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Biomechanics and behaviour in the sea urchin *Paracentrotus lividus* (Lamarck, 1816) when facing gradually increasing water flows

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ABSTRACT

Water motion, because of its potential to dislodge intertidal organisms, plays a crucial role in shaping marine communities as it creates available spaces suitable for interactions, settlement and colonization. To understand how water flow influences the behavioural ecology of benthic species such as echinoids, we investigated how the sea urchin *Paracentrotus lividus* (Lamark, 1816) can cope with increasing flow velocities through a biomechanical and behavioural approach. Whereas sea urchins maintained in static conditions for several weeks showed weak adhesive properties, they immediately reacted to increasing hydrodynamic forces. Sea urchins were dislodged at a flow velocity of about 70 cm s^{-1}, with a few individuals enduring up to 90 cm s^{-1}. This response was modulated by two behavioural strategies: (1) at low flow velocities, an escaping strategy characterized by fast upstream locomotion relying on tube feet; and (2) above a threshold flow, a streamlining strategy characterized by changes in overall shape and spines orientation, accompanied by a fast decrease of the animal's movement until complete immobility. Although the threshold at which the switch in behaviour occurs and the detachment velocities were both probably underestimated because individuals were aquarium-acclimatized, the behavioural sequence reported reveals how *P. lividus* can avoid or withstand rough weather conditions. From an ecological perspective, the occurrence of a range of water velocities too slow to dislodge sea urchins but sufficient to inhibit their active movement is relevant to understand how echinoids can structure benthic communities by controlling macroalgae development through their grazing activity.

List of Abbreviation

Abbr.	Parameters	Units	Equations
Dir_{Mov}	Direction of sea urchin active movement	Degrees	
Dl/Dr/Ul/Ur	Downstream (D) or upstream (D) quadrants, to the left (l) or right (r) of the flow		
d_T	Ambital test diameter	mm	
F_{disk}	Detachment force of a single tube foot disk	N	
F_H	Hydrodynamic force	N	

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	$F_H = 0.5\, \rho\, u^2 \sqrt{(C_D * Spr)^2 + (C_L * Spl)^2}$, ρ: seawater density (Kg m^{-3}); u: water velocity ($m\, s^{-1}$); Cd and Cl: drag and lift coefficients for *Strongylocentrotus purpuratus* obtained from Denny and Gaylord (1996); Spr and Spl: profile and planform projected surface areas (m^2)		
F_{urchin}	Detachment force of whole sea urchin	N	
Flow1′	Flow regime 1: flow velocity increments every minute		
Flow2′	Flow regime 2: flow velocity increments every two minutes		
h_T	Test height	mm	
Pl or Pr	Planform (Pl) or profile (Pr) zones (A/B/C/D) for spines angle		
S_{disk}	Adhesive surface area of a single tube foot disk	mm^2	
S_{urchin}	Adhesive surface area of whole sea urchin	mm^2	$S_{urchin} = S_{disk} *$ *number of adoral tube feet*
T_{disk}	Tenacity of a single tube foot disk	MPa	$T_{disk} = (F_{disk}/S_{disk})$
T_{urchin}	Sea urchin tenacity	MPa	$T_{urchin} = (F_{urchin}/S_{urchin})$
TF_{att}	Density of attached tube feet relative to oral test surface area	mm^{-2}	$TF_{att} =$ (*number of attached tube feet*$/\pi * (d_T/2)^2$)
$TF_{att}\%$	Percentage of attached tube feet relative to the total number adoral tube feet	%	$TF_{att}\% =$ (TF_{att}/*number of adoral tube feet*) $* 100$
V_{Det}	Detachment velocity of sea urchins	$cm\, s^{-1}$	
V_F	Flow velocity	$cm\, s^{-1}$	
V_{Mov}	Linear velocity of sea urchin active movement	$cm\, s^{-1}$	$V_{Mov} =$ *linear distance travelled/ 5 seconds*

