

# Heteromorphic and isomorphic alternations of generations in macroalgae as adaptations to a seasonal environment

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## ABSTRACT

**Background:** Some macroalgae (seaweeds) have haploid and diploid life forms that differ greatly in size and morphology (heteromorphic life cycle). Others have very similar haploid and diploid life forms (isomorphic life cycle).

**Questions:** What are the optimal reproductive cycles for a heteromorphic species and for an isomorphic species? Under what circumstances will a heteromorphic life cycle be more advantageous than an isomorphic life cycle.

**Mathematical model:** We develop mathematical models for an optimal life cycle in one environment where productivity changes seasonally. The beginning and the end of generations are chosen to maximize the population growth rate.

**Key assumption:** The variety of life cycles observed among macroalgae reflects adaptations to seasonally changing environments.

**Conclusions:** (1) In heteromorphic species, the generation with a large body size should appear in the productive season and the generation with a small body size in the unproductive season. (2) In isomorphic species, algae of different generations should mature when body size reaches a certain common value, regardless of the environment of the generation. However, the length of a generation may vary greatly between seasons. (3) In a strongly seasonal environment, a heteromorphic life cycle is more profitable than an isomorphic life cycle.

*Keywords:* alternation of generations, heteromorphic life cycle, isomorphic life cycle, life-history diversity, macroalgae, seasonal environment.

## INTRODUCTION

Seaweeds, or macroalgae, have very diverse life cycles (Wynne and Loiseaux, 1976; Umezaki, 1977; Nakahara, 1986; Verges *et al.*, 2008). Especially notable is the difference between a heteromorphic life cycle and an isomorphic life cycle. In both life cycles, haploid and diploid generations alternate. However, in heteromorphic species, the size of the multicellular body is very

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different between haploid and diploid generations. For example, in brown algae *Undaria pinnatifida* (Hori, 1993), the large body is diploid and the minute body is haploid, whereas in brown algae *Scytosiphon lomentaria* (Hori, 1993), the large body is haploid and the small one diploid. In contrast, in an isomorphic species such as brown algae *Dictyota dichotoma* (Hori, 1993), haploid and diploid generations are very similar in size and morphology of the multicellular body.

These different life cycles are observed among brown algae (*Undaria pinnatifida*, *Scytosiphon lomentaria*, *Dictyota dichotoma*), among green algae (*Derbesia marina*, *Bryopsis plumosa*, *Ulva pertusa*), and among red algae (*Palmaria palmata*, *Porphyra yezoensis*, *Gelidium elegans*) (Hori, 1993; Yoshida, 1998; Ohno, 2004). This phylogenetic distribution suggests that these differences have evolved many times within distinct groups of species, and that they are likely to be the outcomes of adaptation to the environment, rather than evolutionarily preserved traits.

In a species with heteromorphic alternation of generations, the large-sized generation tends to be in the productive season (i.e. winter) and the small-sized generation tends to be in the unproductive season (i.e. summer). This is true whether the large-sized generation is diploid, as in *Undaria pinnatifida*, or haploid, as in *Scytosiphon lomentaria* (Hori, 1993). In contrast, in the species with isomorphic alternation of generations, both generations are often observed all year round (Nakahara, 1986). They tend to have multiple generations in a single growing season (Katada, 1963; Edwards, 1969, 1970; Nakahara, 1986).

This suggests that life-history patterns among macroalgae might be outcomes of adaptation to a seasonally changing environment. If this is the case, isomorphic alternation of generations should be more suited to the environment with a long season favourable for growth, whereas heteromorphic species would be more suited to a strongly seasonal environment. This conjecture is supported by the observed latitudinal distribution in the fractions of the two types: Nakahara and Masuda (1971) studied the horizontal distribution of green and brown marine macroalgae at 26 localities around the coast of Japan and found that the ratio of the number of species with isomorphic alternation of generations (or no alternation of generations) to the number of species with heteromorphic alternation of generations was higher at low latitude (i.e. south) than at high latitude (i.e. north).

The schedule of life-history events as an outcome of evolutionary adaptation has been discussed for insects (Iwasa, 1991; Iwasa *et al.*, 1992, 1994). Univoltine insects have a single generation and bivoltine insects have two generations in a year. By noting that the larval feeding period is the most strongly constrained by available resources, Iwasa *et al.* (1992) examined the timing of the beginning and the end of the larval period. The model showed that a univoltine life cycle is more advantageous than a bivoltine life cycle at higher latitude. In many marine invertebrates, a generation is composed of a planktonic larval stage and a benthic adult stage. In helminth parasites, to complete the life cycle an individual must go through multiple hosts, such as an intermediate host and definitive host. Iwasa and Wada (2006) discussed the optimal timing of life-history events for species with complex life cycles, and examined the condition in which a life cycle utilizing multiple habitats or multiple hosts is more advantageous than one using a single habitat or a single host. However, their analysis was restricted to non-seasonal environments.

In evolutionary genetics, diploid–haploid alternation of generations has been discussed in terms of the genetic effects of ploidy. The diploid phase is dominant among advanced taxa in terrestrial plants and animals with a complex body structure (Valero *et al.*, 1992; Mable and Otto, 1998). The possible advantages of diploidy over haploidy in forming the major life form

include: diploids can mask recessive deleterious mutations by compensating with a second allele (Crow and Kimura, 1965), accumulate new beneficial mutations at a higher rate (Paquin and Adams, 1983), or evolve more rapidly (Lewis and Wolpert, 1979). On the other hand, many extant taxa are haploid or haploid–diploid, and strong adaptive benefits of diploidy are unable to explain the evolution and persistence of haploids and haploid–diploids (Mable and Otto, 1998). Another evolutionary aspect related to haploid–diploids is the advantages of a biphasic life cycle (Willson, 1981; Mable and Otto, 1998). For example, Hughes and Otto (1999) hypothesized that niche differences between haploid and diploid phases may cause the evolution of biphasic life cycles.

In the present paper, we focus on the ecological adaptation of life cycles of macroalgae in a seasonal environment, under the constraints that the life cycle is biphasic (i.e. the offspring of a diploid body is haploid and the offspring of a haploid body is diploid) and that the life form is linked with the genome (i.e. diploid and haploid can either have vastly different life forms or have similar life forms). We do not assume an inherent difference between being diploid and being haploid.

We develop mathematical models for the optimal life cycle in the environment where productivity changes seasonally. The start and the end of generations are chosen to maximize the population growth rate. Then we discuss the condition in which heteromorphic or isomorphic species are more advantageous than the other.

### MODEL

For simplicity of calculation, we assume that the focal species is monocarpy, or of a single reproductive type. When an algal body reaches maturation, it uses up all the resources for reproduction and dies. We also assume that the sexual generation is hermaphroditic.

In marine algae, body size is a good indicator of reproductive ability as well as growth rate, because the resources required for growth per day increase with body size. Let  $W$  be body size. Based on a comparison of a range of species, metabolic rates are known to depend on body size as power functions of body size, proportional to  $W^\beta$ , and the power  $\beta$  is often 0.75 in the case of animals (Kleiber, 1947), plants (Prothero, 1979), and microbes (Wilkie, 1977). Since the power is less than 1, the rates of respiration, assimilation, growth, and other life processes increase with body size  $W$  but at a slower rate than body size itself. Hence the metabolic rate per unit body size becomes slower as size increases. We here assume that the growth rate of body size is a power function of body sizes, and that power  $\beta$  is 0.75:

$$\frac{dW}{dt} = f(t)W^\beta. \quad (1a)$$

The proportionality coefficient  $f(t)$  depends on the day of the year in which there is a seasonal change in the environment:

$$f(t) = f_0 \exp \left[ a \left( \cos \left( 2\pi \frac{t - t_1}{T} \right) - 1 \right) \right], \quad (1b)$$

where  $t$  is the day and  $T$  is the length of the year. This function reflects all the factors that would affect seasonal changes of algal metabolism (temperature, nutrient availability, grazing intensity, etc.). Growth rate is the fastest when  $t = t_1$ , which is the most productive season for algae (i.e. winter), and it is the slowest when  $t = t_1 - T/2$ , which is the least

productive season for algae (summer). Here,  $a$  indicates the magnitude of seasonality in growth rate  $f(t)$ .

We assume that mortality is independent of body size, as confirmed for inter-tidal red algae (Camus, 1992). The daily mortality is denoted by  $m$ . Hence, survivorship during the individual's lifetime is denoted by:  $\exp[-m(\text{lifetime})]$ .

