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1 **Preferential parasitism of native oyster *Ostrea edulis* over non-native**
2 ***Magallana gigas* by a Polydorid worm**

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9

10 **Abstract**

11 Parasites are important structural components of marine communities that can affect
12 organism fitness and ecological interactions, and the provision of ecosystem services.
13 Here, we investigate the host association of *Polydora ciliata* with two ecologically and
14 economically important oyster species (*Ostrea edulis*; *Magallana gigas*) and examine
15 its impacts on two fitness aspects: condition and shell strength. Our results provide
16 strong inferential evidence of host-specificity by *P. ciliata* with a tendency toward
17 infestation of the native *O. edulis* over the introduced *M. gigas*. Evidence suggests
18 increasing prevalence of parasitism with organismal age, but no clear indication that
19 parasitism leads to reduced condition or shell strength. The prevalence of infection of
20 *O. edulis* by *P. ciliata* over *M. gigas* observed here holds potential implications for
21 species competition and dominance, and their respective population maintenance,
22 which could explain the much lower abundances of *O. edulis* compared to *M. gigas* at
23 specific geographical locations. Additionally, these results hold significance for the
24 aquaculture sector, with parasitism likely to lower production output and decrease the
25 end-product market value.

26

1 **Keywords**

2 Intertidal; Estuary; Ecological interactions; Non-native species; Aquaculture

3

1 **Introduction**

2 Parasites are increasingly recognised as important structural components of marine
3 communities (Firth et al. 2017). They modulate the ecology and biogeography of their
4 host-species, but also indirectly shape the whole community via coincidental effects
5 on the habitat and ecological interactions, particularly in the case of an ecosystem-
6 engineer host (Mouritsen and Poulin 2002). Taxa affected by parasitism include
7 mammals, teleosts (Hoberg and Brooks 2008), birds, molluscs and crustaceans
8 (Mouritsen and Poulin 2002).

9

10 Bivalves are known to be hosts for various parasites that live in their mantles or within
11 their shells (Blake and Evans 1973; Carroll et al. 2015; Diez et al. 2014; Sato-Okoshi
12 et al. 2012). Parasites, by definition, are harmful to their host to a certain degree.
13 Negative effects can vary from minor metabolic changes to more important soft tissue
14 damages (Mouritsen and Poulin 2002). The deleterious effects of Polydorid worms on
15 bivalve host species can vary with the intensity of infestation, but usually lead to
16 physiological deficiencies (Chambon et al. 2007), reduced condition (Ambariyanto and
17 Seed 1991; Chambon et al. 2007; Riascos et al. 2008), and reduced shell strength
18 (Bergman et al. 1982; Kent 1981; Korringa 1951). This in turn affects important
19 ecological and biological processes, such as predator-prey interactions (Ambariyanto
20 and Seed 1991) and behaviour (Riascos et al. 2008).

21

22 Increasingly, the implications of parasitism for the bivalve aquaculture industry are
23 being considered (Clements et al., 2017; Diez et al. 2011; Royer et al. 2006; Simon
24 and Sato-Okoshi 2015), not least due to the negative economic and health
25 consequences parasitic infestation can cause. For example, parasites can cause the

1 formation of mud blisters (Blake and Evans 1973; Korringa 1952; Nell 2007) that affect
2 sensory and aesthetic parameters, reducing the quality of the product (Korringa 1951;
3 Lafferty et al. 2015) and negatively affecting the economic value, as well as acting as
4 a vector of disease (Lafferty et al. 2015; Powell et al. 2015).

5

6 In the UK, the native European flat oyster, *Ostrea edulis*, and the non-native invasive
7 Pacific oyster, *Magallana gigas*, are commercially valuable aquaculture species
8 (Lemasson et al. 2017). In addition, they are both ecosystem engineers (sensu Jones
9 et al. 1996) that provide numerous ecosystem services, such as reef formation,
10 erosion control, improvement of water quality and food provision (Herbert et al. 2012).
11 Although historically *O. edulis* was highly abundant in the UK (Orton 1937), their
12 continued decline has led to protection and extensive restoration programs (Woolmer
13 et al. 2011). In contrast, *M. gigas* continues to spread polewards facilitated by the
14 warming of sea surface waters (Rinde et al. 2016; Thomas et al. 2016; Townhill et al.
15 2017). In the Wadden Sea, there has been a gradual shift from native mussel beds to
16 invasive oyster beds following their introduction in 1986 (Kochmann et al. 2008), yet
17 recent studies have shown that both species can co-exist without detrimental
18 ecosystem impacts (Buschbaum et al. 2016; Reise et al. 2017). In Plymouth Sound
19 UK, mixed oyster beds of both *O. edulis* and *M. gigas* occur, but *M. gigas* are
20 increasingly prevalent (pers. observations). Although it is likely that some level of
21 competition for space and resources takes place, the ecological impact of *M. gigas* on
22 *O. edulis* remains unclear and may not alter associated assemblages (Zwerschke et
23 al. 2016).

