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Rhythmic natural selection over intertidal and brackish water genotypes: Simple formulations for testing hypothesis

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ABSTRACT

Tidal cycles at benthic habitats induce a set of periodic environmental changes in variables like salinity, temperature and sediment water content which are able to stress benthic organisms. Consequently, a natural selection temporally correlated with tides affects the fitness of genotypes (w_i) depending on their adaptation degree. Classic population genetics demonstrate that (1) rhythmic w_i is more restrictive than equivalent spatial variations to preserve genetic variance, and (2) mean fitness of the population ($\overline{w}$) does not have to be enhanced by genetic variance (${\sigma^2}_w$). The present study develops a simple replicator dynamics-based model of continuous selection, where w_i of multiple asexual genotypes fluctuates as a sinusoid. The amplitude of w was set as 0.5 $(1 - w_{\min})$, whereas the ratio of tide period to generation time (h) was defined. Overall, the model shows that if $h > 1$, then the success of an advantageous genotype is exposed to randomness, and $\overline{w}$ may decrease over generations. In contrast, if $h < 1$ the success is deterministic, is limiting co-dominance, and only depends on $w_{\min}$. The amount of different genotypes buffers the decay of ${\sigma^2}_w$ and hence increases cohesiveness. Finally, the reliability of the model is analyzed for a set of target intertidal and brackish water organisms.

1. Introduction

Intertidal habitats are dynamic features which are structured by the interactions of physical elements such as tidal and current movements, emersion effects, salinity and temperature conditions (Carter, 1988; Lara et al., 2012). Estuarine habitats are also exposed to these variations, caused by tidal and wind forcing, fluctuations in fresh water input, frontal discontinuities and bathymetric changes, among others (Framiñan and Brown, 1996). These tidally forced environments represent stress conditions for those organisms which are not able to escape unfavorable conditions, implying pressure over the community's genotypic structure.

Spatial and temporal heterogeneity of benthic species composition, distribution and genes expression have often been related to these environmental variables (Kinne, 1964; Koehn, 1980; McKew et al., 2011; Zardi et al., 2011). The genetic distribution of benthic species is mostly patchy, and it consists on fragments of population linked at local scale. Such genetic structure could be caused by both cohesiveness and differentiation mechanisms, including natural selection before or after settlement (Larson and Richard, 1999; Slatkin, 1985). This differentiation mechanism favors the most advantageous genes or genotypes which out-compete the deleterious ones, thus resulting in a general increase of the fitness within genetic structure (Hedrick, 1985; Violle et al., 2011). Natural selection acting after settlement has been observed in populations of benthic organisms from disturbed areas, promoting genetic variance at small scales (Johannesson et al., 1995; Zardi et al., 2011).

On the other hand, temporal heterogeneity also contributes to the differentiation of genetic structure (Larson and Richard, 1999). Rhythmic temperature and desiccation stress determines the distributional limit and genetic structure of populations inhabiting the intertidal zone (Connell, 1961; Wethey, 1984). Benthic and brackish water organisms propagate under a temporally changing environment which involves a fluctuating natural selection (Derycke et al., 2006; McKew et al., 2011). The consequences of these fluctuations when correlating with tidal rhythms have been briefly studied as a simple mathematical formulation. Classic population genetics demonstrate that under fluctuating selection (1) conditions are more restrictive than equivalent spatial heterogeneity to preserve genetic variance, and (2) mean fitness of the population does not have to be enhanced by genetic variance (Bürger and Krall, 2004; Lande and Shannon, 1996; Lande, 2007). Tidal rhythms may allocate a co-dominance of closely related genotypes when the dispersal of deleterious forms is favored (De Meester et al., 2012) although natural selection may prevail over dispersion (Zardi et al., 2011). Under an unconnected genetic structure, a short generation time facilitates not only the rapid fixation of advantageous genotypes, but also the genetic drift of small size populations (Futuyma, 1997;

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Lessios et al., 1994). In contrast, long generation times promote the long-term fixation, although genetic variance may eventually return to an initial state (Kisdi, 2002).

Furthermore, whether a generation time is short or long enough when compared to tidal period, should be mathematically addressed. Previous models of fluctuating selection are very robust and useful if quantitative genetics is available (Bürger and Krall, 2004; Lande and Shannon, 1996). However, because (a) several benthic and brackish water organisms exhibit total or partial asexual reproduction behavior (Hino and Hirano, 1977; King and Snell, 1980; Serra and King, 1999) and (b) natural selection is continuous over generations, some simplifications are allowed when just demography is available. In this sense, a replicator dynamics is a powerful mathematical tool which simplifies the mechanism of genotype propagation, and fits with assumptions (a) and (b) (Garay, 2008).

