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

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Abstract

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

1 **Keywords**

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

3

Introduction

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

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

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

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

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

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

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

Methods

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

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

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

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

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

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

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

Results

Species comparison

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

Size class comparison within species

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

Condition index (CI) and shell strength

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

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: *(row total*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
Magallana gigas		69	*(33.5)*	18	*(13.9)*	5	*(44.6)*	92
Ostrea edulis		1	*(36.5)*	11	*(15.1)*	88	*(48.4)*	100

b)		No Infection		Low Level		High Level		Total
Magallana gigas	Small	53	*(41.2)*	2	*(10.8)*	0	*(2.99)*	55
	Large	16	*(27.8)*	16	*(7.24)*	5	*(2.01)*	37
Ostrea edulis	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*			
χ2	df	*P*	Outcome
141.73	2	<0.001	*Ostrea edulis > Magallana gigas* ***

b)

Size class: Small vs Large				
	χ2	df	*P*	Outcome
Magallana gigas	33.49	2	<0.001	Large>Small***
Ostrea edulis	1.097	2	0.578	Large=Small

*** p<0.001

Discussion

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

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

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

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

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

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

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

Conclusion

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

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Figure legends

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

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

Supplementary Material
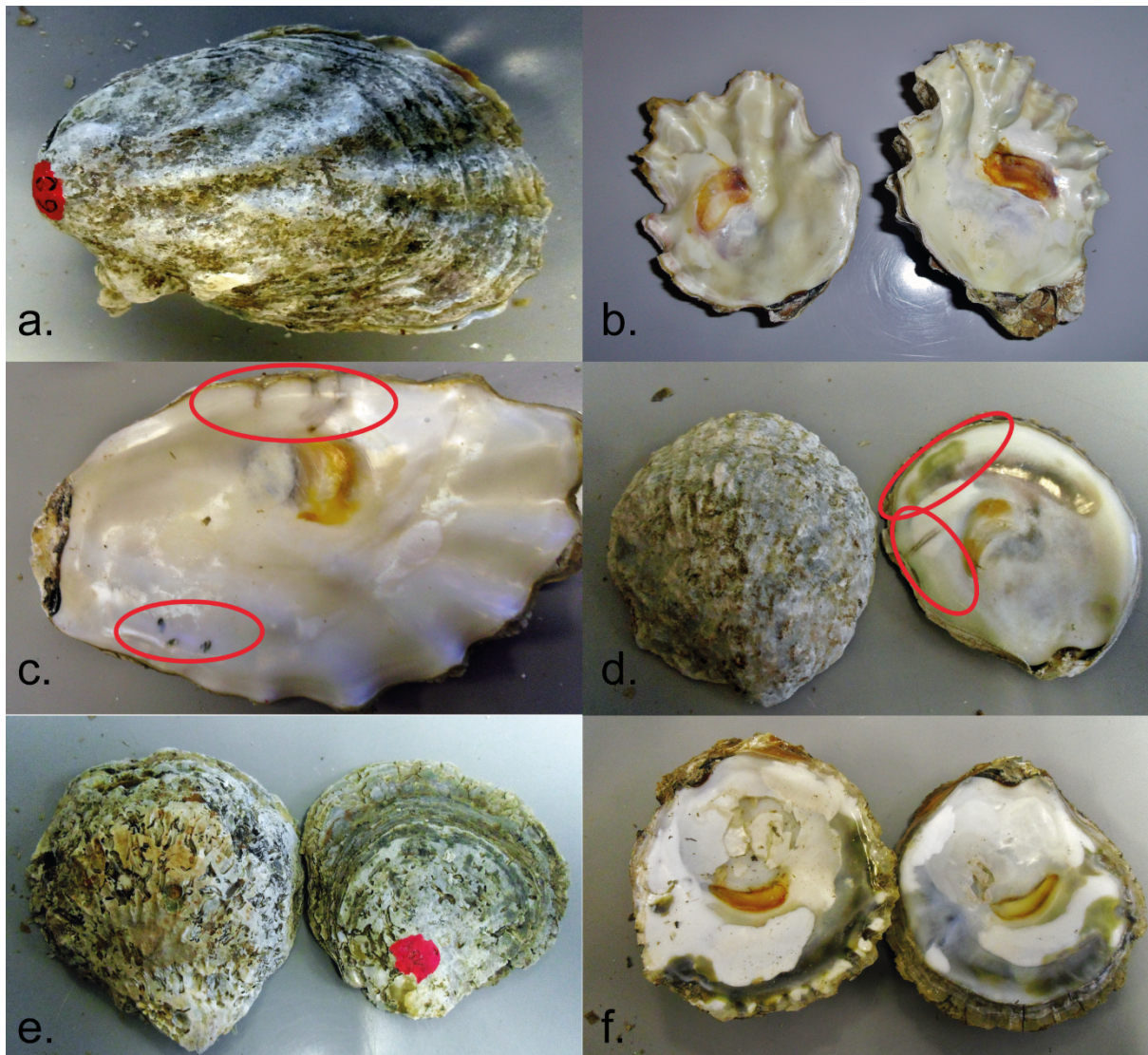
Supplementary Fig. 1 a) Outside view of the uninfected shell of a large *Magallana gigas*. b) Inside view of uninfected shells of a small *M. gigas*. c) Inside view of the shell of a large *M. gigas* with low level of worm infection, depicted by the presence of burrows (red circles). d) Outside and inside 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
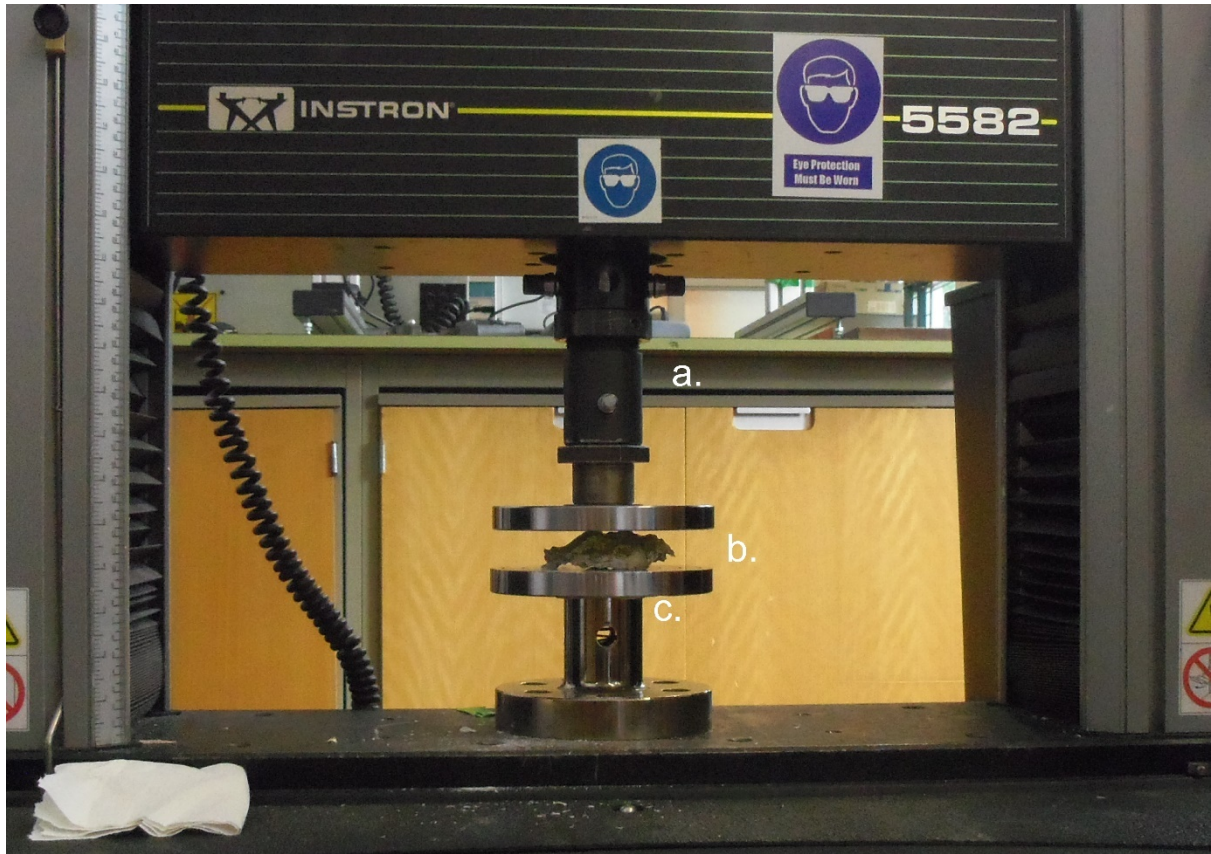
Supplementary Fig. 2: Experimental set-up of oysters' adductor muscle strength

assessment. a. Instron cell load. b. hook glued to the c. oyster. d. clamps. e. metal

plate.