Outcompeted and overfished: Competitive exclusion by the invasive gastropod *Crepidula fornicata* is a threat to recovery of the European native oyster *Ostrea edulis* in the Solent, UK (#29415)

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Outcompeted and overfished: Competitive exclusion by the invasive gastropod *Crepidula fornicata* is a threat to recovery of the European native oyster *Ostrea edulis* in the Solent, UK

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The decline of the European oyster *Ostrea edulis* across its biogeographic range has been driven largely by over-fishing and anthropogenic habitat destruction, often to the point of functional extinction. However, other negatively interacting factors attributing to this catastrophic decline include disease, invasive species and pollution. In addition, a relatively complex life history characterised by sporadic spawning renders *O. edulis* biologically vulnerable to over-exploitation. As a viviparous species successful reproduction in *O .edulis* populations is density dependent to a greater degree than broadcast spawning oviparous species such as the pacific oyster *Crassostrea (Magallana) gigas*. Here we report on the benthic assemblage of *Ostrea edulis* and the invasive gastropod *Crepidula fornicata* across three actively managed harbours in one of the few remaining *O. edulis* fisheries in the UK. Long-term data reveals a significant decrease in oyster densities between 1998 and 2017, and an ecological shift to benthic dominance by *Crepidula fornicata*. Grab surveys recorded extremely low densities of 0 ±0, 0.2 ±0.2, 0.1 ±0.1 *O. edulis* / m^2 (mean ±SE) and 84.1 ±24.5, 174.3 ±34.5 and 306.0 ±106.0 *Crepidula fornicata* / m^2 (mean ±SE) in Portsmouth, Langstone and Chichester Harbours respectively. Chichester Harbour *O. edulis* seabed densities have decreased significantly from 8.0 ±2.7 to 0.1 ±0.1 / m^2 (mean ±SE) whilst *C. fornicata* has increased from 181.2 ±40.7 to 306.0 ±106.0 / m^2 (mean ±SE) since 1998. The lack of recovery of *Ostrea edulis* despite fishery closures indicates competitive exclusion by *C fornicata* is preventing recovery of *O.edulis* due to a lack of habitat heterogeneity or suitable settlement substrate. Large scale population data reveals that mean *O. edulis* length and width has decreased significantly across all year and site groups from 2015 to 2017, with a narrowing demographic structure. An absence of juveniles and lack of multiple cohorts in the remaining population suggests fishing effort exceeds biological output and recruitment is poor. In the Langstone & Chichester 2017 sample 98% of the population is assigned to a single cohort (modal mean 71.20 ± 8.78 mm, max length). There is evidence of small scale (<5km) geographic population structure between connected harbours; the 2015 Portsmouth and Chichester populations exhibited disparity in the most frequent size class with 36% within 81-90mm and 33.86% within 61-70 mm respectively . The prevalence of the disease Bonamiosis supports this population structure. Infection rates of *O.edulis* by *Bonamia ostreae* was 0% in Portsmouth Harbour (n=48), 4.1 % in Langstone (n=145) and 21.3 % in Chichester (n=48) populations. This data collectively indicates that *O. edulis* is on the brink of ecological collapse within the Solent without intervention to mitigate the competitive displacement by *Crepidula fornicata* in the form of biologically relevant fishery policy and recruitment substrate management.