The aim of the present study is to perform a replicator-dynamics based model of continuous natural selection, where the fitness of multiple asexual (or sibling) genotypes fluctuates as a sinusoid. Equations were applied to simulate dimorphism or even polymorphism adaptations. The model was used to discuss whether generation time and minimum fitness of organisms (1) determine the out-compete of deleterious genotypes, (2) influence on the dominance or co-dominance period of emergent advantageous, and (3) adjust the relationship between the mean fitness and the genetic variance of a virtual intertidal population. Conclusions represent a first step towards a heuristic comprehension of rhythmic natural selection modulating genetic structure, and particularly within tidally forced habitats.

2. Material and methods

2.1. Model architecture and assumptions

Environmental stressors that accounts for natural selection pressure (EnvS; salinity, temperature, sediment water content) are associated with tidal dynamics. Along near-shore systems (tidal flats, estuaries, etc.) tidal wave is a harmonic function (Godin, 1988)

$$z(t) = z_0 + \sum_{j=1}^{R} A_j \cos\left(\left(\frac{2\pi}{T_j}\right) t - a_j\right) \tag{1}$$

where $z(t)$ and z_0 are observable and mean water levels, T_j, A_j and a_j are the tidal period, amplitude and phase lag of the component j, and R is the number of resolvable harmonics. Evolution of EnvS is expected to follow the same trend described by Eq. (1), i.e. changes can be considered harmonics (e.g. pore-water salinity within sandy and muddy intertidal; temperature within upper part of sediments) or at least their periodicity similar to tides (Chapman, 1981; Johnson and Shick, 1977; Johnson, 1967; Rocha, 1998).

Natural selection is included in population dynamics by the relative fitness (w_i). Such variable is the ratio of the genotype specific growth rates, and depends on survival, fecundity or other factors that determines whether the genes will be passed to the future generations (Hedrick, 1985).

$$w_i = \frac{\lambda_i}{\lambda_{\max}} = f_i(t) \tag{2}$$

where λ_i is the specific growth rate of genotype i and $\lambda_{\max}$ is the specific growth rate of the most advantageous genotype. Given that natural selection pressure is due to EnvS, the function $f_i(t)$ from Eq. (2) is also assumed to follow a sinusoid:

$$w_i\,(t) = \frac{1}{2}(k_i + 1) - \frac{1}{2}(k_i - 1)\sin\left(\frac{2\pi t}{T}\right) \tag{3}$$

and the period T typically taking 12 h (semidiurnal tides) or 24 h (diurnal tides). The parameter k_i represents the minimum value of w_i during the tidal cycle. In case of asexual reproduction organisms, or when m sibling forms are considered, propagation of the different m genotypes can be modeled as a continuous time replicator dynamics (Garay, 2008):

$$\frac{dX_i}{dt} = X_i(w_i - \overline{w})\lambda_{\max} \tag{4}$$

$$\overline{w}(t) = \sum_{i=1}^{m} X_i(t) w_i(t) \tag{5}$$

where X_i is the relative abundance of the genotype i, t is the time (h) and $\overline{w}$ is the average fitness of the population. By Eq. (4), propagation rate is assumed proportional to the relative advantage over the mean population (Garay, 2008). The variable t can be easily converted to an equivalent number of generations (n) by considering generation time$\approx \frac{1}{\lambda_{\max}}$ (Margaleft, 1986).

For the special case of a dimorphism ($m = 2$), Eqs. (3) and (5) can be replaced in Eq. (4), and the integration from $n = 0$ to $n = n$ yields:

$$\frac{X_n}{(1 - X_n)} = \frac{X_0}{(1 - X_0)} e^{-\left[0.5(1-k)\left(n - \frac{h}{2\pi}\left(\cos\left(\frac{2\pi n}{h}\right) - 1\right)\right)\right]} \tag{6}$$

where X_0 and X_n are the relative abundances of the deleterious genotype and h is the ratio between the tidal period (T) and the generation time. If $h > 1$, a complete turn-over of the population takes less than one-fold T; vice versa (i.e. generation time longer than tidal period), if $0 < h < 1$. Evolution of the advantageous genotype can be simply estimated with $1 - X_n$.

