

1 FACILITATORS MAINTAIN SPECIES RICHNESS AS ABIOTIC STRESS  
2 INCREASES

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9 *Abstract:* High levels of abiotic stress typically reduce biodiversity in natural  
10 communities. However, facilitators are predicted to increase in relative importance  
11 with stress and may buffer this loss of diversity. Using field manipulations, we  
12 examined how benthic species richness associated with mimics of the tubeworm,  
13 *Lanice conchilega*, varied with tube density (facilitator trait) and current speed  
14 (abiotic stress) on a muddy-sand shore. Four densities of mimic (0%, 0.1%, 1%, and  
15 10% roughness density, RD) were inserted into the sediment at low (control) and  
16 high current speeds generated by experimental Venturi flumes (disturbance).  
17 Facilitator trait had no effect on species richness in the controls, but there was a  
18 significant positive relationship between trait and richness in the flumes. Reduced  
19 species numbers caused by the disturbance increased to levels similar to controls by  
20 RD = 10%. Tubeworms were facilitating small organisms that live at the sediment-  
21 water interface, *Pygospio elegans* and *Corophium spp.*. Here, community benefits  
22 correlated with a significant increase in sediment shear strength, indicating that  
23 mimics were preventing erosion. We demonstrated that facilitators buffer  
24 anthropogenic stress and maintain biodiversity and could be a useful tool in  
25 conservation and management.

26 KEYWORDS: Facilitation, Abiotic stress, Biodiversity, Trait, *Lanice conchilega*,  
27 Sand-mason, Bioengineering, Sediment shear strength, Mimics, Context  
28 dependency, Ecosystem function

## 29 INTRODUCTION

30 Interactions between species are often ephemeral, varying circumstantially with  
31 parameters including population density and abiotic stress (Brooker & Callaghan  
32 1998). The idea that these interactions vary contextually, but predictably is central to  
33 community ecology, yet our understanding of when interactions change is  
34 incomplete (e.g. Bertness & Callaway 1994, Rodriguez 2006, Brooker et al. 2008).  
35 Here, we consider how the pervasiveness of facilitation may determine how systems  
36 respond to abiotic stress and in turn influence species richness.

37 It is well understood that the presence of facilitating species within a system strongly  
38 influences the shape of conceptual richness-function models as they can contribute  
39 disproportionately to function (Naeem 1998, Solan et al. 2004, Larsen et al. 2005).  
40 Furthermore, how these facilitator species respond to disturbance could alter the  
41 species richness of communities as they may prevent extinctions of associated  
42 species by ameliorating abiotic stress (Bruno & Bertness 2001). Understanding this  
43 contextual shift in interactions could lead to more accurate predictions of how  
44 richness will be affected by stress in natural systems and may allow better  
45 conservation and management strategies to be developed (Kremen & Ostfeld 2005,  
46 Crain & Bertness 2006, Halpern et al. 2007).

47 Facilitation via stress amelioration is expected to be more important in physically  
48 stressed, rather than benign, habitats (the facilitation-stress hypothesis Bertness &  
49 Callaway 1994). In addition, the shape of the relationship between facilitator traits  
50 (e.g. size or density) and species richness is also predicted to shift with abiotic stress  
51 (trait-diversity hypothesis, Bruno & Bertness 2001). In benign habitats, as a  
52 facilitator trait – such as size or density - increases, it is unlikely to have any effect on

53 associated species because the facilitator is not required (Figure 1a). Conversely, in  
54 more stressful environments, species richness is likely to be low if facilitator traits are  
55 too low to ameliorate the stress (Heck & Wetstone 1977). The facilitation-richness  
56 paradigm shifts if competitive exclusion is considered, as at medium to high stress,  
57 competition will manifest once the stress is fully ameliorated (Figure 1b).

58 Field studies supporting this facilitation-stress theory have come from a limited  
59 number of natural systems. Most empirical evidence comes from terrestrial plant  
60 (Sthultz et al. 2007, Brooker et al. 2008) and saltmarsh (Bertness & Hacker 1994)  
61 communities, with fewer studies from marine rocky shores (Bertness et al. 1999). In  
62 order to formulate broad conceptual models of the interrelatedness of facilitation-  
63 stress and facilitator trait-richness we require empirical evidence from multiple  
64 systems. Currently, there is limited evidence from intertidal, sedimentary systems.  
65 Such habitats are ideal for testing facilitation-stress theories as they are amongst the  
66 most productive and diverse systems on Earth and experience sharp temporal and  
67 spatial gradients of stress (Suchanek 1994).

68 The sand mason, *Lanice conchilega*, is a polychaete worm that inhabits intertidal  
69 and subtidal sediments (Callaway 2006, Rabaut et al. 2007, Van Hoey et al. 2008).  
70 *L. conchilega* constructs a characteristic tube, composed of cemented coarse sand  
71 grains, with the anterior end of the tube topped with a fringe of tentacles projecting 1-  
72 4 cm from the sediment (Zühlke 2001). Tubes can be as long as 65 cm and are  
73 typically of 0.5 cm diameter (Ziegelmeier 1952, 1969). Sand mason tubes facilitate  
74 by providing a refuge from predation, oxygenating the sediment at depth and by  
75 promoting sediment deposition (Van Hoey et al. 2008). They can also prevent  
76 sediment erosion by decelerating current flow and increasing sediment shear

77 strength, a sediment's maximum resistance to shearing stresses (Lambe & Whitman  
78 1985, Jones & Jago 1993, Friedrichs et al. 2000).

