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Roll, right, repeat: short-term repeatability in the self-righting behaviour of a cold-water sea cucumber

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Abstract

For many benthic marine invertebrates, inversion (being turned upside-down) is a common event that can increase vulnerability to predation, desiccation and unwanted spatial transport, and requires behavioural ‘self-righting’ to correct. While self-righting behaviour has been studied for more than a century, the repeatability (R) – the portion of behavioural variance due to inter-individual differences – of this trait is not well understood. Heritability and the evolution of animal behaviour rely on behavioural repeatability. Here, we examined the self-righting technique of a cold-water holothurid, *Parastichopus tremulus*, and assessed the repeatability of this behaviour. Under laboratory conditions, *P. tremulus* consistently used muscle contractions to curl its body and roll itself back to an upright position, which provided for rapid ($\bar{x} \pm \text{SD} = 96.7 \pm 49.8$ s) and highly repeatable ($R = 0.75$) self-righting in the short term that varied between individuals (range of individual average righting times = 34.8–217.0 s). Righting time tended to increase with animal size; however, substantial variation was evident at comparable sizes, as average righting time ranged from 34.8–155.5 s for animals ~20 cm in body length. Contrary to previous studies on other echinoderms, we found no evidence of improved righting times for *P. tremulus* over time. This study ultimately provides the first detailed documentation of self-righting behaviour for *P. tremulus* and suggests that this species displays a high degree of repeatability for this trait in the short term.

Introduction

Benthic organisms are often challenged with inversion (i.e. being dislodged from the benthos such that the ventral side of the body is oriented away from the benthos toward the water column) resulting from wave action or from falling off vertical surfaces (Blake, 1981). While inverted, these animals are vulnerable to predation, desiccation and unwanted transport due to water currents, all of which can influence survivorship (Penn & Brockmann, 1995). For example, Penn & Brockmann (1995) reported that quicker self-righting reduced the probability of stranding for intertidal horseshoe crabs. Furthermore, righting response time is often associated with stress physiology, as stressed animals tend to right slower than less-stressed animals (Lawrence & Cowell, 1996). Consequently, employing ‘self-righting’ strategies (i.e. actively regaining proper orientation) that minimize the time spent inverted is adaptively beneficial for benthic fauna that experience inversion regularly.

Self-righting behaviour is common to many benthic marine invertebrates. In this context, echinoderms are perhaps the most well-studied (Hyman, 1955; Reese, 1966). For example, self-righting in sea stars has been extensively studied since the 19th century (Jennings, 1907) and righting responses in sea urchins are well documented (Challener & McClintock, 2017). As such, righting behaviour in echinoderm taxa can provide a model system for exploring broad questions in behavioural ecology.

An area of contemporary interest for behavioural ecologists is behavioural repeatability. Behavioural repeatability is reflected by within-individual consistency and between-individual variation for a given behaviour (Briffa *et al.*, 2013) and is typically measured as the proportion of phenotypic variance encompassed by inter-individual differences (denoted as R ; Roche *et al.*, 2016). Mathematically, repeatability is calculated as

$$R = s_A^2 / (s_A^2 + s^2)$$

where s_A^2 is inter-individual variance and s^2 is intra-individual variance over time (Bell *et al.*, 2009). Repeatability is a crucial component of behavioural theories, including animal personality (Gosling, 2001; Roche *et al.*, 2016), behavioural syndromes (Sih *et al.*, 2004a, 2004b), temperament (Reale *et al.*, 2007) and behavioural coping styles (Koolhaas *et al.*, 1999). Bell *et al.* (2009) suggested that behaviour can be viewed as significantly repeatable at $R \geq 0.37$ and studies have since used this threshold as evidence for or against repeatability (e.g. Gutowsky *et al.*,

2016). Repeatable variation in behaviour between individuals is related to fitness traits such as reproductive success and survival (see Smith & Blumstein, 2008 for review) and can be influenced by the environment (Réale & Festa-Bianchet, 2003; Dingemans *et al.*, 2004). Furthermore, it is recognized that individual repeatability is a requirement for the heritability of behavioural traits (Falconer & Mackay, 1996). As such, behavioural repeatability within individuals can moderate behavioural variation in animal populations and can influence selection for behavioural traits within a population (Réale & Festa-Bianchet, 2003; Dingemans *et al.*, 2004).