24

1 *Polydora ciliata*, a parasitic worm affecting shellfish, has long been known to occur in
2 the South-West of the UK (Kent 1977) and in Plymouth waters, due to the occurrence
3 of Devonian limestone, a choice settlement substrate for the species (Dorsett 1961).
4 Oysters found along Plymouth Sound shores present signs of parasitism by Polydorid
5 worms (pers. observations), with a preference for *O. edulis* as the host species. To
6 date, the rate and prevalence of parasitism have not been reported, but based on
7 observations, it is hypothesised that parasitism may be in part responsible for the
8 reductions in abundance and high mortality of *O. edulis* (e.g. Naciri-Graven et al.
9 1998). If this is true, the physiological consequences of differential parasitism between
10 the two species of oysters could help to explain the abundance pattern observed, by
11 slowing the recovery of *O. edulis* and facilitating the spread of *M. gigas*, with important
12 ecological and economic outcomes.

13

14 Here, we investigated the host association of *Polydora ciliata* between *Ostrea edulis*
15 and *Magallana gigas* found in Plymouth Sound, UK, in relation to oyster size (proxy
16 for age), and examined if their condition index (tool widely used in the aquaculture
17 sector to evaluate the overall quality and health of bivalves (Knights, 2012; Marin et
18 al., 2003)) - and shell strength (indication of resistance to durophagous predators)
19 were affected.

20

21 **Methods**

22 'Large' and 'small' (see size-specifications below) individuals of each species were
23 hand-collected at low tide during four sampling events through 2015-2016 (as part of
24 separate studies) from the same low-intertidal site in Plymouth Sound (50°23'29.95"N,
25 004°13'16.77"W). Organisms were randomly selected within the chosen size bracket

1 and brought back in buckets without seawater to the Marine Biology and Ecology
2 Research Centre at Plymouth University. 'Large' *Magallana gigas* were collected in
3 July 2015, 'large' *Ostrea edulis* in January 2016, 'small' *M. gigas* in August 2016, and
4 'small' *O. edulis* in November 2016. The average duration of each sampling event
5 varied between one (for *M. gigas*) and two (for *O. edulis*) hours.

6 The maximum dorso-ventral length of each individual was measured to the nearest
7 millimetre using Vernier callipers (Mitutoya, Japan). Each individual was categorized
8 as being either 'small' (<70 mm in length for *O. edulis*; <100 mm in length for *M. gigas*)
9 or 'large' (>70 mm in length for *O. edulis*; >100 mm in length for *M. gigas*) before being
10 destructively sampled to assess the degree of parasitism by *Polydora ciliata* using
11 macroscopic examination of the inside and outside of the valves. Oyster parasitism
12 was described using one of three possible infection-level categorical classifications:
13 *uninfected* (no visible sign of infection), *infected low-level* (less than 10 visible
14 burrows), or *infected high-level* (more than 10 visible burrows) (Supplementary Figure
15 1). Differences in worm infection between species and between size classes within
16 species were assessed using a contingency table and χ^2 test of association.

17

18 The condition index (CI) of 20 randomly selected individuals from each species was
19 determined following the method recommended by Lucas and Beninger (1985): $CI =$
20 $(\text{dry meat weight} / \text{dry shell weight}) \times 100$. Dry tissue weight and dry shell weight were
21 determined after each oyster was shucked using an oyster knife and oven-dried at
22 105°C in pre-weighed aluminium trays for up to 48h. Tissues were considered 'dry'
23 after three successive measurements of the same mass. As nearly 100% of *O. edulis*
24 shells selected were infected, we could not assess the effect of worm infection on its
25 CI. Instead, we investigated the effect of infection level on the CI of *M. gigas* separately

1 first using a single factor Analysis of Variance (ANOVA) after checking for
2 homogeneity of variances using Levene's Test ('car' package). We then assessed
3 differences between highly-infected *O. edulis* and highly-infected *M. gigas*. using a
4 Welch two-sample t-test, after checking for normality of distribution and homogeneity
5 of variances using Shapiro-Wilk test and Levene's test, respectively.

