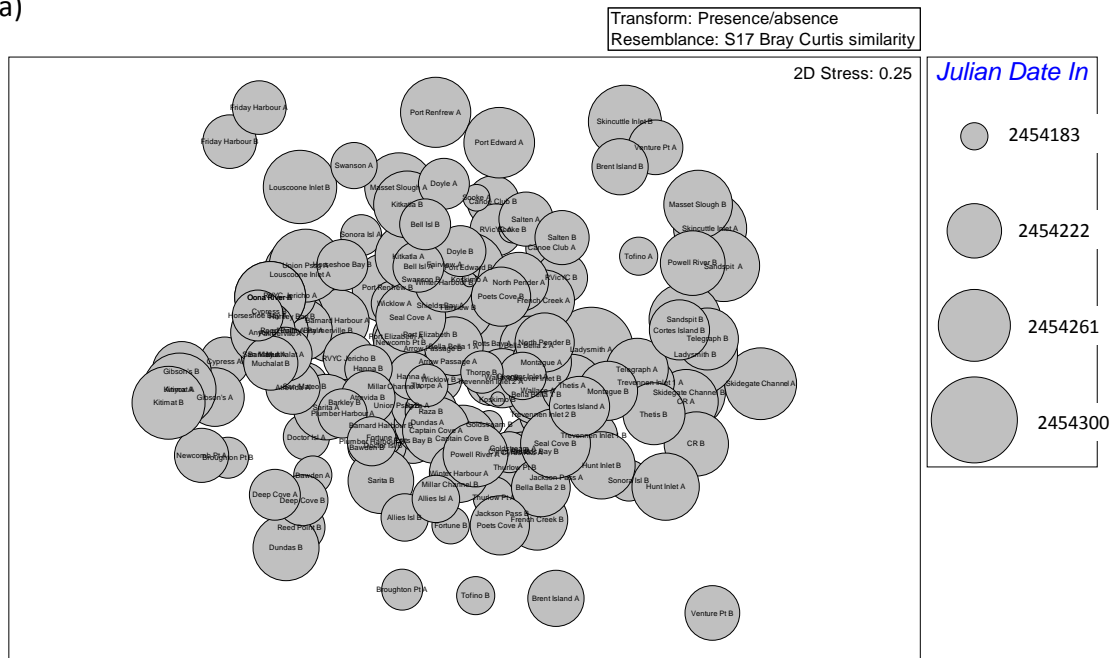


**Figure 13.** The relationship of species richness with the Julian date of deployment of each sample.

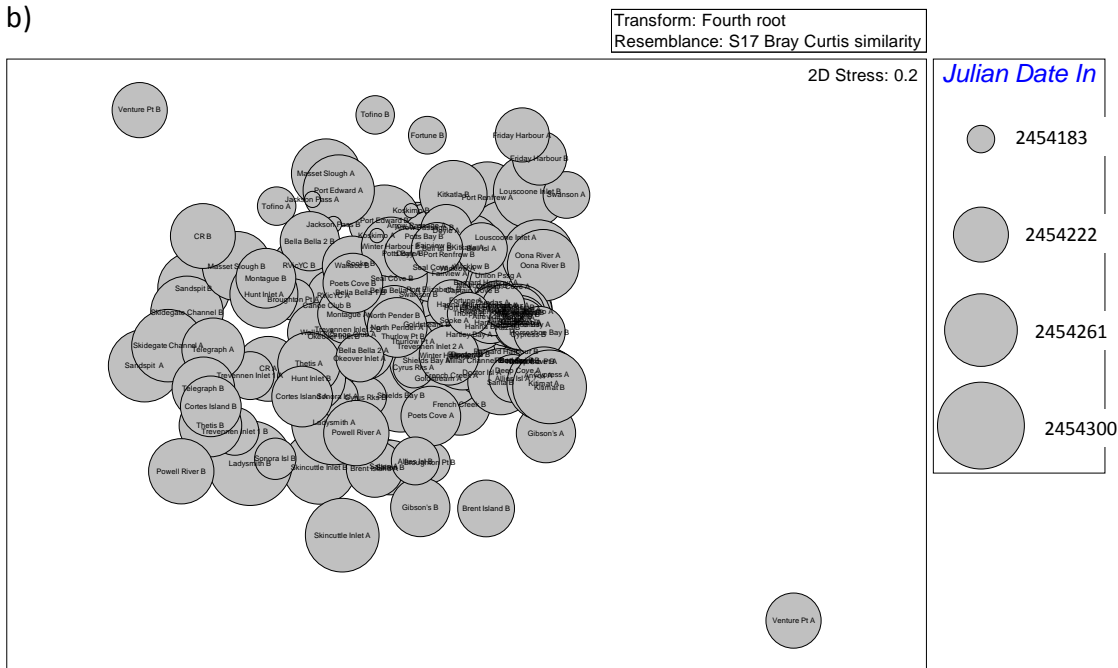


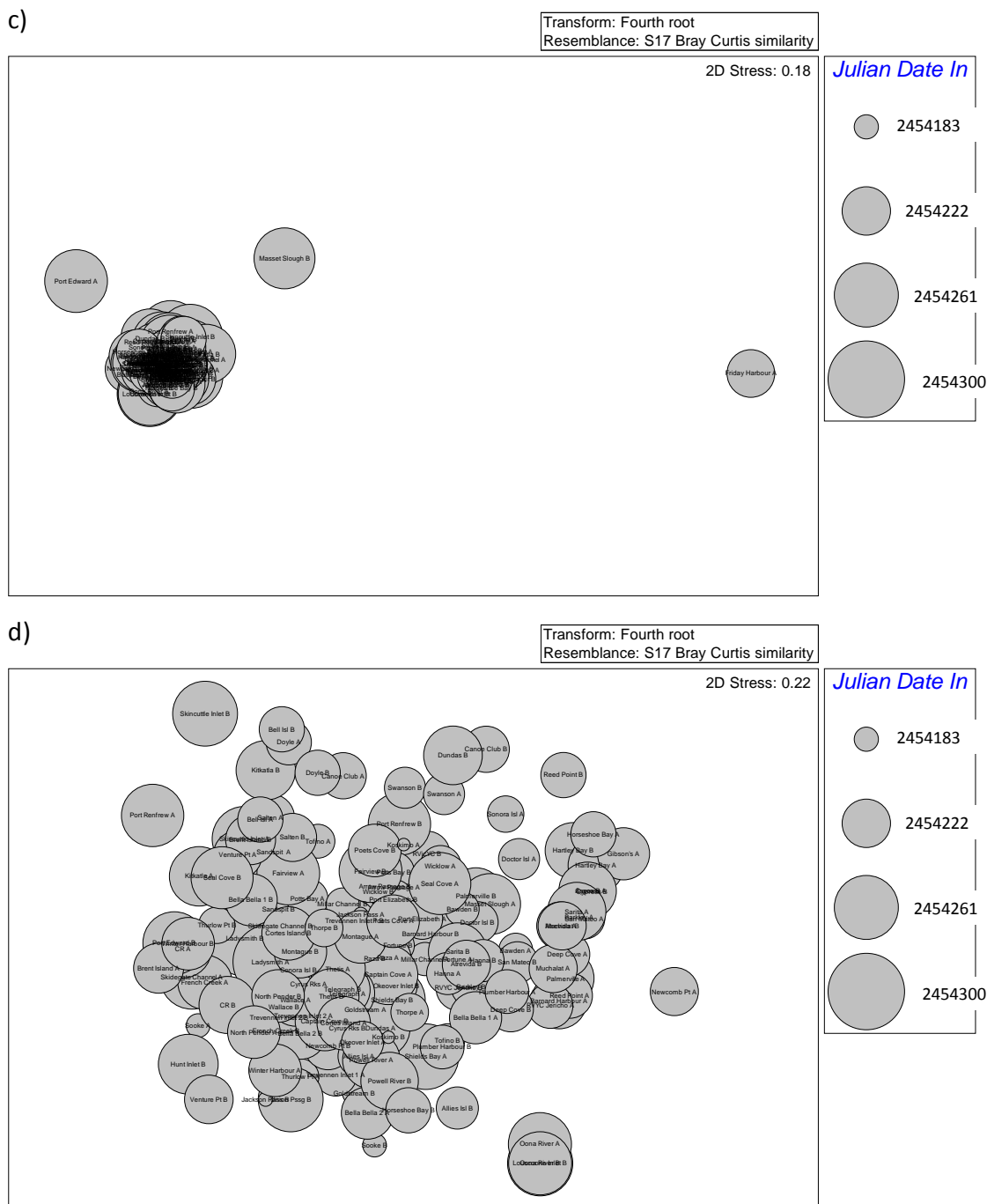
**Figure 14.** The relationship of the (cube root) percent free space available with the Julian date of deployment of each sample.

a)



b)





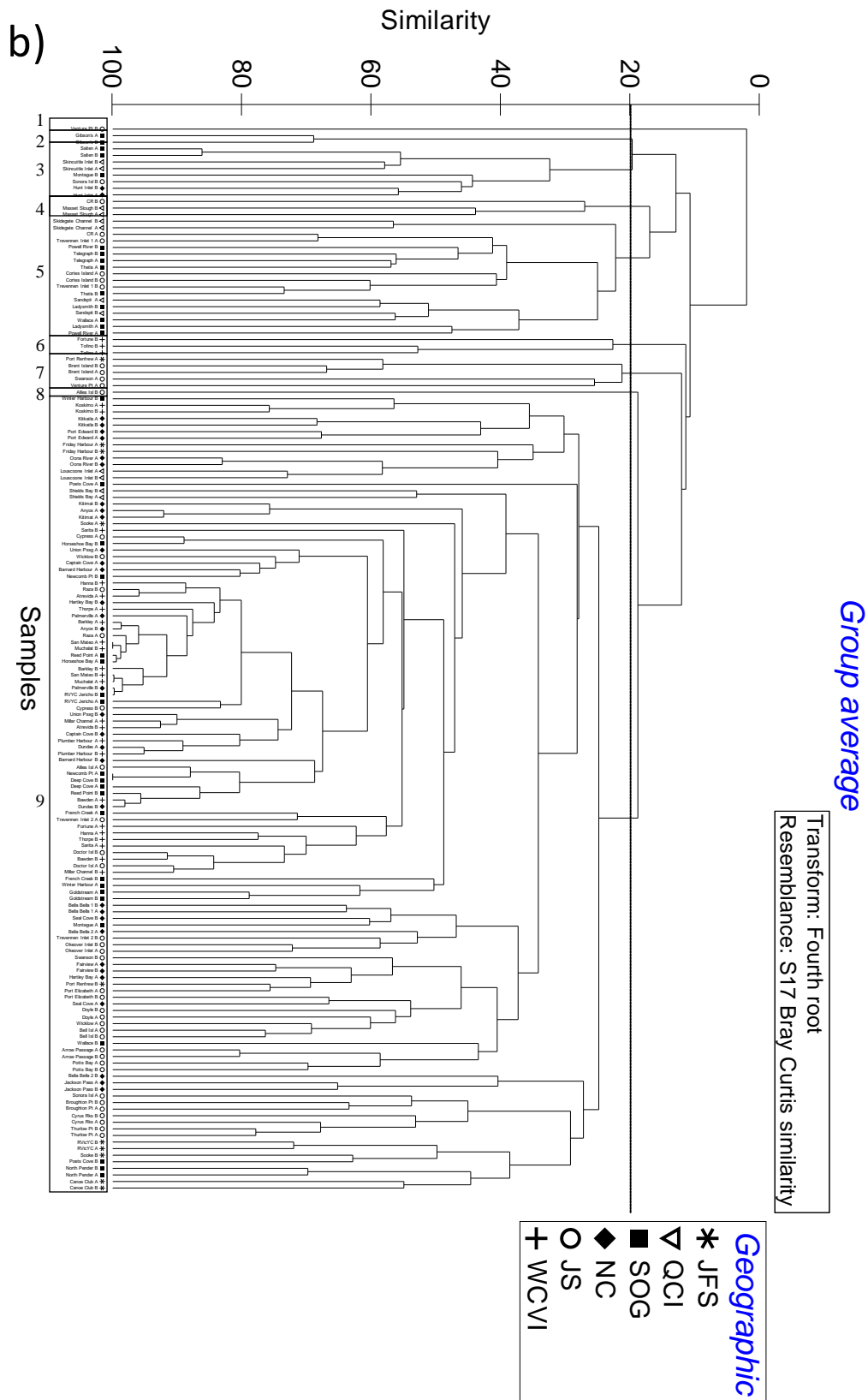
**Figure 15. Two dimensional MDS bubble plots of the Julian date of deployment for a) species presence, b) sessile species abundances, c) motile species abundances and d) motile species abundance for samples excluding Friday Harbor A (JFS), Masset Slough B (QCI), and Port Edward A (NC). Increasing bubble size corresponds to a later deployment date**

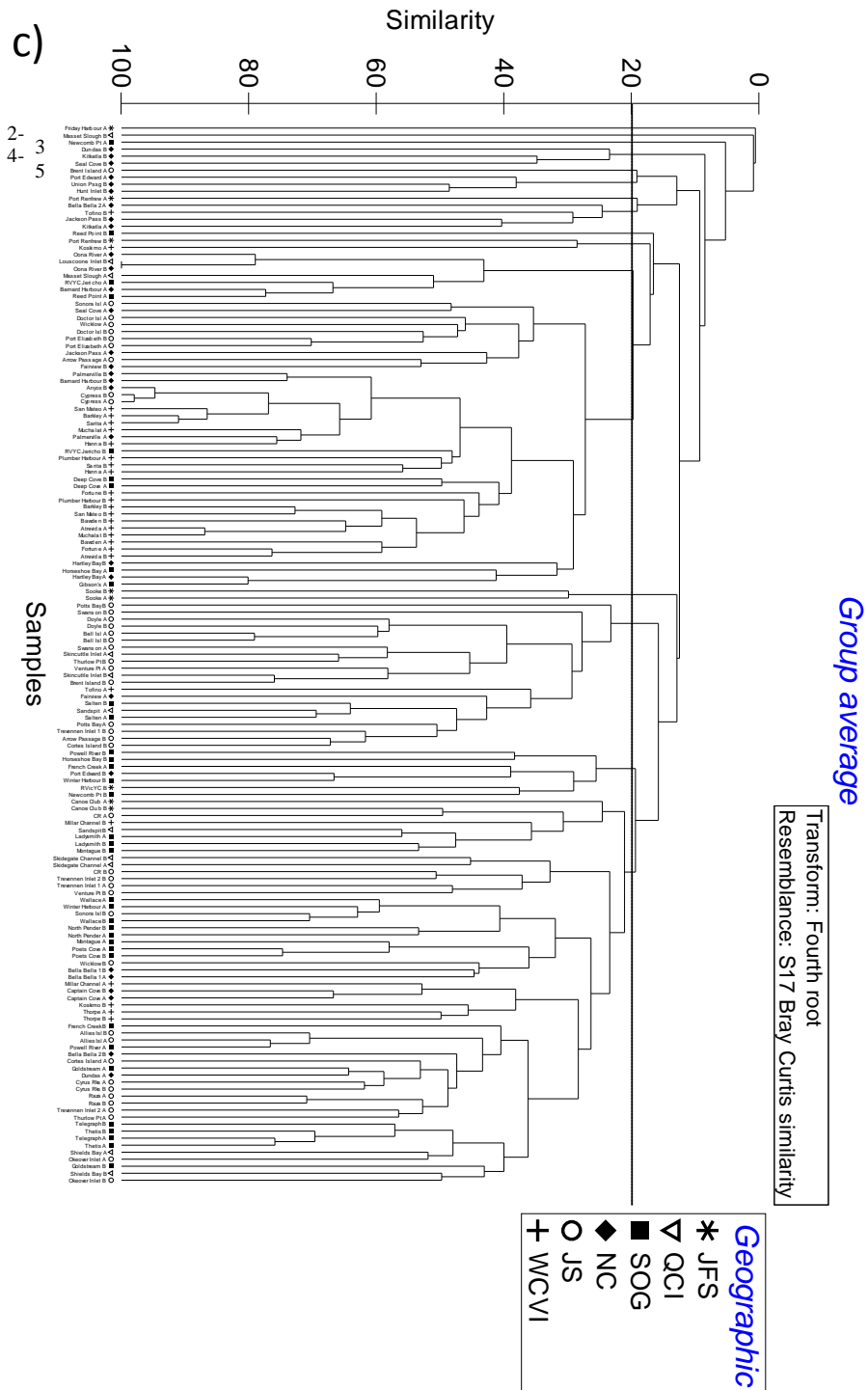
### Geographic area and species assemblages

Similarities in community composition occurred across the geographic areas for species presence (ANOSIM:  $r=0.202$ ,  $p=0.001$ ; Figure 16a), the sessile species abundance data (ANOSIM:  $r=0.141$ ,  $p=0.001$ ; Figure 16b), and the motile species abundance data (ANOSIM:  $r=0.185$ ,  $p=0.001$ ; Figure 16c) of each site.