A variety of behaviours spanning a diverse array of fauna are reported to be repeatable (Bell *et al.*, 2009) and benthic marine organisms are no exception. For example, repeatability has been widely reported for startle responses in sea anemones (Sinn *et al.*, 2008; Briffa & Greenaway, 2011; Rudin & Briffa, 2012; Briffa *et al.*, 2013). Repeatability has also been documented in the escape response of the queen scallop, *Aequipecten opercularis* (Laming *et al.*, 2013). Self-righting behaviour in echinoderms is also thought to be repeatable (Polls & Gonor, 1975). Empirical studies of self-righting repeatability in echinoderms are, however, limited to only two recently published studies (to the best of our knowledge). Gutowsky *et al.* (2016) reported repeatable ($R = 0.47$) and improved self-righting behaviour in the Caribbean sea star, *Oreaster reticulatus*, while Buccheri *et al.* (2019) found moderately repeatable ($R = 0.36$) self-righting in tropical holothurids from the Great Barrier Reef.

Although well documented for other echinoderm taxa, studies on self-righting techniques in holothurids (i.e. sea cucumbers) are lacking, with the exception of a few species (Pearse, 1908; Olmsted, 1917; Berrill, 1966). Furthermore, sea cucumbers are increasingly targeted for aquaculture purposes globally (Lovatelli *et al.*, 2004; Han *et al.*, 2016), particularly as bottom feeders in Integrated Multitrophic Aquaculture operations (Nelson *et al.*, 2012; Zamora *et al.*, 2018). Therefore, more basic knowledge is needed. Only a single study on self-righting repeatability in holothurids exists to our knowledge (Buccheri *et al.*, 2019), which reports that self-righting in three species from the Great Barrier Reef was borderline repeatable ($R = 0.36$). As such, it is largely unclear if holothurid righting behaviour is repeatable. Studies on self-righting behaviour and its repeatability in holothurid echinoderms are thus needed, particularly given the importance of this behaviour in predator avoidance and survival (Penn & Brockmann, 1995).

With a global interest in sea cucumber aquaculture, various species are being considered for farming. A common species being explored for aquaculture in Scandinavia is the red sea cucumber, *Parastichopus tremulus*, a subtidal epibenthic deposit feeder which uses short tentacles for feeding (20 tentacles arranged in a ring and surrounded by papillae). Spine-like papillae are sparsely scattered along a firm body that can reach a length of ~50 cm. Three rows of short tube feet (ambulacral podia; with little elongation capability) line the ventral side of the body, providing for a mobile lifestyle and adherence to hard substrate. In the Gullmar Fjord on the Bohuslän Archipelago of the west coast of Sweden, *P. tremulus* typically occur at 35–80 m depth where numerous predators exist, including sun stars (*Crossaster papposus* and *Solaster endeca*), shrimp (*Pandalus borealis*), fish (*Gadus morhus* and *Melanogrammus aeglefinus*) and (likely) large crabs (*Lithoides maja*) (Francour, 1997). This sea cucumber can occupy soft-bottom areas and is commonly found on silt-covered hard substrates and adhering vertical surfaces (Picton & Morrow, 2016), from which falling off is common (Blake, 1981). Consequently, self-righting is important for predator avoidance, and repeatable variation in individual righting times may play a role in maintaining behavioural variation under different levels of predation pressure (Réale & Festa-Bianchet, 2003).

In this study, we describe (in detail) the self-righting technique employed by this species. We also tested the repeatability of self-righting for adults and assessed whether or not self-righting time was related to body size. We hypothesized that self-righting times for individual *P. tremulus* would be moderately repeatable (based on results of Buccheri *et al.*, 2019 for other holothurids) and positively related to body size.