However, Eq. (4) should be numerically solved when $m > 2$. This is the case of several adaptive forms against EnvS, e.g. as a polymorphism (Bittencourt-Oliveira et al., 2009; Dvornyk and Nevo, 2003), Therefore, a finite linear transformation of Eq. (4) should be considered:

$$\Delta X_{i,n} \approx X_{i,n}\left(w_{i,n} - \overline{w_n}\right) \tag{7}$$

$$X_{i,n+1} = X_{i,n} + \Delta X_{i,n} \tag{8}$$

with the restriction of keeping constant the total relative abundance

$$\sum_{i=1}^{m} (\Delta X_i) = 0. \tag{9}$$

Under such settings, a variance of the fitness of the population ($\sigma^2{}_w$) can be defined as a proxy of the total genetic variation which is affected by natural selection.

$$\sigma^2{}_{w,n} = \sum_{i=1}^{m} X_{i,n}\left(w_{i,n} - \overline{w_n}\right)^2 \tag{10}$$

The $\sigma^2{}_w$ is always >0 and is typically related to $\overline{w}$ by the classical Fischer's theorem of natural selection (Garay, 2008; Lande, 2007):

$$\Delta\overline{w_{n,n+1}} = \sigma^2{}_{w,n}. \tag{11}$$

Whether the fitness of the population evolves according to Eq. (11), and increases from its current state to the next generation, depends on some restrictions to (a) the fitness dynamics (i.e. constant, random fluctuation or deterministic trend), (b) the thresholds on long-run fitness parameters, and (c) the propagation mechanism (Hedrick, 1985; Lande, 2007). Consequently, Eq. (11) should be checked to fit under a rhythmic fitness (i.e. according to Eq. (3)), and no previous guess may be assumed.

2.2. Simulations and statistics

Some specific scenarios were considered to run the proposed model, thus implying different input parameters (i.e. a set of h and k), as well as particular biological restrictions. Firstly, a dimorphism against EnvS was run by simply assuming $w_b = 1$ for the advantageous genotype and the sinusoid $w_a = f_a(t)$ for the deleterious one (see Eq. (3)). The ratio of relative abundances of deleterious/advantageous genotypes (X_a/X_b) was estimated over successive generations (n), and the values of h and k ranged between 1–10 and 0.25–0.75, respectively. Secondly, the effect of an emergent advantageous genotype (X_b) within a previous homogeneous population (X_a) was simulated by setting the initial (X_a/X_b) = 99. The extent at which both genotypes coexist or dominate was studied with the Shannon index of diversity (Margaleft, 1986):

$$H = -\sum_{i=1}^{2} X_i \log_2 X_i. \tag{12}$$

Such index becomes maximum in case of the greatest evenness (i.e. co-dominance of both genotypes, $H = 1$), and is extremely reduced during the dominance of any genotype ($H \approx 0$). At this sense, the number of generations with $H \approx 1$ is a proxy of the lag on the advantageous genotype to become fixed within the population. This lag was characterized for several values of k ($k = 0.25, 0.5, 0.75$) and $h = 10$.

Thirdly, Fischer's theorem described in Eq. (11) was checked to fit under the rhythmic fitness characterized by the model. For this purpose, the values of $\overline{w}$ and $\sigma^2{}_w$ were calculated over successive generations of a dimorphism, and their linear relationship was estimated with the determination coefficient (R^2, $\alpha = 0.05$). Finally, three types of polymorphisms against EnvS were run with Eqs. (7)–(9) ($m = 2$, 6 and 10; $k_i = 0.25$–1), and the evolution of $\overline{w}$ and $\sigma^2{}_w$ over successive generations was compared. This simulation describes how $\sigma^2{}_w$ fluctuates as a function of the number of genotypes.

3. Results

Overall, the model reflects an out-competition of the deleterious genotype when the ratio between both genotypes of the dimorphism (X_a/X_b) is simulated (Fig. 1). The relative abundance of this genotype exponentially decreases with the number of generations (n), regardless the value of h or k. If $h \gg 1$ then a fluctuating component is observed within the out-competition trend; its amplitude clearly increases as h does. In contrast, if $h \approx 1$ then no fluctuating component is observed, and the deleterious X_a monotonically decreases.

