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Morphometry and mechanical design of tube foot stems in sea urchins: a comparative study

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Abstract

To withstand hydrodynamic forces, sea urchins rely on their adoral tube feet, which are specialized for attachment. Although it has been often suggested that the degree of development of these tube feet is intimately related to the maximum environmental energy a species can withstand, it has never been demonstrated by mechanical testing. To address this subject, we studied the mechanical properties of the stem of adoral tube feet from three species of sea urchins, *Arbacia lixula*, *Paracentrotus lividus* and *Sphaerechinus granularis*, which have distinct taxonomic, ecological and morphological characteristics. The tube feet of the three species have a very similar morphology. When a tensile force is applied to the tube foot stem, the connective tissue is the only tissue layer bearing the load. The mechanical properties of this tissue give the tube feet an ideal balance of extensibility (139–166%), strength (23–29 MPa) and stiffness (152–328 MPa), which together produce a material with adequate toughness (2.5–2.9 MJ/m^3) to absorb the impact of waves and currents, and thus to resist the environmental challenges of the habitats in which sea urchins live. Extended stems of *P. lividus* were significantly stiffer (328 MPa) than those of the other two species (152 and 183 MPa, for *A. lixula* and *S. granularis*, respectively). No interspecific difference was found in terms of extensibility, strength, initial stiffness and toughness between the tube feet from the three species. The difference in local distribution between the species investigated is therefore not only explained by the mechanical properties of their tube feet, but may involve other factors such as tube foot number and arrangement, tube foot disc tenacity or sea urchin size.

Keywords: Mechanical properties; Ultrastructure; Connective tissue; Tube feet; Echinodermata; Echinoidea

1. Introduction

Echinoids are exclusively benthic animals. Among the different sea urchin appendages, both the primary spines and the coronal tube feet participate in several activities in relation to the substratum. These activities

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are locomotion and maintenance of position (involving mostly adoral appendages), and righting and covering reactions (involving mostly aboral appendages) (Lawrence, 1987). Coronal tube feet are located in the five ambulacra, from the edge of the apical system to the edge of the peristomeal membrane. They consist of an enlarged and flattened distal extremity, the disc, which makes contact with the substratum and a proximal extensible cylinder, the stem, which connects the disc to the test. Both the stem and the disc consist of four tissue layers: an inner myomesothelium, a connective tissue layer, a nerve plexus, and an outer epidermis (Kawaguti, 1964; Nichols, 1966; Florey and Cahill, 1977; Flammang and Jangoux, 1993).

In every echinoid species investigated, the tube feet on the adoral surface have always a thicker stem wall and a wider disc compared with those of the aboral surface (Smith, 1978). These morphological differences are accompanied by mechanical differences: adoral tube feet are significantly more extensible and stronger than aboral tube feet (Leddy and Johnson, 2000) and may also have more adhesive power (Smith, 1978, Flammang, 1996).

Regular echinoids generally inhabit rocky or other types of hard bottoms exposed to wave action, although some species are found on soft bottoms in sheltered areas. It has been reported that echinoid species belonging to different taxa and inhabiting different environments possess different types of tube feet, and that a general correlation might exist between the degree of development of the tube feet and the maximum environmental energy that a species can withstand (Sharp and Gray, 1962; Smith, 1978). To withstand hydrodynamic forces, sea urchins are able to adhere strongly but temporarily to the substratum with their adoral tube feet. The tenacity with which an individual can anchor to a surface is determined partly by the number of tube feet which are involved. In addition, the strength of attachment depends on the strength of the tube foot itself, which is determined by the tensile strength of the stem and the adhesive power of the disc (Sharp and Gray, 1962; Smith, 1978). However, when a sea urchin is subjected to a constant pull, the majority of tube feet rupture before the terminal disc is detached from the substratum (Smith, 1978; Santos et al., unpublished observation), and therefore, the strength of the stem could limit tube foot attachment strength.

The aim of the present study was to characterize the biomechanics of tube feet in different species of regular echinoids and see if there is a correlation between mechanical properties and habitat. To address this question, we studied the material properties of the stem of adoral tube feet from three common European species, *Arbacia lixula* (Linné, 1758), *Paracentrotus lividus* (Lamarck, 1816) and *Sphaerechinus granularis* (Lamarck, 1816), which have distinct taxonomic, ecological and morphological characteristics.

2. Materials and methods

Specimens of the three species were collected in the Mediterranean Sea (Banyuls-sur-mer, France) in a semi-sheltered rocky area with sandy bottoms. The arbacioid *A. lixula* and the echinid *P. lividus* were collected between 1 and 3 m in depth but, although the two species co-occurred in the same rocky area, individuals of the former were usually observed deeper than individuals of the latter. The temnopleuroid *S. granularis* was found at about 10 m in depth on a sandy bottom area. After collection, the animals were kept in re-circulating aquariums at 14–15 °C and 33‰.

2.1. Morphometric and ultrastructural analysis of tube foot stem

The mean values of the cross-sectional areas of each tissue layer of the tube foot stem from each sea urchin specimen were obtained using tube feet dissected after the mechanical tests (see Section 2.2.). These tube feet were fixed in Bouin's fluid for 24 h, subsequently dehydrated in a sequence of graded ethanol and embedded in paraffin wax. They were then cut transversely into 7-μm-thick sections with a Microm HM 340 E microtome. The sections were mounted on clean glass slides and stained with Masson's Trichrome. Measurements were made with a Leica Laborlux light microscope equipped with a graduated eyepiece on sections taken halfway between the base and the disc of the tube foot.