79 Bed stabilisation by tubeworms is density dependent (Bolam & Fernandes 2002). As  
80 roughness density (RD; the percentage of total surface covered) increases, a new  
81 benthic boundary layer is created above the epibenthic structures until water  
82 interacts with the tubes as if they were a solid structure. Friedrichs et al. (2000)  
83 found that for tubes similar to a sand mason's, a switch from destabilising to  
84 stabilising conditions occurred at RD 2-4.5% (872-1961 tubes.m<sup>-2</sup>) and pure  
85 skimming flow was established at RD 4.5-8.8% (1961-3836 tubes.m<sup>-2</sup>). Such  
86 numbers are not uncommon, as aggregations of *L. conchilega* can reach 20,000  
87 n.m<sup>-2</sup> subtidally (Ropert & Dauvin 2000) and 10,000 n.m<sup>-2</sup> intertidally (Ziegelmeier  
88 1952). Small groups of tubes may influence adjacent organisms by providing a  
89 refuge and alternately destabilising the sediment (Callaway 2006). Any change in  
90 flow regime will have a large impact on how benthic species between the structures  
91 are influenced (Biles et al. 2003), but no empirical study has specifically examined  
92 how interactions and diversity associated with tubeworms vary with flow regime. In  
93 other words, the ability of the tubeworms to facilitate by buffering stress associated  
94 with increased flow. Here, we use sand mason tube mimics to effectively partition  
95 and isolate this specific mechanism of facilitation as other interactions (e.g. with the  
96 fringe or sand grains) are not imitated (Woodin 1978, Friedrichs et al. 2000,  
97 Callaway 2006). We consider tubeworm mimic density to be a facilitator trait.

98 We hypothesize that increasing densities of mimics will increase sediment shear  
99 strength. Furthermore, we hypothesise that any increase in shearing strength in  
100 these high current habitats will have positive effects on the associated community,  
101 effectively increasing species richness. We predict that this relationship will be

102 polynomial, due to competitive exclusion acting at high tube densities. Conversely,  
103 in benign, low current systems, we expect facilitator trait (tube density) to have  
104 neutral effects on communities based on the trait-diversity hypothesis.

105 METHODS

106 Through field manipulations, we examined the effects of tubeworm mimic density on  
107 benthic species richness and an ecosystem function (sediment shear strength) at  
108 low (control) and high (disturbance) current speeds.

109 *Site selection*

110 Experiments were carried out at Traeth Melynog on Anglesey, NW Wales (53°8'N,  
111 4°21'W). Current speed was manipulated as a stressor. Current speed is naturally  
112 low on the shore and so was left as a control. High current speeds were generated  
113 using experimental Venturi flumes aligned with predominate tidal current to  
114 concentrate flow over our experimental plots (after Zühlke & Reise 1994). Flumes  
115 consisted of two boards made of marine plywood and measuring 50 cm x 200 cm  
116 fixed into the sediment 50 cm apart using steel stakes (Figure 2a). Four sections of  
117 oyster netting measuring 50 cm x 200 cm, were then attached to the ends of the  
118 boards and staked out to form funnels.

119 Within the flumes and in the surrounding sediment, four densities of *L. conchilega*  
120 mimic were inserted into the sediment. Mimics were straws of length 15 cm and 0.5  
121 cm  $\varnothing$ , inserted to a depth of 12 cm (Figure 2b). Densities were based on roughness  
122 densities obtained from previous studies to ensure a skimming flow was achieved  
123 (Friedrichs et al. 2000): none (0%), low (0.1%), medium (1%), and high (10%)  
124 density. We thus had a total of eight treatments: four densities of tube mimic at both  
125 low (no flume) and high (flume) current speeds. Plots were all randomly located  
126 within the same biotope, so the benthic species pool was the same, and were placed  
127 at a minimum distance of 10 metres from each other.

128 One month after setup the benthic community was sampled and sediment shear  
129 strength between the mimics and in the no mimic plots was measured. The flumes  
130 were then moved and reinserted into the sediment at a minimum distance of five  
131 metres from any previous treatments and away from any obvious sediment  
132 disturbance. The experiment was then repeated and ran a total of five times to  
133 provide replication (5 replicates per treatment) from April 11<sup>th</sup> to May 14<sup>th</sup> (33 days),  
134 May 14<sup>th</sup> to June 13<sup>th</sup> (30 days), June 13<sup>th</sup> to July 18<sup>th</sup>(35 days), October 2<sup>nd</sup> to 31<sup>st</sup>  
135 (29 days) (all 2008) and December 8<sup>th</sup> 2008 to January 6<sup>th</sup> 2009 (29 days).

