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Analysis of a Population of *Colpomenia peregrina* in British Columbia: Relationships with environment and primary substrate

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An intertidal population of *Colpomenia peregrina* (SAUV.) HAMEL (Phaeophyceae) macrothalli was studied and the data were analysed using Principal Components Analysis. The plant's relationship with other members of the community and various physical factors were examined. *Colpomenia peregrina* was found to occur in environments with intermediate values for temperature, salinity, daily solar radiation, daylength, daytime air exposure and nightime air exposure. Seasonal extremes of these variables (winter and summer) coincided with low *C. peregrina* percent cover. The floristic composition of the community did not seem to influence the occurrence of *C. peregrina* other than high *Lithothrix aspergillum* cover coinciding with low *C. peregrina* cover. *Colpomenia* appeared to be selective of its substrate in some cases.

Key Index Words: Colpomenia; *ordination*; *Scytosiphonales*; *substrate*; *synecology*.

Colpomenia peregrina (Sauv.) Hamel is a saccate brown alga which is widely distributed in temperate seas. It is an ephemeral plant which overwinters as a microscopic filamentous thallus (VANDERMEULEN 1984). The macrothalli are frequently epiphytic and have some characteristics which suggest an opportunistic role in algal communities (VANDERMEULEN and DEWREEDE 1986). Laboratory experiments have indicated that the seasonal abundance of *C. peregrina* in British Columbia may be primarily driven by fluctuations in the physical environment (VANDERMEULEN 1986).

The research presented here describes the relationship between *Colpomenia* abundance and the physical and biological environment in which the plants are found. A population of *C. peregrina* was monitored at Bath Island, British Columbia. Information was gathered on *Colpomenia* percent cover, the cover of all primary substrate algal species in the community (non-epiphytes) and selected environmental variables. Principal components analysis was used to help elucidate relationships in the data set.

Materials and Methods

Details of study site and sampling methods are presented in VANDERMEULEN and DEWREEDE (1986). The study site was at Bath Island in Georgia Strait, British Columbia (49° 09′ N, 123° 40′ W). An intertidal *Colpomenia peregrina* population was studied on the southeast side of the island. The shore is a large sandstone rock slab, moderately exposed to wave action but with strong tidal longshore currents.

The site was usually sampled at high tide by use of SCUBA. The logistics of underwater sampling and the length of time that could be spent at the field site prohibited

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examination of more than three quadrats on any one field trip. Three permanent quadrats (1 m×1 m) were established at the field site between April and May 1979. Q1 at 1.3 m, Q2 at 0.5 m and Q3 at 0.3 m above Canadian Chart Datum. The quadrats were marked on the shore with expansion bolts secured in the substrate (holes were made by a pneumatic drill powered with compressed air from a SCUBA tank). Aluminum frames strung with nylon garden twine provided 81 or 100 coordinates used to estimate the true percent cover of *C. peregrina*.

At the same time as percent cover of *C. peregrina* was estimated by the line intercept method the percent cover of all primary substrate, including algal species and bare substrate, was also estimated. When a *Colpomenia* plant was seen at a line intercept the substrate it was growing on was recorded as well. In this manner the primary cover within a quadrat was calculated to a total of 100% and *C. peregrina* was considered secondary cover upon the primary substrate. *Colpomenia* was the only secondary cover organism examined. The quadrats were examined approximately once a month from April 1979 to September 1981. Twenty nine visits were made in total (28 for Q1).

Three measures of diversity were calculated from the percent cover data from each quadrat on each sampling day, species richness (S), the Shannon-Wiener index (H′) and equibility (J′) (PIELOU 1974). The numbers obtained from the calculations were just used to estimate the heterogeneity of primary cover within a quadrat, not to measure the true species diversity. The percent cover of *C. peregrina* was not included in the calculations as it was considered secondary cover. For comparative purposes bare substrate was also considered a "species" which could add to "diversity".

The information gathered on the substrates upon which individual *C. peregrina* plants were growing was used to measure substrate preference of the *Colpomenia* plants. A chi-square method outlined by BROWER and ZAR (1977) was utilized to test if *Colpomenia* was being selective. The calculation required that at least two *C. peregrina* plants be recorded in the quadrat and at least two different substrates be available in the quadrat.

