

Autecological studies on *Chondrus nipponicus* Yendo (Gigartinales, Rhodophyta)

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Seasonal fluctuations in biomass, blade size (stage class) and frequency of reproductive plants and reproductive blades, and the proportion of tetrasporophytes and gametophytes were investigated in *Chondrus nipponicus* Yendo (Gigartinales, Rhodophyta) growing in Oshoro Bay on the west coast of Hokkaido, Japan. The blade size of each individual plant fluctuates seasonally: from spring to summer larger blades increase in frequency and from autumn to winter they decrease. In accordance with this fluctuation the biomass of individual plants (and the population) changes, the maximum biomass being present in August and the minimum in January. Reproduction is seasonally restricted from July to March. Reproductive structures are formed on larger blades in summer and, progressively, on smaller blades in autumn. This seasonal fluctuation can be quantified according to a *R/T* (total individual reproductive biomass/total individual biomass) index. The proportion of tetrasporophytes and gametophytes is virtually 1 : 1.

Key Index Words: Autecology—*Chondrus*—*Chondrus nipponicus*—*Gigartinales*—*Gigartinales*—*life-history strategy*—*perennial alga*—*Rhodophyta*.

Carrageenan-producing algae are important seaweed resources. Many carrageenophytes (*Chondrus*, *Gigartina*, *Rhodoglossum*, *Mastocarpus*, *Ahnfeltiopsis*, etc.) grow in Japanese waters, but no autecological studies *in situ* have been carried out except for *Chondrus yendoi* Yamada et Mikami (Hasegawa and Fukuhara 1952, 1955 as *Iridophycus cornucopiae*, Funano and Hasegawa 1964), which differs from *Iridaea cornucopiae* Postels et Ruprecht (Mikami 1965). In this study we have attempted to analyze the seasonal fluctuations in biomass, blade size (stage class) and frequency of reproductive blades per individual, and to determine the proportion of sporophytes and gametophytes of *Chondrus nipponicus* Yendo for the elucidation of nuclear phase composition in wild populations.

Chondrus nipponicus resurrected recently by Brodie *et al.* (1991) includes the alga previously known as *C. crispus* Stackhouse in Japan (Mikami 1965). This species differs from genuine *C. crispus* from the Atlantic in gross morphology, internal vegetative anatomy and

post-fertilization events in the developing carposporophyte (Brodie *et al.* 1991). *Chondrus nipponicus* is distributed mainly in areas influenced by the Tsushima Warm Current and its terminal branch, the Tsugaru Warm Current, viz, along the coasts of Sea of Japan of Honshu and Hokkaido and the Pacific coasts of northern Honshu and southern Hokkaido.

Morphological characteristics of *Chondrus nipponicus* have been described by Mikami (1965, as *C. crispus*) and Brodie *et al.* (1991). This species has a *Polysiphonia*-type life history in the laboratory (Brodie *et al.* 1991); however, it has been shown that the proportion of tetrasporophytes and gametophytes of species of *Chondrus* and the related genus *Iridaea* differs in wild populations. Tetrasporophyte dominance in *Iridaea cordata* (Turner) Bory populations has been reported by Hansen and Doyle (1976) at Monterey, California and Dyck *et al.* (1985) for sites along the coast of Oregon. Gametophyte dominance has been demonstrated for *I. cor-*

data populations in Washington (Dyck *et al.* 1985, May 1986) and British Columbia (Dyck *et al.* 1985). The proportion of both generations of *Chondrus crispus* changes along a vertical gradient with gametophytes being more abundant in the upper subtidal zone and tetrasporophytes dominant in deeper water in New Hampshire (Mathieson and Burns 1975) and in the Maritime Provinces of Canada (Craigie and Pringle 1978).

Materials and Methods

Field observations and collections of *Chondrus nipponicus* were made in Oshoro Bay ($43^{\circ}13'N$, $140^{\circ}52'E$) on the west coast of Hokkaido near the lectotype locality, Yagishiri Island (Brodie *et al.* 1991). Tidal range is narrow in Oshoro Bay as it is on shores facing the Sea of Japan. The daily tidal ranges are 20–35 cm throughout a year at Otaru near Oshoro Bay (Japan Meteorological Agency 1989). The monthly mean sea level is lowest in March (about 10 cm) and highest in Au-

gust (about 30 cm) and fluctuates between these extremes (Masuda and Horiuchi 1988). This species grows on rocks or ledges below low-water mark. The vertical growing range is within 1 m. Four study sites (–40 cm) were established in March 1989 (Fig. 1): 1, 2, moderately wave-exposed area; 3, fully wave-exposed area and 4, in a tidal pool at a sheltered locality. At each site, two *C. nipponicus* subpopulations growing on ledges were selected using an iron-frame quadrat of 50×50 cm. Corners of each quadrat were marked with nails hammered into the rock and tagged with colored plastic tape.

