Life history of Porphyra hollenbergii Dawson (Bangiales, Rhodophyta) from the Gulf of California, México

Article *in* Phycologia · September 2011

DOI: 10.2216/10-58.1

CITATIONS
6

READS
383

4 authors, including:

Juan M. López-Vivas
Autonomous University of Baja California Sur
66 PUBLICATIONS **311** CITATIONS

SEE PROFILE

Isai Pacheco-Ruiz
Autonomous University of Baja California
96 PUBLICATIONS **942** CITATIONS

SEE PROFILE

Charles Yarish
University of Connecticut
234 PUBLICATIONS **7,518** CITATIONS

SEE PROFILE

Phycologia (2011) Volume 50 (5), 520–529 Published 30 September 2011

Life history of *Porphyra hollenbergii* Dawson (Bangiales, Rhodophyta) from the Gulf of California, México

Juan Manuel López-Vivas[1,2,3], Isaí Pacheco-Ruiz[2], Rafael Riosmena-Rodríguez[3]* and Charles Yarish[4]

[1]*Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Km 107 Carretera Tijuana-Ensenada, A.P. 458, Ensenada, Baja California CP. 22860, México*

[2]*Instituto de Investigaciones Oceanológicas, Universidad Autónoma de Baja California, Km 107 Carretera Tijuana-Ensenada, A.P. 458, Ensenada, Baja California CP. 22860, México*

[3]*Universidad Autónoma de Baja California Sur, Programa de Investigación en Botánica Marina, Departamento de Biología Marina, Km 5.5 Carretera al Sur, A.P. 19-B, La Paz, Baja California Sur 23080, México*

[4]*Department of Ecology & Evolutionary Biology, University of Connecticut, One University Place, Stamford, Connecticut 06901-2315 USA*

López-Vivas J.M., Pacheco-Ruiz I., Riosmena-Rodríguez R. and Yarish C. 2011. Life history of *Porphyra hollenbergi* Dawson (Bangiales, Rhodophyta) from the Gulf of California, México. *Phycologia* 50: 520–529. DOI: 10.2216/10-58.1

The life history of *Porphyra hollenbergii* Dawson, a species endemic to the Gulf of California (Mexico), was investigated in relation to temperature, photoperiod and photon fluence rates. The hypothesis was that its life history is controlled by extremes of temperature ($< 10°C$ to $> 30°C$), photoperiod (short/neutral/long) and photon fluence levels (low/high light). Culture experiments were set up using a factorial $5 \times 5 \times 3$ design with five photon fluence levels (10, 20, 40, 60 and 80) µmol photons m^{-2} s^{-1}), five temperatures (10, 15, 20, 25 and 30°C) and three photoperiods [8:16, 12:12 and 16:8 light:dark (L:D)]. For the gametophyte phase, the optimal release of zygotospores was at 15°C, with photon fluence level of 60 µmol photons m^{-2} s^{-1} and long photoperiod 16:8 L:D. Germination was best at 20°C, a photon fluence level of 60 µmol photons m^{-2} s^{-1} and under a long photoperiod 16:8 L:D. The abundance of archeospores differed significantly at temperatures of 25 and 30°C. The number of archeospores mm^{-2} of the conchocelis tufts was significantly different in the long photoperiod 16:8 L:D when compared with the neutral 12:12 and short 8:16 L:D. The abundance of conchosporangia at temperatures of 15, 25 and 30°C were different and differed from the other conditions. In addition, abundance of conchosporangia mm^{-2} were significantly different in all photoperiod treatments. Conchospores were released after 6 weeks at 10°C, 20 µmol photons m^{-2} s^{-1} at 8:16 L:D. On the basis of our results, we found that water temperatures were the limiting factor for conchocelis growth. However, it is the combination of photoperiod and high water temperatures that are the environmental conditions that appear to control the development of archeospores and conchospores. *Porphyra hollenbergii* life history is controlled by an array of factors at each stage, strongly suggesting the environmental influence of the habitat on this species.

Key Words: Archeospores, Conchocelis, Conchospores, Endemic, Environmental, Reproduction

INTRODUCTION

Porphyra is a commercially important genus that is dependent on cultivation practices and the need to bring in new cultivars and species into production (Pereira & Yarish 2010). The basic knowledge of the life history of *Porphyra* species has been investigated since the mid 20th century by Drew (1954), Conway & Cole (1977), Hawkes (1977, 1978), Cole & Conway (1980), Notoya *et al.* (1992a, b, 1993a, b), Kornmann (1994); Nelson & Knight (1996), Notoya (1997) and Lindstrom *et al.* (2008). Most of these studies were primarily concerned with temperate species life histories and their environmental regulation but rarely were there any from subtropical or tropical areas.

Among the six *Porphyra* species recognized in the Mexican Pacific, the life history is only known for *Porphyra gardneri* Hawkes (Hawkes 1977, 1978) in the northeast Pacific; *Porphyra perforata* J. Agardh (Hollenberg 1958; Martínez 1990; Polne-Fuller & Gibor 1990) in California; *Porphyra suborbiculata* Kjellman (Freshwater & Kapraun 1986; Monotilla & Notoya 2004) from northwest Pacific and Atlantic (Japan and North Carolina, respectively) and *Porphyra thuretii* Setchell & Dawson (Conway & Cole 1977; Hawkes 1981) in the northeast Pacific (Washington and British Columbia). However, little is known from any populations of these taxa from their southern boundary limits, i.e. from the Mexican Pacific. Even less is known about the life history of *Porphyra hollenbergii* Dawson (Dawson 1944, 1953; Krishnamurthy 1972), a species endemic to the Gulf of California.

The Gulf of California is located in the transitional area from the tropical to temperate biogeographic regions in the Mexican Pacific. The Gulf of California is a sea with exceptionally high primary productivity (Álvarez-Borrego *et al.* 1978; Álvarez-Borrego & Lara-Lara 1991), has a wide range of seawater temperatures and photoperiods along its length and has been isolated from the eastern Pacific Ocean for about 1.3 to 3.5 million years (Johnson & Ledesma-Vázquez 2009). The Gulf of California is also periodically

* Corresponding author (riosmena@uabcs.mx).

affected by major oceanographic events such as El Niño. However, little is known about the environmental control of its seaweed populations (West & Guiry 1981; Scrosati 2001a, b; Pacheco-Ruiz *et al.* 2003). For the endemic *P. hollenbergii*, we expected the conchocelis phase to be the most tolerant phase of its life history, enabling this taxon to survive the extremes of temperature and photoperiodic conditions in the Gulf of California (Álvarez-Borrego 1983; Blanco-Betancourt *et al.* 2004; Martínez-Díaz de León *et al.* 2006).

Dawson described *P. hollenbergii* in 1944 from the Gulf of California (Dawson 1944). He mentioned that *P. hollenbergii* is very similar to *P. perforata* f. *segregata* Hus. The species was described as dioecious, epilithic, membranous, pale rose (female) tending toward greenish (vegetative) in color and yellow at the margins (male), with packets of eight zygotospores and 64–128 spermatangia. Since its original description by Dawson, *P. hollenbergii* has only been found at six localities around the central Gulf of California (Dawson 1944, 1953; Aguilar-Rosas *et al.* 2007). The foliar phase of this species is distributed in the rocky intertidal zone above 50–170-cm mean tide level and develops from December to May when the thalli disappear when water temperatures are above 25°C.

The objectives of our study were to unravel the environmental complexities of the life history of *P. hollenbergii*. Our goals were: (1) to determine the optimal conditions (temperature, photon fluence levels and photoperiod) in which the conchocelis phase develops; (2) to evaluate if there are additional reproductive propagules in the conchocelis phase such as archeospores, conchospores, and protothalli (terminology after Nelson *et al.* 1999: 409); and (3) to determine the optimal conditions for conchosporangia development and release of the conchospores.