In the species presence data (Figure 16a and Table 13), Friday Harbor had a community composition that was very dissimilar from the rest of the samples (only 10% similarity) due to the influence of only one sessile species, *B. crenatus*. Two samples from the Johnstone Strait, Venture Point B and Brent Island A, were the next two samples with dissimilar community compositions due to the influence of only one polychaete species, *C. occidentale*. Eighty samples (cluster 7), from all geographic regions, had species assemblages that were primarily influenced by the presence of *Mytilus* sp., *B. crenatus*, and Amphipod complex 2 (60% of the similarity). Also influential in this species assemblage was *Lichenopora* sp., *H. arctica*, *E. quadrioculata*, *N. vexillosa*, and *N. procera*. Fifty-eight samples (cluster 8), from all geographic areas except WCVI, were influenced by 15 species that each shared a proportionally low percent of the similarity of the cluster.







**Figure 16. Hierarchical cluster dendrograms of sample community composition based on a) species presence, b) sessile species abundances, and c) motile species abundances. Geographic areas are denoted by the following symbols: Juan de Fuca Strait (JFS)-asterisks, Queen Charlotte Islands (QCI)- open triangles, Strait of Georgia (SOG)-solid squares, North coast of mainland BC (NC)- solid diamonds, Johnstone Strait (JS)- open circles, and West coast of Vancouver Island (WCVI)- crosses. Square blocks with numbering emphasise the clusters based on 20% similarity.**

**Table 13. The influential species of the clusters observed at the 20% similarity level for the species presence in the samples.**

Species	Average abundance	Average similarity	Similarity/ SD	Percent contribution	Cumulative percent
<b>Cluster 1 (Friday Harbor A and B)- average cluster similarity is 28.57</b>					
<i>B. crenatus</i>	1.00	28.57	NA	100.00	100.00
<b>Cluster 2 (Venture Point A and Brent Island b)- average cluster similarity is 20.00</b>					
<i>C. occidentale</i>	1.00	20.00	NA	100.00	100.00
<b>Cluster 3 (Salten A to Skincuttle Inlet A)- average cluster similarity is 42.33</b>					
<i>J. staudei</i>	1.00	13.00	4.04	30.72	30.72
<i>C. anomala</i>	0.71	7.05	0.90	16.64	47.36
<i>N. procera</i>	0.71	5.85	0.88	13.81	61.17
<i>M. membranacea</i>	0.71	5.70	0.88	13.47	74.63
<i>Lichenopora</i> sp.	0.57	3.32	0.60	7.85	82.48
<b>Cluster 4 (Masset A and B)- average cluster similarity is 37.04</b>					
<i>Haliclona</i> sp.	1.00	7.41	N/A	20.00	20.00
<i>P. s. potswaldi</i>	1.00	7.41	N/A	20.00	40.00
<i>Lichenopora</i> sp.	1.00	7.41	N/A	20.00	60.00
<i>C. annulata</i>	1.00	7.41	N/A	20.00	80.00
<i>C. inflata</i>	1.00	7.41	N/A	20.00	100.00
<b>Cluster 5 (Port Renfrew A to Tofino A)- average cluster similarity is 26.70</b>					
<i>C. infundibuliformis</i>	1.00	5.82	8.77	21.80	21.80
<i>Lichenopora</i> sp.	1.00	5.82	8.77	21.80	43.60
<i>S. s. elongata</i>	0.067	2.15	0.58	8.05	51.65
<i>C. laeviscula</i>	0.067	2.15	0.58	8.05	59.71
<i>P. cornutus</i>	0.067	1.96	0.58	7.34	67.05
Gammaridea INDET	0.067	1.96	0.58	7.34	74.39
<i>S. insignis</i>	0.067	1.71	0.58	6.40	80.79
<b>Cluster 6 (Broughton Point B to Kitimat A)- average cluster similarity is 42.52</b>					
<i>Mytilus</i> sp.	1.0	39.39	2.20	92.62	92.62
<b>Cluster 7 (Dundas B to Doctor Island B)- average cluster similarity is 33.34</b>					
<i>Mytilus</i> sp.	0.98	9.71	2.05	29.14	29.14
<i>B. crenatus</i>	0.78	6.22	0.98	18.64	47.78
Amphipod complex 2	0.66	4.64	0.79	13.93	61.71
<i>Lichenopora</i> sp.	0.45	1.58	0.45	4.75	66.46
<i>H. arctica</i>	0.44	1.46	0.46	4.39	70.85
<i>E. quadrioculata</i>	0.42	1.34	0.43	4.02	74.87
<i>N. vexillosa</i>	0.34	1.14	0.34	3.43	78.30
<i>N. procera</i>	0.39	1.08	0.40	3.24	81.54
<b>Cluster 8 (Poets Cove A to Cyrus Rocks B)- average cluster similarity is 27.83</b>					
<i>N. procera</i>	0.76	4.07	1.07	14.62	14.62
<i>Mytilus</i> sp.	0.66	2.94	0.82	10.55	25.17
<i>S. japonica</i>	0.59	2.47	0.69	8.88	34.06
<i>C. occidentale</i>	0.57	2.14	0.66	7.69	41.74
<i>P. occidentalis</i>	0.53	1.89	0.61	6.81	48.55
<i>E. quadrioculata</i>	0.53	1.89	0.60	6.78	55.33
<i>B. violacues</i>	0.45	1.28	0.48	4.61	59.95
<i>O. dichotoma</i>	0.40	0.98	0.41	3.52	63.47
<i>M. borealis</i>	0.38	0.84	0.40	3.02	66.48
<i>Halichondria</i> spp.	0.34	0.81	0.35	2.90	69.39
<i>C. inflata</i>	0.34	0.69	0.35	2.48	71.86
<i>S. columbiana</i>	0.31	0.69	0.31	2.47	74.33
Amphipod complex 1	0.29	0.60	0.29	2.14	76.48

Species	Average abundance	Average similarity	Similarity/SD	Percent contribution	Cumulative percent
Juvenile seastars	0.29	0.56	0.29	2.03	78.50
<i>Metridium</i> sp.	0.29	0.50	0.29	1.79	80.29

In the sessile species abundance data (Figure 16b and Table 14), the community composition of Venture Point B was the most dissimilar (only 5% similarity) to all other samples. Only *D. occidentalis* and a small amount of unknown spirorbid were present in this sample. Two groups of samples separate at 10% similarity based primarily on whether *Mytilus* sp. was dominant in the sample community or not. There were roughly nine species associations found along the coast; most of which were in samples from more than one geographic area. There were 121 (75%) samples (cluster 9), from all geographic areas, that were influenced by the abundance of *Mytilus* sp., *B. crenatus*, and *Lichenopora* sp. The *Mytilus* sp. and *B. crenatus* association was a particularly strong one, as within this large cluster there was a smaller grouping of 53 samples sharing 55% similarity. More than 90% of this similarity was influenced by the abundances of just *Mytilus* sp. and *B. crenatus*. Allies Island B (cluster 8) was the only sample within the *Mytilus* sp. dominated sites to have a significant percent (86%) cover of *B. schlosseri*. A relatively large number of samples from the SOG, QCI, and JS had a species assemblage influenced by the abundance of *S. japonica*, *Halichondria* spp., *B. violaceus*, *C. pallasiana*, and *O. dichotoma*.

**Table 14. The influential species of the clusters observed at the 20% similarity level for the samples' sessile species abundance data.**

Species	Average abundance	Average similarity	Similarity/SD	Percent contribution	Cumulative percent
<b>Cluster 1 (Venture Point B)</b>					
<b>Cluster 2 (Gibson's A and B)- average cluster similarity is 68.93</b>					
<i>Conopeum reticulum</i>	2.96	53.57	NA	77.72	77.72
<i>Mytilus</i> sp.	1.19	15.36	NA	22.28	100.00
<b>Cluster 3 (Salten A to Hunt A)- average cluster similarity is 41.65</b>					
<i>Clytia</i> sp.	2.51	24.11	1.99	57.88	57.88
<i>S. columbiana</i>	0.97	6.30	0.99	15.14	73.02
<i>Lichenopora</i> sp.	0.54	2.63	0.50	6.31	79.33
<i>P. occidentalis</i>	0.61	2.16	0.51	5.20	84.53
<b>Cluster 4 (CR B to Masset A)- average cluster similarity is 32.65</b>					
<i>C. inflata</i>	1.95	17.40	1.59	53.29	53.29
<i>S. japonica</i>	0.91	4.01	0.58	12.27	65.55
<i>P. s. potswaldi</i>	1.42	3.39	0.58	10.37	75.93
<i>Haliclona</i> sp.	0.74	2.85	0.58	8.72	84.65

<b>Cluster 5 (Skidegate B to Powell River A)- average cluster similarity is 32.01</b>					
<i>S. japonica</i>	1.43	7.87	1.09	24.57	24.57
<i>Halichondria</i> spp.	1.43	6.66	0.68	20.81	45.38
<i>B. violaceus</i>	1.24	6.52	0.89	20.38	65.76
<i>C. pallasiana</i>	0.89	3.18	0.44	9.92	75.68
<i>O. dichotoma</i>	0.61	1.42	0.38	4.42	80.10
<b>Cluster 6 (Fortune B to Tofino A)- average cluster similarity is 32.73</b>					
<i>A. polyoum</i>	2.06	20.19	3.63	61.69	61.69
<i>C. infundibuliformis</i>	1.03	5.45	0.58	78.33	78.33
<i>Lichenopora</i> sp.	0.70	3.85	0.58	90.10	90.10
<b>Cluster 7 (Port Renfrew A to Venture Point A)- average cluster similarity is 33.65</b>					
<i>O. dichotoma</i>	1.76	16.87	0.61	50.14	50.14
<i>M. membranacea</i>	1.11	13.97	0.95	41.51	91.65
<b>Cluster 8 (Allies Island B)</b>					
<b>Cluster 9 (Winter Harbour B to Canoe Club B)- average cluster similarity is 38.10</b>					
<i>Mytilus</i> sp.	2.22	23.04	1.28	60.45	60.45
<i>B. crenatus</i>	1.11	7.11	0.75	18.65	79.11
<i>Lichenopora</i> sp.	0.53	1.72	0.43	4.52	83.63

There were a number of sites (RVicYC A, Louscoone Inlet A, Masset B, Boughton A and B, Union Passage A, Port Ed A, Hunt Inlet A, Gibson's B, Friday Harbor B, Anyox A, and Kimimat A and B) along the coast that did not have any motile species. In the motile species abundance data for the remaining sites (Figures 16c and Table 15), Friday Harbor A and Masset Slough B had community compositions that were very different (less than 5% similarity) from the rest of the samples. Friday Harbor A had a single *Notocomplana* sp. present, whereas Masset Slough B had two unidentified nemertean and a single *M. fernaldi*. Fifty-five samples (cluster 16), from all geographic areas, had species assemblages where over two thirds of the similarity was attributed to the abundance of just three species: *N. procera*, *C. occidentale* and *E. quadrioculata*. Forty-one samples (cluster 12), from all geographic areas except the QCI and JFS, were influenced strongly (80% of similarity) by the abundance of Amphipod complex 2, *N. vexillosa*, and *G. oregonense*. Twenty-one samples (cluster 14), from all areas except JFS, has a species assemblage influenced by the abundance of *J. staudei*, *N. procera*, and *C. anomala*.

**Table 15. The influential species of the clusters observed at the 20% similarity level for the samples' motile species abundance data.**

Species	Average abundance	Average similarity	Similarity/SD	Percent contribution	Cumulative percent
<b>Cluster 1 (Friday Harbor A)</b>					
<b>Cluster 2 (Masset Slough B)</b>					
<b>Cluster 3 (Newcomb Point A)</b>					
<b>Cluster 4 (Dundas B to Seal Cove B)-average cluster similarity is 27.26</b>					
<i>L. chloranota</i>	1.06	11.56	8.27	42.40	42.40
Amphipod complex 3	1.03	4.33	0.58	15.88	58.29
<i>E. habei</i>	0.84	4.20	0.58	15.40	73.69
<i>P. cornutus</i>	0.80	3.64	0.58	13.36	87.05
<b>Cluster 5 (Brent Island A)</b>					
<b>Cluster 6 (Port Ed A to Hunt Inlet B)- average cluster similarity is 41.60</b>					
<i>E. habei</i>	1.17	34.20	3.21	82.22	82.22
<i>C. occidentale</i>	0.73	7.40	0.58	17.78	100.00
<b>Cluster 7 (Port Renfrew A)</b>					
<b>Cluster 8 (Bella Bella 2 A to Kitkatla A)- average cluster similarity is 24.91</b>					
<i>C. occidentale</i>	1.05	11.26	3.25	39.11	39.11
Gammaridae INDET	1.03	5.66	0.87	19.66	58.77
<i>P. cornutus</i>	0.92	5.64	0.81	19.60	78.36
Doridacea INDET	0.50	2.11	0.41	7.33	85.70
<b>Cluster 9 (Reed Point B)</b>					
<b>Cluster 10 (Port Renfrew B to Koskimo A) average cluster similarity is 28.56</b>					
Syllidae INDET	1.25	7.76	NA	27.16	27.16
<i>C. laeviscula</i>	1.78	7.76	NA	27.16	54.32
<i>N. procera</i>	1.09	6.52	NA	22.84	77.16
Amphipod complex 2	1.09	6.52	NA	22.84	100.00
<b>Cluster 11 (Oona A to Reed Point A)- average cluster similarity is 54.30</b>					
Amphipod complex 1	1.43	44.94	2.17	82.77	82.77
<b>Cluster 12 (Sonora Island A to Gibsons's A)- average cluster similarity is 36.74</b>					
Amphipod complex 2	1.92	23.63	2.01	64.33	64.33
<i>N. vexillosa</i>	0.72	4.54	0.58	12.36	76.69
<i>G. oregonense</i>	0.53	2.61	0.38	7.09	83.78
<b>Cluster 13 (Sooke A and B)- average cluster similarity is 29.90</b>					
<i>Monocorophium</i> sp.	1.60	15.71	NA	52.53	52.53
<i>M. borealis</i>	1.52	14.91	NA	47.47	100.00
<b>Cluster 14 (Potts Bay B to Cortes Island B)-average cluster similarity is 35.41</b>					
<i>J. staudei</i>	1.81	18.54	2.24	52.37	52.37
<i>N. procera</i>	0.75	5.92	0.71	16.72	69.09
<i>C. anomala</i>	0.89	4.51	0.50	12.74	81.82
<b>Cluster 15 (Powell River B to Newcomb Point B)- average cluster similarity 30.99</b>					
<i>N. procera</i>	1.20	29.18	2.66	94.16	94.16
<b>Cluster 16 (Canoe Club A to Okeover Inlet B)- average cluster similarity is 28.38</b>					
<i>N. procera</i>	1.28	8.87	1.32	31.25	31.25
<i>C. occidentale</i>	0.86	5.53	0.89	19.47	50.72
<i>E. quadrioculata</i>	0.80	4.84	0.83	17.05	67.77
<i>M. borealis</i>	0.66	2.49	0.51	8.76	76.54
Amphipod complex 1	0.53	1.53	0.34	5.40	81.93

Despite the strong similarity in community composition across geographic areas, pairwise comparisons of the geographic regions do show that there are some differences in the species assemblages of the area. Although adjacent geographically, the JFS and WCVI differ in community composition based on species presence (Pairwise ANOSIM:  $r=0.672$ ,  $p=0.001$ ; Table 16), sessile species abundance (Pairwise ANOSIM:  $r=0.518$ ,  $p=0.001$ ; Table 16), and motile species abundance (Pairwise ANOSIM:  $r=0.664$ ,  $p=0.001$ ; Table 16).