Daily salinities and temperatures for surface waters (0.9 m) off Entrance Island (49° 12′ N, 123° 48′ W) were obtained from Dr. L.F. GIOVANDO, Institute of Ocean Sciences, Sidney, B.C. This was the closest site to Bath Island where daily sampling of surface waters occurred (approx. 9 km distant). There was some evidence that the physical characteristics of the water at Entrance Island were very similar to those at Bath Island due to prevailing longshore currents (GIOVANDO 1973). Salinity and temperature data collected at Bath Island were similar to the data from Entrance Island collected on the same day (VANDERMEULEN 1984).

Daily solar radiation and daylength measurements for Departure Bay, Nanaimo (49° 12′ N, 123° 57′ W) were obtained from Environment Canada's monthly radiation summary reports (ANONYMOUS 1979, 1980, 1981). This was the closest site to Bath Island where daily pyranometer information was recorded (approx. 22 km distant).

Daily tidal information for Silva Bay, Gabriola Island (49° 09′ N, 123° 42′ W) was obtained from Canadian Tide and Current Tables Volume 5 (ANONYMOUS 1979,

Table 1. Variables used for ordinations of environmental data.

Variable	Item
V1	Temperature (°C)
2	Salinity (‰)
3	Solar radiation (Megajoules/m^2/day)
4	Daylength (hours/day)
5	Number of days plants exposed
6	Number of hours of day exposure
7	Number of nights plants exposed
8	Number of hours of night exposure
9	Percent cover of *Colpomenia*

1980, 1981). This was the closest "tidal secondary port" to Bath Island (2 km distant).

A list of variables used in the environmental ordination is given in Table 1. The information on environmental variables gathered for each Bath Island quadrat was divided into 14 day time periods. Each time period represented the two weeks prior to a particular sampling day in the field. This length of time was representative of the life span of *C. peregrina* (VANDERMEULEN 1984). The average value for a particular variable was then calculated for each time period at each quadrat. A similar method has been employed

Table 2. Variables used for ordinations of percent cover cover data.

Var.	Item	Seasonality*				Q**
		Spring	Summer	Fall	Winter	
V1	*Fucus distichus*	++	++	+++	+++	Q1
2	*Bossiella orbigniana*+*Corallina vancouveriensis*	++++	+++	+++	+++	Q2
3	*Lithothrix aspergillum*	++++	++++	++++	+++	Q3
4	*Rhodomela larix*+*Odonthalia floccosa*	++	++	++	+	Q2
5	*Ralfsia fungiformis*+other species	+++	+++	+++	++++	Q1
6	crustose base of *Prionitis lanceolata*	++++	+++	++	++++	Q3
7	bare sandstone substrate	++	+++	+++	+	Q1(−)
		++	+++	+++	+++	Q2
8	*Hildenbrandia* spp.	++	++	++	+++	Q1
9	*Prionitis lanceolata*	+	++	+	+	Q3
10	*Sargassum muticum*	+	+	+	−	Q2(+)
11	*Lithothamnium* (?)+*Lithothrix* crust	+	+	+	+	Q2(−)
12	*Analipus japonicus*	++	++	+	++	Q1
13	*Ulva* spp.+*Monostroma* spp.	+	++	++	+	Q1
14	*Botryoglossum farlowianum*	+	+	−	−	Q3
15	*Microcladia coulteri*+*M. borealis*	++	+	−	−	Q1
16	*Iridaea heterocarpa, I. cordata* +*Gigartina* sp.	+	+	+	+	Q1(+)
17	*Lomentaria hakodatensis*	+	+	+	−	Q2
18	*Petrocelis franciscana*	++	++++	+	+	Q1
19	*Cryptosiphonia woodii*	+	++	−	−	Q1
20	*Ceramium* spp.	+	−	++	−	Q1
21	*Calliarthron tuberculosum*	+	+	+	+	Q2
22	diatoms	++	+	−	−	Q1
23	green crust (not identified)	+	−	+	−	Q1
24	*Colpomenia peregrina*	+	−	−	−	Q1
		++	+	+++	−	Q2
		+	+	+	−	Q3
25	H′					
26	J′					
27	S					

* Dates for the different seasons as defined in VANDERMEULEN and DEWREEDE (1986). (−) not present; (+) <5% cover; (++) 5–15%; (+++) 16–30%; (++++) 31–70%.

** Seasonality data taken from this quadrat (item most common here). (+) or (−) annual fluctuation in cover for this item correlates (p>0.05) with *Colpomenia*.

