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Sperm swimming in the polychaete *Galeolaria caespitosa* shows substantial inter-individual variability in response to future ocean acidification



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ABSTRACT

The rapidity of ocean acidification intensifies selection pressure for resilient phenotypes, particularly during sensitive early life stages. The scope for selection is greater in species with greater within-species variation in responses to changing environments, thus enhancing the potential for adaptation. We investigated among-male variation in sperm swimming responses (percent motility and swimming speeds) of the serpulid polychaete *Galeolaria caespitosa* to near- ($\Delta\text{pH} -0.3$) and far-future ocean acidification ($\Delta\text{pH} -0.5$). Responses of sperm swimming to acidification varied significantly among males and were overall negative. Robust sperm swimming behavior under near-future ocean acidification in some males may ameliorate climate change impacts, if traits associated with robustness are heritable, and thereby enhance the potential for adaptation to far-future conditions. Reduced sperm swimming in the majority of male *G. caespitosa* may decrease their fertilization success in a high CO₂ future ocean. Resultant changes in offspring production could affect recruitment success and population fitness downstream.

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The rapidity of anthropogenic marine climate change intensifies the pressure for marine organisms to adapt and survive (Hoegh-Guldberg and Bruno, 2010; Doney et al., 2012; Zeebe, 2012). Selection for phenotypes resilient against environmental changes may increase a species' adaptation potential, if traits associated with robustness are heritable. In such cases, the scope for selection will be greater in species that exhibit naturally large inter-individual variation in responses (Sunday et al., 2011; Foo et al., 2012; Schlegel et al., 2012).

Climate change impacts on vulnerable gametes are particularly likely to have flow-on effects, especially in broadcast spawners (Hofmann et al., 2010; Kroeker et al., 2010). Here, selection against susceptible phenotypes may, if heritable, quickly reduce the genetic composition and diversity of subsequent life stages. A resultant gene bottleneck could have severe consequences for overall species fitness (Reed and Frankham, 2003; Frankham, 2005).

An increasing number of studies are focusing on responses of gametes to future ocean conditions across a range of broadcast spawning species (Wicks and Roberts, 2012; Gazeau et al., 2013), particularly in echinoderms (e.g., Caldwell et al., 2011; Reuter et al., 2011; Schlegel et al., 2012). With the exception of a recent study by Lewis et al., (2012), polychaetes have been largely overlooked. This is perplexing as they are common foundation species that modify environments and enhance biodiversity (Smith et al., 2005), and are important as fouling organisms (Bulleri et al., 2005), and soft sediment bioturbators (Coleman and Williams, 2002).

We investigated the sperm swimming behavior of the serpulid polychaete *Galeolaria caespitosa* (Lamarck 1818) under CO₂-induced ocean acidification. *G. caespitosa* is a tube building filter feeder that dominates the mid intertidal region on moderate to extremely exposed rocky shores along the temperate Australian intertidal environment (Edgar, 1997; Bulleri et al., 2005). Due to its tolerance to hyposaline conditions, this species also commonly occurs in estuarine environments (Tait et al., 1984). *G. caespitosa* has a complex life history, where dioecious adults are reproductively mature during most months of the year. Gametes fertilize externally and develop into free swimming planktotrophic larvae that mature into demersal larvae (Andrews and Anderson, 1962; Marsden and Anderson, 1981). After settlement, larvae metamorphose into juveniles that build and reside in a carbonate tube

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cemented to the substrate (Smith et al., 2013). The fertilization kinetics are well documented for *G. caespitosa* (Kupriyanova and Havenhand, 2002; Kupriyanova and Havenhand, 2005; Kupriyanova, 2006). *G. caespitosa* is used as a model species in studies on the evolution of polyandry and sperm competition (e.g., Evans and Marshall, 2005; Styan et al., 2008; McLeod and Marshall, 2009) as well as in ecotoxicological assessments (Moran and Grant, 1993; Ross and Bidwell, 2001).

Here, we focused on among-male variation in sperm swimming responses to future ocean acidification. Following the A1FI scenario (IPCC, 2007), we exposed sperm to seawater conditions predicted for near- ($p\text{CO}_2 = 970 \mu\text{atm}$, year 2100) and far-future CO_2 scenarios future ($p\text{CO}_2 = 1600 \mu\text{atm}$, year 2300), and recorded impacts on the proportion of motile sperm and their swimming speeds. Based on a previous study on individual variation in sperm swimming in sea urchins (Schlegel et al., 2012), we hypothesized that there will be substantial variation in the responses of swimming capabilities in individual sperm.

