

**Life history phases in *Iridaea cordata* (Gigartinaceae):
relative abundance and distribution from
British Columbia to California***

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A rapid procedure for determining the life history stage of some (non-reproductive) red algae has been developed, based on carrageenan type. Using this methodology the life history phases of *Iridaea cordata* from five sites in Barkley Sound and from Vancouver harbour (British Columbia) showed a dominance of gametophytic blades (ca. 60% gametophytic). Within Barkley Sound there was a trend towards fewer gametophytes in areas of greater wave exposure. When about 8000 blades from 12 populations were sampled in July, 1982, from Oregon to California, the proportion of gametophytic blades was low in northerly populations (ca. 11%) and tended to be higher in more southern populations (ca. 78-90%). These data are discussed in terms of a previous life history model suggested for *Iridaea cordata* from California.

Key Index Words: Algal ecology; carrageenans; Iridaea; life histories.

Introduction

HANSEN and DOYLE (1976) and HANSEN (1977) suggested that populations of *Iridaea cordata* from California may have an *in situ* life history different from the simple *Polysiphonia*-type. In studies on the growth and population structure of *I. cordata* these authors found that tetrasporophytic blades were more abundant than male and female gametophytes in natural populations of *I. cordata*. HANSEN and DOYLE (1976) and HANSEN (1977), sampled four populations throughout the year and concluded that plants regrew primarily from long-lived crusts rather than re-establishing from spores derived from reproductively mature plants. FOSTER (1982) came to a similar conclusion

for *I. flaccida* (SETCHELL et GARDNER) SILA. Growth, reproductive maturation, and senescence of blades occurred throughout the year, but with a larger proportion of the population experiencing senescence during the winter months (HANSEN 1977, FOSTER 1982). Throughout the year tetrasporophytic blades were most common, except in spring when numbers were approximately equal.

There is an element of paradox in this model. If sexual reproduction predominates, the tetrasporangial blades should produce a large number of gametophytic plants which in turn should produce gametangial blades in the next season. However, gametophytic blades consistently made up only a minor part of the populations they studied. HANSEN and DOYLE (1976) and HANSEN (1977) proposed several mechanisms whereby dominance of tetrasporophytes could be maintained: (i) tetrasporangial crusts are hardier

* This paper is dedicated to Professor Robert F. Scagel on the occasion of his retirement (1986).

and longer lived than gametangial crusts, (ii) tetraspores have a higher mortality than carpospores, and (iii) apomeiosis. The last of these can occur in culture (KIM 1976). Apomeiosis appeared advantageous in explaining the expenditure of energy necessary to produce the large number of spores observed in *I. cordata* (HANSEN 1977).

Dominance of tetrasporophytic blades does not, however, appear to be the rule for all populations of *I. cordata* on the west coast of North America. ADAMS (1971), examined three sites in British Columbia and found gametophytic blades to be equal or greater in number than tetrasporangial blades from May to August, after which the tetrasporophytes became more abundant.

The research described in this paper was undertaken to determine if dominance of gametophytes occurs on the exposed west coast of Vancouver Island as well as in the more sheltered areas of the Strait of Georgia and Vancouver harbour. In addition, a series of samples was taken along the Oregon and California coasts to determine if changes in population structure could be observed over this range.

In order to process large numbers of plants, and to quickly separate gametophytic from tetrasporophytic blades in samples where large numbers of thalli may be sterile, a modification of the resorcinol test described by CRAIGIE and LEIGH (1978) was used. The CRAIGIE and LEIGH method tests for 3, 6-anhydrogalactose which is a constituent of K-carrageenan (YAPHE and ARSENAULT 1965). The modification we used for analysis of all samples taken in this study, involved adding reagent directly to the dried algal sample, bypassing the autoclaving step. This modification was tested for consistency and also compared to results obtained by the CRAIGIE and LEIGH methodology.