As expected, the amount of n required for the out-competition of X_a mainly depends on its fitness (k, Fig. 1): As k value decreases, fewer generations are needed to become out-competed. According to the model, when simulating $k = 0.25$, X_a takes around 20 generations to be reduced to 0.1% of the total; values of $k = 0.75$ yields the same decrease for $n = 60$.

A specific trend is observed when an advantageous genotype (X_b) emerges within a homogeneous population of deleterious genotype (X_a, Fig. 2). Firstly, X_a exhibits dominance due to its major proportion, but then X_b becomes dominant as a result of its adaptive advantage. Furthermore, the length of co-dominance restricts to a single breakpoint of H (Fig. 2), and the final fixation of X_b does not apparently depend on h (data not shown).

Despite this outcome, if $h \gg 1$ then the fraction of both genotypes may remain constant during several generations of X_a dominance (Fig. 2). Because the length of this period coincides with low levels of X_b, its fixation may be sensible to additional random effects. Moreover, when the amplitude on rhythmic fitness is reduced by setting $k \approx 1$, a longer co-dominance period is found (Fig. 3). Levels of H also reflect that the length of the co-dominance increases as k does (Fig. 3).

Fig. 4 shows the calculated Δw and $\sigma^2{}_w$ for different h values. With the exception of $h = 1$, linear regression deviates from Fischer's theorem. This is accomplished by: a) low values of determination coefficient (e.g. $R^2 = 0.37$ for $h = 0.6$), b) regression slopes diverging from the theoretical ($a = 1$), and c) $\Delta w < 0$, in contrast with the idea which states that $\overline{w}$ should increase over successive generations. However, if h equals to simple harmonic multiples (i.e. $h = 1/2, 1/3, 1/4$, etc., data not shown), $\overline{w}$ and $\sigma^2{}_w$ vary according to Fischer's theorem. This fact suggests that, in order to improve genetic structure, certain level of synchronicity between reproduction rhythm and EnvS is needed.

Large fluctuations of $\overline{w}$ are mainly observed during early generations, but reduce as n increases. Moreover, the amplitude of these fluctuations is related with the amount of genotypes (m, Fig. 5a). When dimorphism is analyzed against other polymorphisms, lower amplitude and a sharper decrease are observed, thus suggesting that fewer generations are required in order to stabilize $\overline{w}$. Furthermore, a similar behavior is observed for $\sigma^2{}_w$ (Fig. 5b). Maximum $\sigma^2{}_w$ values are observed during early generations and reduce as n increases. Dimorphism shows higher values than other polymorphisms, but drops to almost zero for $n > 10$. In opposite, polymorphism takes a greater amount of generations to be negligible and hence, out-competition of deleterious genotypes is slower than dimorphism. Consequently, a higher amount of genetic diversity provides the population more stability against EnvS.

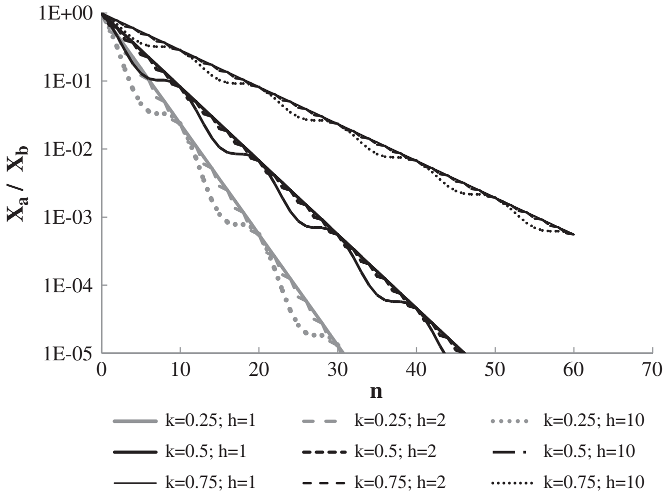

Fig. 1. Ratio of deleterious/advantageous genotypes (X_a/X_b) over successive generations (n) as a function of different values of k and h.

