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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 (\bar{w}) does not have to be enhanced by genetic variance (σ_w^2). 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 \bar{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 σ_w^2 and hence increases cohesiveness. Finally, the reliability of the model is analyzed for a set of target intertidal and brackish water organisms.

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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)

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

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).

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

where λ_i is the specific growth rate of genotype i and λ_{\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:

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

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):

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

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

where X_i is the relative abundance of the genotype i , t is the time (h) and \bar{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 $\approx \frac{1}{\lambda_{\max}}$ (Margalef, 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:

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

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:

$$\Delta X_{i,n} \approx X_{i,n} (w_{i,n} - \bar{w}_n) \quad (7)$$

$$X_{i,n+1} = X_{i,n} + \Delta X_{i,n} \quad (8)$$

with the restriction of keeping constant the total relative abundance

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

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

$$\sigma_{w,n}^2 = \sum_{i=1}^m X_{i,n} (w_{i,n} - \bar{w}_n)^2 \quad (10)$$

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

$$\Delta \bar{w}_{n,n+1} = \sigma_{w,n}^2. \quad (11)$$

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.

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