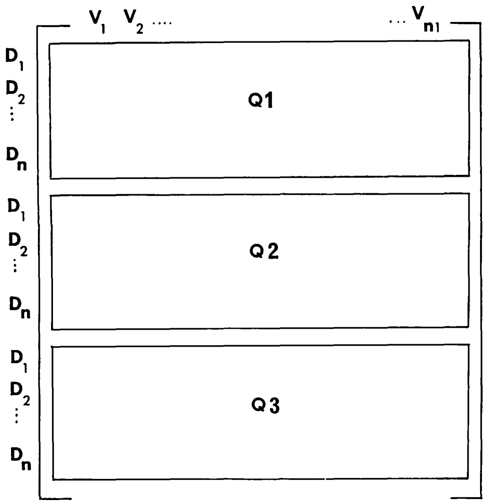

Fig. 1. General form of data matrix used. V=variable, and D=sampling day.

by THOM (1983). The form of the data matrix produced is shown in Fig. 1.

The data matrix was analysed using principal components analysis (PCA) on the MIDAS statistical package (FOX and GUIRE 1976). All variables were standardized (scaled to unit variance) where appropriate in order to remove the effects of different variable scales of measure. In many cases the variables were tested for normality using a G test (SOKAL and ROHLF 1981) prior to the standardization. The ordination methods were used to suggest relationships between variables and the samples, not to function as statistical analyses of such relationships (JEFFERS 1978, JOHN *et al.* 1980, GAUCH 1982).

PCA was also applied to the percent cover data for the quadrats over the sampling period. Variables used for the ordination are shown in Table 2. Standardizations and G tests were done as for the environmental data.

Results

Almost all of the G tests showed that the environmental variables were not significantly different from normal. The ordination method used was assumed to be robust enough to prevent the few instances

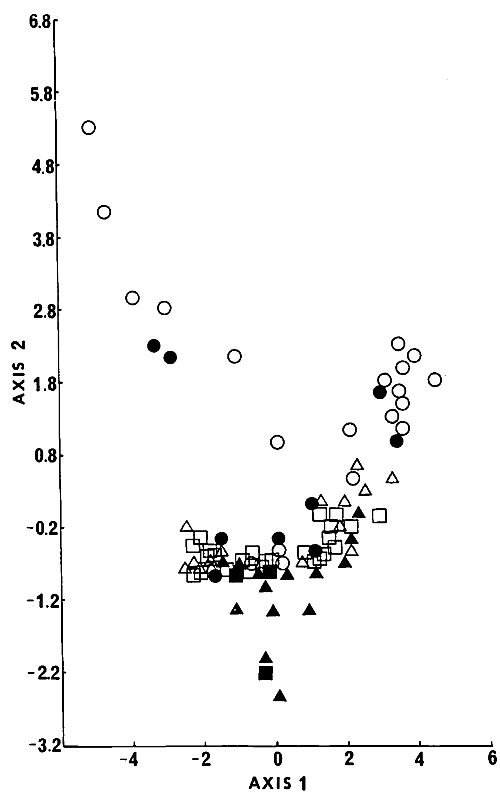

Fig. 2. Scatter plot of a PCA of Bath Island environmental data. Observations with greater than 1.0% cover of *C. peregrina* are shaded. N=86. ○, Q1 observations; △, Q2 observations; □, Q3 observations. 50.4% of total variance accounted for in Axis 1.

of non-normal data use from changing the results (JOHN *et al.* 1980).

Fig. 2 shows the results of the PCA analysis of environmental data. Axis 1 of that scatter plot is composed almost equally of each of the first eight variables (Table 3). The far left of that axis represents an environment of low temperature, high salinity, low solar radiation, short daylength, little daytime air exposure and frequent nighttime air exposure. This was the wintertime environment at Bath Island (VANDERMEULEN 1984). The summer observations are all on the right on Axis 1, an environment of high temperature, low salinity (due to the freshet of the Fraser River), high solar radiation, long daylength, frequent daytime air exposure and little night-

Table 3. Contribution of variables for Fig. 2 scatter plot. Refer to Table 1 for names of variables.

Variable	Axis 1	Axis 2
V1	0.373	−0.007
2	−0.390	−0.109
3	0.419	−0.025
4	0.424	0.0009
5	0.333	0.387
6	0.319	0.388
7	−0.265	0.546
8	−0.264	0.546
9	−0.021	−0.301

time air exposure (VANDERMEULEN 1984). The spring and fall observations occur between those two extremes on Axis 1. *Colpomenia* is most abundant in intermediate positions along this axis (shaded symbols). Note that of the three quadrats Q1 has the widest range along this axis. This means that the environmental conditions in this quadrat fluctuated more over time than in Q2 or Q3. Axis 2 is most strongly represented by nighttime air exposure of the plants (V7 and V8). Q1 again shows the widest range along this axis.

