



## Seasonal occurrence and reproduction of *Hypnea charoides* (Rhodophyta) in Tung Ping Chau, N.T., Hong Kong SAR, China

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**Key words:** Hong Kong, Tung Ping Chau, *Hypnea charoides*, reproductive seasonality, algal population dynamics

### Abstract

Seasonal occurrence and reproduction in populations of *Hypnea charoides* Lamouroux were investigated along two coastal shores, A Ma Wan and Lung Lok Shui, in Tung Ping Chau, N. T., Hong Kong SAR, China, from 1996 to 1999. Annual growth of these populations was initiated in early winter (November–December) and ended in late spring (April–May). Mean length of *H. charoides* in A Ma Wan was significantly negatively correlated with photoperiod ( $r = -0.359$ ,  $n = 38$ ,  $p < 0.05$ ) and seawater temperature ( $r = -0.669$ ,  $n = 38$ ,  $p < 0.05$ ). Vegetative plants were dominant but relatively high abundance in tetrasporic plants was observed at the end of each growing season. Percentage occurrence of tetrasporic plants was significantly positively correlated with seawater temperature in samples collected at  $-1$  m CD ( $r = 0.635$ ,  $n = 19$ ,  $p < 0.05$ ),  $-2$  m CD ( $r = 0.690$ ,  $n = 13$ ,  $p < 0.05$ ) and from drifted populations ( $r = 0.705$ ,  $n = 17$ ,  $p < 0.05$ ), suggesting that increase in seawater temperature might induce tetrasporogenesis of *H. charoides* in A Ma Wan. Plants in Lung Lok Shui were mostly vegetative but 100% tetrasporic samples were collected at  $-1$  m CD during an unusual growth period in October 1998. High abundance of tetrasporic plants was also observed at a depth of  $-10$  m CD on 9 April 1998 (97.5%) and 22-April 1999 (90%). Significantly negative correlation was found in percentage occurrence of vegetative plants at  $-10$  m CD with photoperiod ( $r = -0.553$ ,  $n = 14$ ,  $p < 0.05$ ) and seawater temperature ( $r = -0.855$ ,  $n = 8$ ,  $p < 0.05$ ). Dominance of vegetative and tetrasporic plants and rarity of cystocarpic plants in both A Ma Wan and Lung Lok Shui suggested that the life span of *H. charoides* might be very short and/or majority of the plants underwent apomeiosis to complete their life cycles in Tung Ping Chau.

### Introduction

Algae and seagrasses play very important roles in structuring the marine community as they are the dominant primary producers. Their population dynamics greatly affect those of all the other organisms. However, little attention has been paid in this aspect in algal vegetation studies. For population dynamic analysis, seasonal growth and reproduction have been of considerable interest to many phycologists. They are known to be closely tied to changes in different environmental conditions and the availability of resources. Among these parameters, light and temperature are the physical factors which have been most widely investigated with respect to the growth and reproductive responses

of marine algae (Burns & Mathieson, 1972a,b; Adey, 1973; Mathieson & Burns, 1975; De Wreede, 1976; Kapraun, 1978; Prince & O'Neal, 1979; Schoschina et al., 1996; Voskoboinikov et al., 1996; Zamorano & Westermeier, 1996; Vásquez et al., 1998). This is particularly so in many red algal species where irradiance and photoperiod have received the greatest attention as factors that control their reproductive processes. Out of the 46 red algae examined by various authors, 38 species showed that the development or release of their reproductive structures was a type of photoperiodic responses (see review by Murray & Dixon, 1992). Many of these responses were also associated with changes in temperature and some, in nutrient levels. This indicates that temperature or nutrient concentrations could

\*<sup>1</sup> Strong seasonality in growth and reproduction (tetraspore formation).  
\*<sup>2</sup> Short life cycle (history): an adaptation to cope with the preference of this species of seaweed for the cooler winter waters and shorter days (shorter duration of sunlight hours)

modify or block the inductive effects of photoperiod. Ranges of temperature, irradiance, or photoperiod can therefore serve as thresholds that trigger growth or reproduction in many algae.

Many marine red algae have a triphasic life cycle characterized by a diploid generation of tetrasporophyte, a haploid generation of gametophyte and a diploid generation of carposporophyte that develops on the female gametophyte. Natural populations of these marine algae, however, do not always have equal proportions of these generations at any one time. The dominance of one generation (phase) over the other is commonly reported. For example, gametophyte was found to be the dominant generation in populations of *Gigartina skottsbergii* Setchell et Gardner (Piriz, 1996; Zamorano & Westermeier, 1996), whereas tetrasporophyte was dominant in populations of *Rhodymenia howeana* Dawson (Vásquez et al., 1998). Several hypotheses have been advanced to explain the significance of these differences in phase dominance as part of the life history strategy of these algae. Environmental factors, such as temperature, photoperiod, irradiance, have also been shown to affect phase dominance in different seasons within a year (Dyck & De Wreede, 1995; Piriz, 1996; see also review by Murray & Dixon, 1992).

Hong Kong (22° 12' N; 114° 6' E) is located in the southeastern part of China. It experiences a subtropical, highly seasonal monsoonal climate with annual die-off of the intertidal epibiota (Williams, 1993). The weather in summer (June–August) is hot (mean air temperature = 30°C) and wet while that in winter (December–February) is cool (mean air temperature = 17°C) and dry (Kennish et al., 1996; see also Hodgkiss, 1984). This characteristic monsoonal climate also brings about marked differences in the seawater conditions (more particularly in temperature). Being an important component of many coastal communities, most intertidal marine algae in Hong Kong display clear seasonal patterns in which they start to grow in winter and disappear in summer (Hodgkiss & Lee, 1983). Their diversity, abundance or zonation patterns were strongly influenced by the monsoonal nature of Hong Kong's climate (Kennish et al., 1996; Kaehler & Williams, 1996). Strong sunlight was suggested to be the major factor responsible for their seasonal pattern of distribution (Hodgkiss, 1984). Nonetheless, distribution patterns of subtidal algal populations have never been studied in Hong Kong except for some anecdotal observations. In Tung Ping Chau, an island in the northeastern part of Hong Kong, for

example, subtidal populations dominated by *Hypnea charoides* Lamouroux also show a seasonal pattern in both their occurrence and reproduction. However, details of this seasonal pattern are not known, especially with respect to the occurrence and abundance of the different reproductive stages (phases).

This study investigated the seasonal growth and reproduction of *H. charoides* in Tung Ping Chau with an attempt to relate these seasonal patterns with the variations in photoperiod and seawater conditions, e.g. temperature and nutrient concentrations. This is the first study of its kind in Hong Kong waters.

## Materials and methods

### Study site

Field experiments were carried out along the rocky shores of A Ma Wan and Lung Lok Shui in Tung Ping Chau, Hong Kong (Fig. 1). A Ma Wan, which is facing the northeast, is a more sheltered area, while Lung Lok Shui, located on the southwest side of the island, is subjected to strong waves generated by the SE monsoon. In winter, a number of algal species grow densely on the siltstone substratum, which forms a series of slightly inclined terraces (15° to 20°) lying perpendicularly to the shore, at a depth of -1 to -3 m CD (Chart Datum) in A Ma Wan. These marine algae include *Colpomenia sinuosa* (Roth) Derbes & Solier, *Dictyota* spp., *Enteromorpha* spp., *Galaxaura fruticulosa* Kjellman, *Hypnea* spp., *Padina arborescens* Holmes, *P. australis* Hauck, *Sargassum* spp. and *Ulva* spp., with *Hypnea charoides* being one of the most dominant red algal species observed. Areas beyond -3 m CD are dominated by coral communities. In Lung Lok Shui, similar inclined terraces (15° to 20°) are also found, but in contrast to A Ma Wan, *Sargassum* spp. are the most dominant, canopy-forming species growing on these terraces. Compared with A Ma Wan, marine algae in Lung Lok Shui are far more dominant than corals, growing from -1 to -10 m CD.

### Populations of *Hypnea charoides*

Individuals of *Hypnea charoides* are either loosely attached on the rocky substratum forming clumps or are entangled with other marine algae (e.g. *Sargassum* spp.). Many of them, however, are easily swept away by waves and thus become drifted in the water column. In A Ma Wan, comparatively, more attached and drifted individuals are observed. An attached population

\*1 climate of Hk is subtropical seasonal monsoonal with hot wet summer and cool, dry winter

length of day

The main topic for study!

= new science!