MATERIAL AND METHODS

Female specimens of *P. hollenbergii* were collected on 30 April 2004 at the type locality of Agua Verde Bay, Baja California Sur, 25°32′29.79″N, 111°07′40.45″W. After a morphological evaluation of the plants, voucher material was deposited in the Phycological Herbarium of the Universidad Autónoma de Baja California Sur (FBCS 11232-11236) and submitted for DNA sequencing (GenBank accession no. AY794401, used by Lynch *et al.* 2008). The surface of the blades was cleaned softly with a cotton ball using sterilized seawater. Experiments were designed to understand the main limiting factors for conchocelis development. Small areas of reproductive tissue were excised and placed in Petri dishes with Provasoli's enriched medium (PES) plus 4 mg l^{-1} germanium dioxide (GeO_2) (within the range suggested by Lewin 1966) and left overnight at 15°C, 25 μmol photons $m^{-2}s^{-1}$ and 12:12 light:dark (L:D) photoperiod. Zygotospores were liberated and transferred to new Petri dishes (100-mm diameter) containing PES (Provasoli 1968; Bold & Wynne 1985; Andersen *et al.* 2005). An antibiotic mixture (2 ml l^{-1}) (streptomycin, penicillin, ampicillin 1 g l^{-1} each) was used to control cyanobacteria. The resulting conchocelis cultures were deposited into the culture collection of the Instituto de Investigaciones Oceanológicas (Mex I), Ensenada, Mexico. They were maintained at 15°C, a photon fluence level of 80 μmol photons m^{-2} s^{-1} and 8:16 L:D photoperiod.

Conchocelis growth experiments

A factorial designed experiment $5 \times 5 \times 3$ was started using five 'tufts' of conchocelis 1.5 to 2.0 mm in diameter in Petri dishes in 20-ml volume with PES with temperatures of 10, 15, 20, 25 and 30°C; at photon fluence levels of 10, 20, 40, 60 and 80 μmol photons m^{-2} s^{-1}; and at photoperiods of 8:16, 12:12 and 16:8 L:D (VWR, model 2015 diurnal growth incubators chamber).

Conchocelis tufts were placed in 0.5-litre flasks with PES and gently aerated with air stones, under 15°C, 30 ± 5 μmol photons $m^{-2}s^{-1}$ and at 12:12 L:D, for 4 to 5 weeks to increase biomass. For these experiments, conchocelis tufts were again ground, using a common kitchen grinder, and passed (aided by a spatula) through a 70-μm filter onto a 50-μm filter (glass fibre filter). The filaments trapped by the second filter, between 50 and 70 μm in size, were then resuspended in seawater. One-millilitre aliquots of this mixture were inoculated in Corning cell wells (six-well plates with lid, 10-ml volume) and placed under different combinations of light (25 and 75 μmol photons m^{-2} s^{-1}), temperature (10, 15 and 20, 25 and 30°C) and photoperiod (16:8, 12:12 and 8:16 L:D). The medium was changed weekly.

The growth of conchocelis under the experimental conditions was recorded weekly, as an increase in the area (α), according to the formula:

$$\alpha = \pi/n\left(\sum_{1}^{n}\left(D_1/2\right)^2\right)$$

This formula is based upon a circle's area, where the ray ($D_1/2$) is obtained from the mean of two perpendicular diameter measurements for each conchocelis (D_1). The area values were used to calculate specific growth rates (μ), as the mean percent increase per day, using the formula (Pereira *et al.* 2004):

$$\mu = [\ln(\alpha_2/\alpha_1)]100/t$$

where α_2 and α_1 are the conchocelis area at the end and at the beginning of the experiment and t is the number of days. This formula (DeBoer *et al.* 1978) assumes that growth is exponential and was also used by Chopin *et al.* (1999), Stekoll *et al.* (1999) and by Pereira *et al.* (2004).

Archeospore formation

The filaments growing under the conditions described above were monitored to determine reproductive condition. Archeospore formation was identified by the presence of a small peduncle (in conchospores this is not present). The number of archeospores was determined per square millimeter of conchocelis.

Conchosporangia formation

The filaments grown under the conditions described above were also monitored for conchosporangia formation and

release. The number of conchosporangia within the first 30 random observations in each well was recorded each week. The percentage of reproductive conchocelis tufts was calculated. Simultaneously, vegetative conchocelis tufts from several conditions were transferred to different environmental conditions. Several combinations of changes in temperature, photoperiod and light intensity were tested. These conchocelis were also followed weekly, as described before, for conchosporangia formation.

All experiments were started using five tufts of conchocelis 0.5 to 2.0 mm in diameter in Petri dishes of 20-ml volume. A three-way ANOVA was used with software from SigmaStat (Version 3.5, 2006) *a posteriori* analysis on the basis of Tukey's multiple range test (Sokal & Rohlf 1995; Zar 1999). Normality and homogeneity of variances were checked before performing the ANOVA.

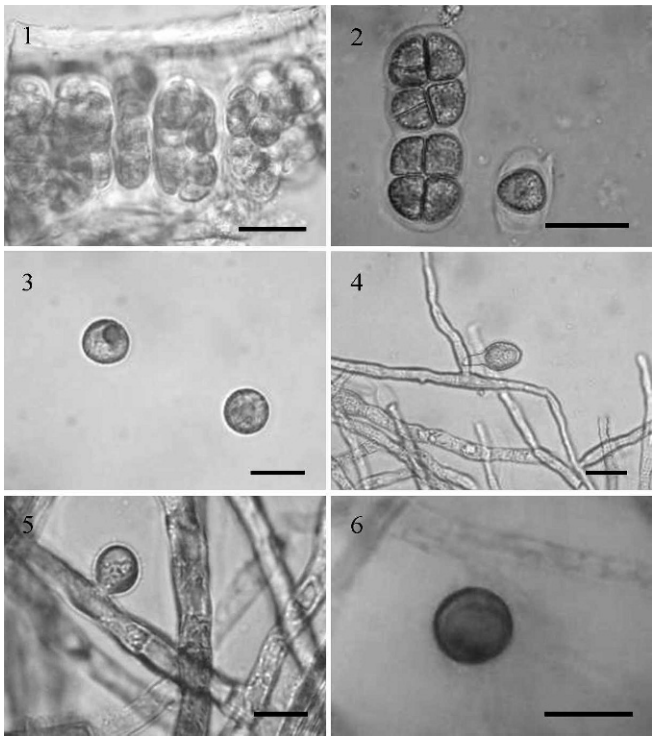
RESULTS

During the experiment we were able to find and identify mature zygotosporangia at the exact moment of release (Figs 1, 2). Afterward we were able to keep zygotospores alive that produced the conchocelis phase from germinated zygotospores (Figs 3, 4). We were able to observe archeospore formation in the conchocelis phase and the release and survival of archeospores (Figs 5, 6). Both branched (Figs 7, 9, 10) and unbranched conchosporangia (Fig. 8) developed. Mature conchosporangia released conchospores that started to grow (Figs 11–13) into separate yellow male and purple female gametophytic thalli (Figs 14–17). The release of zygotospores from the gametophytic phase of *P. hollenbergii* was observed between 10 and 25°C, 10 and 80 μmol photons m^{-2} s^{-1} and at 16:8, neutral 12:12 and short 8:16 L:D photoperiods. These zygotospores germinated between 10 and 30°C to form the conchocelis phase.

Conchocelis growth

The growth of the conchocelis phase of *P. hollenbergii* occurred in a broad range of temperatures (10–30°C), at all photon fluence levels (10, 20, 40, 60 and 80 μmol photons m^{-2} s^{-1}) and in all photoperiods (8:16, 12:12 and 16:8 L:D) (Fig. 18). The best growth rates were observed at 20°C and photon fluence levels of 40–60 μmol photons m^{-2} s^{-1} in both long (16:8 L:D resulting in 6.48 ± 0.54% increase of filaments area d^{-1}) and day-neutral photoperiod (12:12 L:D resulting in 6.43 ± 0.43% area d^{-1}). In contrast, the best growth rate observed at 30°C was just 2.24 ± 0.18% area d^{-1}, under a short photoperiod of 8:16 L:D and at a photon fluence level between 10 and 20 μmol photons m^{-2} s^{-1}. All data were normal ($P = 0.145$), homoscedastic ($P = 1.000$) and the three-way ANOVAs showed that only water temperature caused significant differences ($P < 0.001$), whereas photon fluence level ($P > 0.05$), photoperiod ($P > 0.05$) and their interactions ($P > 0.05$) did not (Table 1).

