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Effects of wave exposure on population and reproductive phenology of an algal turf, *Gelidium pusillum* (Gelidales, Rhodophyta), Songkhla, Thailand

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ABSTRACT

The effect of wave exposure on the population and reproductive phenology of the common red alga, *Gelidium pusillum* (Stackhouse) Le Jolis, was investigated between July 2003 and June 2004, at Suan Song Tha Le, Songkla Province, Thailand. Lengths of thalli, percentage cover, percentage of reproductive fronds and the number of reproductive structures were examined monthly in relation to different degrees of wave exposure (sheltered vs. exposed), temperature, rainfall, day length and tidal cycles. Frond length and percentage cover of *G. pusillum* were different among sites and seasons. Shorter fronds were found on the exposed shore which had a greater percentage cover. Fronds bleached and died off during the summer months (April and May), which resulted in shorter fronds and reduced percentage cover in June. The thalli reproduced throughout the year, with a predominance of tetrasporophytes. The highest percentage of tetrasporic fronds was 33% in February 2004 and 13% of cystocarpic fronds in April 2004, but male gametophytic fronds were never observed. Rainfall showed a strongly negative influence on reproduction since no reproductive fronds were observed during the rainy season (R^2 = 0.49, P = 0.01). The dominance of *G. pusillum* at this study site and throughout elsewhere in turf habitats might be a function of persistent vegetative growth, densely clumped, and the ability to reproduce almost throughout the entire year.

1. Introduction

Exposure to wave action is generally considered to be an important factor in the distribution and abundance of intertidal organisms (Lewis, 1964; Stephenson and Stephenson, 1972; Denny, 1998). It is also well known to influence size, morphology and distribution patterns. Organisms on wave-swept shores are often much smaller than those in more wave-protected habitats (Lewis, 1968; Menge, 1976; Blanchetter, 1997; Prathep et al., 2007). Wave exposure also influences the community structure via water motion (Lobban and Harrison, 1994). Propagule dispersal, fertilization, settlement and recruitment (Vadas et al., 1990; Serrão et al., 1996) are all affected. Recent studies on the red alga, *Mazzaella oregona* (Mudge and Scrosati, 2003) have shown an inverse relationship between the G:T (gametophyte:tetrasporophyte) ratio and the degree of wave exposure although this is not the case in *M. parksii* (Scrosati and Mudge, 2004).

In the family Gelidiaceae (Order Gelidiales) gametophytes and tetrasporophytes are isomorphic. Various investigators have reported that tetrasporophytic fronds predominate over gametophytic fronds in natural populations (Akatsuka, 1986; Santelices, 1988; Santos and Duarte, 1996). *Gelidium pusillum* (Stackhouse) Le Jolis has a very wide geographic range being reported from UK, continental Europe, Chile and Australia (Dixon and Irvine, 1977; Santelices, 1988; Rueness and Fredriksen, 1998; Millar and Freshwater, 2005). It is an intertidal turf-forming alga with a stoloniferous growth form. The clumped erect fronds could be seasonal, possibly due to variable exposure and desiccation at the upper shore level as well as grazing pressure (Dixon and Irvine, 1977; Santelices, 1988).

In this study we examined (1) the effects of wave exposure, temperature, rainfall, day length and tidal cycles on percentage cover, length of thalli, life phase and fertility of *G. pusillum* population and (2) its reproductive phenology throughout the year.

2. Materials and methods

Preliminary observations revealed that *G. pusillum* is a dominant red alga on many intertidal shores of the Gulf of Thailand in Southern Thailand, e.g. Koh Samui, Chumporn, Nakorn Si Thammarat and Pattani provinces, it can form vast monospecific stands. In Songkhla province, at Suan Song Tha Le (7°13′N, 100°34′W), a high abundance

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Table 1
Summary of length, percentage cover, percentage of reproductive fronds and number of reproductive organs of *G. pusillum* at the sheltered and exposed areas during July 2003–June 2004 at Songkhla province, Thailand.

