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The mechanisms of filter feeding on oil droplets: Theoretical considerations

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ABSTRACT

Filter feeding animals capture food particles and oil droplets from the fluid environment using cilia or appendages composed of arrays of fibers. Here we review the theoretical models that have provided a foundation for observations on the efficiency of particle capture. We then provide the mathematical theoretical framework to characterize the efficient filtration of oil droplets. In the aquatic and marine environments oil droplets are released from the decay of organisms or as hydrocarbons. Droplet size and flow velocity, oil-to-water viscosity ratio, oil-water interfacial tension, oil and water density difference, and the surface wettability, or surface texture, of the filter fiber are the key parameters for oil droplet capture. Following capture, capillary force maintains the droplet at its location due to the oil-water interfacial tension. If the oil-coated fiber is subject to any external force such as viscous or gravitational forces, it may deform and separate from the fiber and re-enter the fluid stream. We show oil droplet capture in *Daphnia* and the barnacle *Balanus glandula*, and outline some of the ecological unknowns regarding oil capture in the oceans. Awareness of these mechanisms and their interrelationships will provide a foundation for investigations into the efficiency of various modes of filter feeding on oil droplets.

1. Introduction

Filter feeders use a diverse range of filamentous appendages to capture food from the water (Riisgård and Larsen, 2010). Although most appendages essentially consist of arrays of bristles or cylinders, some behave as sieves to intercept particles from suspension passing through (e.g. bands of stiff cilia, setae, or mucous nets), while others create feeding currents or act as paddles to direct pockets of fluid for further processing (e.g. flagella, cirri, or tentacles) (Riisgård and Larsen, 2010; Vogel, 1994). With respect to food capture (i.e. particles or oil droplets), the structure and motion of the fibres, and their interaction with the flow of water, form the essence of the filtering mechanism. The capture of particles has been explored from theoretical (Rubenstein and Koehl, 1977), experimental (Koehl, 2004; Labarbera, 1978; Riisgård and Larsen, 2010), and modeling perspectives (Koehl, 2003; Shimeta and Jumars, 1991; Vogel, 1994; Spielman and Goren, 1968). Experimental (Almeda et al., 2013) and modelling (Nepstad et al., 2015) perspectives of oil capture by filter feeders have been addressed. Here we provide a theoretical basis of oil droplet capture and retention by filter-feeding appendages. From here onwards, we adopt the terminology of those that contributed before us, and refer to these diverse appendages as fibers, and treat them as cylindrical, solid, surfaces.

Oil droplets in the aquatic and marine environment may be derived from animals, plants, algae, microbes or fossil hydrocarbons. Oil may be nutritionally rich or a toxic component of the filter-feeding diet (Conover, 1971; Jónasdóttir, 1999; Miller et al., 2000; Friedman and Strickler, 1975). It is used by zooplankton to modulate buoyancy (Miller et al., 2000; Thorisson, 2006), and as part of the diet of copepods it increases the production of eggs (Thorisson, 2006; Jónasdóttir, 1999; Demott and Dörthe, 1997). The capture and ingestion of oil, most significantly by zooplankton, provides the entry point into the aquatic food webs that can terminate with top predators including humans (Turner and Ferrante, 1979; Longhurst and Williams, 1992). Oil that is peletized into fecal castings is a key link in the global carbon cycle (Siegel et al., 2014). Oil occurs in aquatic environments as large surface slicks, as sub-surface blobs, down to micron-sized oil droplets. Droplets form due to the natural shear created by waves, or natural and industrial surfactants (dispersant) (Rico-Martínez et al., 2013). The ingestion of micron-sized oil droplets, those within the size range consumed by filter-feeders, is significant and documented (Rico-Martínez et al., 2013; Almeda et al., 2014, 2013), but the interaction between these organisms and the oil particles are not. The mechanics of filter feeding on micron-sized droplets, by animal appendages, is lesser known, and is the subject of this review.

Oil-water-fiber interaction is a complex problem and requires an extensive review of the fundamentals of fluid dynamics and interface science. In Sect. 2, we review the theoretical basis of solid particle capture from a fluid dynamic perspective, that includes a discussion of

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Nomenclature

Bo	Bond number
Ca	capillary number
D	particle diffusivity (m^2/s)
F_d	drag force (N)
F_g	gravitational force (N)
g	gravitational acceleration (m/s^2)
G	dimensionless number for intensity of gravitational deposition
h	maximum thickness of oil coating a fiber (m)
K	Boltzmann's constant ($g{\cdot}cm^2{\cdot}s^{-2{\cdot}o}K^{-1}$)
l	wetting length on a fiber (m)
L	Inter-fiber distance (m)
m	mass (kg)
n	dimensionless oil film thickness ($=h/R_f$)
p	oil-to-water viscosity ratio
Pe^{-1}	dimensionless number for intensity of diffusion deposition
R	radius (m)
$\overline{R}$	dimensionless number for intensity of direct interception
Re	Reynolds number
St	Stokes number for intensity of inertial interaction
T	temperature (Kelvin)
U	velocity (m/s)
$\mathbf{v}_T$	terminal velocity m/s
V	dimensionless volume of oil on fiber (m^3)
$\mathbf{x}_s$	stopping distance (m)
μ	viscosity ($Pa{\cdot}s$)
ρ	density (kg/cm^3)
σ	interfacial tension N/m
θ	contact angle (degrees)
δ	boundary layer thickness (m)