**Table 16. The influential species that account for the difference in community composition for the JFS with the WCVI.**

Species	Avg abundance JFS	Avg abundance WCVI	Avg Dissimilarity	Diss./SD	Percent contribution	Cumulative percent
<b>Species presence</b>						
<i>N. vexillosa</i>	0.00	0.85	4.04	1.57	4.88	4.88
Amphipod complex 2	0.20	0.73	3.13	1.04	3.78	8.66
<i>H. arctica</i>	0.00	0.65	2.74	1.13	3.31	11.98
<i>Mytilus</i> sp.	0.60	0.88	2.24	0.71	2.70	14.68
<i>E. quadrioculata</i>	0.10	0.54	2.23	0.93	2.69	17.38
<i>B. violaceus</i>	0.60	0.04	2.16	1.13	2.62	19.99
<b>Sessile species abundance</b>						
<i>Mytilus</i> sp.	1.05	2.57	12.43	1.11	16.28	16.28
<i>O. dichotoma</i>	1.01	0.28	6.05	0.79	7.92	24.20
<i>B. crenatus</i>	1.75	1.01	5.64	1.25	7.38	31.57
<i>B. violaceus</i>	1.09	0.07	4.80	1.10	6.28	37.86
<i>H. arctica</i>	0.00	0.76	4.41	1.08	5.78	43.63
<i>Lichenopora</i> sp.	0.35	0.53	3.41	0.95	4.47	48.10
<b>Motile species abundance</b>						
Amphipod complex 2	0.27	1.43	9.77	1.09	10.82	10.82
<i>N. vexillosa</i>	0.00	1.17	8.44	1.54	9.34	20.16
<i>G. oregonense</i>	0.18	0.47	3.95	0.70	4.37	24.53
<i>E. gracile</i>	0.25	0.59	3.81	0.83	4.22	28.75
<i>E. quadrioculata</i>	0.25	0.59	3.65	0.94	4.04	32.79
<i>N. procera</i>	0.43	0.49	3.50	0.92	3.88	36.66

In the richness data, *N. procera* and *H. arctica* were prominent in WCVI samples but absent from JFS samples. Additionally, Amphipod complex 2, *Mytilus* sp. and *E. quadrioculata* were found in many more samples along the WCVI. The tunicate *B. violaceus* was found more prominently in the JFS. In the sessile species data a large proportion of this difference is attributed to the fact that *Mytilus* sp. was far more abundant on the WCVI. *O. dichotoma*, *B. crenatus*, and *B. violaceus* were more

abundant in the JFS. In the motile species data a large proportion of the observed difference is attributed to the fact that both Amphipod complex 2 and *N. vexillosa* were far more abundant on the WCVI.

The QCI and WCVI also differed in community composition based on species presence (Pairwise ANOSIM:  $r=0.659$ ,  $p=0.001$ ; Table 17), sessile species abundance (Pairwise ANOSIM:  $r=0.614$ ,  $p=0.001$ ; Table 17), and motile species abundance (Pairwise ANOSIM:  $r=0.637$ ,  $p=0.001$ ; Table 17). In the species richness data a number of species (Amphipod complex 2, *Mytilus* sp., *H. arctica*, *B. crenatus*) were more prevalent in WCVI samples. Additionally, *N. vexillosa* was not present in any QCI samples, though it was in WCVI samples. In the sessile species data, *Mytilus* sp. were far more abundant in WCVI samples than QCI samples (accounts for over 19% of the dissimilarity). *S. japonica* and *C. pallasiana* were more abundant in QCI samples, whereas *B. crenatus* and *H. arctica* were more abundant in WCVI samples. In the motile species data the difference between the two areas was driven by the strong abundance of Amphipod complex 2 and *N. vexillosa* in the WCVI relative to the QCI samples.

**Table 17. The influential species that account for the difference in community composition for the QCI with the WCVI.**

Species	Avg abundance QCI	Avg abundance WCVI	Avg dissimilarity	Diss./SD	Percent contribution	Cumulative percent
<b>Species presence</b>						
<i>N. vexillosa</i>	0.00	0.85	4.61	1.65	5.38	5.38
Amphipod complex 2	0.17	0.73	3.72	1.13	4.35	9.74
<i>Mytilus</i> sp.	0.25	0.88	3.54	1.22	4.13	13.87
<i>H. arctica</i>	0.08	0.65	3.02	1.11	3.53	17.41
<i>B. crenatus</i>	0.33	0.65	2.68	0.96	3.14	20.54
<b>Sessile species abundance</b>						
<i>Mytilus</i> sp.	0.46	2.57	16.63	1.55	19.45	19.45
<i>S. japonica</i>	1.02	0.03	6.36	1.02	7.45	26.89
<i>B. crenatus</i>	0.36	1.01	6.29	1.23	7.36	34.25
<i>H. arctica</i>	0.12	0.76	5.13	1.15	6.01	40.25
<i>C. pallasiana</i>	0.79	0.00	4.73	0.83	5.53	45.79
<b>Motile species abundance</b>						
Amphipod complex 2	0.24	1.43	10.47	1.12	11.67	11.67
<i>N. vexillosa</i>	0.00	1.17	8.78	1.58	9.78	21.45
<i>N. procera</i>	0.91	0.49	5.18	1.08	5.77	27.21
Amphipod complex 1	0.50	0.53	4.74	0.84	5.29	32.50
<i>J. staudei</i>	0.57	0.15	4.07	0.77	4.53	37.03

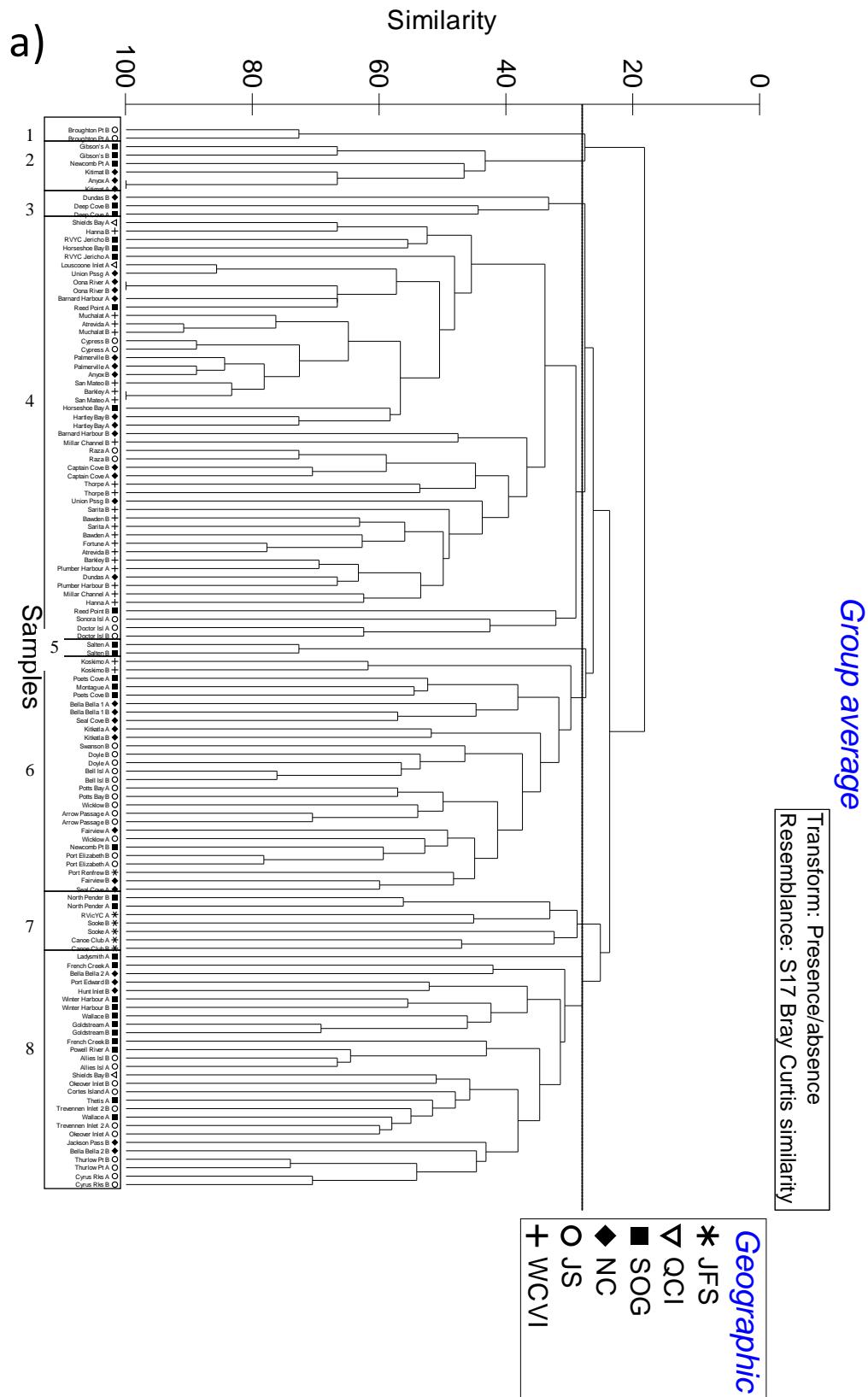
The QCI and NC differed in community composition based only on the sessile species abundance data (Pairwise ANOSIM:  $r=0.527$ ,  $p=0.001$ ; Table 18). *Mytilus* sp., *B. crenatus*, and *Lichenopora* sp. are much more abundant on the NC than the QCI. *S. japonica* was more abundant in the QCI samples. *C. pallasiana* was present in the QCI but not the NC.

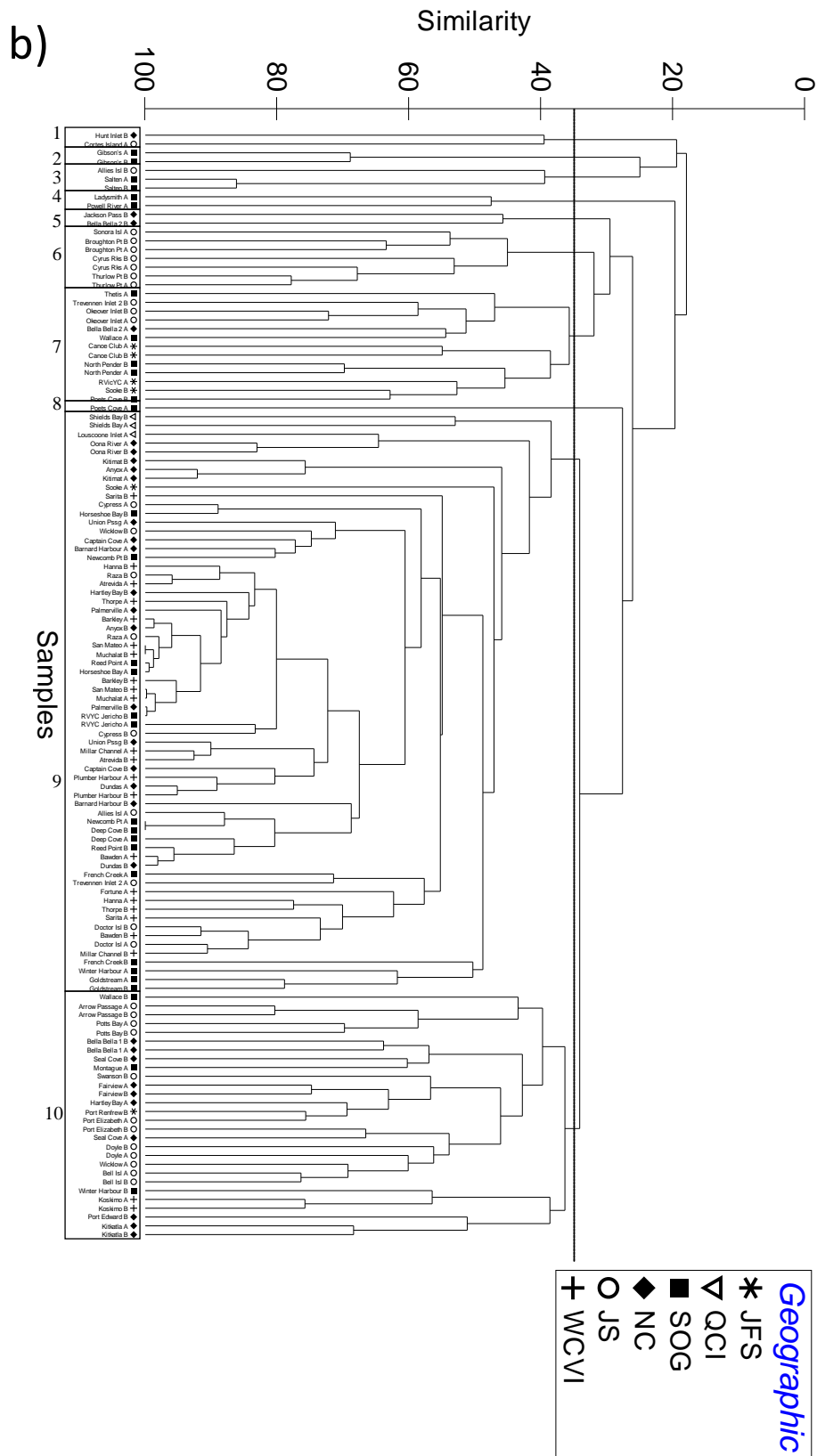
**Table 18. The influential species that account for the difference in community composition for the QCI with the NC.**

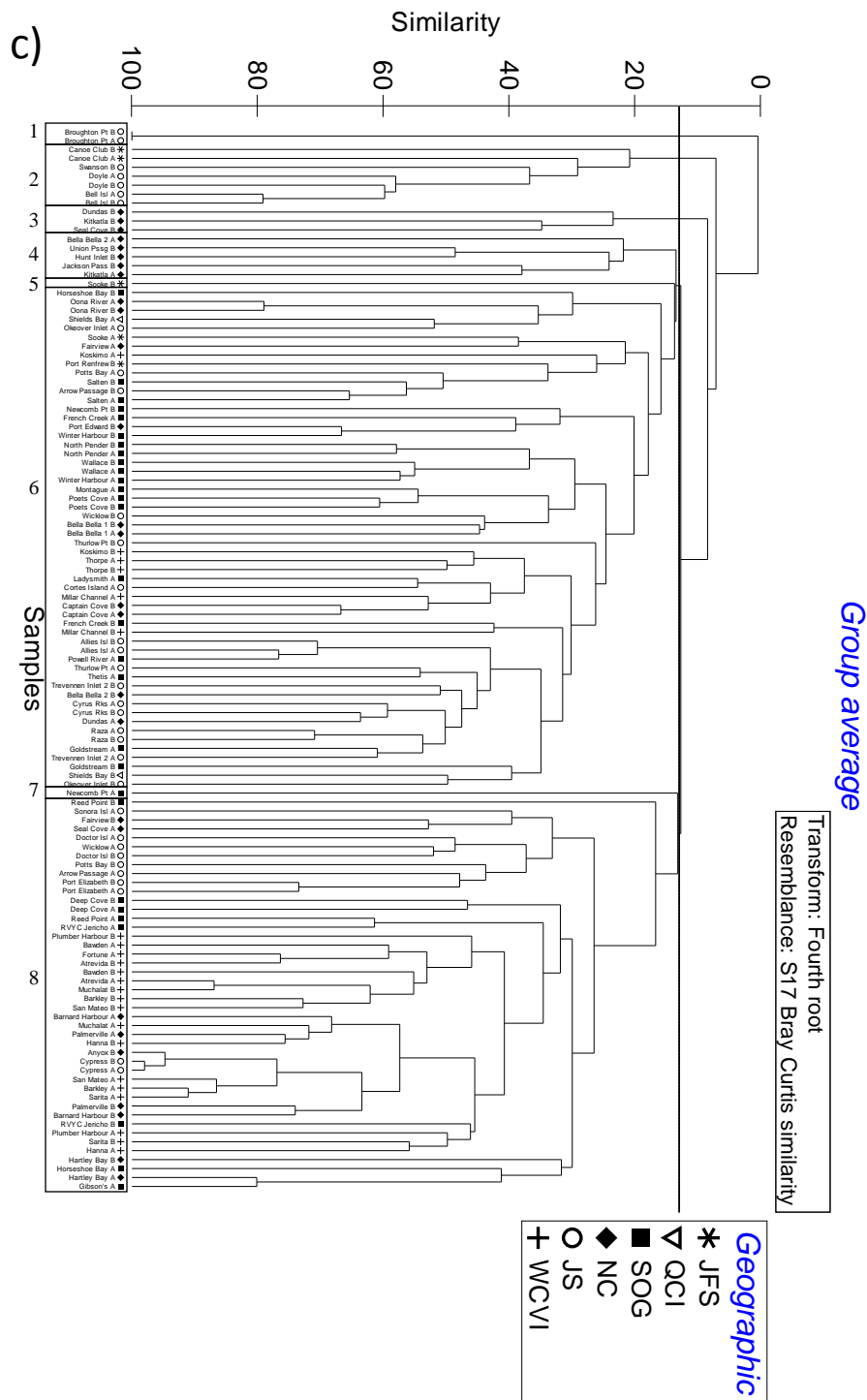
Species	Avg abundance QCI	Avg abundance NC	Avg dissimilarity	Diss./SD	Percent contribution	Cumulative percent
<b>Sessile species abundance</b>						
<i>Mytilus</i> sp.	0.46	1.88	11.74	1.28	13.77	13.77
<i>B. crenatus</i>	0.36	1.14	7.22	1.09	8.47	22.25
<i>S. japonica</i>	1.02	0.22	6.19	1.00	7.26	29.51
<i>Lichenopora</i> sp.	0.44	0.67	4.74	0.91	5.56	35.07
<i>C. pallasiana</i>	0.79	0.00	4.51	0.80	5.29	40.36

#### **Patterns in the *Mytilus* sp. community**

*Mytilus* sp. was present in 78% (126/162) of the samples. *Mytilus* sp. community composition had no relationship with geographic area based on species presence (ANOSIM:  $r=0.161$ ,  $p=0.001$ ; Figure 17a), sessile species abundance data (ANOSIM:  $r=0.107$ ,  $p=0.001$ ; Figure 17b), or motile species abundance data (ANOSIM:  $r=0.136$ ,  $p=0.001$ ; Figure 17c).