1. Introduction

In coastal environments, marine organisms are constantly exposed to the action of moving water whether it is driven by regular tidal regime, by continuous wave surge or by infrequent storm events. When a mass of moving water flows over a benthic animal, two main hydrodynamic forces are generated simultaneously: pressure drag, acting parallel to the substratum in the direction of flow, pushes the organism downstream; and lift, acting perpendicular to the substratum and to the flow, pulls the animal away from the substratum (Denny, 1988; Denny, 1991). Acceleration reaction, acting in the direction of flow, was believed to apply large forces on organisms (Denny, 1985; Denny et al., 1985), but at the small spatial scale of the intertidal zone, is not a force commonly imposed on surf-zone organisms (Gaylord, 2000). The resultant of drag and lift forces tends to detach the organism from the substratum, leaving behind free patches for settlement and invasion for other species (Paine and Levin, 1981). Therefore, interaction with moving water plays a fundamental role in the ecology of organisms by modulating the way they relate with other species and how they influence their habitat.

As hydrodynamic forces are highly variable in severity and duration, benthic organisms inhabiting the intertidal rocky shore should rely on a variety of strategies to withstand water motion (*e.g.*Cohen-Rengifo et al., 2017; Denny, 1987; Koehl, 1984; Siddon and Witman, 2003; Stewart and Britton-Simmons, 2011; Vogel, 1994). On the short term, these organisms can display specific behaviours such as seeking refuges or clamping and streamlining the body against the substratum since shape modification is an effective way to reduce hydrodynamic forces (Dance, 1987; Ellem et al., 2002; Koehl, 1999; Vogel, 1994; Stewart and Britton-Simmons, 2011). On the medium term, they can modulate their adhesion by regulating the production of adhesive compounds (Toubarro et al., 2016). On the long term, they can adapt their morphology and mechanical properties through phenotypic plasticity (Cohen-Rengifo et al., 2017; Trussell, 1997).

Echinoids are active biological agents in benthic community dynamics and ecosystems productivity around the globe. They often play a key ecological role by controlling the biomass and development of benthic macrophytes through their grazing activity (Boudouresque and Verlaque, 2007; Kitching and Thain, 1983; Scheibling, 1996). Hydrodynamics is known to be an important factor largely influencing the life history of echinoids at levels ranging from the individual (settlement, morphology, feeding and growth) to the community (migration, abundance and distribution patterns) (Boudouresque and Verlaque, 2007; Cohen-Rengifo et al., 2017; Denny et al., 1985; Hereu et al., 2004; Jacinto and Cruz, 2012; Leichter and Witman, 1997; Siddon and Witman, 2003; Turon et al., 1995; Vogel, 1994). Consequently, many studies have been conducted, both in the field and in the laboratory, to investigate the influence of hydrodynamics on sea urchin behaviour and survival. In the field, movement and grazing were reduced in *Strongylocentrotus droebachiensis* subjected to increased turbulence and wave height (Lauzon-Guay and Scheibling, 2007; Mann, 1973). Likewise, during periods of turbulence, *Paracentrotus lividus* moved towards the deep (Dance, 1987), while *Centrostephanus coronatus* halved the number of individuals emerging from their burrows (Lissner, 1980). All these studies indicated an inverse relationship between hydrodynamics and echinoids' activity. They also showed that it is technically difficult to observe sea urchin behaviour and to measure local flow velocities directly in wave-swept environments, appealing for the necessity of *ex situ* experimental approaches. Several studies focusing on the effects of flow on attachment capacity, movement and feeding behaviour of echinoids have thus been conducted under controlled-flow conditions in laboratory flume tanks. Tuya et al. (2007) measured the flow velocity at detachment for *P. lividus* (80 to 120 $cm\, s^{-1}$), *Diadema antillarum* (65 to 75 $cm\, s^{-1}$) and *Arbacia lixula* (180 to 200 $cm\, s^{-1}$). Movement of the echinoid *Strongylocentrotus nudus* was inhibited at a flow velocity of 70 $cm\, s^{-1}$, though feeding rate was already reduced at a velocity of 30 $cm\, s^{-1}$ and ceased at ∼40 $cm\, s^{-1}$ (Kawamata, 1998). Several *Strongylocentrotus* species exhibit a streamlining behaviour when exposed to flows, orientating their spines downwards to mitigate hydrodynamic forces (George and Carrington, 2014; Stewart and Britton-Simmons, 2011). This behaviour, however, can affect the efficiency of particle capture (George and Carrington, 2014).

These previous works attest that, although large hydrodynamic forces can potentially dislodge organisms from the substratum, weaker

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