Collections of all plants from per unit holdfast area have chiefly been employed in previous studies of the autecology of *Chondrus* (Prince and Kingsbury 1973, Mathieson and Burns 1975) and *Mastocarpus* (Burns and Mathieson 1972, as *Gigartina*) species with dense growth forms and individual plants are impossible to identify within such populations. *Chondrus nipponicus*, however, does not form such dense populations at any study site

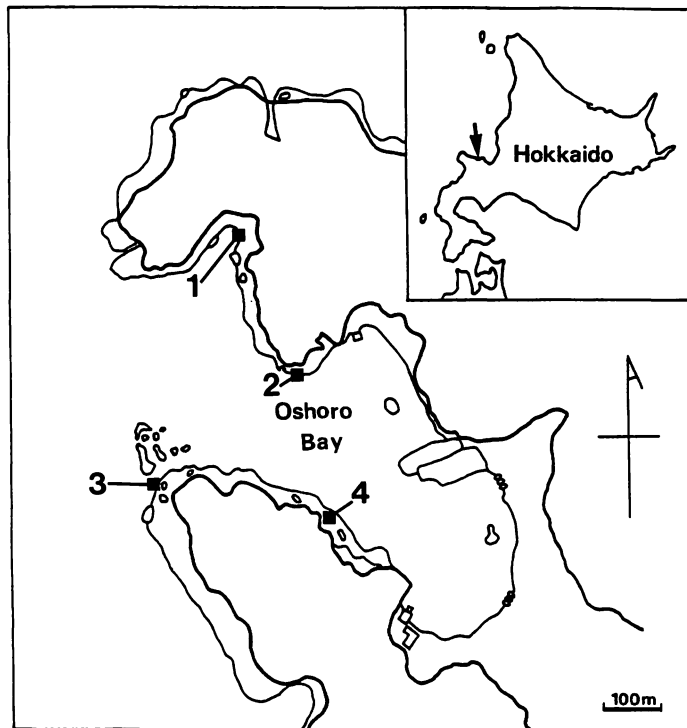


Fig. 1. Map of Oshoro Bay, showing four study sites.

and careful observations *in situ* with a water glass made the recognition of each individual composed of a holdfast and many upright blades possible. Plants growing in each quadrat were recorded: 50 and 32 individuals in each of quadrats at site 1, 54 and 28 at site 2, 56 and 21 at site 3 and 28 and 21 in site 4 at the beginning of this observation. Four-six individuals with holdfasts from each site were haphazardly sampled using scrapers at the beginning of each month from March 1989 to February 1990. Plants with very large numbers of upright blades (more than 100) were occasionally collected. Vertical sections of discoid holdfasts of such samples revealed a portion in which a holdfast was overgrown by another holdfast (Taylor *et al.* 1981). Such samples were excluded from our data.

Fresh specimens were measured individually as follows: 1) number of blades under a dissecting microscope, 2) length of each blade after removal from the holdfast, 3) number of branches on each blade. The presence or absence of proliferations and reproductive structure of each blade were also recorded. Procarpic blades were determined by the presence of refractive supporting cells at the tips of branches under a dissecting microscope and confirmed by sections of small portions under a compound microscope. Cystocarpic and tetrasporangial blades were determined by the protruding cystocarps and round to oval, non-protruding tetrasporangial sori, respectively, under a dissecting microscope. Younger cystocarps and tetrasporangial sori were distinguished by checking for procarps on the blades. Spermatangial blades were identified

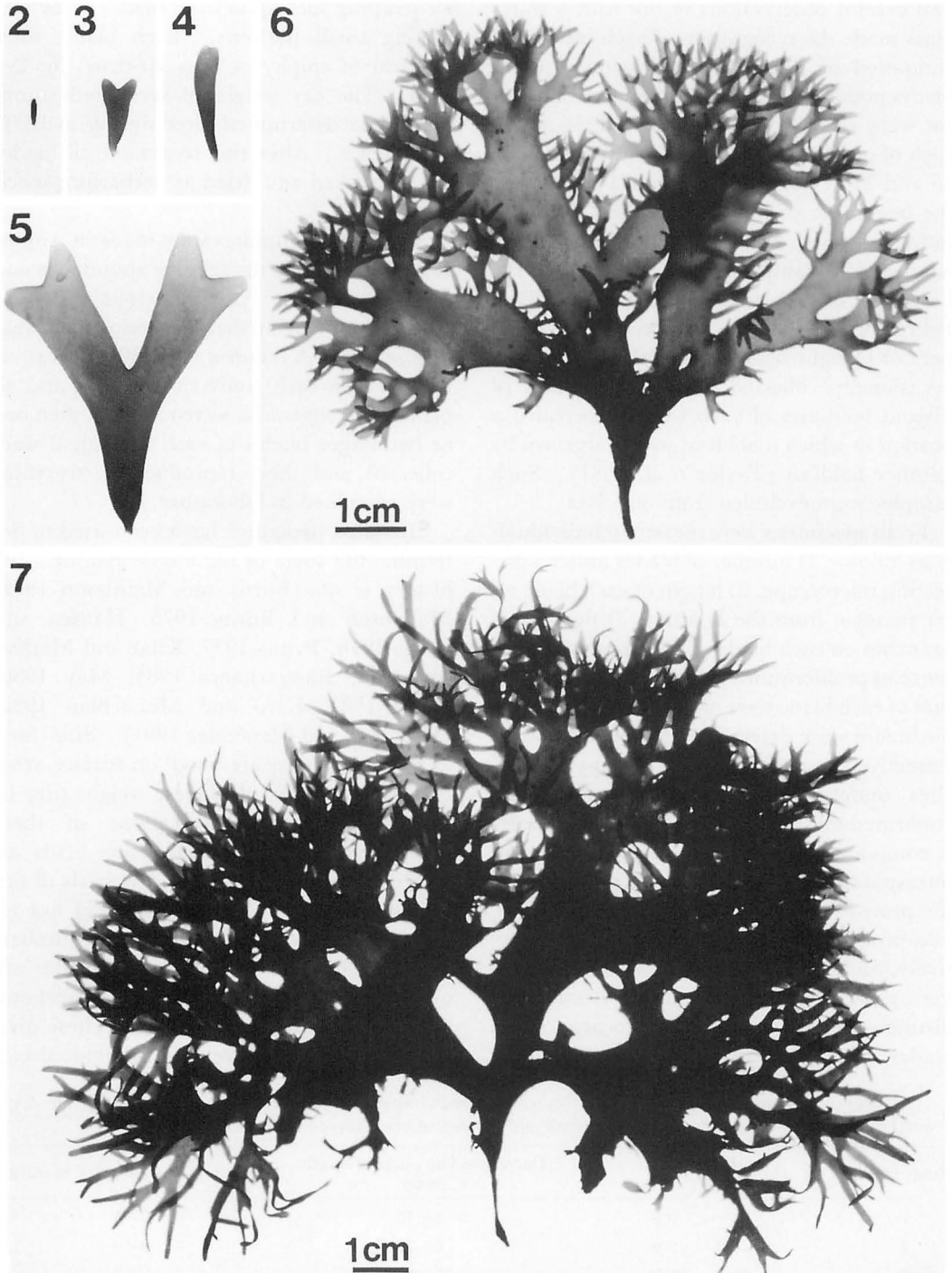
by scraping spermatia from blades or by sectioning small portions. Each blade, after removal of epiphytes, was air-dried for 2-3 days. The dry weight of each blade numbered was determined after drying at 85°C for 20-24 h. After this treatment all blades were re-soaked and dried as herbarium specimens.