### 136 *Community analysis*

137 Intertidal macrofauna communities were sampled to a depth of 15 cm using a PVC  
138 suction-corer (123 mm internal diameter) after the treatments. Seven cores were  
139 taken in each treatment plot and their contents combined to ensure that a sufficient  
140 amount of fauna was sampled. Samples were then sieved *in situ* through a 500 µm  
141 sieve and any macrofauna retained in the sieve were fixed in 4% buffered formalin.  
142 During subsequent laboratory analysis, all macrofauna organisms were identified to  
143 the lowest taxonomic classification possible and enumerated.

### 144 *Sediment cohesion*

145 At each plot, sediment shear strength was measured to examine if sand masons  
146 influence biodiversity through changes in sediment cohesion. Sediment shear  
147 strength was measured *in situ* using a torvane (Kravitz 1970). A torvane consists of  
148 a series of blades mounted on a spring which are pushed into the sediment. The  
149 instrument is then rotated until failure occurs i.e. the blades slip. A dial on top of the  
150 torvane records the maximum sediment shear strength. Six measurements were  
151 taken per plot each time and a mean calculated to account for patchiness.

152 *Statistical analysis*

153 General linear models (GLM) were used with a Gaussian error structure to  
154 investigate whether current speed and/ or tubeworm mimic density significantly  
155 influenced species richness or shear strength ( $N.m^{-2}$ ) (normality and homogeneity of  
156 variance tests; Appendix 1). The interaction between current speed and mimic  
157 density was also calculated to see whether any effect of density was significantly  
158 modified by current speed. A series of GLMs were then used to test for the effects of  
159 current and RD on the abundance of the ten most common species ( $\log(n+0.1)$   
160 transformed). Here, a Bonferroni correction was used to maintain the familywise  
161 error rate at 0.05 by testing each hypothesis against a higher statistical significance  
162 ( $\alpha/n$ ). Multivariate analyses were conducted using PRIMER 6 to see whether  
163 facilitated communities differed in species composition compared with the control  
164 treatment (Clarke 1993, Clarke & Gorley 2006). Species abundances were initially  
165  $\sqrt{\sqrt{\cdot}}$ -transformed to down-weight contributions of outliers in multivariate tests (Clarke  
166 & Gorley 2006). Intersample similarities were then calculated using the Bray–Curtis  
167 similarity coefficient (Bray & Curtis 1957) and ordinated using non-metric  
168 multidimensional scaling (MDS) (e.g. Kruskal & Wish 1978).

169 RESULTS

170 *Species richness*

171 Species richness varied significantly with flow speed and tube density, and the  
172 interaction between these two factors (Table 1; Figure 3). In general, species  
173 numbers were significantly lower in flume treatments compared to controls and  
174 increased with mimic density. The increase in species numbers with mimic density  
175 was significantly greater in flume treatments and there was no discernible effect of  
176 density on richness in the controls.

177 *Physico-chemical changes*

178 Sediment shear strength varied significantly with tube density and flow regime, but  
179 this time with no interaction (Table 3; Figure 4). Shear strength was significantly  
180 greater in controls compared to flumes and increased with mimic density regardless  
181 of flow.

182 *Species responses to tubeworm mimics*

183 Of the ten most common species, the density of six varied strongly with flow regime  
184 and/ or RD (Table 3; Figure 5; Appendix 2). *Hydrobia ulvae* and *Oligochaeta* were  
185 less abundant in flumes compared to controls and were unaffected by tubeworm  
186 mimics. The abundance of *Capitella capitata* was lower in flumes, but increased in  
187 density with mimics regardless of flow. *Macoma balthica* was unique, in that it  
188 decreased in density with mimics regardless of flow. Only *P. elegans* and  
189 *Corophium spp.* varied significantly after the strict Bonferroni correction estimated  
190 the critical significance level at 0.005. *Pygospio elegans* and *Corophium spp.* were  
191 lower in flumes and decreased with tubeworm mimics in controls, but increased in  
192 density with them in flumes.

193 *Community changes*

194 Sampled communities were largely similar between controls and formed two closely  
195 related, but distinct clusters with flume communities associated with RDs of 1-10%  
196 (A and B) (Figure 6). In general, communities in flumes with lower densities of mimic  
197 formed two separate assemblages (C and D). As RD increased in flumes the  
198 communities typically became more similar to controls.

199 Seasonal effects did not influence how trait-richness relationships varied with stress  
200 here (see Appendix 3).

201 DISCUSSION AND CONCLUSIONS

202 By examining interactions between tubeworm densities (facilitator trait), current  
203 speed (abiotic stress) and associated species richness, we showed for the first time  
204 that the facilitation-stress hypothesis applies to polychaete bioengineers that  
205 facilitate by decreasing bed shear stress in flow-dominated marine systems. The  
206 facilitation-stress paradigm is based on the assumption that facilitation through  
207 stress amelioration is relatively more important in physically stressed systems where  
208 facilitators can ameliorate that particular stressor (Sthultz et al. 2007, van  
209 Wesenbeeck et al. 2007). Although this has been demonstrated for a number of  
210 terrestrial (Brooker et al. 2008) and intertidal systems (Bertness et al. 1999), it has  
211 not until now been observed in tubeworms that modify near-bed hydrodynamics. By  
212 increasing sediment shear strength, our tubes buffered erosion of the sediment  
213 (Friedrichs et al. 2000, Callaway 2006). Under normal flow conditions, this increase  
214 in sediment cohesion had no effect on community structure, but at high flow speeds,  
215 species richness and densities of particular species were maintained relative to  
216 controls. Thus, as abiotic stress increased, the bioengineering role of the tubeworm  
217 changed from neutral to keystone as their role became unique within the community.