Filtered seawater (FSW; $0.22 \mu\text{m}$ filtered) was aerated with a CO_2 /air mixture to achieve CO_2 treatments. Seawater temperature and salinity (Table 1) were measured for each replicate ($n = 23$) using an IQ Sensor net (MIQ/T2020, WTW). Microprocessor CO_2 injection units were set to maintain stable pH_{NBS} levels of 8.1 (controls, no CO_2 added; $p\text{CO}_2 = 427 \mu\text{atm}$), 7.8 ($p\text{CO}_2 = 971 \mu\text{atm}$) and 7.6 ($p\text{CO}_2 = 1597 \mu\text{atm}$), following the A1FI scenario (IPCC, 2007). Total alkalinity was determined for every third replicate ($n = 7$) by titration (HI 3811 Alkalinity kit, Hanna Instruments), all other parameters of the CO_2 system were calculated using CO_2 -SYS (Lewis and Wallace, 1998) and the dissociation constants of Dickson and Millero, (1987) (Table 1).

Clumps of large *G. caespitosa* (tube openings of 2+mm diameter) were collected from intertidal rock platforms in Fairlight, Sydney, Australia ($33^\circ 48' 1''\text{S}$, $151^\circ 16' 3''\text{E}$) in November and December 2011, and held in a recirculating seawater system at Macquarie University. Individuals were used in experiments within 48 h of collection.

Collection of gametes followed the protocol by Kupriyanova and Havenhand, (2002). Individual *G. caespitosa* were carefully removed from their calcareous tubes and inspected for ripeness. Individual males, characterized by creamy white lower abdomens, were placed into separate petri dishes. Removal of the males from their tubes caused instantaneous spawning in mature individuals. Males that did not immediately release gametes were discarded. Sperm from spawning individuals were collected with Pasteur pipettes from each male, and held “dry” on ice in Eppendorf tubes (one for each individual) until immediately prior to use (within 15 min of release). A total of 23 mature males were tested.

Sperm motility experiments were conducted in a temperature-controlled room at $20 \pm 0.5^\circ\text{C}$ and followed established protocols (Havenhand et al., 2008; Havenhand and Schlegel, 2009; Schlegel et al., 2012). “Dry” sperm ($\sim 0.5\text{--}1 \mu\text{l}$) were diluted in 1.5 ml of seawater of each pH immediately before use (final concentrations of $1\text{--}2 \times 10^4$ sperm μl^{-1}). Ten replicate sperm suspensions were freshly prepared for each pH treatment and for each male. A drop of sperm suspension ($\sim 60 \mu\text{l}$) was placed between an albumin-coated microscope slide and cover slip, separated by a 0.75 mm thick O-ring. Sperm movements were video recorded immediately

after suspension using a digital video camera (SMX-160; at 25 frames s^{-1}) mounted on a compound microscope (Olympus BX51). Videos were post-processed and 2s-clips were analyzed using CellTrak 1.3 (Motion Analysis Corporation) for the proportion of motile sperm (defined as sperm moving faster than $15 \mu\text{m s}^{-1}$) and their swimming speed. A total of 10 replicate recordings were made for 10 separate sperm suspensions for each male and pH treatment.

All percentage data were arc-sin transformed prior to statistical analyses (Quinn and Keough, 2002). Data were assessed for homogeneity of variances among individuals using Levene’s test, before using two-way ANOVA (pH fixed, male random) to test pH effects on percent motility and speed of motile sperm. Differences between means were compared *post hoc* using Tukey’s test. Among-male responses were assessed using logarithmic response ratios (LnRR; natural log of treatment response divided by control response; Hedges et al., 1999). Upper and lower boundaries for 95% confidence intervals around mean LnRRs were determined by bootstrapping in R (100,000 iterations). All other analyses were carried out using SPSS™.

