

Variation in gametophyte dominance in populations of *Chondrus verrucosus* (Gigartinaceae, Rhodophyta)

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SUMMARY

We describe the abundance, including spatial and temporal variability, of phases of the isomorphic *Chondrus verrucosus* Mikami from Japan. *Chondrus verrucosus* occurred in a dense (~90% cover) and temporally stable bed on a small, isolated rocky outcrop (Oyakoiwa) in Shizuoka Prefecture. Small vegetative fronds were always much more abundant than large vegetative and fertile fronds over the spring to late summer periods in 1999 and 2000. Over the same period, fertile carposporophytic fronds were generally more abundant than fertile tetrasporophytic fronds, and fertile male fronds appeared infrequently at low densities. Using the resorcinol-acetal test, we determined the proportion of gametophytes and tetrasporophytes in three populations of *C. verrucosus*: Oyakoiwa and Noroshi (Shizuoka) in the summers of 1999 and 2000 and Kamehana Point (Miyagi) in autumn 2000. All populations had a significantly higher proportion of gametophytes than tetrasporophytes in both years, although gametophytic proportions were lower at Noroshi (~70%) than at Oyakoiwa (~80%) and Kamehana Point (~97%). However, examination of all isolated individuals sampled on Noroshi showed equal proportions of each phase in 1999, but gametophyte dominance (74%) in 2000. Differences in dispersal and spore production between phases are discussed as mechanisms potentially contributing to variation in gametophyte dominance.

Key words: dispersal, gametophyte, isomorphic, macroalgae, phase dominance, resorcinol-acetal test, tetrasporophyte.

INTRODUCTION

Gametophyte dominance has been described for several members of the Gigartinaceae in North America (Mathieson & Burns 1975; Craigie & Pringle 1978; Bhattacharya 1985; May 1986; Scrosati *et al.* 1994; Dyck & De Wreede 1995; Scrosati 1998), Chile (Hannach & Santelices 1985; Gonzalez & Meneses

1996) and Sweden (Lindgren & Åberg 1996). Moreover, studies have found that the pattern of gametophyte dominance for *Chondrus crispus* Stackhouse on rocky substrata is generally temporally stable over short (monthly) and long (annual to decadal) time-scales (May 1986; Scrosati *et al.* 1994; Scrosati & Mudge 2004a,b). In Japan, seasonal variation in the number of fertile gametophytic and tetrasporophytic thalli has been examined for *Chondrus yendoi* Yamada *et* Mikami (as *Iridophycus cornucopia* (Postels *et* Ruprecht) Setchell *et* Gardner – Hasegawa and Fukuhara 1952; Hasegawa and Fukuhara 1955), but no estimates of the total proportions (including fertile and non-fertile thalli) of gametophytes and tetrasporophytes in a population have been made, despite the relatively high species diversity within the Gigartinaceae in Japan.

Chondrus verrucosus Mikami often occurs in isolated areas along the central Pacific coast of Japan, but usually in quite dense populations (>50% cover; A. Bellgrove, pers. obs. 1999–2008). This suggests that this species is capable of both long-distance dispersal as well as short-distance dispersal within a population and/or vegetative regeneration. Fertile thalli can be observed all year round, but there have been no studies of the seasonality of reproduction or relative differences between phases for this species.

Several models have been proposed in published reports to explain gametophyte dominance in the Gigartinaceae (Bhattacharya 1985; Hannach & Santelices 1985; May 1986; Luxoro & Santelices 1989; Gonzalez & Meneses 1996; Lindgren & Åberg 1996; Fierst *et al.* 2005). However, for *Chondrus verrucosus* and other Japanese Gigartinaceae, it is premature to test models explaining mechanisms controlling population dynamics, without first describing the patterns of distribution and any variability in these patterns (Underwood *et al.* 2000). Therefore, to assess the generality of patterns found for members of the Gigartinaceae in America and

