# No whirlwind romance: typhoons, temperature and the failure of reproduction in *Caulacanthus okamurae* (Gigartinales, Rhodophyta)

## HAN GIL CHOI[1], KI WAN NAM[1] AND TREVOR A. NORTON[2]

[1] *Department of Marine Biology, Pukyong National University, Nam-gu, Pusan, 608–737, Korea*
[2] *Port Erin Marine Laboratory (School of Biological Sciences, University of Liverpool), Port Erin, Isle of Man IM9 6JA, UK*

The red alga *Caulacanthus okamurae* Yamada occurs commonly on the coasts of South Korea, but reproductive plants have rarely been found in the field. Seasonality of field populations was examined and the temperature responses of growth and reproduction were determined in laboratory cultures. In the field, monthly average temperatures of surface seawater ranged from $12.7 °C \pm 0.73$ (SD) to $21 °C \pm 1.19$. Monthly mean biomass in $25 \times 25$ cm quadrats ($n = 3$) ranged from $11.2 \pm 9.6$ g m$^{-2}$ (SD) to $148.8 \pm 19.2$ g m$^{-2}$ in wet weight with minimal biomass in February 1995 and maximal values in August. In culture, the growth of vegetative plants and germination of tetraspores of *C. okamurae* occurred at temperatures from 13 to 27 °C. Tetrasporangia, gametangia and cystocarps were formed at 19 °C and above, but not at 13 or 16 °C, indicating that reproduction is directly affected by seawater temperature. On the basis of these data, seawater temperature was above the critical temperature for reproduction from August to October (20–21 °C) yet only three plants with tetrasporangial branches were found in the field. In September the biomass of *C. okamurae* declined sharply following severe storm damage. Thus, the absence of reproductive organs in field populations of *C. okamurae* may occur because they inhabit a seasonally stressful habitat, in which typhoon damage removes branches before the water temperature becomes favourable for reproduction.

Key words: biomass, *Caulacanthus okamurae*, Korea, germination, growth, reproduction, seasonality, storm damage, temperature

## Introduction

It is well known that seawater temperature is an important factor influencing growth and reproduction of seaweeds and often determines their geographical distribution (for reviews see Breeman, 1988; Murray & Dixon, 1992; Pakker & Breeman, 1996; Pakker *et al.*, 1996). Seaweeds growing in an unfavourable temperature regime close to their geographical boundary are frequently sterile (Dixon, 1965; Norton & Parkes, 1972; Cullinane *et al.*, 1980; Kain & Norton, 1990; Lüning, 1990; Murray & Dixon, 1992; Orfanidis *et al.*, 1999). Such sterility has been reported for many red algae including *Chondracanthus* (as *Gigartina*) *acicularis* (Guiry & Cunningham, 1984) and *Caulacanthus ustulatus* (Rueness, 1997), both of which maintained their populations by vegetative propagation, and rarely produced reproductive organs even when other environmental conditions seemed favourable to sexual reproduction (Dixon, 1965; Guiry & Cunningham, 1984). For many species, asexual

Correspondence to: H. G. Choi. e-mail: hangilchoi@hotmail.com

perennation is the norm for populations at the limits of their geographical range (Dixon, 1965).

*Caulacanthus okamurae* Yamada (which may be synonymous with *C. ustulatus*; see Rueness & Rueness, 2000) is a red alga that inhabits the upper intertidal zone of exposed rocky shores in Korea, China and Japan, and reaches its northern known limit in Hokkaido (43°06′ N, 144°06′ E; Yamada, 1933). The plants at Hokkaido are completely sterile and here the inshore surface water temperatures are lower than elsewhere in the range of this species. So at first glance this seems to be a typical example of marginal sterility where reproduction has been suppressed by unfavourable temperatures. However, fertile plants of *C. okamurae* have rarely been found in the field even on shores far distant from the geographical boundaries of its distribution (Norris & Wynne, 1968; Searles, 1968; Lee *et al.*, 2001). Cystocarpic and tetrasporangial plants have been recorded only twice in Korea (Lee & Lee, 1981; Lee *et al.*, 2001) and cystocarpic plants only once in Japan (Segi, 1952), although here tetrasporangial plants occur more frequently, but only in the warmer waters in the south (Kamura, 1963). Thus it

seems that factors other than, or additional to, water temperature must be at play.