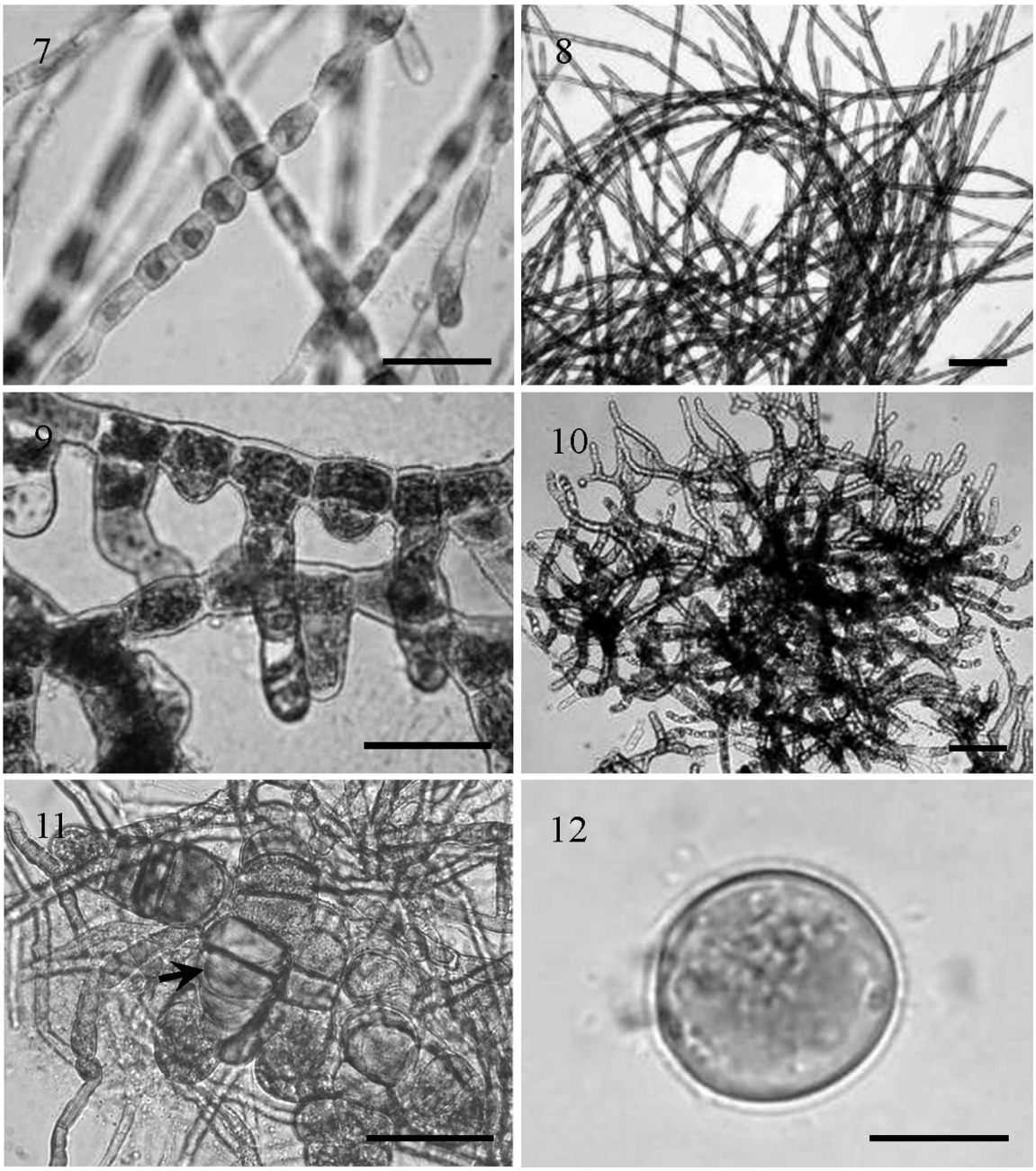
Tukey's *a posteriori* multiple range test applied to the relative growth rate showed a significant difference between the water temperature from 15 to 20°C; both conditions had the highest rate of growth. It also showed that the rate of growth at these two temperatures was significantly different from the other temperatures tested (10, 25 and 30°C, $P < 0.001$).



Figs 1–6. Reproductive structures of the gametophyte and sporophyte stages in the life history of *Porphyra hollenbergii.* Scale bar = 50 μm in all figures.
Fig. 1. Mature zygotosporangia.
Fig. 2. Zygotosporangia being released.
Fig. 3. Zygotospores free living.
Fig. 4. Filaments of the conchocelis phase at 15°C, photoperiod 16:8 L:D and photon fluence rate of 40 μmol photons m^{-2} s^{-1}.
Fig. 5. Archeospore formation in the conchocelis phase at 10°C, photoperiod 12:12 L:D and photon fluence rate of 60 μmol photons m^{-2} s^{-1}.
Fig. 6. Free-living archeospore from the conchocelis phase of *Porphyra hollenbergii* at 10°C, photoperiod 12:12 L:D photon fluence rate of 60 μmol photons m^{-2} s^{-1}.