Materials and methods

Animal collection and husbandry

Adult *Parastichopus tremulus* ($N = 17$) were collected from the Gullmar Fjord (40–80 m depth) as by-catch in lobster pots and were held for more than one year under laboratory conditions at a nearby public aquarium (Havets Hus, Lysekil, Sweden; 2.2 km from the centre) in flow-through aquaria with seawater (33 m depth) from the fjord. With the exception of two animals which remained at Havets Hus, sea cucumbers from the public aquarium were transferred to the Sven Lovén Centre for Marine Infrastructure – Kristineberg (58.249700°N 11.445074°E; near Fiskebäckskil, Sweden and hereafter referred to as 'Kristineberg') in March 2019 ($N = 15$). They were subsequently held in a flow-through laboratory tank under ambient deep seawater conditions in the fjord (6–9 °C) until May 2019 when the temperature was stabilized at 7 °C. One day before the experiment, the seawater temperature was increased to 10 °C to match the seasonal increase in natural temperatures at which the animals would be exposed. The animals at Havets Hus ($N = 2$) were maintained in seawater at 10 °C from catch until the self-righting trials. During holding, the animals at both locations were maintained in flow-through seawater at ambient salinity (mean of hourly measurements 33.1 ± 0.8 SD) and fed *ad libitum* with a mixture of mud and algae (*Sargassum thunbergii*).

Behavioural experiments

We used all 17 animals including those at Kristineberg ($N = 15$) and Havets Hus ($N = 2$). Trials at Kristineberg were conducted on 19 June 2019 and at Havets Hus on 28 June 2019. At both locations, self-righting assays were conducted under constant abiotic conditions with individual animals contained in the same seawater tank; the animals were permitted to feed up until the experiment. Behavioural trials were conducted in the original holding tank to minimize effects of handling on righting behaviour; long-term holding of the animals minimized effects of short-term captivity on self-righting (Bose *et al.*, 2019). Individuals were identified visually by tracking distinctive morphological characteristics. For each self-righting trial, individual *P. tremulus* were gently inverted by hand and the time taken for the animal to right itself was recorded using a stopwatch. An individual was considered righted when both sides of the dorsal surface touched the bottom of the tank. Preliminary observations suggested that the vast majority of individuals righted in less than 3 minutes (180 s). We therefore terminated an individual trial if the animal did not successfully self-right in 5 min and allocated the individual a self-righting time of 300 s; however, this only occurred in a single instance ($N = 1$ out of 85 observations). A total of five trials were conducted. At Kristineberg, once all animals had righted in a given trial, the next trial commenced immediately and individuals were tested in the same sequence in each trial. This provided ~20 min of recovery time between each trial for each individual, which was comparable to a recent study of echinoderm self-righting repeatability (Gutowsky *et al.*, 2016). At Havets Hus, we also allowed the two animals ~20 min in between trials for consistency. Once all five trials were completed, the body length