**Figure 17. Hierarchical cluster dendrograms of *Mytilus* sp. samples' community composition based a) species presence, b) sessile species abundances, and c) motile species abundances. Geographic areas are denoted by the following symbols: Juan de Fuca Strait (JFS)- asterisks, Queen Charlotte Islands (QCI)- open triangles, Strait of Georgia (SOG)- solid squares, North coast of mainland BC (NC)- solid diamonds, Johnston Strait (JS)- open circles, and West coast of Vancouver Island (WCVI)- crosses. Square blocks with numbering emphasise the clusters at the designated similarity level.**

In the species richness data (Figure 17a and Table 19), 80 samples (cluster 4), from all geographic areas except the JFS, were influenced primarily by the presence of *Mytilus* sp., *B. crenatus*, Amphipod complex 2, *N. vexillosa*, *H. arctica*, and *G. oregonense*. The grouping of 28 samples (cluster 6), from all geographic areas except JS, was influenced by the presence of thirteen species but most prominently by *Mytilus* sp., *B. crenatus*, and *Lichenopora* sp. Another grouping of 28 samples, including samples from JS, NC, SOG, and QCI, was influenced by the species association of *Mytilus* sp. with *N. procera*, *E. quadrioculata*, and *C. occidentale*.

**Table 19. The influential species of the *Mytilus* sp. clusters observed at the 28% similarity level for species presence in the samples.**

Species	Avg abundance	Avg similarity	Similarity/SD	Percent contribution	Cumulative percent
<b>Cluster 1 (Broughton A and B)- average cluster similarity is 72.73</b>					
<i>P. occidentalis</i>	1.00	18.18	NA	25.00	25.00
<i>Mytilus</i> sp.	1.00	18.18	NA	25.00	50.00
<i>Styela</i> sp.	1.00	18.18	NA	25.00	75.00
<i>S. droebachiensis</i>	1.00	18.18	NA	25.00	100.00
<b>Cluster 2 (Gibson's A to Kitimat A)- average cluster similarity is 52.44</b>					
<i>Mytilus</i> sp.	1.00	50.22	2.90	95.76	95.76
<b>Cluster 3 (Dundas B to Deep Cove A) - average cluster similarity is 37.04</b>					
<i>Mytilus</i> sp.	1.0	11.11	$6.59 \times 10^7$	30.00	30.00
<i>N. vexillosa</i>	1.0	11.11	$6.59 \times 10^7$	30.00	60.00
<i>H. arctica</i>	0.67	3.70	0.58	10.00	70.00
<i>Triplana</i> sp.	0.67	3.70	0.58	10.00	80.00
<b>Cluster 4 (Shields Bay A to Doctor Island B)- average cluster similarity is 40.13</b>					
<i>Mytilus</i> sp.	1.00	12.89	2.68	32.12	32.12
<i>B. crenatus</i>	0.76	7.67	0.99	19.11	51.23
Amphipod complex 2	0.74	7.10	1.00	17.70	68.94
<i>N. vexillosa</i>	0.42	1.89	0.43	4.70	73.64
<i>H. arctica</i>	0.42	1.59	0.44	3.97	77.61
<i>G. oregonense</i>	0.34	1.50	0.34	3.75	81.36
<b>Cluster 5 (Salten A and B)- average cluster similarity is 72.73</b>					
<i>Clytia</i> sp.	1.00	9.09	NA	12.50	12.50
<i>Balanus</i> sp.	1.00	9.09	NA	12.50	25.00
<i>Mytilus</i> sp.	1.00	9.09	NA	12.50	37.50
<i>Lichenopora</i> sp.	1.00	9.09	NA	12.50	50.00
<i>B. schlosseri</i>	1.00	9.09	NA	12.50	62.50
<i>N. procera</i>	1.00	9.09	NA	12.50	75.00
<i>J. staudei</i>	1.00	9.09	NA	12.50	87.50
<i>C. laeviuscula</i>	1.00	9.09	NA	12.50	100.00
<b>Cluster 6 (Koskimo A to Seal Cove A)- average cluster similarity is 36.90</b>					
<i>Mytilus</i> sp.	1.00	6.11	4.39	16.59	16.59
<i>B. crenatus</i>	0.86	4.66	1.50	12.66	29.25
<i>Lichenopora</i> sp.	0.82	4.19	1.31	11.38	40.63
<i>A. polyoum</i>	0.68	2.74	0.87	7.44	48.07
<i>N. procera</i>	0.61	2.09	0.71	5.69	53.76

Species	Avg abundance	Avg similarity	Similarity/SD	Percent contribution	Cumulative percent
Amphipod complex 2	0.57	1.80	0.67	4.89	58.65
<i>P. cornutus</i>	0.54	1.62	0.60	4.41	63.06
<i>O. dichotoma</i>	0.50	1.41	0.55	3.82	66.88
<i>J. staudei</i>	0.43	1.13	0.45	3.07	69.95
<i>E. quadrioculata</i>	0.43	1.09	0.44	2.96	72.91
<i>P. occidentalis</i>	0.46	1.09	0.50	2.95	75.86
<i>C. mutica</i>	0.43	1.00	0.45	2.72	78.58
<i>C. occidentale</i>	0.39	0.78	0.40	2.11	80.69
<b>Cluster 7 (North Pender B to Canoe Club B)- average cluster similarity is 32.95</b>					
<i>B. crenatus</i>	1.00	6.21	9.20	18.84	18.84
<i>Mytilus</i> sp.	1.00	6.21	9.20	18.84	37.69
<i>B. violaceus</i>	1.00	6.21	9.20	18.84	56.53
<i>C. inflata</i>	0.71	2.86	0.92	8.69	65.22
<i>M. borealis</i>	0.57	1.62	0.62	4.91	70.13
<i>S. japonica</i>	0.43	0.93	0.39	2.81	72.94
<i>P. occidentalis</i>	0.43	0.90	0.40	2.72	75.66
<i>N. procera</i>	0.43	0.88	0.40	2.66	78.32
<i>E. quadrioculata</i>	0.43	0.86	0.40	2.60	80.92
<b>Cluster 8 (French Creek A to Cyrus Rocks B)- average cluster similarity is 35.56</b>					
<i>Mytilus</i> sp.	1.0	7.39	4.03	20.79	20.79
<i>N. procera</i>	0.75	3.95	1.04	11.10	31.88
<i>E. quadrioculata</i>	0.71	3.53	0.95	9.93	41.81
<i>C. occidentale</i>	0.68	2.98	0.89	8.39	50.19
<i>P. occidentalis</i>	0.57	2.21	0.66	6.22	56.41
Juvenile seastars	0.50	1.72	0.54	4.84	61.25
<i>S. japonica</i>	0.50	1.65	0.54	4.65	65.90
<i>O. dichotoma</i>	0.50	1.55	0.54	4.37	70.27
Amphipod complex 1	0.43	1.26	0.44	3.53	73.80
<i>H. arctica</i>	0.46	1.21	0.50	3.40	77.21
<i>M. borealis</i>	0.43	1.06	0.45	2.98	80.19

In the sessile species abundance data (Figure 17b and Table 20), the largest group of samples (cluster 9) included 66 samples from all geographic regions and was influenced almost entirely by the abundance of just *Mytilus* sp. and *B. crenatus*. There were small groups of samples (clusters 1-6) where there were species more influential than *Mytilus* sp. In particular, two sites from the NC (cluster 5) were more strongly influenced by the abundance of *C. inflata*, *S. insignis*, *A. polyoum*, and *Metridium* sp.

**Table 20. The influential species of the *Mytilus* sp. clusters observed at the 35% similarity level for the samples' sessile species abundance data.**

Species	Avg abundance	Avg similarity	Similarity/ SD	Percent contribution	Cumulative percent
<b>Cluster 1 (Hunt Inlet B and Cortes Island A)- average cluster similarity is 39.54</b>					
<i>C. annulata</i>	1.93	11.20	NA	28.34	28.34
<i>Mytilus</i> sp.	1.39	10.84	NA	27.41	55.74
<i>S. japonica</i>	1.68	10.84	NA	27.41	83.15
<b>Cluster 2 (Gibson's A and B)- average cluster similarity is 68.93</b>					
<i>C. reticulum</i>	2.96	53.57	NA	77.72	77.72
<i>Mytilus</i> sp.	1.19	15.36	NA	22.28	100.00
<b>Cluster 3 (Allies Island B to Salten B)- average cluster similarity is 55.03</b>					
<i>B. schlosseri</i>	2.29	22.69	10.22	41.23	41.23
<i>Clytia</i> sp.	2.06	11.49	0.58	20.89	62.12
<i>Mytilus</i> sp.	0.96	10.21	11.10	18.55	80.67
<b>Cluster 4 (Ladysmith A and Powell River A)- average cluster similarity is 47.56</b>					
<i>C. pallasiana</i>	2.04	20.28	NA	42.64	42.64
<i>O. dichotoma</i>	1.55	15.68	NA	32.96	75.60
<i>Mytilus</i> sp.	1.15	11.60	NA	24.40	100.00
<b>Cluster 5 (Jackson Pass B and Bella Bella 2 B)- average cluster similarity is 45.78</b>					
<i>C. inflate</i>	3.01	19.00	NA	41.51	41.51
<i>S. insignis</i>	1.32	8.59	NA	18.75	60.26
<i>A. polyoum</i>	2.09	7.22	NA	15.77	76.03
<i>Metridium</i> sp.	1.25	5.59	NA	11.98	88.02
<b>Cluster 6 (Sonora Island A to Thurlow Point A)- average cluster similarity is 51.68</b>					
<i>P. occidentalis</i>	1.48	15.21	2.56	29.44	29.44
<i>Mytilus</i> sp.	1.60	13.26	2.26	25.67	55.10
<i>C. inflate</i>	1.30	8.82	1.39	17.06	72.17
<i>Styela</i> sp.	0.60	5.21	0.90	10.09	82.26
<b>Cluster 7 (Thetis A to Poets Cove B)- average cluster similarity is 41.53</b>					
<i>Mytilus</i> sp.	1.62	8.96	3.17	21.54	21.54
<i>B. violaceus</i>	1.68	8.06	1.73	19.40	40.94
<i>C. inflate</i>	1.42	5.98	1.03	14.41	55.35
<i>O. dichotoma</i>	1.41	4.42	0.78	10.65	66.00
<i>S. japonica</i>	1.04	2.91	0.67	7.00	72.99
<i>B. crenatus</i>	0.90	2.24	0.58	5.40	78.39
<i>P. occidentalis</i>	0.57	1.69	0.60	4.07	82.46
<b>Cluster 8 (Poets Cove A)</b>					
<b>Cluster 9 (Shields Bay B to Goldstream B)- average cluster similarity is 58.24</b>					
<i>Mytilus</i> sp.	2.86	44.94	3.08	77.16	77.16
<i>B. crenatus</i>	1.05	8.82	0.75	15.14	92.30
<b>Cluster 10 (Wallace B to Kitkta B)- average cluster similarity is 42.71</b>					
<i>Mytilus</i> sp.	1.64	10.83	2.87	25.35	25.35
<i>B. crenatus</i>	1.69	9.99	1.56	23.40	48.75
<i>Lichenopora</i> sp.	1.21	6.43	1.27	15.07	63.81
<i>A. polyoum</i>	1.23	4.63	0.70	10.84	74.65
<i>O. dichotoma</i>	1.01	3.02	0.46	7.07	81.72

In the motile species abundance data (Figure 17c and Table 21), a group of 56 samples (cluster 6) included samples from all the geographic regions and about two thirds of the similarity within this cluster was influenced by the abundance of *N. procera*, *E.*

*quadrioculata*, and *C. occidentale*. The next largest grouping included samples from the SOG, JS, NC, and WCVI and was largely driven by the abundance of Amphipod complex 2, *N. vexillosa*, and *G. oregonense*.

**Table 21. The influential species of the *Mytilus* sp. clusters observed at the 14% similarity level for the samples' motile species abundance data.**

Species	Avg abundance	Avg similarity	Simil./SD	Percent contribution	Cumulative percent
<b>Cluster 1 (Broughton Point A and B)- average cluster similarity is 100.00</b>					
<i>S. droebachiensis</i>	1.00	10.00	NA	100.00	10.00
<b>Cluster 2 (Canoe Club B to Bell Island B)- average cluster similarity is 37.64</b>					
<i>C. mutica</i>	1.46	16.82	4.26	44.67	44.67
<i>J. staudei</i>	1.80	11.56	0.92	30.72	75.39
<i>C. anomala</i>	1.53	8.82	0.87	23.43	98.82
<b>Cluster 3 (Dundas B to Seal Cove B)- average cluster similarity is 27.26</b>					
<i>L. chloranota</i>	1.06	11.56	8.27	42.40	42.40
Amphipod complex 3	1.03	4.33	0.58	25.88	58.29
<i>E. habeii</i>	0.84	4.20	0.58	15.40	73.69
<i>P. cornutus</i>	0.80	3.64	0.58	13.36	87.05
<b>Cluster 4 (Bella Bella 2 A to Kitkatla A) - average cluster similarity is 27.04</b>					
<i>C. occidentale</i>	1.08	16.94	4.84	62.66	62.66
<i>E. habeii</i>	0.50	2.64	0.32	9.76	72.42
<i>P. cornutus</i>	0.54	1.72	0.32	6.38	78.80
<i>E. blomstrandii</i>	0.40	1.70	0.32	6.30	85.10
<b>Cluster 5 (Sooke B)</b>					
<b>Cluster 6 (Hoseshoe Bay B to Okeover Inlet B)- average cluster similarity is 24.63</b>					
<i>N. procera</i>	1.24	9.25	1.38	35.57	37.57
<i>E. quadrioculata</i>	0.78	4.38	0.77	17.79	55.36
<i>C. occidentale</i>	0.66	2.62	0.60	10.63	66.00
Amphipod complex 1	0.48	1.66	0.29	6.74	72.73
<i>M. borealis</i>	0.54	1.63	0.40	6.63	79.36
Juvenile seastars	0.40	1.28	0.36	5.18	84.54
<b>Cluster 7 (Newcomb Point A)</b>					
<b>Cluster 8 (Reed Point B to Gibson's A)- average cluster similarity is 35.05</b>					
Amphipod complex 2	1.90	23.87	2.11	68.10	68.10
<i>N. vexillosa</i>	0.64	3.54	0.50	10.10	78.20
<i>G. oregonense</i>	0.50	2.25	0.35	6.41	84.61

There were some differences in *Mytilus* sp. community composition based on pairwise comparisons of the geographic areas. The JFS and WCVI differed in *Mytilus* sp. community composition based on species presence (Pairwise ANOSIM:  $r=0.814$ ,  $p=0.001$ ; Table 22), sessile species abundance (Pairwise ANOSIM:  $r=0.780$ ,  $p=0.001$ ; Table 22), and motile species abundance (Pairwise ANOSIM:  $r=0.730$ ,  $p=0.001$ ; Table

22). In the richness data this difference was influenced by the fact that *N. vexillosa* and *H. arctica* were prominent in WCVI samples but not in any JFS samples. The opposite was true for *B. violaceus* and *B. gracilis* for the JFS. Additionally, Amphipod complex 2 was far more prominent in WCVI samples. In the sessile species abundance data the difference was, again, largely driven by the abundance of *B. violaceus* in the JFS and its absence along the WCVI. Additionally, the *Mytilus* sp. was far more abundant in WCVI samples. In the motile species abundance data the difference can largely be attributed to the abundance of both Amphipod complex 2 and *N. vexillosa* in the WCVI samples as compared to the JFS samples.

