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Small-scale temporal variation in propagule supply of an intertidal red alga

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Information on the variability in supply of algal propagules is scarce, hindered by the difficulty in identifying propagules, but this variability may affect the distribution and abundance of algal assemblages. This study examined the small-scale (½ hourly to hourly) temporal variation in propagule supply of *Chondrus verrucosus* (Gigartinaceae, Rhodophyta) over a dense, isolated bed in south-eastern Japan in summer and winter of 1999. Either 0.5 litre scoop samples or 5 litre pump samples were collected ½ hourly to hourly over 13, 22.5, and 30 h on three occasions in summer (June & July) and 32 h on one occasion in winter (December). Sampling was conducted around either the new moon (two occasions in summer) or full moon (one occasion in both summer and winter) and incorporated full tidal sequences including daytime (summer) and nighttime (winter) low-low (LL) tides. *Chondrus verrucosus* was the only red alga with spores within the size range of 15–20 μm that was fertile in the study area and surrounds at the time of sampling facilitating identification of spores. Spores in scoop samples were settled onto Petri dishes and identified on the basis of cell shape, colour and size. Pump samples were filtered onto transparent membrane filters and identified using epifluorescence microscopy: *C. verrucosus* spores fluoresced bright yellow and were easily distinguished from other micro-organisms of similar size, which fluoresced red or green. Results showed that while propagules could be found in the water column at most times, propagule supply of *C. verrucosus* was greatest during the 1–2 h period following LL tides. Variability in propagule supply was less than in previous studies examining surface or offshore waters. Spore release is thought to be stimulated by either desiccation or salinity changes associated with periods of emersion at low tide followed by re-immersion on incoming tides.

KEY WORDS: *Chondrus verrucosus,* Propagule supply, Spore release, Supply-side ecology, Temporal variation, Tidal rhythm

INTRODUCTION

To understand the potential role recruitment may play in community organization, we must have knowledge of the dispersal distances (and thus possible sources) of the organisms involved and the temporal and spatial variability in propagule supply. The small size and difficulty in identification of algal propagules and germlings has so far limited this field of study. Additionally, on intertidal rock platforms, particularly on wave-exposed coasts, the danger associated with sampling at higher tidal states often limits studies to the low tide or early flood-tide period (e.g. Bellgrove *et al.* 2004). The most notable *in situ* studies of dispersal and settlement have been on fucoids such as *Sargassum* spp. with large, multicellular propagules (after Deysher & Norton 1982; Kendrick & Walker 1991; Kendrick 1994; Kendrick & Walker 1995) or *Silvetia compressa* (J. Agardh) Serrão, Cho, Boo & Brawley (previously *Pelvetia compressa*), which has large (80–100 μm) nonmotile zygotes (Johnson & Brawley 1998). Similarly, studies of the abundance of propagules in the water column (Hruby & Norton 1979; Amsler & Searles 1980; Zechman & Mathieson 1985; Fredriksen *et al.* 1995; Bellgrove *et al.* 1997, 2004) have usually involved the collection of water samples that were then cultured in the laboratory to facilitate identification of post-settlement stages. However, due to potential variability in settlement success and growth in culture, these studies provide only indirect estimates of propagule supply in the field (Norton 1992). Recent work by Graham (Graham 1999; Graham & Mitchell 1999; Graham 2003) using microphotometric methods to distinguish individual kelp zoospores of closely related species in water samples, gives exciting hope for the development of this field in the case where propagules are not easily distinguished from other species.

Chondrus verrucosus Mikami is a red, intertidal alga with an assumed triphasic, isomorphic life cycle and *in situ* fertilisation (Taylor & Chen 1994). This species is fertile throughout the year, though fertile carposporophytic and tetrasporophytic fronds may be present at different times (Bellgrove & Aoki, unpublished data). Both the carpospores and tetraspores are nonmotile and relatively large (15–20 μm) for algae. These features may suggest dispersal of this species may generally be limited to metres from adult plants (Santelices 1990), yet it is commonly found in isolated areas on the Pacific coast of Japan, indicating that it may be capable of at least occasional longer distance dispersal. A dense population of *C. verrucosus* occurs on a small rocky outcrop in Oura Bay, Izu Peninsula, isolated by at least 90 m from the next closest population. Waves break over the outcrop creating a semi-exposed environment in an otherwise relatively sheltered bay. This system lends itself to water sampling at all tidal states, where it might otherwise be dangerous and/or impossible on more extensive rocky shores. Additionally, *C. verrucosus* is the only red alga in the vicinity that is fertile year-round and has spores within the 15–20 μm range, aiding identification of spores without the need for expensive, specialised equip-