Subscripts

f	fiber
o	oil droplet
p	particle
s	solid
w	water

the mechanisms of particle capture introduced to the biology community by Rubenstein and Koehl (1977). In Sect. 3, a comprehensive review to colloid and interface science is provided. Some of the practical processes and problems that relate the science of emulsion and wettability to aquatic animals is given. In Sect. 4, the capture and release mechanisms of oil droplet by fibers are discussed. We introduce the role of different parameters including oil-to-water viscosity ratio, oil-water interfacial tension, oil-water density difference, and the wettability of the fiber on the success of oil droplet capture and detachment. The capturing and detachment of an oil droplet from a fiber is quantified using appropriate dimensionless numbers. Finally in Sect. 5, real examples of oil droplets interacting with *Daphnia* and barnacles are shown.

2. Mechanisms of solid particle capture by fibers: a review

2.1. Capture by single fiber

Rubenstein and Koehl (1977) introduced a set of simplified equations, to the biology community, that form the basis of particle capture by fibers and pores. Particles may be captured (filtered) through inertial interaction, gravitational deposition, direct interception, diffusion deposition, or sieving. They proposed non-dimensional numbers to estimate the encounter efficiency "intensities" of filtration for different mechanisms. The proposed dimensionless numbers account for filter size, particle size, fluid viscosity and velocity and other parameters, and remain the fundamental tools of most present-day animal-fluid studies.

Fluid mechanical models of filter-feeding generally assume a steady, viscous, incompressible flow with free stream velocity (U_w) over a smooth, stationary cylinder with infinite length, and the particle is spherical, and flows in the direction of the free stream normal to the axis of the cylinder (Fig. 1a). This model requires the knowledge of two well-known problems in the literature of fluid dynamics: 1) Viscous flow over a cylinder, and 2) viscous flow over a spherical solid particle. These problems are summarized in Fig. 1.

Consider the motion of a particle with radius R_p and mass m_p moving at velocity U_p in a viscous fluid (e.g. water) having viscosity and density of μ_w and ρ_w, respectively, flow at velocity of U_w. The particle is under the influence of gravity in the y-direction, where g is the gravitational acceleration. At low Reynolds numbers (Stokes' low-Reynolds number solution), the force balance on the moving particle in vector form is:

$$m_p\frac{d\mathbf{U}}{dt} = F_d + F_g = -6\pi\mu_w R_p(U_p - U_w) + m_p g \tag{1}$$

The left side of Eq. (1) describes the acceleration of the moving particle $\left(\frac{d\mathbf{U}}{dt}\right)$, where m_p is the mass of the particle. The right side of Eq. (1) is the sum of all external forces (i.e, drag and gravitational forces). Drag force always exists whenever there is a velocity difference between the particle and the free stream flow, and the negative sign implies that the drag force is in the opposite direction of the flow. After simplifying Eq. (1) using some mathematical maneuvers (see Chen (1955); Harrop and Stenhouse (1969); Lee and Liu (1982); Yeh and Liu (1974) for details), the stopping distance and terminal velocity of a particle moving in a fluid is obtained. These two parameters, defined below, are used to determine the efficiency of particle capture by a fiber.

Stopping distance: The distance over which a particle velocity will reach zero ($U_p = 0$) if the fluid flow ceased is known as the stopping distance. The cause of the "ceasing of the flow" can be due to the particle entering the boundary layer of the fiber. The stopping distance is defined as:

$$\mathbf{x}_s = \frac{2R_p^2(\rho_p - \rho_w)U_w}{9\mu_w} \tag{2}$$

Terminal velocity: If fluid flow is ceased, after long enough time, the particle will only move in the y-direction and reach a steady velocity that is caused only by gravitational forces, also known as the terminal velocity:

$$\mathbf{v}_T = \frac{2R_p^2(\rho_p - \rho_w)g}{9\mu_w} \tag{3}$$

Eqs. (2) and (3) are the fundamental equations used to describe the efficiency of particle capture.

2.1.1. Inertial interaction

If there is a density difference between the particle and the fluid, the particle will have momentum, thus its trajectory will deviate from the fluid streamlines around the fiber. This deviation will cause the particle to be captured by the fiber (Fig. 1b). Inertial interaction is characterized using the Stokes number that is the ratio of the stopping distance to the fiber radius

$$St = \frac{\mathbf{x}_s}{R_f} = \frac{2R_p^2(\rho_p - \rho_w)U_w}{9\mu_w R_f} \tag{4}$$