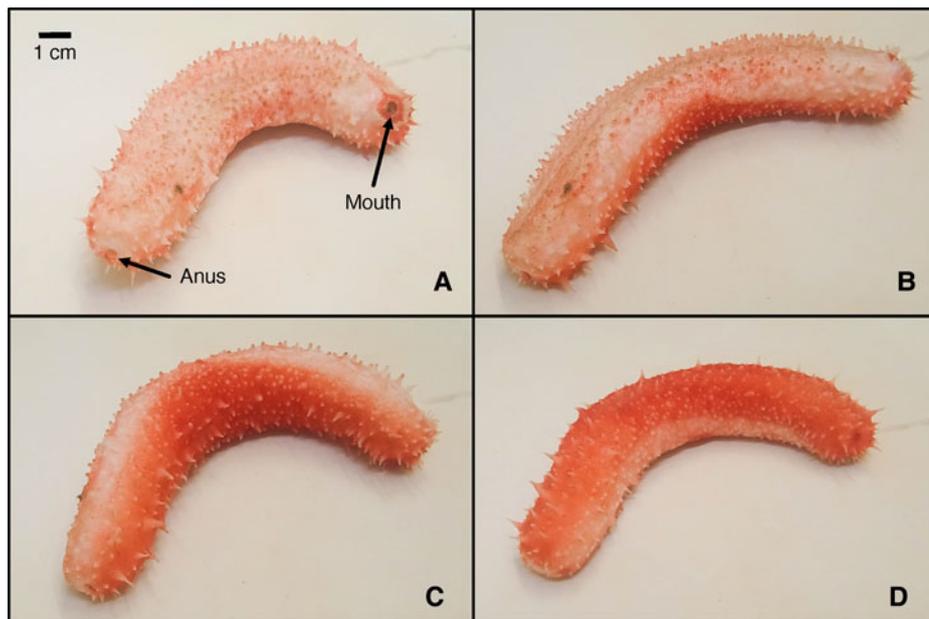


Fig. 1. Photographic sequence of a self-righting event for an individual *Parastichopus tremulus* showing the animal: (a) initially inverted; (b) as it began to roll to its right-hand side using muscle contractions; (c) approximately half-way through the righting process; and (d) fully righted.

of each individual was measured while the animals were in a relaxed state. To describe the behaviour, we first assessed the technique visually and recorded notes on the righting method; after the trials were completed, the righting of a subset of individuals was video recorded to further characterize the behaviour (see Supplementary Files S1 and S2 for videos).

Data analyses

All statistical analyses were conducted using R version 3.5.3 (R Core Team, 2019) with a statistical threshold of $\alpha \leq 0.05$. All raw data and annotated R Script can be found in Supplementary Files S3 and S4, respectively. Fixed effects of trial, location (Kristineberg or Havets Hus), their interaction (trial \times location), and body length (covariate) on self-righting time were tested by building a linear mixed model (LMM), with individual ID as a random variable, using the *lmer* function in the *lmerTest* package (Kuznetsova *et al.*, 2017) and subsequently using the *anova* function to determine fixed effects. The raw self-righting data initially violated the assumptions of homoscedasticity and residual normality based on visual assessments of Q-Q plots and histograms for normality, and residual fitted plots for homoscedasticity (see Supplementary File S4). The statistical test was therefore conducted on ln-transformed righting time values, which did not violate assumptions (see Supplementary File S4). The relationship between body length and the average self-righting time (individual⁻¹) was further explored using a linear model (LM). Repeatability (R) in self-righting time (and the corresponding 95% confidence interval) was estimated with generalized linear mixed models (GLMM) and Bayesian interpretation according to Dingemans & Dochtermann (2013). The GLMM was built using the *MCMCglmm*() function (*MCMCglmm* package; Hadfield, 2010) and the *posterior.mode*() and *HPDinterval*() functions were used to estimate repeatability and the corresponding 95% confidence interval (CI), respectively (code adapted from Roche *et al.*, 2016). The model included the fixed effects of trial, location, their interaction (trial \times location), and body length, with individual ID as a random variable; the model therefore provided a measure of adjusted repeatability (accounting for variance associated with fixed effects).

Two previous studies report that echinoderms have the propensity to improve self-righting performance over time (i.e. self-righting

times decrease as number of trials increases, which can be indicative of habituation or learning; Migita, 2012; Gutowsky *et al.*, 2016). To further explore the propensity for improved self-righting performance, we tested the individual relationships between trial and righting time for statistical significance using linear regression. We then placed individuals into one of three categories: (1) 'null' responders, defined as individuals with a non-significant regression slope; (2) 'worsened' responders, defined as individuals with a significantly positive slope (i.e. self-righting time increased – or worsened – with increasing trials); and (3) 'improved' responders, defined as individuals with a significantly negative slope (i.e. self-righting time decreased – or improved – with increasing trials). The proportion of individuals in each category was calculated as a measure of self-righting improvement.