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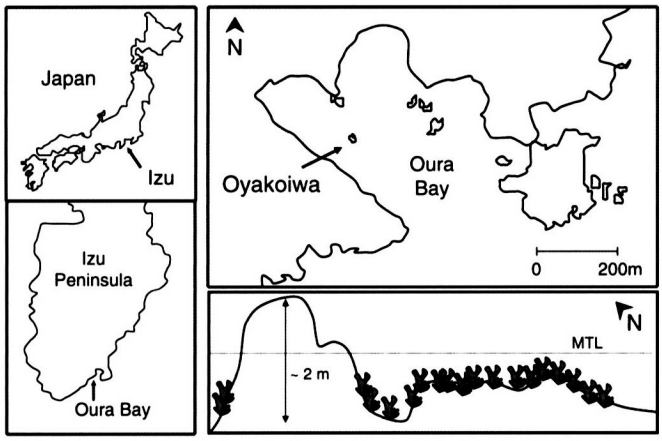


Fig. 1. Study area, Japan, showing the location of Izu Peninsula (top left); Izu Peninsula (bottom left); Oura Bay, showing the location of Oyakoiwa (top right) and schematic longitudinal section through Oyakoiwa showing mean tidal level (MTL) and the distribution of *Chondrus verrucosus* (bottom right).

ment (*sensu* Graham 1999). The aim of this study was to examine small-scale (½ hourly to hourly) temporal variation in the abundance of spores of *C. verrucosus* in the water column immediately above a dense, isolated bed. The specific questions being asked were: when does maximum propagule supply occur, is propagule release associated with tidal or diurnal rhythms and how long do propagules remain in the water column?

MATERIAL AND METHODS

Study site

Sampling was conducted in the area of Oyakoiwa, a small (7 × 5 m) rocky outcrop composed of tuff breccia (Machida 1972), in Oura Bay, Izu Peninsula, Shizuoka Prefecture, Japan (34°40′N, 138°57′E) (Fig. 1). Oura Bay is a relatively sheltered embayment but is exposed to seasonal storms and typhoons (particularly in summer) where waves up to 1 m may enter the bay (Bellgrove, unpublished observation). Oyakoiwa is separated from the nearest rock platform by approximately 150 m and the andesite rock wall demarcating the southwest boundary of the bay by approximately 90 m. The rocky outcrop provides an obstacle to water movement resulting in waves crashing over the outcrop and creating a semi-exposed environment even under relatively calm conditions elsewhere in the bay (Bellgrove, unpublished observation). Machida (1972) observed differences in wave cut benches within Oura Bay suggesting within-bay differences in wave action and abrasion forces, which is consistent with observations of water movement around Oyakoiwa. *Chondrus verrucosus* occurs in a dense (approximately 90% cover) and stable bed dominating the lower-mid intertidal area of the outcrop (Bellgrove & Aoki, unpublished data; Fig. 1).

Study species

Chondrus verrucosus is a dioecious, perennial, benthic red alga that occurs in the eulittoral zone on rocky substrata, mainly in the central region of the Pacific coast of Japan (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. Haploid tetraspores give rise to haploid male and female gametophytes and diploid carposporophytes then develop in the female gametangia after *in situ* fertilisation. Diploid carpospores then give rise to diploid tetrasporophytes. As fertilisation occurs *in situ*, the main dispersive propagules are assumed to be the carpospores and tetraspores. Fertile carposporophytic and tetrasporophytic fronds can be observed throughout the year, while fertile male fronds are present less regularly (Bellgrove & Aoki, unpublished data).

Sampling protocol

To ascertain the period of peak propagule abundance and the supply of propagules of *Chondrus verrucosus*, water sampling was conducted on four occasions in 1999. Two types of samples were collected: *scoop* and *pump* samples. 0.5 litre scoop samples and/or 5 litre pump samples were collected hourly (except where otherwise stated) throughout the tidal cycle, intermitted only for LL tide when the water was too low for effective sampling (Table 1). Sampling recommenced with the first incoming waves washing over the *C. verrucosus* bed, approximately 1.5–2 h after LL tide. On all occasions four replicate samples were collected from different areas within 10 cm above the *C. verrucosus* bed at each sampling time.