\*2

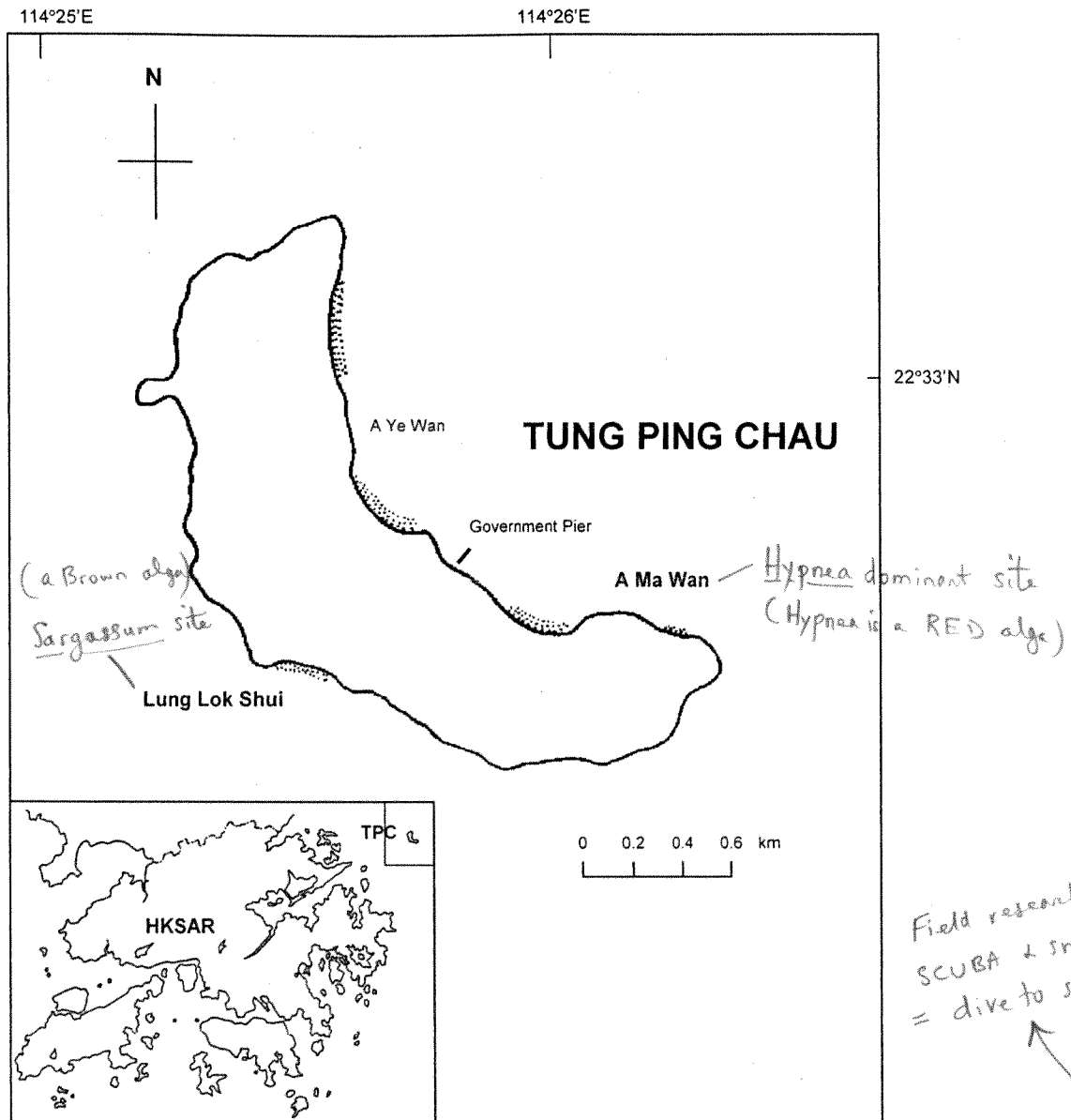


Figure 1. Map of Tung Ping Chau, showing the locations of A Ma Wan and Lung Lok Shui. The location of Tung Ping Chau (TPC) is shown in the insert map of Hong Kong Special Administrative Region (HKSAR).

of *H. charoides* is found on the inclined terraces at  $-1$  m CD while another grows on the corals (alive or dead) at  $-2$  to  $-3$  m CD. Drifting individuals are mostly found at a depth of  $-2$  to  $-3$  m CD. In Lung Lok Shui, most of the clumps are found entangled with the holdfast of *Sargassum* spp. on the terraces at  $-1$  to  $-3$  m CD while a much deeper population was observed at a depth of  $-10$  m CD.

#### Measurement of plant length

Measurement of plant length and sample collection of *Hypnea charoides* were carried out by SCUBA or by snorkeling in both A Ma Wan and Lung Lok Shui. One hundred individuals (clumps) were haphazardly selected and measured at a depth of  $-1$  to  $-2$  m CD every two weeks from January 1997 to June 1999 in each site. Plant length was measured from the base to the tip of each clump of *H. charoides*. Due to typhoons or strong monsoon, field trips were sometimes interrupted (especially to Lung Lok Shui). Therefore, *in situ*

✓ \* haphazard sampling: V. good and more honest and meaningful than (so-called) random sampling!

length measurement could not be carried out regularly at exactly biweekly intervals and at times, had to be delayed for one or two weeks. All the plants measured in A Ma Wan were attached individuals while those in Lung Lok Shui were individuals entangled with the holdfasts of *Sargassum* spp.

#### Examination of reproductive structures

To examine the reproductive structures of *Hypnea charoides*, samples were collected at approximately biweekly intervals during the growing seasons from January 1996 to June 1999. At each sampling in A Ma Wan, 30 individuals (clumps) were haphazardly collected from the population attached on the siltstone substratum at a depth of -1 m CD and another 30 were from the population attached on corals at depths of -2 to -3 m CD. Additional drifting samples (30 individuals at each sampling) within the water column of -2 to -3 m CD were also collected. In 1999, an extra 30 attached samples were collected approximately biweekly (February–April) at a depth of -5 m CD for further examination. In Lung Lok Shui, 30 drifting individuals entangled with *Sargassum* spp. (fronds or holdfasts) were collected at depths of -1 to -2 m CD. Starting from April 1998, additional samples (30 individuals at each sampling) were collected from a depth of -10 m CD. All the plants collected were taken back to the laboratory and examined under the microscope for the presence or absence of reproductive structures (cystocarps vs. tetrasporangia). Search for male plants was also attempted. The occurrence of different reproductive stages (phases) was expressed as a percentage of the number of cystocarpic, tetrasporic or vegetative plants over the total number of plants observed.

#### Environmental parameters

Information on photoperiod over the sampling period was obtained based on the sunrise and sunset data from the Hong Kong Observatory. Seawater temperature was recorded by temperature probes (Minilog TP, Vemco Inc., Halifax, Canada) in both A Ma Wan and Lung Lok Shui over the study period. These probes were set to record the bottom temperature every 30 min and were retrieved for replacement approximately every other month. In A Ma Wan, the temperature probe was placed at a depth (-1 to -2 m CD) in between the -1 m CD and -2 to -3 m CD populations. There was no significant difference in the seawater temperature between -1 m and -3 m CD.

Hence, only one set of temperature data was collected. In Lung Lok Shui, three temperature probes were placed, respectively, at depths of -1 m CD, -2 to -3 m CD and -10 m CD. However, due to strong waves and possible human interferences, temperature probes at -1 m CD were frequently lost. So, only data recorded at -2 to -3 m CD and -10 m CD were available. For nutrient analysis, three water samples (mostly surface water) were collected from A Ma Wan and Lung Lok Shui at approximately bi-weekly intervals. Concentrations of ammonium ions, nitrites, nitrates and phosphates were determined by an autoanalyzer in the laboratory using the standard methods prescribed by the American Public Health Association (APHA, 1995).

#### Statistical analysis

Pearson Product Moment Correlation (SigmaStat, Jandel Scientific Software) was used to correlate the patterns of change in mean plant length and percentage occurrence of reproductive phases with variations in the environmental parameters investigated.

## Results

#### Seasonal occurrence and growth of *Hypnea charoides*

Populations of *Hypnea charoides* in A Ma Wan were observed from January to May in 1997, from January to April in 1998 and from December 1998 to May in 1999 (Fig. 2). Mean plant length ( $\pm$ SD) was first measured in January 1997. It reached its maxima on 16 February 1997 ( $17.0 \pm 9.5$  cm), 11 April 1998 ( $11.7 \pm 6.8$  cm) and 21 March 1999 ( $14.0 \pm 4.0$  cm) and minima on 8 March 1997 ( $10.6 \pm 4.5$  cm), 24 January 1998 ( $4.8 \pm 2.0$  cm) and 11 May 1999 ( $4.1 \pm 1.3$  cm) respectively in the three growing seasons from 1996 to 1999 (Fig. 2). The population usually appeared as creeping thalli or as very short branches at the start or the end of each growing season.

In Lung Lok Shui, *H. charoides* normally appeared within the same period as in A Ma Wan, from January to May in 1997, January to April in 1998 and from January to April in 1999 (Fig. 2). However, many individuals were also observed from July to December in 1998 during an unusual bloom. Plant length measurement started in January 1997. The maximum values were  $12.8 \pm 6.1$  cm on 3 May 1997,  $10.0 \pm 5.7$  cm on 22 April 1998 and  $20.1 \pm 6.1$  cm on 22 April 1999

\*3 = x(3) sets of winter data (V. good)

A nice seasonal pattern : well done Corsica !!

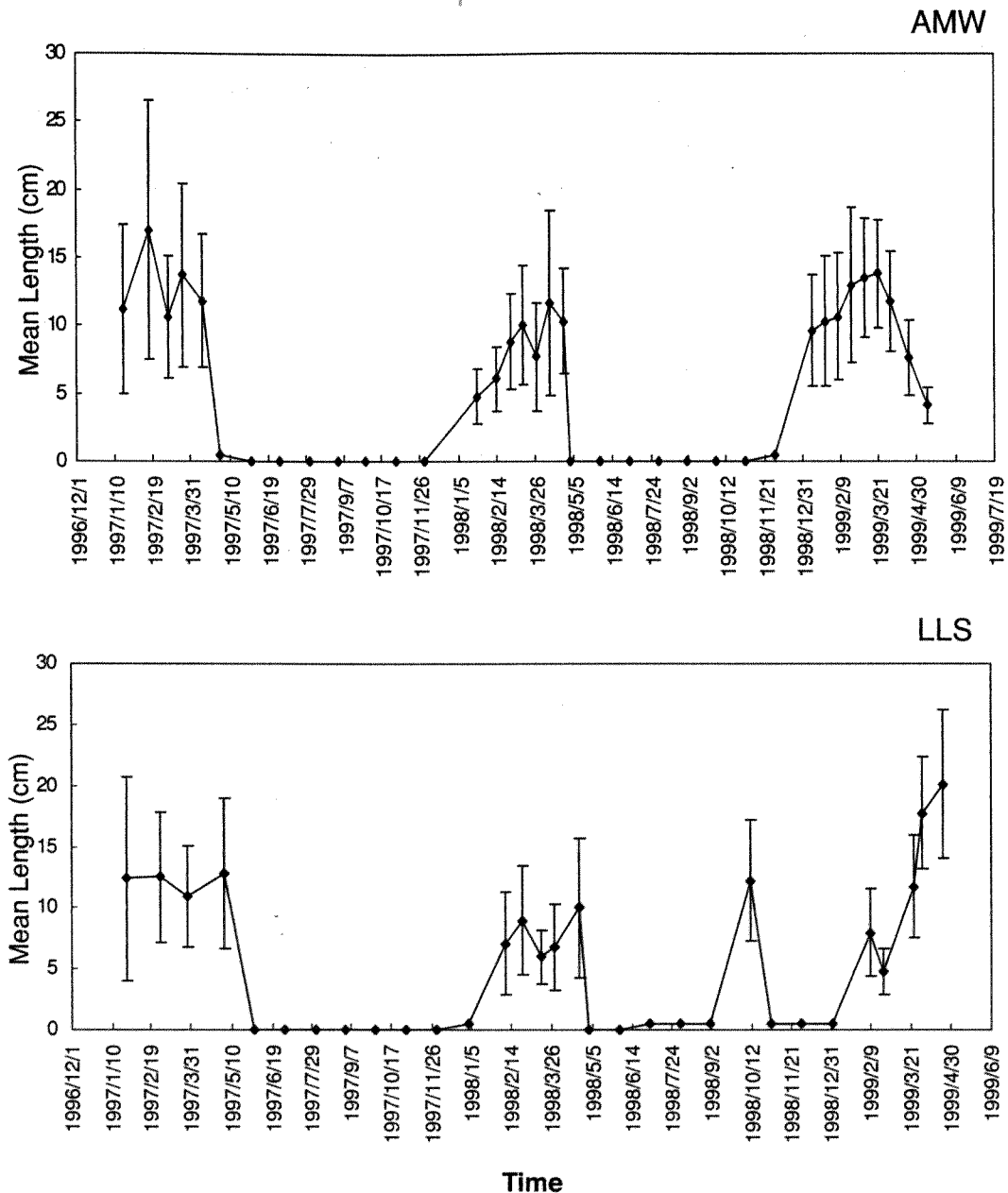


Figure 2. Variation in mean length (cm  $\pm$  SD) of *Hypnea charoides* ( $n = 100$ ) at  $-1$  to  $-2$  m CD in A Ma Wan (AMW) and Lung Lok Shui (LLS) from January 1997 to June 1999.

while the minimum values were  $10.9 \pm 4.1$  cm on 28 March 1997,  $6.0 \pm 2.2$  cm on 16 March 1998 and  $4.7 \pm 1.9$  cm on 23 February 1999 in the three growing seasons from 1997 to 1999 (Fig. 2).