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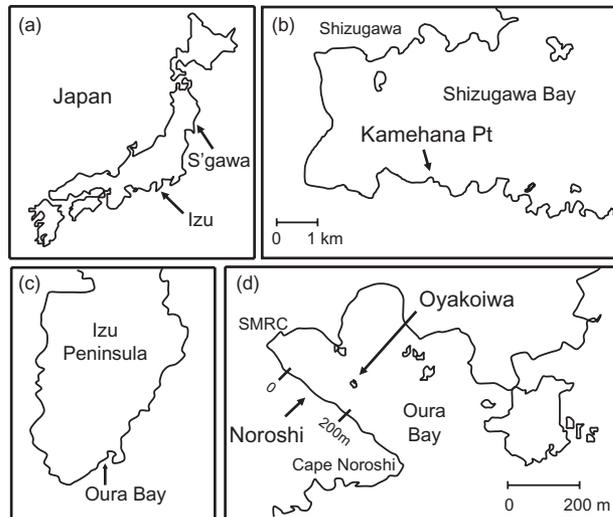


Fig. 1. Study area. (a) Japan, showing the locations of Izu Peninsula and Shizugawa Bay (S'gawa); (b) Shizugawa Bay, showing the location of Kamehana Point and the township of Shizugawa; (c) Izu Peninsula; (d) Oura Bay, showing the location of Oyakoiwa and the 200 m transect on Noroshi. SMRC, Shimoda Marine Research Center.

Europe, this study aimed to determine the proportion of gametophytes and tetrasporophytes in three spatially isolated populations of *C. verrucosus* in Japan, and to see whether these proportions varied annually. Additionally, in one very dense population (Oyakoiwa) we examined the temporal stability of the population and the monthly variation in the production of fertile fronds relative to vegetative fronds over two successive spring to late summer periods. We hypothesized that the perennial habit of *C. verrucosus* would lead to populations that are temporally and spatially stable with respect to abundance and proportions of gametophytes and tetrasporophytes. Moreover, we expected these populations to be gametophyte-dominated. In contrast, we hypothesized that the periodicity of fertility amongst gametophytes and tetrasporophytes may be temporally variable.

MATERIALS AND METHODS

Study sites

Sampling was conducted at two sites within Oura Bay, Izu Peninsula, Shizuoka Prefecture (34°40'N, 138°57'E) and one site close to the northern extent of the distribution of *Chondrus verrucosus* (Yoshida 1998; Tanaka 2004) at Kamehana Point, Shizugawa Bay, Miyagi Prefecture (38°38'N, 141°28'E), Japan (Fig. 1). The first site, Oyakoiwa, is a small (7 m × 5 m) isolated rocky outcrop composed of tuff breccia (Machida 1972), separated from the nearest rock

platform by approximately 150 m. The second site, Noroshi, is a sharply sloping andesite (Machida 1972) rock wall on Cape Noroshi, demarcating the south-west boundary of the bay, and approximately 90 m from Oyakoiwa at the closest point. The third site, Kamehana Point, is a gently sloping boulder shore composed of pretertiary sedimentary rock (Anon 1983). *Chondrus verrucosus* occurs in a dense bed dominating the lower to mid-intertidal area of Oyakoiwa (40–80 cm above chart datum (nearly lowest low water), MN Aoki, unpubl. data, 1998–2000) and in both dense and sparse patches along Noroshi, within a 2 m band on the near vertical wall. Similarly, it occurs in dense and sparse patches in the lower to mid-intertidal area of Kamehana Point, but thalli are generally smaller than in Oura Bay (A. Bellgrove, pers. obs. 2000). The tidal range for Oura Bay is 2 m (from 20 cm below to 180 cm above chart datum); sea temperatures typically range from 13 to 27°C (14–26°C monthly means) and air temperatures from 5 to 31°C (8–29°C monthly means) (Shimoda Marine Research Center, unpubl. data, 1950–2008). The tidal range of Kamehana Point is 170 cm (from 10 cm below to 160 cm above chart datum); sea temperatures typically range from 5 to 24°C (6–23°C monthly means) (Shizugawa Nature Center, unpubl. data, 1999–2008) and air temperatures for nearby Ishimaki city (38°25'N, 141°18'E) range from –2.8 to 26.9°C (0.5–23.5°C monthly means) (SDMO 2005). Tides for both Oura and Shizugawa Bays follow a mixed tidal pattern with typically two unequal ebb and two flood tides per lunar day; in Oura Bay, Oyakoiwa is usually only immersed on one low tide per day during spring tides, but high tides are of relatively equal magnitude throughout both the lunar cycle and year.