Scoop samples were collected in 0.5 litre clear acrylic jars

Table 1. Sampling regime for water samples collected from above Oyakoiwa during daytime low-low (LL) tides on three occasions in June and July 1999 and nighttime LL tides on one occasion in December 1999.[1]

Date	Method	Start	Finish	Sampling frequency	Duration	Lunar phase
16–17 Jun.	scoop	2:00 AM 16 Jun. 1 h after HL tide	12:30 AM 17 Jun. 1 h before HL tide	hourly	22.5 h	NM
29 Jun.	scoop	8:30 AM 29 Jun. 3 h before LL tide	9:30 PM 29 Jun.* 3 h after HL tide	hourly	13 h	FM
15–16 Jul.	scoop & pump	10:00 AM 15 Jul. 3 h before LL tide	3:30 PM 16 Jul. 2.5 h after LL tide	½ hourly: 10:00 AM–4:00 PM 15 Jul., 3:00 PM–4:00 PM 16 Jul., hourly all other times	30 h	NM
22–24 Dec.	pump	6:00 PM 22 Dec. 5 h before LL tide 7:00 PM 23 Dec. 5 h before LL tide	4:00 AM 23 Dec. 5 h after LL tide 3:00 PM 24 Dec. 3 h after HL tide	½ hourly: 1:00 AM–4:00 AM 23 Dec., 2:00 AM–4:00 AM 24 Dec., hourly all other times	11 h 21 h	FM

[1] HL, high-low; NM, 2 days after new moon; FM, during full moon; *, abandoned due to torrential rains and turbulent waters.

with the bottom half of a Petri dish (60 mm diameter) attached to the screw-on lid of each jar with Blutac re-usable adhesive (Bostik, Thomastown, Vic., Australia). Sampling was conducted from a small anchored boat pulled up over the bed during sampling. Inverted jars were fixed to a pole and pushed through the water column to the algal bed, then tipped to the side and swept over an area of bed, releasing the trapped air bubble and thus sampling the water from immediately above the bed to a maximum height of 10 cm (jar mouth diameter 7.2 cm). Capped jars were inverted, placed in a cooler box (without ice) and returned to the laboratory every 3 h where they were placed in a dark 15°C room for between 24 and 48 h to facilitate spore settlement onto the Petri dishes, and then exposed to a 15L : 9D cycle (natural day length) until counts had been completed (within 3 days of collection). To avoid potentially confounding slight variations in light and temperature conditions within the controlled temperature (CT) room or time elapsed until spores were counted with the time of collection, samples were haphazardly arranged within the CT room (i.e. not in groups) and samples were then randomly selected for counting. Spores were counted with the aid of an inverted microscope (IX 70, Olympus Corporation, Tokyo, Japan). Each sample was subsampled to expedite processing time and avoid degradation of spores in later counted samples: 10 (first occasion) or 15 (second and third occasions) fields of view at ×100 magnification were haphazardly chosen for each Petri dish and the number of spores within counted and then pooled for each sample. Checks outside the subsampled area ensured that no large clumps of spores were missed. Higher magnification was used to confirm identification. Spores were identified on the basis of cell shape, colour and size, as at the time of sampling, *C. verrucosus* was the only red alga with spores within the size range of 15–20 μm that was fertile in the study area and surrounds.