In July 1998, the population of *H. charoides* in Lung Lok Shui appeared as short branches entangled around the bases of *Sargassum* spp. This growth period was much earlier than what was normally observed. At the end of September, plants were observed to have two growth forms: prostrate and erect. The

prostrate parts appeared like a vegetative mat adhering onto the rocky substratum whereas the erect parts were long and bushy. Both of them exhibited healthy greenish red in coloration. They grew so rapidly and covered almost the whole area that was normally dominated by *Sargassum* spp. at that period of time. Measurement was done on the erect plants only once on 11 October 1998 ( $12.2 \pm 4.9$  cm) as all these plants disappeared during the following visit to Lung Lok Shui in Novem-

ber 1998. Only short creeping branches were observed thereafter (November 1998 to January 1999).

### *Reproductive seasonality*

During the period from 1996 to 1999, the  $-1$  m CD attached population of *Hypnea charoides* in A Ma Wan appeared in winter and early spring and disappeared completely in the summer (Fig. 3). All the plants observed from December 1996 to February 1997 were vegetative. Tetrasporic plants were first observed on 23 March 1997 and 15.9% of the plants were tetrasporic. This percentage occurrence increased to 50% on 13 April 1997. The next growing season (starting from January 1998) also showed dominance of vegetative plants and 13.3% of the plants were tetrasporic on 11 April 1998. This percentage increased to 60% on 25 April 1998. Cystocarpic plants were rarely seen and found only on 13 December 1998 (6.7%). When compared with the previous two growing seasons, the percentage occurrence of tetrasporic plants was relatively low during the growth period in 1999, with a maximum of 30% recorded on 3 April 1999.

Drifted and attached samples at  $-2$  to  $-3$  m CD were collected for examination starting from 1997 and 1998 respectively (Fig. 4). Drifted samples were first collected in March 1997 and majority of them were vegetative. Percentage occurrence of tetrasporic plants increased from 3.3% (23 March) to 56.7% (13 April) in 1997 and cystocarpic plants were only recorded on 23 March (3.3%). In 1998, no cystocarpic plants were observed and tetrasporic plants were only found in April, with an increase from 60% (11 April) to 82.8% (25 April). However, cystocarpic plants occurred quite frequently in the growing season from December 1998 to March 1999. In spite of this, the percentage occurrence of cystocarpic plants remained very low, ranging from 3.3% on 21 February 1999 to 8.3% on 13 December 1998. Similarly, tetrasporic plants were found in all the samples collected in the second growing season, ranging from 3.3% on 21 February 1999 to 58.3% on 13 December 1998.

For attached samples at  $-2$  to  $-3$  m CD, majority of the plants were vegetative (Fig. 4). A few cystocarpic plants were observed on 3 February (3.3%) and 25 April (6.5%) in 1998. Tetrasporic plants were only found in April 1998 with a maximum percentage of 90% on 25 April. In the second growing season from December 1998 to April 1999, however, they were present in all the samples collected, ranging from 3.3%

on both 7 February and 7 March 1999 to 50% on 3 April 1999.

All the plants (100%) collected at a depth of  $-5$  m CD in 1999 from A Ma Wan were vegetative in February. This percentage occurrence dropped to 6.7% on 3 April when majority (83.3%) of the plants became tetrasporic. Only few cystocarpic plants (10%) were observed on 3 April 1999.

In Lung Lok Shui, the population of *H. charoides* at  $-1$  to  $-2$  m CD appeared in January and disappeared in May 1997 (Fig. 5). Majority of the plants were vegetative and 23.3% of them were tetrasporic on 29 March 1997. This percentage increased to 46.7% on 3 May 1997. In 1998, all the plants (100%) observed in February and March were vegetative but 80% of them were tetrasporic on 22 April 1998. In July 1998, when some individuals reappeared apparently earlier than normal as small clumps, all of them (100%) were vegetative. In September, however, they grew very quickly and 41.7% of the plants became tetrasporic. By October, all of them (100%) were tetrasporic. After this period, there were only creeping parts left behind. Tetrasporic plants were observed again in the following January 1999 (23.3% on 3 January) and this percentage occurrence rose to 66.7% on 22 April 1999. No cystocarpic plants were found in Lung Lok Shui during the whole study period.

Samples of *H. charoides* were first collected at a depth of  $-10$  m CD in April 1998 and most of the plants were tetrasporic (97.5% on 9 April). In the following growing season in December 1998, 30% of the plants were tetrasporic and this percentage increased to 90% on 22 April 1999. Majority of the plants remained vegetative in January and February in 1999.

### *Other observations*

Among all the individuals of *Hypnea charoides* examined, the presence of cystocarps and tetrasporangia on the same branch was occasionally observed. The first one was found in Lung Lok Shui on 3 May 1997 and another one among the drifted samples in A Ma Wan on 25 April 1998. This phenomenon was not common during the whole study period. Of hundreds of plants observed, only two individuals were found to bear both of these structures.

Although attempts were made to look for male plants, they were not successful.

\*<sup>1</sup> Impressive: a very rapid reproductive phase! \*<sup>2</sup> *Hypnea* was only around for ~5 months per year.

\*<sup>2</sup>

interesting!

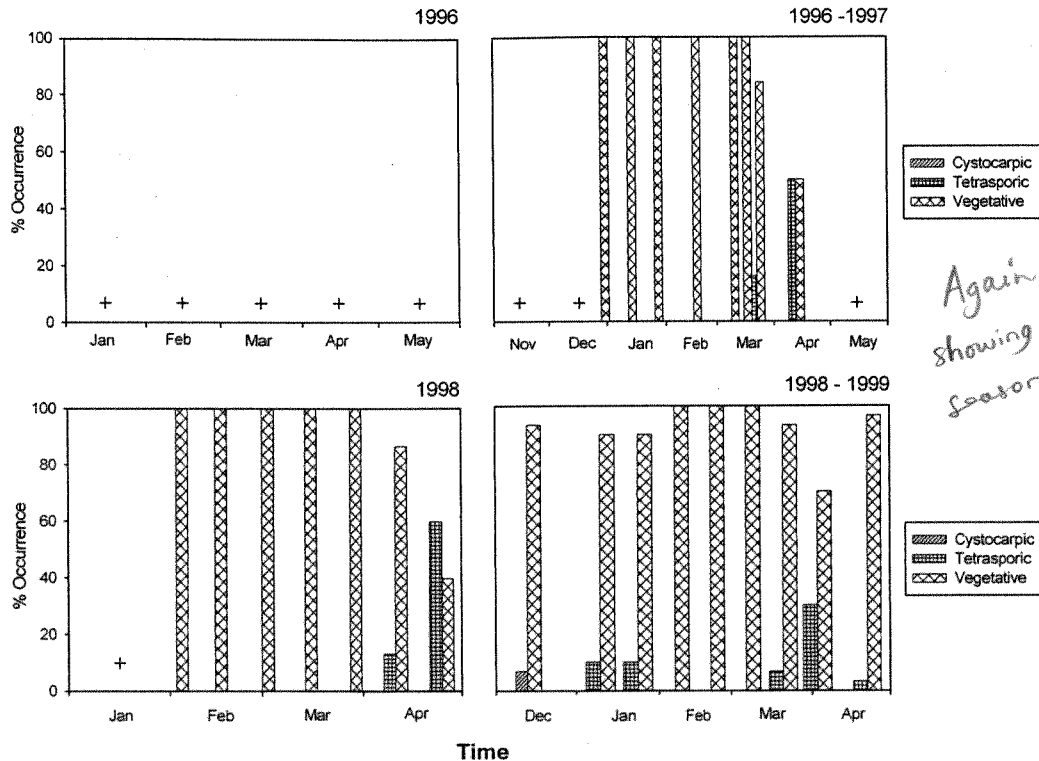


Figure 3. Seasonal occurrence and percentage of reproductive phases in attached population of *Hypnea charoides* ( $n = 30$ ) at  $-1$  m CD in A Ma Wan from January 1996 to June 1999. Only those months when *H. charoides* was present are shown. "+" = months when *H. charoides* was present, but percentage of reproductive phases was not estimated.

#### Environmental parameters

From January 1996 to June 1999, the mean monthly photoperiod was recorded to be the longest in July (13.5:10.5h L:D), while the shortest was in December (10.75:13.25h L:D) in 1996, 1997 and 1998 (Fig. 6).

Mean monthly water temperature was calculated as an average of all the temperatures recorded at 30 min interval within a month by the temperature probe. In A Ma Wan, the mean temperature of seawater at  $-1$  to  $-2$  m CD varied from a maximum of  $29.5^{\circ}\text{C}$  in August 1998 to a minimum of  $16.0^{\circ}\text{C}$  in February 1996 (Fig. 6). Slight fluctuations were observed during 1997 and the overall mean values were relatively lower than those of the other study years. In Lung Lok Shui, mean temperature at  $-2$  to  $-3$  m CD varied from a maximum of  $29.7^{\circ}\text{C}$  in August 1998 to a minimum of  $16.7^{\circ}\text{C}$  in February 1998 during the period from January 1998 to June 1999 (Fig. 6). While at  $-10$  m CD (measured only from December 1998 to June 1999), mean seawater temperature decreased from  $19.5^{\circ}\text{C}$  in December 1998 to a minimum of  $17.9^{\circ}\text{C}$  in January and February in 1999 and rose to  $26.7^{\circ}\text{C}$  in June 1999.