Although there have been no studies of wave exposure or water flow within Oura Bay, Machida (1972) observed differences in wave cut benches suggesting within-bay differences in wave action and abrasion forces. Oyakoiwa and Noroshi are typically both moderately exposed to wave action in an otherwise relatively sheltered embayment (A. Bellgrove, pers. obs. 1999–2008). However, Oura Bay is exposed to seasonal storms and typhoons (particularly in summer) where waves up to 1 m may enter the bay and wave forces increase, particularly over Oyakoiwa and Noroshi (A. Bellgrove, pers. obs. 1999–2006). Similarly, wave exposure has not been quantified at Kamehana Point, but generally the reef is moderately exposed, with high wave exposure during seasonal storms and typhoons (K. Tanaka, pers. comm. 2000).

Study species

Chondrus verrucosus is a dioecious, perennial, benthic red alga that occurs in the eulittoral zone on rocky

substrata, primarily in the central region of the Pacific coast of Japan (Mikami 1965; Yoshida 1998). Although the life cycle of *C. verrucosus* has not specifically been studied, it is assumed to follow the triphasic life cycle of other members of the genus (Taylor & Chen 1994). Gametophytes and tetrasporophytes are morphologically similar. Tetraspores give rise to male and female gametophytes and carposporophytes then develop in the female gametangia after *in situ* fertilization. Carpospores then give rise to tetrasporophytes. As fertilization occurs *in situ*, the main dispersive propagules are assumed to be the carpospores and tetraspores.

Proportion of tetrasporophytes and gametophytes

The population of *C. verrucosus* on Oyakoiwa was surveyed monthly around the full moon from May to August 1999 and March to June 2000 for the number of fertile carposporophytic, tetrasporophytic and male fronds and the number of large (≥ 2 branches) and small (< 2 branches) vegetative fronds in 10 haphazardly placed, 25 × 25 cm quadrats. Sampling between August 1999 and March 2000 and after June 2000 was not possible due to swells associated with typhoons and consequent insufficient field time up until October of each year, and then night time low tides through until March, when accurate counts of fertile tetrasporophytic and male fronds could not be made under head lamps. In July and August 2000 the few calm days around the full moon were used for sampling for a concurrent study (Bellgrove & Aoki 2006). However, daytime observations of the populations were made by snorkel periodically during autumn and winter months. Although not quantified, fertile carposporophytic and tetrasporophytic fronds were observed during these times; fertile male fronds were observed less frequently; and the overall cover did not fluctuate greatly. Identification of fertile male fronds was initially confirmed in the laboratory by sectioning spermatia, and was thereafter identified in the field with the naked eye. Spermatia appeared as irregular dark splotches over the mid to distal portions of fertile male fronds. To assess the temporal stability of the algal bed over spring and summer of two consecutive years, monthly surveys of the percentage cover of *C. verrucosus* in 10 haphazardly placed, 50 × 50 cm 100-point quadrats on Oyakoiwa were also conducted from May to September 1999 and March to September 2000.

To determine the proportion of each phase on Oyakoiwa, Noroshi and Kamehana Point, different sampling designs were used due to the nature of the populations. On Oyakoiwa 20, 25 × 25 cm quadrats were surveyed and a 6 mm tissue punch taken from one frond of each individual (totals: 220 and 274 individu-

als in 1999 and 2000, respectively). The potential for spore coalescence in the Gigartinaceae is recognized (Tveter & Mathieson 1976; Santelices *et al.* 1999) but for the purposes of this study, an individual was defined as one clump of upright fronds, which may have formed either from a single spore (genet) or from coalescence of two or more spores (consistent with Scrosati & Mudge 2004b). Where the boundary between adjacent clumps was unclear due to the diffuse holdfast, we conservatively grouped potentially two clumps as one. The population on Noroshi stretches for over 200 m, but within a narrow vertical belt. This population was surveyed along a 200 m transect (Fig. 1) in which a 6 mm tissue punch was taken from each individual along the transect and the position recorded for later comparisons (totals: 870 and 744 individuals in 1999 and 2000, respectively). At Kamehana Point a 6 mm tissue punch was taken from 243 haphazardly selected individuals over the reef. Tissue punches were also taken from fertile tetrasporophytes and female gametophytes from each site as test controls. The population on Oyakoiwa was sampled on 28 July 1999 and again on 5 June 2000, Noroshi was sampled on 11 and 12 July 1999 and on 4 July 2000, and Kamehana Point was sampled on 17 October 2000.