The aim of our study was to explain the reproductive reluctance of *Caulacanthus okamurae* in order to test the null hypothesis that water temperature is not responsible for the absence of reproduction in this species. In addition the phenology of a natural population of *C. okamurae* not growing at the limits of its range was studied in order to identity other factors that may be influential in reproductive success or failure on the shore, and the effects of temperature on growth and reproduction were also examined in the laboratory.

## Materials and methods

The geographical distribution of *Caulacanthus okamurae* was determined from a search of the literature and the examination of specimens in the herbaria of the Department of Marine Biology, Pukyong National University, Korea and the Department of Biology, Chonju University, Korea.

*Caulacanthus okamurae* occurs in the upper intertidal zone between 2·0 and 2·5 m above lowest astronomical tide (LAT) and usually forms patches of low turf on rocks, shells or barnacles. It also occasionally grows together with *Gelidium pusillum* (Stackhouse) Le Jolis and *Ulva pertusa* Kjellman.

From December 1994 to November 1995 monthly collections of *C. okamurae* were taken from the shore at Cheongsapo near Pusan, Korea (35°09′ N, 129°11′ E). Additional field observations were made at the same locality in 1999. On each occasion, all plants within three randomly placed quadrats (25 × 25 cm) were collected using a scraper. Samples were examined for reproductive status under a stereomicroscope after transportation to the laboratory. The biomass of each sample was measured as wet weight, following removal of surface moisture with paper towel.

Measurements of daily surface seawater temperatures over the experimental period were obtained from the Korea Institute of Ocean Science, which is situated only 2·5 km from the sampling site.

### Laboratory cultures

Plants of *C. okamurae* were collected from Cheongsapo, Pusan, Korea, on 20 April 1995. The plants were transported to the laboratory and cleaned by using a paint brush and rinsing several times with filtered seawater to remove silt and detritus. All plants collected from the field were non-reproductive and were cultured in a flask containing 200 ml of PES medium (Provasoli, 1968). Vegetative tips were repeatedly excised until the culture was unialgal. Stock cultures of vegetative plants were maintained at 16 °C, 14:10 h light:dark (LD) and 60 µmol m$^{-2}$ s$^{-1}$.

Growth and reproduction were studied at five different temperatures (13, 16, 19, 23 and 27 °C). Daylength (14:10 h LD) and irradiance (60 µmol m$^{-2}$ s$^{-1}$) remained constant as these conditions were found to be optimal for growth and tetrasporogenesis in preliminary experiments. Temperature was controlled to within ± 1 °C and light

was provided by four 40 W cool-white fluorescent tubes. The culture medium was changed once a week throughout the experimental period.

### Growth

Plants (0·5 mg wet weight) were cut from stock vegetative thalli and incubated in beakers with 100 ml of medium for 40 days. Five plants were put in each of four replicate beakers at each temperature. All 20 vegetative plants of each treatment were weighed together to an accuracy of 0·01 mg. Surface moisture of the plants was removed with paper towel before weighing the plants. Relative growth rate (RGR) was calculated for each replicate using the equation:

$$\mathrm{RGR} = (\ln W_t - \ln W_0)/t$$

where $W_0$ is the initial wet weight and $W_t$ is the wet weight after $t$ days.

### Reproduction

*Gametangia.* A total of 40 glass slides with sporelings were prepared by inoculating tetraspores which had been released at 23 °C and 60 µmol m$^{-2}$ s$^{-1}$. Four replicate Petri dishes, each containing 50 ml of medium and two slides, were placed in five different temperatures (13, 16, 19, 23 and 27 °C) at 60 µmol m$^{-2}$ s$^{-1}$. Settlement density of spores was about 100 spores cm$^{-2}$. Reproductive status of the young plants was monitored under a stereomicroscope every 5–10 days. Fertility (%) was determined after 65 days by counting gametangial plants and total plants (> 60 per replicate) under a stereomicroscope.