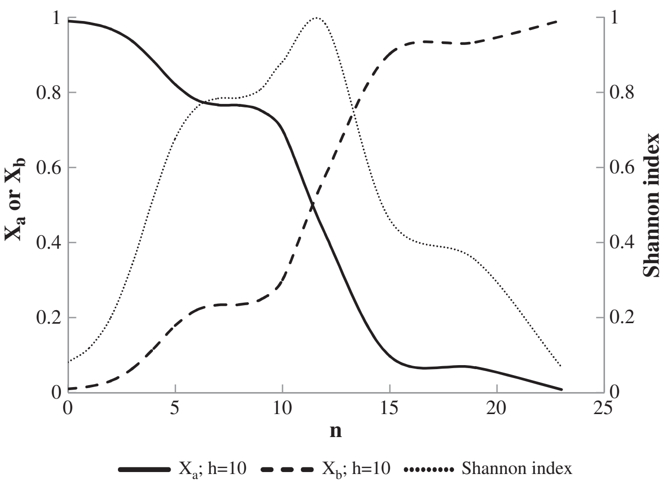

Fig. 2. Evolution of relative abundances (left axis) and Shannon index (right axis) when an advantageous genotype (X_b) emerges. Initial ratio $X_a/X_b = 99$.

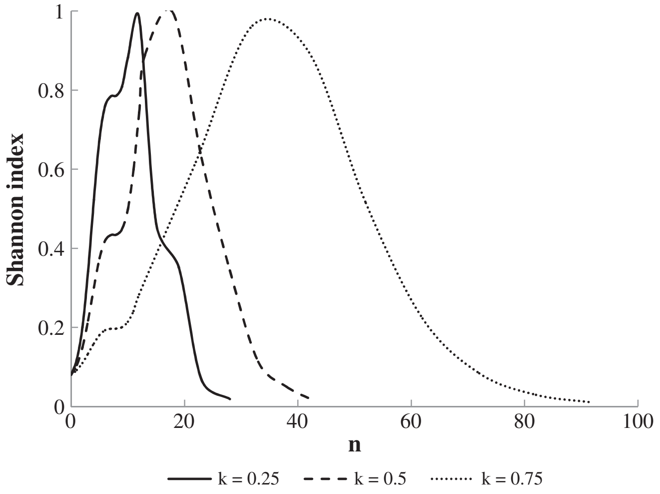

Fig. 3. Shannon index as a function of different *k* values for a simulated dimorphism.

4. Discussion

4.1. Model reliability

Due to the nature of the continuous replicator dynamics, the model is useful to analyze the temporal genetic structure of populations with asexual propagation (Garay, 2008) which is widely spread over benthic and brackish water organisms (Hino and Hirano, 1977; King and Snell, 1980; Serra and King, 1999). Given that stressing and transitional environments may enhance such mechanism over sexual reproduction (Eckert, 2002), this restriction seems reasonable at the community level. Asexual propagation is associated with short fluctuation periods of EnvS, although genetic recombination plays a central role under long fluctuation periods (Bürger, 1999). In addition, the model can be extended to organisms of dormant sexual reproduction and sibling non-recombinant genotypes, which is the case of the brackish water rotifer *Brachionus* spp. (Serra and King, 1999).

The model also assumes that genotypes cannot avoid EnvS and its rhythms, i.e. the genotype dispersion to favorable environments is not allowed. This fact limits the reliability to (a) benthic organisms of reduced or absent mobility and (b) brackish water organisms exposed to rhythmic salinity changes. Nevertheless, natural selection is recognized to be more relevant than genotype dispersion for the genetic structure of tidally forced populations (Zardi et al., 2011).