Air-dried samples were identified as either tetrasporophytes or gametophytes using the resorcinol-acetal test (Craigie & Leigh 1978; Craigie & Pringle 1978; Garbary & DeWreede 1988) based on the presence or absence of kappa-carrageenan. Preliminary tests with >50 samples of fertile tetrasporophytes and female gametophytes reliably identified (100% success) samples of *C. verrucosus* using the resorcinol-acetal test.

Statistical analyses

Data were analyzed with simple and complex ANOVAs. Assumptions of normality and homogeneity of variances were checked with box plots and residual plots (Quinn & Keough 2002). Data were fourth-root transformed to improve normality where necessary. Tukey's post-hoc test was used for unplanned pairwise comparisons between sampling times after ANOVA. Where significant interactions were found in two-factor ANOVAs, we used simple main effects analysis (SME) to compare the main factor of interest using the MS_{error} and df_{error} from the two-factor ANOVAs as the error terms (Quinn & Keough 2002). All analyses were carried out using Systat v7.01.

RESULTS

There was a significant difference in the percentage cover of *Chondrus verrucosus* on Oyakoiwa over time ($F_{11,108} = 2.413$; $P < 0.001$), but this difference was

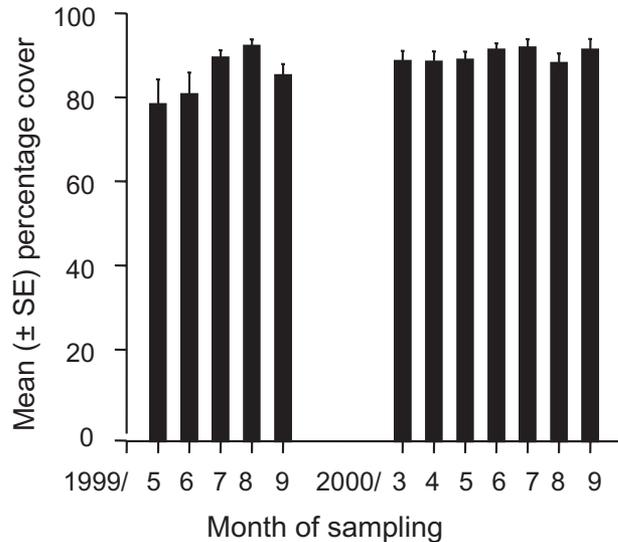


Fig. 2. Mean (\pm standard error (SE)) percentage cover of *Chondrus verrucosus* on Oyakoiwa from May to September in 1999 and March to September in 2000.

caused by two outliers in May and June 1999, which were sampled at the lower extent of the distribution of *C. verrucosus*. When these two replicates were removed from the analysis the cover of *C. verrucosus* was stable over time averaging 90.5% (\pm 0.5 SE) ($F_{11,106} = 1.743$; $P = 0.074$; Fig. 2). Fertile carposporophytic and tetrasporophytic fronds were found on all sampling dates but fertile male fronds appeared less regularly and in lower abundance (Fig. 3a). Due to the absence of fertile male fronds in May and June 1999 and missing values when field time limitations prevented counts of small vegetative fronds in June 2000, the assumptions of a two-factor (frond type and date) ANOVA for the complete dataset were violated. However, analysis of the number of fertile carposporophytic and tetrasporophytic fronds over time indicated that the patterns of abundance and period of maximum fertility were not the same (significant interaction: $F_{6,114} = 3.408$; $P = 0.004$), but on most dates there were more fertile carposporophytic than tetrasporophytic fronds (simple main effects: $F_{1,114} = 27.780$; $P < 0.001$; Fig. 3a). The abundance of small vegetative fronds fluctuated over time with highest densities in May of each year (Fig. 3b). The densities of large vegetative fronds were low at most times (Fig. 3b) with most fronds with two or more branches being fertile.