Materials and Methods

Acetal resorcinol reagent was prepared as outlined in CRAIGIE and LEIGH (1978) and added directly to excised portions of air-

dried thalli. Material was designated as tetrasporophytic if no (or only very slight) color reaction occurred, and gametophytic if the reagent mixture became pink to red. Spectrophotometric analyses were done to determine whether the revised procedure was monitoring the same color reaction as that of CRAIGIE and LEIGH (1978). The test was initially carried out on plants of *I. cordata* from British Columbia and *Chondrus crispus* STACKHOUSE from Nova Scotia, Canada.

Increase in color intensity of the reaction product with increase in biomass of the alga was measured for dry weights from 0.5 to 16 mg (Fig. 1). All reactions proceeded for 60 sec at 86°C in 2 ml of reagent diluted with an additional 2 ml of reagent prior to reading the absorbance. Increase in color intensity of the reaction product with increase in reaction time was measured at intervals from 15 to 150 sec (Fig. 2). All readings were done at 510 nm using a Perkin-Elmer UV-VIS Spectrophotometer Model 139. Complete visible spectra (350–700 nm) for the reaction products of both gametophytic and tetrasporophytic material of *I. cordata* and *C. crispus*, utilizing both the CRAIGIE and LEIGH method and our modification, were performed on a Unicam Sp 800A Ultraviolet Recording Spectrophotometer (Fig. 3).

Preliminary samples in British Columbia were taken at Dixon Island, Wizard Island, First Beach, Second Beach, and Execution Rock (Fig. 4) in Barkley Sound, Vancouver Island, and Stanley Park in Vancouver harbour during 1981. Sampling in each case was done in a 0.5 m wide belt transect located from the upper to lower intertidal zone through an area densely populated by *I. cordata*. From each blade in the transect greater than 5 cm in height, a disk 6 mm in diameter (ca. 3 mg dry weight) was removed with a single hole paper punch.

At First Beach, Barkley Sound, four sites were chosen along a wave exposure gradient. At each site three vertical transects were sampled (July 6–12, 1982) using 0.5 m² qua-

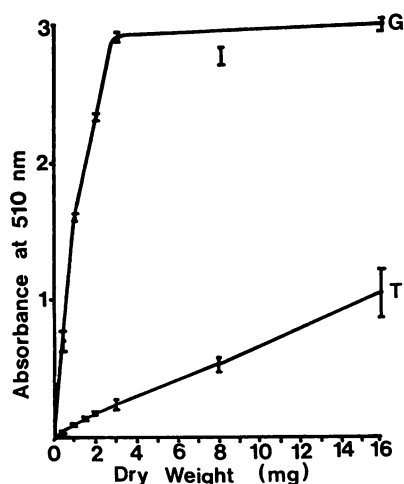


Fig. 1.

Fig. 1. Absorbance at 510 nm for modified resorcinol test in gametophytic (G) and tetrasporophytic (T) plants at different dry weights. (Mean \pm S. E., $n=6$)

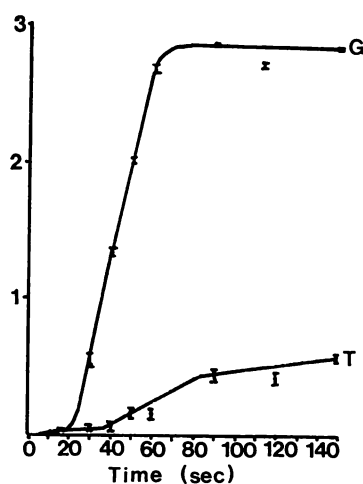


Fig. 2.

Fig. 2. Absorbance at 510 nm for modified resorcinol test in gametophytic (G) and tetrasporophytic (T) plants at different reaction times. (Mean \pm S. E., $n=6$)