Pump samples increased the water volume sampled and thus likelihood of spores being collected. A bilge pump (CB-P80A Hitachi Ltd, Tokyo, Japan; 100 V, 50 Hz, 130 W, 40 l min^{-1}) powered by a generator on the boat was used. The pump was fitted with a plastic pipe (22 mm internal diameter) and funnel (125 mm maximum internal diameter, 80 mm height), increasing the suction area and decreasing the pump pressure so that thalli were not sucked into the pump. As the pump requires a continuous flow of water, the funnel was held over the bed for approximately 30 sec to allow drainage from the hose and pump before sample collection commenced. This was repeated between replicates over different areas of the bed to ensure independent replicates. Each sample was collected by 'vacuuming' a different area of approximately 1 m^2 within 10 cm (funnel height 8 cm) above the *C. verrucosus* bed. Samples were filtered through a series of 300, 100, 40 and 10 μm mesh filters; the 10 μm fractions were washed into 50 ml jars with microfiltered (to 0.45 μm) seawater, formalin was added to 8% final concentration and then stored in the dark at 4°C until processed. The 10 μm fractions were vacuum filtered at a pressure of 15–20 mm Hg onto Cyclopore track etched polycarbonate transparent membrane filters (3.0 μm pore size, 25 mm diameter, catalogue number 7062-2512; discontinued but replaced by 7091-2510, Whatman International Ltd, Maidstone, UK). Initially the filtration pump was turned off for the last 1 ml of each sample to allow gravity fed filtration and minimise damage to spores (after Graham & Mitchell 1999) but as spore damage was negligible regardless, the filtration pump ran continuously to maximise efficiency. The membrane filters were mounted on glass slides in Olympus nonfluorescent immersion oil and sealed with nail polish (Graham & Mitchell 1999). Slides were stored at 4°C until examined with the aid of epifluorescence microscopy [Nikon Optiphot microscope with blue (450–490 nm) excitation filters, Tokyo, Japan]. *Chondrus verrucosus* spores autofluoresced bright yellow and were easily distinguishable from other micro-organisms of similar size, which fluoresced red or green, and other red algal spores by size (~5 μm spores were occasionally trapped by the 10 μm filter, possibly entangled in mucilage). The number of *C. verrucosus* spores in each pump sample were counted in a subsampled area of 10 parallel, haphazard transects across the filter at ×200 magnification. Spore counts for the 10 transects were pooled for each sample. No degradation in autofluorescence was observed even after 5 months storage.

In both scoop and pump samples it was impossible to visually distinguish carpospores from tetraspores of *C. verrucosus* as they are morphologically similar in size, shape, colour and autofluorescence. Spore counts thus potentially represent a combination of both carpospores and tetraspores.

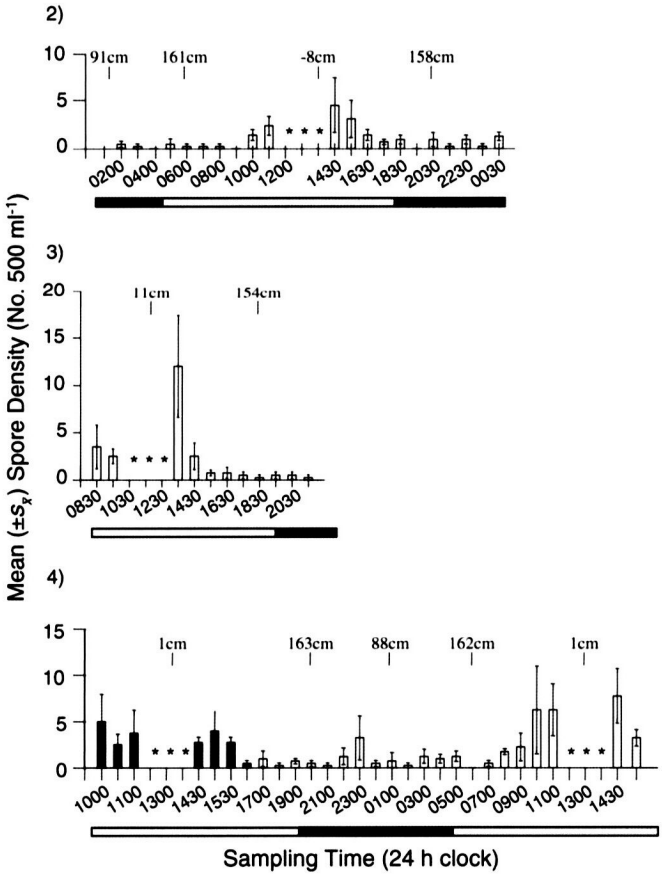
Surface seawater temperatures were recorded at the time of each scoop and pump sample collection on all occasions. Humidity data are from Shimoda Marine Research Centre, collected daily at 10:00 AM in Oura Bay.

Statistical analyses

Data were analysed with one-way analyses of variance (ANOVAs) for each occasion with time of sampling as a fixed factor. The relationships between abundance of propagules and water surface temperatures were analysed with Pearson's correlation. Assumptions of normality and homogeneity of variances were checked with box plots and residual plots. Data were fourth-root transformed to meet assumptions of normality where necessary. Tukey's *post hoc* test was used for unplanned pairwise comparisons between sampling times after ANOVA. Because Tukey's test controls the family-wise Type I error rate to the nominated α-level (in this case $\alpha = 0.05$) (Quinn & Keough 2002), this reduces the power of any individual pairwise comparison to detect significant differences, particularly when a large number of pairwise comparisons are made (as in these data sets). However, we can be more confident that any significant differences detected are real differences.