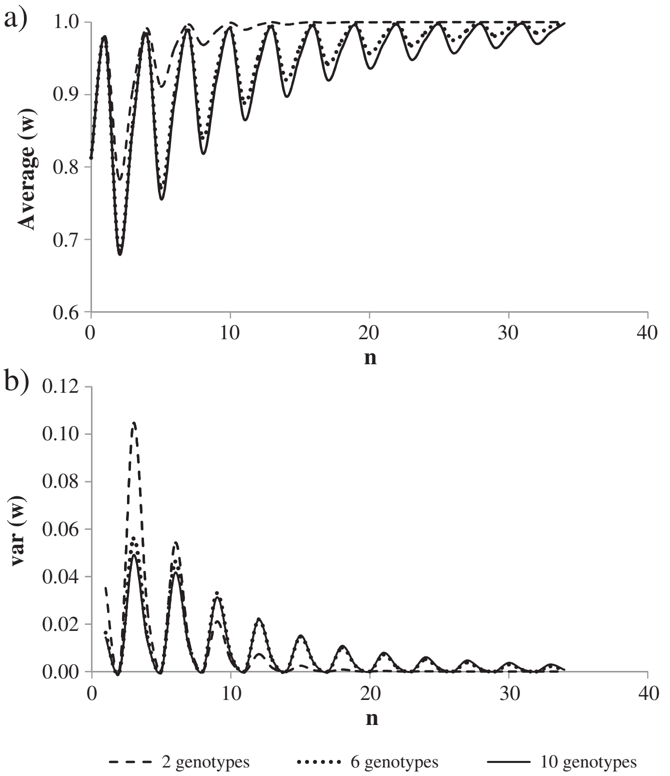

Fig. 5. a) Fluctuating average fitness (average *w*) and b) fluctuating variance of fitness (var *w*) of different polymorphisms ($m = 2, 6, 10$) over successive generations (n).

Despite of the abovementioned restrictions, the model may be applied to several target organisms. Table 1 summarizes some estimations of *h* for occurring organisms meeting condition 'a' or 'b' (i.e. cyanobacteria, diatoms and rotifers). Data were calculated for both semidiurnal and diurnal tides, and reflect different specific growth

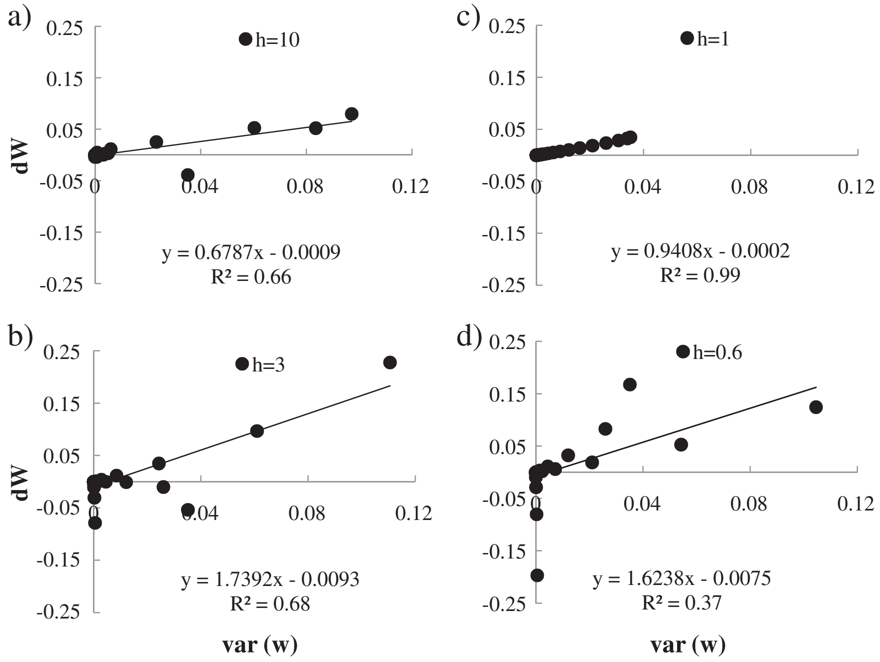

Fig. 4. Relationship between fitness increase (*dw*) and its variance (var (*w*)) for different levels of *h*: a) $h = 10$; b): $h = 3$; c) $h = 1$; d) $h = 0.6$.

Table 1
Summary of some estimations of h for occurring intertidal and brackish water cyanobacteria, diatoms and rotifers.

Species	Group	μ Max (day^{-1})	Tg (day)	h (semidiurnal)–h (diurnal)	Reference
Microcystis sp.	Cyanobacteria	0.275	3.636	0.138–0.275	Krüger and Eloff (1978) and Foy et al. (1976)
Microcystis aeruginosa	Cyanobacteria	0.800	1.250	0.295–0.810	Nicklisch and Kohl (1983), Watanabe and Oishi (1985), and Van der Westhuizen and Eloff (1985)
Anabaena oscillarioides	Cyanobacteria	0.800	1.250	0.400–0.800	Vincent and Silvester (1979)
Anabaena spiroides	Cyanobacteria	0.900	1.111	0.450–0.900	Seki et al. (1981)
Anabaena variabilis	Cyanobacteria	1.100	0.909	0.550–1.100	Collins and Boylen (1982) and Foy et al. (1976)
Aphanizomenon flos aquae	Cyanobacteria	1.200	0.833	0.090–1.200	Uelinger (1981) and Konopka and Brock (1978)
Synechocystis sp.	Cyanobacteria	0.680	1.471	0.340–0.680	Sheng et al. (2011)
Thalassiosira pseudonana	Diatom	1.710	0.585	0.855–1.710	López Elías et al. (2009)
Chaetoceros muelleri	Diatom	1.730	0.578	0.865–1.730	Medina-Reyna and Cordero-Esquivel (2004)
Brachionus quadridentatus	Rotifer	0.504	1.984	0.252–0.638	Ajah (2010)
Brachionus rotundiformis	Rotifer	1.960	0.510	0.980–1.960	Cabrera (2008)