Additional samplings were made in August 1990 to determine the relative abundance and the distribution of gametophytes and tetrasporophytes at their reproductively mature season. A quadrat (50 × 50 cm) was established on each study site (Fig. 1) and all plants of *C. nipponicus* were mapped, then one or two larger blades of each individual were collected and their reproductive structures were examined in laboratory.

Size class structures have been used to determine the stage of the foliose red algal life history *in situ* (Burns and Mathieson 1972, Mathieson and Burns 1975, Hansen and Doyle 1976, Pybus 1977, Kilar and Mathieson 1978, Bhattacharya 1985, May 1986, Sharp 1987, Lazo and McLachlan 1989, Fernández and Menéndez 1991). Size classes in these reports are based on surface areas of blades, lengths of blades, weight (dry or wet) or various combinations of these parameters. Upright blades were firstly assigned to one of 5 classes on the basis of dry weight (Table 1). This sorting did not always conform with blade length or numbers of branches (Table 1). Upright blades are usually divided dichotomously or subdichotomously with increase in length. These divisions result in an increase of individual bio-

Table 1. Stage classes of individual blades of *Chondrus nipponicus* discriminated on the basis of the dry weight. Corresponding ranges of blade length and number of branches are also given.

Stage class	Range (mg)	Corresponding range of length (mm)	Corresponding range of branches
1	- 0.9	2- 10	0- 1
2	1.0- 9.9	6- 28	0- 4
3	10.0- 99.9	18- 60	1- 8
4	100.0- 999.9	41- 94	1-14
5	1000.0-9999.9	76-120	12-14
6	eroded blade after spore or spermatial release		



Figs. 2-7. Living blades of *Chondrus nipponicus* collected in Oshoro Bay, showing representatives of the discriminated stage classes based on individual dry weight: 2, stage class 1; 3, 4, stage class 2; 5, stage class 3; 6, stage class 4; 7, stage class 5. Scale in Fig. 6 also applies to Figs. 2-5.

Table 2. Seasonal fluctuations in number of blade per individual (mean \pm SD), biomass per individual (dry weight, mean \pm SD), frequency of reproductive individuals (FRI), frequency of reproductive blades (FRB) and *R/T* index (total individual reproductive biomass to the total individual biomass) in Oshoro Bay population of *Chondrus nipponicus* during March 1989 and February 1990. Average seawater temperatures (ST) and daylengths (DL) were also given.

Month	Individuals examined	Number of blade	Biomass (mg)	FRI (%)	FRB (%)	<i>R/T</i> index (%)	ST (°C)	DL (h)
March	20	36.2 \pm 10.4	565 \pm 174	5	0.1	2	4.6	11.95
April	16	37.1 \pm 9.3	867 \pm 373	0	0	0	7.1	13.45
May	16	37.7 \pm 8.6	1185 \pm 600	0	0	0	10.3	14.68
June	14	38.3 \pm 13.8	1616 \pm 640	0	0	0	14.3	15.32
July	16	44.9 \pm 19.3	2083 \pm 677	63	10	52	19.1	15.02
August	14	45.5 \pm 21.7	2495 \pm 973	100	28	93	22.7	13.91
September	16	40.5 \pm 13.4	1852 \pm 980	100	24	98	20.3	12.53
October	14	40.7 \pm 12.1	870 \pm 420	100	20	86	15.7	11.04
November	18	37.8 \pm 14.8	560 \pm 400	100	15	80	11.5	9.74
December	16	38.1 \pm 19.6	313 \pm 220	88	11	59	8.0	8.71
January	16	35.6 \pm 16.6	249 \pm 112	38	4	20	4.9	9.41
February	20	35.6 \pm 18.4	413 \pm 181	15	3	16	3.8	10.53