218 Furthermore, we demonstrated that the facilitator trait-species richness hypothesis  
219 (Bruno & Bertness 2001) applies to these epibenthic facilitators that buffer stress by  
220 increasing sediment shear strength. As facilitator trait (tube density) increased in the  
221 low current treatments, it had no effect on species richness; the current was not  
222 sufficient to disturb the community and facilitation was therefore not required to  
223 buffer the disturbance. At higher current speeds, the relationship shifted so that  
224 there was a significant positive relationship between facilitator trait and species  
225 richness. It is likely that, as tube density increased even further, competitive

226 exclusion would have begun to operate (Bruno & Bertness 2001). Here there was  
227 an insufficient spread of RDs to observe whether a logarithmic or polynomial model  
228 would have better explained the shape of the relationship. Furthermore, competitive  
229 exclusion will likely be stronger in nature as here mimics only competed for space,  
230 not other resources. Additional studies using real *L. conchilega* at a broader range  
231 of RDs could be used to partition multiple mechanisms of facilitation and competition  
232 at various stress levels.

233 From our regression, in high stress systems, the richest communities are predicted  
234 to occur as RD approaches 10%. Previous studies have shown that under similar  
235 conditions skimming flow is achieved at RD 4.5-8.8% for a current speed of 5 cm.s<sup>-1</sup>  
236 (Friedrichs et al. 2000). Here, we demonstrated that benefits to the community can  
237 be detected at much lower densities. Commensalisms with real *L. conchilega* tubes  
238 are common in nature, but we did not expect them to operate here due to the lack of  
239 a sand fringe and realistic surface for attachment (Callaway 2003b, a, 2006). Thus,  
240 low tube densities may simply have been facilitating by increasing habitat  
241 heterogeneity and providing some basic form of refuge from predation (Van Hoey et  
242 al. 2008).

#### 243 *Trophic group amensalism*

244 *L. conchilega* benefits specific organisms (*Corophium* spp. and *Pygospio elegans*)  
245 seemingly based on their traits. Organisms profiting from mimics are small, surface  
246 dwelling organisms. *Corophium* spp. (mud shrimps) are burrow-dwellers and are  
247 found in sheltered environments, where tidal flow is weak (<0.51 m.s<sup>-1</sup>) (Hughes &  
248 Gerdol 1997). They emerge at high tide to feed and would not be able to re-  
249 establish themselves in the sediment if flow was too fast (Hughes 1988) or the  
250 sediment was fluidised (Jensen 1985). *P. elegans* is a small (<15 mm), tube-

251 dwelling spionid that lives in relatively sheltered environments (Bolam 2004).  
252 Although not observed here, it is possible that at even higher stresses, such species  
253 would be promoted by facilitation to the detriment of other species (trophic group  
254 amensalism) (Rhoads & Young 1970, Snelgrove & Butman 1994). Both *P. elegans*  
255 and *Corophium spp.* are also known increase sediment shear strength in natural  
256 systems (Meadows & Tait 1989). An amensalism between stabilising suspension  
257 feeders and destabilising deposit feeders has been described previously and  
258 suggests that at very high densities of tubeworm, deposit feeding species such as *A.*  
259 *marina* and *C. edule* may be negatively impacted (Rhoads & Young 1970,  
260 Volkenborn & Reise 2006).

#### 261 *Facilitation over complete stress gradients*

262 Most empirical facilitation-stress studies only consider extremes of abiotic stress as  
263 we did here. Future work needs to look at how relationships change over an entire  
264 stress gradient to see if more complex facilitation-stress models are realistic (Travis  
265 et al. 2006). For example, it is still unknown whether facilitation increases gradually  
266 with stress or whether there is a threshold at which it suddenly becomes manifest  
267 (Crain & Bertness 2006). Furthermore, facilitation through stress amelioration is only  
268 expected to increase in importance until abiotic stress reaches such a level that it  
269 can no longer be sufficiently buffered (Bruno & Bertness 2001). Studies have found  
270 that at extremely high levels of abiotic stress, any benefits provided by a facilitator  
271 would be overwhelmed by its own resource use (Maestre & Cortina 2004). This  
272 relationship was not observed here, possibly due to mimics not imitating competition  
273 fully. In addition, we may assume that at very high current speeds where they  
274 cannot remain imbedded, tubes would no longer be able to buffer stress effectively.