RESULTS

On all four sampling occasions and for both scoop and pump samples, there was significant temporal variation in the density of *C. verrucosus* spores in the water column over the algal bed on Oyakoiwa [$F_{(20,61)} = 3.383$, $F_{(10,33)} = 2.732$, $F_{(27,84)} = 3.568$, $F_{(25,77)} = 7.544$, $F_{(28,86)} = 17.213$ for scoop samples collected on the first three sampling occasions and pump samples collected on the third and fourth sampling occasions, respectively; $P < 0.05$ for all ANOVAs]. However, the densities of spores in scoop samples collected on the first three occasions were very low (Figs 2–4). Despite this, there was a weak



Figs 2–4. Mean number (±s_x) of *Chondrus verrucosus* spores in 0.5 litre scoop samples collected between 16–17 June 1999 (Fig. 2), on 29 June 1999 (Fig. 3), and between 15–16 July 1999 (Fig. 4). In this and subsequent figures dark shaded bars indicate samples collected every 30 min – all other samples were collected hourly; stars indicate that no samples were collected during low-low tide; white and black horizontal bars beneath the X-axis indicate periods of light and dark respectively; and heights at the top of each figure represent tidal height above or below chart datum.

trend for greater densities of spores in samples collected in the hour preceding and the hour following the LL tide (Figs 2–4). This was particularly noticeable on the second (late June) sampling occasion and for the second LL tide period on the third (mid-July) sampling occasion (Figs 3, 4). This pattern was stronger for the pump samples collected after the second LL tide period on the third (mid-July) sampling occasion (Fig. 5). However, the samples collected around the LL tide on July 15 contained much lower densities of spores than after the LL tide on July 16 (Fig. 5). The same strong pattern was evident for the pump samples collected on the fourth (December) sampling occasion with the highest densities of spores in the samples collected within 1 h after both LL tide periods sampled (Fig. 6).

For the scoop samples collected on all three occasions and the pump samples collected on the third occasion (mid-July) there was only a very small proportion of *post hoc* pairwise comparisons that were significant, but almost all were comparisons with samples collected within 1 h after the LL tide, and also 1 h before the LL tide for the third occasion (Table 2). Over one third of the pairwise comparisons of pump samples collected in December (fourth sampling occasion) were significant (Table 2) and 78% of these involved samples collected within 1 h after the LL tide; the remaining significant pairwise comparisons involved samples collected between 1–2 h after LL tide (Table 2).

The numbers of spores in the 5 litre pump samples were obviously much greater than in the 0.5 litre scoop samples, though still surprisingly low given the amount of water sampled and proximity to the bed (Figs 5, 6). Spores of *C. verrucosus* were, however, present, at least in low concentrations, at most sampling times, particularly during the summer collections (first three occasions) (Figs 2–6). There were no significant relationships between surface water temperatures and the number of spores in the water column (Pearson's r = 0.429, 0.390, 0.056, 0.188, −0.269 for the three sampling occasions when scoop samples were taken and the two sampling occasions when pump samples were taken, respectively; $P > 0.05$ for all correlations).