When the individual matures, it produces eggs or spores of the next generation and dies. For simplicity, we call both eggs and spores 'eggs' in the following. Let  $W(t)Q$  be the amount of resources for reproduction, where  $Q$  is the fraction of body mass available for producing eggs or spores ( $0 < Q < 1$ ). Let  $\omega_{\text{next}}$  be the size of an egg in the next generation. The number of eggs to be produced is  $W(t)Q/\omega_{\text{next}}$ . Only a small fraction of eggs can settle successfully into a suitable habitat. Settlement success is denoted by  $S$  ( $0 < S < 1$ ). Hence the reproductive success of an alga is given by:

$$\left[ \begin{array}{c} \text{reproductive} \\ \text{success} \end{array} \right] = \frac{W(t)QS}{\omega_{\text{next}}}. \quad (2)$$

We assume that the time required for egg incubation, and the time for a newly hatched larva to settle into its habitat, are rather short.

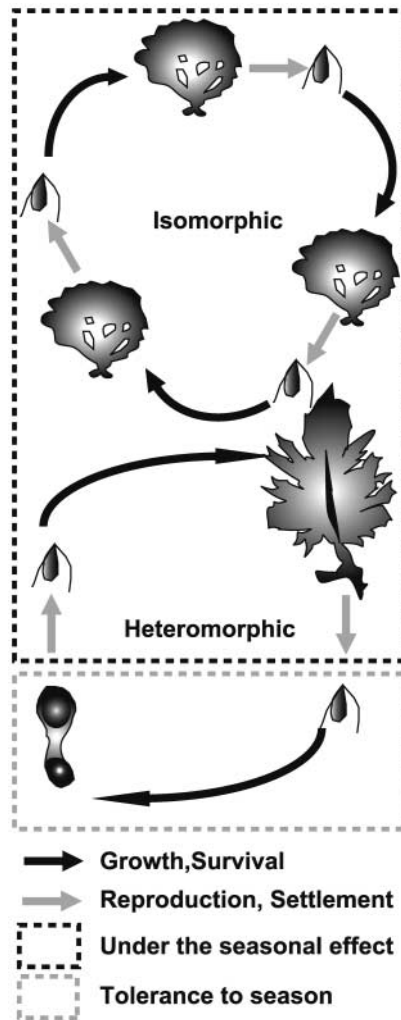
To evaluate the adaptedness of different types of life cycle of macroalgae, we calculate the expected rate of population growth in a year. A year may include multiple generations. In this paper, we consider two different types of life cycles of macroalgae: heteromorphic and isomorphic alternations of generations, as illustrated in Fig. 1.

### Heteromorphic life cycle

We first consider the heteromorphic life cycle. We assume that there are two generations in a year. The suffixes (1 or 2) of parameters ( $\omega$ ,  $m$ ,  $Q$ , and  $S$ ) distinguish generations within a year. The first generation has a large body and experiences fast growth rate, acquiring energy and nutrients from the environment. The growth rate is strongly affected by seasonal changes of the environment, and it also suffers a risk of biomass loss and mortality due to herbivory or physical disturbances. In contrast, the second generation has a very small body hiding within a small space, such as within an oyster shell (Hori, 1993), in which the alga is protected from herbivores and physical disturbance. The second generation has a slower growth rate but suffers a smaller daily mortality than the first generation.

Let  $x$  be the day on which the first generation starts to grow, and let  $y$  be the day on which the first generation matures and gives birth to the second generation. The second generation starts its life at  $y$  and continues to grow until day  $x + T$ , the same day  $x$  in the following year. At  $x + T$ , the second generation reproduces and gives birth to the first generation in the next year. We assume that the first generation starts to grow after the most unproductive season ( $t_1 - T/2 < x$ ).

Body size follows the differential equation:  $dW_1/dt = f(t)W_1^\beta$  from  $t = x$  (the initial size is  $\omega_1$ ) to  $t = y$ . Survivorship until maturation is  $e^{-m_1(y-x)}$ . The number of individuals in the second generation that are produced by an adult of the first generation and can settle safely is  $W_1(y)Q_1S_1/\omega_2$ . The second generation grows from  $t = y$  (the initial size is  $\omega_2$ ) to  $t = T + x$ , and body size follows the differential equation:  $dW_2/dt = g_0W_2^\beta$ . We assume that growth efficiency is a constant  $g_0$  because the hiding generation is protected from the seasonal environmental changes and disturbances (herbivory or physical disturbance). We also



**Fig. 1.** Heteromorphic and isomorphic alternation of generations. The heteromorphic life cycle includes two generations in a year. The first generation produces a large algal body and is strongly affected by seasonal change of environment. The second generation remains small in size and is not affected by seasonal changes. The isomorphic life cycle includes  $k^*$  generations in a year. All generations form a fast-growing large algal body and are affected by seasonal change of environment.

assume that the growth rate of the second generation is slower than that of the first generation:  $g_0 < f(t)$  holds for all  $t$ . On the other hand, daily mortality is less in the second generation than in the first generation ( $m_2 < m_1$ ). Environmental resistance and defence against herbivores differ between generations (Nakahara, 1986; Verges *et al.*, 2008). Survivorship until maturation is  $e^{-m_2(T+x-y)}$ . The expected size of the next generation produced by an adult of the second generation is  $W_2(x+T)Q_2S_2/\omega_1$ .

The population growth rate per year is given as:

$$\begin{aligned}
\phi_h(x, y) &= \frac{W_1(y)Q_2S_2}{\omega_2} e^{-m_2(T+x-y)} \frac{W_2(T+x)Q_1S_1}{\omega_1} e^{-m_1(y-x)} \\
&= \frac{Q_1Q_2S_1S_2}{\omega_1\omega_2} e^{-m_2T} \left( (1-\beta) \int_x^y f(t)dt + \omega_1^{1-\beta} \right)^{\frac{1}{1-\beta}} \\
&\quad \times \left( (1-\beta)g_0(T+x-y) + \omega_2^{1-\beta} \right)^{\frac{1}{1-\beta}} e^{-(m_1-m_2)(y-x)}.
\end{aligned} \tag{3}$$

The annual rate of population growth  $\phi_h$  is a function of dates for the beginning and end of two generations:  $x$  and  $y$ . We consider the optimal choices of  $x$  and  $y$  that achieve the maximum of  $\phi_h$ .

#### *Optimal timing of heteromorphic alternation of generations*

Candidates for the optimal timing ( $x^*$ ,  $y^*$ ) are found by calculating the partial derivatives of  $\ln\phi_h$  and by setting them equal to zero:

$$\left. \frac{\partial \ln\phi_h}{\partial x} \right|_{x=x^*} = \frac{-f(x^*)}{(1-\beta) \int_x^y f(t)dt + \omega_1^{1-\beta}} + \frac{g_0}{(1-\beta)g_0(T+x-y) + \omega_2^{1-\beta}} + (m_1 - m_2) = 0, \tag{4a}$$

$$\left. \frac{\partial \ln\phi_h}{\partial y} \right|_{y=y^*} = \frac{f(y^*)}{(1-\beta) \int_x^y f(t)dt + \omega_1^{1-\beta}} + \frac{-g_0}{(1-\beta)g_0(T+x-y) + \omega_2^{1-\beta}} - (m_1 - m_2) = 0. \tag{4b}$$

From equations (4a) and (4b),  $x^*$  and  $y^*$  are obtained numerically. We also can derive a simple condition:

$$f(x^*) = f(y^*). \tag{5}$$

The solution that satisfies equation (5) is the local optimum, as shown in Appendix A. Since function  $f(x)$  has a single peak,  $x^*$  is before the peak date ( $t_1 - T/2 < x^* < t_1$ ), and  $y^*$  is after the peak date ( $t_1 < y^* < T + x^*$ ). In addition, since function  $f(t)$  given by equation (1b) is symmetric around the peak,  $x^*$  and  $y^*$  are equally distant from the date of the peak growth rate, as illustrated in Fig. 2.