#### 275 *Facilitators could buffer regime shifts and restore perturbed habitats*

276 Facilitators could potentially restore disturbed and defaunated habitats. The  
277 potential restorative power of polychaetes has already been well documented in  
278 classic successional models and empirical studies (Pearson & Rosenberg 1978,  
279 Rhoads & Germano 1986). Fast-growing, opportunistic polychaetes quickly colonise  
280 and stabilise defaunated sediment, allowing other benthic species to then succeed  
281 them (e.g. Rosenberg 1976, Passchier & Kleinhans 2005, Volkenborn et al. 2009).  
282 Furthermore, broad evidence from plant communities suggests that stress-  
283 ameliorating facilitators have the potential to buffer disturbances (Callaway 1997,  
284 Callaway et al. 2005). Our work indicates that if sand masons were present in a  
285 benign system that changed to a flow-dominated one, tubeworms could prevent a  
286 change in species richness. This further demonstrates the potential for using  
287 facilitators as tools in conservation projects (Crain & Bertness 2006, Halpern et al.  
288 2007). However, detailed knowledge of specific systems is warranted to ensure that  
289 facilitators do not unintentionally (from the managers' viewpoint) facilitate unwanted  
290 species, such as invasive species (Shouse 2003).

291 ACKNOWLEDGEMENTS

292 We are grateful to Ian Nicholls for aiding in construction of the experimental flumes  
293 and to Gwynne Parry Jones at the School of Ocean Sciences for helping us deploy  
294 them. Thanks also to Nick Jones, Eilir Morgan, Charlotte Bentley and David  
295 Reynolds for help with sampling.

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426

TABLES

427

Table 1: General linear model of the effects of tubeworm density (0-10% RD) and

428

current regime (low/ high speed) on associated benthic species richness ( $R^2 =$

429

66.57%))

Source	df	F	P
RD	3	5.56	0.003
Flow	1	16.67	<0.001
RD x flow	3	10.13	<0.001

430

431 Table 2: General linear model showing the effects of tubeworm density (0-10% RD)  
432 and current regime (low/ high speed) on associated sediment shear strength ( $R^2 =$   
433 51.12%)

Source	df	F	p
log(RD+0.1)	3	9.71	<0.001
Flow	1	3.07	0.090
Interaction	3	0.43	0.734

434

435 Table 3: GLMs of the effects of tubeworm mimic density (RD 0-10%) on species abundance under different hydrodynamic  
 436 conditions (control/ high current speed); species trait information from [www.marlin.ac.uk/biotic](http://www.marlin.ac.uk/biotic); critical significance level = 0.005.

Taxon	Habit and feeding method	Mimic density (log(RD+0.1))			Flow speed		Interaction	
		R <sup>2</sup>	F	p	F	p	F	p
<i>Hydrobia ulvae</i>	Surface deposit feeder	0.359	1.64	0.200	11.66	0.002	0.44	0.724
OLIGOCHAETA	Free-living detritivore	0.216	0.69	0.566	5.76	0.022	0.33	0.803
<i>Scoloplos armiger</i>	Burrow- dwelling sub-surface deposit feeder	0.280	2.74	0.059	1.66	0.207	0.85	0.478
<i>Pygospio elegans</i>	Tube-dwelling surface suspension/ deposit feeder	0.931	33.45	*<0.001	160.45	*<0.001	57.69	*<0.001
<i>Cerastoderma edule</i>	Surface suspension feeder	0.117	0.99	0.408	0.86	0.361	0.14	0.936
<i>Eteone cf. longa</i>	Free-living predator/ scavenger	0.121	0.65	0.587	1.65	0.208	0.27	0.849
<i>Bathyporeia spp.</i>	Free-living scavenger/ omnivore	0.188	0.78	0.513	0.73	0.400	1.45	0.247
<i>Corophium spp.</i>	Burrow-dweller surface suspension/ deposit feeder	0.728	4.87	*0.007	24.12	*<0.001	15.68	*<0.001
<i>Macoma balthica</i>	Burrow-dweller surface deposit/ suspension feeder	0.335	3.05	0.042	1.67	0.206	1.77	0.172
<i>Capitella capitata</i>	Sub-surface deposit feeder	0.386	3.45	0.028	4.66	0.039	1.69	0.188

438 FIGURE LEGENDS

439 Figure 1: a) Conceptual models of how facilitation and species richness may relate at  
440 three levels of ambient stress (low, medium and high): at low stress the facilitator is  
441 not required and at the higher stresses, the facilitator trait must reach a certain level  
442 before ameliorating stress and influencing species richness. b) Includes competitive  
443 exclusion, expected to operate when stress is ameliorated completely (after Bruno &  
444 Bertness 2001). Richness is greatest at intermediate levels of stress

445 Figure 2: a) Venturi flume designed to increase current speed over a treatment area  
446 b) deployment device to implant tubeworm mimics in the sediment at a high density  
447 treatment (4358 tubes.m<sup>-2</sup>)

448 Figure 3: Relationship between facilitator trait (log (tubeworm RD+1)) and associated  
449 species richness at two levels of abiotic stress, low (control) and high current speed  
450 (flume)