Variations in the concentrations of ammonium ions, nitrites, nitrates and phosphates in seawater samples collected from A Ma Wan and Lung Lok Shui during the study period (August 1996 to June 1999) were also recorded. In A Ma Wan, concentrations of ammonium ions, nitrates and phosphates did not fluctuate (mostly remained at a level below  $1\ \mu\text{M l}^{-1}$ ) except a very sharp peak ( $21.5\ \mu\text{M l}^{-1}$ ) was recorded on 10-May 1999 for ammonium ions. Similarly, nitrate concentration remained steady, with values around or below  $1\ \mu\text{M l}^{-1}$ , but a sharp peak ( $22.3\ \mu\text{M l}^{-1}$ ) was also recorded on 10-May 1999. While for phosphates, concentration rose from  $0.4\ \mu\text{M l}^{-1}$  (24-September 1998) to a level higher than  $3\ \mu\text{M l}^{-1}$  (from November 1998 to April 1999) and a maximum of  $5.1\ \mu\text{M l}^{-1}$  was reached on 16 June in 1999.

Similar results were recorded in Lung Lok Shui, except that a sharp peak ( $14.5\ \mu\text{M l}^{-1}$ ) was observed in the concentration of nitrites on 6 October 1996. For all the other periods of sampling, nitrite concentration remained around or below  $1\ \mu\text{M l}^{-1}$ . For the other three nutrients, fluctuations occurred starting from November 1998. Concentrations of both ammonium

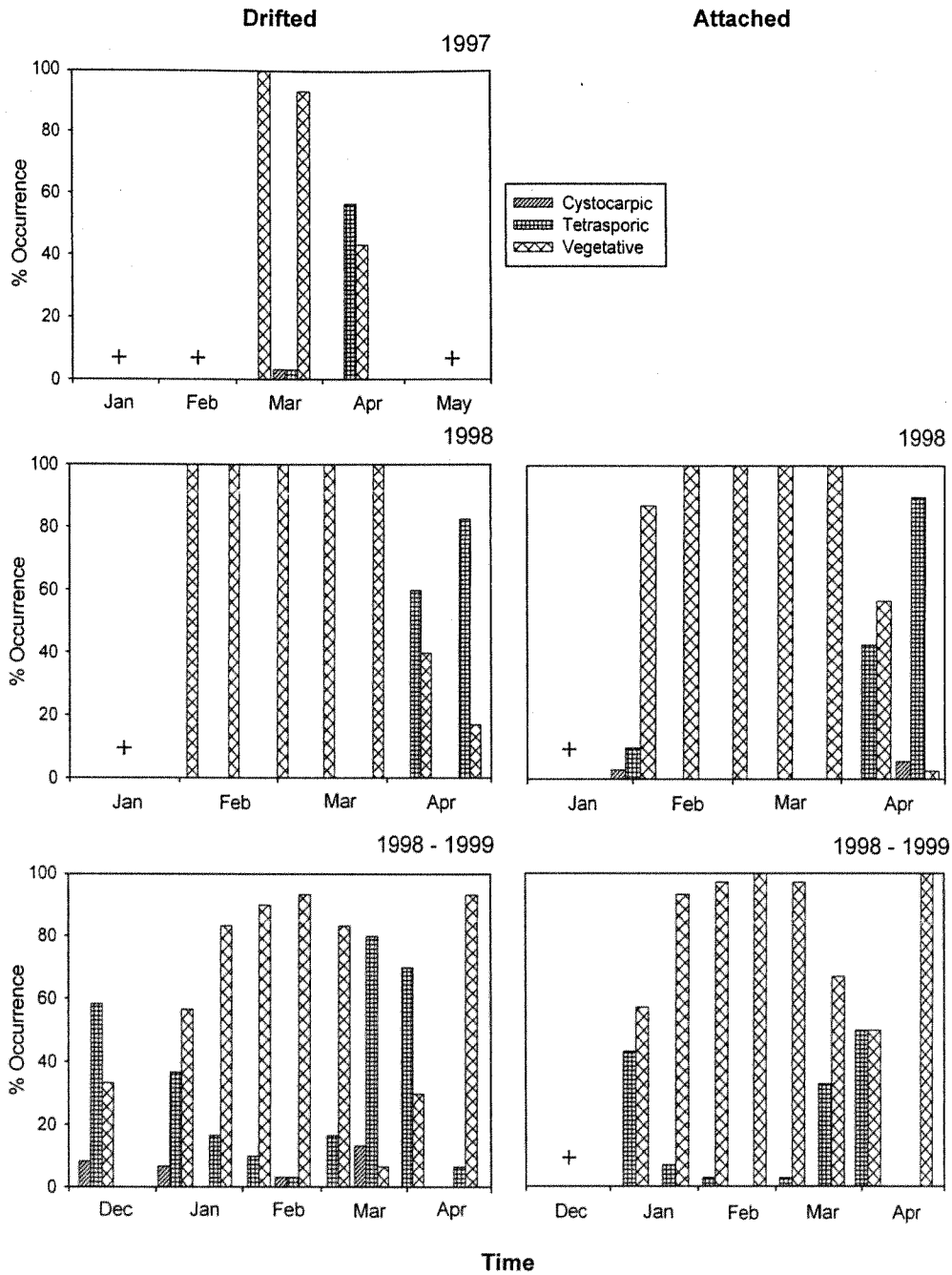


Figure 4. Seasonal occurrence and percentage of reproductive phases in drifted and attached populations of *Hypnea charoides* ( $n = 30$ ) at  $-2$  to  $-3$  m CD in A Ma Wan from January 1997 to June 1999. Only those months when *H. charoides* was present are shown. "+" = months when *H. charoides* was present, but percentage of reproductive phases was not estimated.

ions and phosphates varied from  $1 \mu\text{M l}^{-1}$  to  $3 \mu\text{M l}^{-1}$  in 1999. While for nitrates, three peaks were recorded on 10 January ( $7.9 \mu\text{M l}^{-1}$ ), 7 February ( $8.7 \mu\text{M l}^{-1}$ ) and 30 May ( $10.8 \mu\text{M l}^{-1}$ ) in 1999.

*Statistical analysis*

In A Ma Wan, the mean length of *Hypnea charoides* was significantly negatively correlated with photoperiod ( $r = -0.359, n = 38, p < 0.05$ ) and seawater temperature ( $r = -0.669, n = 38, p < 0.05$ ) but was not significantly correlated with any nutrient concentration in seawater. No correlation analysis

i.e. growth of this Red alga species was max in winter (cooler water & shorter days).



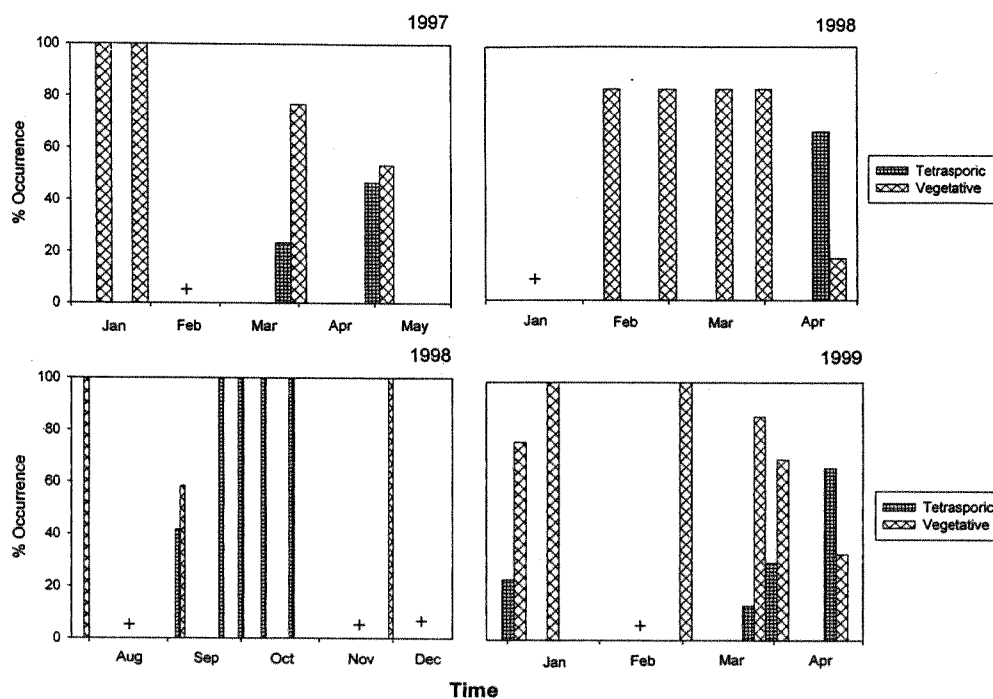


Figure 5. Seasonal occurrence and percentage of reproductive phases in attached population of *Hypnea charoides* ( $n = 30$ ) at  $-1$  to  $-2$  m CD in Lung Lok Shui from January 1997 to June 1999. Only those months when *H. charoides* was present are shown. "+" = months when *H. charoides* was present, but percentage of reproductive phases was not estimated.

was carried out to relate the percentage occurrence of cystocarpic plants in  $-1$  m CD attached samples with any physical parameters due to the small sample size of cystocarpic plants. Percentage occurrence of tetrasporic plants in  $-1$  m CD attached samples was significantly negatively correlated with photoperiod ( $r = -0.533$ ,  $n = 24$ ,  $p < 0.05$ ) but positively correlated with seawater temperature ( $r = 0.635$ ,  $n = 19$ ,  $p < 0.05$ ), while that of vegetative plants was negatively correlated with both photoperiod ( $r = -0.510$ ,  $n = 24$ ,  $p < 0.05$ ) and seawater temperature ( $r = -0.635$ ,  $n = 19$ ,  $p < 0.05$ ). Percentage occurrence of cystocarpic plants in attached and drifted samples at depths of  $-2$  to  $-3$  m CD was not significantly correlated with any physical parameters. In attached samples, the percentage occurrence of tetrasporic plants showed a significant positive correlation with seawater temperature ( $r = 0.690$ ,  $n = 13$ ,  $p < 0.05$ ) but that of vegetative plants showed a negative correlation ( $r = -0.685$ ,  $n = 13$ ,  $p < 0.05$ ). Similarly, a significant positive correlation was found in the percentage occurrence of tetrasporic plants of drifted samples with seawater temperature ( $r = 0.705$ ,  $n = 17$ ,  $p < 0.05$ ) whereas a negative correlation was observed in that of vegetative plants ( $r = -0.689$ ,  $n = 17$ ,  $p < 0.05$ ). No significant correlations were

found in percentage occurrence of tetrasporic and vegetative plants in both attached and drifted samples at  $-2$  to  $-3$  m CD with photoperiod and nutrient concentrations.