The population of *C. verrucosus* on Oyakoiwa was strongly gametophyte-dominated in both 1999 and 2000, with no significant difference in the phase proportions between years (Fig. 4a,b). The population of *C. verrucosus* within a 200 m transect on Noroshi also had a significantly higher proportion of gametophytes than tetrasporophytes in both 1999 and 2000, but the

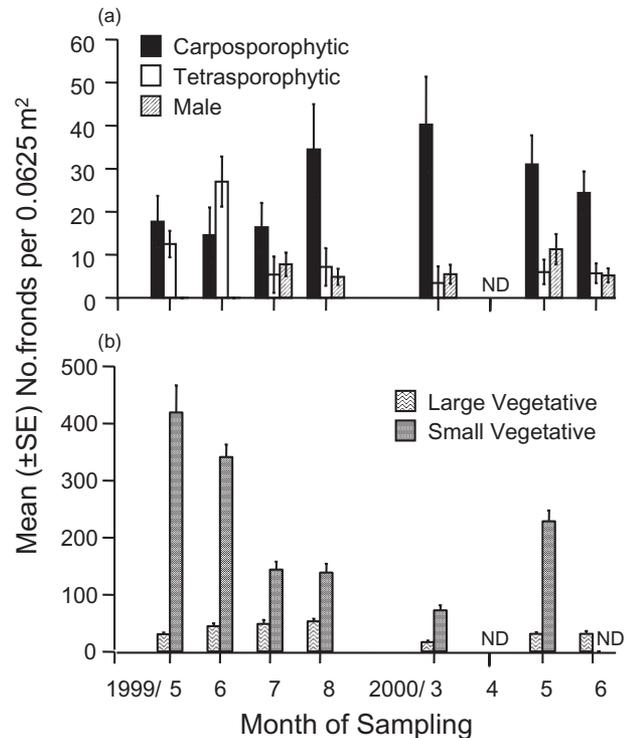


Fig. 3. Mean (\pm standard error (SE)) density (in 0.0625 m²) of (a) fertile carposporophytic, tetrasporophytic and male fronds; and (b) small (<2 branches) and large (\geq 2 branches) vegetative fronds from May to August 1999 and March to June 2000.

G:T ratios were consistently lower than those for Oyakoiwa (average 2.0 vs. 4.1, respectively; Fig. 4c,d). When we examined the phase proportions for individuals (= clumps) on Noroshi that were isolated from other individuals by at least 20 cm, we found no significant difference between phases in 1999, but significant gametophyte dominance in 2000 (Fig. 4e,f). The population of *C. verrucosus* at Kamehana Point was also very strongly gametophyte-dominated in autumn 2000 (96.7% gametophytes, data not shown).

DISCUSSION

The population of *Chondrus verrucosus* on Oyakoiwa was very dense and stable over spring and summer in consecutive years. However the proportions of fertile and vegetative fronds fluctuated, with the highest number of small vegetative fronds in spring. This potentially indicates a period of high recruitment or vegetative regeneration in spring, but winter and autumn data would need to be collected to confirm this. The number of vegetative fronds always greatly exceeded the number of fertile fronds, consistent with the findings of Scrosati *et al.* (1994) for *Chondrus crispus* in Canada. At most times there were many more fertile carposporophytic than tetrasporophytic fronds of *C. verrucosus*.