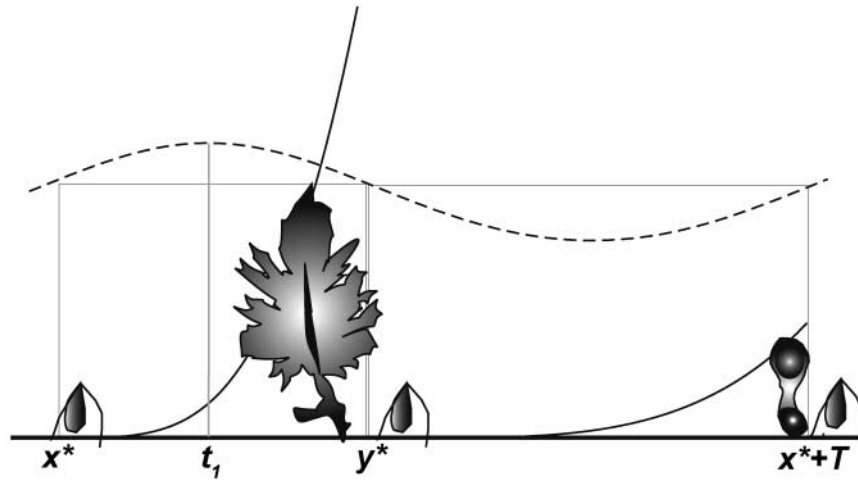
#### *Parameter dependence*

Figure 3 illustrates the length of the first generation within a year  $(y^* - x^*)/T$  obtained from numerical simulations for a range of parameter values. The length of the first generation decreases with the intensity of seasonality,  $a$ . This implies that the length of the period for the fast growing generation forming a large body size becomes shorter as the seasonality of the environment increases.

The length of the first generation also decreases with the difference in the daily mortality between two life forms:  $m_1 - m_2$ .

It also decreases with the productivity of the habitat for the first generation ( $f_0$ ) and with the ratio of the productivity of the two generations ( $g_0/f_0$ ), but the dependence on these parameters is less pronounced than the dependence on  $a$  or  $m_1 - m_2$ .

The relative length of the first generation does not change much with  $\omega_1$  and  $\omega_2$ , but there is a very small decreasing tendency with  $\log_{10}\omega_2$ . It clearly increases with parameter  $\beta$ .



**Fig. 2.** The optimal timing of a heteromorphic life cycle. The horizontal axis represents time,  $t$ . The solid line indicates the algal growth size of individuals. Optimal  $x^*$  and  $y^*$  are timings of alternation of generations. The dotted line indicates the coefficients of power function growth of the first and second generations,  $f(t)$  and  $g_0$ .  $f(t)$  has a single peak at  $t = t_1$  and is symmetric around the peak date. Note that  $x^*$  and  $y^*$  are located distant from the peak date.

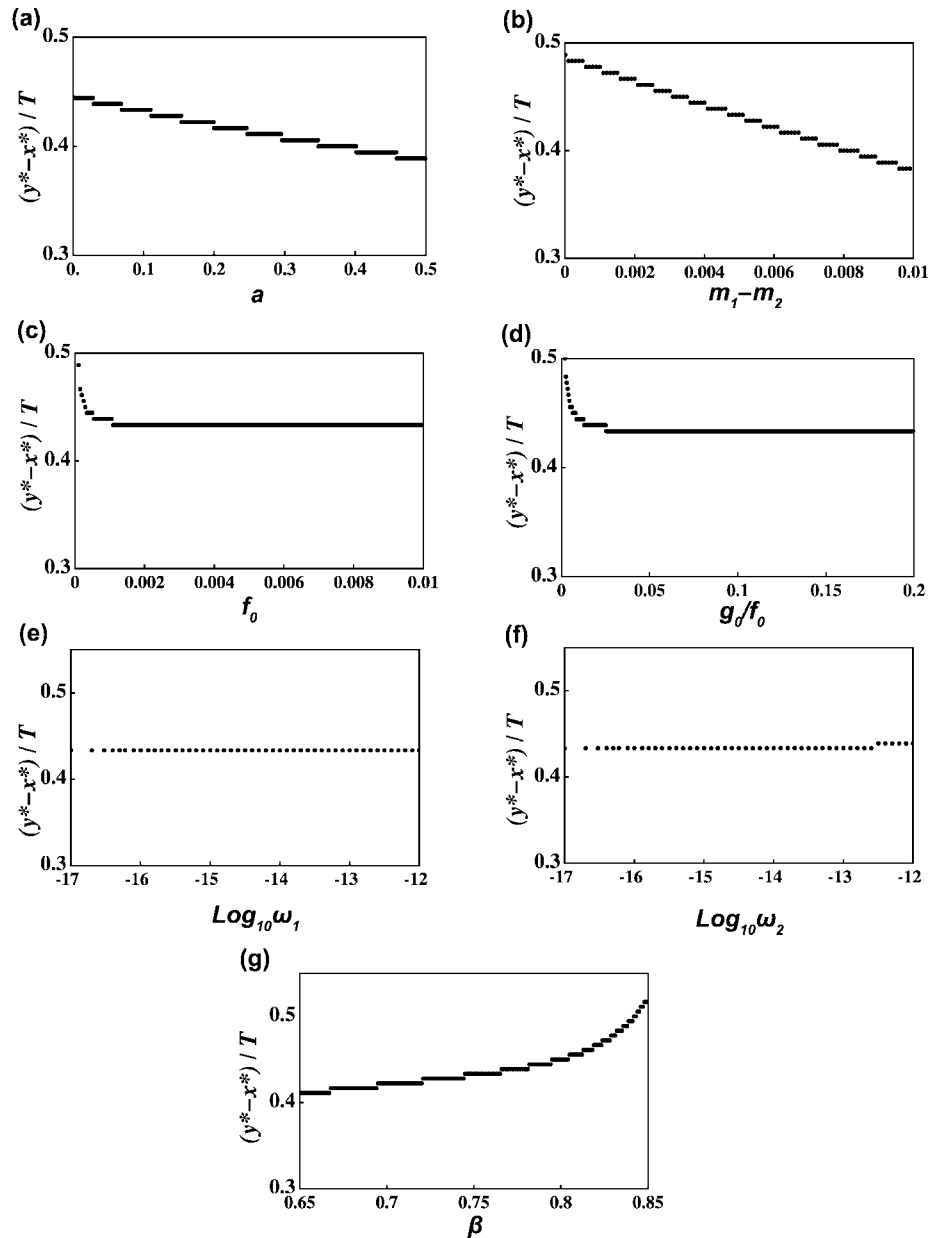
### Isomorphic life cycle

Next, we consider the isomorphic life cycle. We assume that there are  $k$  generations in a year, and that productivity changes seasonally. All parameters ( $\omega$ ,  $m$ ,  $Q$ ,  $S$ ) have the same values between generations, because different generations are physiologically equal (Littler *et al.*, 1987).

We denote the length of a year by  $T$ . Let  $x_1$  be the day on which the first generation of a year starts to grow from an egg or spore. With  $j = 2, 3, \dots, k - 1$ , let  $x_j$  be the day on which the  $(j - 1)$ th generation reproduces and the  $j$ th generation starts to grow from an egg or a spore. Let  $x_k$  be the day on which the last generation of a year starts growing. This last generation grows until day  $x_1 + T$ .

Algae in the first generation start growing at  $t = x_1$  ( $W_1(x_1) = \omega$ ) and their body size follows the differential equation:  $dW_1/dt = f(t)W_1^p$ . They become mature at  $t = x_2$  and give birth to the next generation. Survivorship until maturation is  $e^{-m(x_2 - x_1)}$ . The number of offspring (the second generation) produced by a single adult of the first generation and settle successfully is  $W_1(x_2)QS/\omega$ . With  $j = 2, 3, \dots, k - 1$ , the  $j$ th generation starts at  $t = x_j$ , matures at  $t = x_{j+1}$ , and gives birth to the next generation. Survivorship until maturation is  $e^{-m(x_{j+1} - x_j)}$ . The number of offspring produced by a single adult of the  $j$ th generation and settle successfully is  $W_j(x_{j+1})QS/\omega$ . The  $k$ th generation grows from  $t = x_k$  to  $t = T + x_1$ , where  $T$  is the length of the year. The number of the newly settled individuals for the first generation of the following year who were produced by a single adult of the previous generation in the current year is  $W_k(x_{T+x_1})QS/\omega$ .