**Table 22. The influential species in the *Mytilus* sp. samples that account for the differences in community composition for the JFS with WCVI.**

Species	Avg abundance JFS	Avg abundance WCVI	Average dissimilarity	Diss./ SD	Percent contribution	Cumulative percent
<b>Species presence</b>						
<i>N. vexillosa</i>	0.00	0.87	3.53	2.26	4.45	4.45
<i>B. violaceus</i>	0.83	0.00	3.13	1.92	3.95	8.40
Amphipod complex 2	0.17	0.78	2.71	1.38	3.41	11.82
<i>B. gracilis</i>	0.67	0.00	2.53	1.30	3.19	15.01
<i>H. arctica</i>	0.00	0.70	2.50	1.39	3.15	18.16
<b>Sessile species abundance</b>						
<i>B. violaceus</i>	1.57	0.00	6.82	1.76	9.79	9.79
<i>Mytilus</i> sp.	1.75	2.90	6.44	1.52	9.24	19.03
<i>O. dichotoma</i>	1.04	0.31	5.37	0.82	7.70	26.73
<i>B. crenatus</i>	2.06	1.15	5.20	1.19	7.46	34.19
<i>H. arctica</i>	0.00	0.80	3.72	1.31	5.34	39.53
<i>C. inflata</i>	0.83	0.00	3.55	0.86	5.09	44.62
<b>Motile species abundance</b>						
Amphipod complex 2	0.24	1.57	9.98	1.27	11.13	11.13
<i>N. vexillosa</i>	0.00	1.19	8.08	1.75	9.01	20.15
<i>M. borealis</i>	0.81	0.04	4.52	1.10	5.04	25.19
<i>c. mutica</i>	0.52	0.26	4.42	0.82	4.93	30.12
<i>G. oregonense</i>	0.28	0.53	4.30	0.82	4.79	34.91
<i>E. gracile</i>	0.20	0.62	3.75	0.88	4.18	39.09

The QCI and WCVI also differed in *Mytilus* sp. community composition based on species presence (Pairwise ANOSIM:  $r=0.570$ ,  $p=0.008$ ; Table 23), sessile species abundance (Pairwise ANOSIM:  $r=0.647$ ,  $p=0.014$ ; Table 23), and motile species abundance (Pairwise ANOSIM:  $r=0.557$ ,  $p=0.023$ ; Table 23). In the richness data this

difference was largely attributed to the fact that four species (*N. vexillosa*, Amphipod complex 2, *H. arctica*, *Lichenopora* sp.) were far more prominent in the WCVI samples, while three more species (*C. pallasiana*, *S. japonica*, *M. borealis*) were far more prominent in the QCI samples. In the sessile species abundance data the difference was largely attributed to the abundance of *Mytilus* sp. on the WCVI compared to the QCI. *B. crenatus* was also more abundant in WCVI samples whereas *S. japonica*, *O. dichotoma*, and *Lichenopora* sp. were more abundant in the QCI. In the motile species abundance data the Amphipod complex 2 and *N. vexillosa* were more abundant on the WCVI whereas *M. borealis*, Amphipod complex 1, and *N. procera* were more abundant in QCI samples.

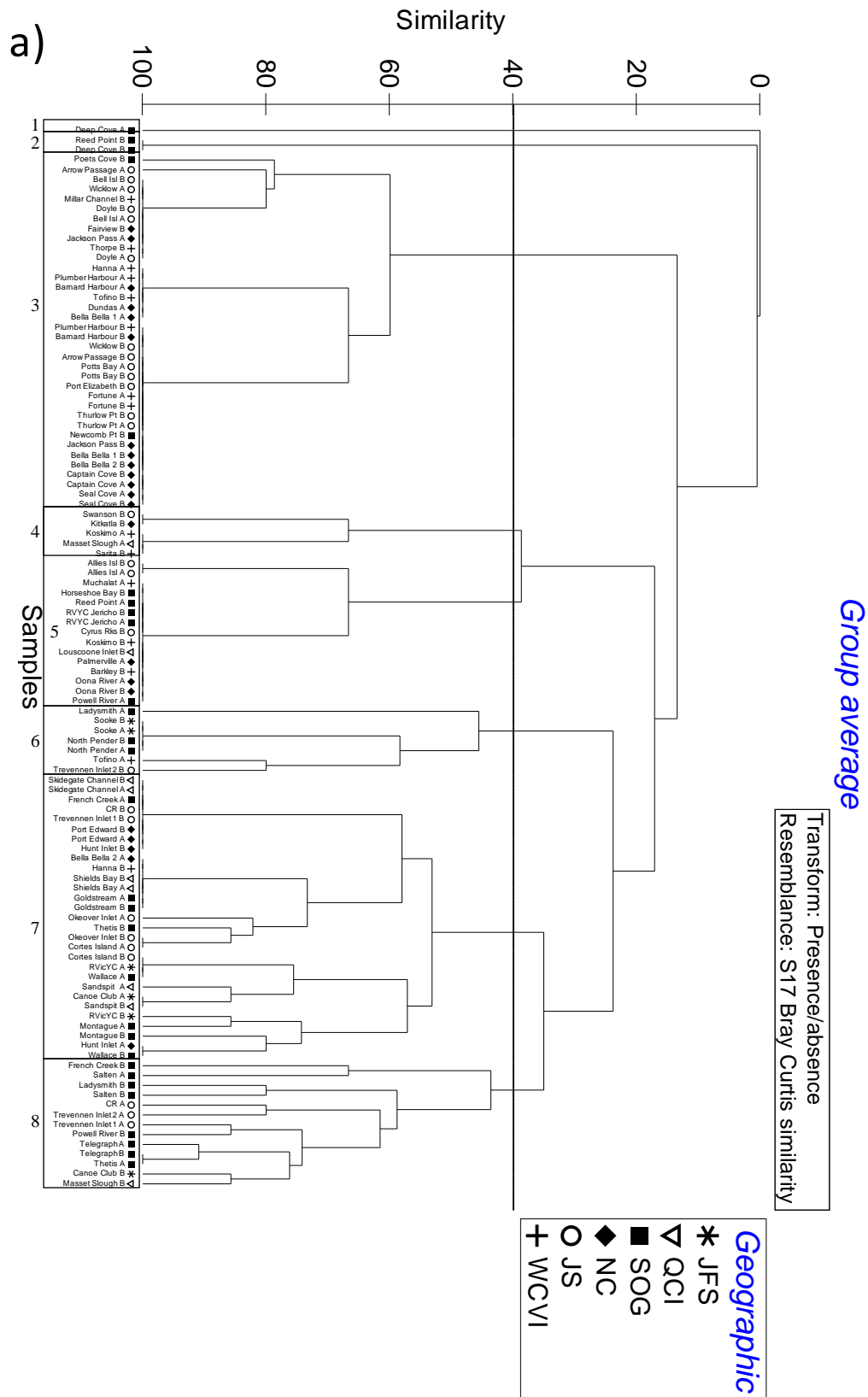
**Table 23. The influential species in the *Mytilus* sp. samples that account for the differences in community composition for the QCI with WCVI.**

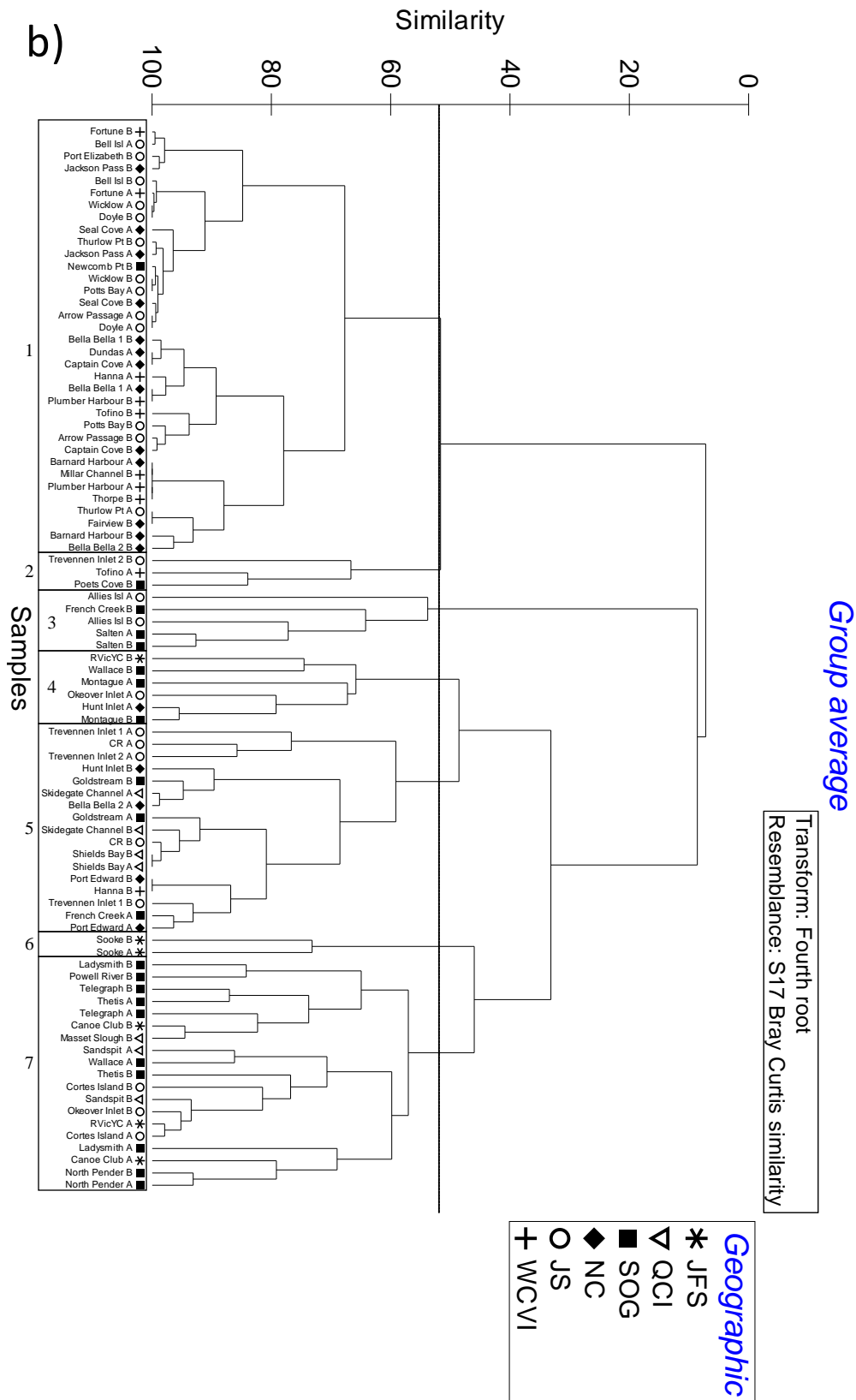
Species	Avg abundance QCI	Avg abundance WCVI	Average dissimilarity	Diss./SD	Percent contribution	Cumulative percent
<b>Species presence</b>						
<i>N. vexillosa</i>	0.00	0.87	5.06	1.57	7.17	7.17
Amphipod complex 2	0.33	0.78	3.91	0.99	5.54	12.71
<i>H. arctica</i>	0.33	0.70	3.05	0.98	4.33	17.04
<i>Lichenopora</i> sp.	0.33	0.43	2.81	0.74	3.98	21.02
<i>C. pallasiana</i>	0.67	0.00	2.79	1.20	3.95	24.97
<i>S. japonica</i>	0.67	0.04	2.78	1.15	3.94	28.90
<i>M. borealis</i>	0.67	0.04	2.76	1.18	3.92	32.82
<b>Sessile species abundance</b>						
<i>Mytilus</i> sp.	1.86	2.90	10.23	1.14	17.20	17.20
<i>S. japonica</i>	0.97	0.04	5.93	1.31	9.98	27.17
<i>O. dichotoma</i>	0.83	0.31	5.64	1.06	9.48	36.66
<i>Lichenopora</i> sp.	0.53	0.51	5.64	0.88	9.48	46.14
<i>B. crenatus</i>	0.72	1.15	5.62	1.46	9.45	55.59
<b>Motile species abundance</b>						
Amphipod complex 2	0.71	1.57	7.83	1.03	9.56	9.56
<i>N. vexillosa</i>	0.00	1.19	7.19	1.69	8.79	18.35
<i>M. borealis</i>	1.34	0.04	6.98	3.11	8.52	26.87
Amphipod complex 1	1.37	0.51	6.59	1.16	8.05	34.92
<i>N. procera</i>	1.34	0.45	5.76	1.65	7.04	41.96

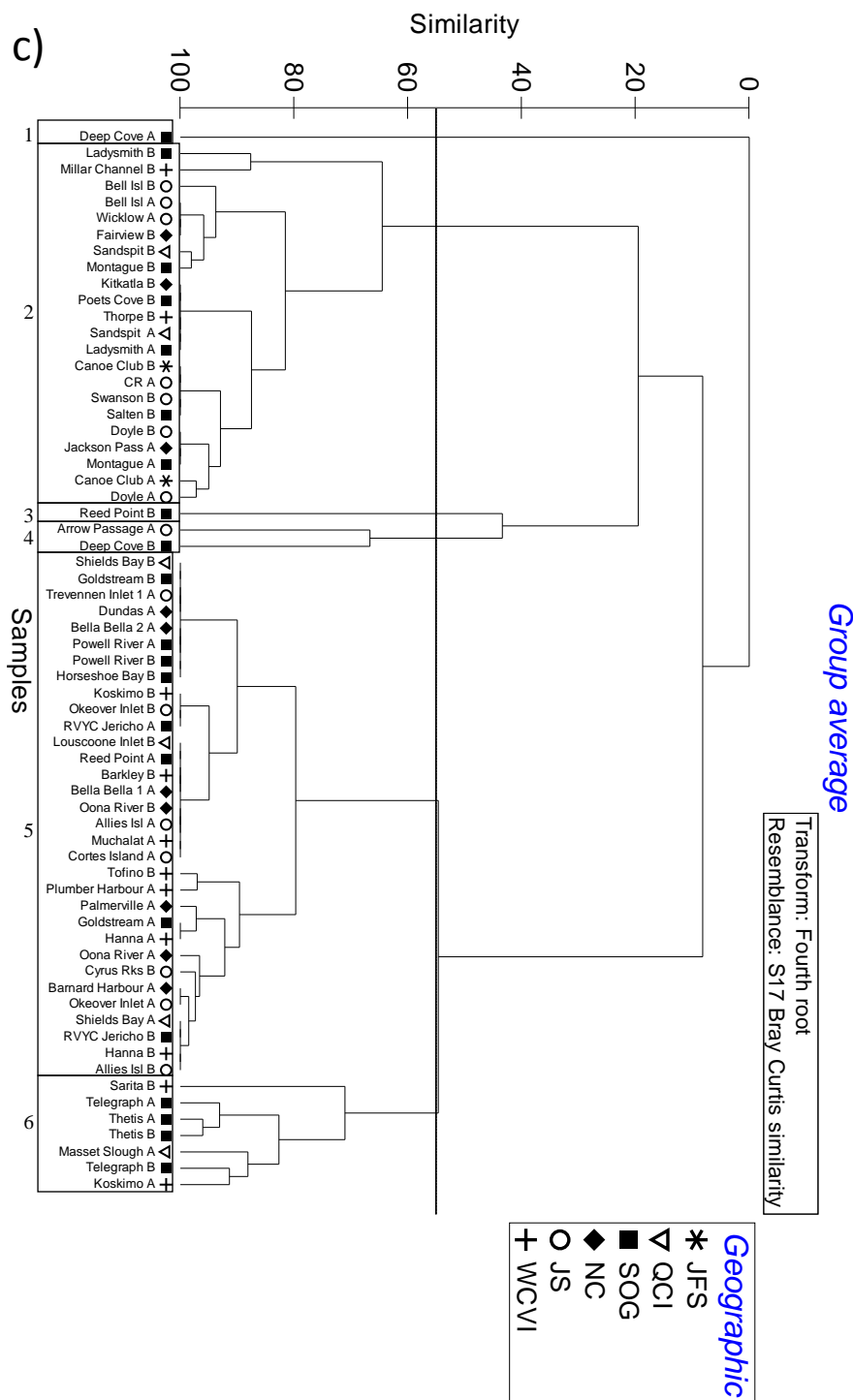
### **Patterns in the Introduced species community**

Eleven introduced species, seven sessile and four motile, were found in this study. These introduced species were present in 67% (108 /162) of the samples (this includes the Amphipod complex 1 containing both a native and non-native species). Sessile introduced species were present in 82 of these samples and motile introduced species were present in 65 samples. There was a weak relationship between introduced species assemblages and geographic area based on species presence (ANOSIM:  $r=0.090$ ,  $p=0.001$ ; Figure 18a), sessile species abundance (ANOSIM:  $r=0.174$ ,  $p=0.001$ ; Figure 18b), and motile species abundance (ANOSIM:  $r=-0.049$ ,  $p=0.969$ ; Figure 18c).

In the introduced species richness data there were groups of samples that shared 100% similarity and spanned a number of the geographic areas (Fig 18a and Table 24). Three samples (Deep Cove A and B, and Reed Point B) had low similarity with the other samples due to the presence of a single species, *P. cornuta*. The largest grouping of samples (36 from cluster 3) from JS, WCVI, SOG, and NC was influenced by primarily by the presence of *A. polyoum*. A group of samples from all geographic areas (cluster 7) was influenced by the presence of *S. japonica*.







**Figure 18** Hierarchical cluster dendrograms of introduced species samples' community composition based on a) species presence, b) sessile species abundances, and c) motile species abundances. Geographic areas are denoted by the following symbols: Juan de Fuca Strait (JFS)- asterisks, Queen Charlotte Islands (QCI)- open triangles, Strait of Georgia (SOG)-solid squares, North coast of mainland BC (NC)- solid diamonds, Johnstone Strait (JS)- open circles, and West coast of Vancouver Island (WCVI)- crosses. Square blocks with numbering emphasise the clusters at the designated similarity level.