	N	Sheltered area	Exposed area	Site		Month		Site × Month	
		Mean ± S.E.	Mean ± S.E.	SS (%)	*P*	SS (%)	*P*	SS (%)	*P*
Length (cm)	150	0.759 ± 0.007	0.736 ± 0.005	1	<0.001	1	<0.001	1	<0.001
% Coverage	10	35.14 ± 1.65	63.01 ± 1.87	3	<0.001	22	<0.05	2	<0.001
% Reproductive frond	12	15.66 ± 3.22	15.88 ± 4.81	0	0.93	6	<0.001	2	<0.001
% Tetrasporophyte	12	14.61 ± 3.01	12.92 ± 4.04	23	<0.001	34	<0.001	30	<0.001
% Carposporophyte	12	1.05 ± 0.44	2.97 ± 2.01	1	<0.001	1	<0.001	1	<0.001
No. of tetrasporic sori/frond	150	7.38 ± 0.06	9.62 ± 0.96	0	0.69	0	<0.001	2	<0.001
No. of cystocarp/frond	150	0.06 ± 0.02	0.36 ± 0.08	1	<0.001	1	<0.001	1	<0.001

Two-way ANOVA for length, % Coverage, % reproductive frond, % tetrasporophyte, % carposporophyte, number of tetrasporic sori/frond and number of cystocarp/frond, sites (sheltered vs. exposed sites) and months as factors and their interactions. Percentage of variance is explained by a factor (SS = (100 × factor SS/total SS), and the level of significance (*P*).

of *G. pusillum* was found over a 1 km long artificial rocky wall, in the intertidal range between 0.7 and 1.0 m. mean seawater level. *G. pusillum* is directly exposed to wave motion which is especially high during the monsoon season (October–March). In sheltered areas on the wall, thallus does not directly face the ocean and therefore is less exposed to wave splash. Water velocity was measured 15 min interval for an hour at high tide in May 2004 at both exposed and sheltered areas, using a MINI Current Meter model SD-6000 (Sensordata, Norway). The water velocity at the exposed site was two times greater than at sheltered one: 0.034 ± 0.007 m/s (mean ± S.E.) and 0.016 ± 0.006 m/s, respectively.

Each month between July 2003 and June 2004, three hundred fronds were sampled from ten 50 cm × 50 cm quadrats on both sheltered and exposed areas of the rocky wall. Quadrats were placed haphazard at the mid-shore level, 15 fronds from each quadrat were collected randomly and measured for length and examined for reproductive status. Razor blade cross-sections were stained using 1% aniline blue and examined for spermatangia, cystocarps and tetrasporic sori (Fredriksen et al., 1994). In addition, we have not seen any grazing mark on the fronds, thus herbivory was unlikely to influence growth and coverage of *G. pusillum* at the sites.

Temperature, rainfall, day length and tidal cycles were monitored to assess any correlation with percentage cover, length of thalli, percentage of reproductive fronds and number of different reproductive phases. The dataset were provided by the Thai Meteorological Department, NICA (National Institute of Coastal Aquaculture), Songkhla and Royal Thai Navy.

Two-way ANOVA was employed to test the differences in percentage cover, length of thalli, life phase and numbers of each reproductive phase among sites and seasons using SPSS, version 15.0, temperature, rainfall, day length and tidal cycles were used as covariates. When necessary, data were transformed to meet the assumptions of the parametric test. Multiple comparisons were made following Zar (1984) when there were significant differences between treatments. The potential relationship between percentage cover, length, percentage of reproductive fronds, life phase and number of each reproductive phase and temperature, rainfall, day length and tidal cycle were assessed using stepwise multiple regression. The aim was to select those combinations of variables that were associated with percentage cover, length, percentage of reproductive fronds, life phase and number of each reproductive phase of *G. pusillum*, to give information on the types of factors that might be controlling population and reproduction of *G. pusillum*.

3. Results

There were small variations in temperature and tidal cycle throughout the year. The average temperature was 27.9 ± 0.2 °C, the highest temperature was 29.5 °C in April 2004 and the lowest was 26.6 °C in December 2003. The highest tide was 1.25 m above mean sea level in December 2003 and the lowest tide was 0.54 m in August 2003, the tide was low during daytime between March and August. There was variation in day length, the longest day was 15 h/day in September 2003 and the lowest was 12 h/day in December 2003. The highest variation was observed in rainfall, the average rainfall was 170 ± 41 mm. The highest rainfall was 580 mm during the beginning of monsoon, in October 2003 and the lowest was 15 mm in mid of dry season, March 2004.

Variation in length of *G. pusillum* fronds was observed among sites and time of year (Table 1). Specimens from the sheltered shore were significant taller than those on the exposed shore in many months (Fig. 1a). The average longest frond was 1.04 ± 0.03 cm (mean ± S.E.) on the sheltered shore during July 2003. On the exposed shore the average shortest frond was 0.6 ± 0.01 cm during May 2004. Many bleached tips were observed in late April and beginning of May.