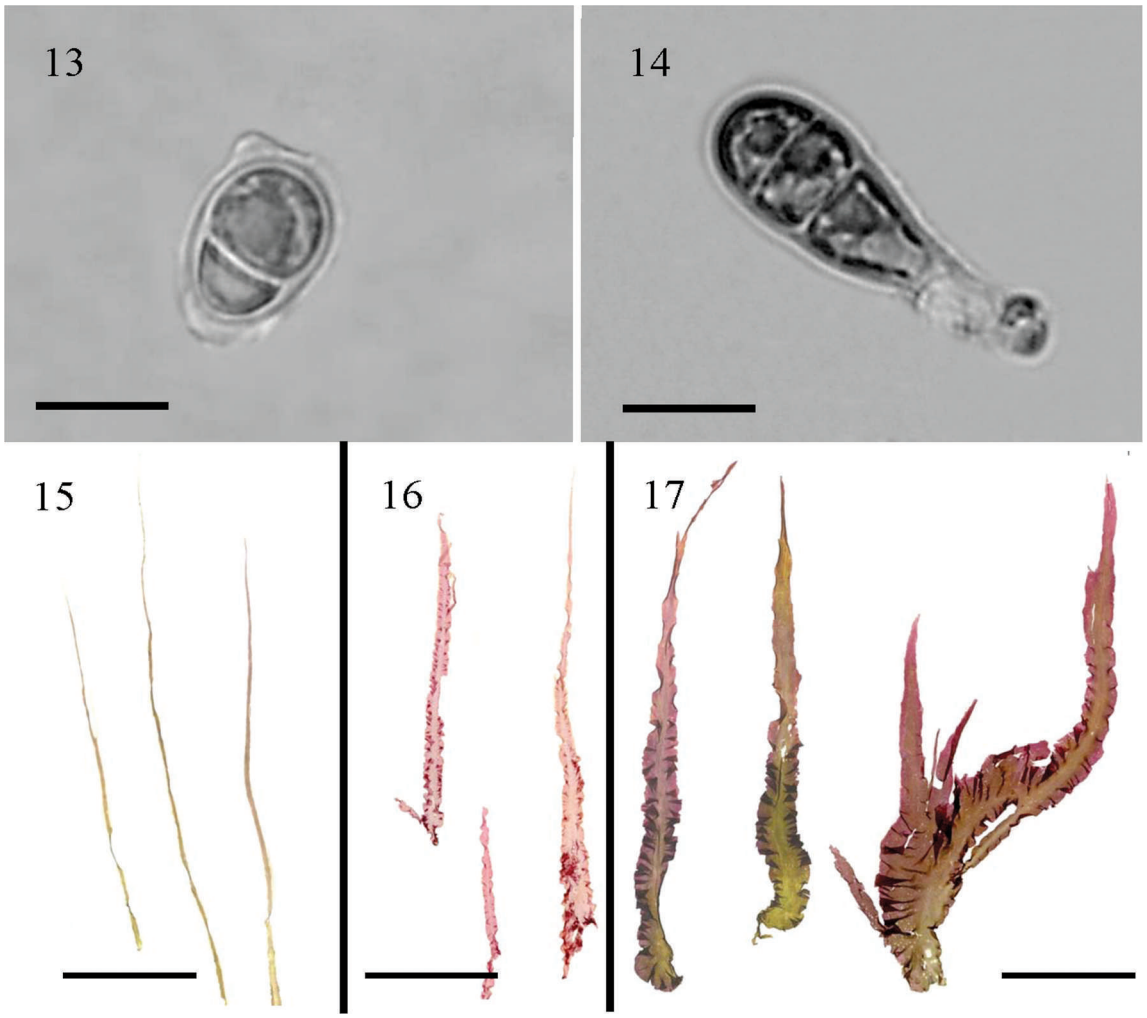
Archeospore production

The archeospores that were produced by the conchocelis were spherical and had red stellate chloroplasts (Fig. 6). Archeospores were released during the entire experiment under all conditions tested. They developed as lateral outgrowths of the conchocelis filaments, being attached by a small peduncle (Fig. 5) and reaching a diameter of 3.0–4.5 μm. They were most abundant (Fig. 19) at 25–30°C, photon fluence levels of 10–20 μmol photons m^{-2} s^{-1} under either long 16:8 L:D or short photoperiod 8:16 L:D with a maximum number of 24.85 ± 7.34 archeospores mm^{-2}. Lower abundances, 2.47 ± 2.64 archeospores mm^{-2} (Fig. 19), were found at 10, 15 and 20°C, photon fluence levels of 10 μmol photons m^{-2} s^{-1} and a neutral photoperiod 12:12 L:D. The three-way ANOVA showed that abundances of archeospores mm^{-2} were significantly different with water temperature ($P < 0.001$) and photoperiod ($P < 0.001$), whereas the photon fluence level did



Figs 7–12. Reproductive structures of the conchocelis stage of *Porphyra hollenbergii.*
Fig. 7. Immature conchosporangia without ramifications. Scale bar = 50 μm.
Fig. 8. Immature conchosporangia without ramifications, growing at 10°C, photoperiod 16:8 L:D and photon fluence rate of 60 μmol photons m^{-2} s^{-1}. Scale bar = 50 μm.
Fig. 9. Conchosporangia with branches. Scale bar = 50 μm.
Fig. 10. Conchosporangia with branches, growing at 25°C, photoperiod 16:8 L:D and a photon fluence rate of 40 μmol photons m^{-2} s^{-1}. Scale bar = 50 μm.
Fig. 11. Conchosporangia mature after 60 days at 30°C, photoperiod 8:16 L:D and photon fluence rate of 20 μmol photons m^{-2} s^{-1}. Scale bar = 20 μm.
Fig. 12. Conchospore released after 60 days at 10°C, photoperiod 8:16 L:D and photon fluence rate of 20 μmol photons m^{-2} s^{-1}. Scale bar = 10 μm.

not significantly influence archeospore abundance ($P > 0.05$) (Table 2). The Tukey's *a posteriori* analysis showed that the abundance of archeospores differed significantly at temperatures of 25 and 30°C ($P < 0.001$). At 30°C there was a higher number of archeospores mm^{-2} than at 10, 15 and 20°C ($P < 0.001$), and at 25°C archeospores were more abundant per mm^{-2} than at 15 and 20°C ($P = 0.019$ and $P = 0.091$). The number of archeospores mm^{-2} of the conchocelis tufts was significantly different in the long photoperiod 16:8 L:D when compared with the neutral 12:12 L:D ($P = 0.001$) and short photoperiod 8:16 L:D ($P = 0.049$).



Figs 13–17. Gametophyte stage of the life history of *Porphyra hollenbergii.* Scale bar = 50 μm (Figs 13, 14) and 2 cm (Figs 15–17).
Fig. 13. Conchospore development 3 days after its release.
Fig. 14. Conchospores 1 week after release with a gametophyte differentiated by its bipolar growth.
Fig. 15. Pale yellow male gametophyte of *Porphyra hollenbergii* from Bahía Agua Verde strain after 3 months.
Fig. 16. Pale rose young gametophyte thalli after 2 months.
Fig. 17. Red- and green-colored female gametophyte thalli after 3 months.

Conchosporangia formation

The conchosporangia were formed at all positions on the conchocelis filaments (lateral, medial, apical). Between 10 and 20°C, the conchosporangia filaments did not branch and the cells had different morphologies: rectangular, cubic or elliptical (Figs 7–11). These filaments were more robust and densely branched at 25 and 30°C, with immature conchosporangial cells that were 35–40 μm long and 25–30 μm wide. The conchosporangia were present at week three and matured after week six. The optimal conditions for conchosporangial production were 30°C, under a photon fluence level of 20 μmol photons m^{-2} s^{-1} and at a short photoperiod 8:16 L:D (Fig. 20). However, released conchospores were found only after 6 weeks at 10°C (Fig. 12), under a photon fluence level of 20 μmol photons m^{-2} s^{-1} in a short photoperiod (8:16 L:D). The highest density of conchosporangia, ≈79 ± 0.093 mm^{-2}, was found at 25 and 30°C, under a photon fluence level of 10 and 20 μmol photons m^{-2} s^{-1} in a short photoperiod (8:16 L:D). The lowest values 0.05 ± 4.63 mm^{-2} of conchosporangia were found at 15 and 20°C, and at a day-neutral photoperiod (12:12 L:D). Three-way ANOVA showed significant differences between temperature ($P < 0.001$) and photoperiod ($P < 0.001$), but not photon fluence levels in the abundances of conchospores mm^{-2} ($P > 0.05$) (Table 3). The *a posteriori* Tukey's test showed that the abundance of conchosporangia at temperatures of 15, 25 and 30°C were different ($P < 0.05$) and differed from the other conditions. The abundance of conchosporangia mm^{-2} was not significantly different ($P = 0.083$) at 10 and 20°C. In addition, abundance of conchosporangia mm^{-2} was significantly different ($P < 0.05$) in all photoperiod treatments. The abundance of conchosporangia mm^{-2} between the photon fluence level combinations did not display any significant differences ($P > 0.05$).

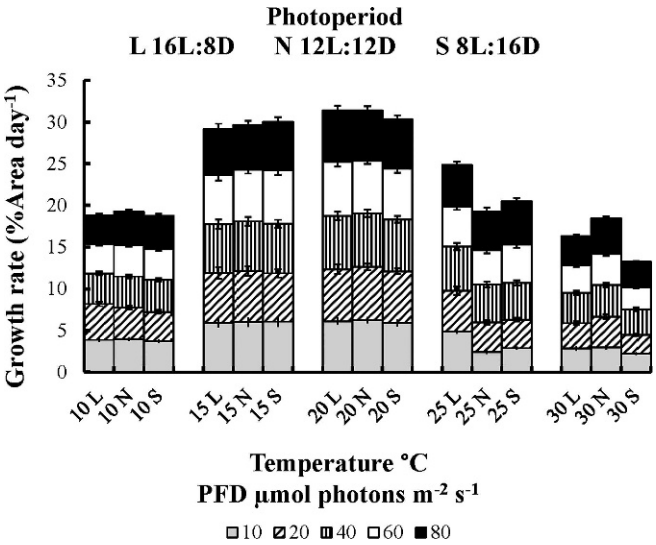


Fig. 18. *Porphyra hollenbergii.* Average growth rates of conchocelis under different combinations of temperatures (10, 15, 20, 25 and 30°C), photoperiod (16:8, 12:12 and 8:16 L:D) and photon fluence rate (10, 20, 40, 60 and 80 µmol photons m^{-2} s^{-1}).