**Table 24. The influential species of the introduced species clusters observed at the 40% similarity level for species presence in the samples.**

Species	Avg abundance	Avg similarity	Similarity/SD	Percent contribution	Cumulative percent
<b>Cluster 1 (Deep Cove A)</b>					
<b>Cluster 2 (Reed Point B and Deep Cove B)- average cluster similarity is 100.00</b>					
<i>P. cornuta</i>	1.00	1.00	NA	1.00	100.00
<b>Cluster 3 (Poets Cove B to Seal Cove B)- average cluster similarity is 75.85</b>					
<i>A. polyoum</i>	1.00	70.61	3.60	93.09	93.09
<b>Cluster 4 (Swanson B to Sarita B)- average cluster similarity is 80.00</b>					
<i>C. mutica</i>	1.00	65.00	4.45	81.25	81.25
<b>Cluster 5 (Allies Island B to Powell River A)- average cluster similarity is 91.75</b>					
Amphipod complex 1	1.00	91.27	6.09	99.48	99.48
<b>Cluster 6 (Ladysmith A to Trevennen Inlet 2B)- average cluster similarity is 67.62</b>					
<i>B. violaceus</i>	1.00	65.71	2.75	97.18	97.18
<b>Cluster 7 (Skidegate Channel B to Wallace B)- average cluster similarity is 62.79</b>					
<i>S. japonica</i>	1.00	50.59	2.77	80.56	80.56
<b>Cluster 8 (French Creek B to Masset B)- average cluster similarity is 61.00</b>					
<i>B. schlosseri</i>	1.00	32.63	2.92	53.49	53.49
<i>S. japonica</i>	0.62	9.16	0.71	15.01	68.50
<i>B. violaceus</i>	0.62	8.75	0.72	14.34	82.84

In the introduced sessile species abundance data (Figure 18b and Table 25), 35 samples (cluster 1), from the SOG, JS, WCVI, and NC, had a high level of similarity based on the abundance of *A. polyoum*. Seventeen samples (cluster 5) from all geographic regions except JFS were influenced by the abundance of *S. japonica*. Nineteen samples (cluster 7) from SOG, JFS, JS, and QCI were influenced by the presence of *B. violaceus* in association with *S. japonica*.

**Table 25 The influential species of the introduced species clusters observed at the 52% similarity level for the samples' sessile species abundance data.**

Species	Avg abundance	Avg similarity	Similarity/SD	Percent contribution	Cumulative percent
<b>Cluster 1 (Fortune B to Bella Bella 2 B)- average cluster similarity is 77.52</b>					
<i>A. polyoum</i>	1.83	77.52	5.11	100.00	100.00
<b>Cluster 2 (Trevennen Inlet 2 B to Poets Cove B)- average cluster similarity is 72.47</b>					
<i>A. polyoum</i>	1.40	38.96	6.74	53.77	53.77
<i>B. violaceus</i>	1.30	33.50	7.80	46.23	100.00
<b>Cluster 3 (Allies Island A to Salten B)- average cluster similarity is 65.51</b>					
<i>B. schlosseri</i>	1.85	65.51	4.42	100.00	100.00
<b>Cluster 4 (RVicYC B to Montague B)- average cluster similarity is 70.48</b>					
<i>S. japonica</i>	1.23	33.83	3.95	48.00	48.00
<i>A. polyoum</i>	1.16	32.09	4.97	45.52	93.53
<b>Cluster 5 (Trevennen Inlet I A to Port Edward A)- average cluster similarity is 72.80</b>					
<i>S. japonica</i>	1.57	72.12	4.62	99.07	99.07

<b>Cluster 6 (Sooke A and B)- average cluster similarity is 73.21</b>					
<i>B. violaceus</i>	1.15	73.21	NA	100.00	100.00
<b>Cluster 7 (Ladysmith B to North Pender A)- average cluster similarity is 63.78</b>					
<i>B. violaceus</i>	1.99	43.91	3.31	68.86	68.86
<i>S. japonica</i>	1.22	16.80	1.00	26.34	95.20

In the introduced motile species data (Figure 18c and Table 26) the similarity between samples was high as the community composition was based on only four species. Deep Cove A had a low similarity to all other samples due to the abundance of *P. cornuta*. Thirty-two samples (cluster 5), with samples from all geographic regions except the JFS, were influenced by the abundance of Amphipod complex 1. Twenty-two samples (cluster 2), from all geographic areas, were influenced by the abundance of *C. mutica*.

**Table 26. The influential species of the introduced species clusters observed at the 58% similarity level for the samples' motile species abundance data.**

Species	Avg abundance	Avg similarity	Similarity/ SD	Percent contribution	Cumulative percent
<b>Cluster 1 (Deep Cove A)</b>					
<b>Cluster 2 (Ladysmith B to Doyle A)- average cluster similarity is 83.65</b>					
<i>C. mutica</i>	1.48	83.65	6.73	100.00	100.00
<b>Cluster 3 (Reed Point B)</b>					
<b>Cluster 4 (Arrow Passage A to Deep Cove B)- average cluster similarity is 66.67</b>					
<i>P. cornuta</i>	1.00	66.67	NA	100.00	100.00
<b>Cluster 5 (Shields Bay B to Allies Island B)- average cluster similarity is 86.92</b>					
Amphipod complex 1	1.36	86.92	9.30	100.00	100.00
<b>Cluster 6 (Sarita B to Koskismo A)- average cluster similarity is 81.92</b>					
Amphipod complex 1	2.03	47.46	57.93	57.93	57.93
<i>C. mutica</i>	1.44	34.46	42.07	42.07	100.00

Pairwise comparisons did show some geographic differences in introduced species community composition. JFS and WCVI differed based on introduced species presence data (Pairwise ANOSIM:  $r=0.605$ ,  $p=0.001$ ; Table 27), and sessile species abundance data (Pairwise ANOSIM:  $r=0.735$ ,  $p=0.001$ ; Table 27). The difference was largely influenced by the abundance and prevalence of *B. violaceus* and *S. japonica* in the JFS samples compared with the WCVI samples. *A. polyoum* was both more abundant and more prevalent on the WCVI. Amphipod complex 1 was only found on the WCVI not in the JFS.

**Table 27. The influential species in the introduced species samples that account for the differences in community composition for the JFS with WCVI.**

Species	Avg abundance JFS	Avg abundance WCVI	Avg dissimilarity	Diss./SD	Percent contribution	Cumulative percent
<b>Species presence</b>						
<i>B. violaceus</i>	1.00	0.07	26.74	2.16	30.63	30.63
Amphipod complex 1	0.00	0.60	16.67	1.06	19.09	49.72
<i>A. polyoum</i>	0.17	0.60	16.00	1.00	18.33	68.05
<i>S. japonica</i>	0.67	0.07	14.89	1.26	17.06	85.11
<b>Sessile species abundance</b>						
<i>B. violaceus</i>	1.82	0.17	38.46	2.51	43.95	43.95
<i>A. polyoum</i>	0.22	1.38	29.34	1.42	33.53	77.48
<i>S. japonica</i>	0.96	0.08	17.18	1.27	19.64	97.11

JFS and NC differed based on introduced sessile species abundance data (Pairwise ANOSIM:  $r=0.7572$ ,  $p=0.002$ ; Table 28). This difference was largely attributed to the fact that *B. violaceus* was abundant in JFS samples and was not found on the NC. Additionally, *S. japonica* was more abundant in JFS samples whereas *A. polyoum* was more abundant in NC samples.

**Table 28. The influential species in the introduced species samples that account for the differences in community composition for the JFS with NC.**

Species	Avg abundance JFS	Avg abundance NC	Average dissimilarity	Diss./SD	Percent contribution	Cumulative percent
<b>Sessile species abundance</b>						
<i>B. violaceus</i>	1.82	0.00	39.65	3.75	45.22	45.22
<i>A. polyoum</i>	0.22	1.20	26.66	1.23	30.41	75.62
<i>S. japonica</i>	0.96	0.42	18.86	1.15	21.51	97.13

There was a very weak relationship between community composition and the type of manmade structure the settlement arrays were suspended from for introduced species presence (ANOSIM:  $r=0.076$ ,  $p=0.004$ ), sessile species abundance (ANOSIM:  $r=0.091$ ,  $p=0.001$ ), and motile species abundance (ANOSIM:  $r=0.008$ ,  $p=0.369$ ). However, pairwise comparisons did reveal that there was a difference in introduced species community structure for sessile abundance between fish farm samples and shellfish aquaculture samples (Pairwise ANOSIM:  $r=0.517$ ,  $p=0.001$ ; Table 29). *A. polyoum* was far more abundant at fish farms than at shellfish aquaculture sites. *B. schlosseri* was

more abundant at shellfish sites and both *B. violaceus* and *S. japonica* were only found at shellfish sites.

**Table 29. The influential species in the introduced species samples that account for the differences in community composition for the Fish farm samples with Shellfish samples.**

Species	Avg abundance Fish farm	Avg abundance Shellfish	Average diss.	Diss./ SD	Percent contribution	Cumulative percent
<b>Sessile species abundance</b>						
<i>A. polyoum</i>	1.97	0.43	39.13	1.86	49.17	49.17
<i>S. japonica</i>	0.00	0.74	16.82	1.07	21.12	70.31
<i>B. schlosseri</i>	0.17	0.52	13.64	0.68	17.14	87.45
<i>B. violaceus</i>	0.00	0.52	9.99	0.78	0.78	100.00

## Discussion

### Depth

The species richness observed at the surface was lower than at one meter depth. The community at the surface likely had more extreme environmental conditions compared to one meter below the surface, which could have had effects on the recruiting larval population, post settlement mortality rates (*e.g.* Hunt and Scheilbling 1997), and adult community disruption (*e.g.* Sugden *et al* 2007). The recruiting larval population would have experienced higher mortality rates due to physiological stress associated with elevated levels of pollution from oil and gasoline from nearby boats and machinery, stronger UV radiation, as well as lower salinities and fluctuations in temperature due to freshwater runoff (Pechenik 1987 cited in McEdward 1995). Physically the larval recruits would also have had to deal with increased turbulence at the surface caused by boat activity and wave action from surface winds. Though increased turbulence can have beneficial effects by increasing feeding encounters (Rothschild and Osborn 1988) and aiding in dispersal (MacKenzie and Leggett 1991) it also increases the likelihood of predator-prey encounters, thereby increasing mortality (summarised in McEdward 1995). Osman (1977) also found that, in general, larval settlement increased with depth over the first few meters of the water column. Many abiotic factors, such as light, currents, and salinity, have been shown to vary with depth and these abiotic factors are favoured differently and utilized as settlement cues by different species in various ways (Osman 1977, Keough 1983, Rodriguez *et al.* 1993). The similar percent free space available at

both depths indicated that, though fewer species were reaching the A depth level, the species that were able to recruit to the community were strong space competitors.

The depth sampled did not have a strong effect on the overall community composition. The clustering of the two depth samples from each site indicated the strong effect of local dynamics of larval recruitment. Despite the possible abiotic differences facing the larvae recruiting to different depths within a site, the suite of larvae was likely to be most similar within a site (Brown 1984). There are many abiotic and biotic factors that may affect the presence and abundance of larval species within the plankton that vary on such a wide range of temporal and spatial scales that the local dynamics of the larval populations really shape the recruitment to a community (Osman 1977, Caley *et al.* 2006).

The difference in community composition between the two depth levels was greatest for the motile species abundance data. Though many of the species likely inhabit and spend most of their lifetime in the sessile community, many motile species may be transient. Motile species do not provide the same insight into the successional processes of the community but they are integral components of the community. The small-scale movement of motile species in a community has a positive influence on local biodiversity (Kerr *et al.* 2002). In fact, Davidson *et al.* (2004) suggested that, due to a combination of high motile species richness and their low overall abundance in communities, we may be underestimating the functional role of motile invertebrate species in communities.

### **Timing**

The species richness of the samples decreased as the settlement arrays were deployed later in the year. The longer a settlement array was in the water, the more likely it was to be encountered by recruiting species. The deployment date not only reflected more physical time in the water column, but was also tied to the seasonality in reproduction and recruitment of most invertebrate species. The peak spawning periods for most planktotrophic and lecithitrophic larvae in the Northeast Pacific is the late spring to early summer (April to June) (Reitzel *et al.* 2004). In brooding species, recruitment is more variable and may occur throughout the year but there are still general key recruitment periods through the spring and summer (Reitzel *et al.* 2004). The earliest settlement arrays in this study were deployed beginning in March. The earlier deployed

settlement arrays were in the water for the key recruitment period of all types of larvae and would therefore be more likely to have more species present. The last few settlement structures were not deployed until the summer season. These settlement arrays were not submerged during the main recruitment season of most species and it is likely that fewer species were available for recruitment. These settlement structures also had less time for the established species to compete and utilize the available space in the community. The increase in available free space with the increasing date of deployment reflected the insufficient time to colonize and compete for space on the settlement arrays.

Very little of the variation in the data was actually explained by the trends of decreasing diversity and increasing free space available with later deployment dates. The date of deployment also did not have a strong effect on the community composition. It was unexpected that seasonality had no effect on community composition as it is thought to be one of the most important factors in determining the composition of a community. The initial colonization of a substrate is determined by the abundance of local larvae and the abundance of local larvae is largely determined by selectivity and seasonality (Osman 1977). I believe the effects of timing/seasonality were weak in this study as there were strong similarities in community composition along the coast and that there are a multitude of additional variables that contributed to the outcome of the community (explored further in following sections *e.g.* salinity, presence of predators, etc.).

The date that the settlement arrays were collected had no significant effect on the richness and percent free space available. The settlement arrays were collected from the fall to early winter (Sept-Dec), a timeframe that did not span the peak recruitment periods. Therefore it is unlikely that we missed any large recruitment events when the settlement arrays were pulled earlier in this timeframe. However, the fact that the percent free space was not affected is surprising. Any increase in time submerged would only provide species with more time to compete for free space available. One possible explanation is that the species in the community were no longer growing as they were entering winter and environmental conditions were less than favourable.

## Geographic area and species assemblages

### Geographic area

The geographic areas outlined in the introduction have a number of unique oceanographic and geographic features. Despite these features there was no strong effect of the geographic area on invertebrate fouling community composition across all geographic regions. The development of an epibenthic community is a complex process. I collected the settlement arrays five to six months after deployment. The communities of the settlement arrays were in an early successional stage and the species observed had already survived the settlement, recruitment, and early successional stages of the community. At each stage in this process there are a myriad of abiotic and biotic factors that contribute to the success or failure of a species. Studies have highlighted the effects of proximity to seafloor (Glasby 1999), shoreline configuration (Archambault and Bourget 1999), pollution (Agard *et al.* 1993), predators (Estes and Palmisano 1974), disturbance (Warwick and Clarke 1993), as well as temperature and salinity (Tettelback and Rhodes 1981) on species richness and community structure. Unfortunately, due to the large-scale effort of this study, very little information was collected on these and other potentially influential factors.

Geographic and latitudinal effects have been researched and documented worldwide in the marine environment (*e.g.* Connolly and Roughgarden 1999, Roy *et al.* 2000, Connolly *et al.* 2001, Ellingsen *et al.* 2005). However, a number of studies have found that other factors better explain observed latitudinal/geographic patterns or that there are no latitudinal/geographic patterns at all. Roy *et al.* (1998) found that diversity trends for prosobranch gastropods were best described by solar energy input and likely tied to productivity. I examined epibenthic communities that were primarily composed of suspension feeding organisms and it is probable that the community structure and species abundances were tied to primary productivity. Productivity is linked to oceanographic and topographic features such as upwelling, fluvial transport, and even headlands and capes (Ebert and Russell 1988, Zacharias and Roff 2001). The large-scale geographic regions that I designated may have been too large to reflect the smaller scale patterns of variability in production along the coast. Ellingsen and Gray (2002) found that diversity along the Norwegian continental shelf was linked not to latitude but to habitat

heterogeneity and variability. In this study the surfaces of the settlement arrays were uniform along the entire coast but the habitat of the area in which the settlement arrays were hung was not. Habitat heterogeneity and variability are very fine scale features that would not be well reflected by the large-scale geographic regions.

The reason that no geographic effects were evident in the epibenthic invertebrate community of the settlement arrays was that there was such a strong similarity in species associations along the length of the coast. Studies by Zacharias and Roff (2001) and Ardisson and Bourget (1992) also found weak effects of geographic areas due to the similarity of species associations within their study areas. The geographic area sampled by Ardisson and Bourget (1992) was smaller than our coastline, and for the most part, the similarities in their species associations could be explained by the natural dispersal of the larvae by oceanographic features. It is very likely that the dispersal of the larvae along the length of the coast was additionally facilitated by both natural and anthropogenic vectors. In fact, one of the common factors between my study of the BC coast and Ardisson and Bourget's study (1992) is that we both employed anthropogenic structures for sampling the local epibenthic communities. These anthropogenic structures (in my case docks at marina, shellfish and finfish aquaculture sites) may be selecting communities with species that can do well on these artificial surfaces, that are often in these stressed environments, and that are closely associated with potential vectors (boats, shellfish gear, etc.). In addition to serving as possible vectors of dispersal (Glasby and Connell 1999), research conducted in Australia (summary in Glasby and Connell 1999, Connell 2000, Connell 2001) has shown that particularly pontoons (as well as pilings) have an effect on community composition when compared to their local natural counterparts. Connell (2000 and 2001) highlight that the differences in community composition may be attributed to the fact that these man-made structures provide novel habitat, to the fact that they are not subjected to the influence of the tide, and to their close proximity to the surface (*i.e.* light). There is no way of knowing whether the communities that developed on the settlement arrays in this study reflected natural communities along the coast, or were simply communities reflecting the species found on local artificial structures. We did have a few settlement arrays suspended from buoys in natural environment but these buoys were removed earlier than expected due to inclement

weather. Simkanin (unpublished data) has found that the number of introduced tunicate species, and their relative abundances, is much greater in marinas compared with adjacent natural rock habitat. The findings by Simkanin indicate that we may in fact be sampling a community that is not a direct reflection of the natural local community and is biased towards introduced species.