There was variation in percentage cover of *G. pusillum* both among sites and time of year (Table 1). The highest percentage cover was 83 ± 2% during July 2003 on the exposed area (Fig. 1b). A significantly greater percentage cover of *G. pusillum* was found on the exposed area throughout the study (Table 1). The lowest percentage cover was 40 ± 6% in October on the exposed shore; and the lowest

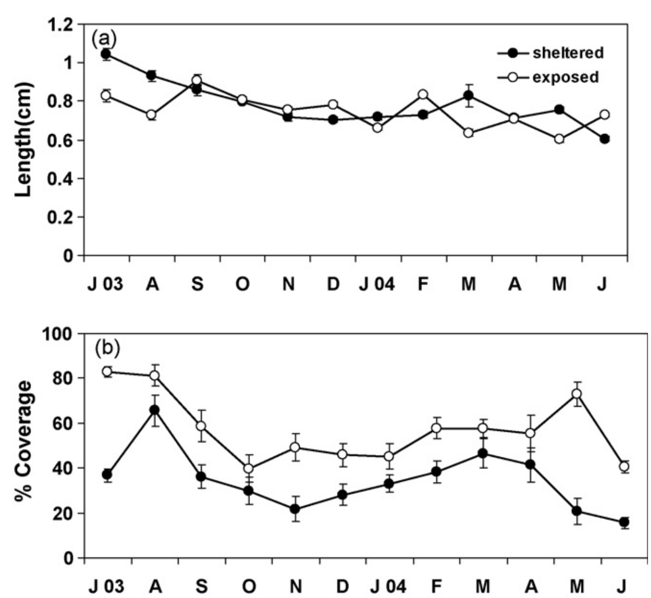

Fig. 1. *Gelidium pusillum* population. Variations in length (a) and % coverage (b) between sheltered and exposed areas throughout the year (mean ± S.E.).

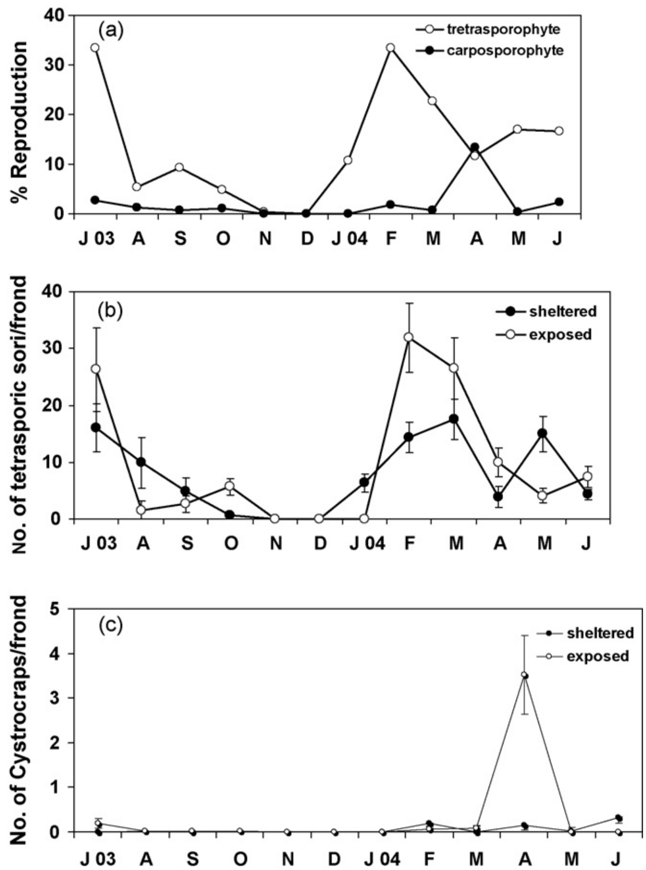

Fig. 2. *G. pusillum* population. Variations in % reproduction (a), number of tetrasporic sori/frond (b) and number of cystrocarps/frond (c) between sheltered and exposed areas throughout the year (mean ± S.E.).