In Lung Lok Shui, significant correlations with environmental parameters were only found in samples collected from the depth of  $-10$  m CD. For these samples, the percentage occurrence of vegetative plants was significantly negatively correlated with both photoperiod ( $r = -0.553$ ,  $n = 14$ ,  $p < 0.05$ ) and seawater temperature ( $r = -0.855$ ,  $n = 8$ ,  $p < 0.05$ ).

## Discussion

### *Seasonal occurrence and growth of Hypnea charoides*

Annual growth of populations of *Hypnea charoides* in Tung Ping Chau was initiated in early winter (November–December) and ended in late spring (April–May). These periods were when photoperiod and seawater temperature showed marked changes. Since photoperiod and temperature are environmental signals for seasonal change (Lüning, 1990), it might be inferred that they are among the most important factors responsible for the seasonal growth of *H. char-*

\*<sup>1</sup> Very nice finding: well done Corisca! \*<sup>2</sup> Temp + daylength are environmental signals!

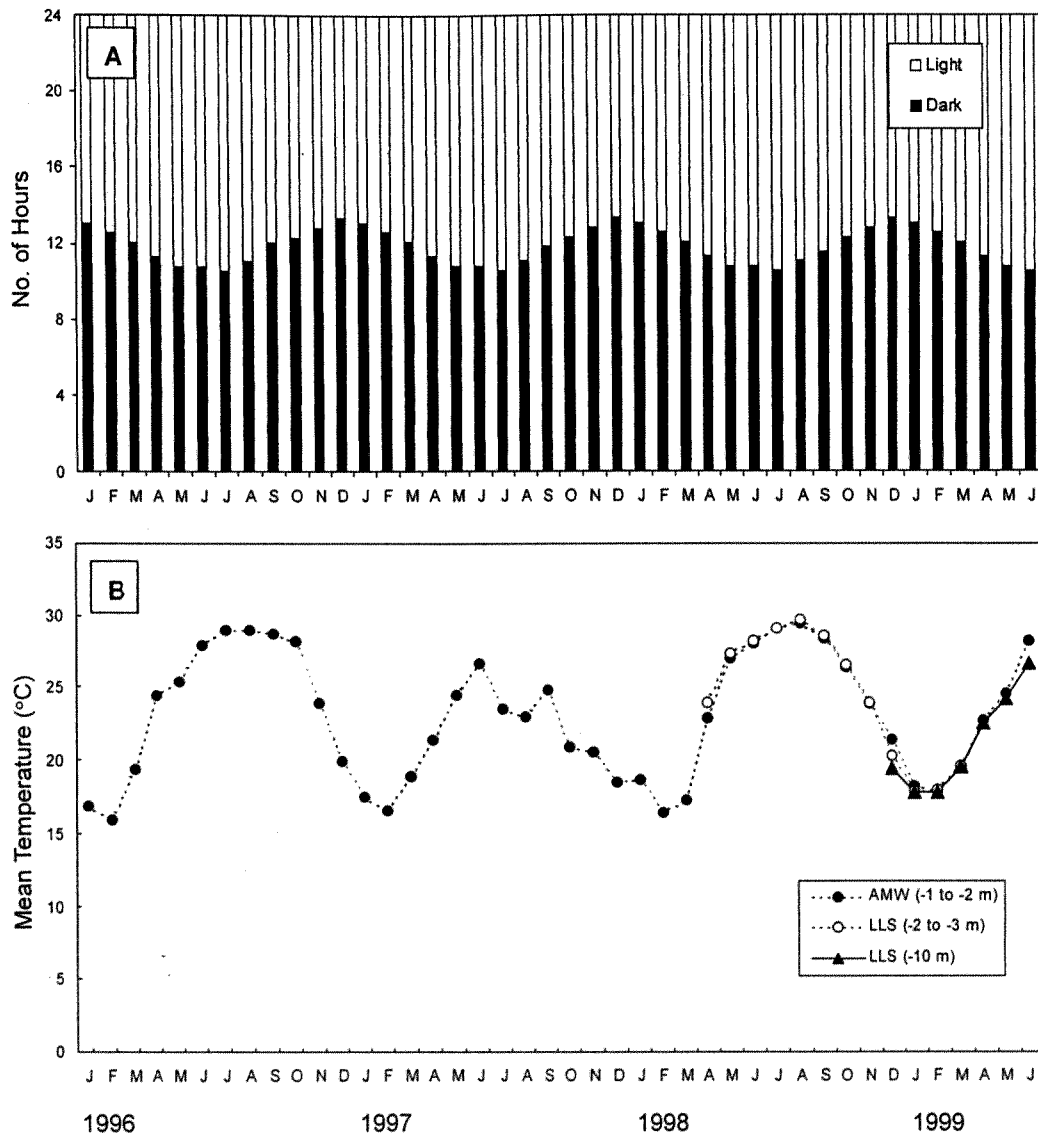


Figure 6. Mean monthly variations in (A) photoperiod and (B) seawater temperature ( $^{\circ}\text{C}$ ), recorded at depth of  $-1$  to  $-2$  m CD at A Ma Wan (AMW),  $-2$  to  $-3$  m CD and  $-10$  m CD at Lung Lok Shui (LLS), from January 1996 to June 1999. Standard deviations are not shown.

*oides* in Tung Ping Chau. Besides these two parameters, high nutrient content of seawater is also an ecological factor that favours algal growth, particularly in winter as marine algae start to consume their reserve materials for growth during this period (Lüning, 1990). The effects of different nutrients (e.g. nitrates and phosphates) on algal growth have been documented in many studies in addition to the influences of light and temperature (e.g. Kilar & Mathieson, 1978; Zinoun & Cosson, 1996; Hurtado-Ponce & Pondevida, 1997; Reani et al., 1998; see also Murray & Dixon, 1992). However, algal growth is not always favoured by high nutrient content. In *Gracilariopsis bailinae* Zhang et Xia, for example, plants grew well with a

low concentration of nutrients (Rabanal et al., 1997). While in some economic marine algae, like *Chondrus crispus* Stackhouse (Neish et al., 1977) and *Hypnea musciformis* (Wulfen) J. V. Lamouroux (Guist et al., 1982), the carrageenan production of thalli increased under reduced nitrogen availability. Nitrogen in the form of ammonium ions was even toxic to *Solieria chordalis* (C. Agardh) J. Agardh at high concentrations (Brown, 1995).

In the present study, annual growth of *H. charoides* was correlated with shorter photoperiod and lower seawater temperature, implying that decrease in photoperiod and seawater temperature could initiate its growth in A Ma Wan. The results from the shallow

water samples further indicate that change in seawater temperature might be more critical in such initiation than the photoperiod. Photoperiod is more predictable year after year, but change in seawater temperature is not. The timing of the initiation of growth of *H. charoides* populations is not consistent over the years. Populations of *H. charoides* in shallow water of A Ma Wan were first recorded in November 1996 when seawater temperature dropped from 28.2 °C (October 1996) to 24 °C (November 1996) and disappeared after May 1997 when seawater temperature rose from 24.5 °C (May 1997) to 26.7 °C (June 1997). In 1998, *H. charoides* first appeared in December 1998 when seawater temperature dropped from 23.9 °C (November 1998) to 21.5 °C (December 1998) and disappeared after April 1999 when seawater temperature rose from 22.8 °C (April 1999) to 24.6 °C (May 1999). This pattern was less clear in 1997 when the temperature fluctuated more irregularly. Mean temperature lower than 24 °C was recorded in October, but population of *H. charoides* did not appear until January 1998. However, the population disappeared in May 1998, at a time when temperature rose from 23 °C in April to 27.1 °C in May. The lowest seawater temperature throughout the whole study period was 16 °C recorded in February 1996. It thus appears that population of *H. charoides* in A Ma Wan grows best within a mean temperature range from 16 °C to 24 °C but culture experiment may be needed to further investigate such relationship.

In contrast, none of the physical parameters investigated was significantly correlated with the growth of *H. charoides* at -1 to -2 m CD in Lung Lok Shui, suggesting that factors other than photoperiod, seawater temperature and nutrient concentrations were also important in structuring its growth pattern. The apparent irregular growth pattern of *H. charoides* populations in Lung Lok Shui may be due to the much stronger wave action in the study site. This caused fragmentation of the algal thalli and resulted in various sizes of individuals in the population. Strong wave action may also explain why plants of *H. charoides* are mostly found entangled with *Sargassum* spp., a plant with a strong holdfast, rather than being attached on the substratum directly.

The unusual sudden appearance of *H. charoides* from July to November in 1998 also contributed to the irregular growth pattern of *H. charoides* observed in Lung Lok Shui. Although the reason for the appearance of this growth period is unknown, the ability of *H. charoides* to survive and grow during summer

months (i.e. longer photoperiod and warmer temperature) could not be ruled out. In some algal species, seasonal growth was not entirely controlled by physical factors alone but may be due to endogenous regulations (Molenaar & Breeman, 1994, 1997; Voskoboinikov et al., 1996; Makarov et al., 1999), allowing survival of these species under adverse conditions. Some tropical algae also exhibited no evident responses to environmental parameters (e.g. irradiance, temperature and salinity), indicating a natural ability to adapt to different marine conditions (Dawes et al., 1999). In a review of life history, reproduction and phenology of *Gracilaria*, Kain & Destombe (1995) found that there was no evidence of *Gracilaria* species anticipating the seasons by being triggered by a repeatable seasonal condition (e.g. photoperiod or water temperature) for optimal exploitation of predictable conditions. It seems that such species are responders (*sensu* Kain, 1989) and they grow when they can, when the environment allows. For the populations of *H. charoides* in Lung Lok Shui, there might also be some endogenous regulations involved in their growth. Perhaps they are similar to some *Gracilaria* spp. that they grow whenever they can.