6

7 Another subsample of individuals from each species (n=26 for *Magallana gigas*; n=28
8 for *Ostrea edulis*) was randomly selected and the mechanical strength of their left
9 valve measured using a vertical compressive force applied to the shell using a force
10 transducer (Instron Testing System, Instron, USA). The left valve of each oyster shell
11 was placed cup-down directly underneath the cell load and the force profile for each
12 oyster recorded (Supplementary Figure 2). For each oyster, the force required to break
13 the valve in half was recorded. Again, as nearly 100% of *O. edulis* shells selected were
14 infected, we could not assess the effect of worm infection on its shell strength, and
15 instead we investigated the effect of infection level on the shell strength of *M. gigas*
16 separately first using a single factor Analysis of Variance (ANOVA) after checking for
17 homogeneity of variances using Levene's Test ('car' package). Multiple regression
18 was used to analyse shell strength data, with "Species" set as the fixed factor and shell
19 weight (g) as the continuous covariate in the model. The "step()" function was used to
20 assess the best model to select, based on Akaike Information Criterion values.
21 Diagnostics plots were used to visually assess model assumptions that the residuals
22 were unbiased and homoscedastic. Where necessary, data were log-transformed to
23 meet assumptions.

24

1 All analyses were performed using the public domain package *R* [version 3.3.1] (R
2 Core Team, 2018) with significance indicated by p-values < 0.05.

3

4 **Results**

5 Species comparison

6 In total, shells of 92 *Magallana gigas* and 100 *Ostrea edulis* were analysed. There
7 were significant differences in the degree of infection between species, with 25% and
8 99% of *M. gigas* and *O. edulis* displaying parasitism by *Polydora ciliata*, respectively
9 (Fig 1). *Ostrea edulis* was statistically more infected by the worm than *M. gigas* (Table
10 1a, Table 2a).

11

12 Size class comparison within species

13 For *M. gigas*, there was significant differences in infection level with individual size
14 (Table 1b), with large oysters showing significantly higher levels of infection than small
15 oysters (21 'large' out of the 23 infected) (Table 2b, Fig 1). In contrast, the level of
16 infection of *O. edulis* (99%) appeared irrespectively of individual size (49.5% of
17 infected individuals were 'small', and 50.5% were 'large') (Table 1b, Table 2b, Fig 1).

18

19 Condition index (CI) and shell strength

20 Worm infection did not alter the CI of *M. gigas* ($F_{2,17} = 0.612$; $p = 0.554$), which
21 averaged at 3.9 ± 0.2 (Fig. 2a) The mean CI of highly-infected *O. edulis* (3.5 ± 0.3)
22 was not significantly different from that of highly-infected *M. gigas* (3.9 ± 0.8 ; $t_{4.1} =$
23 0.42 , $p = 0.70$) (Fig 2b).

24

1 The mechanical strength of *M. gigas* was unimpacted by worm infestation ($F_{2,20} = 1.1$;
 2 $p = 0.34$; Fig 2c), but the strength of oyster shells significantly differed between species
 3 ($F_{7,46} = 14.3$; $p < 0.001$) depending on shell weight (Fig 2d). There was no difference
 4 in shell strength between species in lower weight oysters (23-50 g), after which, the
 5 shell strength of *M. gigas* continued to increase to a maximum strength of 4.4 kN; over
 6 3x greater than the maximum strength of *O. edulis* (1.3 kN) although the heaviest
 7 individual of *M. gigas* was nearly 3x heavier (323 g) than the heaviest *O. edulis* (109
 8 g). Comparing the heaviest *O. edulis* and equivalent mass *M. gigas*, the shell strength
 9 of *M. gigas* was on average (0.9 kN), 4.4x stronger than that of *O. edulis* (0.2 kN), with
 10 larger *O. edulis* seemingly losing shell strength with increasing mass (Fig 2d).