CO_2 -induced ocean acidification significantly reduced the overall proportion of motile sperm and their swimming speeds compared to present day (ambient) conditions (Fig. 1A, Table 2). Responses among individual males, however, varied substantially (Fig. 1B). While sperm from the majority of *G. caespitosa* males were less motile and slower under near-future conditions compared to present ambient conditions ($\Delta\text{pH} -0.3$; Fig. 1B, Table 3), sperm from some males ($n = 7$) showed either slightly increased motility and/or swimming speed, or no change in these parameters. Only few males ($n = 3$) showed robust sperm swimming under far-future conditions ($\Delta\text{pH} -0.5$; Table 3).

For percent sperm motility, upper and lower bound 95% confidence intervals around individual log response ratios (LnRR) were equivalent to changes of +4.6% to -38.7% at $\Delta\text{pH} -0.3$ (Fig. 1B); and of -13.4% to -46.6% at $\Delta\text{pH} -0.5$.

For speed of motile sperm, 95% confidence intervals around LnRRs were equivalent to changes of +0.7% to -24.8% at $\Delta\text{pH} -0.3$; and of -9.2% to -38.2% at $\Delta\text{pH} -0.5$.

We found substantial, and significant, variation in sperm swimming responses among single males of *G. caespitosa* to CO_2 -induced ocean acidification. Overall percent sperm motility and sperm swimming speeds declined significantly under ocean acidification. Sperm from a minority of males seemed robust to near-future acidification scenarios ($\Delta\text{pH} -0.3$), showing no, or even positive, responses. Even fewer males were robust to far-future acidification scenarios ($\Delta\text{pH} -0.5$). If this robustness to near-future conditions is heritable, it could act as a base for adaptation to far-future conditions (Sunday et al., 2011), provided that adaptation can occur within the relatively short time frame of predicted future ocean acidification.

The inter-male variability we observed was not unexpected: *G. caespitosa* naturally exhibit high intra-specific variation in sperm swimming behavior (Kupriyanova and Havenhand, 2002, Fig. 1A). The extent to which this variability depends on seasonal changes in reproductive condition and temperature is unknown. Further, the substantial range in sperm responses among individuals to ocean acidification observed here – from highly positive to

Table 1
Seawater parameters. pH_{NBS} , temperature (T), salinity (Sal), and total alkalinity (A_T) were measured directly and used to calculate partial CO_2 pressures ($p\text{CO}_2$) and seawater saturation states for calcite (Ω_{Ca}) and aragonite (Ω_{Ar}) using CO_2 -SYS (see text). Data are means \pm S.E. $n = 23$ for pH, T and Sal. $n = 7$ for A_T .

pH_{NBS}	T ($^\circ\text{C}$)	Sal	A_T ($\mu\text{eq kg}^{-1}$)	$p\text{CO}_2$ (μatm)	Ω_{Ca}	Ω_{Ar}
8.10 ± 0.01	20 ± 0.5	35 ± 0.1	2029 ± 5	427	3.40	2.21
7.80 ± 0.01	20 ± 0.5	35 ± 0.1	2029 ± 5	971	1.90	1.24
7.60 ± 0.01	20 ± 0.5	35 ± 0.1	2029 ± 5	1597	1.25	0.81

