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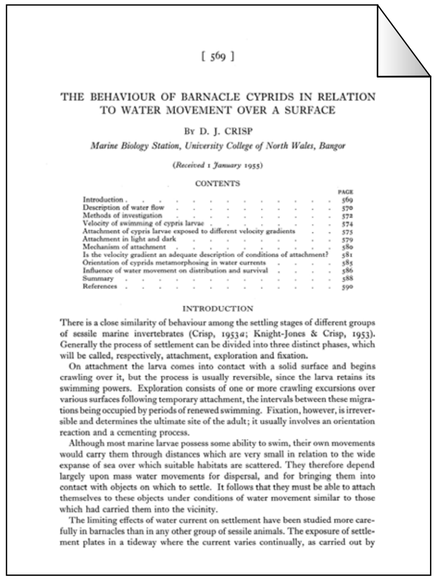
A CLASSIC HYDRODYNAMIC ANALYSIS OF LARVAL SETTLEMENT



[569]

THE BEHAVIOUR OF BARNACLE CYPRIDS IN RELATION TO WATER MOVEMENT OVER A SURFACE

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CONTENTS

INTRODUCTION

There is a close similarity of behaviour among the settling stages of different groups of sessile marine invertebrates (Crisp, 1953*a*; Knight-Jones & Crisp, 1953). Generally the process of settlement can be divided into three distinct phases, which will be called, respectively, attachment, exploration and fixation.

On attachment the larva comes into contact with a solid surface and begins crawling over it, but the process is usually reversible, since the larva retains its swimming powers. Exploration consists of one or more crawling excursions over various surfaces following temporary attachment, the intervals between these migrations being occupied by periods of renewed swimming. Fixation, however, is irreversible and determines the ultimate site of the adult; it usually involves an orientation reaction and a cementing process.

Although most marine larvae possess some ability to swim, their own movements would carry them through distances which are very small in relation to the wide expanse of sea over which suitable habitats are scattered. They therefore depend largely upon mass water movements for dispersal, and for bringing them into contact with objects on which to settle. It follows that they must be able to attach themselves to these objects under conditions of water movement similar to those which had carried them into the vicinity.

The limiting effects of water current on settlement have been studied more carefully in barnacles than in any other group of sessile animals. The exposure of settlement plates in a tideway where the current varies continually, as carried out by

Per R. Jonsson writes about D. J. Crisp's 1955 publication on the behaviour of barnacle cyprids in relation to water movement over a surface.

Dennis Crisp began his academic education in Cambridge, where he studied natural sciences with a broad coverage in physics, chemistry and biology (see biography by Fogg and Southward, 1992). His first scientific achievements dealt with physico-chemical mechanisms involved in protein surface affinity. This background, combined with a deep interest in zoology, led to a post at a commercial testing station for studies of corrosion and fouling on man-made surfaces in the marine environment. Here, Crisp began his life-long research to understand the factors controlling the settlement behaviour of the larval stage of marine organisms. During the golden era of British marine larval biology in the 1950s, he rapidly became one of the most influential scientists in the development of larval ecology. During his career he published several comprehensive studies detailing the responses of marine larvae to environmental factors in their quest for a suitable site to metamorphose into the sedentary, adult life stage (e.g. Crisp, 1955, 1974; Crisp and Barnes, 1954; Crisp and Meadows, 1963). Crisp's classic paper on the effect of water flow on the settlement of barnacle larvae, published in *The Journal of Experimental Biology* in 1955, continues to have a positive citation trend 50 years after its publication. The growing citation frequency attests to how far ahead of his time he was in applying hydrodynamic theory to understand larval responses to water flow in the boundary layer just above the surface of the attachment site.

