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Behavioural modification of local hydrodynamics by asteroids enhances reproductive success

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ABSTRACT

The reproduction of apex species, such as sea stars, is important for sustaining many marine ecosystems. Many sea star species reproduce externally, introducing gametes in the turbulent benthic boundary layer. Sea stars often aggregate and adopt characteristic behaviour, such as arched posturing, while spawning. Here we quantify, for the first time, the hydrodynamic advantages of postural changes and the extent to which they enhance the efficiency of external reproduction. Hydrodynamic and fertilisation kinetic theoretical modelling were used to provide context and comparison. The arched posture was clearly important in the downstream advection of gametes. Digital particle image velocimetry, acoustic doppler velocimetry and dye release experiments indicated reduced wake and lower shear stresses downstream of arched sea stars, which increased downstream transport of gametes compared to those in the flat position. In all cases, sperm concentration decay rates of two orders-of-magnitude over distances < 20 cm were inferred from fluorometry, confirming the requirement for close aggregation. The level of turbulence and hence downstream gamete dilution was increased by greater current speeds and a rougher seabed. Both an arched posture and hydrodynamic conditions may improve external reproduction efficiency, with behavioural mechanisms providing the primary contribution.

1. Introduction

Sea stars are an important group (Lawrence, 2013), playing a crucial ecological role by serving as voracious predators, prey and detritivores, as well as regulating and maintaining ecosystem structure and functioning (Clark, 1968; Paine, 1969; Uthicke et al., 2009). The majority of sea star species are dioecious and spawn externally (Naylor, 2011). For most species, males and females congregate on an annual basis and release gametes into the turbulent benthic boundary layer (Barker and Nichols, 1983). Sea water temperature change is considered a factor in triggering the external spawning of gametes (Hancock, 1958; Minchin, 1987; Mercier and Hamel, 2009). During spawning events, asteroids congregate in large numbers (Hancock, 1958; Clark, 1968) and females release millions of eggs into the water column (*Asterias* sp. may release 2.5 million eggs per individual over two hours; Clark, 1968), with males ejecting spermatozoa to facilitate external fertilisation (Clark, 1968). Many echinoderms modify their behaviour during spawning, for example by aggregating (Young et al., 1992) or modifying their position and posture, for example by rising from a flat to an arching posture (Fig. 1). The benefits gained by these behaviours have not been quantified.

Asterias rubens Linnaeus, 1758, is one of the most common sea stars in the North Atlantic and often used as a model species to represent the Asteroidea, owing to its typical size, morphology and function (Vevers, 1949; Barker and Nichols, 1983; Nichols and Barker, 1984). *A. rubens* inhabits both smooth sandy surfaces as well as rough rocky surfaces (Naylor, 2011). The size of sexually mature specimens is between 10 and 30 cm diameter (Hayward and Ryland, 1995). Spawning occurs during spring months when gonads are fully ripe (Nichols and Barker, 1984).

External fertilisation in the turbulent benthic boundary layer would appear to be an inefficient method of reproduction (Denny and Shibata, 1989), but is commonly used by a range of invertebrates and vertebrates (Yund, 2000; Crimaldi and Zimmer, 2014). The motility and locomotory abilities of released gametes is negligible (Denny, 1988) and viability of oocytes (< 24 h) and spermatozoa (< 5 h) is short (Vogel et al., 1982; Denny and Shibata, 1989; Williams and Bentley, 2002). Therefore, successful external fertilisation is reliant on high gamete concentrations and turbulent mixing (Levitan et al., 1991; Crimaldi and Zimmer, 2014). Flow velocities of < 0.10 m/s on an uneven substrate can provide sufficient turbulent mixing to aid successful fertilisation (Denny, 1988). Inadequate turbulence may result in

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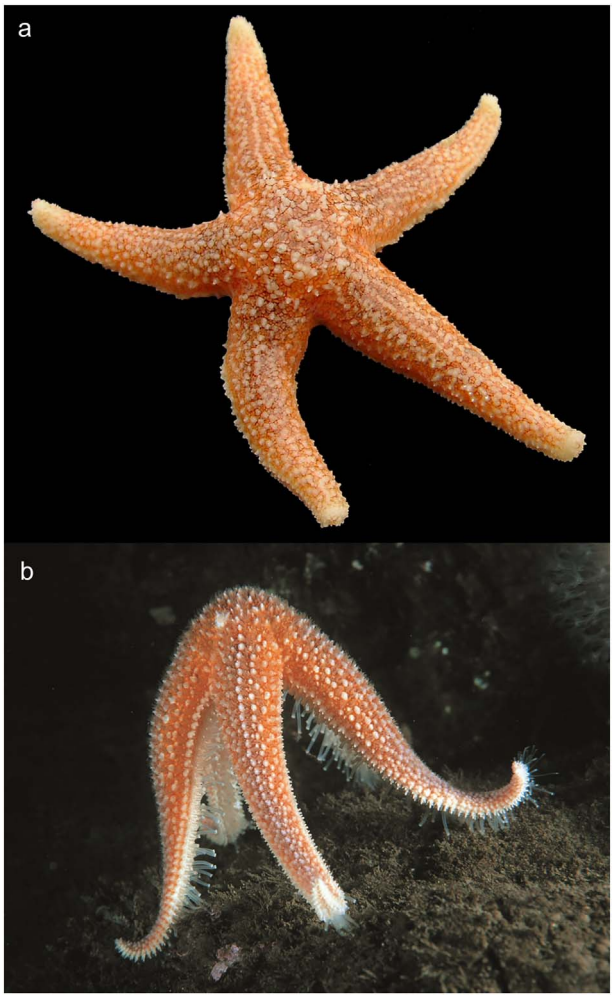