*Cystocarps.* To determine whether fertilization and cystocarp formation were affected directly by low temperatures, tetraspores were cultured at 23 °C, 14:10 h LD and 60 µmol m$^{-2}$ s$^{-1}$ until plants formed gametangia. Female and male plants were then isolated into flasks, each containing 500 ml of PES medium, and incubated at 23 °C for 10 days to ensure that female plants had not been fertilized before they were isolated. Four replicate groups of five female and two male plants (height *c*. 3 cm), were then transferred to both 16 °C and 19 °C. After 2 weeks, the numbers of females bearing cystocarps were determined.

*Tetrasporangia.* Apical fragments (5 mm) were excised from stock vegetative tetrasporangial thalli of *C. okamurae* and were chosen randomly. Twenty Petri dishes each with five apical fragments of *C. okamurae* were prepared and four Petri dishes were allocated to each of the five different temperatures as described above. The plants were monitored every 2 days, for a period of 21 days, to determine whether tetrasporangia had been formed.

### Germination

Tetraspores released at 23 °C and 60 µmol m$^{-2}$ s$^{-1}$ were inoculated onto cover slips in Petri dishes containing 50 ml of medium. Two Petri dishes, each with five cover slips, were placed in each of five incubators at 13, 16, 19, 23 and 27 °C. Germination was recognized under a microscope 10 days after inoculation by the initiation of rhizoid cells. The results were expressed as percentage germination, out of at least 200 spores at each temperature.

### Statistical analysis

Statistical analyses were done using STATISTICA v. 5.0. A one-way ANOVA was used to test the effects of temperature on spore germination, gametangial formation and relative growth rate. When significant differences between means were detected, the Tukey test was applied (Sokal & Rohlf, 1995). Homogeneity of variance was tested using Cochran's test (Underwood, 1997). Where necessary, data were transformed to meet the assumptions of the parametric statistics. For example, gametangial formation and germination were arcsine-transformed.

## Results

### Field observations

Monthly average temperatures of surface seawater based on daily data ranged from $12.7\ ^{\circ}\text{C} \pm 0.73$ (SD) to $21\ ^{\circ}\text{C} \pm 1.19$ and the average temperature over the year was $16.4\ ^{\circ}\text{C}$ (Fig. 1).

Monthly mean biomass (wet weight) of triplicate samples varied substantially from $11.2 \pm 9.6\ \text{g m}^{-2}$ (SD) to $148.8 \pm 19.2\ \text{g m}^{-2}$ during the survey period (Fig. 1). Average biomass increased from February to August and then declined sharply in September with minimal biomass recorded in February 1995. Three plants with tetrasporangial branches were found in September 1995, but no gametangial or cystocarpic plants were found at any time throughout the monitoring period. Further qualitative surveys in 1999 failed to reveal any fertile plants.

### Laboratory cultures

### Growth

Growth of vegetative plants occurred at all the temperatures tested ($13-27\ ^{\circ}\text{C}$). Relative growth rates increased significantly with increasing temperature (ANOVA, $F_{4,15} = 1259.75$, $p < 0.001$) and maximal growth of *C. okamurae* occurred at $23\ ^{\circ}\text{C}$ (Fig. 2). A Tukey test showed that there were significant differences between all temperatures except $23\ ^{\circ}\text{C}$ and $27\ ^{\circ}\text{C}$.

### Reproduction

*Gametangia.* Gametangial plants were first observed in the $27\ ^{\circ}\text{C}$ treatment 45 days after inoculation. Male plants appeared 2–4 days earlier than females. No gametangia were observed in the $13\ ^{\circ}\text{C}$ or $16\ ^{\circ}\text{C}$ treatments even after 65 days, but the percentage of fertile plants increased with temperature between $19\ ^{\circ}\text{C}$ and $27\ ^{\circ}\text{C}$ (Fig. 3). There was a significant difference in development of gametangia between treatments (ANOVA, $F_{4,15} = 201.51$, $p < 0.001$). A Tukey test showed that there were significant differences between all treatments except $13\ ^{\circ}\text{C}$ and $16\ ^{\circ}\text{C}$. Cystocarps appeared 1 week after gametangia.