In his 1955 paper, Crisp addressed a now central issue in marine larval ecology, namely if and how microscopic larvae can actively select final settlement sites on shores and seabeds exposed to water flows more than 100× faster than larval swimming speeds. In a series of elegant experiments, Crisp explored how barnacle larvae (cyprids) respond to water flow at the surface of a potential attachment site, and how flow speed may prevent swimming cyprids from making an initial attachment to a surface. In well-defined flow regimes Crisp first determined the swimming capability of different species of cyprids. He then tested the ability of free-swimming cyprids to attach to surfaces exposed to different flow speeds. His pioneering approach was to focus on the local flow speed at the scale of the settling larva (ca. 0.5 mm), rather than the free-stream flow speed away from the seabed. By applying hydrodynamic theory Crisp was perhaps the first to explicitly point out the significance of the velocity gradient of water (the boundary layer), which is always present close to any surface, to aquatic organisms. In his experiments Crisp used glass tubes of different diameters to create a series of velocity gradients at the attachment surface. Crisp knew that the velocity distribution in laminar water flow through pipes is easily determined and he could relate larval attachment probability to the local flow speed acting on the larvae when making contact with the solid surface. He showed that local flow speeds of a few cm s^{-1} stimulated cyprid attachment, which then declined sharply when he increased flow speeds to 10–20 cm s^{-1}. Crisp also found that cyprids, once attached, could use their antennae to walk along the substrate surface at even higher local flow speeds than 10–20 cm s^{-1}. Crisp explained the cyprid's ability to remain attached by showing that the hydrodynamic drag acting on the cyprid body was considerably less than the predicted adhesion force generated by its antennae against the substratum. He concluded that of all the processes involved in larval settlement, initial adhesion is the most sensitive to flow speed.

Crisp also found an interesting correspondence between the swimming velocity of cyprids and the local flow speed that resulted in maximum attachment. He proposed a mechanism of site selection based on flow, where cyprids approaching the surface swim against the current (rheotaxis) and attach when local flow speed coincides with their swimming speed. However, he offered no explanation as to how the suspended cyprid could obtain some frame of reference against which it could exercise a rheotactic response. This mechanism of larval choice still remains to be tested. With the inclusion of a boundary layer Crisp partly resolved the debate of how larvae could settle in water currents where the free-stream flow greatly exceeds larval swimming speeds. A limitation in Crisp's analysis is that all his experimental boundary layers were laminar, whereas most marine attachment sites likely experience turbulent water flow. Crisp was well aware of this simplification, but at that time empirical information about time-dependent turbulent boundary-layer flow was not available. Recent work shows that the prediction of settling probability is much more complex in turbulent boundary layers (Abelson and Denny, 1997; Crimaldi, 2002).

The key innovation in Crisp's paper was the rigorous inclusion of hydrodynamic theory to gain an understanding of the flow conditions and forces acting on the small scale of larvae. Possibly because he was trained in physics and chemistry Crisp had the theoretical ability to cross the traditional discipline boundaries and combine hydrodynamic theory and experimental ecology. It is probably fair to say that the power of applying hydrodynamic analysis to better understand larval settlement was not fully recognized at the time of publication. The biological audience was apparently not prepared for the physical message. The significance of the boundary layer and hydrodynamic forces took time to diffuse into the marine biological community. However, Crisp's paper clearly foreshadows the successful application of hydrodynamics in aquatic ecology that developed in the 1980s. I can only guess that research following in the footsteps of Crisp's paper was stimulated by his quantitative use of hydrodynamic theory (e.g. Butman, 1987; Eckman et al., 1990; Mullineaux and Butman, 1991). It is clear that the issue of flow effects on larval settlement first raised in Crisp's 1955 paper is now at the core of larval ecology research.

Personally, I am deeply impressed with the scholarship evident in Crisp's work, how ahead of his time he was with this publication, and the skill he showed in his experiments on live larvae. In a recent paper on the settlement of barnacle cyprids in different flow environments (Jonsson et al., 2004) we found that the data on critical flow speeds for attachment in cyprids presented in Crisp's paper are still the best available, despite the tremendous developments in high-speed video recording and flow measurement techniques in recent years. In his classic 1955 paper, Dennis Crisp reported a very fine piece of research with both theoretical and empirical qualities. Few scientific reports stand the test of time so well.

A PDF file of the original paper can be accessed online: http://jeb.biologists.org/cgi/content/full/208/18/3431/DC1

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