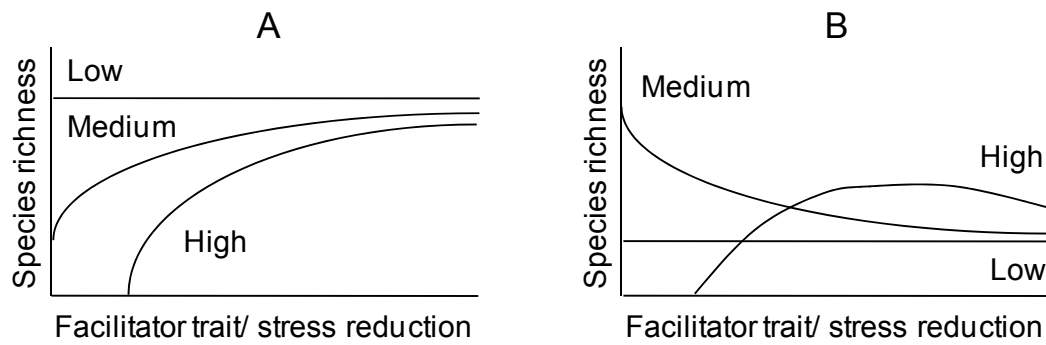
451 Figure 4: Relationship between facilitator trait (log (tubeworm RD+0.1)) and sediment  
452 shear strength (N.m<sup>-2</sup>) at two levels of abiotic stress, low (control) and high current  
453 speed (flume)

454 Figure 5: Relationship between facilitator trait (log (tubeworm RD+0.1)) and species  
455 density at two levels of abiotic stress, low (control) and high current speed (flume) for  
456 the ten commonest species in field study sites

457 Figure 6: MDS ordination showing the effects of tubeworm mimic density (RD 0-  
458 10%) on community structure ( $\sqrt{\sqrt{}}$ -transformed) under different hydrodynamic  
459 conditions (control/ high current speed); dashed lines represent significant clusters at  
460 a 68% similarity level (SIMPROF). In general, clusters A and B denote control

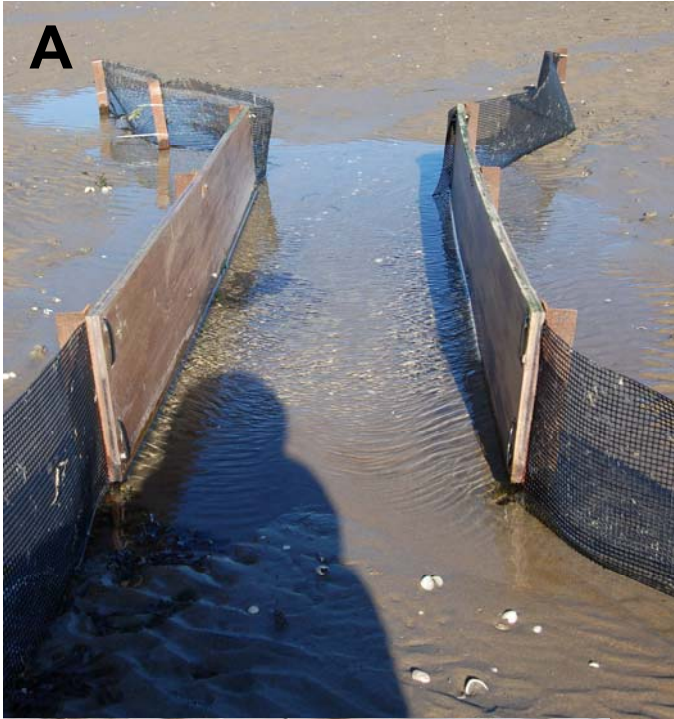
461 communities and flume communities with 1-10% RD, whilst clusters C and D

462 represent flume communities with 0-1% RD.



464

465 Figure 1: a) Conceptual models of how facilitation and species richness may relate at  
466 three levels of ambient stress (low, medium and high): at low stress the facilitator is  
467 not required and at the higher stresses, the facilitator trait must reach a certain level  
468 before ameliorating stress and influencing species richness. b) Includes competitive  
469 exclusion, expected to operate when stress is ameliorated completely (after Bruno &  
470 Bertness 2001). Richness is greatest at intermediate levels of stress



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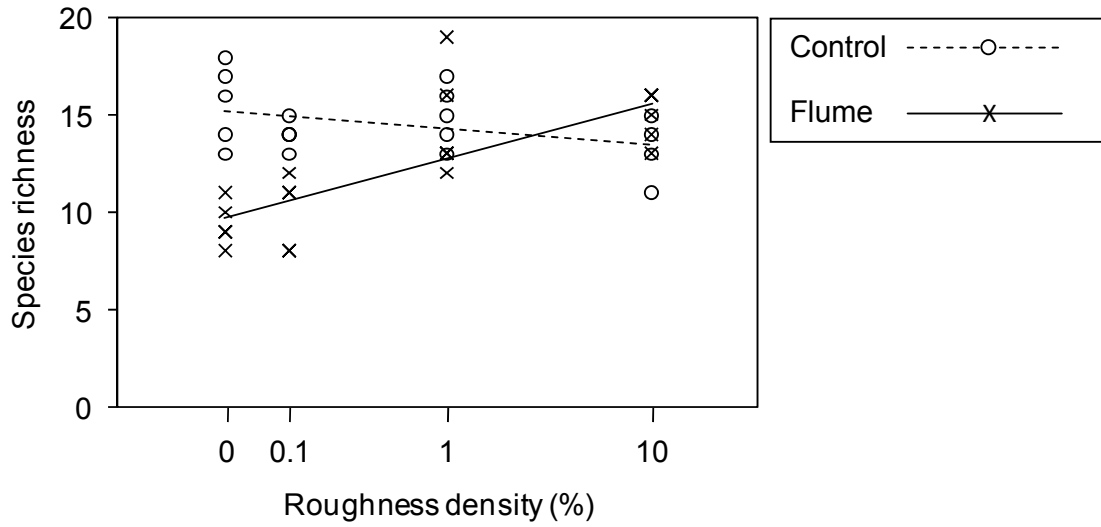