11

12 **Table 1:** Recorded counts of oyster shells for each infection level a) by species, b) by
 13 size class within each species. Expected values are shown in brackets and calculated
 14 as: $(\text{row total} * \text{column total}) / n$, where n is the total number of observations. No infection:
 15 no burrows observed; Low level: 1-10 burrows; High level: >10 burrows observed.

16

a)		No Infection	Low Level	High Level	Total
<i>Magallana gigas</i>		69 (33.5)	18 (13.9)	5 (44.6)	92
<i>Ostrea edulis</i>		1 (36.5)	11 (15.1)	88 (48.4)	100

b)		No Infection	Low Level	High Level	Total
<i>Magallana gigas</i>	Small	53 (41.2)	2 (10.8)	0 (2.99)	55
	Large	16 (27.8)	16 (7.24)	5 (2.01)	37
<i>Ostrea edulis</i>	Small	0 (0.49)	6 (5.39)	43 (43.1)	49
	Large	1 (0.51)	5 (5.61)	45 (44.9)	51

17

18

19 **Table 2:** Summary of the χ^2 analyses results for a) species comparisons and b) size
 20 class within each species comparisons.

21

a) **Species: *Magallana gigas* vs *Ostrea edulis***

χ^2	df	P	Outcome
141.73	2	<0.001	<i>Ostrea edulis</i> > <i>Magallana gigas</i> ***

b) **Size class: Small vs Large**

	χ^2	df	P	Outcome
<i>Magallana gigas</i>	33.49	2	<0.001	Large>Small***
<i>Ostrea edulis</i>	1.097	2	0.578	Large=Small

*** p<0.001

1

2 Discussion

3 This study aimed to investigate the prevalence of the parasite, *Polydora ciliata*, in two
 4 commercially valuable oyster species, *Ostrea edulis* and *Magallana gigas*, and assess
 5 the physiological implications of infection on two aquaculture-relevant fitness
 6 measures. Simon (2011) suggested that polydorid worms demonstrate no host
 7 specificity, yet our results provide strong inferential evidence of host-specificity by
 8 *P. ciliata*, with in particular, a tendency toward infestation of the native *O. edulis* over
 9 the introduced *M. gigas*. Several other studies have also demonstrated host-specificity
 10 by *Polydora* worms (Calvo et al. 2000; Calvo et al. 1999; Diaz et al. 2011), also with
 11 tendency of infection prevalence and intensity toward native species
 12 (*Crassostrea virginica*) over introduced species such as *Crassostrea ariakensis* and
 13 *M. gigas*.

14

15 To date, the mechanisms behind infestation and the traits that dictate host selection
 16 remain unclear. Infection by *Polydora* worms begin with the settlement of a planktonic
 17 larvae onto the oyster shell, which after reaching sexual maturity is able to multiply
 18 and colonize the shell (Blake and Evans 1973). Due to the gregarious nature of the
 19 larvae, species-specific chemical cues from the shells are likely to influence settlement
 20 and host preference (Blake and Evans 1973). Given the preference here for settlement

1 onto the shells of native *O. edulis* over invasive *M. gigas* perhaps an evolved attraction
2 to *O. edulis* exists in *P. ciliata* that has not yet had time to develop towards *M. gigas*.
3 Additionally, chemical cues emanating from epibionts are also known to influence
4 polydorid worm settlement. For instance, Diaz et al. (2016) reported that polydorid
5 infestation of ribbed mussels *Aulacomya atra* was positively related to the presence
6 and abundance of serpulid polychaetes and crustose algae growing on the shells. The
7 authors concluded that the settlement of polydorid larvae may have been triggered by
8 chemical cues produced by the epibionts (Diaz et al. 2016). However, neither species
9 of oysters in our study appeared to host such epibionts (pers. observations). Shell
10 aspects such as surface roughness, area available for colonisation, and thickness,
11 which vary amongst species, are also important factors for invertebrate larval
12 settlement choice. The shell morphologies of *O. edulis* and *M. gigas* are quite distinct
13 (Hu et al. 1993); *M. gigas* possess a thick frilled shell, usually elongated with prominent
14 ribs, whereas *O. edulis* has a thinner rounded shell with obvious concentric flat scales.
15 While not assessed here, thinner shells have been shown to be a cause of higher
16 susceptible to infection, with infected oysters also displaying more important
17 physiological impacts (Bishop and Hooper 2005; Calvo et al. 1999). Additionally, while
18 not tested in this study, differences in bivalve shell microstructural arrangement can
19 explain differences in strength and toughness (MacDonald et al. 2009). It is therefore
20 possible that *O. edulis* biomineralisation processes lead to crystallographic
21 orientations and shell characteristics that favour the settlement, boring action, and
22 colonisation of *P. ciliata*.