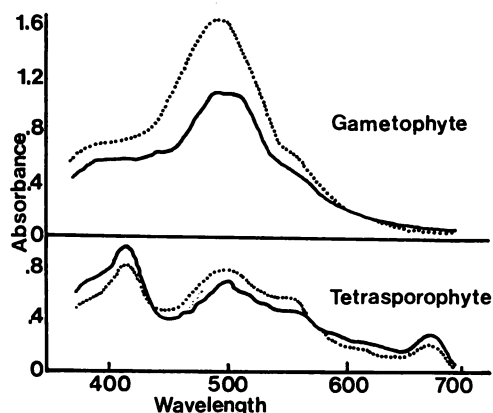


Fig. 3. Absorption spectra of reaction products of modified resorcinol test for gametophytic and tetrasporophytic plants of *Iridaea cordata* (solid line) and *Chondrus crispus* (dotted line).

drats; disks were collected from all blades in each transect. The vertical extent of the sampling varied with topography and exposure, but each transect included the lowest and highest extent of the *Iridaea* population. The lowest elevation sampled in each site was +0.2 m, the highest ranged from +1.0 m (sites 2 and 3) to +1.6 m (site

1); average sampling height was 0.66 ± 0.34 m. After an arc-sin transformation to normalize data (SOKAL and ROHLF 1973), results were analyzed using an ANOVA to examine differences in life history stages among sites and tidal heights. At each site any quadrat with less than 30 individual blades was excluded from the analysis. Site 2 was excluded for this reason.

Twelve sites along the Oregon and California coasts were sampled between July 18-26, 1982 (Fig. 5). At each site representative areas were subjectively selected with dense growths of *Iridaea cordata*. In order to minimize bias, site selection was done from a distance before the population had been examined. At each site all blades in 4 to 10 separate 0.5 m^2 areas were punched and combined for analysis.

In April, 1983, Pigeon Point (California) was resampled. Five 625 cm^2 quadrats were placed randomly along a 50 m transect line in the upper (+67 to +39 cm above mean lower low water) extent of the *Iridaea* bed, and seven additional quadrats were placed in the same fashion in the lower (+15 to -5 cm) extent of the *Iridaea* bed. Data were

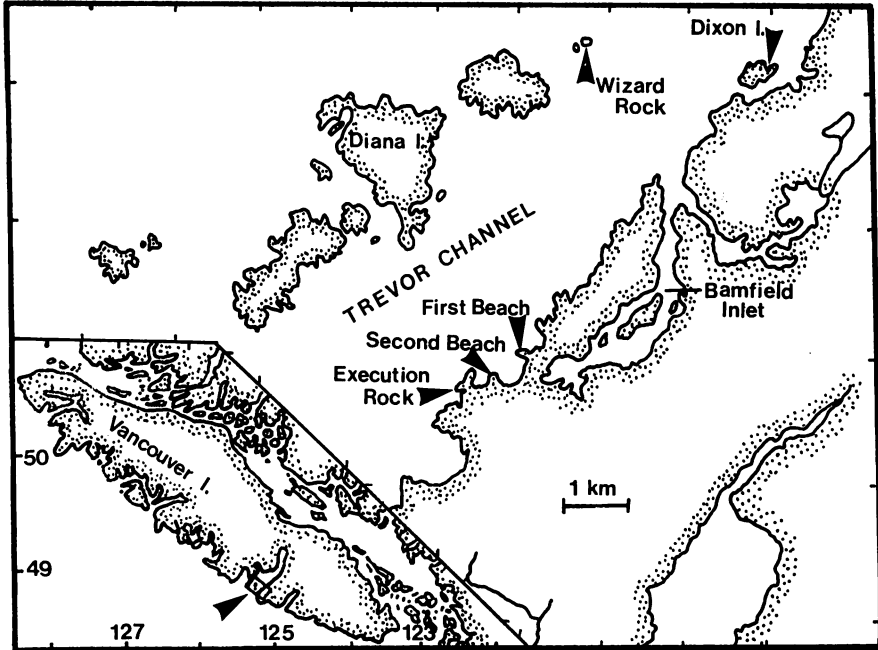


Fig. 4. Details of collection sites in Barkley Sound (arrows) with insert of Vancouver Island showing general location (box and arrow) of sampling area.