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473 Figure 2: a) Venturi flume designed to increase current speed over a treatment area

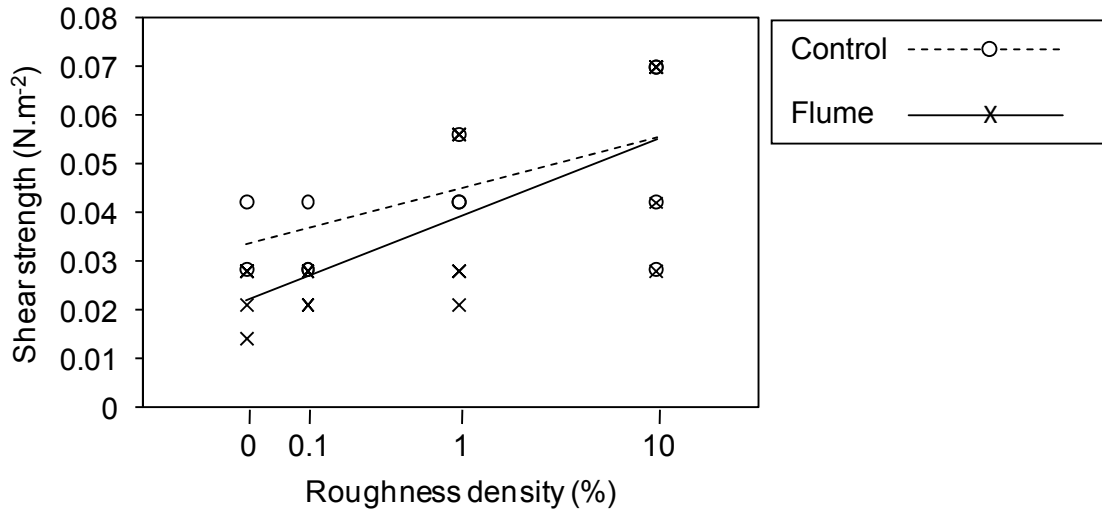
474 b) deployment device to implant tubeworm mimics in the sediment at high density

475 (4358 tubes.m<sup>-2</sup>)