mass of blade. Differences in biomass between blades with the same length are caused by the incidence of branching. The widths of blades probably also affect their biomass, although blade widths were not assessed. On the other hand, palmately divided blades are frequently found also. These blades have a higher incidence of branching than the dichotomously or subdichotomously divided blades with the same dry weight. The development of proliferations and an increase of thicknesses may contribute to an increase in biomass. Accordingly, the growth stage of blades of *C. nipponicus*, which are so much branched and produce numerous proliferations, is best shown by dry weight. Dry weight may allow meaningful comparisons between different populations of the species concerned and between different species. Selected blades of 5 stage classes are shown in Figures 2-7. Furthermore, wave-eroded blades after spore or spermatial release were frequently observed. In the previous reports these blades have been included in the smaller classes (Hansen and Doyle 1976, Kilar and Mathieson 1978). We provided these blades with one class (class 6 in Table 1). Thus, our class is not the size class but the stage class.

To quantify reproductive maturation the

relationship between the total individual reproductive biomass (*R*) to the total individual biomass (*T*) was investigated according to the formula *R/T* as proposed by Hansen (1977) for *Iridaea cordata*. The resulting value ranges from 0 to 1.0. As the value approaches 1.0, the component of reproductively mature biomass approaches 100% (Hansen 1977). The *R/T* index (*R/T* \times 100) is shown as a percentage (see Table 2).

Daylengths in Oshoro Bay were calculated according to a formula and table given by Suzuki (1987). Seawater temperatures were provided from Oshoro Marine Biological Station of Hokkaido University. Voucher specimens are preserved in the herbarium, Faculty of Science, Hokkaido University, Sapporo (SAP).

Results

Seasonal fluctuations in biomass

Plants of *Chondrus nipponicus* growing at the four study sites did not show any spatial difference in biomass and in the pattern of seasonal fluctuation. For example, mean individual biomass of each study site in August is 2429 mg at 1, 2370 mg at 2, 2386 mg at 3 and 2369 mg at 4 and that in February is 391 mg

at 1, 392 mg at 2, 415 mg at 3 and 404 mg at 4. No significant differences in individual biomass between gametophytes and tetrasporophytes were found. In August mean individual biomass of male gametophytes is 2325 mg, that of female gametophytes 2821 mg and that of tetrasporophytes 2402 mg. The data from each site, including different generations, were totaled monthly and averaged. Annual fluctuations in average individual biomass is shown in Table 2. The minimum biomass was present in January and then increased from February to summer with a peak in August; it subsequently decreased.

Seasonal fluctuations in blade size

Each individual of *Chondrus nipponicus* is composed of many upright blades and a discoid holdfast. The number of blades varies according to individuals. The largest number recorded was 60-70 and the smallest 10-20; however, standard deviations are usually large (Table 2). No significant seasonal difference in the number of blades was found. [Comparison of means test between the largest number recorded month (August) and the smallest number recorded month (January), d.f. = 24, $t = 1.26$; $p > 0.2$.] Individuals with large blade numbers had larger holdfasts and individuals with small blade numbers had smaller holdfasts. The latter were collected during January and February and this may be an indication of different ages, but, as we could not carry out a demographic analysis of the population, ages of individual plants could not be determined.

The blades are different in size to each other. Figures 8 and 9 shows the seasonal change of stage class structures determined on the basis of the categories given in Table 1. No difference in this character was found according to study sites and generations. The data collected from each site were totaled monthly and averaged. There were general increases of larger blades and their frequency from January to August in accordance with an increase in biomass. In January, the largest blades belonged to stage class 4, but they

represented only a few percent of individual plants. Blades of this class increased in number from February onward. In June, larger blades belonging to class 5 began to appear and increased in number during the summer months. From September to January a decrease in the frequency of larger blades occurred. In any season the smallest blades of class 1 were found among larger blades on every individual.

From October, smaller individuals consisting of a small holdfast and a few upright blades less than 1 cm long began to appear. These were probably young plants derived from sporelings. However, it had been impossible to discriminate these plants from young *Chondrus yendoi* with certainty from October to December. The data from the plants during these months were therefore not included in our results. Their specific identity was established from January onward. These plants strongly suggested the occurrence of new sporelings.

Seasonal fluctuations of reproductive blades

Reproductive individuals appeared first in July and all individuals collected from August to November were reproductive. Reproductive individuals decreased in number during the winter months (Table 2).