23

24 Whereas there were no differences in infection with oyster size in *O. edulis*, here
25 bigger *M. gigas* were linked with higher infection rate. This is consistent with the

1 general assumption that infection can be related to the size of the organisms, with
2 bigger organisms displaying higher levels of infection (Ambariyanto and Seed 1991;
3 Riascos et al. 2008; Royer et al. 2006). This is often explained by both an increase in
4 shell surface for colonization with growth, and a longer exposure to the parasite with
5 age, therefore increasing the probability of infection (Diaz et al. 2016).

6

7 Although not the direct cause of mortality, infection can eventually lead to death
8 through sub-lethal effects. Infection can bring about important negative physiological
9 consequence, such as reduction in flesh weight and overall condition, decrease in
10 reproductive output, and lowering of the immune system (Royer et al. 2006). For
11 instance, the condition index (CI) of ribbed mussels *A. atra* was significantly negatively
12 related to polydorid infestation levels (Diez et al. 2016). Here however, the CI of
13 *M. gigas* appeared unimpacted by worm infection, but interestingly was similar to that
14 of *O. edulis*. Because nearly 100% of *O. edulis* individuals collected were infected with
15 *Polydora* sp., we could not determine whether uninfected individuals have inherently
16 higher CI than *M. gigas*, and if infection led to a reduction in condition. Reduction in
17 shell strength as a consequence of infection was recorded in *Placopecten*
18 *magellanicus* and *Mytilus edulis*, and was linked to increased predation susceptibility
19 (Bergman et al. 1982; Kent 1981). Here in contrast to previous findings, the shell
20 strength of *M. gigas* remained similar across infection levels, meaning that its
21 mechanical properties were not altered by the presence of the worm. Additionally,
22 shells of *O. edulis* were notably weaker than those of *M. gigas*, making them easier
23 prey for durophagous predators. However, we could not compare the strength of
24 infected vs uninfected *O. edulis* as all individuals were infected, and therefore, we
25 cannot decipher between the possibility that infection might have affected its shell

1 strength and rendered it weaker, with potential implications for predator-prey
2 interactions, and the possibility that its shell is inherently weaker than those of
3 *M. gigas*.

4

5 **Conclusion**

6 The differential infection by *P. ciliata* between *O. edulis* and *M. gigas* observed here,
7 with *M. gigas* apparently more resistant to infection, holds potential implications for
8 species competition and dominance, and their respective population maintenance in
9 Plymouth Sound. Although infection did not appear to negatively impact *M. gigas*
10 condition and strength, we could not assess whether infection affected *O. edulis*.
11 Regardless, *O. edulis* clearly appears less resistant to durophagous predators. These
12 effects can influence community interactions and have implications for its long-term
13 resilience and survival, which could explain the much lower abundances of *O. edulis*
14 compared to *M. gigas* observed in Plymouth Sound populations (pers. observations).
15 Finally, given the economic value of both *M. gigas* and *O. edulis* in the UK, these
16 findings also hold significance for the aquaculture sector, with parasitism likely to lower
17 production output and decrease the end-product market value.