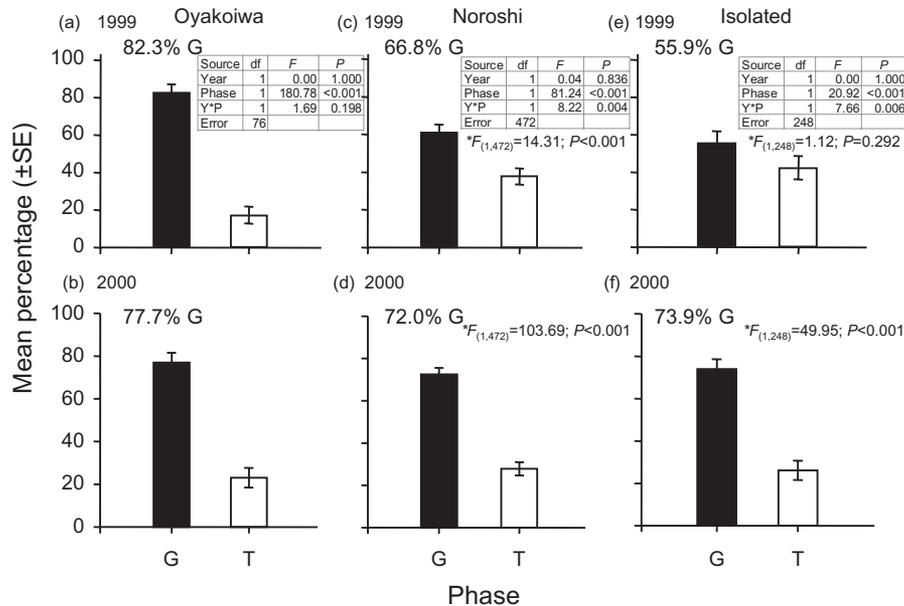


Fig. 4. Mean (\pm standard error (SE)) percentage of gametophytes and tetrasporophytes at Oyakoiva in (a) 1999 (b) 2000; in a 200 m transect on Noroshi in (c) 1999 (d) 2000; and as individuals isolated by >20 cm on Noroshi in (e) 1999 (f) 2000. Included are inserts of two-factor ANOVAs comparing the percentage of gametophytes and tetrasporophytes (Phase) between 1999 and 2000 (Year) for Oyakoiva, Noroshi and isolated individuals, respectively. Y*P, year*phase interaction; *, F - and P -values from simple main effects analyses comparing the percentage of gametophytes and tetrasporophytes for each year; G, gametophytes; T, tetrasporophytes.

Similarly, Bhattacharya (1985) and Mathieson and Burns (1975) generally found a higher proportion of fertile carposporophytic than tetrasporophytic fronds of *C. crispus* in the north-eastern Atlantic Ocean throughout the year; Prince and Kingsbury (1973) found a greater proportion of fronds bearing carposporic than tetrasporic sori from December to March in Plymouth, Massachusetts, with tetrasporic fronds more abundant than carposporic at other times. Conversely, Scrosati *et al.* (1994) found similar proportions of fertile carposporophytic and tetrasporophytic fronds in reproductive clumps of *C. crispus* in Nova Scotia, Canada between June and October. In other studies based on numbers of fertile thalli, Hasegawa and Fukuhara (1955) found almost twice as many fertile female (carposporophytic) gametophytes as tetrasporophytes of *Chondrus yendoi* (as *Iridophycus cornucopiae*) in Hakodate, northern Japan; Hannach and Santelices (1985) found a predominance of carposporophytic thalli of *Mazzaella laminarioides* (Bory) Fredericq and *Sarcothalia crispata* (Bory) Leister (as *Iridaea laminarioides* Bory and *I. ciliate* Kützing, respectively) in central Chile and Lindgren and Åberg (1996) found more fertile tetrasporophytes of *C. crispus* in northwestern Sweden than carposporophytes, although overall fertility was very low. It is worth noting however, that Prince and Kingsbury (1973) caution that reproductive periodicity may not be accurately recorded by the presence or absence of sori alone, because of different stages of

development of the spores within, and the persistence of sori once spores are released. For *C. verrucosus* intact and ruptured sori were clearly distinguishable and fertile fronds were only scored if intact sori were present; the level of maturity of spores, however, was not assessable.

In this study, fertile carposporophytic and tetrasporophytic fronds were abundant at different times, but showed no consistent temporal patterns between years. Other studies have found fertile carposporophytic fronds to be more abundant in late summer-winter for *C. crispus* (Mathieson & Burns 1975), summer for carposporophytic thalli of *M. laminarioides* (as *I. laminarioides*) and autumn for tetrasporophytic thalli of the same species (Hannach & Santelices 1985; Luxoro & Santelices 1989), and summer maxima for biomass of fertile tetrasporophytic fronds of *Chondracanthus chamissoi* (C. Agardh) Kützing (Gonzalez & Meneses 1996). However, to adequately assess seasonality in fertility, studies must be conducted over multiple years to account for interannual variation relative to seasonal variation. Of the studies describing seasonal patterns, only Mathieson and Burns (1975) had sufficient interannual replication (2 years) to be confident of the seasonal patterns described, but their data also showed noteworthy spatial and interannual variation in the abundances of fertile fronds (figs 7–9 in Mathieson & Burns 1975). Although the present study was conducted over shorter intra-annual time scales than the

studies described above with data from spring to late summer only, repeated sampling over two consecutive years allows us to conclude that, at least for spring to late summer, there was no consistent seasonality in fertility of *C. verrucosus*.