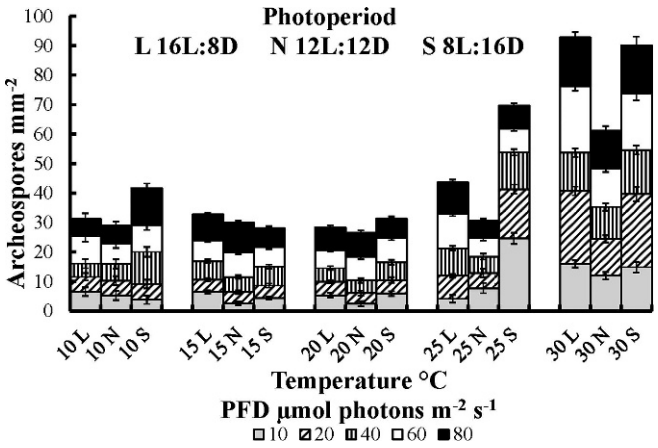


Fig. 19. Number of archeospores from the conchocelis phase of *Porphyra hollenbergii* under different combinations of temperature (10, 15, 20, 25 and 30°C), photoperiod (16:8, 12:12 and 8:16 L:D) and photon fluence rate (10, 20, 40, 60 and 80 µmol photons m^{-2} s^{-1}).

DISCUSSION

On the basis of the results presented, the life history of the dioecious species *P. hollenbergii* falls within the type IV classification of Notoya (1997). Only zygotosporangia and spermatangia were observed in the gametophytic phase. Archeospores, conchosporangia branches and conchospores were found in the conchocelis phase. Protothalli and protoplasts were not found as described by Cole & Conway (1980), Kornmann (1994) and Notoya (1997). No other structures (archeospores, neutral spores, agamospores or endosporangia) (Kornmann 1994; Nelson & Knight 1995; Nelson *et al* 1999) were found in the gametophytic phase, as observed for other dioecious species of *Porphyra* (Notoya 1997).

In the conchocelis phase, water temperature and photoperiod were the determining factors for the growth and development of reproductive structures as reported elsewhere for other species of *Porphyra* (Freshwater & Kapraun 1986; Waaland *et al.* 1990; Notoya 1997; Ruangchuary & Notoya 2003; Pereira *et al.* 2004, Tables 4–6). The lack of influence of photon fluence level on life history is also commonly reported in the literature for *Porphyra* spp. (Waaland *et al.* 1987).

The optimal temperature for growth of conchocelis of *P. hollenbergii* was between 15 and 20°C, which is similar to that reported for other subtropical species including *Porphyra spiralis* var. *amplifolia* E.C. Oliveira & J. Coll and *Porphyra vietnamensis* T. Tanaka & Pham-Hoàng Ho

Table 1. Three-way ANOVA on the effects temperature, photon fluence rates and photoperiod on the growth rates of the conchocelis phase of *Porphyra hollenbergii*.

Source of variation	df	Sum of squares	Mean square	*F*	*P*	Significance
Temperature	4	5.0870	1.2720	148.83	<0.001	*
Photon fluence rates	4	0.0472	0.0118	1.3800	0.239	NS
Photoperiod	2	0.0380	0.0190	2.2230	0.109	NS
Temperature × photon fluence rates	16	0.1150	0.0072	0.8450	0.634	NS
Temperature × photoperiod	8	0.0763	0.0095	1.1170	0.35	NS
Photon fluence rates × photoperiod	8	0.0050	0.0006	0.0734	1	NS
Temperature × photon fluence rates × photoperiod	32	0.0345	0.0011	0.1260	1	NS

* Significant at $P < 0.001$; NS, not significant.

Table 2. Three-way ANOVA on the effects temperature, photon fluence rates, and photoperiod on the number of archeospores from the conchocelis phase of *Porphyra hollenbergii*.

Source of variation	df	Sum of squares	Mean square	*F*	*P*	Significance
Temperature	4	1158.396	289.599	33.601	<0.001	*
Photon fluence rates	4	46.846	11.711	1.359	0.27	NS
Photoperiod	2	141.223	70.612	8.193	<0.001	*

* Significant at $P < 0.001$; NS, not significant.

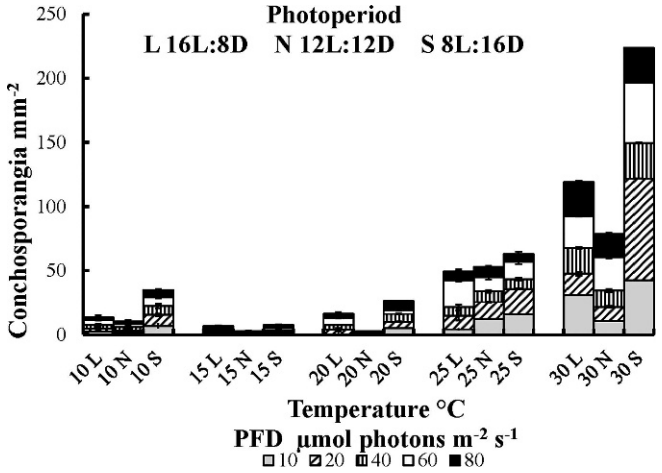


Fig. 20. Number of conchosporangia produced by *Porphyra hollenbergii* under different combinations of temperature (10, 15, 20, 25 and 30°C), photoperiod (16:8, 12:12 and 8:16 L:D) and photon fluence rate (10, 20, 40, 60 and 80 µmol photons m^{-2} s^{-1}).

(Table 4; Ruangchuary & Notoya 2003; Sahoo *et al.* 2006). Cool temperate species, such as *Porphyra miniata* (C. Agardh) C. Agardh (Chen *et al.* 1970), *Porphyra linearis* (Bird *et al.* 1972), *Porphyra purpurea* (Lu & Yarish 2010) and *Porphyra torta* (Waaland *et al.* 1987), have optimal growth between 5 and 15°C and photon fluence levels of 5–100 µmol photons m^{-2} s^{-1}. Other species, like *Porphyra seriata* Kjellman and *P. linearis* Greville (Israel *et al.* 1999; Kim & Notoya 2004) have the same optimum development as reported in our study. The conchocelis phase of *P. hollenbergii* develops when water temperatures are between 14 and 30°C (Blanco-Betancourt *et al.* 2004; Martínez-Díaz de León *et al.* 2006). However, this type of development is inhibited in September when the temperatures are above 30°C (Blanco-Betancourt *et al.* 2004; Martínez-Díaz de León *et al.* 2006). This growth response is similar to other seaweeds from the Gulf of California that have an alternate microscopic phase (such as in *Chondrachanthus squarrulosus* as described in Pacheco-Ruíz & Zertuche-González 1999).

The archeospores in the conchocelis phase of *P. hollenbergii* occurred under all tested experimental conditions. This strongly suggests that the conchocelis phase perennates throughout the year in the Gulf of California by reproducing itself via archeospores (Tseng & Chang 1956; Conway & Cole 1977; Chen *et al.* 1970), potentially an adaptation to subtropical environments. Archeospores of the conchocelis phase have not been reported in both tropical and temperate species with exception of *Porphyra abbottiae*, which produces archeospores only in one condition, 11°C, short photoperiod and 40 µmol photons $m^{-2}s^{-1}$ (Lindstrom *et al.* 2008).