About one half of the G tests of the percent cover variables showed that the variiables were not normally distributed, probably due to the nature of percent cover data. Proportions are frequently not normally distributed and the many zero entries in percent cover data compound that problem. As for the environmental data the ordination method used was assumed to be robust enough to prevent non-normal data from changing the results (JOHN *et al.* 1980).

Fig. 3 shows the results of the PCA analysis of percent cover data. Axis 1 is composed mainly of *Fucus* (0.283), *Hildenbrandia*

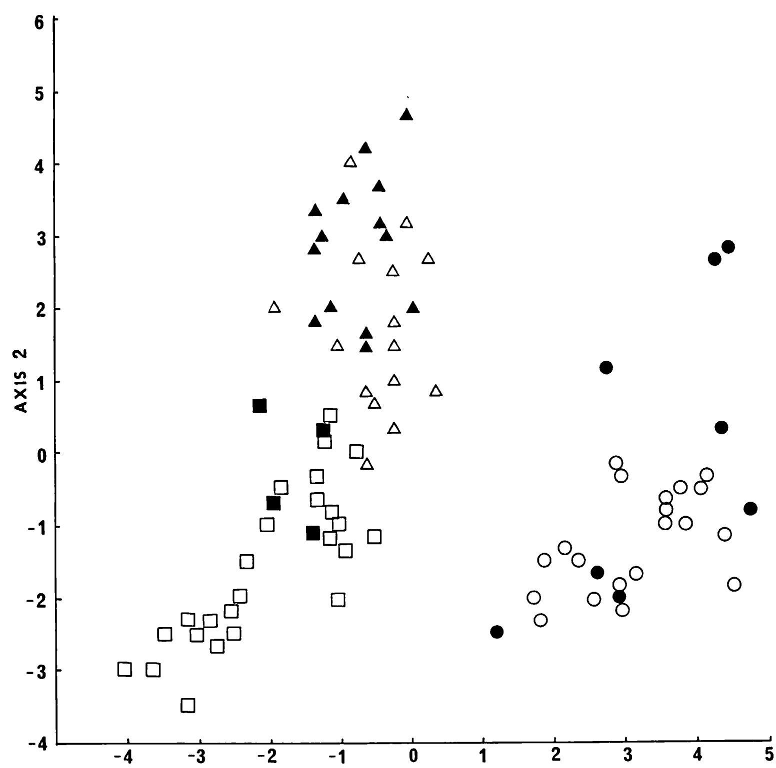

Fig. 3. Scatter plot of a PCA of Bath Island percent cover data. N=86. Refer to Fig. 2 for symbols. 20.5% of total variance accounted for in Axis 1.

Table 4. Contribution of variables used for Fig. 3 scatter plot. See Table 2 for variable names.

Variable	Axis 1	Axis 2
V1	0.283	−0.122
2	−0.115	0.364
3	−0.357	−0.125
4	−0.253	0.269
5	0.260	−0.043
6	−0.165	−0.119
7	0.191	0.123
8	0.305	−0.079
9	−0.199	−0.183
10	−0.101	0.231
11	−0.133	0.234
12	0.260	−0.176
13	0.197	−0.051
14	−0.067	0.291
15	0.108	0.233
16	0.226	0.036
17	−0.010	0.177
18	0.104	−0.143
19	0.101	−0.010
20	0.186	0.025
21	−0.089	0.130
22	0.102	0.068
23	0.171	−0.057
24	−0.041	0.202
25	0.248	0.333
26	0.263	0.224
27	0.126	0.364

(0.305) and *Lithothrix* (−0.357) percent cover (Table 4). This axis separated out those quadrats containing *Lithothrix* (Q2 and Q3) on the left, while Q1 data points are on the right as it was the only quadrat to contain *Fucus*. Axis 2 represents increasing *Bossiella* percent cover and increasing H′ and S as one moves up the axis. Q2 separates out on the upper half of the scatter plot because of its high *Bossiella* cover and relatively high diversity values compared to Q3. It is interesting to note that low diversity values coupled with high percent cover of *Lithothrix* (the lower left hand corner of the scatter plot) seem to represent a community in which *Colplomenia* was not abundant. No other trend could be noted between *Colpomenia* abundance (shaded symbols) and the cover values or diversity measures used.

Table 5. Substrate selectivity of *Colpomenia* (Q1 data).