Then the expected rate of multiplication in a year, or the expected number of individuals in the following year produced from a single adult that existed in the same season of the previous year, is:



**Fig. 3.** The fraction of the fast-growing generation for the optimal growth schedule. The vertical axis is the optimal generational balance  $(y^* - x^*)/T$ . The horizontal axis indicates: (a) strength of seasonality,  $a$ ; (b) differential mortality,  $m_1 - m_2$ ; (c) growth rate of large-sized generations,  $f_0$ ; (d) the ratio of growth rate between two generations,  $g_0 / f_0$ ; (e) logarithmic egg size,  $\log_{10} \omega_1$ ; (f) logarithmic egg size,  $\log_{10} \omega_2$ ; (g) parameter  $\beta$ . Unless stated otherwise, parameters are:  $f_0 = 0.005$ ,  $a = 0.1$ ,  $t_1 = 270$ ,  $T = 360$ ,  $g_0 = 0.0005$ ,  $\beta = 0.75$ ,  $m_1 - m_2 = 0.005$ ,  $\omega_1 = 10^{-15}$ ,  $\omega_2 = 10^{-15}$ .



$$\begin{aligned} \phi_i &= \frac{W_1(x_2)QS}{\omega} e^{-m(x_3-x_2)} \times \dots \times \frac{W_k(x_1+T)QS}{\omega} e^{-m(T+x_1-x_k)} \\ &= \left(\frac{QS}{\omega}\right)^k e^{-mT} \left( (1-\beta) \int_{x_1}^{x_2} f(t)dt + \omega^{1-\beta} \right)^{\frac{1}{1-\beta}} \times \dots \times \left( (1-\beta) \int_{x_k}^{T+x_1} f(t)dt + \omega^{1-\beta} \right)^{\frac{1}{1-\beta}}. \end{aligned} \quad (6)$$

$\phi_i$  is the ‘annual rate of population growth’. The timing of the start and end of generations is a function of  $x_1, \dots, x_k$ . We calculate the optimal values of  $x_1, \dots, x_k$  that maximize  $\phi_i$ .

*Optimal timing of isomorphic alternation of generations*

Candidates for the optimal timing ( $x_1^*, \dots, x_k^*$ ) can be found by calculating the partial derivatives of  $\ln\phi_i$ , the logarithm of the annual population growth rate, and by setting them equal to zero:

$$\left. \frac{\partial \ln\phi_i}{\partial x_1} \right|_{x_1=x_1^*} = \frac{f(x_1^*)}{(1-\beta) \int_{x_k}^{T+x_1} f(t)dt + \omega^{1-\beta}} + \frac{-f(x_1^*)}{(1-\beta) \int_{x_1}^{x_2} f(t)dt + \omega^{1-\beta}} = 0, \quad (7a)$$

$$\left. \frac{\partial \ln\phi_i}{\partial x_j} \right|_{x_j=x_j^*} = \frac{f(x_j^*)}{(1-\beta) \int_{x_{j-1}}^{x_j} f(t)dt + \omega^{1-\beta}} + \frac{-f(x_j^*)}{(1-\beta) \int_{x_j}^{x_{j+1}} f(t)dt + \omega^{1-\beta}} = 0, \quad (7b)$$

where  $j = 2, 3, \dots, k - 1$ .

$$\left. \frac{\partial \ln\phi_i}{\partial x_k} \right|_{x_k=x_k^*} = \frac{f(x_1^*)}{(1-\beta) \int_{x_{k-1}}^{x_k} f(t)dt + \omega^{1-\beta}} + \frac{-f(x_k^*)}{(1-\beta) \int_{x_k}^{T+x_1} f(t)dt + \omega^{1-\beta}} = 0. \quad (7c)$$

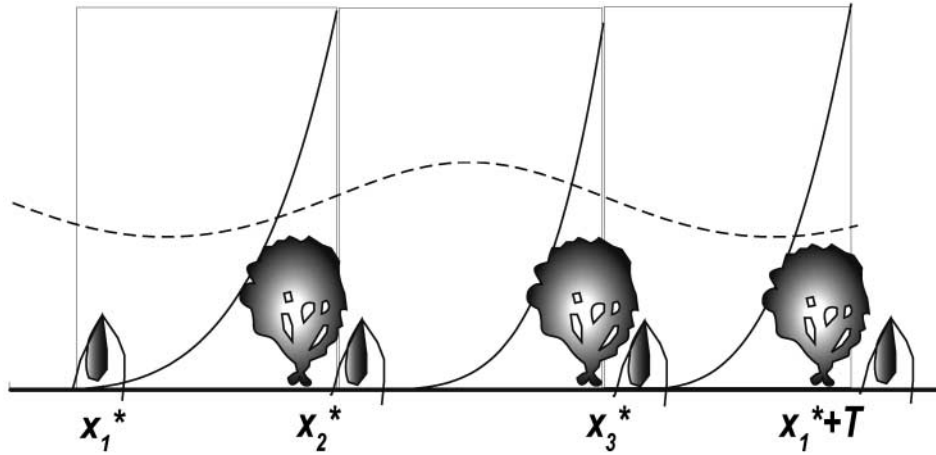
From equations (7a), (7b), and (7c), we have the following condition for the optimality of  $x_1^*$  and  $x_k^*$ :

$$\int_{x_1}^{x_2} f(t)dt = \dots = \int_{x_{k-1}}^{x_k} f(t)dt = \int_{x_k}^{T+x_1} f(t)dt = \frac{\int_0^T f(t)dt}{k}. \quad (8)$$

This equation indicates that the area under the curve  $f(t)$  from  $t = 0$  to  $t = T$  is the same between  $k$  generations, as illustrated in Fig. 4. We call this the ‘equal-area rule’.

Equation (8) does not specify the day for the start of the first generation. When the number of generations  $k$  is given, and if the day at which the first generation begins is chosen arbitrarily, then the beginning of other  $k - 1$  generations  $x_2^*, \dots, x_k^*$  is determined automatically by equation (8).

Note that equal-area rule is only a necessary condition for the local optimality. A solution satisfying equation (8) may be a local minimum or other non-optimal stationary point. To examine the local optimality, we need to calculate the Hessian matrix, as explained in Appendix B. We can prove that for  $k = 2$  and  $k = 3$ , the local optimality is satisfied for all the solutions satisfying the equal-area rule. For  $k \geq 4$ , some of the solutions satisfying the equal-area rule are local optima, but others are not (see Appendix B).



**Fig. 4.** The optimal timing of isomorphic life cycles. The horizontal axis represents day of the year,  $t$ . The solid lines indicate the size of algal body. The optimal timings for the starts and ends of generations are  $x_1^*$ ,  $x_2^*$ , and  $x_3^*$  ( $k^* = 3$ ). The dotted line indicates the coefficients of growth rate,  $f(t)$ . Note that areas under the curve  $f(t)$  for different generations are equal, and the maturation sizes of all generations are the same between generations. The length of generations differs markedly between seasons.

There can be multiple solutions that are local optima. To search for the global optimum, we need to compare  $\phi$  between different local optima.

Note that if the integral  $\int_{x_j}^{x_{j+1}} f(t)dt$  is the same for different generations ( $j = 1, 2, \dots, k$ ), the final size  $W(x_{k+1})$  is the same for all generations in a year. This implies that the length of a generation may differ between generations. The generation in a favourable season should be a lot shorter than one in an unfavourable season.

#### Number of generations in a year

The number of generations per year  $k$  cannot be specified by the local optimality condition given by equation (8) alone. We can construct the optimal life cycle for any given  $k$ . But to choose the best  $k$ , we need to compare the performance for different  $k$ .