Results

Our behavioural observations showed that *P. tremulus* did not use their tube feet to self-right, but rather used longitudinal muscles along the body wall to re-orient themselves to a righted position using a 'rolling' motion (Figure 1, Supplementary Files S1 and S2). While not recorded empirically, many individuals tended to curl their body into a 'C-shape' prior to rolling (e.g. Figure 1). Rolling appeared to occur simultaneously across the entire body length of the animals and was not initiated by the anterior or posterior end of the body. In all observations of self-righting, each individual employed the same general strategy of righting, suggesting a single method of self-righting for this species.

Individual self-righting times ranged between 25 and 240 s ($\bar{x} \pm \text{SD} = 96.1 \pm 52.7$ s) with the exception of a single observation where the individual did not right itself in 5 min (Trial 1; individual righted the anterior end of its body but failed to properly re-orient the posterior end). Results also indicated a substantial degree of repeatability in self-righting for adult *P. tremulus*, with an adjusted repeatability measure (accounting for effects of trial, location, and body size) of $R = 0.75$ (95% CI = 0.52–0.87) (Figure 2a). Variation in self-righting time was not significantly related to trial, location, (LMM: $F_{4,60} = 0.211$, $P = 0.931$), location (LMM: $F_{1,14} = 0.003$, $P = 0.961$), nor their interaction (LMM: $F_{4,60} = 0.257$, $P = 0.904$), but was marginally related to body length (LMM: $F_{1,14} = 4.14$, $P = 0.061$). There was a positive relationship between individual body length and mean righting time

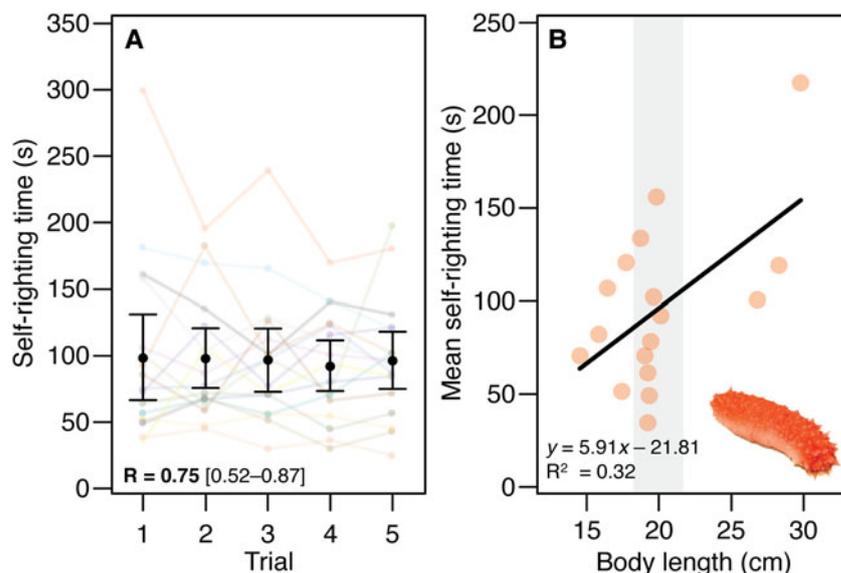


Fig. 2. (a) Individual ($N = 17$) self-righting times across the five trials for *Parastichopus tremulus*. Black points and error bars represent the mean \pm 95% CI for self-righting time in each trial. R is the adjusted measure of repeatability (accounting for effects of trial, location and body length) and the values in brackets represent the upper and lower bounds of the 95% CI. (b) The relationship between mean righting time and body length. Each point represents an individual. The grey bar highlights the variation in mean righting time for individuals ~ 20 cm body length.

(LM: $F_{1,15} = 6.936$, $P = 0.019$; Figure 2b). Nonetheless, substantial variation existed for similarly sized individuals, as mean righting times for individuals ~ 20 cm body length ranged from 34.8–155.5 s (Figure 2b).

Only two of the 17 individuals exhibited a significant linear relationship between trial and righting time, while righting time was not related to trial for most (15/17, 88%). Of those two individuals, one displayed a positive relationship (ID8), while the other displayed a negative relationship (ID6) (Supplementary File S4).