The frequency of reproductive blades fluctuates seasonally: 10% in July, more than 20% during the following three months, and then decreasing until early spring (Table 2). The frequency of reproductive blades in each stage class is given in Figures 8 and 9. During August and January all blades more than 100 mg in dry weight (stage class 4) reached reproductive maturity. The frequency of reproductive blades between 10.0-99.9 mg (stage class 3), however, varied seasonally. These blades increased from August through November and then decreased. These fluctuations were quantified according to the *R/T* index shown in Table 2. In July, 52% of the total biomass among individual blade samples was reproductively mature. This percentage increased toward September when 98% of the total biomass formed reproductive struct-

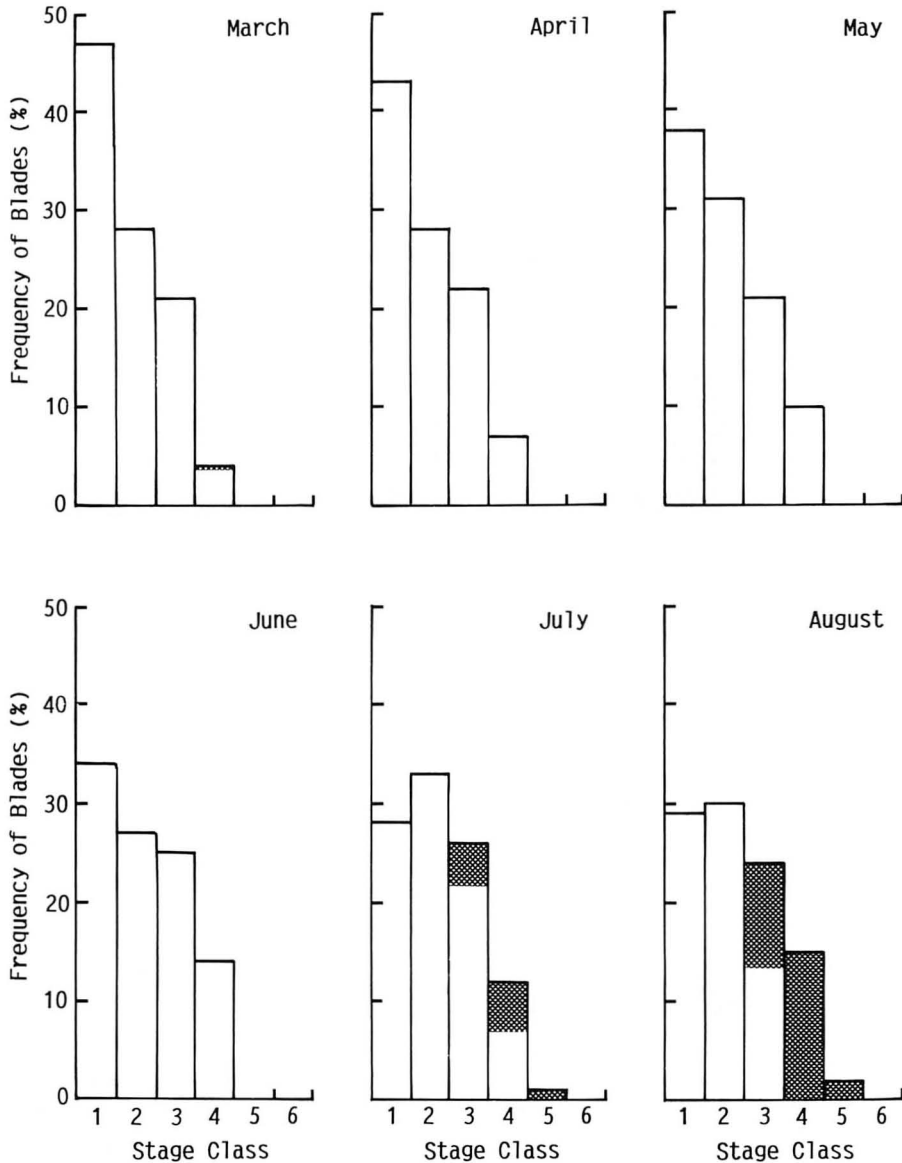


Fig. 8. Stage class structures of blades in Oshoro Bay population of *Chondrus nipponicus* from March to August. Shaded portions, showing the frequency of reproductive blades.

ures. Reproductive blades collected in February and March were only cystocarpic and had a few cystocarps. The occurrence of smaller, reproductive blades between 1.0-9.9 mg (stage class 2) was restricted during October and December. The smallest reproductive blade was 4.8 mg in dry weight and 15 mm in length.

Tetraspores and carpospores were released after the disintegration of the outer tissue

covering tetrasporangial sori or cystocarps and older reproductive blades had many holes. These blades were vulnerable to wave exposure. Spermata are released through the surface cuticle and the soral portion is also vulnerable, becoming eroded by wave action. Such eroded blades of tetrasporophytes and both gametophytes (stage class 6) began to appear in September, lasting until January, and then disappeared. Several of them