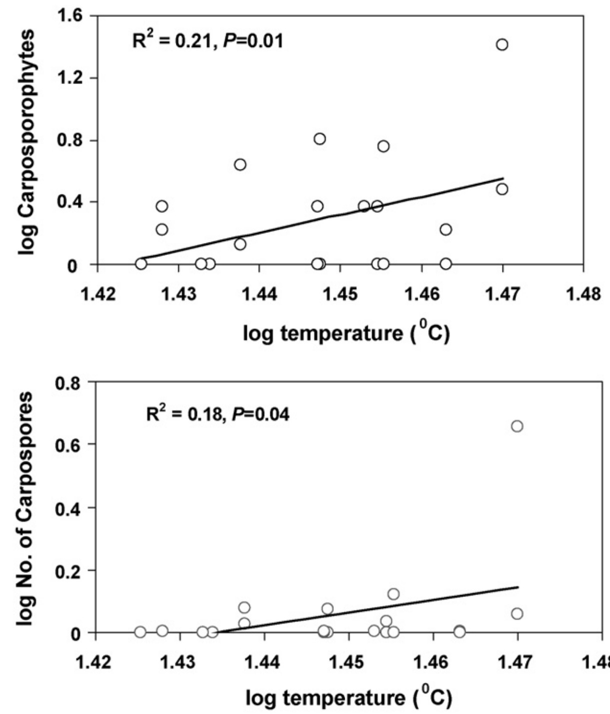

Fig. 3. Significant correlation between temperature and % cystocarpic frond and number of cystrocarps/frond of *G. pusillum*.

percentage cover of the sheltered shore was 8 ± 3 in June 2004, after the bleaching phenomenon observed.

Seasonal variation in percentage of reproduction was striking. *G. pusillum* reproduced throughout the year, except for November and December 2003, the beginning of the rainy season (Fig. 2a). Both tetraspores and carpospores were observed, but spermatangia were never found in this study. There was a high percentage of tetrasporophytes in this population. For example, more than 33% of tetrasporophytes were found in July 2003 and Febuary 2004. Only a few carposporophytes were found.

We observed variation in number of tetrasporic sori of *G. pusillum* among sites and months. In general the thalli produced great numbers of tetraspores. The highest number of tetrasporic sori was 31.9 ± 6.0 sori/frond in January 2004, however, as mentioned above, there were no reproductive fronds in November and December 2003 (Fig. 2b). There were variations of number of cystocarpic specimens among sites and months. The highest number was 3.52 ± 0.09 cystocarps/frond in April 2004 at the exposed shore site (Fig. 2c). This suggests that there were male gametophytes in the previous months.

Stepwise multiple regression revealed that percentage cover and length of *G. pusillum* were not significantly influenced by temperature or rainfall ($P > 0.05$). However, low tide occurred between late morning to early afternoon in summer months, thus *G. pusillum* was exposed to stronger irradiance and longer hours in the air. We also observed fronds bleaching; the bleached fronds died off later and washed away during the rainy season.

Reproduction and the number of reproductive structures exhibited a correlation with temperature and rainfall. High temperature not only stressed reproduction but also caused the plants to die off. However, an increase in temperature was correlated with higher numbers of carposporophyte (Fig. 3). Rainfall caused a decrease in salinity to <10 psu during the rainy season. This low salinity also correlated with low reproduction as expressed in percentage of reproductive fronds (Fig. 4). No reproductive fronds were observed during the mid-rainy season from November–December 2003.

4. Discussion

The presence of a greater number of tetrasporophytes than carposporophytes, and only a few male or female gametophytes confirm the reports for the family Gelidaceae (Akatsuka, 1986; Santelices, 1988; Servière-Zaragoza and Scrosati, 2002). In this study the number of cystrocarps was influenced by wave exposure. The cystocarps observed were on thalli from the exposed area just after the rainy season, a situation that might be caused by the greater water motion which could increase the success of fertilization by enhancing the ability of the nonmotile spermatia to encounter the trichogyne of the carpogonium.

Plants reproduced throughout the year, a condition which, together with vegetative reproduction, probably accounts for a high percentage cover of this species in the study sites, 16–83% coverage of *G. pusillum* on the shore. The dense stand of algal-forming turf can persist under high stress along the intertidal shore (Hay, 1981; Guiry and Womersley, 1993). Fronds could grow into two directions both as creeping axes and as uprights the former withstands the high wave motion and provides as base for the shorter upright axes such as were found in the wave-exposed area. Although this species is known as a perennial plant, the upright fronds bleached during summer months and when the apical tips became weak, the fronds became shorter and died, decreasing the coverage of the plants two months shortly after. This is similar to the pattern of many other turf-forming red algae (Beach and Smith, 1996; Scrosati and DeWreede, 1998).

