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DYNAMICS AND SCALING OF THE TENTACLES OF SQUID

Muscular hydrostats are muscular organs that lack hard skeletal support and instead rely on a tightly packed, three-dimensional array of muscle for support and movement. Examples include the arms and tentacles of cephalopods, the tongues of many mammals, reptiles and amphibians and the elephant's trunk. The movements of a muscular hydrostat depend on its size and shape, the properties and arrangement of its tissues, as well as the activation and three-dimensional arrangement of its muscle fibres. The mechanical properties and arrangement of the tissues presumably vary according to the functional demands the system has to fulfill, and are expected to depend on the peak mechanical load, which varies with animal size. Thus, muscular hydrostats are expected to grow allometrically. To explore this hypothesis, the functional design of the tentacles in squid was studied by a combination of mathematical modeling and morphological and experimental observations.

The muscular stalks of the two tentacles of a squid are rapidly extended (typical extension time 30 ms; peak extension speed nearly 2.5 m/s, c.f. Kier & Van Leeuwen, 1997) during prey capture. The distal portions of the tentacles, the clubs, do not elongate and are used to adhere to the prey with arrays of suckers. The extensor muscle fibres are optimally oriented in transverse planes. A forward dynamics model of the tentacle was developed (Van Leeuwen and Kier, 1997), which incorporates the basic muscle architecture and basic muscle physiological properties. The model predicts the extension movements (as measured by Kier & Van Leeuwen, 1997) remarkably well after some unknown parameters were adjusted within physiological limits. Interestingly, the model predicts that the unusually short myosin filaments observed previously in the extensor muscles (range 0.5–1.0 micrometers, unique for the animal kingdom!) are required for the remarkable extension of the tentacles. The predicted filament length for the tip should probably be increased slightly, because we have found that the amount of extensor muscle decreases slightly from the base to the tip (figure 1), whereas a constant muscle mass distribution was assumed previously. The model predicts also the observed slender shape of the tentacles: addition of tissue in the radial direction has little effect on the extension speed. Several other aspects were predicted by the model, which are currently tested. (1) It is predicted that the sarcomeres should be longer at the base of the stalk than at the tip. This is due to a difference of the mechanical load of the sarcomeres along the stalk. (2) The mechanical load of the extensor muscles tends to increase with size. This may be compensated for by a relative decrease in the size of the terminal club with increase in tentacular size. Indeed, at hatching, the terminal club of the squid *Sepioteuthis lessoniana* represents 70 % of the length of the tentacle but by the fifth week after hatching only 50% of the length (Kier, 1996). The increase in mechanical load could also be compensated for by an increase in the relative proportion of extensor fibres or by longer myofilaments in the extensor fibres. These predictions are tested with measurements made on an ontogenetic growth series of squid specimens.

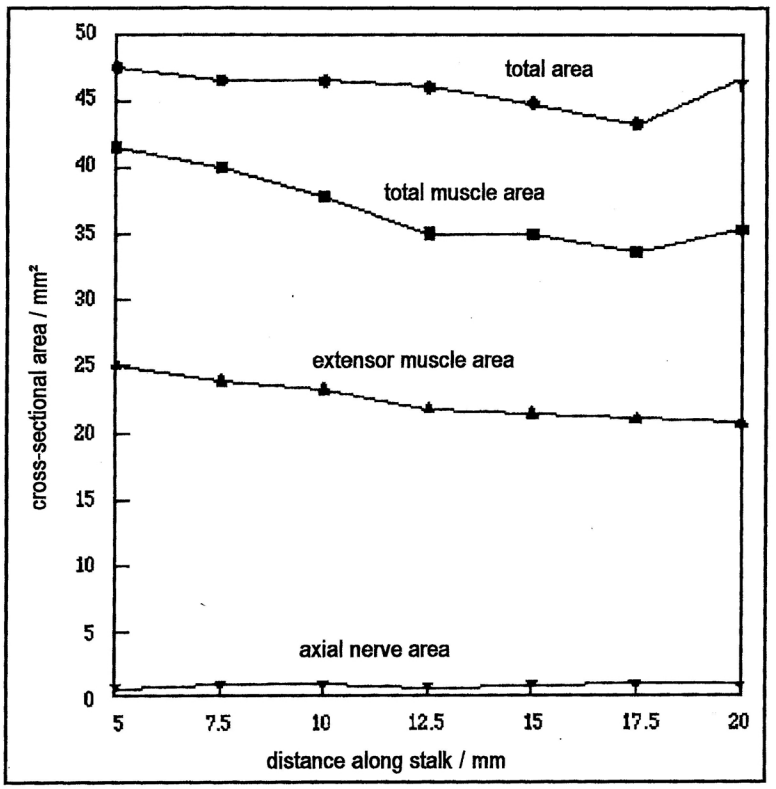

Fig. 1 Areas measured from cross-sections along the stalk of *Sepiotheutis*. Both the total muscle area and the area of the extensor muscles decrease sligthly along the stalk.

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