18

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3

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5

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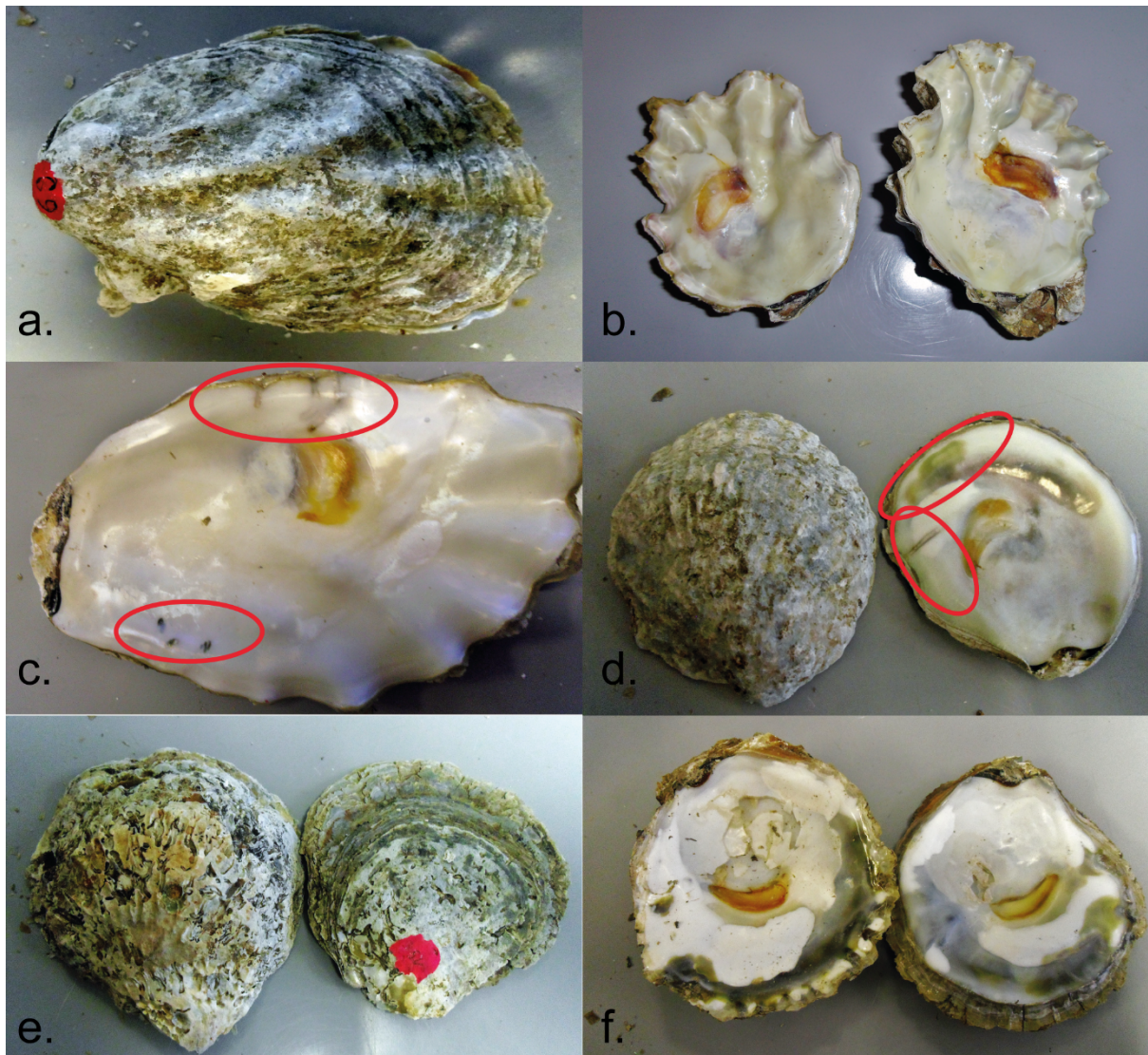
1 **Figure legends**

2 **Fig. 1** Percentage of *Magallana gigas* (n=92) and *Ostrea edulis* (n=100) shells being
3 infected by the parasitic worm *Polydora ciliata*, grouped by small and large size
4 classes. Uninfected: no burrows observed; Low Level: 1-10 burrows; High Level: >10
5 burrows.