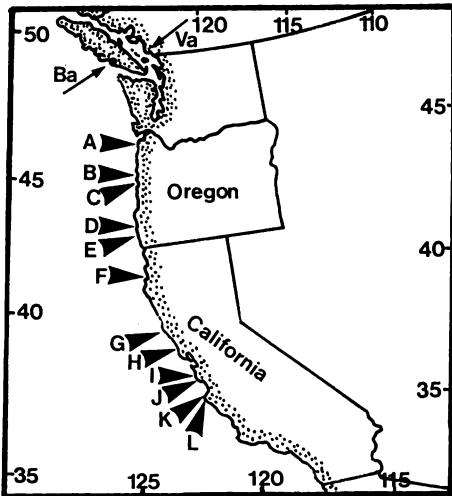


Fig. 5. Map of western North America from Vancouver Island to California indicating sampling locations: Va, Vancouver; Ba, Barkley Sound; A-E, Oregon; A, Indian Beach, Ecola State Park; B, Otter Rock; C, Seal Rock; D, Cape Arago; E, Cape Blanco; F-L California; F, Patrick's Point; G, Point Arena Lighthouse Station; H, University of California Marine Station, Bodega Bay; I, Pigeon Point; J, Davenport, California; K, Point Pinos, Pacific Grove; L, Point Joe, 17 Mile Drive.

analyzed with a one-way ANOVA to test for differences in numbers of tetrasporophytic versus gametophytic blades with respect to tidal height.

All carrageenan analyses were performed utilizing the modified resorcinol reagent test described earlier. Plants were analyzed in batches of ca. 75 disks and several disks of known life history phase were included with each batch as controls.

Note on the taxonomy of *Iridaea cordata* var. *cordata*.

The taxonomy of the *Iridaea cordata* complex in western North America is poorly understood. The bulk of the plants sampled in this study comply with concepts of *I. cordata* var. *cordata* in most modern treatments (e.g. ABBOTT 1971) and are similar to plants identified by SCAGEL (1973) from Barkley Sound. In Barkley Sound, however, plants in more wave exposed sites tended toward the morphology referred to as var. *splendens* (ABBOTT 1971), and some plants

in the upper part of the *Iridaea* zone in California may be referable to *I. flaccida*. Regardless of the potential confusion of *I. cordata* and *I. flaccida*, no differences in proportion of life history stages were recorded at different tidal heights (+0.2 to +1.6 m and -0.05 to +0.7 m) in either Barkley Sound (First Beach) or California (Pigeon Point) respectively. FOSTER (1982) suggests that there is little basis for the separation of *I. flaccida* and *I. cordata* and that these taxa may be conspecific. Our observations are consistent with this synonymy. *I. cordata* var. *cordata*, *I. cordata* var. *splendens* and *I. flaccida* form an apparent continuum in morphology.

Results

Gametophytic tissue of *I. cordata* showed a sharp increase in absorbance at 510 nm as the mass of tissue was increased from 0 to 3 mg. With greater mass there was little or no measurable increase in absorbance. Tetrasporophytic tissue showed an increase in absorbance over the entire 0 to 16 mg range used in the experiment (Fig. 1). Gametophytic tissue also showed an increase in absorbance with reaction time, from 0 to 60 sec, but with little or no increase thereafter (Fig. 2). Tetrasporophytic tissue showed an increase over the entire 0 to 150 sec range tested. Maximum separation of color intensity occurred at about 60 sec using 3 mg dry weight.

Examination of the complete visible spectra of the reaction products of gametophytic and tetrasporophytic plants of *I. cordata* showed different spectra for the two stages (Fig. 3). *C. crispus*, the plant for which the test was first used and from which the different carageenans contributing to these spectra were first isolated (McCANDLESS *et al.* 1973), also shows different spectra for the two stages. Spectra for both plants show a single broad absorption peak at 510 nm for gametophytic tissue. Tetrasporophytic tissue produced spectra with three peaks having maxima at 413, 500, and 672 nm. The absorption spectra

were the same as those generated from tissues prepared according to the methodology of CRAIGIE and LEIGH (1978).