*Cystocarps.* All female plants produced cystocarps within 2 weeks of being transferred from $23\ ^{\circ}\text{C}$ to $19\ ^{\circ}\text{C}$ and carpospores were released 2–3 days later, but those transferred from $23\ ^{\circ}\text{C}$ to $16\ ^{\circ}\text{C}$ did not produce cystocarps.

*Tetrasporangia.* Tetrasporangia were formed within 3 weeks at 19, 23 and $27\ ^{\circ}\text{C}$, but not at 13 or $16\ ^{\circ}\text{C}$ (Table 1). Release of tetraspores took place 2–5 days after the appearance of tetrasporangial branches. After releasing spores, some tetrasporangial branches degenerated at $27\ ^{\circ}\text{C}$, but not at lower temperatures, where they remained healthy and produced new branches. Immature plants grown at $19\ ^{\circ}\text{C}$ gradually formed tetrasporangia, but those at 13 and $16\ ^{\circ}\text{C}$ did not, even after 4 months.
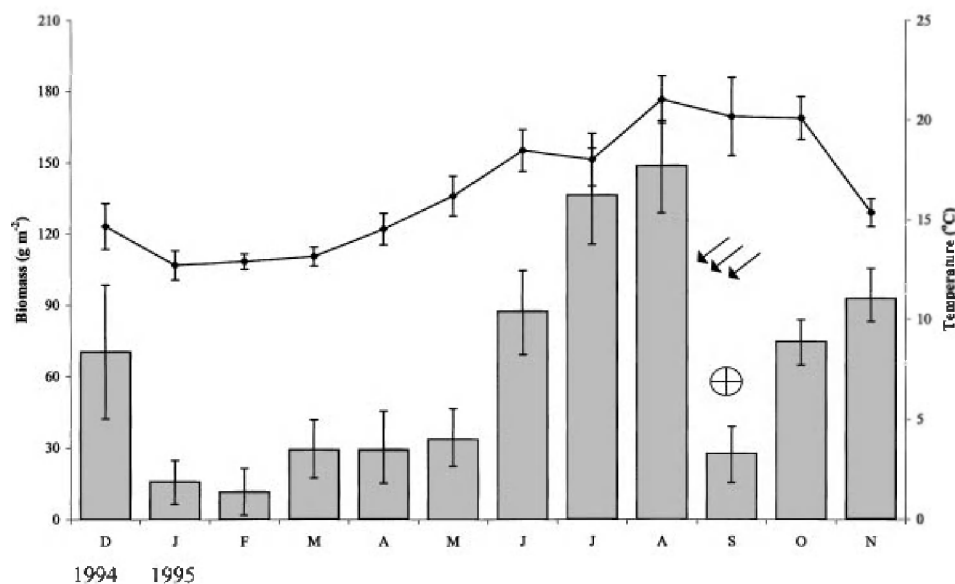