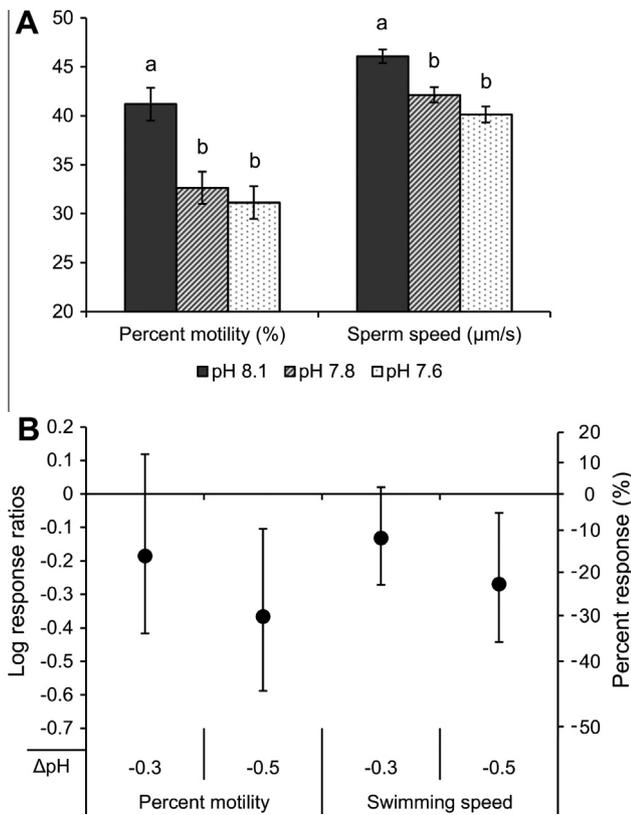


Fig. 1. Impacts of CO₂-induced ocean acidification on sperm swimming behavior in *Galeolaria caespitosa*. (A) Proportion of motile sperm and their swimming speeds at different pH levels mediated by addition of CO₂. Data are means ± S.E. Lower case letters indicate significantly different groups at *P* = 0.05 (Tukey's test). (B) Variation in sperm responses among individual males. Data are shown as bootstrapped mean individual response ratios (log of treatment response divided by control response) ±95% confidence intervals (CI) (left axis) and percent response (%) ±95% CI (right axis). Larger CIs indicate greater among-male variability in responses. *n* = 23.

Table 2
Two-way ANOVA results for effects of CO₂-induced ocean acidification on (A) proportion of motile sperm and (B) speed of motile sperm in *Galeolaria caespitosa*. pH = fixed, male = random. Significant effects (*P* < 0.05) are shown in bold.

	df	MS	F	P
(A) Percent sperm motility				
pH	2	1.147	5.705	0.006
Male	22	1.850	68.519	<0.001
pH * Male	44	0.201	7.370	<0.001
Residual	621	0.027		
(B) Speed of motile sperm				
pH	2	2440.287	10.696	<0.001
Male	22	1439.402	17.441	<0.001
pH * Male	44	228.914	2.774	<0.001
Residual	604	82.528		

negative (Fig. 1B) – suggests that these responses are not reaction norms. Such large variation in responses increases the scope for selection of rare sperm phenotypes robust to future acidification (Pistevos et al., 2011; Sunday et al., 2011; Foo et al., 2012; Schlegel et al., 2012), which may contribute disproportionately more to subsequent generations. This selection may thus ameliorate ocean acidification effects on a species, if traits associated with acidification resistance are heritable. In this context, it is important to stress the need for adequately replicated studies on climate change impacts in order to accurately estimate the extent of inter-individual variation (Havenhand et al., 2010). Resilience to near-future climate change observed in the sperm of some males could act as a

Table 3
Effects of CO₂-induced ocean acidification on percent sperm motility and sperm swimming speeds for each male *Galeolaria caespitosa*.

pH Male	Percent motility (%)		Sperm speed (mm s ⁻¹)			
	pH 8.1	pH 7.8	pH 7.8	pH 7.6	pH 8.1	pH 7.8
A	43.95	4.35	4.69	50.72	33.07	33.49
B	37.07	48.81	36.32	30.95	33.13	33.78
C	30.87	28.79	11.09	52.56	43.29	36.04
D	11.53	13.65	4.35	35.03	41.10	26.57
E	9.94	16.37	2.92	50.80	29.49	19.00
F	27.17	22.80	17.30	45.24	41.60	34.25
G	36.50	28.40	29.64	42.15	37.83	41.32
I	37.98	22.30	35.22	47.54	53.35	45.13
J	27.03	13.54	27.03	33.36	28.01	29.95
K	12.80	5.91	6.97	41.54	38.90	34.29
L	29.09	9.72	6.07	48.06	41.12	31.07
M	22.70	22.35	32.96	33.39	33.17	33.17
N	61.10	61.14	60.83	51.96	49.67	49.13
O	7.40	12.97	26.27	44.20	37.39	46.73
P	54.79	49.35	15.91	42.47	45.70	46.70
Q	74.92	78.41	60.23	57.78	58.26	53.32
R	34.96	32.85	35.81	46.04	37.80	35.93
S	64.49	67.04	68.89	50.80	47.13	48.61
T	66.76	38.24	35.70	42.54	40.45	39.89
U	65.48	37.37	63.59	50.48	52.67	46.82
V	76.51	11.78	19.64	59.57	44.73	51.65
W	84.85	84.20	87.57	50.99	48.37	48.44
X	42.35	37.26	28.21	49.56	43.32	42.17
Mean	41.75	32.51	31.18	45.99	41.72	39.45
S.E.	4.78	4.78	4.85	1.58	1.61	1.85

stepping stone for adaptation to far-future conditions, if gathering of advantageous alleles through recombination in subsequent generations can outrun the rapidity of predicted ocean acidification. Consequently, simultaneous selection against susceptible phenotypes could quickly reduce genetic diversity, with flow-on consequences for species fitness and competitive ability (Reed and Frankham, 2003; Frankham, 2005).