Samples of 3 mg dry weight, when combined with the resorcinol reagent for 60 sec, produced a sufficient difference in color intensity to make visual separation of gametophytic and tetrasporophytic samples simple and consistent. All samples taken from Barkley Sound, Vancouver harbour, and Oregon and California were approximately 3 mg dry weight and were subjected to 60 sec reaction time at 86°C.

The initial survey of life history stages in Barkley Sound showed that variation occurred at the same site over time and between nearby sites at the same time. However, gametophytic blades were most common (55–90%) in 12 out of 15 samples. Similarly, four samples taken in Vancouver harbour during the spring of 1981 also showed a predominance (80%) of gametophytic blades.

Sampling done at First Beach in 1982 at sites with varying wave exposure, revealed a patchy distribution of gametophytes and tetrasporophytes. Results of ANOVA demonstrated no apparent relationship between tidal height and relative numbers of gametophytic and tetrasporophytic blades. Pooling of all the samples at a site (Fig. 6)

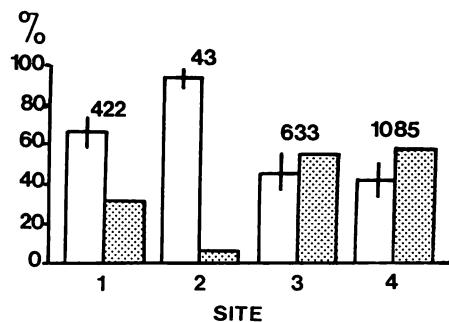


Fig. 6. Histograms showing proportions of gametophytic (clear) and tetrasporophytic (stippled) plants at four sites along a wave force exposure gradient (one is least exposed) at First Beach, Barkley Sound. Numbers above sites are the total number of plants sampled. Error bars denote \pm one standard deviation.

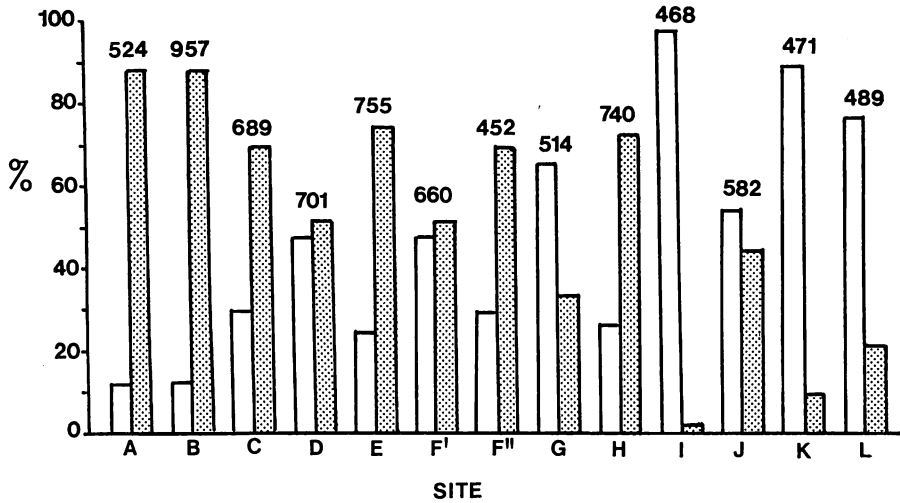


Fig. 7. Histograms showing proportions of gametophytic (clear) and tetrasporophytic (stippled) plants at sites in Oregon and California. (F', Abalone Rock; F'', Wedding Rock). See legend for Fig. 5 for other site names.

reveals an apparent trend toward tetrasporophyte dominance with increasing wave exposure. ANOVA showed a significant difference ($p=0.05$) between site 1 and sites 3 and 4.

Senescence of virtually all blades of *Iridaea* occurred late in October at First Beach, with only a few widely scattered blades overwintering. This was also reported by HRUBY (1975) for populations in Washington State, U.S.A., and by FOSTER (1982) for *I. flaccida* in California. Blade initiation occurred early in March, with rapid growth occurring for the first two or three months and then decreasing during the summer.