**Fig. 1.** Monthly variations in mean seawater temperature and mean biomass of *Caulacanthus okamurae* at Cheongsapo, Pusan, Korea, from December 1994 to November 1995. Histograms represent mean biomass ($n = 3$). Bars show standard deviations. ($\oplus$) denotes the presence of tetrasporangial plants. Arrows show the incidence of hurricanes.
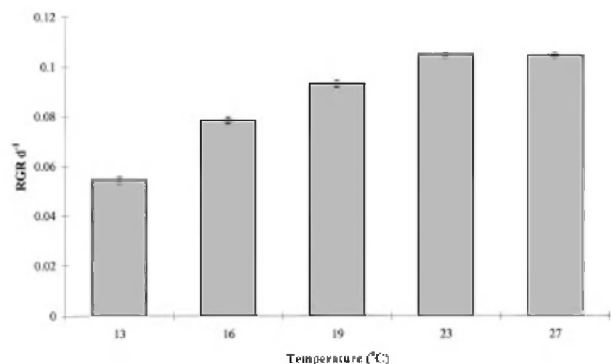
**Fig. 2.** The effect of temperature on relative growth (RGR) rate per day of *Caulacanthus okamurae*. Plants were grown at 14:10 h light:dark (LD) and 60 µmol m$^{-2}$ s$^{-1}$ for 40 days. Bars show 95% confidence intervals ($n = 4$).
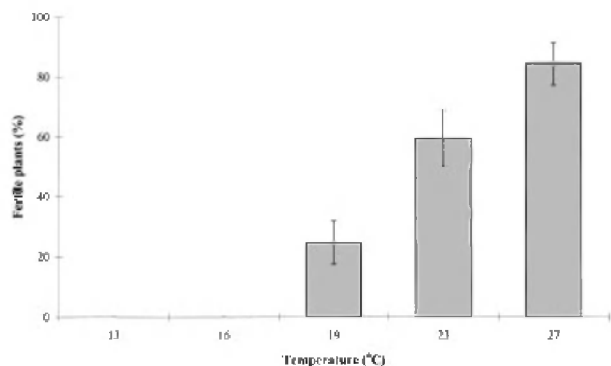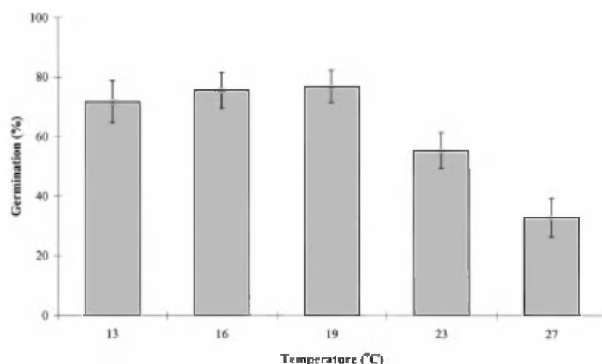


**Fig. 4.** The effect of temperature on the germination of *Caulacanthus okamurae* tetraspores. Plants were cultured for 10 days at 14:10 h LD and 60 µmol m$^{-2}$ s$^{-1}$. Bars show 95% confidence intervals ($n = 10$).



**Fig. 3.** The effect of temperature on gametangial formation in *Caulacanthus okamurae*. Plants were cultured from tetraspores for 65 days at 14:10 h LD and 60 µmol m$^{-2}$ s$^{-1}$. Bars show 95% confidence intervals ($n = 4$).

**Table 1.** Number of plants with tetrasporangial branches at various temperatures after 3 weeks

| Temperature (°C) | Total plants ($n$) | Fertile plants ($n$) | |
|---|---|---|---|
| | | 14 days | 21 days |
| 13 | 20 | 0 | 0 |
| 16 | 20 | 0 | 0 |
| 19 | 20 | 0 | 13 |
| 23 | 20 | 3 | 20 |
| 27 | 20 | 8 | 20 |

Plants were grown at 14:10 h LD and 60 µmol m$^{-2}$ s$^{-1}$. Total plants represent four replicate dishes each containing five plants.

*Germination*

The percentage germination of tetraspores ranged from 32·8% to 77·0%, and was greatest at 19 °C (Fig. 4). Percentage germination of tetraspores was significantly greater at 13 and 16 °C than at 23 and 27 °C (ANOVA, $F_{4,45} = 31·41, p < 0·001$). A Tukey test showed a significant difference between the 19, 23 and 27 °C treatments but not between the 13, 16 and 19 °C treatments.

**Discussion**

Sterile plants of *C. okamurae*, collected from the shore in April 1995, became fertile when grown above 19 °C in culture, but not at 13 °C and 16 °C. Fertile plants were not found in the field population at Cheongsapo, probably because the water temperature at this time of year did not exceed 14·5 °C. In Hokkaido, at the northern boundary of *C. okamurae*'s range, the average seawater temperature in summer is 16–18 °C (Ohno & Largo, 1998) and all the plants are sterile (Yamada, 1933; Searles, 1968). Thus the reproduction of *C. okamurae* would also be limited by water temperature close to its geographical limits.

