

Temperature Effects on Gametophyte Life-History Traits and Geographic Distribution of Two Cryptic Kelp Species

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Abstract

A major determinant of the geographic distribution of a species is expected to be its physiological response to changing abiotic variables over its range. The range of a species often corresponds to the geographic extent of temperature regimes the organism can physiologically tolerate. Many species have very distinct life history stages that may exhibit different responses to environmental factors. In this study we emphasized the critical role of the haploid microscopic stage (gametophyte) of the life cycle to explain the difference of edge distribution of two related kelp species. *Lessonia nigrescens* was recently identified as two cryptic species occurring in parapatry along the Chilean coast: one located north and the other south of a biogeographic boundary at latitude 29–30°S. Six life history traits from microscopic stages were identified and estimated under five treatments of temperature in eight locations distributed along the Chilean coast in order to (1) estimate the role of temperature in the present distribution of the two cryptic *L. nigrescens* species, (2) compare marginal populations to central populations of the two cryptic species. In addition, we created a periodic matrix model to estimate the population growth rate (λ) at the five temperature treatments. Differential tolerance to temperature was demonstrated between the two species, with the gametophytes of the Northern species being more tolerant to higher temperatures than gametophytes from the south. Second, the two species exhibited different life history strategies with a shorter haploid phase in the Northern species contrasted with considerable vegetative growth in the Southern species haploid stage. These results provide strong ecological evidence for the differentiation process of the two cryptic species and show local adaptation of the life cycle at the range limits of the distribution. Ecological and evolutionary implications of these findings are discussed.

Citation: Oppliger LV, Correa JA, Engelen AH, Tellier F, Vieira V, et al. (2012) Temperature Effects on Gametophyte Life-History Traits and Geographic Distribution of Two Cryptic Kelp Species. PLoS ONE 7(6): e39289. doi:10.1371/journal.pone.0039289

Editor: Debashish Bhattacharya, Rutgers University, United States of America

Received: February 6, 2012; **Accepted:** May 21, 2012; **Published:** June 18, 2012

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Funding: Support from the following programs is acknowledged: CONICYT-FRENCH EMBASSADY (PhD grant to LVO), French Ministry of Education and Research (PhD grant to FT), "Collège Doctoral Franco-Chilien", "ARCUS" of the French Ministry of Foreign Affairs and FCT-CNRS collaborative funding. This study is part of the research programs FONDAP 1501-0001 6 Program 7, ANR ECOKELP (ANR BDIV 012), Pôle Mer Bretagne, FONDECYT 1060493, Laboratoire International Associé "Dispersal and Adaptation of Marine Species" (LIA DIAMS), and FCT scholarships SFRH/BPD/7153/2001 and SFRH/BPD/63703/2009. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

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Introduction

Understanding the mechanisms that limit geographical distributions of species has long been a key question in both ecology and evolutionary biology [1,2] and it is generally accepted that multiple causes (both biotic and abiotic) can be interacting. Variations of geographic species range resulting from current climatic change have been widely demonstrated, including, for example, poleward movements of species' range boundaries in fish [3], mammals [4], birds [5], butterflies [6], and seaweeds [7]. Predictions of range shift are generally based on statistical relationships between the current species distribution and selected environmental variables. However, physiological limitations can constrain the distribution ranges and abundance of organisms [8]. There is a clear need for improved understanding of how the variation of environmental factors in space and time affect critical fitness components such as survival and reproduction [2,9].

To study the mechanisms that constrain a species' distribution, a highly informative zone is the edge of the range itself [10,11], particularly to study evolutionary processes. First, because marginal populations tend to occur in patches, genetic drift is expected to be stronger than in central populations where distribution is continuous [12]. As a consequence, marginal populations are expected to be genetically deprived, leading to a higher sensitivity to environmental changes in comparison with central populations. Furthermore, when dispersal is too low, even small abiotic variations in space and/or in time may have a large impact on the persistence of these local populations [12]. However, marginal populations may also be a place where local adaptation occurs, due to the particular environmental conditions, although this process depends on the relative genetic isolation of the marginal populations and on the species' dispersal capacity.

Temperature is considered as the most important factor determining the geographic distribution of numerous species, as

it affects survival, reproduction and/or growth [13]. This is particularly true for benthic marine macroalgae [14]. Kelps (Laminariales, Phaeophyceae) are mainly cold temperate species occurring from polar to inter-tropical zones. They play a major ecological role by structuring the ecosystem and are commercially exploited for alginate extraction [15]. At low latitudes, their range edge is generally determined by warm temperatures and nutrient limitation (see for review Steneck et al. 2002). In the tropics, kelps are restricted to deep-water cool habitats [16,17] confirming the effect of temperature on kelp distribution.