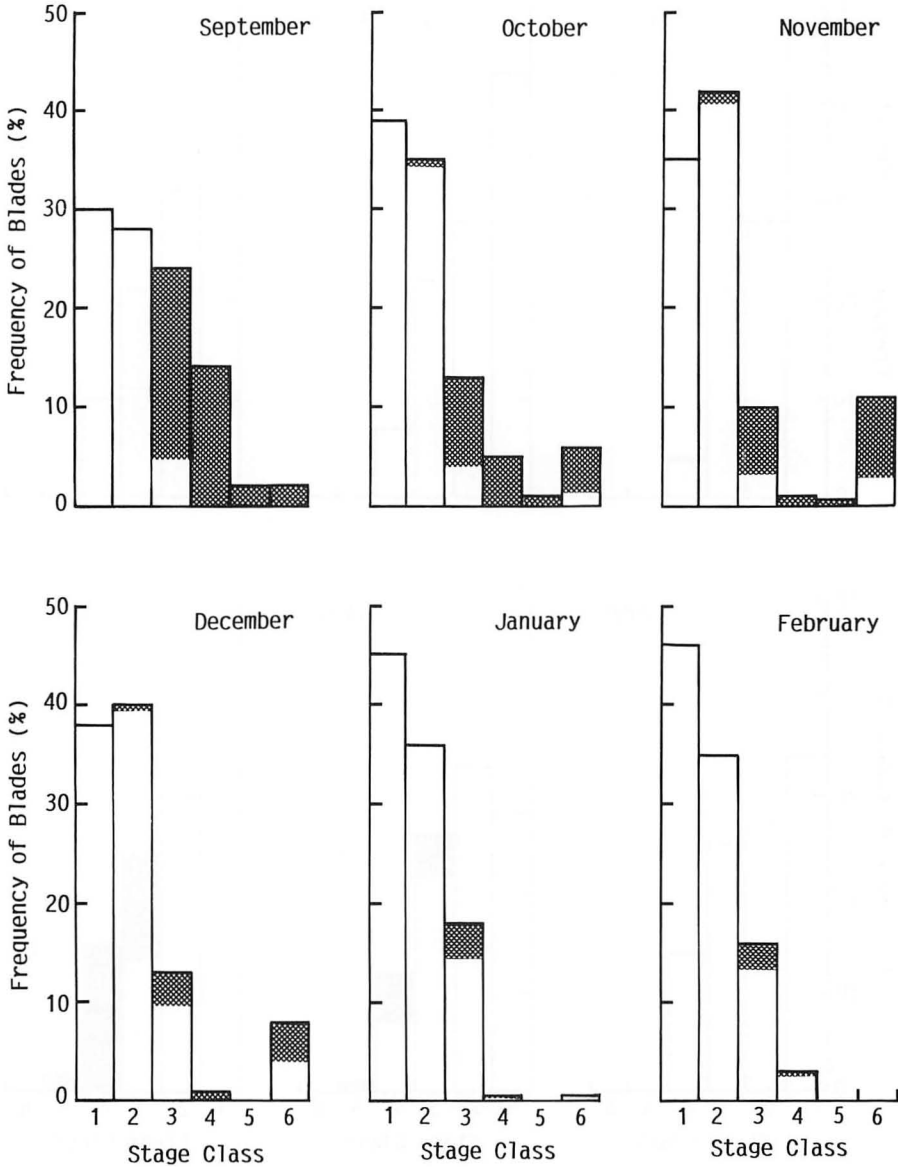


Fig. 9. Stage class structures of blades in Oshoro Bay population of *Chondrus nipponicus* from September to February. Shaded portions, showing the frequency of reproductive blades.

had no reproductive structures as a result of wave action. The loss of these blades from holdfasts during the winter months might be promoted by increased wave action resulting from increased winds in winter.

Tetraspore and/or carpospore release was tested from August to March. All plants examined released tetraspores or carpospores except for cystocarpic plants collected in February and March. These cystocarpic plants

were maintained in a culture room at 15°C, 8:16 h light : dark cycle—where gametogenesis, carposporophyte development and carpospore release were observed (Brodie *et al.* 1991)—for 4 days, but they did not release carpospores. In section the cystocarps appeared to be mature and have healthy carposporangia. Spore release studies were not carried out in July.

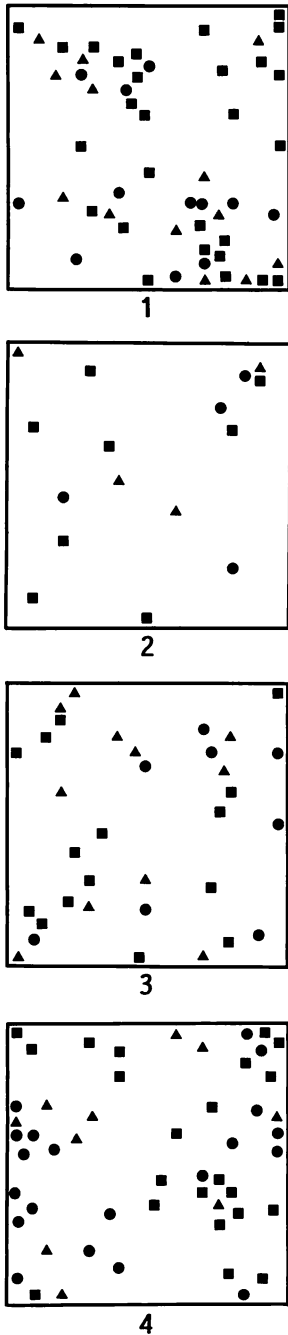


Fig. 10. Distribution of tetrasporophytes and gametophytes of *Chondrus nipponicus* in each quadrat of 2500 cm² at four study sites in Oshoro Bay. ■, tetrasporophyte; ●, female gametophyte; ▲, male gametophyte.

Proportion of tetrasporophytes and gametophytes

The relative abundance of tetrasporophytes and gametophytes in August 1990 at each study site is shown in Table 3. All these samples had an almost 1 : 1 ratio of tetrasporophytes and gametophytes. Their distribution is illustrated in Figure 10. In most cases tetrasporophytes, male and female gametophytes grew intermixed in each quadrat (2500 cm²).