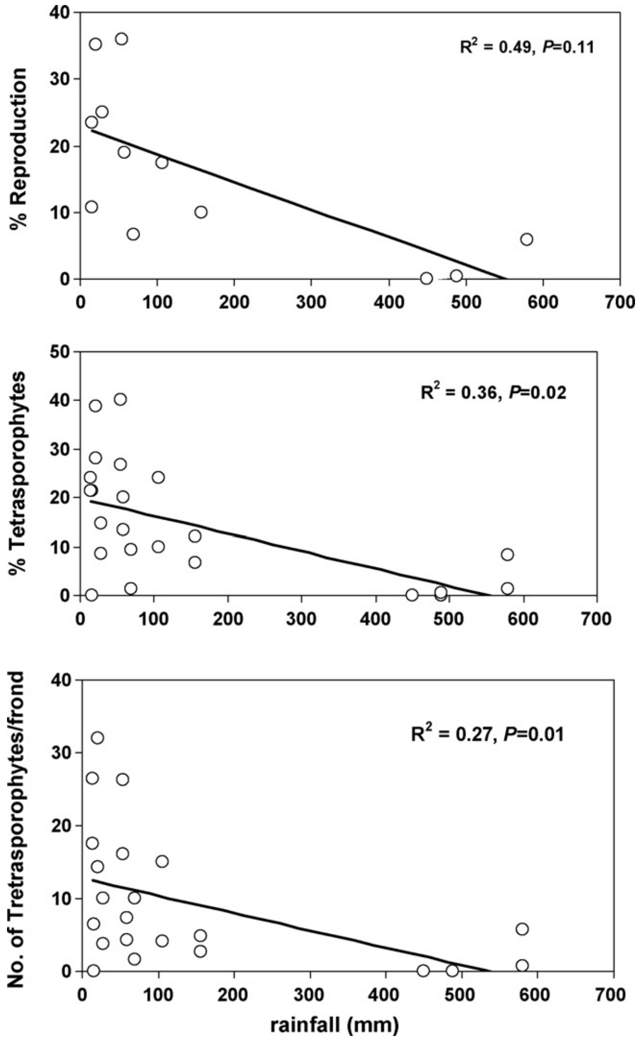

Fig. 4. Significant correlation between rainfall and % reproductive fronds, % tetrasporic fronds and number of tetrasporic sori/frond of *G. pusillum*.

The onset of tetraspore and carpospore production did not reflect a physiological trade-off between resource allocation to vegetative growth and allocation to reproduction as suggested by Harper and Ogden (1970). *G. pusillum* reproduced spores throughout the year, except in November and December, without any decline of length, density or die off. Although known to be perennial, reproduction was not reduced as hypothesized (Bell, 1984a) by the idea that plants reduce allocation to individual growth or general maintenance (Bell, 1984b; Obeso, 2002) in favor of reproductive cell formation or vice versa. It is possible that resources at the site exceed the requirements. Nutrient levels were high throughout the year. The highest were found during the rainy season: NO_3 was 0.12 mg N l^{-1} and PO_4 was 0.024 mg P l^{-1}. High concentrations of nutrients from urban runoff as well as from agriculture and aquaculture around the basin (Panapitukkul et al., 2005; Chevakidagarn, 2006) are well-known.

Rainfall, which decreased the salinity, might be expected to inhibit reproduction. Although increased temperature caused bleaching and later die off, the decline of reproduction might be due to lower salinity. Our salinity results showed great variation between 9 and 26 psu; and salinity was less than 10 psu during the rainy season (unpublished data). A salinity stress lower than 15 psu was reported to reduce growth rate by almost five times in some *Gelidium* spp. (Oliger and Santelices, 1981). This is known to cause a decrease in productivity and reproduction in many red algae and now in *G. pulsillum* as well.

There were no shifts of life phase between seasons and sites in *G. pusillum* as has been observed in *Mazzaella* spp. (Mudge and Scrosati, 2003; Scrosati and Mudge, 2004). A predominance of tetrasporophytes is a common feature in *Gelidium* (Montalva and Santelices, 1981; Carter, 1985; Akatsuka, 1986; Macler and West, 1987; Santelices, 1990; Melo and Neushul, 1993; Sosa et al., 1993). Carmona and Santos (2006) have recently tested the advantages of tetrasporophytes over the gametophytes in *G. sesquipedale* through their ecophysiological performance. They found that there were no significant differences either in the photosynthesis rate, nitrogen uptake, nitrate reductase activity, or biochemical composition of phases, but there was an advantage in vegetative recruitment and spore production. The dominance of tetrasporophytes of *G. sesquipedale* does reflect the success of this turf-forming alga throughout the world.

The G:T ratio of *G. pulsillum* in our study was 1:14; the G:T ratio in *Gelidium* may be as high as 1:20. Abbott (1980) suggested that this might be because of the failure in the viability of tetraspores, which are the sources of gametophytes and/or the enhanced capability of carpospores to produce tetrasporophytes. Although we found some mature red tetraspores and carpospores in our study, newly recruited plants were rarely observed. After release, spores could be washed away or trapped within the turf, hence form new thalli within the patch.

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