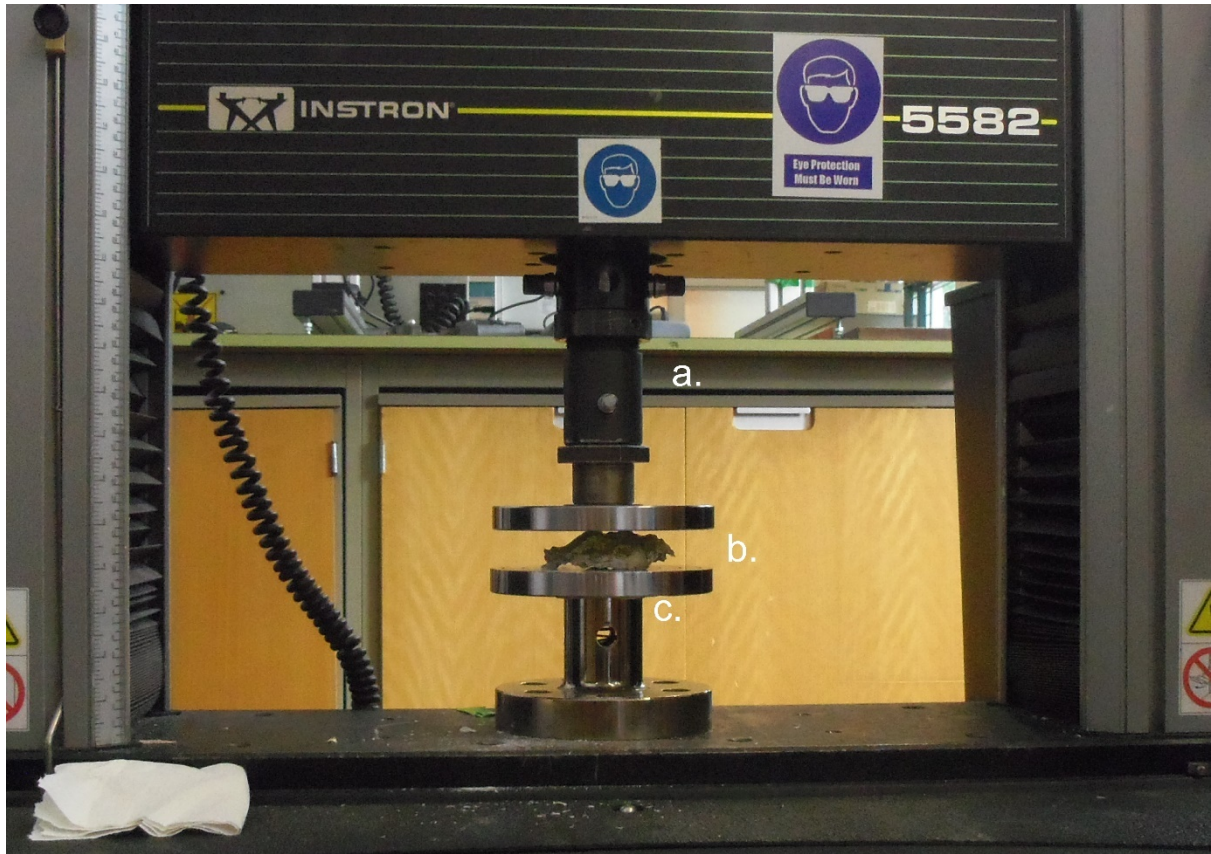
6

7 **Fig. 2** a) Condition index of *Magallana gigas* grouped by infection level. b) Condition
8 index of highly-infected individuals of *Ostrea edulis* (n=19) and *Magallana gigas* (n=4).
9 Data presented as means \pm standard error (s.e). c) Strength of the lower valve of shells
10 of *Magallana gigas* grouped by infection level. Data presented as means \pm standard
11 error (s.e). kN=kilo newton. d) Variation in shell strength with shell weight. *Ostrea*
12 *edulis* (grey): $y = 0.017x^2 - 0.0001x - 0.03$, $R^2 = 0.30$; *Magallana gigas* (black): $y = 3 \times 10^{-7}x^3 - 0.0002x^2 + 0.026x - 0.279$, $R^2 = 0.59$
13

1 **Supplementary Material**



Supplementary Fig. 1 a) Outside view of the uninfected shell of a large *Magallana gigas*. b) Inside view of uninfected shells of a small *M. gigas*. c) Inside view of the shell of a large *M. gigas* with low level of worm infection, depicted by the presence of burrows (red circles). d) Outside and inside views of the shell of a large *Ostrea edulis* with low-level of worm infection manifested by burrows and mud blisters (red circles). e) Outside view and inside view. f) of a large *O. edulis* displaying high-level of worm infection



1

2 **Supplementary Fig. 2:** Experimental set-up of oysters' adductor muscle strength
3 assessment. a. Instron cell load. b. hook glued to the c. oyster. d. clamps. e. metal
4 plate.