Discussion

Our results suggest that adult *P. tremulus* employ a single and consistent ‘rolling’ method of self-righting. This method provides reasonably fast righting times that are highly consistent within individuals with an apparent lack of habituation or improvement in the short term. Furthermore, while some of the inter-individual variation in righting times can be explained by body size, there was substantial variation among similarly sized individuals. Collectively, these results suggest that individual adult *P. tremulus* consistently employ a successful self-righting strategy that varies across individuals and differs from other echinoderms.

Echinoderm self-righting behaviours typically involve, at least to some degree, activity of the tube feet. Tube feet serve multiple functions, including (but not limited to) adhesion, locomotion, feeding (Smith, 1937; Flammang, 1996), photoreception (Ullrich-Lüter *et al.*, 2011) and self-righting (Lawrence, 1976a, 1976b; Ghiold, 1983; Migita *et al.*, 2005). The use of tube feet in self-righting requires strong adhesive capability, which is typically associated with the presence of adhesive secretions (Flammang & Jangoux, 1992). Holothurids (including *P. tremulus*) share a similar tube foot morphology to adhesive-secreting taxa (Smith, 1937) and some use tube feet for self-righting (*Sclerodactyla briareus*: Pearse, 1908); however, we found no evidence of tube feet being involved in the self-righting behaviour of *P. tremulus*. This is likely due to the fact that *P. tremulus* only have three rows of tube feet (Barnes, 2008) which are comparably shorter and less extendible than other species that use tube feet for self-righting (E. Schagerstrom, personal observations). While adaptively beneficial for keeping the body close to the substrate and reducing the probability of dislodgement (which suits the ecology of this species), short tube feet would not fare well in self-righting as they would not readily allow *P. tremulus* to adhere to a

horizontal surface when inverted. Similarly, while some holothurids use their tentacles for self-righting (*Opheodesoma spectabilis*: Berrill, 1966; *Synaptula hydriformis*: Olmsted, 1917), we did not observe *P. tremulus* using tentacles for righting. Like its tube feet, the tentacles of *P. tremulus* are comparably shorter than other species and are probably not useful for self-righting. Instead, this species used longitudinal muscle contractions to roll itself back to an upright position. This is consistent with Olmsted (1917), who noted that, in addition to using tentacles, *S. hydriformis* would sometimes retract its tentacles, contract its body, and roll to reorient itself upright. Our behavioural observations suggest that morphological constraints in tube feet and tentacle size preclude their use for self-righting in *P. tremulus*.

Our results align with previous reports suggesting that echinoderm self-righting is repeatable (Gutowksy *et al.*, 2016; Buccheri *et al.*, 2019). Interestingly, however, the righting time repeatability for *P. tremulus* observed in our study was more than two times greater than that reported for holothurids on the Great Barrier Reef (Buccheri *et al.*, 2019). This may have resulted from the fact that we studied self-righting repeatability in a single species under stable environmental conditions, while Buccheri *et al.* (2019) studied three species under different temperature conditions. We also used a different species than Buccheri *et al.* (2019), which has different biology and perhaps different constraints with respect to self-righting behaviour. Conversely, it may be that attributes of different locations or climate regions result in higher repeatability in holothurid self-righting, or that different species are simply more repeatable than others. Repeatability of self-righting may have fitness consequences for holothurids (Dingemanse & Réale, 2005), as proper orientation can allow for more effective escape responses from potential predators (i.e. increased mobility). For *P. tremulus*, proper orientation may also provide a degree of camouflage from predators against a sedimentary backdrop, whereas the animals would be more conspicuous while inverted because of their white underside. Spine-like papillae on the dorsal side of the animals may also provide protection from predation. As such, there is likely an adaptive advantage to righting faster and righting times may be heritable, as behavioural responses to mortality factors such as predation are known to be heritable (Åbjörnsson *et al.*, 2004). Studies of heritability and selection on righting response time and its repeatability, however, remain absent from the literature.

