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Internal brooding favours pre-metamorphic chimerism in a non-colonial cnidarian, the sea anemone *Urticina felina*

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The concept of intraorganismal genetic heterogeneity resulting from allogeneic fusion (i.e. chimerism) has almost exclusively been explored in modular organisms that have the capacity to reproduce asexually, such as colonial ascidians and corals. Apart from medical conditions in mammals, the natural development of chimeras across ontogenetic stages has not been investigated in any unitary organism incapable of asexual propagation. Furthermore, chimerism was mainly studied among gregarious settlers to show that clustering of genetically similar individuals upon settlement promotes the occurrence of multi-chimeras exhibiting greater fitness. The possible occurrence of chimeric embryos and larvae prior to settlement has not received any attention. Here we document for the first time the presence of natural chimeras in brooded embryos and larvae of a unitary cnidarian, the sea anemone *Urticina felina*. Rates of visible bi- and multi-chimerism of up to 3.13 per cent were measured in the broods of 16 females. Apart from these sectorial chimeras, monitored fusion events also yielded homogeneous chimeric entities (mega-larvae) suggesting that the actual rates of natural chimerism in *U. felina* are greater than predicted by visual assessment. In support of this assumption, the broods of certain individuals comprised a dominant proportion (to 90%) of inexplicably large embryos and larvae (relative to oocyte size). Findings of fusion and chimerism in a unitary organism add a novel dimension to the framework within which the mechanisms and evolutionary significance of genetic heterogeneity in animal taxa can be explored.

Keywords: chimera; fusion; genetic heterogeneity; allorecognition; marine invertebrate

1. INTRODUCTION

Our understanding of life histories largely relies on the concept of the individual, which is intrinsically associated with genetic homogeneity and uniqueness [1]. However, intraorganismal genetic heterogeneity (IGH) has now been shown to occur naturally in protists, fungi, plants and animals [2], questioning the definition of individuality, with vast implications in ecology and evolution. Until recently, the significance of IGH was essentially dismissed because of its presumed rarity, even though supporting evidence for genetic homogeneity is equally scarce [2]. While not always clearly distinguished in the literature, two main types of IGH can be defined on the basis of functional origin and genetic change. Mosaicism is the outcome of genetic variations within an organism that may be caused by somatic mutations or other processes, whereas chimerism is the result of allogeneic fusion. In this sense, chimerism is primarily restricted to algae and colonial marine organisms with pelagic propagules (sponges, hydroids, corals, bryozoans and ascidians), while mosaicism also commonly occurs in unitary animals as well as in clonal and aclonal plants [2,3]. A broad definition of a chimera states that it is an organism that simultaneously harbours cell populations from two distinct fertilization products (zygotes), whether via coalescence or through an exchange (e.g. blood twins and foetal–maternal chimeras in humans [4]).

As evidence of their natural occurrence accumulates, chimeric entities are becoming a focus of interest in trying to determine the mechanisms and evolutionary significance of genetic heterogeneity. Much like the mythological monsters, chimeras in animal taxa are often perceived as aberrant and generally found to be detrimental in terms of relative fitness costs and benefits for the chimeric state compared with genetically homogeneous conspecifics [2,5]. However, while the negative outcome of natural chimerism has been documented in juvenile colonies of soft corals [6], important rates of chimerism (2–5%) have been measured in wild adult populations of hermatypic corals [7]. Of the several potential benefits that have been suggested to explain the prevalence of chimeric entities (e.g. increased growth, reproductive output or survivorship) very few have so far been demonstrated, except greater fitness of multi-chimeras in colonial ascidians and corals [5,8]. This finding is in line with the assumption that greater genetic variability translates into more versatile physiological qualities enabling chimeras to better cope with environmental changes.

The mechanisms that might promote or prevent chimerism have been examined in the hopes of shedding some light on this puzzling phenomenon. In soft corals and colonial hydroids, a window of opportunity was

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