### Species assemblages

In the species presence data the samples from Friday Harbor showed very little similarity to the other samples based on the presence of just one barnacle species, *B. crenatus*. The Friday Harbor site was the last site collected during the winter. It is likely that this site is subjected to runoff associated with the heavy rainfalls of coastal BC winters. The extremes in water temperature and salinity may have killed off most of the species on the settlement array, leaving behind the sessile barnacle.

The species assemblage of *Mytilus* sp., *B. crenatus*, and Amphipod complex 2 was found on samples from all geographic areas. The *Mytilus* sp. complex likely contained three different species, and their hybrids, whose natural and introduced ranges span from Alaska to Mexico (Lamb and Hanby 2005). This species complex is also known as one of the most common bivalves along temperate and Arctic coastlines (Milne and Milne 1973). I explore patterns within this community in the subsequent section because of the prevalence and abundance of this species complex in this study, combined with the fact that *Mytilus* sp. increase habitat heterogeneity and harbour other organisms (Tsuchiya 2002). The co-occurring barnacle, *B. crenatus*, also has a native range that spans the length of our study area and is well known for fouling the hulls of ships and other artificial structures (Lamb and Hanby 2005). Barnacles and mussels are often found in close association in the rocky intertidal and many *Mytilus* sp. larvae are known to settle amongst filamentous algae, barnacles, and the byssal threads of their own genus (Dayton 1971). Often these *Mytilus* sp. are seen to attach and grow directly on top of the barnacles (Dayton 1971) as was seen frequently in this study. *B. crenatus* may therefore be an important foundation species that actually facilitates the settlement of *Mytilus* sp. larvae. The Amphipod complex 2 found living among the barnacles and mussels included *Gnathopleustes pugettensis* and *Eogammarus oclairi*. *G. pugettensis* belongs to the family Pleustidae which are common in fouling communities as commensalists, egg

predators, and microparasites of other invertebrates (Carlton 2007). *E. oclairi* is from the family Anisogammaridae which are free-living, benthic, and epibenthic omnivores and zooplankton predators that inhabit a variety of shallow marine habitats (Carlton 2007). Neither of these species has been reported in epibenthic community studies as most focus on sessile and large motile fauna.

The next largest grouping of samples for the species presence data had a species assemblage of 15 species each sharing a relatively low influence. The similarities of the samples were also much lower in this group of samples so patterns of association for most of these species were better explored in the abundance data.

In the sessile species abundance data, the prevalence and abundance of the *Mytilus* sp. - *B. crenatus* association was again quite apparent, this time in association with the encrusting bryozoan *Lichenopora* sp. The *Lichenopora* genus is under major taxonomic revision and is tentatively placed with the *Disporella* genus; both are known for their discoid colonies encrusting a variety of hard substrates and other invertebrate species (Carlton 2007). I found *Lichenopora* sp. encrusting a variety of substrates but most prominently on the shells of both the mussels and barnacles. Fuller (1936) found a similar species assemblage (though it included a few additional species) in a fouling community in Maine. Fuller (1936) described a pattern of settlement and growth that reflects the community structure I observed in this species association. The barnacles settled first, followed shortly by the mussel community. There was period of growth before the *Lichenopora* sp. were found to settle and grow. This reflects the most common composition I observed, which was of a base of barnacles with mussels growing among and on top of them, and little disks of *Lichenopora* sp. on the mussels, barnacles, and any available free space. These observed patterns of growth also reflected the theory developed by Coe (1932) that, despite the broad recruitment period of most encrusting bryozoans, a number of species delay recruitment until their hosts, such as bivalves and barnacles, have had time to grow to a sufficient size.

In the sessile abundance data, the next largest cluster included samples from three geographic areas (SOG, QCI, and JS). The five most influential species were *S. japonica*, *Halichondria* spp., *B. violaceus*, *C. pallasiana*, and *O. dichotoma*. Interestingly, these influential species are all introduced or cryptogenic species. *S.*

*japonica* was likely introduced from Japan with the Pacific oyster and now occurs in areas along most of the coast extending from BC to South America. It is an extremely well adapting species that has become the most dominant encrusting bryozoan in much of the Pacific Northwest (Lamb and Hanby 2005). The *Halichondria* spp. complex in this study likely includes at least one cryptogenic/introduced species (Carlton personal communication). One species likely prominent in this complex is the introduced *Halichondria (Halichondria) bowerbanki* which is common on floating docks and pilings (Carlton 2007). *B. violaceus* is a colonial tunicate species that may encrust any hard substrate. This species has been introduced from Asia and occurs in locations from BC to northern Baja California (Lamb and Hanby 2005). *C. pallasiana* is another encrusting bryozoan that is almost cosmopolitan in distribution (Carlton 2007). *O. dichotoma* is a cryptogenic species that spans the range from Alaska to the tropics (Carlton 2007). The *Obelia* genus is known for hanging from docks and algae (Lamb and Hanby 2005). The fact that these cryptogenic and introduced species are associated suggests that they are likely introduced and/or transported via a similar vector. It is also very interesting that the cluster includes samples from three of the geographic regions. One of the introduced species, *B. violaceus*, is a brooding tunicate with larvae that are only in the water column for a very short period of time (Carver *et al.* 2006). This species was only introduced to BC in 2001 (Carver *et al.* 2006) and, based on the reproductive strategy and the natural circulation of the coast, it is unlikely that this species was able to spread between SOG and QCI based on natural dispersal alone. Therefore, this species assemblage may provide some insight into how these introduced organisms are able to spread along the coast. This species assemblage was found at sites that were either marinas or shellfish aquaculture sites. The marinas utilised in this study were primarily for recreational boats, and it is unlikely that they would travel the distance to the QCI. All the marinas with this assemblage were in close proximity to areas with a history of having the high density of aquaculture activities (based on information compiled by Herborg and Therriault 2007). It is possible that one of the major vectors of introduction of these species to our coast is aquaculture with the recreational boat activities aiding in the secondary spread of these species. Introduced species assemblages will be further explored in a subsequent section.

In the motile species abundance data, a large proportion of the samples were clustered based on three species assemblages. The species assemblage of *N. procera*, *C. occidentale* and *E. quadrioculata* was present in the most number of samples. *N. procera* is a predatory polychaete whose native range spans from southern Alaska to California and is commonly found on pilings, in mussel beds, and on rocky or silty substrates (Lamb and Hanby 2005). *E. quadrioculata* is another predatory worm which belongs to the Phyllodocidae family which contains the most common and conspicuous active predators in shallow water habitats, particularly associated with hard substratum (Carlton 2007). *C. occidentale* is a polychaete in the family Chrysopetalidae which are active scavengers and carnivores. *C. occidentale* is thought to be more southern in distribution along the coast (Carlton 2007), so it is possible that this study reveals a range expansion, or a possible misidentification to species level. The main characteristic that unites this species assemblage is that all three of the species are active predators. Across all geographic regions, these samples with this species assemblage were likely the ones with an abundance of prey items.

The next most prominent assemblage, was not found in any samples from the QCI or JFS, and was influenced by the abundance of Amphipod complex 2, *N. vexillosa*, and *G. oregonense*. This assemblage is likely formed as the species co-inhabit mussel communities. This relationship will be further explored in the subsequent section, but as previously discussed and highlighted in the species richness data the Amphipod complex 2 forms a strong association with *Mytilus* sp. and *B. crenatus*. *N. vexillosa* is a predatory polychaete also known for hiding in amongst barnacle and mussel clusters (Lamb and Hanby 2005). *G. oregonense* is an intertidal isopod whose habitat is usually described as simply ‘under rocks’ (Lamb and Hanby 2005) though they have also been observed living among mussel and barnacle communities (Brook *et al.* 1994).

The third species assemblage is *J. staudei*, *N. procera*, and *C. anomala*. *J. staudei* belongs to the family Ischyroceridae and are among the most common amphipods of fouling communities. Amphipods in the family are known for constructing tubes on hard substrates in areas of high water velocity (Carlton 2007). *N. procera* are predatory polychaetes that also secrete mucus tubes from which they emerge to feed (Lamb and Hanby 2005). *C. anomala* is a caprellid amphipod that aggregates on any emergent

substratum, including other invertebrates such as hydroids and bryozoans (Carlton 2007). Caprellids are grazers of the microalgae collected on the substratum to which they cling or they can be suspension feeders (Carlton 2007). The preferred habitat features described for these three species suggest that this species assemblage is found where there are relatively strong current flows. The strong flow would facilitate the aeration of the tubes for *J. staudei* and *N. procera* while also provides ample currents to facilitate the suspension feeding for *C. anomala*.

Ardisson and Bourget (1992) described certain ecological traits shared by the species in their assemblage that describe their association: planktotrophic pelagic development, the ability to maintain themselves in the upper layer of the water column during the larval phase prior to settlement, and the capacity to live continuously immersed during the adult phase. The various species assemblages observed in my study share many of these traits; they also have the capacity to live continuously immersed and must be able to maintain themselves in the upper layer of the water column, though for a number of a species this is a very short time period. The difference in my study is that species of the assemblages not only have planktotrophic larvae but also lecithotrophic larvae or are brooders. Instead as the third shared ecological trait I will highlight that the species within these assemblages are usually good space competitors or are gregarious in nature.

The species assemblages identified in the study usually spanned multiple geographic ranges and were dominated by relatively few species. In space limited environments the biological interactions of competition for space often leads to the dominance by one or few species. This dominance largely depends on a number of factors which determine which species arrive first and is further affected by a combination of so many factors that, particularly when sharing a similar larval pool, there are number of community outcomes are possible (Osman 1977, Dean and Hurd 1980). In addition to the attributed features described in the previous paragraph these species were likely so influential in this study because their natural range extends the length of the study area, they are the species best suited to recruit to man-made/artificial structures, and they are easily transported by natural or anthropogenic factors.

### Species assemblages related to geographic area

The WCVI differed from both the JFS and QCI in terms of community composition based on the species presence, sessile species abundance, and motile species abundances. It becomes apparent that most of the differences are driven by the *Mytilus* sp. and associated species (e.g. *H. arctica*, *N. vexillosa*, and Amphipod complex 2). The WCVI samples were primarily dominated by *Mytilus* sp. communities whereas the JFS and QCI had relatively low abundances of *Mytilus* sp. and were instead driven by introduced and cryptogenic species (JFS-*B. violaceus* and *O. dichotoma*, QCI- *S. japonica* and *C. pallasiana*). The WCVI is characterised as open ocean coast with numerous warm inlets and bays (Gillespie 2007). These warm bays and inlets would facilitate the retention of larvae and the stepwise progression of communities along the coast. The WCVI is also not subjected to as many anthropogenic activities as the JFS and QCI. The JFS likely had such a strong introduced/cryptogenic community composition as it is the busiest waterway for commercial vessels along the BC coast (Herborg and Therriault 2007). The QCI also had a surprisingly strong representation of introduced/cryptogenic species as the few sites we had in the QCI were where there are historic records of aquaculture activity and where the few human settlements are located. Both the JFS and WCI also had fewer samples than the other geographic regions which may contribute to the observed differences.

The QCI and NC differ in community composition for only the sessile species abundance data. This indicates that two areas share a similar species pool and that it is simply the most abundant or dominant species that differs between the geographic regions. Again, the observed difference is attributed to the abundance of the *Mytilus* sp. – *B. crenatus* – *Lichenopora* sp. assemblage on the NC compared to the abundance of the bryozoans *S. japonica* and *C. pallasiana* in the QCI. The NC most closely resembles the WCVI in terms that it consists of a series of inlets and fjords, but is much colder due to influences of glacial runoff. The *Mytilus* sp. – *B. crenatus* – *Lichenopora* sp. is likely the assemblage that is best adapted to cold and relative low saline waters.

### Patterns in the *Mytilus* sp. community

The *Mytilus* sp. complex was the most prominent and abundant species in this study. *Mytilus* sp. was found all along the coast, though differences in its abundance did contribute to observed differences between geographic areas. Along with its abundance and prominence in this study, we also want to look at the community structure associated with *Mytilus* sp. as they provide habitat for many organism. The surface of *Mytilus* sp. shells provide secondary space of epizootic growth and many organisms recruit to and seek refuge in among the byssal threads attaching to the substratum (Paine 1974, summarized in Ragnarsson and Raffaelli 1999, Tsuchiya 2002). Tsuchiya (2002) summarises that, in addition to other abiotic and biotic factors, the community structure within a mussel bed will likely be affected by the age and size structure of the mussels, the patch size, the proximity and abundance of local algal growths, and the presence of gaps within the bed. In this section we can explore the patterns of community composition within the mussel community along the coast and look at the species assemblage inhabiting these communities.

In the species presence data, the most common species assemblage was *Mytilus* sp., *B. crenatus*, Amphipod complex 2, *N. vexillosa*, *H. arctica*, and *G. oregonense*. The association of most of these species was highlighted in the previous section, especially the *Mytilus* sp.-*B. crenatus*-Amphipod complex 2 association. *N. vexillosa* and *G. oregonense* are both motile species that forage and seek refuge in the structural complexity of a *Mytilus* sp. community. The only species not previously mentioned is the bivalve *H. arctica*. *H. arctica* is a small sessile bivalve species that was frequently observed in samples but did not occupy much space within the community as it was so small. *H. arctica* is a nestling bivalve that uses byssal threads to attach to a substratum and is often found within mussel beds, algal holdfasts, on pilings, and in fouling clumps. This species was once primarily an Arctic species that has likely spread southward by boating and shipping activity (Lamb and Hanby 2002, Carlton 2007). The next most prominent association is that of *Mytilus* sp., *B. crenatus*, and *Lichenopora* sp. Again, the association of *Mytilus* sp. and *B. crenatus* has been previously discussed. The surface of the mussel shells provided idea habitat for the *Lichenopora* sp. This assemblage was observed in all geographic regions except the JS. The unique feature of the JS that may

be limiting the settlement of *Lichenopora* sp. in the mussel community is that it is an area of such turbulent mixing.

The next most prominent species assemblage was that of *Mytilus* sp. with *N. procera*, *E. quadrioculata*, and *C. occidentale*. This species assemblage was missing the typical *Mytilus* sp.-*B. crenatus* association. It is likely that at these sites the *Mytilus* sp. complex actually settled before *B. crenatus* larvae. If this were the case, the competitively dominant *Mytilus* sp. larvae likely excluded *B. crenatus*. This species assemblage highlights the importance of recruitment and settlement timing because if *B. crenatus* settles first it may act as foundation species that facilitates the settlement of the *Mytilus* sp. complex (Dayton 1971). However, if the *Mytilus* sp. larvae settle first, the mussel complex will inhibit the settlement of *B. crenatus* (Dean and Hurd 1980). This also reiterates the importance of local dynamics and timing to the local recruiting larval pools. The three associated worm species are predators and scavengers that likely forage and seek refuge among the byssal threads of the mussels.

The association and abundance of *Mytilus* sp.-*B. crenatus* is again evident in the sessile species abundance data. However, there were associations along the coast where *Mytilus* sp. was present but not the most influential species in the community. This is surprising, as once mussels species are established in a community they will inhibit the growth and settlement of other sessile species (Dayton 1971, Dean and Hurd 1980). It is possible that at the sites where other species dominate the samples either a) *Mytilus* sp. recruitment and settlement timing was later than the other dominants species, b) the other species are superior space competitors, or c) there are environmental factors at these sites that allow these other species to be competitively dominant. The clustering of the two NC sites was influenced by the abundance of *C. inflata*, *S. insignis*, *A. polyoum* and *Metridium* sp. Any of the previously listed possibilities may have lead to the dominance of other species in these samples. It is likely that *C. inflata* was able to recruit to the settlement arrays earlier than the *Mytilus* sp. complex as it is a solitary tunicate that broods throughout the year (Strathmann 1987). Additionally, *Corella willmeriana*, a close relative of *C. inflata*, has a very rapid growth rate that would give this species a strong competitive edge (Lambert 1968, Schooner and Greene 1981). *S. insignis* is a sabellid polychaete commonly seen on docks and pilings. It could have beaten the

*Mytilus* sp. larvae to the settlement arrays as it has been seen to spawn in the laboratory as early as January, as well as in April-May, though field observations record the spawning season in July (Strathmann 1987). The *Alcyonidium* genus is under taxonomic revision and is being introduced worldwide (Carlton 2007). As such, there is little information available on its competitive nature or reproductive strategies along our coast. Regardless, *A. polyoum* is a very good space competitor as it is a colonial encrusting bryozoans and is able to cover a large area of space through asexual reproduction. It is not likely that *Metridium* sp. settlement was earlier than that of *Mytilus* sp. as its spawning period is May-August (Reitzel *et al.* 2004). However, *Metridium* sp. are species that become strong space competitors with time. They settle as small individuals that have relatively large growth spurts where they effectively increase the diameter of their pedal disk. This species can also perform asexual reproduction called pedal laceration to increase members in the aggregation and take over more space (Sebens 1979).