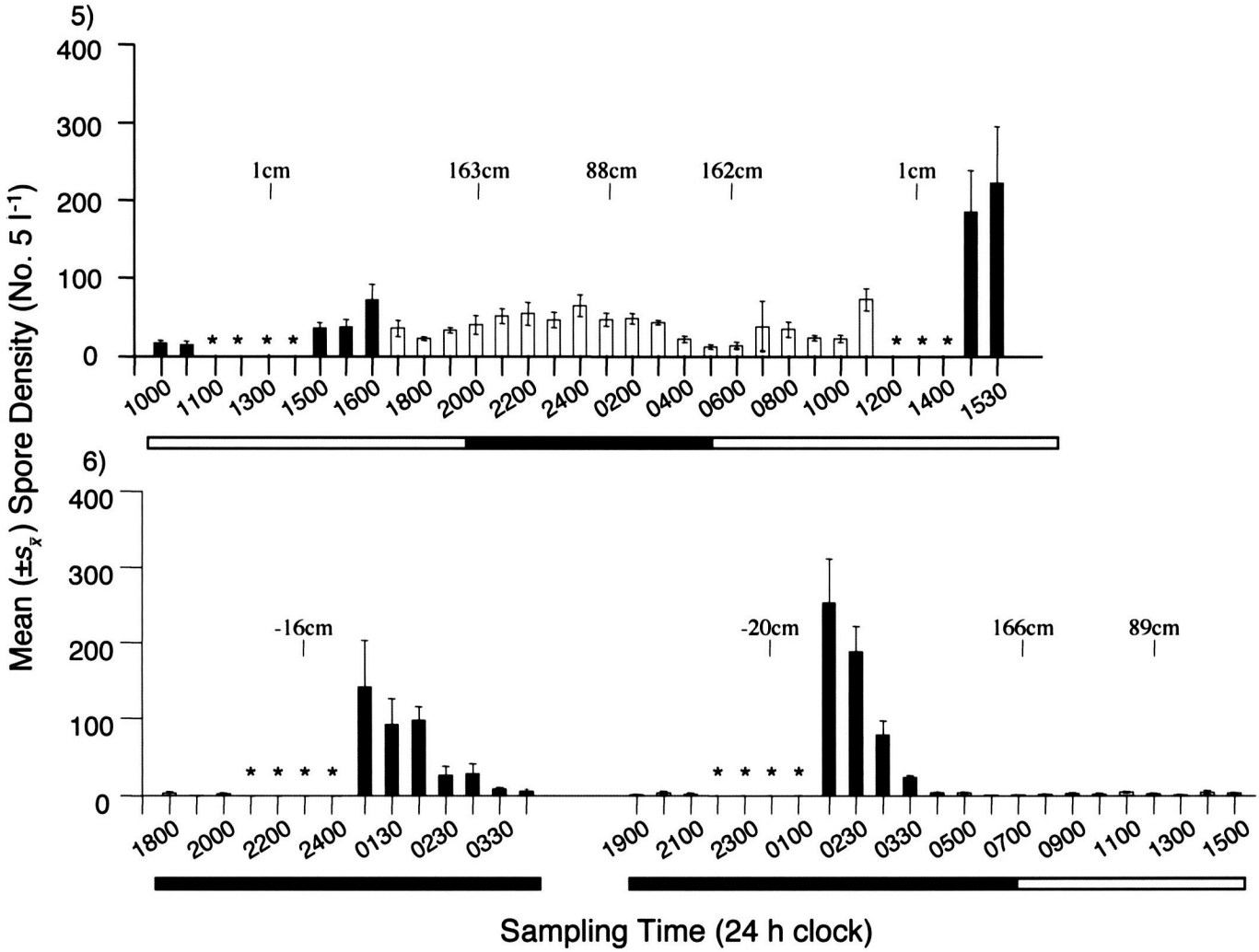
DISCUSSION

Densities of spores of *C. verrucosus* were generally highest in the water samples collected within the first hour (and sometimes into the second hour) of the incoming tide washing over the algal bed. This pattern was stronger for the 5 litre pump samples, in which higher densities of spores were sampled, than for the 0.5 litre scoop samples. Due to the small size of Oyakoiwa, once the tide began to come in, the bed of *C. verrucosus* was usually covered by water within an hour, though sometimes still partially emerged with receding waves. On some occasions (summer collections) the samples collected during the hour or two preceding LL tide also tended towards high densities of spores. At these times, although the water level was still high enough to cover the bed and collect water samples, the bed was often exposed on receding waves.

The methods for collecting propagules used in this study relied on sufficient water being present over the algal bed, and thus sampling was intermitted during LL tides when the algal bed was emerged. It is therefore not possible to know what spore densities were during these times.

One possible explanation for the observed peaks in spore densities following LL tides is that spores of *C. verrucosus* are released continuously, but accumulated in the algal bed during LL tide when water was not moving through, and were then suspended in relatively high densities once the incoming tide washed over the bed. The presence of low densities of spores at most times in summer also supports this hypothesis. However, Ngan & Price (1983) found that of 48 species of benthic red algae studied in the laboratory, species with free cystocarps (projecting above the thallus surface) released most spores within a 1 or 2 h period, and periods of tetraspore release in these species were similarly brief. Additionally, most species had only one period of spore release within a 24 h period. *Chondrus verrucosus* also produces free cystocarps and thus this explanation of continuous spore release is unlikely. Additionally, the data for December do not support a model of continuous spore release.