Changes in sperm swimming behavior affect fertilization success (Vogel et al., 1982; Styan and Butler, 2000; Styan et al., 2008). Positive relationships between fertilization success and sperm concentration – influenced by percent motility – as well as sperm swimming speeds have been reported for this species (Kupriyanova and Havenhand, 2002; Kupriyanova, 2006). Sperm swimming speeds are reported to be enhanced under increased water temperatures (Kupriyanova and Havenhand, 2005), and therefore future ocean warming could ameliorate acidification-related reductions in sperm swimming speeds, particularly during warmer summer temperatures (Hobday and Lough, 2011). For the majority of *G. caespitosa*, however, potential positive effects of ocean warming on sperm swimming speeds would likely be swamped by the substantial negative effects of ocean acidification on percent motility that we observed (Fig. 1). Naturally occurring sperm limitation scenarios (Williams et al., 1997) could thereby be exacerbated, decreasing reproductive output in affected males. Conversely, reduced sperm swimming under acidified conditions could increase sperm longevity due to lowered consumption of limited endogenous energy provisioning (Mita and Nakamura, 1998). Greater sperm longevity may increase chances of successful fertilization if sperm–egg-encounter rates remain sufficient over prolonged periods of time (Leviton, 2000; Marshall, 2002). Impacts of CO₂-driven ocean acidification on sperm swimming behavior of *G. caespitosa* may interact with other acidification impacts on fertilization variables such as male–female compatibility, egg competition or polyspermy block efficiency (Evans and Marshall, 2005; Marshall and Bolton, 2007). Negative impacts of CO₂-induced ocean acidification have also been reported for later life-history stages of serpulid tubeworms, such as weaker calcareous tubes

(Chan et al., 2012; Smith et al., 2013). Resultant cumulative effects on reproductive success and survivorship are likely to exacerbate the rate or intensity of selection pressure of climate change.

Patterns of sperm swimming responses of *G. caespitosa* to CO₂-induced acidification observed here were similar to those of *Arenicola marina* sperm in lowered seawater pH (Pacey et al., 1994). Sperm activation in *A. marina* was delayed and sperm speed was reduced in HCl-acidified seawater (pH < 7.6). Interestingly, our findings are very different to those from a study on the related serpulid species *Pomatoceros lamarckii* (Lewis et al., 2012). Sperm speeds of *P. lamarckii* were robust to CO₂-induced pH reductions, percent motility was significantly reduced, but responses were non-linear. These findings may be explained by differences in experiment design and sample size (5 pooled assays (Lewis et al., 2012) vs 23 single individuals in this study). As outlined earlier, conducting adequately replicated studies will help to clarify whether these differences are caused by high inter-individual variability or differences in average responses between species.

In conclusion, the substantial inter-individual variation in sperm responses observed here may ameliorate effects of future climate change, if the traits that drive phenotype robustness are heritable. Sperm from some *G. caespitosa* will be better equipped to cope with acidification than others, creating 'winners' and 'losers' in a future acidified ocean (Schlegel et al., 2012). This observed resilience to near-future conditions could increase the potential for adaptation to far-future conditions, if gathering of advantageous alleles can occur quickly enough. Likewise, rapid selection against phenotypes susceptible to acidification may quickly reduce genetic diversity and lead to severe flow-on consequences for fitness and competitive ability downstream. Very few studies to date have investigated climate change impacts on polychaete species (Chan et al., 2012; Lewis et al., 2012; Wicks and Roberts, 2012; Smith et al., 2013), despite their vital importance to marine ecosystems worldwide. Consequently, further research on these organisms is imperative as their success or loss might severely change the habitat structure and community composition of future marine ecosystems.

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