During this unusual, sudden growth period, *H. charoides* was observed to exhibit a heterotrichous organization, i.e. its thallus was differentiated into a prostrate and an erect form. Members of the red algal order Gigartinales, to which *H. charoides* belongs, possess this categorization of thalli into two types of growth forms. An initial basal layer is first formed which then gives rise to filaments that form erect axes (Murray & Dixon, 1992). In *Cryptopleura ramosa* (Hudson) Kylin ex Lily Newton or *Plocamium cartilagineum* (Linnaeus) P. S. Dixon, the realized developmental pathway for their particular mode of erect or prostrate growth appeared to be correlated with irradiance (Dixon, 1973). Though factors that induce *H. charoides* to exhibit heterotrichy are not known, it appears that heterotrichy could be a means of increasing the opportunities to successfully perennate its thallus throughout any open space (Murray & Dixon, 1992).

#### *Reproductive seasonality*

Effects of seawater temperature on phenology of marine algae have been well documented in the past (e.g. Adey, 1973; De Wreede, 1976; Luxoro & Santelices, 1989; Narasimha Rao, 1995; Voskoboinikov et al., 1996). Although in some cases, water temperature *per se* does not directly affect algal re-

\* These two different growth forms are, themselves, another type of biodiversity. Taxonomically, ecologists may need to take this bio-variation into account and not 'score' two separate species when, in fact, there is only one!

production, it may initiate the reproductive events in conjunction with other environmental parameters like irradiance/photoperiod (Kapraun, 1978; Prince & O'Neal, 1979) and/or nutrient concentrations (Reed et al., 1996; Stimson et al., 1996; Rabanal et al., 1997). In some red algal species, photoperiod and seawater temperature were found to be particularly important to reproductive events (Molenaar & Breeman, 1994; Molenaar et al., 1996; Zamorano & Westemeier, 1996; Hall & Murray, 1998). In the present study, variations in photoperiod and seawater temperature seemed to play a more important role in controlling the occurrence of reproductive plants in the population of *H. charoides* in A Ma Wan than that in Lung Lok Shui. It was more obvious in the attached samples collected at -1 m CD in A Ma Wan, in which shorter photoperiod and higher temperature were more favourable for the growth of tetrasporic plants. Besides, percentage occurrence of tetrasporic plants in attached and drifted samples at depths of -2 to -3 m CD was also enhanced by higher temperature, indicating that increasing seawater temperature may favour tetrasporogenesis in the populations of *H. charoides* in A Ma Wan. Induction of tetrasporogenesis by change in water temperature was also reported in other red algal species. In a population of *Gracilaria heteroclada* (Montagne) Feldmann & G. Feldmann in Central Philippines, a positive correlation ( $r = 0.6586$ ) was obtained between the percentage occurrence of tetrasporophytes and seawater temperature (Luhan, 1996). A sudden rise in water temperature (+ 5 °C) together with a decrease of incident light could even trigger a massive tetraspore release in *Gracilaria bursa-pastoris* (S.G. Gmelin) P.C. Silva (Marinho-Soriano et al., 1998). The onset and end of the growth and reproductive seasons may also be triggered by many factors other than temperature (Dring, 1974; Lobban & Harrison, 1994). Nevertheless, none of the other environmental parameters investigated appeared to induce development of reproductive plants in both A Ma Wan and Lung Lok Shui.

Throughout the whole study period, cystocarpic plants were very rare and even absent in Lung Lok Shui. The populations of *H. charoides* in Tung Ping Chau were dominated by vegetative and tetrasporic plants. Natural populations do not always have equal proportions of isomorphic generations. Although it was evident that the gametophytic:sporophytic ratio of fronds in populations of *Chondrus crispus* in sublittoral Prince Edward Island of Canada was a result of stochastic events, with both generations having equal

chances of becoming established (Lazo et al., 1989), cystocarpic plants of the same species were found to be relatively more common and abundant than tetrasporic plants in other places (Mathieson & Burns, 1975). Piriz (1996) observed clear predominance of cystocarpic plants in the population of *Gigartina skottsbergii* Setchell & N.L. Gardner in Argentina, suggesting that there were differential adaptive strategies for each growth phase in its life cycle. Predominance of gametophytes was also reported in other red algae, like *Iridaea cordata* (Turner) Bory de Saint-Vincent (May, 1986), *Iridaea laminarioides* Bory de Saint-Vincent (Luxoro & Santelices, 1989) and *Mazzaella cornucopiae* (Postels & Ruprecht) Hommersand (Scrosati, 1998). On the contrary, the rarity of gametophytes and/or the predominance of tetrasporophytes were more commonly documented in many other red algal species (e.g. Hansen & Doyle, 1976; Kaliaperumal & Umamaheswara Rao, 1982; Vásquez et al., 1998; Cecere et al., 2000; Reis & Yoneshigue-Valentin, 2000).

In addition to rarity of cystocarpic plants, male plants were also not examined in the present study. This could underestimate the present reproductive analysis. Absence of male plants and rare occurrence of female ones in *Hypnea* species were also reported in other places like India (Rama Rao, 1977) and Brazil (Schenkman, 1989; Reis & Yoneshigue-Valentin, 2000). Two questions were raised by Schenkman (1989): (1) Why are fertile gametophytes so rare even if there is high production of tetraspores in several genera of Rhodophyta? (2) Could the reason be the apomeiotic division of the sporangia or a greater ability of diploid plants to propagate vegetatively in comparison with the haploid phase (see also Dixon, 1973; Searles, 1980), or neither?

There are several explanations for the first question. Cecere et al. (2000) stated that gametophytes, which were ephemeral, might die back soon after reproduction or might become reproductive when they were still so small to be underestimated (see also Breeman et al., 1988). Similarly, Reis & Yoneshigue-Valentin (2000) thought that the reason why male plants of most red algae were rarely recorded was likely to be that the male plants manifested themselves during a very short period of time or it was a bit difficult to recognize them. While Mathieson (1989) explained that relatively longer lifespan of tetrasporophytes in wild populations allowed them to produce more upright thalli per plant and thus they became more robust under stressful conditions. In a culture

\* This ecological observation may be part of eco-diversity in which habitat type influences biology; in this case reproduction!

study of *Stictosiphonia hookeri* (Harvey) Harvey from different localities, West et al. (1996) suggested two possibilities to explain the low frequency of gametophytes: (1) tetraspores do not survive germination due to their low viability, thus survival and dispersal are probably achieved by vegetative growth and fragmentation (see also Hansen & Doyle, 1976 and Cecere et al., 2000), (2) gametophytes reproduce and die more quickly than tetrasporophytes do. All these would lead to rare occurrence of gametophytes and a prevalence of tetrasporophytes (see also Rama Rao, 1977).

For the second question, both suggestions are possible. Variations in gametophyte-to-sporophyte ratios could be attributable to greater fecundity and survivorship (relative fitness) of one phase or to asexual phenomena, such as vegetative propagation and/or apomixis (see Hawkes, 1990). In certain algal species, apomixis can occur by means of apogamy/parthenogenesis or apomeiosis. Since in red algae, vegetative reproduction is an important and widespread strategy to maintain their populations in one place, many of them are able to develop apomeiotic tetrasporangia, thus giving rise to a life history in which new tetrasporophytes develop directly from tetraspores (Hansen & Doyle, 1976; Rama Rao, 1977; Hoyle, 1978; Magne, 1987; see also Hawkes, 1990; Murray & Dixon, 1992). Hence, the phenomenon showing high frequency of tetrasporophytes in certain species of the family Hypneaceae suggested that the principal reproductive mode could be resulted from apomeiosis (West & Hommersand, 1981). Nevertheless, Schenkman (1989) believed that the *Hypnea* population studied in Brazil maintained itself mainly by vegetative reproduction rather than apomeiosis as normal meiosis was observed in the tetrasporangia in a previous study (Schenkman, 1986).

Since *Hypnea* species exhibit isomorphic life cycles, the many vegetative plants of *H. charoides* observed in Tung Ping Chau during the growing seasons could be either infertile gametophytes or tetrasporophytes. If the suggestions mentioned above, i.e. that gametophytes might die soon after reproduction (Cecere et al., 2000) or that they manifested themselves only during a very short period of time (Reis & Yonshigue-Valentin, 2000), are applicable to populations of *H. charoides* in Tung Ping Chau, the processes from fertilization of gametes to the development of carposporophytes and from carpospores to tetrasporophytes should be relatively short. This leads to the rare occurrence of cystocarpic plants. The tetrasporophytes became fertile and released tetraspores at the

end of the growing season. These tetraspores persisted in summer months and then gave rise to gametophytes in the next growing season, completing the life cycles. However, the viability of free-floating spores is exceedingly low and this is true for tetraspores (Santelices 1990; Lobban & Harrison, 1994). Then, how could they survive in summer? Hoffmann & Santelices (1991) suggested that this role could be fulfilled by developing into microscopic forms that remained in a state of suspended growth. Some algal species existed as a microthallus phase (e.g. prostrate disc-like phases) in order to survive adverse conditions like intense high summer temperatures and ice scour (Schoschina et al., 1996). In *Acanthophora najadiformis* (Delile) Papenfuss populations in the Ionian Sea, Cecere et al. (2000) explained that due to their inviability, tetraspores were substituted by propagules, which could act either as perennating organs or resting organs to overcome unfavourable environmental conditions. Such kinds of (asexual) propagules was found to have a substantially greater amount of nutrient reserves and greater photosynthetic potential than the spores (Cruz Adames & Ballantine, 1996). Hence, it is possible that tetraspores of *H. charoides* in Tung Ping Chau are able to develop and exist in a form (e.g. sporelings or propagules) that can survive during summer and then grow into adult plants when the conditions are optimal (i.e. late fall to winter).

Despite the low percentage occurrence of reproductive plants in populations of *H. charoides* in A Ma Wan during the whole study period, the frequency of observing cystocarpic (drifted samples) and tetrasporic (-1 m CD, -2 to -3 m CD and drifted samples, also in Lung Lok Shui populations) plants was relatively higher in 1999. There are several possibilities: (1) the process from fertilization of gametes to the development of tetrasporophytes was prolonged, increasing the chances of observing cystocarpic plants; (2) the tetraspores produced in the previous growing season in 1998 might undergo apomeiosis and develop into a tetrasporophyte; (3) the ripening of tetrasporangia was premature. These observed phenomena might be a response to stressful environment conditions (e.g. severe fluctuations of nutrient concentrations in seawater in 1999). The real reasons, however, could not be determined at present.