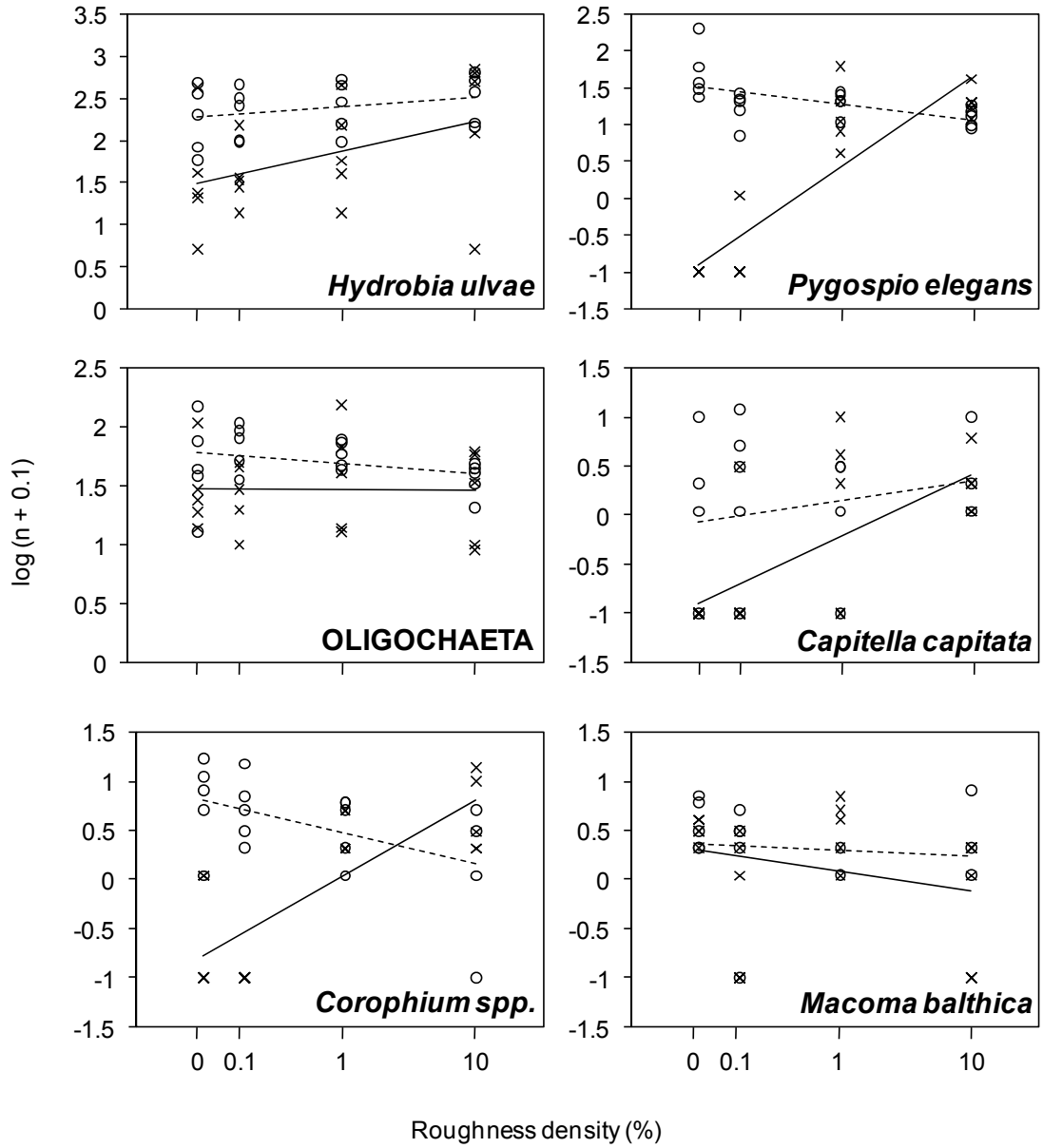
476

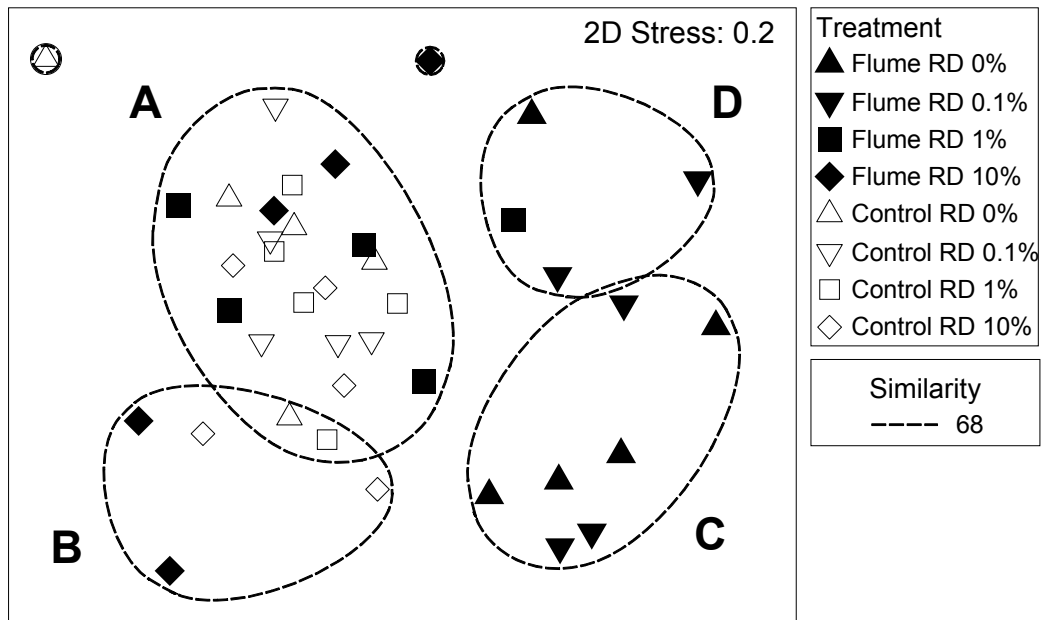
477 Figure 3: Relationship between facilitator trait ( $\log(\text{tubeworm RD}+1)$ ) and associated  
 478 species richness at two levels of abiotic stress, low (control) and high current speed  
 479 (flume); a logarithmic trendline is fitted to the high stress trait-richness relationship  
 480 based on the original trait-richness hypothesis (Bruno & Bertness 2001).



481

482 Figure 4: Relationship between facilitator trait (log (tubeworm RD+0.1)) and sediment  
 483 shear strength (N.m<sup>-2</sup>) at two levels of abiotic stress, low (control) and high current  
 484 speed (flume).





487

488 Figure 6: MDS ordination showing the effects of tubeworm mimic density (RD 0-  
 489 10%) on community structure ( $\sqrt{\sqrt{\cdot}}$ -transformed) under different hydrodynamic  
 490 conditions (control/ high current speed); dashed lines represent significant clusters at  
 491 a 68% similarity level (SIMPROF). In general, clusters A and B denote control  
 492 communities and flume communities with 1-10% RD, whilst clusters C and D  
 493 represent flume communities with 0-1% RD.