If there is a seasonal schedule of growth satisfying the equal-area rule in isomorphic life cycles of macroalgae, the annual rate of population growth becomes

$$\phi_i(k) = (QS)^k \left( \frac{(1-\beta) \int_0^T f(t)dt}{k\omega^{1-\beta}} + 1 \right)^{\frac{k}{1-\beta}} e^{-mT}, \quad (9a)$$

and maturation size is

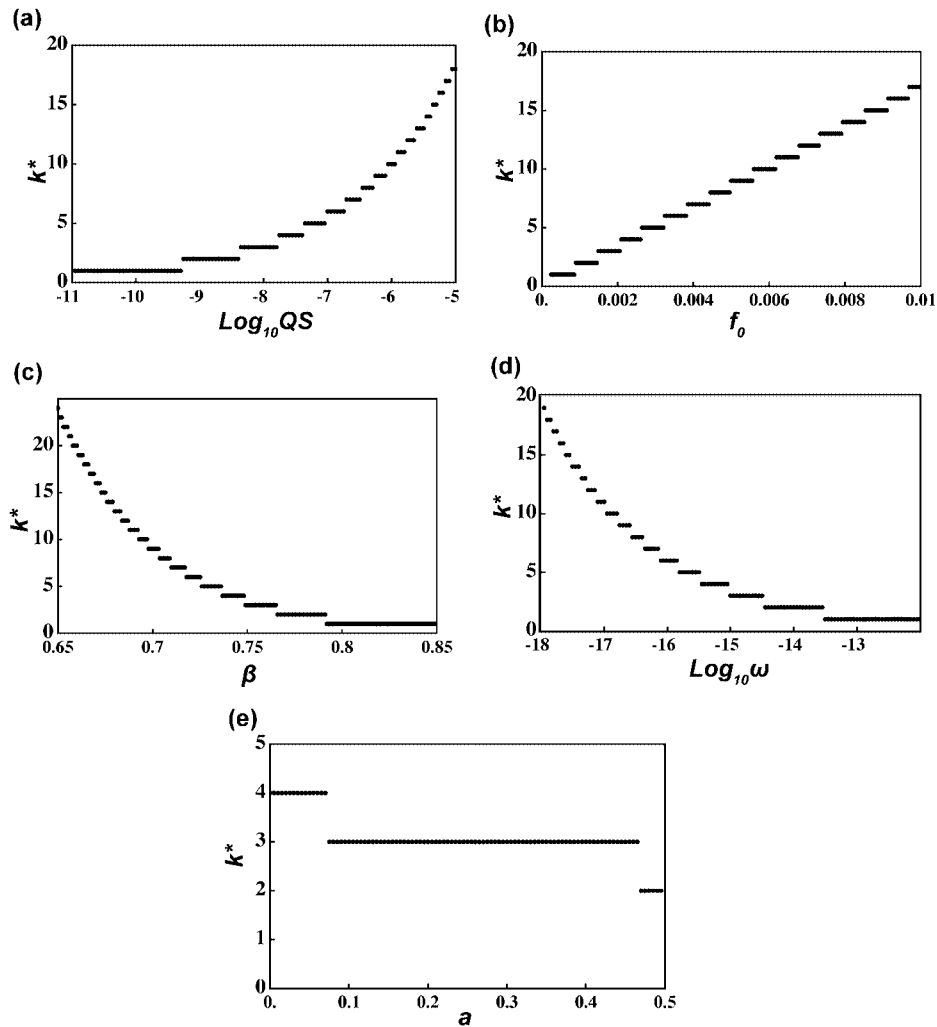
$$W_1(x_2) = \dots = W_k(T + x_1) = \left( \frac{(1-\beta) \int_0^T f(t)dt}{k} + \omega^{1-\beta} \right)^{\frac{1}{1-\beta}}. \quad (9b)$$

Both are functions of  $k$  only. The annual population growth rate is a function of the number of the generation  $k$ , but is independent of the day of the first generation  $x_1$ .

The optimal number of generations per year is calculated by comparing equation (9a) for different  $k$  calculated numerically. Figure 5 illustrates the optimal number of generations ( $k^*$ ) for different parameter values.

Note that  $\phi_i$  depends on  $Q$  and  $S$  through their product  $QS$ . As illustrated in Fig. 5a, the optimal number of generations  $k^*$  increases as  $QS$  increases.

As shown in Fig. 5b, the optimal number of generations increases with  $f_0$ , indicating that the number of generations should be greater in a more productive environment. In contrast,



**Fig. 5.** The optimal number of generations for isomorphic species. The vertical axis represents the optimal number of generations,  $k^*$ . The horizontal axis represents: (a) parameter  $\log_{10} QS$ ; (b) growth rate of large-sized generation,  $f_0$ ; (c) parameter  $\beta$ ; (d) logarithmic egg size,  $\log_{10} \omega$ ; and (e) strength of seasonality,  $a$ . Unless stated otherwise, parameters are:  $f_0 = 0.002$ ,  $a = 0.1$ ,  $\beta = 0.75$ ,  $\omega = 10^{-15}$ ,  $Q \times S = 10^{-8}$ .

the optimal number of generations decreases with parameter  $\beta$ . It also decreases with the size of eggs (or spores)  $\omega$  shown in Fig. 5c and 5d respectively.

The number of generations tends to decrease with an increase in strength of seasonality  $a$ , but this dependence on  $a$  is weaker than the dependence on other parameters.

#### Maturation size

Figure 6 illustrates the optimal size at maturity [ $\log_{10} W_i(k^*)$ ] given by equation (9b). The horizontal axis represents a focal parameter with all the other parameters fixed. The graph is composed of a number of line segments, each corresponding to the same optimal number of generations  $k^*$ . Between different line segments there is a discontinuous change in the optimal size at maturity.

For example, in Fig. 6a the line has a negative slope, implying that the optimal size at maturity decreases as the strength of seasonality  $a$  increases when we compare the cases with the same number of generations. But when the strength of seasonality increases further,  $k$  becomes smaller and the size at maturity jumps to a much greater value.

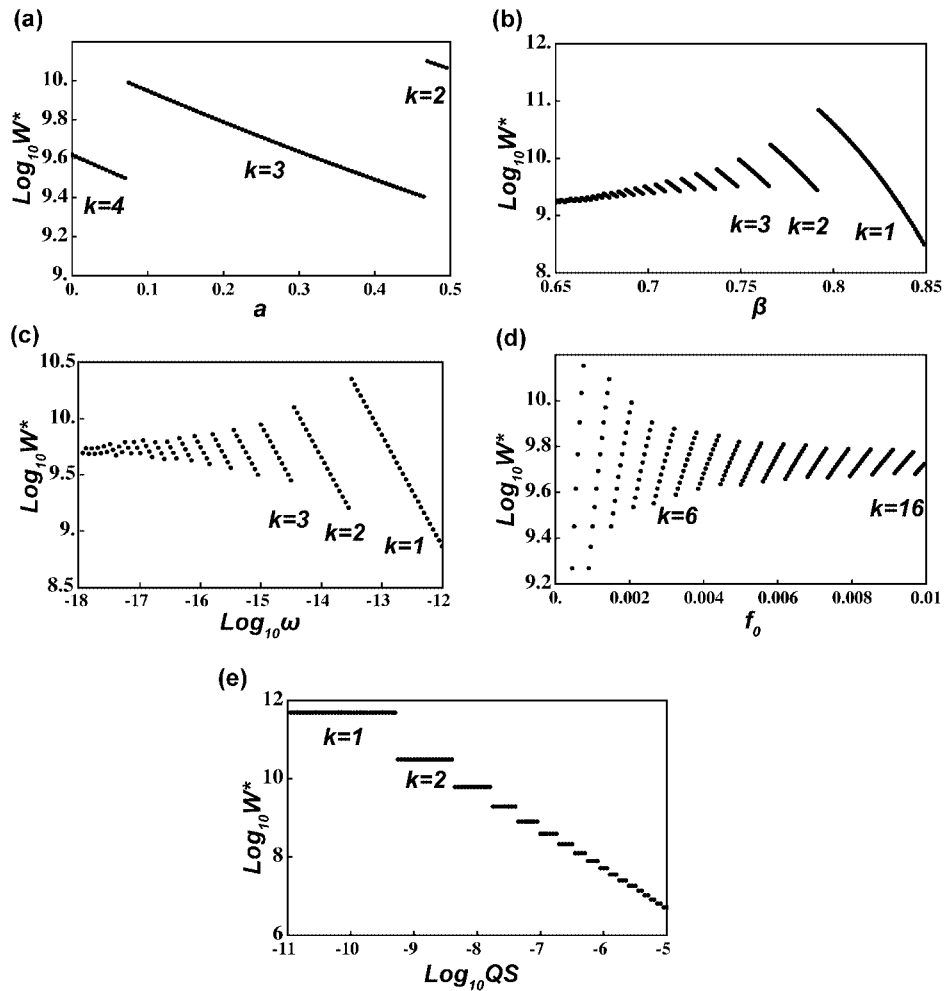
Figures 6b, 6c, and 6d indicate how the optimal size at maturity changes with different parameters. Note that the overall trend in size is rather stable because the change within the same  $k$  is in the opposite direction to the large change that occurs when  $k$  shifts. However, we cannot expect a similar size at maturity for different parameter values because the fluctuation of the optimal size is very large. Since the vertical axis represents a logarithmic scale, fluctuations of a small magnitude in the graph may correspond to a very large difference in the optimal size at maturity.