Population recruitment of *H. charoides* during the growing season was thought to be provided by vegetative fragmentation as the timing of occurrence and reproduction were similar among different groups of samples in A Ma Wan. Many drifted samples were

\*' apomixis = asexual reproduction .

apogamy = the development of the sporophyte directly from the gametophyte without the formation of gametes. The resulting sporophyte has the same chromosome # as the gametophyte.

found at the beginning of the growing season, suggesting that the loosely attached individuals could easily disperse themselves (or branches) in order to populate the whole area. The stability of this free-floating population ensured the vegetative fragmentation as an effective means of population recruitment of *H. charoides* in A Ma Wan (see Perrone & Cecere, 1997). Without considering the unusual, sudden growth of *H. charoides* in 1998, similar pattern of vegetative fragmentation and population recruitment would likely be occurring in Lung Lok Shui. This process of population recruitment is more likely to happen in Lung Lok Shui as indicated by the fact that thalli of *H. charoides* were mostly found entangled with *Sargassum* spp. rather than loosely attached on the substratum. Furthermore, this might be an adaptation to populate a place with strong wave action. The relatively high abundance of tetrasporic plants in Lung Lok Shui could also be another adaptation of *H. charoides*. Tetrasporophytes could be more resistant to hydrodynamic forces (Scrosati, 1998). In addition, the high abundance of tetrasporic plants (100%) observed in October 1998 during the unusual growth period might be the result of selective forces acting in different ways on the different phases, with one phase better adapted than the other (Zamorano & Westmeier, 1996; Reis & Yoneshigue-Valentin, 2000). It could also be a response of *H. charoides* populations to some undetected changes induced by the plants themselves to the surroundings. Selection will favor rapid growth, early reproduction, and short life spans in unstable areas (Lobban & Harrison, 1994). Among algae, different types of stress induce different physiological responses, resulting in different ecological outcomes (Davison & Pearson, 1996).

The onset of reproduction coinciding with the end of the growth phase has been recorded in several red algal species (Burns & Mathieson, 1972b; Kilar & Mathieson, 1978; Kain & Norton, 1990; Voskoboinikov et al., 1996; Molenaar & Breeman, 1997). In this study, populations of *H. charoides* in A Ma Wan became tetrasporic when the growing season came to the end. This could be advantageous as there would be more free substrata due to the mortality of many other marine algae during this period (Kim & De Wreede, 1996; Scrosati, 1998).

\* Most interesting.

#### *Occurrence of cystocarps and tetrasporangia on the same thallus in Hypnea charoides*

During the examination of reproductive structures in *Hypnea charoides*, presence of cystocarps and tetrasporangia on the same branch was observed twice (25 April 1998 in A Ma Wan and 3 May 1997 in Lung Lok Shui). Abnormal pairing of these two reproductive organs had been recorded in certain red algae, like *Cystoclonium purpureum* (Hudson) Batters (Gigartinales), *Chondria baileyana* (Montagne) Harvey (Ceramiales) (Edelstein et al., 1974), *Polysiphonia harlandii* Harvey (Cheung et al., 1984) and many *Gracilaria* species (see Kain & Destombe, 1995). Plants can bear both structures either on separate parts of the thallus or on the same. Explanations, suggested by Kain & Destombe (1995), include the *in situ* germination of tetraspores (enabling gametophytes to develop as epiphytes on parental tetrasporophytes), the coalescence of spores or basal discs arising from spores to form a chimaera, mitotic recombination during cell division (resulting in occurrence of diploid male and female cells on the same tetrasporophyte), a natural mutation during which female expression is repressed, allowing the formation of carpogonia on male plants which thus became bisexual, and finally, incomplete formation of cross-walls in tetrasporangia. Though it is not clear which explanation(s) would be more applicable to the populations of *H. charoides* in Tung Ping Chau at the moment, this could be a strategy for the tetraspores to survive and germinate. The percentage occurrence of cystocarpic plants in both A Ma Wan and Lung Lok Shui could also be underestimated. This phenomenon of having both gametangial and non-gametangial sexual reproductive structures on a single thallus was not commonly recorded in Hong Kong (see Cheung et al., 1984). The present finding is thus a first record for *H. charoides* in Hong Kong.

#### Acknowledgements

This paper benefited from valuable comments from Professors H. M. Lam, C. K. Wong (Chinese University of Hong Kong (CUHK)) and S. W. Phang (University of Malaya). Special thanks are given to staff of Marine Science Laboratory for using the facilities and the following people for their kind assistance in the field: Louis Y. Cheung, Theo C. H. Hui, Donna C. Lee, May S. H. Liu, Henry T. W. Tam, Eva K. Y. Tso, Dickson C. C. Wong, Icy W. S. Yip and Y. H.

Yung. This project was supported by various CUHK University Grants Council Direct grants to POA.

## References

- Adey, W. H., 1973. Temperature control of reproduction and productivity in a subarctic coralline alga. *Phycologia* 12: 111–118.
- APHA (American Public Health Association), 1995. Standard Methods for the Examination of Water and Waste Water (19th edn). American Public Health Association, Washington, DC.
- Breeman, A. M., E. J. S. Meulenhoff & M. D. Guiry, 1988. Life history regulation and phenology of the red alga *Bonnemaisonia hamifera*. *Helgoländer wiss. Meeresunters.* 42: 535–551.
- Brown, M. T., 1995. Interactions between environmental variables on growth rate and carrageenan content of *Solieria chordalis* (Solieriaceae, Rhodophyceae) in culture. *J. appl. Phycol.* 7: 427–432.
- Burns, R. L. & A. C. Mathieson, 1972a. Ecological studies of economic red algae. II. Culture studies of *Chondrus crispus* Stackhouse and *Gigartina stellata* (Stackhouse) Batters. *J. exp. mar. Biol. Ecol.* 8: 1–6.
- Burns, R. L. & A. C. Mathieson, 1972b. Ecological studies of economic red algae. III. Growth and reproduction of natural and harvested populations of *Gigartina stellata* (Stackhouse) Batters in New Hampshire. *J. exp. mar. Biol. Ecol.* 9: 77–95.
- Cecere, E., O. D. Saracino, M. Fanelli & A. Petrocelli, 2000. Phenology of two *Acanthophora najadiformis* (Rhodophyta, Ceramiales) populations in the Ionian Sea (Mediterranean Sea). *Bot. mar.* 43: 109–117.
- Cheung, K. W., K. Y. Lee & I. J. Hodgkiss, 1984. The occurrence of tetrasporangia and cystocarps on the same thalli in *Polysiphonia harlandii* (Rhodophyta: Ceramiales) (Note). *Bot. mar.* 27: 571–572.
- Cruz Adames, V. M. & D. L. Ballantine, 1996. Asexual reproduction in *Laurencia poiteaui* (Rhodomelaceae, Rhodophyta). *Bot. mar.* 39: 75–77.
- Davison, I. R. & G. A. Pearson, 1996. Stress tolerance in intertidal seaweeds. *J. Phycol.* 32: 197–211.
- Dawes, C. J., J. Orduña-Rojas & D. Robledo, 1999. Response of the tropical red seaweed *Gracilaria cornea* to temperature, salinity and irradiance. *J. appl. Phycol.* 10: 419–425.
- De Wreede, R. E., 1976. The phenology of three species of *Sargassum* (Sargassaceae, Phaeophyta) in Hawaii. *Phycologia* 15: 175–183.
- Dixon, P. S., 1973. *Biology of the Rhodophyta*. Hafner Press, New York: 285 pp.
- Dring, M. J., 1974. Reproduction. In Stewart, W. D. P. (ed.), *Algal Physiology and Biochemistry*. Blackwell Scientific Publications: 814–833.
- Dyck, L. J. & R. E. De Wreede, 1995. Patterns of seasonal demographic change in the alternate isomorphic stages of *Mazzaella splendens* (Gigartinales, Rhodophyta). *Phycologia* 34: 390–395.
- Edelstein, T., C. J. Bird & J. McLachlan, 1974. Tetrasporangia and gametangia on the same thallus in the red algae *Cystoclonium purpureum* (Huds.) Batt. and *Chondria baileyana* (Mont.) Harv. *Br. Phycol. J.* 9: 247–250.
- Guist, G. G., Jr., C. J. Dawes & J. R. Castle, 1982. Mariculture of the red seaweed, *Hypnea musciformis*. *Aquaculture* 28: 375–384.
- Hall, J. D. & S. N. Murray, 1998. The life history of a Santa Catalina Island population of *Liagora californica* (Nemaliales, Rhodophyta) in the field and in laboratory culture. *Phycologia* 37: 184–194.
- Hansen, J. E. & W. T. Doyle, 1976. Ecology and natural history of *Iridaea cordata* (Rhodophyta; Gigartineae): population structure. *J. Phycol.* 12: 273–278.
- Hawkes, M. W., 1990. Reproductive strategies. In Cole, K. M. & R. G. Sheath (eds), *Biology of the Red Algae*. Cambridge University Press, Cambridge: 455–476.
- Hodgkiss, I. J., 1984. Seasonal patterns of intertidal algal distribution in Hong Kong. *Asian mar. Biol.* 1: 49–57. \*
- Hodgkiss, I. J. & K. Y. Lee, 1983. *Hong Kong Seaweeds*. Urban Council, Hong Kong. \*
- Hoffmann, A. J. & B. Santelices, 1991. Banks of algal microscopic forms: hypotheses on their functioning and comparisons with seed banks. *Mar. Ecol. Prog. Ser.* 79: 185–194.
- Hoyle, M. D., 1978. Reproductive phenology and growth rates in two species of *Gracilaria* from Hawaii. *J. exp. mar. Biol. Ecol.* 35: 273–283.
- Hurtado-Ponce, A. Q. & H. B. Pondevida, 1997. The interactive effect of some environmental factors on the growth, agar yield and quality of *Gracilariopsis bailinae* (Zhang et Xia) cultured in tanks. *Bot. mar.* 40: 217–223.
- Kaehler, S. & G. A. Williams, 1996. Distribution of algae on tropical rocky shores: spatial and temporal patterns of non-coraline encrusting algae in Hong Kong. *Mar. Biol.* 125: 177–187.
- Kain (Jones), J. M., 1989. The seasons in the subtidal. *Br. Phycol. J.* 24: 203–215.
- Kain (Jones), J. M. & C. Destombe, 1995. A review of the life history, reproduction and phenology of *Gracilaria*. *J. appl. Phycol.* 7: 269–281.
- Kain (Jones), J. M. & T. A. Norton, 1990. Marine ecology. In Cole, K. M. & R. G. Sheath (eds), *Biology of the Red Algae*. Cambridge University Press, Cambridge: 377–422.
- Kaliaperumal, N. & M. Umamaheswara Rao, 1982. Seasonal growth and reproduction of *Gelidiopsis variabilis* (Greville) Schmitz. *J. exp. mar. Biol. Ecol.* 61: 265–270.
- Kapraun, D. F., 1978. Field and culture studies on growth and reproduction of *Callithamnion byssoides* (Rhodophyta, Ceramiales) in North Carolina. *J. Phycol.* 14: 21–24.
- Kennish, R., G. A. Williams & S. Y. Lee, 1996. Algal seasonality on an exposed rocky shore in Hong Kong and the dietary implications for the herbivorous crab *Grapsus albolineatus*. *Mar. Biol.* 125: 55–64. \*
- Kilar, J. A. & A. C. Mathieson, 1978. Ecological studies of the annual red alga *Dumontia incrassata* (O. F. Müller) Lamouroux. *Bot. mar.* 21: 423–437.
- Kim, J. H. & R. E. DeWreede, 1996. Effects of size and season of disturbance on algal patch recovery in a rocky intertidal community. *Mar. Ecol. Prog. Ser.* 133: 217–228.
- Lazo, M. L., M. Greenwell & J. McLachlan, 1989. Population structure of *Chondrus crispus* Stackhouse (Gigartineae, Rhodophyta) along the coast of Prince Edward Island, Canada: distribution of gametaphytic and sporophytic fronds. *J. exp. mar. Biol. Ecol.* 126: 45–48.
- Lobban, C. S. & P. J. Harrison, 1994. *Seaweed Ecology and Physiology*. Cambridge University Press, Cambridge.
- Luhan, M. R. J., 1996. Biomass and reproductive states of *Gracilaria heteroclada* Zhang et Xia collected from Jaro, Central Philippines. *Bot. mar.* 39: 207–211.
- Lüning, K., 1990. *Seaweeds: Their Environment, Biogeography and Ecophysiology*. John Wiley & Sons, Inc., New York.
- Luxoro, C. & B. Santelices, 1989. Additional evidence for ecological differences among isomorphic reproductive phases of *Iridaea laminarioides* (Rhodophyta: Gigartinales). *J. Phycol.* 25: 206–212.