In all the conditions tested, conchosporangial branches and conchosporangia were observed in *P. hollenbergii.* However, the best conditions for conchosporangia formation were found at 30°C, 12:12 L:D and under a photon fluence level of 40 µmol photons $m^{-2}s^{-1}$, which is similar to *Porphyra dioica* (Holmes & Brodie 2004) and *P. vietnamensis* (Sahoo *et al.* 2006) (Table 5). Conchospore release was found after 6 weeks as in other species of *Porphyra* (Waaland *et al.* 1983, 1990; Ávila *et al.* 1986; Freshwater & Kapraun 1986; Stekoll *et al.* 1999; Sidirelli-Wolff 1992; Notoya & Nagaura 1998; Kim 1999; Orfanidis 2001; Ruangchuary & Notoya 2003; Pereira *et al.* 2004; Sahoo *et al.* 2002, 2006). However, conchospore release only occurred between 10 and 15°C and at short day lengths, which correspond to winter conditions in the Gulf of California (Blanco-Betancourt *et al.* 2004; Martínez-Díaz de León *et al.* 2006). In other species, *Porphyra rosengurtii* (Kapraun & Luster 1980), *Porphyra columbina* (Ávila *et al.* 1986), *P. abbottiae* (Hannach & Waaland 1989), *P. vietnamensis,* Lewmanomont & Chittpoolkusol (1993), *Porphyra leucosticta* (Gargiulo *et al.* 1994; Orfanidis 2001), *Porphyra lacerata* (Notoya & Nagaura 1999),

Table 3. Three-way ANOVA on the effects of temperature, photon fluence rates and photoperiod on the number conchosporangia of *Porphyra hollenbergii.*

Source of variation	df	Sum of squares	Mean square	*F*	*P*	Significance
Temperature	4	11.466	2.867	144.399	<0.001	*
Photon fluence rates	4	0.151	0.0378	1.904	0.134	NS
Photoperiod	2	1.454	0.727	36.614	<0.001	*

* Significant at $P < 0.001$; NS, not significant.

Table 4. Comparative analysis of the optimal conditions for growth of the dioecious species of *Porphyra.*

Species[1]	Growth rates[2]	Photon fluence rates (µmol photon m^{-2} s^{-1})	Temperature (°C)	Photoperiod	References
P. dentata	6-mm diameter; ND	40, 10–25	20	14:10 &12:12 L:D	Kim 1999; Sahoo *et al.* 2002
P. dioica	20% area d^{-1}	25–75	15–20	8:16, 12:12 & 16:8 L:D	Pereira *et al.* 2004
P. lacerata	4-mm diameter	40	15–25	14:10 & 10:14 L:D	Notoya & Nagaura 1998
P. linearis	200-mm^2 diameter	10–20	15–20	16:8 L:D	Varela-Alvarez *et al.* 2004
P. pseudolanceolata	7.1% area d^{-1}	100	15	ND	Waaland *et al.* 1990
P. pseudolinearis	4.3-mm diameter; 8.8% V d^{-1}	40, 160	7–20	14:10 & 8:16 L:D	Kim 1999; Stekoll *et al.* 1999
P. hollenbergii	6.5% area d^{-1}	40–60	15–20	12:12 L:D	This work

[1] In all the species the original name was preserved in all the tables even if it has been changed.
[2] ND, not done; V, volume.

Table 5. Comparative analysis of the optimal conditions for conchosporangia production in the dioecious species of *Porphyra*.

Species[1]	Photon fluence rates (μmol photon m^{-2} s^{-1})	Temperature (°C)	Photoperiod	Time (days)	References
P. angusta	20–80	27–29	9:15 & 14:10 L:D	14	Chiang & Wang 1980
P. dentata	10–80	10–30, 10–25	14:10 & 10:14; 12:12 L:D	42, 14	Kim 1999; Sahoo *et al.* 2002
P. dioica	25–75	5–20, 10–15	16:8; 8:16 & 12:12 L:D	21–42, 35–50	Holmes & Brodie 2004; Pereira *et al.* 2004
P. koreana	10–80	15–25	14:10 & 10:14 L:D	14	Kim & Notoya 2003
P. lacerata	40	25	14:10 & 10:14 L:D	35	Notoya & Nagaura 1998
P. linearis	5–40	15–20	16:8 L:D	30	Varela-Alvarez *et al.* 2004
P. pseudolanceolata	35–40	6–10	12:12 & 14:10 L:D	14–21, 30–40	Waaland *et al.* 1990
P. pseudolinearis	10–80	10–25	14:10 L:D	49	Kim 1999; Park *et al.* 2003
P. hollenbergii	20–40	10	8:16 L:D	40–50	This work

[1] In all the species the original name was preserved in all the tables even if it has been changed.

Table 6. Comparative analysis of the optimal conditions for conchospore release in the dioecious species of *Porphyra*.

Species[1]	Photon fluence rates (μmol photon m^{-2} s^{-1})	Temperature (°C)	Photoperiod	Time (days)	References
P. dentata	10–80	20 to 15	12:12, 10:14 L:D	14	Kim 1999; Sahoo *et al.* 2002
P. lacerata	40	25 to 10–15–20	14:10, 10:14 L:D	7–14	Notoya & Nagaura 1998
P. linearis	20	20	16:8 L:D	40–50	Varela-Alvarez *et al.* 2004
P. pseudolanceolata	30–40	6–10	12:12, 14:10 L:D	14–21, 30–40	Waaland *et al.* 1990
P. pseudolinearis	10–80	20 to 15	10:14 L:D	14	Kim 1999
P. hollenbergii	20	10	8:16 L:D	45–52	This work

[1] In all the species the original name was preserved in all the tables even if it has been changed.

Porphyra moriensis (Notoya & Miyashita 1999) and *P. linearis* (Katz *et al.* 2000), conchospore release occurs after a decrease in temperature and a change in photoperiod, which differs from our study (Table 6).

We found that water temperature was the main limiting factor for the conchocelis growth. However, it is the combination of photoperiod and high water temperatures that are the environmental conditions that appear to control the development of archeospores and conchospores. The foliar phase only develops below 25°C (López-Vivas, unpublished data) and when water temperature increases above that level the alternate phase appear to survive in more extreme conditions in the gulf. *Porphyra hollenbergii* life history is controlled by a variety of factors for each stage of its life history (vegetative and reproductive in the conchocelis phase), thereby strongly suggesting the physical influence of the habitat on the species. However, the possibility that conchocelis is present continuously through the year needs to be re-evaluated as an adaptative mechanism for the fluctuating changes in the Gulf of California oceanographic conditions (Kahru *et al.* 2004; Herrera-Cervantes *et al.* 2007).

ACKNOWLEDGEMENTS

This study was supported by the Mexican Council for the Sciences and Technology (CONACYT-50173Q) that granted a PhD scholarship (CONACYT 157780) and the Autonomous University of Baja California (UABC-0572). We also thank all those who participated in the laboratory work, as well as Alberto Gálvez T. and Biology students at UABC and personnel from UABCS herbarium for their assistance during the fieldwork. We thank the support of the Connecticut Sea Grant College Program, the National Marine Aquaculture Initiative (National Oceanic and Atmospheric Administration, US Department of Commerce) and US Agency for International Development Training, Internships, Exchanges, and Scholarships program between the Universidad Autónoma de Baja California and the University of Connecticut (UABC-UCONN).

REFERENCES

Aguilar-Rosas R., Aguilar-Rosas L.E., Sánchez-Rodríguez I., Broom J.E. & Nelson W.A. 2007. Morfología y distribución de *Porphyra hollenbergii* (Bangiaceae, Rhodophyta) en la costa Pacífico de México. *Revista Mexicana de Biodiversidad* 78: 351–357.

Álvarez-Borrego S. 1983. Gulf of California. In: *Estuaries and enclosed seas* (Ed. by B.H. Ketchum), pp. 427–429. Elsevier, Amsterdam.

Álvarez-Borrego S. & Lara-Lara J.R. 1991. The physical environment and primary productivity of the Gulf of California. *American Association of Petroleum Geologists Memori* 47: 555–567.

Álvarez-Borrego S., Rivera J.A., Gaxiola-Castro G., Acosta-Ruiz M.J. & Schwartzlose R.A. 1978. Nutrientes en el Golfo de California. *Ciencias Marinas* 5: 21–36.

Andersen R.A., Berges J.A., Harrison P.J. & Watanabe M.M. 2005. Appendix A. Recipes for freshwater and seawater media. In: *Algal culturing techniques* (Ed. by R.A. Andersen), pp. 429–543. Elsevier Academic Press.

Ávila M., Santelices B. & McLachlan J. 1986. Photoperiod and temperature regulation of the life history of *Porphyra columbina* (Rhodophyta, Bangiales) from central Chile. *Canadian Journal of Botany* 64: 1867–1872.

Bird C.J., Chen C.-M. & McLachlan J.R. 1972. The culture of *Porphyra linearis* (Bangiales, Rhodophyta). *Canadian Journal of Botany* 50: 1859–1863.