Discussion

In Oshoro Bay, the occurrence of populations of *Chondrus nipponicus* with virtually equal numbers of tetrasporophytes and gametophytes and the appearance of new sporelings suggest that there is an *in situ* life history involving the regular alternation of both isomorphic generations and these generations have equal chances of becoming established. Plants of both generations have perennial holdfasts from which many upright blades are formed. This species maintains the population by means of the perennial holdfasts and sporeling recruitment.

Upright blade size on each holdfast (=per individual) fluctuates seasonally: from spring to summer larger blades increased in frequency and from autumn to winter they decreased. In accordance with this change, the biomass of individual plants and the whole population fluctuates: the minimum biomass is present in January and the maximum biomass in August. The majority of blades belong to smaller classes at any season (Figs. 8, 9) as reported for *Iridaea cordata* in California (Hansen and Doyle 1976). This can be equally applicable to other morphologically similar perennial species, such as *Chondrus crispus* (Pybus 1977, McLachlan *et al.* 1989) and *Mastocarpus stellatus* (Stackhouse in Withering) Guiry (Pybus 1977, as *Gigartina stellata*).

In Oshoro Bay from early spring to early summer when larger blades began to increase in number the seawater temperatures rose from 4.6°C to 14.3°C and the maximum biomass was evident in August when maximum

Table 3. Relative abundance of tetrasporophytes and gametophytes in the Oshoro Bay population of *Chondrus nipponicus*.

Reproductive phase	Site 1	Site 2	Site 3	Site 4	Total
Tetrasporophytes	28 (54%)	8 (50%)	15 (44%)	22 (42%)	73 (47%)
Female gametophytes	11 (21%)	4 (25%)	8 (24%)	20 (38%)	43 (28%)
Male gametophytes	13 (25%)	4 (25%)	11 (32%)	10 (19%)	38 (25%)

temperatures were 22.7°C. The spring to early summer period was also associated with a corresponding increase in daylength with about 12 h in March and about 15 h in June. A decrease in biomass from autumn to winter is related to the loss of larger reproductive blades and the slow growth of smaller blades by decreasing temperatures and daylengths. According to Kanomata *et al.* (1986), who measured seasonal change in concentrations of nutrients at Yoichi (43°15'N, 140°47.2'E) near Oshoro Bay, ammonium, nitrite, nitrate and phosphate concentrations vary seasonally: high during December and March and low from April to November. Thus, no correlations between seawater nutrient levels and seasonal fluctuations in biomass were found.

The reproductive season of *Chondrus nipponicus* is restricted. Reproductive individuals appeared in July and increased in number during summer and autumn months. They decreased in number during winter months and no reproductive individuals were found from April to June (Table 2). Larger blades first became reproductive and subsequently smaller blades also became reproductive. The critical size of reproductive blades during the season concerned is 4.8 mg in dry weight and 15 mm in length. The delayed disappearance of cystocarpic blades may be due to slow growth of cystocarps during the cold winter months. These blades had a few cystocarps on the lower portions and no procarps on any portions, suggesting that they ceased gametogenesis after fertilization and grew vegetatively. It is questionable whether the cystocarpic blades found in February and March contribute to maintenance of the population studied, because no spores were released from these blades.

Reproductive phenology of the Oshoro

population of *Chondrus nipponicus* was described in an earlier paper (Brodie *et al.* 1991). That description was based on periodic collections during 1977-78 (by H. Kawai), 1984-85 (by K. Kobayashi) and 1988-89 (only winter months by M. Masuda). According to these collections, tetrasporangial plants first appeared in early June. Samples were not collected in late June in 1989. In 1989, tetrasporangium formation might have been delayed a few weeks (not a month), since tetrasporangial plants collected in early July in 1989 had larger sori. Seawater temperatures during the last twenty days of May in 1989 were 10-12°C and about 1°C lower than the corresponding season in 1977. This species may therefore require higher temperatures for tetrasporogenesis.

A laboratory culture experiment suggests that gametogenesis of *Chondrus nipponicus* is a short-day response (Brodie *et al.* 1991). The appearance of spermatangial and procarpic plants in early July is not at odds with such a short-day response. The daylengths in Oshoro Bay are 15.39 h in the last third of June and 15.30 h in the first ten days of July. Short-day plants growing at higher latitudes have longer critical day lengths: 16.5 h for a population of the flowering plant *Xanthium strumarium* L. at 45.5°N (Ray and Alexander 1966), 14 h for the brown alga *Scytosiphon lomentaria* (Lyngbye) Link at 66°N (Lüning 1980), and 16 h for *Ahnfeltiopsis flabelliformis* (Harvey) Masuda at 45.3°N (Masuda unpublished observations). Gametogenesis (and also tetrasporogenesis) decreased from November onward when the daylengths were about 9-10 h (suitable for gametogenesis) and the seawater temperatures were 4-8°C. The photoperiodic response of this species may be only expressed over a particular temperat-

ure. Further studies are needed to clarify the critical levels of daylength and temperature for reproduction of *C. nipponicus*. Hasegawa and Fukuhara (1952) and Funano and Hasegawa (1964) reported the year-round occurrence of cystocarpic and tetrasporangial plants in *Chondrus yendoi* at five localities in Hokkaido. Plants bearing cystocarps and tetrasporangial sori are never totally absent from *Chondrus crispus* populations during a year at Plymouth, Massachusetts (Prince and Kingsbury 1973). The year-round occurrence of reproduction has been known for other geographically distant populations of *C. crispus* also (Tveter-Gallagher *et al.* 1980, McLachlan *et al.* 1988, Guiry personal communication). These two species do not show photoperiodic responses in laboratory cultures (Brodie *et al.* 1991, Masuda unpublished observations).