Date	Chi-square value	Degrees of freedom
May 12 1979	50.8*	8
June 11 1979	2.7	6
March 7 1980	38.8*	9
March 29 1980	23.1*	8
March 1 1981	51.9*	11
March 12 1981	4.1	11

* $p > 0.05$ selection of substrate.

Table 2 indicates that some components of the primary substratum did have an annual fluctuation in percent cover that correlated with that for *Colpomenia*. Bare substrate and *Lithothamnion* crust were negatively correlated while *Sargassum* and *Iridaea* were positively correlated to *Colpomenia*.

The information on substrate selectivity of *Colpomenia* is presented in Table 5. Only Q1 had data which could be analysed by the chi-square method over a number of sampling days. It can be seen that *C. peregrina* does restrict its distribution to certain substrata types on occasion.

Discussion

Colpomenia peregrina abundance appears to be more related to environmental conditions than to the nature of its primary substrate (the algal community in part). PCA analysis of environmental data at Bath Island (Fig. 2) demonstrates that *C. peregrina* is most abundant when environmental conditions are not extreme (fall and spring). Plots of percent cover data over time verify this seasonality (VANDERMEULEN and DEWREEDE 1986) and similar results were found if ordinations were made on data from individual quadrats (VANDERMEULEN 1984). Further evidence supporting a model of environmental control of *Colpomenia* abundance comes from examining individual quadrat points in Fig. 2. Q1 is seen to have had the most extreme environmental fluctuations (wide spread of points along Axis 1), predominantly due to greater exposure, while Q2 and Q3 were quite similar and less variable. Q1 also had a different seasonal percent cover pattern of *C. peregrina* than the other two quadrats (VANDERMEULEN and DEWREEDE 1986).

The composition of primary substrate and the abundance of other algal species does not seem to influence *Colpomenia* abundance. The three quadrats were different floristically (Fig. 3). Each had a different dominant alga, Q1 with *Fucus*, Q2 with *Bossiella* and Q3 with *Lithothrix*. The diversity measures were different in each quadrat as well (Fig. 3). Yet the only relationship that could be deduced was that low diversity quadrats with high *Lithothrix* percent cover coincided with little *Colpomenia* growth (Fig. 3). Correlations of *Colpomenia* percent cover with primary substrate cover (Table 2) do suggest some interaction between *Colpomenia* and the biological environment. For example, the positive correlation between *Sargassum* abundance and *Colpomenia* abundance in Q2 could be considered to be due to *Sargassum* creating a microenvironment favorable for *Colpomenia* growth. However, when *Sargassum* was experimentally removed from this area on the shore no change in *Colpomenia* abundance or seasonality occurred (VANDERMEULEN and DEWREEDE 1986). The other correlations indicated in Table 2 may also have no biological basis other than similar patterns of response to environmentally variable seasonality.

The results of the chi-square tests indicate that *Colpomenia* is "selective" of its substrate in some cases. The selectivity may be due to recruitment on specific surfaces or to selective mortality on other surfaces. No seasonal or quadrat specific trends could be determined and this subject does warrant further investigation.

The hypothesis of environmental control of *Colpomenia* populations generated in this paper has been tested experimentally. Culture work has shown that the high temperature and low salinities of the water at Bath Island in the summer prevent macrothallus formation in *Colpomenia* (VANDERMEULEN 1986). Low water temperature in winter also prevents macrothallus formation (VANDERMEULEN 1986). Field experiments have indicated that *Colpomenia* abundance is not affected by overstory algal species (VANDERMEULEN and DEWREEDE 1986). This result underscores the lack of influence of biological factors on *Colpomenia* abundance. The field and laboratory results both support the environmental control hypothesis for *Colpomenia* abundance in British Columbia.

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VANDERMEULEN, H.・DEWREEDE, R.E.：ブリティシュコロンビアにおける *Colpomenia peregrina* 個体群の解析：環境及び主要基層との関係

褐藻 *Colpomenia peregrina* (SAUV.) HAMEL の潮間帯個体群について調査し，得られたデータを主要構成要素解析法(Principal Components Analysis）により解析した。群集の他の構成種及び物理的要因と *C. peregrina* との関係を検討した結果，本種は中位の温度・塩分・日射・日長・昼間干出・夜間干出をもつ環境のところに出現することが分った。これら諸要因が季節的に極大または極小くとなる時（冬季および夏季）には，本種の被度は低かった。本種の出現は群集の種構成には影響されないようであったが，*Lithothrix aspergillum* の被度が高いところでは本種の被度は低かった。*Colpomenia* は，ある場合には，基層選択性をもつようである。
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