There is a clear trend that the optimal size at maturity decreases with an increase in  $QS$ , shown in Fig. 6e. This implies that the algal body size tends to be greater when successful settlement is more difficult.

### Relative advantage of heteromorphic versus isomorphic species

We compared the performance of the best life-history schedule for heteromorphic species and the best schedule for isomorphic species, by calculating their annual population growth rates. The difference  $\Delta\phi$  ( $\Delta\phi = \phi_h(x^*, y^*) - \phi_i(k^*)$ ) is the relative advantage of the heteromorphic type over the isomorphic type. We assume that power  $\beta$  is kept at 0.75. We also assume that the basic parameters of isomorphic species ( $Q, S, m, f_0, a$ ) are the same as those for the large generation of heteromorphic species ( $Q_1, S_1, m_1, f_0, a$ ), and that the sizes of eggs ( $\omega_i, \omega_1, \omega_2$ ) are the same between generations. Figure 7 illustrates the advantage of heteromorphic type  $\Delta\phi$  obtained from numerical simulations for a range of parameter values. In Fig. 7, the vertical axis is  $\tanh(\Delta\phi)$  in order to make the sign of  $\Delta\phi$  clear.

The relative advantage of a heteromorphic life cycle over an isomorphic life cycle increases with an increase in seasonality ( $a$ ). There is a threshold value of  $a$  at which  $\Delta\phi$  changes its sign. A heteromorphic life cycle is more advantageous ( $\Delta\phi > 0$ ) for  $a$  smaller than the threshold, whereas an isomorphic life cycle is more advantageous ( $\Delta\phi < 0$ ) for  $a$  larger than the threshold (Fig 7a). This implies that a heteromorphic life cycle is more advantageous in a more strongly seasonal environment. A similar conclusion is reached for the dependence on the relative productivity of the slow-growing and fast-growing generations ( $g_0/f_0$ ), the daily mortality of the fast-growing generation ( $m_1$ ), and parameter  $Q_2S_2$ : the relative advantage of a heteromorphic life cycle is positive when these parameters are large (Figs. 7b, 7c, 7d, respectively).

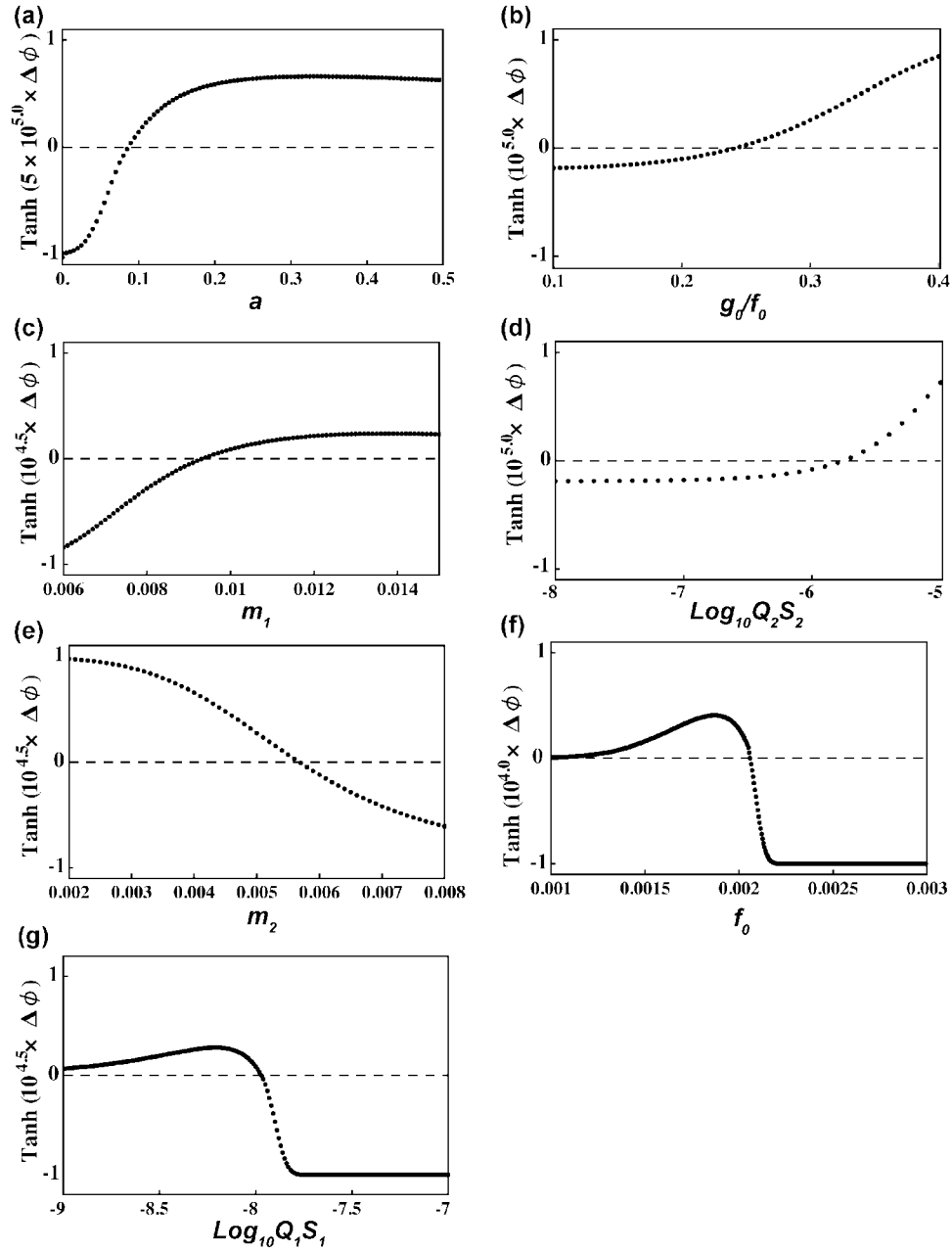


**Fig. 6.** The optimal size at maturity. The vertical axis represent the maturation size  $W_i(k^*)$  in the optimal schedule. Horizontal axis represents (a) strength of seasonality  $a$ ; (b) parameter  $\beta$ ; (c) logarithmic egg size  $\log_{10} \omega$ ; (d) growth rate of large-sized generation  $f_0$ ; and (e) parameter  $\log_{10} QS$ . Unless stated otherwise, parameters are:  $f_0 = 0.002$ ,  $a = 0.1$ ,  $\beta = 0.75$ ,  $\omega = 10^{-15}$ ,  $Q \times S = 10^{-8}$ .

In contrast, the opposite is true for the daily mortality of the slow-growing generation ( $m_2$ ). The relative advantage of a heteromorphic life cycle is positive when  $m_2$  is smaller than a threshold. Similarly, a heteromorphic life cycle is more likely to be advantageous than an isomorphic life cycle when the growth rate in the first generation  $f_0$  and parameter  $Q_1 S_1$  are small (Figs. 7e, 7f, and 7g, respectively).

**DISCUSSION**

In the present paper, we test the hypothesis that the diversity of marine macroalgal life cycles can be understood as adaptations to seasonally changing environments. We may



**Fig. 7.** The advantage of the heteromorphic type versus the isomorphic type with different parameter values. The vertical axis indicates (a) the relative advantage of the heteromorphic type,  $\tanh(\Delta\phi)$ , where  $\tanh(\Delta\phi)$  converges to  $\pm 1$  when  $\Delta\phi$  becomes  $\pm\infty$ . The horizontal axis represents: (a) strength of seasonality,  $a$ ; (b) relative growth rate between two generations,  $g_0/f_0$ ; (c) mortality in the fast-growing generation,  $m_1$ ; (d) parameter  $\log_{10} Q_2 S_2$ ; (e) mortality in the slow-growing generation,  $m_2$ ; (f) growth rate in the fast-growing generation,  $f_0$ ; and (g) parameter  $\log_{10} Q_1 S_1$ . Unless stated otherwise, parameters are:  $a = 0.1$ ,  $f_0 = 0.002$ ,  $m_1 = 0.01$ ,  $Q_1 \times S_1 = 10^{-8}$ ,  $g_0 = 0.0005$ ,  $m_2 = 0.005$ ,  $Q_2 \times S_2 = 2 \times 10^{-6}$ ,  $\beta = 0.75$ ,  $\omega = 10^{-15}$ .

consider the following model for life-history evolution of macroalgae. Suppose that the evolution of their life cycle patterns have the following constraints:

1. A diploid generation and haploid generation must alternate: a diploid generation is followed by a haploid generation, which is followed by another diploid generation.
2. There are two possible life forms: a fast-growing life form is strongly affected by environmental seasonality and suffers high mortality, while a slow-growing life form is less sensitive to seasonality and has low mortality.
3. The life form (fast growing or slow growing) is linked to the genome (haploid or diploid).