It is also possible that spore densities were diluted at higher tidal states, with a larger volume of water washing over the algal bed compared to following LL tides. However, with both the scoop and the pump samples, spores were sampled from



Figs 5, 6. Mean number ($\pm s_x$) of *Chondrus verrucosus* spores in 5 litre pump samples collected between 15–16 July 1999 (Fig. 5) and 22–24 December 1999 (Fig. 6). Bar shading and annotations are as for Fig. 2–4. Note: pump samples could not be collected after 10:30 AM on July 15, and before 3:00 PM on both July 15 and 16 due to an inability of the pump to sample unless completely submerged (cf. scoop samples, Fig. 4).

Table 2. Summarised results from Tukey's *post hoc* tests after ANOVA for scoop and pump samples collected on four occasions in 1999. Data indicate the total number of pairwise comparisons made, the percentage of those that were significant (adjusted $P < 0.05$), and the percentage of significant pairwise comparisons that involved samples collected within 1 h after LL tide. Data in parentheses indicate the percentage of significant pairwise comparisons that involved samples collected within 2 h of LL tide (bold) or 1 h before LL tide (underlined).

Sample type and collection period	Total no. comparisons	% Significant	% Significant within 1 h after LL tide
Scoop samples			
16–17 Jun. 1999	220	1.4	100
29 Jun. 1999	55	3.6	100
15–16 Jul. 1999	378	2.1	75 (<u>12.5</u>)
Pump samples			
15–16 Jul. 1999	325	2.8	66.7 (<u>11.1</u>)
22–24 Dec. 1999	406	34.7	78 (**100**)

within 10 cm above the algal bed, such that dilution should not be a major influence on spore densities. Thus if spores were being released during high tide periods we would expect to see high spore densities in the 10 cm above the algae at these times. This was not the case.

Alternatively, we may infer that times of peak propagule abundance immediately over the algal bed indicate the time of propagule release. As such, it would appear that the release of spores of *C. verrucosus* is related to tidal rhythms. The fact that the same pattern was found for both summer daytime LL tides and winter nighttime LL tides indicates that the stimulus for spore release was related to tidal rhythms rather than diurnal rhythms (cf. Amsler & Neushul 1989). Several species of intertidal algae have been found to release propagules during periods of emersion or after emersion followed by reimmersion (Santelices 1990; Johnson & Brawley 1998). Propagule release for several fucoids is stimulated by limited photosynthesis after periods of successful photosynthesis, as would occur when thalli dry out during low tide (Johnson & Brawley 1998; Pearson *et al.* 1998). However as spores of *C.*

verrucosus were released during periods of darkness surrounding winter LL tides in this study, changes in photosynthesis seem an unlikely release mechanism for this species. Other changes associated with low-tide periods thought to stimulate release in several species, such as desiccation and changes in salinity (Santelices 1990) may more likely stimulate spore release in *C. verrucosus*. While desiccation may be caused by high irradiance during daytime summer low tides, the low humidity associated with Japanese winters (59%, 47% and 63% in the study area for 22–24 December respectively) may similarly desiccate thalli during nighttime winter low tides. Abundance of spores was also positively correlated with patterns of emersion in the period surrounding the LL tide; the algal bed was never fully emerged during HL tides. Additionally, in the laboratory, both carpospore and tetraspore release of *C. verrucosus* can be stimulated by air-drying thalli for 1–2 h and then re-immersing in seawater (Bellgrove, unpublished data); although laboratory methods of stimulating spore-release can be unrelated to natural release mechanisms (Johnson & Brawley 1998).

If spore release in *C. verrucosus* is stimulated by emersion during LL tides, then the peaks in propagule release observed within 1–2 h of re-immersion after LL tide are consistent with the episodes of propagule release observed by Ngan & Price (1983) (see above). However, Ngan & Price (1983) found spore release of most species was associated with predicted high-tide periods in the field, and usually during the lower of the two high tides. In the area of the present study the two daily high tides are usually similar in height, but spore densities were usually very low at these times. Ngan & Price (1983) suggested reduced desiccation stress and increased dispersal potential as benefits for spore release during high tides. Similar benefits could be afforded by release during incoming tides. Conversely, the turbulent waters associated with incoming waves may actually increase spore deposition and reduce dispersal potential.