Our results suggest that larger individuals tend to take more time to self-right in *P. tremulus*. The influence of body size on

echinoderm self-righting is conflicting in the literature. Gutowsky *et al.* (2016) reported that body size had no effect on righting in *O. reticulatus*, while larger individuals of the sea urchin, *Lytechinus variegatus* had slower righting times than smaller conspecifics (Challener & McClintock, 2017). Other studies with echinoderms also suggest that righting times tend to increase with increasing animal size (e.g. *Strongylocentrotus droebachiensis*: Percy, 1973; *S. purpuratus*: Sonnenholzner *et al.*, 2010). Where present, the effect of body size on righting likely reflects differences in surface area:volume ratios across different animal sizes. Compared with larger individuals, the forces generated by smaller animals are greater relative to their body mass because smaller individuals have a smaller mass per unit of cross-sectional area than larger individuals, resulting in faster self-righting times (Weihs, 1977; Schmidt-Nielsen & Duke, 1984; Challener & McClintock, 2017).

Contrary to previous studies on sea stars (Migita, 2012; Gutowsky *et al.*, 2016), we found no evidence of improved righting times for *P. tremulus* under laboratory conditions. Sea stars employ variable methods of self-righting and have a high probability of tangling themselves (Polls & Gonor, 1975; Gutowsky *et al.*, 2016). In contrast, holothurids have a more basic and streamlined body plan, perhaps limiting their ability to alter righting responses, as evidenced by the single method of self-righting we observed. In addition, we conducted experiments in the same tank that the animals were held in for >7 months prior to the experiment to avoid confounding effects of captivity and handling (Bose *et al.*, 2019), while Gutowsky *et al.* (2016) conducted experiments less than one day after animal collection. Indeed, acclimatization time is reported to affect behavioural repeatability (O'Neill *et al.*, 2018). Although the time interval between trials in our experiment may not have been sufficiently long to allow improvement (growth of muscles and neurons necessary to confer improvement can take days), studies reporting improved echinoderm righting performance used similar time periods (Migita, 2012; Gutowsky *et al.*, 2016). It thus appears that *P. tremulus* is unable to improve self-righting times, at least in the short term.

Our study comes with some limitations that are important to acknowledge. We only had 17 individuals and for the relationship between size and righting time, there is a gap between ~21–26 cm body length (Figure 2b). Nonetheless, the three individuals of larger body sizes consistently had a righting time >100 s and the slowest individual was indeed the largest individual. It therefore seems like a size relationship probably exists; however, studies with a larger sample size and a broader size range would be beneficial. It is also important to note that the biological state of individuals and surrounding environmental conditions can affect repeatability but were maintained under constant conditions over the short duration of our experiment. In the same vein, we only tested animals from two locations (although they were from the same population) and only had two individuals from one of those locations (Havets Hus). Further experiments testing effects of biological state, environment, and location and population on self-righting repeatability in holothurids and other echinoderms are warranted.

Conclusions

This study documents self-righting behaviour in *P. tremulus*, suggesting a single method of self-righting. This righting method provided for a high degree of intra-individual repeatability in self-righting times, which varied across individuals (even those of a similar size) in the short term. Our results also suggest that righting times in this species may be a function of body size (smaller animals self-right faster than larger animals), which aligns with numerous other studies in echinoderms and may be

a function of differing surface area:volume ratios at different sizes. Finally, contrary to studies in sea stars, we did not find any evidence of improved behaviour and performance in subsequent trials – a discrepancy which could be explained by taxonomy and/or morphology, or by differences in acclimation time to laboratory conditions.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315419001218>

Data accessibility. All raw data and R code are available as supplementary material.

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Author contributions. JCC and KR conceived the idea and carried out the experiment. JCC analysed data and wrote the manuscript. ES maintained animals during husbandry and provided lab space for the experiment. SD and FJ provided in-kind support and technical guidance. All authors revised and approved the manuscript.

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Conflict of interest. We declare no conflict of interest.

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