\* Hong Kong References

- Magne, F., 1987. Is the frequency of apomeiosis in the Rhodophyta a genetic character? *Hydrobiologia* 151/152: 221–232.
- Makarov, V. N., M. V. Makarov & E. V. Schoschina, 1999. Seasonal dynamics of growth in the Barents Sea seaweeds: endogenous and exogenous regulation. *Bot. mar.* 42: 43–49.
- Marinho-Soriano, E., T. Laugier & M. L. De Casabianca, 1998. Reproductive strategy of two *Gracilaria* species, *G. bursa-pastoris* and *G. gracilis*, in a Mediterranean Lagoon (Thau, France). *Bot. mar.* 41: 559–564.
- Mathieson, A. C., 1989. Phenological patterns of New England seaweeds. *Bot. mar.* 32: 419–438.
- Mathieson, A. C. & R. L. Burns, 1975. Ecological studies of economic red algae. V. Growth and reproduction of natural and harvested populations of *Chondrus crispus* Stackhouse in New Hampshire. *J. exp. mar. Biol. Ecol.* 17: 137–156.
- May, G., 1986. Life history variations in a predominantly gametophytic population of *Iridaea cordata* (Gigartinales, Rhodophyta). *J. Phycol.* 22: 448–455.
- Molenaar, F. J. & A. M. Breeman, 1994. Ecotypic variation in *Phyllophora pseudoceranioides* (Rhodophyta) ensures winter reproduction throughout its geographic regions. *J. Phycol.* 30: 392–402.
- Molenaar, F. J. & A. M. Breeman, 1997. Latitudinal trends in the growth and reproductive seasonality of *Delesseria sanguinea*, *Membranoptera alata* and *Phycodrys rubens* (Rhodophyta). *J. Phycol.* 33: 330–343.
- Molenaar, F. J., A. M. Breeman & L. A. H. Venekamp, 1996. Ecotypic variation in *Cystoclonium purpureum* (Rhodophyta) synchronizes life history events in different regions. *J. Phycol.* 32: 516–525.
- Murray, S. N. & P. S. Dixon, 1992. The Rhodophyta: some aspects of their biology. III. *Oceanogr. mar. biol. Ann. Rev.* 30: 1–148.
- Narasimha Rao, G., 1995. Seasonal growth, biomass, and reproductive behavior of three species of red algae in Godavari estuary, India. *J. Phycol.* 31: 209–214.
- Neish, A. C., P. F. Shacklock, C. H. Fox & F. J. Simpson, 1977. The cultivation of *Chondrus crispus*. Factors affecting growth under greenhouse conditions. *Can. J. Bot.* 55: 2263–2271.
- Perrone, C. & E. Cecere, 1997. Regeneration and mechanisms of secondary attachment in *Solieria filiformis* (Gigartinales, Rhodophyta). *Phycologia* 36: 120–127.
- Piriz, M. L., 1996. Phenology of a *Gigartina skottsbergii* Setchell et Gardner population in Chubut Province (Argentina). *Bot. mar.* 39: 311–316.
- Prince, J. S. & S. W. O'Neal, 1979. The ecology of *Sargassum pteropleuron* Grunow (Phaeophyceae, Fucales) in the waters off South Florida I. Growth, reproduction and population structure. *Phycologia* 18: 109–114.
- Rabanal, S. F., R. Azanza & A. Hurtado-Ponce, 1997. Laboratory manipulation of *Gracilariopsis bailinae* Zhang et Xia (Gracilariales, Rhodophyta). *Bot. mar.* 40: 547–556.
- Rama Rao, K., 1977. Studies on Indian Hypneaceae. II. reproductive capacity in the two *Hypnea* over the different seasons. *Bot. mar.* 20: 33–39.
- Reani, A., J. Cosson, A. Parker & D. Zaoui, 1998. Seasonal variation of growth, carrageenan content and rheological properties of *Cystoclonium purpureum* (Huds.) Batters (Rhodophyta, Cystocloniaceae) from the Calvados Coast (France). *Bot. mar.* 41: 383–387.
- Reed, D. C., A. W. Ebeling, T. W. Anderson & M. Anghera, 1996. Differential reproductive responses to fluctuating resources in two seaweeds with different reproductive strategies. *Ecology* 77: 300–316.
- Reis, R. P. & Y. Yoneshigue-Valentin, 2000. Phenology of *Hypnea musciformis* (Wulfen) Lamouroux (Rhodophyta, Gigartinales) in three populations from Rio de Janeiro State, Brazil. *Bot. mar.* 43: 299–304.
- Santelices, B., 1990. Patterns of reproduction, dispersal and recruitment in seaweeds. *Oceanogr. mar. biol. Ann. Rev.* 28: 177–276.
- Schenkman, R. P. F., 1986. Cultura de *Hypnea* (Rhodophyta) in vitro como subsidio para estudos morfológicos, reprodutivos e taxonomicos. Ph. D. thesis, Inst. Biociências, Universidade de São Paulo, Sao Paulo, Brazil.
- Schenkman, R. P. F., 1989. *Hypnea musciformis* (Rhodophyta): ecological influence on growth. *J. Phycol.* 25: 192–196.
- Schoschina, E. V., V. N. Makarov, G. M. Voskoboinikov & C. van den Hoek, 1996. Growth and reproductive phenology of nine intertidal algae on the Murman Coast of the Barents Sea. *Bot. mar.* 39: 83–93.
- Scrosati, R., 1998. Population structure and dynamics of the clonal alga *Mazzaella cornucopiae* (Rhodophyta, Gigartinales) from Barkley Sound, Pacific Coast of Canada. *Bot. mar.* 41: 483–493.
- Searles, R. B., 1980. The strategy of the red algal life history. *Am. Nat.* 115: 113–120.
- Stimson, J., S. Larned & K. McDermid, 1996. Seasonal growth of the coral reef macroalga *Dictyosphaeria cavernosa* (Forskål) Børgesen and the effects of nutrient availability, temperature and herbivory on growth rate. *J. exp. mar. Biol. Ecol.* 196: 53–77.
- Vásquez, J. A., A. Vega, B. Matsuhira & C. Faúndez, 1998. Biomass, reproductive phenology and chemical characterization of soluble polysaccharides from *Rhodymenia howeana* Dawson, (Rhodymeniaceae, Rhodymeniales) in Northern Chile. *Bot. mar.* 41: 235–242.
- Voskoboinikov, G. M., A. M. Breeman, C. van den Hoek, V. N. Makarov & E. V. Schoschina, 1996. Influence of temperature and photoperiod on survival and growth of North East Atlantic isolates of *Phycodrys rubens* (Rhodophyta) from different latitudes. *Bot. mar.* 39: 341–346.
- West, J. A. & M. H. Hommersand, 1981. Rhodophyta: life histories. In Lobban, C. S. & M. J. Wynne (eds), *The Biology of Seaweeds*. Blackwell Scientific Publications: 133–193.
- West, J. A., G. C. Zuccarello & U. Karsten, 1996. Reproductive biology of *Stictosiphonia hookeri* (Rhodomelaceae, Rhodophyta) from Argentina, Chile, South Africa and Australia in laboratory culture. *Hydrobiologia* 326/327: 277–282.
- Williams, G. A., 1993. Seasonal variation in algal species richness and abundance in the presence of molluscan herbivores on a tropical rocky shore. *J. exp. mar. Biol. Ecol.* 167: 261–275.
- Zamorano, J. & R. Westermeier, 1996. Phenology of *Gigartina skottsbergii* (Gigartinales, Rhodophyta) in Ancud Bay, southern Chile. *Hydrobiologia* 326/327: 253–258.
- Zinoun, M. & J. Cosson, 1996. Seasonal variation in growth and carrageenan content of *Calliblepharis jubata* (Rhodophyceae, Gigartinales) from the Normandy coast, France. *J. appl. Phycol.* 8: 29–34.

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