μMax: maximum growth rate. Tg: Generation time.

rates as a result of intrinsic traits and contrasting habitats. The values of h ranges between 0.14 and 1.96, thus indicating that generation times are either shorter or longer than tidal periods under model restrictions. According to results, the first case implies a fluctuating component which is absent in the second case. Because $h > 1$ is only found for diurnal tides (Table 1), further research is needed to test how different tidal periods promote dissimilar genetic structures.

Some experimental evidences recognize dimorphism and polymorphism in the adaptive traits against EnvS. For example, the benthic cyanobacteria *Synechocystis* sp. displays a dimorphic variation on the gene *stpA*. This gene encodes the specific glucosylglycerol-phosphate phosphatase, being the glucosylglycerol a quite important osmolyte in response to salinity stress and desiccation. A mutant without *stpA* expression has been isolated (Hagemann et al., 1997). Another example is *Brachionus* sp., because several sibling genotypes of this organism have been isolated, and they exhibit contrasting osmotolerance and fitness against salinity stress (Lowe et al., 2006). In all of these cases, the model run is feasible with few demographic parameters.

4.2. Rhythmic natural selection

Regardless the values of h or initial ratio of genotypes, the model predicts an out-competition of deleterious when dimorphism or polymorphism is simulated. This deterministic trend seems reasonable according to the biotic and abiotic stress defining tidally forced habitats, which favors extinctions and genetic differentiation (Agur and Deneubourg, 1985). When both (a) isolated, (b) non-recombinant and (c) EnvS co-occur, the genetic structure becomes extremely differentiated and σ^2_w approximates to zero (Bürger, 1999). However, increase of the amount of genotypes results in a buffered decrease of σ^2_w (Fig. 5), thus suggesting that a spatially structured polymorphism is a complementary cohesive of out-competition (Bingham et al., 2011; De Meester et al., 2012).

Nevertheless, the parameter h defines two contrasting scenarios. On one hand, if $h \approx 1$ or $h < 1$ then dynamics is similar to a constant w because the sinusoid component is neglected. Consequently, co-dominance within dimorphism was not found, and long generation times limit genetic drift and alternatives to out-competition (Futuyma, 1997). A special case is $h = 1$ or a simple harmonic multiple of T (i.e. $h = 1/2, 1/3, 1/4$, etc.), because w fits to the Fischer's theorem (Fig. 4). As a result, w always increases over successive generations and it improves genetic structure (Garay, 2008; Hedrick, 1985). At this sense, further research is required on the potential maximization of fitness by a circadian or circalunar reproduction (Bentley et al., 1999; Naylor, 1985).

On the other hand, if $h > 1$ then dynamics include the sinusoid component. Co-dominance within dimorphism is feasible (Fig. 3), especially if intrinsic fitness of genotypes is closely related (De Meester et al., 2012; Violle et al., 2011). Another special case is $h \gg 1$, because deleterious dominance may be enlarged when advantageous genotype is emerging (Fig. 2). Low abundance and short generation time presumably result in genetic drift, and it would inhibit the fixation of advantageous genotypes (Futuyma, 1997; Lessios et al., 1994). In addition, dynamics deviates from Fischer's theorem, thus supporting a strong covariance between EnvS and w. The weakness against random fluctuations makes genetic structures diverge from maximum fitness (Lande, 2007).

In summary, a model of rhythmic natural selection has been developed by simply assuming that fitness varies as a sinusoid. The model is reliable to asexual and isolated populations of target intertidal and brackish water organisms. A key parameter is the ratio of tidal period to a characteristic generation time of genotypes. If such parameter exceeds 1, then the success of advantageous genotypes is exposed to randomness and to a lengthy co-dominance with deleterious genotypes. Simulations also show that the mean fitness of the population may fluctuate over early generations, and this effect is enhanced by the amount of different genotypes. These insights should result useful to the future research on the genetic structure of tidally forced populations.

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