A quantitative estimate of multiple fitness components across the life cycle is necessary to understand the mechanisms that define the range limit [18,19]. Because of their complex life cycle, kelps are an especially interesting model. These species display a heteromorphic life history with an alternation of microscopic haploid gametophytes and diploid sporophytes [20] so that their range limit may be determined by the cryptic gametophytic stage. This microscopic stage is quite impossible to observe *in situ* but easy to cultivate in the laboratory from spores compared to the macroscopic sporophytic stage issued from wild individuals. Thermal responses of macroscopic sporophytes and microscopic stages are generally consistent with the geographical distribution of species and strongly depend on the species studied (macroscopic stage: [14,21]; microscopic stages: [22–26]). Tom Dieck [27] hypothesized that the distribution of the five different *Laminaria* species in the Northern Atlantic is following a gradient from cold-temperate to warm-temperate microscopic stage adaptation. In addition, Matson and Edwards [28] suggested that difference in temperature response of the microscopic stages could explain the difference in the location of the southern limit of range distribution between *Pterygophora californica* (less tolerant to warm temperature) and *Eisenia arborea* along the North Eastern Pacific coast. Similarly, the range distribution of two *Ecklonia* species across the cold-to-warm transition of the southern tip of South Africa is positively associated with optimal temperature for growth and fertility of the gametophyte stage [29]. However, very little is known about the variation of response of the microscopic stage to temperature among kelp populations across their entire geographic range.

The South Eastern Pacific temperate coast is particularly interesting to study the effects of temperature fluctuation, because Sea Surface Temperature (SST) shows a complex pattern of both spatial and temporal variability. While a general trend of increasing temperatures with decreasing latitude is described in the Humboldt Current System [30], a patchy structure of thermal conditions along the coast is created by upwelling centers where cold, nutrient-rich subsurface waters are upwelled by equatorward winds [30]. In addition, temporal fluctuations of SST are occurring: (i) at inter-annual scales due predominantly to El Niño Southern Oscillation (ENSO) events, (ii) at the seasonal scale, and (iii) at the synoptic scale (several days), associated to the alternation between high and low atmospheric pressure and rain, mostly in temperate areas, and (iv) at the daily scale for intertidal species, associated to the tidal regimes [31,32]. In comparison to southern regions, the northern part of the Humboldt Current System is dominated by permanent anticyclonic conditions but occasionally strongly affected by ENSO events [30]. At a smaller scale, the marine biogeographic transition zone described around 30°S of latitude in the Chilean coast seems to have unpredictable but high temperature fluctuations at inter-annual scales at the north of 30°S, in contrast to predictable and limited temperature fluctuations at intra-annual scales south of 30°S [31]. Consequently, fluctuating temperatures and the duration of exposure to stress must be considered along with mean temperatures present in the coast.

We chose to study the case of the intertidal kelp *Lessonia nigrescens* for which two cryptic species have been recently identified along the South-eastern Pacific coast [33]. These two kelp species have contrasting geographic ranges: the 'Northern species' occurs between 16°S and 30°S and the 'Southern species' stretches between 29°S and 41°S (Fig. 1). Further studies have shown that these two species are reproductively isolated [34] and were never found co-existing in the same location, even within the transition zone between the two range distributions (from 29°S to 30°14'S), where a mosaic of pure populations either of the Northern or Southern species was observed whatever the scales [33,35]. Because of the contrasting distribution ranges, the species experience different environmental conditions such as water temperature with the Northern species occurring in warmer waters than the Southern species. They are also differentially exposed to environmental disturbances. For example, during the El Niño event of 1982/83, a massive mortality affected individuals from the northernmost populations of the Northern species, nevertheless in the affected region, some populations survived in certain localities, such as Iquique (20°S, [36]). It has been hypothesized that this survival could have been the result of local adaptation to high temperatures [36,37].

Using these two cryptic species of the *Lessonia*, we aimed to test the following hypotheses regarding the tolerance to temperature stress of microscopic stages: (i) the Northern species is expected to be more tolerant to high temperature than the Southern species, and (ii) local adaptation within each species is expected as a differential thermal tolerance among populations across geographic range. Particularly, we expected that marginal populations, located in the transition zone, would present singular responses to temperature.

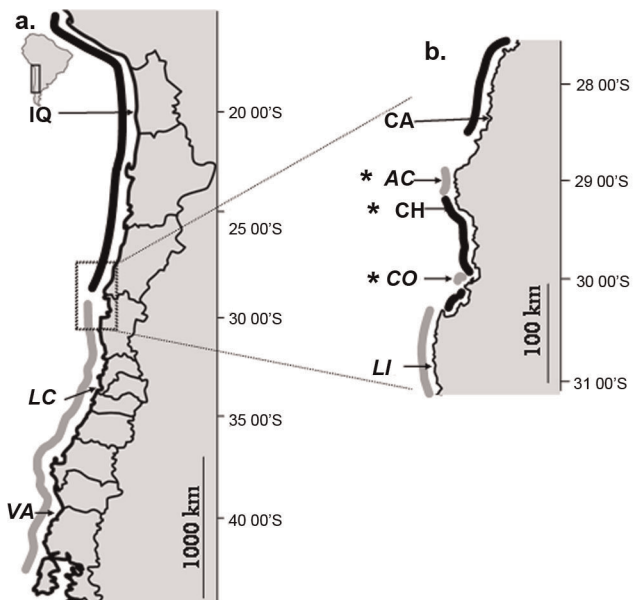


Figure 1. Distribution of Northern and Southern cryptic species of *Lessonia nigrescens*: (a) along the Chilean coasts, (b) detail of the transition zone (28–31°S). The range distribution of the Southern species is represented in grey (names in italics) and of the Northern species in black. Marginal populations are indicated by an asterisk. See Table 1 for details.

doi:10.1371/journal.pone.0039289.g001