Then, there are four possible combinations: both diploid and haploid generations are fast growing; both are slow growing; the diploid generation is fast growing but the haploid generation is slow growing; and the haploid generation is fast growing but the diploid generation is slow growing. In our model, the first combination is classified as isomorphic while the last two combinations are classified as heteromorphic. These three combinations are represented by *Ulva pertusa*, *Undaria pinnatifida*, and *Porphyra yezoensis*, respectively. The second combination is unknown, but isomorphic brown algae *Ralfsia fungiformis* might be an example of this combination because both generations develop a crustose thallus (Hori, 1993).

### Optimal seasonal schedule

In the model for heteromorphic alternation of generations, there are two generations in a year. One generation takes a fast-growing life form with high mortality due to predation or physical disturbance, while the second generation takes a very small body size with a low growth rate but low mortality. Optimally, the fast-growing generation should overlap with the season that is favourable for growth.

The length of the fast-growing generation should depend on the balance between the advantages of faster growth of the large-sized generation and the lower mortality of the small-sized generation. A stronger seasonality (large  $a$ ) and a greater difference in mortality between the two life forms (large  $m_1 - m_2$ ) make the optimal length of the fast growth season shorter.

Since environmental seasonality is stronger at higher than at lower latitudes, parameter  $a$  would be larger at high latitude. The model suggests that the length of the fast-growing generation for heteromorphic species is likely to be longer at low than at high latitude.

We also discuss the relative advantage of two types of life cycles (Fig. 7). We conclude that the heteromorphic species is more advantageous than the isomorphic species in the more strongly seasonal environment. This suggests that heteromorphic species should be more dominant at higher latitude than isomorphic species, which is consistent with the observed pattern (Nakahara and Masuda, 1971).

In the model for isomorphic alternation of generations, we derived the 'equal-area rule' (equation 8) and conclude that maturation size is similar between generations (equation 9b). In addition, in the productive season (i.e. winter), the length of a generation should be shorter than in the unproductive season (i.e. summer).

Isomorphic species tend to have more generations per year in a habitat with a longer season suitable for growth, which is more productive, and is more stable for settlement (Fig. 5). The optimal size at maturity fluctuates markedly when many parameters change

gradually and does not show a clear trend for most parameters (Fig. 6), with one exception: the size at maturity should be large when successful settlement is very difficult ( $QS$  is small). To incorporate the difference in the constraint on size, we need to expand the current model and incorporate the differences in growth rate and mortality between tidal levels that are also dependent on algal body size. This will be an important avenue for future theoretical work.

### Future problems

Our treatment of the life cycle of macroalgae is simplistic. To make the model more realistic, in the future we need to incorporate the following complexities of algal life cycles:

1. *Haplont and diplont types.* Our model focuses on a haplo-diplontic life cycle that includes heteromorphic and isomorphic alternation of generations. Most macroalgae have this life cycle. However, some algal species have life cycles that are of a haplont or diplont type.

Among unicellular algae, a haplontic life cycle is prevalent, in which the diploid phase is a cyst. In the diploid phase, some macroalgae species also exist as a cyst [e.g. *Monostroma nitidum* (Ohno, 2004)]. In the context of our theory, we can treat haplont type macroalgae as a variation of heteromorphic species with  $g_0$  equal to zero.

In a diplontic life cycle, there is no alternation of generations. The algal body consists of diploid cells, and when it matures, after meiosis and immediate syngamy, a diploid zygosis is formed. A diploid zygote is produced from the diploid body and it grows to a diploid algal body. This group includes brown algae *Fucus* and green algae *Codium* (Nakahara, 1986). The macroalgae *Fucus horneri* and *Codium fragile* are known to have one seasonal maturation (Hori, 1993, 1994). In our model, diplont type macroalgae can be treated as a form of isomorphic species that has just one generation in a year ( $k = 1$ ).

2. *Triphasic life cycle.* Red algae have a triphasic life cycle (Umezaki, 1977; Fierst *et al.*, 2005; Verges *et al.*, 2008). There are three phases of body: gametophyte (haploid), carposporophyte (diploid), and tetrasporophyte (diploid). The zygote develops to a diploid carposporophyte on the haploid body. The carposporophyte produces carpospores that develop to diploid tetrasporophytes. To treat the triphasic life cycle within the context of our model, gametophyte and tetrasporophyte correspond to haploid body and diploid body respectively, and carposporophyte corresponds to the reproductive organ of the gametophyte.

3. *Sub-cycle.* Some species are thought to have sub-cycles of the life cycle – a diploid algal body is formed from a diploid parent and a haploid algal body is formed from a haploid parent. Sub-cycles affect the population dynamics of macroalgae (Nakahara, 1986).

For example, a heteromorphic brown algae *Cladosiphon okamuranus* is known to show parthenogenetic development, and their azygotes (zygotes that do not undergo zygosis) develop to a haploid body and neuter-zoospores develop to a diploid body (Hori, 1993). An isomorphic green alga *Ulva pertusa* has sub-cycles in the haploid phase (Hori, 1994). Parthenogenetic development in the sub-cycle of isomorphic species can be discussed within our model because the model does not distinguish between the algal body in the diploid phase and that in the haploid phase.

Sub-cycles can also occur as vegetative reproduction, as exemplified by brown alga *Ecklonia stolonifera* (Ohno, 2004).



4. *Perenniality or repeated reproduction.* Some macroalgae are perennial, and a single algal body undergoes reproduction multiple times. First, perenniality can arise if the algal body survives after the first reproduction. For example, the heteromorphic brown alga *Laminalia japonica* has annual and biennial populations in one community (Hori, 1993). The isomorphic red alga *Gelidium elegans* survives for 2 or 3 years (Ohno, 2004). Second, perenniality can also arise by regeneration of the basal alga body. In many isomorphic species, the algal main body flows away every year but shoots grow up from the basal part (Katada, 1963). Regeneration from the basal part may be important for algae living in harsh environments (Nakahara, 1986).

Species with multi-time maturation often have overlapping generations, exemplified by the heteromorphic green alga *Monostroma nitidum* and by the isomorphic green alga *Ulva pertusa* (Hori, 1993; Ohno, 2004).

5. *Dioecy.* We considered hermaphroditic species only. However, some macroalgae are dioecious, having an algal body with separate sexes. For example, the heteromorphic brown alga *Undaria pinnatifida* and isomorphic green alga *Ulva pertusa* have male and female gametophytes in the haploid phase (Hori, 1993, 1994).

6. *Density dependence.* In the present study, we analysed the annual population growth rate in a density-independent population as a criterion for adaptedness of different life-history schedules and different life-cycle types. However, when the population size increases, the population will be regulated within a finite range by density-dependent mortality or fertility. This does not change the conclusion of the relative advantage of different life-cycle types if the density dependence works equally for all the life-cycle types competing with each other. However, if the density dependence works differently between types, we need to construct a model to show how mortality, growth rate, and fertility would be regulated by the density of the population.

7. *Size-dependent mortality.* Regarding the gradient along the tidal zone, differential mortality  $m_1 - m_2$  should be larger in the upper inter-tidal zone or supra-tidal zone than in the sub-tidal zone because the habitat is exposed to drought for a longer period each day. The model then suggests the greater dominance of a heteromorphic life cycle in the upper inter-tidal and supra-tidal zones than in the sub-tidal zone. However, the opposite pattern is observed – isomorphic species tend to be more abundant in the inter-tidal zone (e.g. *Ulva pertusa*), while heteromorphic species are dominant in the sub-tidal zone (e.g. *Undaria pinnatifida*). This can be understood by considering the constraint of algal body size. In the sub-tidal zone, a large algal body size is an advantage in competition for light and species with a heteromorphic life cycle can become very large, forming a forest-like community. In contrast, in the supra-tidal and upper inter-tidal zones, algal body size is constrained by physical disturbance and algae mature at a relatively small size, with multiple generations in a year, which results in the dominance of isomorphic species.

Despite the many shortcomings of the model, the analysis in this paper provides a new perspective on the evolution of the diversity of life cycles in macroalgae in the context of life-history strategy theory (e.g. Stearns, 1993; Iwasa and Cohen, 1989; summarized in Iwasa, 2000).