In the motile species abundance data, samples from all geographic were influenced by the abundance of *N. procera*, *E. quadrioculata*, and *C. occidentale*. The next largest cluster contained samples from SOG, JS, NC, and WCVI and was influenced by the abundance of Amphipod complex 2, *N. vexillosa*, and *G. oregonense*. These species assemblages have been previously discussed in their likely association within the *Mytilus* sp. community. What is truly surprising in the motile species abundance data is that so few species seem to primarily inhabit the *Mytilus* sp. community. Given the increased level of habitat heterogeneity provided by the community, I speculated that a greater range of species would inhabit the community.

In this section, and previous sections, any differences in geographic area have been strongly tied the prominence and abundance of the *Mytilus* sp. community in one area to the prominence and abundance of introduced/ cryptogenic species in the JFS and QCI. The introduced species in this study are strong space competitors. The only regions where *Mytilus* sp. did not dominate was where introduced and/or cryptogenic species were present. It appears that the introduced/cryptogenic species in this study are able to inhibit the dominance of *Mytilus* sp. in the subtidal fouling community.

### Patterns in the introduced community

In the species assemblage data for the entire dataset, we see likely patterns relating to cryptogenic and introduced species data. By definition, we are unsure whether cryptogenic species have been introduced to an area or not so, to tease out the patterns in the introduction of species along our coast, I will focus on the introduced species only. Seven introduced sessile species and four introduced motile species were identified in this study.

The introduced sessile species include one species of sponge, two bryozoans, and four tunicate species. *Cliona* spp. is a genus of sponge known for boring into bivalve shells and this species was likely introduced with oyster aquaculture from the North Atlantic and western North Pacific (Levings *et al.* 2002). *S. japonica* (= *unicornis*) is an encrusting bryozoan that was first reported along our coast in the 1950s and was likely introduced from Japan along with the Pacific oyster for aquaculture (Dick *et al.* 2005, Carlton 2007). *A. polyoum* (= *gelatinosum*) is another bryozoan species that was keyed out to be the species of European origin. However, the genus *Alcyonidium* is under major taxonomic revision and it likely that along our coast we have a number of native or cryptogenic species that have not yet been identified and described (Carlton personal communication). *B. violaceus* and *B. schlosseri* are colonial tunicates that are becoming increasingly abundant on the east and west coast of Canada. *B. violaceus* was first reported along the BC coast in 2001 and was likely introduced from the Pacific Northwest (Japan) (Carver *et al.* 2006). *B. schlosseri* is a cosmopolitan species, though it originated from the Mediterranean Sea, which has been in BC waters since the early 1900's but has recently seen a substantial population growth (Carver *et al.* 2006). Both species were likely introduced to our coast via oyster aquaculture and continue to be of concern for aquaculture practices as their presence can lead to a direct loss of stock and increased production costs (Carver *et al.* 2006). *S. clava* is a solitary tunicate that has been introduced from the western North Pacific that has just recently taken hold in a few of our coasts' harbours. This species is suspected to have been transported by ships to our coast, though it is also of a great concern as a nuisance species for shellfish aquaculture (Lamb and Hanby 2005). *M. manhattensis* is a solitary tunicate that was introduced to our coast from the western North Atlantic. *M. manhattensis* previously

reported introduced range is further south in Pacific Northeast and its presence on the settlement arrays in this study indicates a northward spread along the coast (Lamb and Hanby 2005).

The motile introduced species include one polychaete and three amphipod species. *P. cornuta* is a spionid polychaete common in estuaries and mudflats that was likely introduced to our coast from the North Atlantic several times (Levings *et al.* 2002, Carlton 2007). The possible vectors of introduction and spread for this species include ballast water, ship fouling, and oyster aquaculture (Heiman *et al.* 2008). The introduced species, *M. acherusicum*, of Amphipod complex 1 is often found in float fouling communities and estuary soft benthos. This species was introduced from the North Atlantic by shipping and is now cosmopolitan in distribution (Carlton 2007). The introduced caprellid amphipod *C. mutica* is an Asian species that was brought to the BC coast via either shipping or oyster aquaculture. This species is gregarious in nature and is often very abundant on hydroids in fouling communities on floats and pilings (Carlton 2007). The final amphipod species *M. nitida* may be introduced from either the North Atlantic or from Asia, though it is difficult to resolve this species from its close Asian relative (Carlton 2007). Interestingly, the sessile and motile introduced species in this study may be introduced and transported by different vectors; the sessile species predominantly by shellfish aquaculture, and the motile species by large shipping activities.

Introduced species assemblage had a weak relationship with geographic area. This result is unexpected as certain geographic areas are likely to host more species. For example, the SOG is home to most of the province's population and has the coast's major shipping port, highest density of aquaculture facilities, and the highest density of small craft moorings (Herborg and Therriault 2007). It is also expected that certain species would be only be present in limited areas because of recent introduction and limited natural dispersal (*i.e.* *B. violaceus*). The geographic effects may be weak in this study because of the fact that we are examining a number of species that not only fill different ecological niches but that also have been introduced by different vectors. In addition, along with their natural sources of introduction to the coast the species are likely being secondarily spread by activities such as recreational boating (Floerl and Inglis 2003,

Ashton *et al.* 2007). Again the nature of this study may also have enhanced the relative presence of introduced species as all the settlement structures were suspended from man-made structures that were in close proximity to potential vectors of spread. Introduced species are also well adapted to exploit novel habitat and withstand the extremes of a stressed environment.

*A. polyoum* was present and abundant in samples from all geographic areas, except JFS and QCI. As has been previously discussed these two geographic areas did not have a strong prevalence or abundance of *Mytilus* sp. and it appears that *A. polyoum* forms a strong association with the *Mytilus* sp. community. The difference in the presence and abundance of *A. polyoum* had a strong influence on the difference in community composition observed for the JFS and WCVI.

A large proportion of the samples were influenced by the presence and abundance of *S. japonica*, as well as by the association of *B. violaceus* and *S. japonica*. These two species were both introduced to this coast via shellfish aquaculture activities. The abundance of these two species in JFS compared to the WCVI largely contributed to the two regions observed differences. The JFS does not have a strong history of supporting aquaculture activities. The JFS is the major travel route for shipping traffic entering the SOG and Puget Sound. The strong presence and abundance in the JFS confirms that these species are being secondarily spread along the coast, potentially by the fouling of recreational boat hulls. The surface outflow from the SOG caused by Fraser-induced estuarine circulation may also facilitate the dispersal of these species from the SOG.

In the motile species abundance data, Amphipod complex 1 was found in samples from all geographic regions except JFS. Unfortunately, this complex contains two species and only one, *M. acherusicum*, of is actually introduced. The inability to resolve this group to the species level means that we can gain little insight into the current distribution and potential vectors of spread for this species within our coast.

The next largest cluster for the motile species abundance data included samples from all geographic regions and was influenced by the abundance of the introduced *C. mutica*. This is actually the first confirmed report of the presence of *C. mutica* in BC waters, though it has been reported along coast of the US and most recently Alaska (Frey *et al.* 2009). *C. mutica* is a caprellid amphipod that lacks a planktonic larval phase and whose

limited dispersal potential is on the scale of a few kilometres per year (Ashton 2006). It is very unlikely that this species was able to spread along the length of our coast in such a short time frame by natural dispersal and was aided by anthropogenic activities. At least one probable anthropogenic vector is commercial vessels, as Frey *et al.* (2009) also found *C. mutica* on the hulls and in the sea-chest of commercial ships entering Canadian dry-docks.

Many of the introduced species in this study were found at greater distances than expected based on natural dispersal alone. By looking at the structure from which each settlement array was suspended, we hoped to gain insight into anthropogenic vectors likely associated with the introduction and spread of introduced species. The general categories consisted of a marina or dock, shellfish aquaculture site, finfish aquaculture sites, or floats. There was a weak relationship of introduced species assemblages with the type of structure from which the settlement arrays were suspended. Pairwise comparisons did indicate that there was a difference in the community structure for the introduced sessile species abundance between fish farm samples and shellfish aquaculture samples. *A. polyoum* was far more abundant at fish farms than at shellfish aquaculture sites. *B. schlosseri* was more abundant at shellfish sites and both *B. violaceus* and *S. japonica* were only found at shellfish sites. This indicates that the vector for *A. polyoum* is different from that of *B. schlosseri*, *B. violaceus*, and *S. japonica*. We already know that *B. schlosseri*, *B. violaceus*, and *S. japonica* were introduced via shellfish aquaculture so it is not surprising that it continues to serve as a vector of transport with the coast. *A. polyoum* appears to be transferred by finfish aquaculture. Finfish aquaculture has been responsible for the introduction of species to our coast, but these are primarily the species they utilise in the industry and the species associated with them (*e.g.* Volpe *et al.* 2000). Encrusting bryozoans are not usually associated with fish species. The fact that *A. polyoum* is more associated with finfish aquaculture than with the shellfish aquaculture may support the theory presented by Carlton (personal communication) that there are actually a number of native and cryptogenic species along the coast not yet described.

Though only 11 introduced species were reported in this study, this by no means represents the total number of marine introduced species whose presence is possible along the BC coast. In this study we simply focused on the shallow subtidal hard

substratum epibenthic species. There are introduced species present in the plankton, soft-sediment, and intertidal environments. Additionally, there are introduced algae, fish, mammal, and marine species. In the Strait of Georgia alone 117 introduced and cryptogenic species have indentified (Levings *et al.* 2002). The wide spread distribution and the abundance of a number of introduced species emphasized that introduced species are a growing concern on the BC coast.

## Summary

By examining patterns in the community composition for the BC coast we can begin to understand the processes that shape the community. In this chapter we first found that though the depth sampled affected the species richness it had no effect on the way the species recruiting to a sample utilised the available space. Depth had very little effect on community composition and high similarities between the depths at a site highlighted the importance of local dynamics for larval recruitment. The timing of settlement structure deployment should have had a greater effect on community composition due to the seasonality of invertebrate reproduction and recruitment. These temporal signals may be partially obscured in this study because of the strong similarity in community composition along the coast and because so many of the abiotic and biotic factors that shape a community vary in space as well as time.

The strong similarity in community composition occurred along the coast because there were several species assemblages that were present in numerous geographic areas. The most prevalent was that of *Mytilus* sp. and associated species. There were differences in community composition between the WCVI with both JFS and QCI. The WCVI was dominated by the *Mytilus* sp. community whereas the JFS and QCI had a greater abundance of introduced/cryptogenic species. The introduced species in this study were strong space competitors. It appears that the introduced/cryptogenic species in this study are able to inhibit the dominance of *Mytilus* sp. in the subtidal fouling community.

Introduced species were found in all geographic areas. New reports from this study include the present of *B. violaceus* in QCI, a northward spread of *M. manhattensis*, the first confirmed report of the presence of *C. mutica* in BC waters. The introduced species assemblages were different on settlement arrays hung from shellfish from those at fin fish sites.

## Conclusions

The development of a subtidal hard substratum epibenthic invertebrate community is complex and is shaped by multiple biotic and abiotic factors acting throughout the life histories of the organisms. In identifying the individual species and studying the patterns in community composition we are able gain a better understanding of these communities and the factors that shape them.

I identified 171 species with an additional 34 categories of unresolved organisms, each containing at least one species. The richness of over 200 species observed in this study is one of the highest reported for studies of epibenthic communities in the northeast Pacific Ocean. We likely saw such high richness because we sampled such a large geographic range and utilised a sampling method that allowed us to look at the entire community while causing minimal damage during the sampling process. However, I was studying this epibenthic community in a very space limited environment and though it was high in species richness, it was also very uneven, being dominated by relatively few species. The dominant species were usually the most influential in species assemblages along the coast. The dominant species observed in this study were very strong competitors, had ranges that included the length of our study area, and had key reproductive periods during the sampling period. The most dominant sessile species was the *Mytilus* sp. complex.

There were no strong geographic patterns in community composition along the coast. Instead, there were strong similarities observed across geographic regions based on species assemblages. The most prominent and abundant community along the whole coastal range was *Mytilus* sp. and its associated species. *Mytilus* sp. most commonly formed an association with the sessile barnacle species *B. crenatus*, the sessile bryozoan species *Lichenopora* sp., and the motile amphipod complex of *G. pugettensis* and *E. oclairi*. The regions where the *Mytilus* sp. associated community did not dominate the dominant species assemblage were usually influenced by introduced and cryptogenic species. The introduced species in this study were strong space competitors and may have been able to inhibit the dominance of *Mytilus* sp. in the subtidal fouling community.

The community composition was not strongly affected by the depth sampled or the timing of sampling. The two depth samples from a site were usually clustered together based on high similarity. I thought that, due to the more extreme environmental

conditions associated with the surface; there would be less similarity between the depths. However, the strong similarity observed within a site highlights the importance of local dynamics of recruiting larval populations. There are so many contributing abiotic and biotic factors, that can vary both spatially and temporally, that recruiting species pools were the most similar within a site.

Community composition is largely influenced by the initial colonization of a substrate. Timing should have had a greater effect on community composition, as initial colonization is determined by the abundance of local larvae, and the abundance of local larvae is largely determined by selectivity and seasonality (Osman 1977). I believe that the effects of timing may have been weakened in part due to the strong similarity of species composition along the coast. Also, the effects of timing may have been diminished because there are a multitude of variables that vary in time and space, but also may vary spatially over time. For example, a species that may be present in all geographic areas may have a peak recruitment period that is tied to water temperature and may spawn earlier in the SOG as opposed to the cold waters of the NC.

Eleven introduced and twelve cryptogenic species were identified in this study. The introduced species *A. polyoum*, *B. violaceus*, *S. japonica*, Amphipod complex 1 (containing *M. acherusicum*), and *C. mutica*, along with the cryptogenic species *O. dichotoma*, were all considered dominant species in this study and were influential species in assemblages that spanned numerous geographic ranges. New reports from this study included the present of *B. violaceus* in QCI, a northward spread of *M. manhattensis*, and the first confirmed report of the presence of *C. mutica* in BC waters. The widespread distribution and abundance of these species emphasised the fact that introduced species are becoming integrated into communities along the BC coast. Introduced species are a growing concern worldwide as they can have important ecological and economic effects on natural communities.

The sampling gear used in this study facilitated and enabled this large-scale survey. The design of the settlement arrays allowed for easy transport of communities, could be easily replicated, and allowed me to look at the entire community while causing minimal damage. I believe the high richness observed in this study was largely attributed to the fact that I was able to transport subsamples of the entire community back to the lab.

There was a strong representation of motile species, which are often overlooked in epibenthic studies and I was able to resolve bryozoans to species level because the colonies and all defining characteristics were left intact. However, introduced species may have been so prevalent in this study because the sampling arrays were always suspended from man-made structures that may be vectors of introduction and spread. Also, man-made structures are often high stress environments (*e.g.* high pollution levels) and we may have been sampling the organisms that were best adapted to these environments. Future studies should consider having an artificial and natural sample from each site to determine whether the sampling arrays are an accurate representation of the local natural environment. The ‘natural’ settlement arrays can be suspended from floats or buoys near rocky habitat at set distances away from the ‘artificial’ arrays. Regardless, these settlement arrays have proven to be an effective tool to be utilised in monitoring the introduction and spread of introduced species along the coast.

The next step in this project is to examine the patterns in community composition in the context of more abiotic factors. Temperature and salinity are usually important abiotic factors that may limit the distribution, growth, and reproductive abilities of species (*e.g.* Epelbaum *et al.* 2008). Temperature and salinity data can be extracted from websites such as the National Oceanic and Atmospheric Administration (NOAA) World Ocean Data (<http://www.nodc.noaa.gov/>). However, in future projects for high-resolution data I would recommend that temperature loggers be affixed to the settlement arrays.

The greatest value gained from this project is that was a pioneer study. It was the first large scale, high resolution study of subtidal epibenthic invertebrate communities for the BC coast. The data gathered on the identity, richness, diversity, and pattern of community composition for invertebrate fouling communities can be used as a baseline for future studies. It fills a knowledge gap that may be increasingly important with the growing global concerns of climate change, human mediated species introductions, and increasing anthropogenic disasters.

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