The populations of *I. cordata* sampled on the Oregon and California coasts from July 18 to 26, 1982 (Fig. 5) revealed unequal quantities of gametophytes and tetrasporophytes in most populations sampled (Fig. 7). Sites from Point Arena south to Pebble Beach, California (except for Bodega Bay), exhibited gametophyte dominance. Sites from Patrick's Point State Park, California north to Ecola State Park, Oregon showed tetrasporophyte dominance.

Two samples were made at Otter Rock, one of attached plants and the other of drift plants. At this site 68% ($N=188$) of the

drift blades were gametophytes whereas only 11% ($N=957$) of the attached blades were that life history stage.

In the April, 1983, samples obtained from Pigeon Point there was a mean gametophyte dominance of 86% ($N=782$). The gametophyte stage dominated in both the upper ($94\% \pm 5\%$, $N=291$) and lower ($83\% \pm 16.4\%$, $N=546$) zone. A one-way ANOVA showed no significant difference between the percent of either gametophytes or tetrasporophytes in the upper and lower zones.

Discussion

Resorcinol reagent added directly to dried, excised algal tissue proved as accurate an indicator of constituent carrageenans (and thus nuclear phase) as is the methodology outlined in CRAIGIE and LEIGH (1978). Our modification results in a large reduction in the time needed to process samples, and non-destructive (and therefore repeated) sampling is possible since only small disks are removed from blades.

The proportions of gametophytes and tetrasporophytes found in *I. cordata* populations along the Oregon and California coasts differ between sites. In their entirety the

twelve samples suggest that tetrasporophytes predominate in the north (northern Oregon) and gametophytes dominate in the south (central-California). However, large differences occurred in samples taken relatively short distances apart. An example of this is between the Pigeon Point sample, with over 80% gametophytes in 1982 and 1983, and the nearby Davenport sample, with just over 50% gametophytes. In addition, samples taken ca. 2.5 km apart at Patrick's Point State Park showed almost 25% more tetrasporophytic blades in the sample from Wedding Rock than from Abalone Rock. The presence of a strong tetrasporophyte dominance in the population of Bodega Bay, within the southern area where gametophyte dominance is most common, further supports the possibility of local variability, as do the samples taken in Barkley Sound, Vancouver Island.

Thus, such a cline of reproductive stages, if it does in fact exist, is quite different from that which was postulated at the beginning of our study on the basis of an apparent gametophyte dominance in the Strait of Georgia (ADAMS 1971) and a reported year-round (except early spring) tetrasporophyte dominance (HANSEN and DOYLE 1976) in central California. Any gradation from dominance of gametophytes in the north to tetrasporophytes in the south was certainly not shown by our samples. Instead, the pattern we found (from Oregon to California) more closely resembles that postulated by DIXON (1965) and described for *Ceramium* by EDWARDS (1973) in which gametophytes dominate the southern ranges of certain Rhodophyta, giving way to a predominance of tetrasporophytes and finally to sterile blades as one progresses northward. It should be noted, however, that our methodology employing a test for chemical differences did not test the hypothesis of DIXON (1965) who recorded reproductively mature blades. Using DIXON's methodology it is possible that equal numbers of tetrasporophytes and gametophytes are in fact present, but that only the tetrasporophytes become reproductively mature in more nor-

thern sites. Using our methodology it would be possible to score an area as having gametophyte dominance when none of the haploid blades might become reproductively mature.

Our samples taken in the Monterey area raise other questions, since they did not confirm the reported dominance of tetrasporophytes for these populations (HANSEN and DOYLE 1976). Instances of gametophyte dominance for an entire year have been reported for *Rhodoglossum affine* and *Gigartina leptorhyncos* (ABBOTT 1980) but not for species of *Iridaea*.

Our sampling at Pigeon Point revealed an 80-90% gametophyte dominance in July, 1982, and an 86% gametophyte dominance in April, 1983, different from the tetrasporophyte dominance reported from this area by HANSEN and DOYLE (1976). This suggests that the proportions of gametophytes and tetrasporophytes in a particular population may change over periods longer than a few years. Such a reversal has occurred at Pigeon Point in the nine years between the work of HANSEN and DOYLE and this study.