The frequency of reproductive individuals in the southern Gulf of St. Lawrence population of *Chondrus crispus* are 24% from May to September and that of reproductive blades is less than 10% (McLachlan *et al.* 1988). These may be characteristic of species with the year-round reproduction in a certain reproductive season. However, *Chondrus nipponicus* has much more abundant reproductive individuals and blades per individual (Table 2). Reproductive blades became eroded after spore or spermatial release. They were designated here as stage class 6 (Fig. 9). These blades lasted until January with a peak frequency in November and then disappeared without production of new proliferations, which suggests that most blades are semelparous (Pianka 1983), though individual plants being iteroparous (Pianka 1983), and have truncated life spans of less than two years. These blades are equivalent to the "stubs" of *Iridaea cordata* mentioned by Hansen and Doyle (1976). As to life spans of upright blades of perennial red algae with tenacious holdfasts, Hansen (1977) shows clearly on the basis of individually tagged blades of *Iridaea cordata* that all blades live for only one year or less. Bhattacharya (1985) described similar life spans for *Chondrus crispus*

blades.

All blades of the smallest class 1 (less than 1.0 mg in dry weight) remained vegetative. The majority of blades of stage class 2 and a few percent of blades between 10.0–99.9 mg (stage class 3) also remained vegetative (Figs. 8, 9). Is there an element of paradox therefore in the production of many blades? Photosynthetic products are not able to allocate sufficiently to reproduction, because too many blades are formed and the production of blades remaining vegetative is a waste of energy. The vegetative blades, however, may represent a stock of blades that can replace old reproductive and/or grazed blades and will become reproductive in the next season. Reproductive structures of *C. nipponicus* are restricted to small portions of blades (Mikami 1965, Brodie *et al.* 1991). This species can supply photosynthetic products for vegetative growth even during the reproductive season as does *Iridaea cordata* (Hansen 1977). An increase in biomass from July to August and the formation of new blades even during the summer reproductive months may support this assumption. Furthermore, some of photosynthetic products can be allocated to the formation of new blades, because this species has no storage organs. The allocation rate to small blades can be quantified by the *R/T* index (Hansen 1977). The maximum of reproductively mature biomass is 98% of the total individual biomass in September (Table 2), which indicates that a small quantity of photosynthetic products is required for the production of the remaining 2%. According to Bhattacharya (1985), who carried out a demographic study of *Chondrus crispus* blades, smaller blades exhibit higher survivorship than larger ones.

Allocation rates of photosynthetic products to reproduction and a stock of blades ("blade bank") can be approximately estimated by the *R/T* index proposed by Hansen (1977). The maximum *R/T* index of *Iridaea cordata* is 90% and the remaining 10% is allocated to a blade bank. The maximum *R/T* index of *C. nipponicus* is 98%. The *R/T* index of these species does not reach 100% and the remaining

photosynthetic products can be allocated to a stock of the next season. This feature is likely to be a general life-history strategy of perennial red algae. The maximum R/T index of annual red algae should, theoretically, be 100%, but such data have not been reported for annual species. The R/T index may be applied to *Dumontia contorta* (Gmelin) Ruprecht as described by Kilar and Mathieson (1978, as *D. incrassata*). In a New Hampshire population of this species blades are 100% vegetative during the early growing season (October through December). Reproductive blades appear from February onward, reaching 100% from May to July (R/T index = 100%), and then all upright blades disappear suddenly. Thus, photosynthetic products of annual algae can be efficiently allocated to reproduction in the season concerned.

Numbers of *Chondrus nipponicus* plants collected in this study were not large and errors in haphazard samplings were unavoidable. However, our results may show the general tendency of seasonal fluctuations in the biomass, stage classes of upright blades and frequency of reproductive plants and blades in the Oshoro Bay population.

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増田道夫・橋本康治：紅藻マルバツノマタ（スギノリ目）の個生態学

北海道忍路湾に生育するマルバツノマタ (*Chondrus nipponicus* Yendo) 個体群の生物体量・葉状体の大きさ・成熟個体と成熟葉状体頻度の季節変動及び四分孢子体と配偶体の出現割合を調査した。春季から夏季にかけて大きな葉状体の頻度が増し、秋季から冬季にかけては、それらの部分あるいは全体の流出によって減少した。この変動に伴って、個体と個体群の生物体量は変化した。最大量は8月で、最小量は1月であった。生殖季節は7月から3月に限定され、生殖器官は夏季から秋季にかけて大きな葉状体から小さな葉状体へと順次形成されていった。この季節変化はR/T指数（成熟葉状体量／全葉状体量）によって量的に把握し得た。四分孢子体と配偶体の出現割合はほぼ1：1であった。(060 札幌市北区北10条西8丁目 北海道大学理学部植物学教室)

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