Although there was both small-scale spatial (between replicate) and temporal variation in the abundance of spores of *C. verrucosus* in the water column above the algal bed, the patterns of maximum abundance were similar for all four occasions of sampling (although the trends are weak for the scoop samples). We may expect, however, to find much greater variation in samples collected at greater distances from the source population due to dilution and potential mortality within the plankton. Indeed studies that have sampled surface waters (Hruby & Norton 1979; Hoffmann & Ugarte 1985; Zechman & Mathieson 1985; Fredriksen *et al.* 1995; Bellgrove *et al.* 1997, 2004) or offshore waters (Amsler & Searles 1980) have found much greater variability than in the present study. In the only other study of small-scale temporal variation in macroalgal propagule supply, Graham (2003) found complex patterns of giant kelp [*Macrocystis pyrifera* (Linnaeus) C. Agardh] zoospore supply associated with small-scale hydrodynamic forces and coupling with reproduction. He also found that zoospores were continuously present in the water column, potentially facilitating year-round recruitment.

While it was impossible to visually distinguish carpospores from tetraspores in samples, in several samples clumps of four spores (or sometimes three with a fourth close by) were observed, still bound by a mucilaginous sheath. These were assumed to be tetraspores. Conversely, mucilage was rarely observed around single spores. The fact that the mucilage remained, binding the spores together after both gravity-fed filtration through the series of mesh filters in the field, and then later vacuum filtration onto the transparent membrane filters, indicates that it is highly resilient. Consequently, mucilage may keep the tetraspores bound together and increase the rate of sedimentation of these aggregated spore bodies relative to individual carpospores (Coon *et al.* 1972; Norton & Fetter 1981; Okuda & Neushul 1981; Norton 1992) or the stickiness might assist adhesion of spore aggregates during turbulent deposition. Conversely, if the difference in the density of the aggregations of tetraspores and the associated mucilage is at least twice the difference in the density of the mucilage and the surrounding seawater, then the mucilaginous sheath may actually increase the buoyancy of tetraspore aggregations (Walsby & Reynolds 1981). Although these measurements have not been made, the former seems more likely due to the increased radius of the tetraspore aggregations relative to that of individual carpospores (Walsby & Reynolds 1981). Either way, the persistent mucilage around tetraspores may possibly result in different dispersal potential for carpospores and tetraspores.

Although maximum spore abundance was associated with the period immediately following LL tides, at least a few spores were found in most samples, particularly those collected during summer. This could be explained by three equally plausible models that remain to be tested: (1) most propagules settle within a relatively short period of time (perhaps through turbulent deposition) with minimal dispersal, and spores remaining in the water column for extended periods may represent the potential for longer distance dispersal; (2) most propagules are carried away from the source population on incoming waves and flood currents potentially facilitating long distance dispersal, and spores remaining above the bed may have been entrapped in local eddies to eventually settle into the local population; (3) tetraspores released in resilient mucilaginous sheaths settle relatively quickly within close proximity of the source bed, while carpospores may be more buoyant (i.e. sink more slowly) and remain in the water column for longer, facilitating longer distance dispersal. Summer in the study area is a time associated with storms and typhoons and it may be possible that spores are more likely to be resuspended, and thus remain in the water column for a longer period of time, than during calmer winter months (Figs 2–5 cf. Fig. 6). The relationship between storm and typhoon-induced swells and currents and long distance dispersal may also prove an interesting area of study.

There is a great need for more studies examining both the temporal and spatial variability in propagule supply and the dispersal potential of macroalgal species, and the contribution of these processes to community structure. While quantitative sampling and identification of early stages present major obstacles to these studies, researchers may be able to use methods such as microphotometry (Graham 1999; Graham & Mitchell 1999; Graham 2003) or species with clearly distinguishable propagules (Deysher & Norton 1982; Kendrick & Walker 1991; Kendrick 1994; Kendrick & Walker 1995; Johnson & Brawley 1998, this study) to advance this field. The results of this study support a model of spore release of *C. verrucosus* being stimulated by emersion at low tide and subsequent re-submersion on incoming tides, perhaps through ei-

ther desiccation or osmotic changes. The stimulus for spore release in this species remains to be tested experimentally however.

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