Fig. 1. *Asterias rubens*, (a) flat (Hillewaert, 2000) and (b) arched (Naylor, 2011). Please access the online version of the paper for a colour figure.

released gametes from each sex failing to meet before they become ineffective (Yund, 2000) and excessive turbulence results in gametes being rapidly diluted, reducing levels of fertilisation success (Pennington, 1985; Denny and Shibata, 1989). At a distance of > 1.00 m, gametes are expected to become too diluted for successful fertilisation to occur (Pennington, 1985; Denny and Shibata, 1989). Optimal downstream sperm concentrations vary across taxa, for example, 10^5 sperm ml^{-1} for gastropods, with no fertilisation occurring below 10^2 sperm ml^{-1} (Baker and Tyler, 2001), and 10^2–10^3 sperm ml^{-1} for bivalves (Styan and Butler, 2000).

Knowledge of hydrodynamic conditions that optimise reproduction in apex species, such as asteroids, is important for predicting their population ecology as well as for management of marine systems. Asteroids are known to be extremely important in the structuring of some marine ecosystems (Paine, 1969, 1980; Uthicke et al., 2009). At high population densities, some asteroid species can cause negative effects and require management. An example of this is for *Acanthaster planci*, the crown-of-thorns sea star, where outbreaks can cause widespread reef-building coral mortality events and active culling measures are put in place to prevent damage to important reef systems (Bos et al., 2013). Asteroids can also cause negative impacts to commercial bivalve fisheries (Lawrence, 2013). Population densities are highly variable (Uthicke et al., 2009) and the prediction of harmful population outbreaks and efficacy of management approaches depends on knowledge of the environmental and biological controls on recruitment (Bos et al., 2013; Caballes and Pratchett, 2017).

The objective of this study was to examine whether individual sea stars could profitably use behavioural mechanisms to improve fertilisation success by modifying their local hydrodynamic regime. This study applied hydrodynamic theory and laboratory experiments to determine key constraints on reproduction in asteroids using both flat and arched postures in a range of flow fields.

2. Experimental methodology

The experimental work was undertaken in a unidirectional flow channel measuring 7.50 m long and 0.30 m wide. Flow rate was controlled using a pump and two depth-averaged flow velocities (flow velocity averaged over the entire depth of the water column) were investigated. These were 0.10 m s^{-1} and 0.25 m s^{-1} and corresponded to relatively "low" and "high" turbulence cases. A sluice gate located downstream of the experimental section was used to control the water depth (Fig. 2), which was set at 0.15 m or 0.30 m during the experiment.

Both sandy (smooth) and rocky (rough) substrates were simulated in the flume. The rough surface consisted of dental plaster slabs into which 40 mm diameter spheres were irregularly set and subsequently removed (Dams, 2015). To simulate sand, skateboard grip tape with a mean particle diameter of 240 μm (equivalent to a fine to medium sand) was affixed to the flume base.

Life sized models were 3D printed in 21 separate components and assembled into flat and arched positions. To simulate the spiny aboral

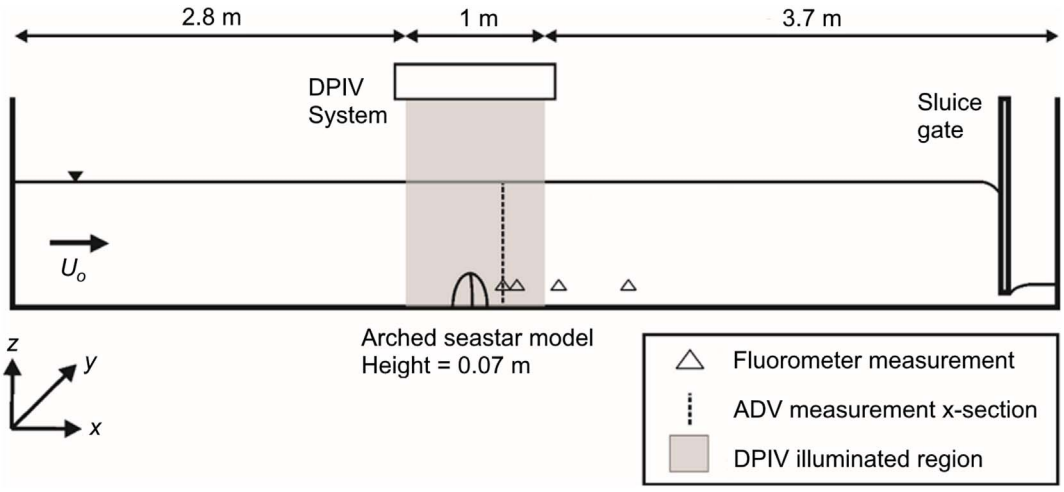

Fig. 2. Schematic diagram of the flume and experimental apparatus.