The populations of *Chondrus verrucosus* on Oyakoiwa and Noroshi were strongly gametophyte-dominated in the summers of 1999 and 2000. Similarly, the population of *C. verrucosus* at Kamehana Point was strongly gametophyte-dominated in autumn 2000. However, there was some variation between populations with approximately 97% gametophytes at Kamehana Point, 80% gametophytes on Oyakoiwa and closer to 70% gametophytes on Noroshi. These results are consistent with those of previous studies that have found significantly higher proportions of gametophytes than tetrasporophytes for several members of the Gigartinaeae (Craigie & Pringle 1978; Bhattacharya 1985; Hannach & Waaland 1986; May 1986; Scrosati *et al.* 1994; Dyck & De Wreede 1995; Lindgren & Åberg 1996), and with the few studies that have reliably shown that these patterns can be consistent over time for perennial species on stable substrata, particularly for the congeneric *Chondrus crispus* (May 1986; Scrosati *et al.* 1994; Scrosati & Mudge 2004a,b). However, we do not believe the spatial variability in the G:T ratios observed in this study can be explained by differences in wave action (Dyck *et al.* 1985; Mudge & Scrosati 2003), as hydrodynamic conditions were perceived to be similar at all sites (see site descriptions).

Many models related to ecologic differences between phases have been proposed to explain gametophyte dominance within the Gigartinaeae including differential susceptibility to grazers (Hannach & Santelices 1985; Luxoro & Santelices 1989; Buschmann 1991) and higher desiccation tolerance of gametophytes potentially due to differences in carrageenan content (Luxoro & Santelices 1989); faster gametophytic growth rates relative to tetrasporophytes, particularly in warmer months (Bhattacharya 1985; Hannach & Santelices 1985; May 1986; Luxoro & Santelices 1989); differences in fertilization rates, spore production and/or survival (May 1986; Lindgren & Åberg 1996; Fierst *et al.* 2005); higher settlement and germination rates for tetraspores (Gonzalez & Meneses 1996) and differential recruitment between phases (Bhattacharya 1985; May 1986). However, several studies have recorded either minor differences in spore production and release rates between phases (Luxoro & Santelices 1989) or much higher levels of carpospore release than tetraspore release (Bhattacharya 1985; May 1986; Luxoro & Santelices 1989; Gonzalez & Meneses 1996), which should theoretically contribute to higher proportions of tetrasporophytes in populations, assuming equivalent spore survival (but see above). Consistent with the latter

findings, we have observed that higher densities of carpospores than tetraspores were released on multiple occasions of induction of spore release of *C. verrucosus* (A. Bellgrove, pers. obs. 2000–2008). Similarly, in modeling the effects of changes in fertilization rate and spore output on the G:T ratios of isomorphic rhodophytes, Fierst *et al.* (2005) suggested that not only should greater energetic investment in gametes (over meiospores) and mechanisms to increase fertilization rates be adaptive, but also that the reduction in the influence of fertilization rate on population structure and growth through increased carpospore output would favor the evolution of a carposporophyte stage. Conversely, it has been suggested for some species that recruitment from spores adds little to the production of fronds relative to perennation of holdfasts, but differential survival of holdfasts may also affect phase ratios (May 1986; Scrosati *et al.* 1994).

Through demographic model iterations, Scrosati and DeWreede (1999) showed that for ecologically similar phases with the lowest possible spore output per phase, a stable gametophyte: tetrasporophyte (G:T) ratio of 2.8 (~74% G) could be achieved for triennial and perennial thalli regardless of the initial G:T ratio. If the carpospore output doubled (see above) the G:T ratio was reduced to 2 (~67% G). However, they also noted that stable G:T ratios of 2.8 could be achieved by compensatory effects of ecologic differences between phases. It is not possible to determine mechanisms driving phase dominance simply from the patterns of distribution and abundance of different phases (Underwood 1990; Underwood 1997; Scrosati & DeWreede 1999; Fierst *et al.* 2005) and indeed Fierst *et al.* (2005) cautioned that one's conclusions can be influenced by the choice of null model.