In our study area, however, seawater temperature was above the critical value of around 19 °C from August to October (20–21 °C). Such temperatures should have encouraged fertility in plants of *C. okamurae*, but their biomass decreased in September 1995 and, except for three records of tetrasporangial branches, the vast majority of the plants remained sterile.

Even when the water temperatures became favourable, *C. okamurae* had no chance to become fertile, because of storm damage to the plants. Three typhoons (named Janis, Oscar and Ryan) passed through this area during late August and September as they do every summer (Ryu, 1983; Ryu *et al.*, 1983; Lee *et al.*, 1994; Lee & Lee, 1998). In 1995 the typhoons dislodged many plants of *C. okamurae* and stripped off all the potentially fertile tissue from the remainder. The survivors subsequently regenerated to make good the damage, and therefore biomass increased progressively between September and October. Exactly the same pattern was again apparent in 1999. Such events are almost certainly

not just a local effect, for typhoons are commonplace throughout the entire range of *C. okamurae*. The storms originate in the tropics and veer northwest skirting the coasts of Korea, China and Japan. Therefore, although sexual reproduction of *C. okamurae* in the field could be curbed by low seawater temperatures, storms remove almost all the tissue before it has matured or achieved the equivalent of a 'ripeness to flower'. Thus what at first sight seems to be a typical example of temperature-controlled sterility close to the geographical limits of the species is, in reality, largely a consequence of seasonal storm damage.

Growth and reproduction are sometimes seen as conflicting processes that compete for the same resources within the plant (Lovett Doust & Lovett Doust, 1988; Silvertown & Lovett Doust, 1993), and seaweeds are no exception (Norton, 1977; De Wreede & Klinger, 1988; Mathieson & Guo, 1992). Gardeners are aware that 'growth follows the knife'. In other words, hard pruning stimulates vegetative growth, but not flowering. Similarly in *Caulacanthus* damage stimulates a burst of regenerative growth to restore the devastated vegetative stands. In any case, for *C. okamurae* the resources for both processes are probably more limited than for most seaweeds because it lives at the upper edge of the inhabitable region of the shore (Kang, 1966; Lee & Lee, 1981). This stressful habitat reduces the resources available, because of intermittent access to nutrients and the frequent interruptions of photosynthesis caused by desiccation when emersed. Hence, following a major setback such as a devastating storm there may not be sufficient energy and resources left over for both growth and reproduction.

Plants that live near to their physiological limits either locally or geographically are not well placed to recover from disasters and perhaps the ideal habit to adopt is to form a turf. Plants in turfs are closely packed and low-lying and thereby less vulnerable to desiccation and wave action. Thus turf-dwellers are the most, indeed sometimes the only, successful seaweeds inhabiting the intertidal zone in the tropics, and the same genera of red algae (including *Caulacanthus*) are found in turfs world wide (Kain & Norton, 1990). Like *Caulacanthus* they are adept at vegetative proliferation from their spreading basal branches, which allows them to cope with annual die back or wave-induced pruning. When the going gets tough, the survivors creep.

We suggest that damage-induced curtailment of reproduction may occur in any area subject to the severe storms (hurricanes, cyclones, typhoons and monsoons) that are a feature of many tropical shores. They devastate the littoral vegetation (Umaheswara Rao & Sreeramulu, 1964; Doty, 1971; Murthy *et al.*, 1978), removing some plants

and pruning back surviving plants to the holdfast or a vegetative tuft (Svedelius, 1906; Underwood, 1998). Indeed such pruning may even be essential for the survival of species that endure habitats with high wave intensity (Santos, 1994).

The timing is of course critical; even severe pruning after the plants have reproduced is of small importance, but the removal of all the larger branches *before* they reach maturity means that the plants are dependent upon vegetative perennation, which serves for survival but not for dispersal and extending their geographical range.

Furthermore, with the growing frequency and severity of El Niño Southern Oscillation events, which often subject plants to the multiple threat of storms and aberrant temperatures, the incidence of reproductive curtailment may well increase.

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