Blanco-Betancourt R., Pacheco-Ruíz I., Guzmán-Calderón J.M., Zertuche-González J.A., Chee-Barragán A., Martínez-Díaz de León A., Gálvez-Telles A. & López-Vivas J.M. 2004. Base de datos de la temperatura del agua de mar en seis bahías de la costa noroccidental del Golfo de California, México. In: *Reportes Técnicos* (Ed. by C. Marinas), pp. 1–35. Instituto de Investigaciones Oceanológicas, Universidad Autónoma de Baja California, Ensenada, México.

Bold H.C. & Wynne M.J. 1985. *Introduction to the algae. Structure and reproduction,* ed. 2. Englewood Cliffs, NJ: Prentice-Hall, 706 pp.

Chen L.C.-M., Edelstein T., Ogata E. & McLachlan J. 1970. The life history of *Porphyra miniata*. *Canadian Journal of Botany* 48: 385–389.

Chiang Y.-M. & Wang J.-C. 1980. A study on the production of conchosporangia in the conchocelis phase of *Porphyra angusta* Okamura et Ueda. *Phycologia* 19: 20–24.

Chopin T., Yarish C., Wilkes R.J., Belyea E., Lu S. & Mathieson A.C. 1999. Developing *Porphyra*/salmon integrated aquaculture for bioremediation and diversification of the aquaculture industry. *Journal of Applied Phycology* 12: 463–472.

Cole K.M. & Conway E. 1980. Studies in the Bangiaceae: reproductive modes. *Botanica Marina* 23: 545–553.

Conway E. & Cole K.M. 1977. Studies in the Bangiaceae: structure and reproduction of the *Conchocelis* of *Porphyra* and *Bangia* in culture (Bangiales, Rhodophyta). *Phycologia* 16: 205–216.

Dawson Y.E. 1944. *The marine algae of the Gulf of California.* The University of Southern California Press, Los Angeles, CA. 452 pp.

Dawson Y.E. 1953. Marine red algae of Pacific Mexico. Part I. Bangiales to Corrallinaceae Subf. Corrallinaideae. University of Southern California, Los Angeles, CA. 258 pp.

DeBoer J.A., Guigli H.J., Israel T.L. & Elia C.F.D. 1978. Nutritional studies of two red algae. I. Growth rate as a function of nitrogen source and concentration. *Journal of Phycology* 14: 261–266.

Drew K.M. 1954. Studies in the Bangioideae. III. The life-history of *Porphyra umbilicalis* (L.) Kütz. Var. *lacinata* (Lightf.) J. Ag. *Annals of Botany* 18: 183–211.

Freshwater D.W. & Kapraun D.F. 1986. Field, culture and cytological studies of *Porphyra carolinensis* Coll et Cox (Bangiales, Rhodophyta) from North Carolina. *Japan Journal of Phycology* 34: 251–262.

Gargiulo G.M., De Masi F., Genovese G. & Tripodi G. 1994. Karyology and effects of temperature and photoperiod on the life-cycle of *Porphyra leucosticta* Thuret in Le Jolis (Bangiales, Rhodophyta) from the Mediterranaen Sea. *Japan Journal of Phycology* 42: 271–280.

Hannach G. & Waaland J.R. 1989. Growth and morphology of young gametophytes of *Porphyra abbottae* (Rhodophyta): effects of environmental factors in culture. *Journal of Phycology* 25: 247–254.

Hawkes M.W. 1977. A field, culture and cytological study of *Porphyra gardneri* (Smith & Hollenberg) comb. nov., (=*Porphyrella gardneri* Smith & Hollenberg), (Bangiales, Rhodophyta). *Phycologia* 16: 457–469.

Hawkes M.W. 1978. Sexual reproduction in *Porphyra gardneri* (Smith et Hollenberg) Hawkes (Bangiales, Rhodophyta). *Phycologia* 17: 329–353.

Hawkes M.W. 1981. *Porphyra nereocystis* and *Porphyra thuretii* (Rhodophyta): Gametophyte morphology, distribution, and occurrence. *Syesis* 14: 97–108.

Herrera-Cervantes H., Lluch-Cota D.B., Lluch-Cota S.E. & Gutiérrez de Velasco G. 2007. The ENSO signature in sea-surface temperature in the Gulf of California. *Journal of Marine Research* 65: 589–605.

Hollenberg G.J. 1958. Culture studies of marine algae. III. *Porphyra perforata*. *American Journal of Botany* 45: 653–656.

Holmes M.J. & Brodie J. 2004. Morphology, seasonal phenology and observations on some aspects of the life history in culture of *Porphyra dioica* (Bangiales, Rhodophyta) from Devon, UK. *Phycologia* 43: 176–188.

Israel A., Katz S., Dubinsky Z., Merrill J.E. & Friedlander M. 1999. Photosynthetic inorganic carbon utilization and growth of *Porphyra linearis* (Rhdodophyta). *Journal of Applied Phycology* 11: 447–453.

Johnson M.E. & Ledesma-Vasquez J. 2009. *Atlas of coastal ecosystems in the western Gulf of California*. The University of Arizona Press, Tucson. 192 pp.

Kahru M., Marinone S.G., Lluch-Cota S.E., Parés-Sierra A. & Mitchell G. 2004. Ocean color variability in the Gulf of California: scales from the El Niño–La Niña cycle to tides. *Deep Sea Research II* 51: 139–146.

Kapraun D.F. & Luster D.G. 1980. Field and culture studies of *Porphyra rosengurtii* Coll et Cox (Rhodophyta, Bangiales) from North Carolina. *Botanica Marina* 23: 449–457.

Katz S., Kizner Z., Dubinsky Z. & Friedlander M. 2000. Responses of *Porphyra linearis* (Rhodophyta) to environmental factors under controlled culture conditions. *Journal of Applied Phycology* 12: 535–542.

Kim N.-G. 1999. Culture studies of *Porphyra dentata* and *P. pseudolinearis* (Bangiales, Rhodophyta), two dioecious species from Korea. *Hydrobiologia* 398/399: 127–135.

Kim N.-G. & Notoya M. 2003. Life history of *Porphyra seriata* Kjellman (Bangiales, Rhodophyta) from Korea in culture. *Proceedings of the International Seaweed Symposium* 17: 435–442.

Kornmann P. 1994. Life histories of monostromatic *Porphyra* species as a basis for taxonomy and classification. *European Journal of Phycology* 29: 69–71.

Krishnamurthy V. 1972. A revision of the species of algal genus *Porphyra* occurring on the Pacific Coast of North America. *Pacific Science* 26: 24–49.

Lewin J. 1966. Silicon metabolism in diatoms. V. Germanium dioxide, a specific inhibitor of diatom growth. *Phycologia* 6: 1–12.

Lewmanomont K. & Chittpoolkusol O. 1993. Life cycle of *Porphyra vietnamensis* Tanaka & Pham-Hoang Ho from Thailand. In: *Proceedings XIV International Seaweed Symposium* (Ed. by A.R.O. Chapman, M.T. Brown & M. Lahaye), pp. 397–400. Kluwer, Brest, France.

Lindstrom S.C., Conitz J.M., Hall S. & Stekoll M.S. 2008. Induction of conchospore release: ecotypic variation in northeast Pacific species of *Porphyra*. *Journal of Applied Phycology* 20: 331–340.

Lu S. & Yarish C. 2010. Photoperiod and temperature interact on conchocelis development of *Porphyra purpurea* (Rhodophyta: Bangiales). *Journal of Applied Phycology* 23: 89–96.

Lynch M.D.J., Sheath R.G. & Müller K.M. 2008. Phylogenetic position and ISSR-estimated intraspecific genetic variation of *Bangia maxima* (Bangiales, Rhodophyta). *Phycologia* 47: 599–613.

Martínez E. 1990. The Conchocelis phase of *Porphyra* (Rhodophyta) in the intertidal of San Juan Island, Washington, USA. *Phycologia* 29: 391–395.