If carpospore output is really as high as laboratory studies suggest (Bhattacharya 1985; May 1986; Luxoro & Santelices 1989; Gonzalez & Meneses 1996; A. Bellgrove, pers. obs. 2000–2008), this may be offset by differences in dispersal potential between phases or spore survival. For successful *in situ* fertilization to occur it would be advantageous for tetraspores to have limited dispersal and settle in close proximity to each other. Carpospores and tetraspores of *C. verrucosus* are similar in size, yet the mucilage surrounding tetraspores on release appears to be very resilient (Bellgrove & Aoki 2006), potentially increasing sinking rates of tetraspores relative to carpospores, and limiting dispersal. Additionally, Santelices *et al.* (1999) found that survival rates for thalli derived from groups of coalescing spores were higher than those from single spores, and that three species of *Chondrus* were indeed capable of coalescence (although *C. verrucosus* was not tested). We have observed potential coalescence of spores of *C. verrucosus* in laboratory cultures, although this has not been quantified (A. Bellgrove, pers. obs. 1999). If

tetraspores are in fact more likely than carpospores to settle in groups due to limited dispersal or resilient binding mucilage (Bellgrove & Aoki 2006), then they may also experience higher rates of coalescence and concomitant higher rates of survival. Conversely, carpospores may remain in the water column longer and be carried further where they may experience higher rates of spore mortality or unsuccessful recruitment. Such differential dispersal and/or survival of tetraspores and carpospores may result in gametophyte-dominated populations as seen in this and other studies (reviewed above). Consistent with this hypothesis, we have shown that peak spore supply occurs immediately following low-low tides, but a few spores remain in the water column throughout the tidal cycle (Bellgrove & Aoki 2006). Thus, the lower G:T ratios on Noroshi (average 2.0) relative to Oyakoiwa (average 4.1) and the G:T ratio of 1 observed for isolated plants on Noroshi in 1999 may result from greater dispersal of carpospores into these populations, potentially washed from Oyakoiwa on flood tides (that move into Oura Bay, flow over Oyakoiwa and tend north-northwest towards to Noroshi) after spore release (Bellgrove & Aoki 2006). In support of this, Fierst *et al.* (2005) implied that distant populations of isomorphic rhodophytes are most likely to be founded by either fragments of carposporophytes or tetrasporophytes, or by carpospores. Such differential dispersal between phases may also help to explain the occurrence of isolated but dense populations of *C. verrucosus*: we propose the model that distant areas may be colonized by carpospores but limited dispersal of tetraspores and potentially higher survival rates due to coalescence leads to dense populations dominated by gametophytes, which may be further sustained by hold-fast perennation.

At present, the difficulty in distinguishing carpospores and tetraspores of *C. verrucosus* in mixed water samples (Bellgrove & Aoki 2006) makes it difficult to experimentally test this model in the field, but continuing developments in this area (e.g. Graham 1999; Graham & Mitchell 1999; Dean & Sigee 2006; A. Bellgrove *et al.*, unpubl. data, 2008) may make it possible in the near future.

It is important to note, however, that the proposed model does not exclude the possibility of other mechanisms (such as those reviewed above) contributing to the patterns of distribution and abundance of gametophytes and tetrasporophytes of *C. verrucosus* or other isomorphic rhodophytes. There are a plethora of examples of interactions (both direct and indirect) (e.g. Hunter & Price 1992; Menge 1992; Wootton 1994; Miller & Hay 1996; Benedetti-Cecchi 2000; Lake 2003) between factors controlling the distribution and abundance of organisms, and isomorphic rhodophytes are unlikely to be an exception. Only by proposing alternative models, experimentally testing them and

eliminating false models (Underwood 1990) can we begin to understand the processes driving the distribution and abundance of gametophytes and sporophytes of isomorphic algae.

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