In re-examining some of the proposed mechanisms by which a tetrasporophytic dominance might be maintained (HANSEN and DOYLE 1976) in the light of our data, the probability of apomeiosis now seems less likely. An apomeiotic population is incapable of producing the gametophyte dominance we found at Pigeon Point. Because of the differences observed in earlier studies and in our data, the various mechanisms proposed by Hansen and Doyle do not appear important in explaining the observations.

One possibility that must be considered is that dominance of any life history stage of *Iridaea* is part of a larger cycle which takes some years before moving from one stage to another. One mechanism which could operate to produce an alternating dominance of reproductive phases is suggested here. For example, once a tetrasporophytic phase became dominant, a subsequent event which resulted in removal (grazing or very low tides combined with hot weather) would enable the spores of the remaining plants

to settle and grow into the gametophytic phase, which would then predominate until the next local catastrophe.

The results from the sampling in Barkley Sound have suggested one environmental mechanism which may contribute to an instance of tetrasporophyte dominance. Sampling at the First Beach site showed that areas of higher wave exposure had significantly more tetrasporophytes than sheltered areas.

Sampling done at Otter Rock, Oregon, showed a tetrasporophyte dominance of 89% in blades attached to rock in the intertidal zone and gametophyte dominance of 68% in a drift sample taken at the same site. This suggests that gametophytic blades are more susceptible to being stripped from rocks by wave action than are the tetrasporophytes.

The patterns of change in populations of *Iridaea cordata*, and the factors controlling these patterns, may be such that only long term studies carried out simultaneously at a large number of sites of varied geography are able to produce a satisfactory picture.

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本村泰三・阪井與志雄：イチメガサ *Carpomitra cabrerae* (褐藻・ケヤリモ目)
胞子体の核分裂の電顕的研究

イチメガサ胞子体の頂毛細胞の核分裂を電顕的に観察した。中間期の核はほぼ球形で、その周囲に1組の中心子が存在している。前期に中心子は複製し分裂極に移動する。核は極のところでくぼみ、多数の微小管が中心子のまわりの高電子密度物質から核のくぼみに伸びている。核小体は消失し始め、染色糸の凝縮が進む。中期には染色糸が赤道面に並ぶが、動原体は観察されない。核膜は両極部分のみが開放し、中心子のまわりの高電子密度物質より紡錘糸が伸びる。後期に、核膜は徐々に破れる。両極間の距離は中期より増し染色糸は両極へと移動する。二つの娘染色体塊の間には中間紡錘糸が観察される。この時期には分裂軸に沿って核領域の近くによく発達した小胞体が観察される。終期には二つの娘核は核膜で包まれ、核小体の再生・染色糸の分散とともに核の体積が増す。(051 室蘭市母恋南町 1-13 北海道大学理学部付属海藻研究施設)

p. 225~232 の論文の和文要約.

L. ディック・R.E. ドゥブリード・D. ガーバリ：ブリティシロコンビアとカリフォルニアにおける紅藻
Iridaea cordata (スギノリ科) の配偶体と四分胞子体の出現と生活史

Iridaea cordata の配偶体と四分胞子体の出現状況を地理的分布を異にする個体群と波浪条件等を異にする個体群について調査した。両世代の藻体の識別は、藻体を含むカラゲenanのタイプを知るために Craigie と Leigh (1978) が開発した resorcinol test を著者等が改変した方法によった。カナダ・ヴァンクーヴァー島とヴァンクーヴァー港の個体群では約60%が配偶体であったが、波の荒い地点から静かな地点にかけて配偶体数比が減少する傾向を示した。アメリカ・オレゴン州からカリフォルニア州中部にかけての太平洋沿岸12点の個体群では、北部では配偶体が約11%で少かったが、南部では78~90%と増加した。しかし、この出現比は地域により、また年により例外も多く見られた。両世代の出現比の違いがどのようにして生ずるかを知るには、多くの地点において出現状況を永年に亘って調査することが必要である。