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#### APPENDIX A: LOCAL OPTIMALITY FOR THE HETEROMORPHIC MODEL

Candidates for the optimal dates  $x^*$  and  $y^*$  satisfy equation (5). We induced  $x^*$  and  $y^*$  as follows:

$$R_1(x, y) = (1 - \beta) \int_x^y f(t) dt + \omega_1^{1-\beta}, \quad (\text{A1a})$$

$$R_2(x, y) = (1 - \beta) g_0(T + x - y) + \omega_2^{1-\beta}. \quad (\text{A1b})$$

Denote  $f = f(x^*) = f(y^*)$ ,  $f'(x^*) = \left. \frac{\partial f(x)}{\partial x} \right|_{x=x^*}$  and  $f'(y^*) = \left. \frac{\partial f(y)}{\partial y} \right|_{y=y^*}$ .

We calculated the second derivatives of the logistic fitness  $\ln \phi_h$  with  $x$  and  $y$  around candidates of optimal timing  $(x^*, y^*)$  which satisfy equation (A1) as:

$$\left. \frac{\partial^2 \ln \phi_h}{\partial x^2} \right|_{x=x^*, y=y^*} = -\frac{f'(x^*)}{R_1} - \frac{(1-\beta)f^2}{R_1^2} - \frac{(1-\beta)g_0^2}{R_2^2}, \quad (\text{A2a})$$

$$\left. \frac{\partial^2 \ln \phi_h}{\partial y^2} \right|_{x=x^*, y=y^*} = \frac{f'(y^*)}{R_1} - \frac{(1-\beta)f^2}{R_1^2} - \frac{(1-\beta)g_0^2}{R_2^2}, \quad (\text{A2b})$$

$$\left. \frac{\partial^2 \ln \phi_h}{\partial x \partial y} \right|_{x=x^*, y=y^*} = \frac{(1-\beta)f^2}{R_1^2} + \frac{(1-\beta)g_0^2}{R_2^2}. \quad (\text{A3})$$

From equation (A3), we can derive the following:

$$\begin{aligned} & \left. \frac{\partial^2 \ln \phi_h}{\partial x \partial y} \right|_{x=x^*, y=y^*}^2 - \left. \frac{\partial^2 \ln \phi_h}{\partial x^2} \right|_{x=x^*, y=y^*} \left. \frac{\partial^2 \ln \phi_h}{\partial y^2} \right|_{x=x^*, y=y^*} \\ &= \frac{f'(x^*)f'(y^*)}{R_1^2} + \frac{(1-\beta)(f'(y^*) - f'(x^*))}{R_1} \left( \frac{f^2}{R_1^2} + \frac{g_0^2}{R_2^2} \right). \end{aligned}$$

Note that  $x^*$  is before the peak and  $y^*$  is after the peak. We have:

$$\left. \frac{\partial^2 \ln \phi_h}{\partial x^2} \right|_{x=x^*, y=y^*} < 0, \quad (\text{A4a})$$

$$\left. \frac{\partial^2 \ln \phi_h}{\partial x \partial y} \right|_{x=x^*, y=y^*}^2 - \left. \frac{\partial^2 \ln \phi_h}{\partial x^2} \right|_{x=x^*, y=y^*} \left. \frac{\partial^2 \ln \phi_h}{\partial y^2} \right|_{x=x^*, y=y^*} < 0. \quad (\text{A4b})$$

Hence the candidate for optimal timing  $(x^*, y^*)$  for a heteromorphic life cycle satisfying equation (5) is the local optimum.

## APPENDIX B: LOCAL OPTIMALITY FOR THE ISOMORPHIC MODEL

From equation (11), we get candidates of optimal condition of  $x_1$  to  $x_k$  that maximize fitness  $\phi_i$ :

$$\int_{x_1}^{x_2} f(t) dt = \dots = \int_{x_{k-1}}^{x_k} f(t) dt = \int_{x_k}^{T+x_1} f(t) dt = \frac{1}{k} \int_0^T f(t) dt. \quad (\text{B1})$$

We calculated the second derivatives of the logistic fitness  $\ln \phi_i$  with  $x_2$  to  $x_k$  around candidates of optimal timings  $(x_2^*, \dots, x_k^*)$  that satisfy the 'equal-area rule' with arbitrary  $x_1$  as:

$$\left. \frac{\partial^2 \ln \phi_i}{\partial x_j^2} \right|_{\text{all } x=x^*} = -2f(x_j^*)^2 \quad j = 2, 3, \dots, k, \quad (\text{B2a})$$

$$\left. \frac{\partial^2 \ln \phi_i}{\partial x_{j+1} \partial x_j} \right|_{\text{all } x=x^*} = f(x_j^*) f(x_{j+1}^*) \quad j = 2, 3, \dots, k-1, \quad (\text{B2b})$$

and other terms are zero. From equation (B2), we can derive the Hessian matrix around candidates of optimal timings  $(x_2^*, \dots, x_k^*)$   $H$  denoted as:

$$H = \begin{pmatrix} -2f(x_2^*)^2 & f(x_2^*)f(x_3^*) & 0 & \dots & 0 \\ f(x_2^*)f(x_3^*) & -2f(x_3^*)^2 & f(x_3^*)f(x_4^*) & 0 & \vdots \\ 0 & f(x_3^*)f(x_4^*) & \ddots & f(x_{k-2}^*)f(x_{k-1}^*) & 0 \\ \vdots & 0 & f(x_{k-2}^*)f(x_{k-1}^*) & -2f(x_{k-1}^*)^2 & f(x_{k-1}^*)f(x_k^*) \\ 0 & \dots & 0 & f(x_{k-1}^*)f(x_k^*) & -2f(x_k^*)^2 \end{pmatrix} \quad (\text{B3})$$

All the eigenvalues are real because matrix  $H$  is symmetric. If all the eigenvalues of  $H$  are negative, we can say that the candidate  $(x_2^*, \dots, x_k^*)$  is a local maximum of the annual population growth rate.

When  $k^* = 2$ , the Hessian matrix is:

$$H_2 = (-2f(x_2^*)^2),$$

where the eigenvalue is negative trivially.

When  $k^* = 3$ , the Hessian matrix is:

$$H_3 = \begin{pmatrix} -2f(x_2^*)^2 & f(x_2^*)f(x_3^*) \\ f(x_2^*)f(x_3^*) & -2f(x_3^*)^2 \end{pmatrix}.$$

From the characteristic equation of  $\det |H_3 - \lambda I|$ , the eigenvalues of  $H_3$  are:

$$\begin{aligned} \lambda_- &= -(f(x_2^*)^2 + f(x_3^*)^2) - \sqrt{(f(x_2^*)^2 - f(x_3^*)^2)^2 + f(x_2^*)^2 f(x_3^*)^2} \\ \lambda_+ &= -(f(x_2^*)^2 + f(x_3^*)^2) + \sqrt{(f(x_2^*)^2 - f(x_3^*)^2)^2 + f(x_2^*)^2 f(x_3^*)^2}. \end{aligned}$$

$\lambda_-$  is negative. To prove negativity of  $\lambda_+$ , we note the following equation:

$$\begin{aligned} (f(x_2^*)^2 + f(x_3^*)^2)^2 &> (f(x_2^*)^2 - f(x_3^*)^2)^2 + f(x_2^*)^2 f(x_3^*)^2 \\ \Leftrightarrow (f(x_2^*)^2 + f(x_3^*)^2) &> \sqrt{(f(x_2^*)^2 - f(x_3^*)^2)^2 + f(x_2^*)^2 f(x_3^*)^2}. \end{aligned}$$

Hence all the eigenvalues of  $H_3$  are negative.

When  $k^* \geq 4$ , we cannot prove negativity of all the eigenvalues of the Hessian matrix analytically. Hence we tried computer simulation and checked negativity of the eigenvalues numerically. We calculated all the eigenvalues with basic parameters ( $f_0 = 0.002$ ,  $a = 0.1$ ,  $\beta = 0.75$ ,  $\omega = 10^{-15}$ ,  $Q \times S = 10^{-8}$ ) numerically. We then calculated all the eigenvalues with different values of parameters. We selected parameters in the same range of parameter dependence as the isomorphic model. From computer simulation, we obtained negativity of all eigenvalues. This suggests that candidates of optimal timings in the isomorphic model may satisfy the local optimality.