Martínez-Díaz de León A., Pacheco-Ruíz I., Delgadillo-Hinojosa F., Zertuche-González J.A., Chee-Barragán R., Blanco-Betancourt R., Guzman-Calderon J.M. & Galvez-Telles A. 2006. Spatial and temporal variability of the sea surface temperature in the Ballenas-Salsipuedes Channel (central Gulf of California). *Journal of Geophysical Research* 111: 1–7.

Monotilla W.D. & Notoya M. 2004. Morphological and physiological responses of *Porphyra suborbiculata* Kjellman (Bangiales, Rhodophyta) blades from five localities. *Botanica Marina* 47: 323–334.

Nelson W.A. & Knight G.A. 1995. Endosporangia – a new form of reproduction in the genus *Porphyra* (Bangiales, Rhodophyta). *Botanica Marina* 38: 17–20.

Nelson W.A. & Knight G.A. 1996. Life history in culture of the obligate epiphyte *Porphyra subtumens* (Bangiales, Rhodophyta) endemic to New Zealand. *Phycological Research* 44: 19–25.

Nelson W.A., Brodie J. & Guiry M.D. 1999. Terminology used to describe reproduction and life history stages in the genus *Porphyra* (Bangiales, Rhodophyta). *Journal of Applied Phycology* 11: 407–410.

Notoya M. 1997. Diversity of life history in the genus *Porphyra. Natural History Research Special Issue* 3: 47–56.

Notoya M. & Miyashita A. 1999. Life history, in culture, of the obligate epiphyte *Porphyra moriensis* (Bangiales, Rhodophyta). *Hydrobiologia* 398/399: 121–125.

Notoya M. & Nagaura K. 1998. Life history and growth of the epiphytic thallus of *Porphyra lacerata* (Bangiales, Rhodophyta) in culture. *Algae* 13: 207–211.

Notoya M. & Nagaura K. 1999. Studies on the growth, in culture, of two forms of *Porphyra lacerata* from Japan. *Hydrobiologia* 398/399: 299–303.

Notoya M., Kikuchi N., Aruga Y. & Miura A. 1992a. *Porphyra kinositae* (Yamada et Tanaka) Fukuhara (Bangiales, Rhodophyta) in culture. *Japan Journal of Phycology* 40: 273–278.

Notoya M., Kihuchi N., Matsuo M., Aruga Y. & Miura A. 1992b. Culture studies of tour species of *Porphyra* (Rodophyta) from Japan. Abstracts and Programme of XIVth International Seaweed Symposium. 109 pp.

Notoya M., Kikuchi N., Aruga Y. & Miura A. 1993a. Life history of *Porphyra tenuipedalis* Miura (Bangiales, Rhodophyta) in culture. *La Mer* 31: 125–130.

Notoya M., Kikuchi N., Matsuo M., Aruga Y. & Miura A. 1993b. Culture studies of four species of *Porphyra* (Rhodophyta) from Japan. *Nippon Suisan Gakkaishi* 59: 431–436.

Orfanidis S. 2001. Cultuire studies of *Porphyra leucosticta* (Bangiales, Rhodophyta) from the Gulf of Thessaloniki, Greece. *Botanica Marina* 44: 533–539.

Pacheco-Ruíz I. & Zertuche-González J.A. 1999. Population structure and reproduction of the carrageenophyte *Chondracanthus pectinatus* in the Gulf of California. *Hydrobiologia* 398/399: 159–165.

Pacheco-Ruíz I., Becerril-Bobadilla F., Zertuche-González J.A., Chee-Barragan A., Gálvez Telles A. & Blanco-Betancourt R. 2003. Effects of El Niño on beds of *Ulva lactuca* along the northwest coast of the Gulf of California, Mexico. *Geofísica Internacional* 42: 447–453.

Park C.S., Hwang E.K. & Sohn C.H. 2003. A stable seeding method for *Porphyra pseudolinearis* Ueda (Rhodophyta): developing a new species for cultivation of *Porphyra* in Korea. *Aquaculture Research* 34: 895–898.

Pereira R. & Yarish C. 2010. The role of *Porphyra* in the sustainable culture systems: physiology and applications. In: *Seaweeds and their role in globally changing environments* (Ed. by A. Israel, R. Einav & J. Seckbach), pp. 339–354. Springer, New York.

Pereira R., Sousa-Pinto I. & Yarish C. 2004. Field and culture studies of the life history of *Porphyra dioica* (Bangiales, Rhodophyta) from Portugal. *Phycologia* 43: 756–767.

Polne-Fuller M. & Gibor A. 1990. Developmental studies in *Porphyra* (Rhodophyceae). III. Effect of culture conditions on wall regeneration and differentiation of protoplasts. *Journal of Phycology* 26: 674–682.

Provasoli L. 1968. Media and prospects for the cultivation of marine algae. In: *Cultures and collections of algae* (Ed. by A. Watanabe & A. Hattori), pp. 63–75. Japan Society Plant Physiology, Hakone, Japan.

Ruangchuary R. & Notoya M. 2003. Physiological responses of blade and conchocelis of *Porphyra vietnamensis* Tanaka et Pham-Hoang Ho (Bangiales, Rhodophyta) from Thailand in culture. *Algae* 18: 21–28.

Sahoo D., Tang X. & Yarish C. 2002. *Porphyra* the economic seaweed as a new experimental system. *Current Science* 83: 1313–1316.

Sahoo D.B., Baweja P. & Kushwah N. 2006. Developmental studies in *Porphyra vietnamensis:* a high-temperature resistant species from the Indian Coast. *Journal of Applied Phycology* 18: 279–286.

Scrosati R. 2001a. Population dynamics of *Caulerpa sertularioides* (Chlorophyta: Bryopsidales) from Baja California, Mexico, during El Niño and La Niña years. *Journal of the Marine Biological Association of the United Kingdom* 81: 721–726.

Scrosati R. 2001b. Predicting the impact of El Niño on seaweeds from Baja California, Mexico. *Marine Biological Association News* 26: 11.

Sidirelli-Wolff M. 1992. The influence of temperature, irradiance and photoperiod on the reproductive life history of *Porphyra leucosticta* (Bangiales, Rhodophyta) in laboratory culture. *Botanica Marina* 35: 251–257.

SigmaStat Version 3.5, Systat Software, Inc.

Sokal R.R. & Rohlf F.J. 1995. *Biometry: the principles and practice of statistics in biological research*. W. H. Freeman, New York. 887 pp.

Stekoll S.M., Lin R. & Lindstrom S.C. 1999. *Porphyra* cultivation in Alaska: conchocelis growth of three indigenous species. *Hydrobiologia* 398/399: 291–297.

Tseng C.K. & Chang T.J. 1956. Conditions of *Porphyra* conchospores formation and discharge and the discharge rhythm. *Acta Botanica Sinica* 5: 33–48.

Varela-Alvarez E., Stengel D.B. & Guiry M.D. 2004. The use of image processing in assessing conchocelis growth and conchospore production in *Porphyra linearis. Phycologia* 43: 282–287.

Waaland J.R., Dickson L.G., Duffield J.E. & Burzycki G.M. 1983. Research on *Porphyra aquaculture. Beihefte zur Nova Hedwigia* 83: 124–131.

Waaland J.R., Dickson L.G. & Duffield J.E. 1987. Conchocelis growth and photoperiodic control of conchospore release in *Porphyra torta* (Rhodophyta). *Journal of Phycology* 23: 399–406.

Waaland J.R., Dickson L.G. & Duffield C.S. 1990. Conchospore production and seasonal occurrence of some *Porphyra* species (Bangiales, Rhodophyta) in Washington State. *Hydrobiologia* 204/205: 453–459.

West J.A. & Guiry M.D. 1981. A life history study of *Gigartina johnstonii* (Rhodophyta) from the Gulf of California. *Botanica Marina* 24: 205–211.

Zar J.H. 1999. *Biostatistical analysis*. Prentice Hall, Englewood Cliffs, New Jersey. 663 pp.

Received 11 August 2010; accepted 23 February 2011
Associate editor: Wendy Nelson