AUTHOR COVER PAGE

Title

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ABSTRACT

The decline of the European oyster *Ostrea edulis* across its biogeographic range has been driven largely by over-fishing and anthropogenic habitat destruction, often to the point of functional extinction. However, other negatively interacting factors attributing to this catastrophic decline include disease, invasive species and pollution. In addition, a relatively complex life history characterised by sporadic spawning renders *O. edulis* biologically vulnerable to over-exploitation. As a viviparous species successful reproduction in *O .edulis* populations is density dependent to a greater degree than broadcast spawning oviparous species such as the pacific oyster *Crassostrea (Magallana) gigas*. Here we report on the benthic assemblage of *Ostrea edulis* and the invasive gastropod *Crepidula fornicata* across three actively managed harbours in one of the few remaining *O. edulis* fisheries in the UK. Long-term data reveals a significant decrease in oyster densities between 1998 and 2017, and an ecological shift to benthic dominance by *Crepidula fornicata*. Grab surveys recorded extremely low densities of 0 ±0, 0.2 ±0.2, 0.1 ±0.1 *O. edulis* / m^2 (mean ±SE) and 84.1 ±24.5, 174.3 ±34.5 and 306.0 ±106.0 *Crepidula fornicata* / m^2 (mean ±SE) in Portsmouth, Langstone and Chichester Harbours respectively. Chichester Harbour *O. edulis* seabed densities have decreased significantly from 8.0 ±2.7 to 0.1 ±0.1 / m^2 (mean ±SE) whilst *C. fornicata* has increased from 181.2 ±40.7 to 306.0 ±106.0 / m^2 (mean ±SE) since 1998. The lack of recovery of *Ostrea edulis* despite fishery closures indicates competitive exclusion by *C fornicata* is preventing recovery of *O.edulis* due to a lack of habitat heterogeneity or suitable settlement substrate. Large scale population data reveals that mean *O. edulis* length and width has decreased significantly across all year and site groups from 2015 to 2017, with a narrowing demographic structure. An absence of juveniles and lack of multiple cohorts in the remaining population suggesting the limited fishing effort

exceeds biological output and recruitment is poor In the Langstone & Chichester 2017 sample 98% of the population is assigned to a single cohort (modal mean 71.20 ± 8.78 mm, maximum length). There is evidence of small scale (<5km) geographic population structure between connected harbours; the 2015 Portsmouth and Chichester populations exhibited disparity in the most frequent size class with 36% within 81-90mm and 33.86% within 61-70 mm respectively . The prevalence of the disease Bonamiosis was monitored and supports this microgeographic population structure. Infection rates of *O.edulis* by *Bonamia ostreae* was 0% in Portsmouth Harbour (n=48), 4.1 % in Langstone (n=145) and 21.3 % in Chichester (n=48) populations. This data collectively indicates that *O. edulis* is on the brink of ecological collapse within the Solent without intervention to mitigate the competitive displacement by *Crepidula fornicata* in the form of biologically relevant fishery policy and recruitment substrate management.

INTRODUCTION

European flat oyster *Ostrea edulis* (Linnaeus, 1758) populations naturally fluctuate due to sporadic reproduction, making the species biologically vulnerable to over-exploitation (Drinkward 1999b). Long-term fishing pressure and habitat destruction has pushed *O. edulis* to functional extinction in many places across Europe (Gross & Smyth 1946**,** Kirby 2004**,** Beck et al 2011**)**. The Solent is no exception; a boom-and-bust fishery, invasive species and disease led to a severe population crash during 2007 from which it has failed to recover despite fishery closures. Baseline data is required to understand the fundamental ecological principles of density, growth, survival, reproduction and recruitment. Furthermore, successful management of this endangered resource requires spatiotemporal scales of demographic variation within the Solent. With large scale restoration efforts planned, this paper reports on baseline data gathered to demographically characterise the remnant population of Ostrea edulis in the Solent and to confirm the extent of threats to restoration, both the benthic extent of the invasive species Crepidula fornicata and infection rates by *Bonamia ostreae*.

Reference?

End of intro?

The native habitat of *Ostrea edulis* (European flat oyster) (Linnaeus, 1758) includes a range of firm substrata from the lower intertidal to subtidal depths up to 80m (Perry & Jackson 2017) across its biogeographic range from Morocco, throughout the Mediterranean and Black seas, to Norway (Lallias et al. 2010). Earliest records identify *O. edulis* shell middens from the Mesolithic period, (Gutiérrez-Zugasti et al. 2011) and cultivation and harvesting since the Roman Empire (Gunther 1897) illustrating the long history of extraction for human consumption.

Native oyster populations throughout Britain remained large and lightly fished up until the early 19th century (Edwards 1997, Key & Davidson 1981). By the mid-19th C demand was high, approximately 700 million oysters were consumed in London during 1864, supporting a sizable UK fleet of 120,000 oyster dredgers (Philpots 1890 in Edwards 1997). In France, historic shell piles contained approximately $5x10^{12}$ oysters (Gruet & Prigent 1986 in Goulletquer & Heral 1997) highlighting both the historic densities and unsustainable extraction of this species. Despite UK governmental legislation put in place by a parliamentary committee (still enforced under the Sea Fisheries (Shellfish) Act of 1967), stocks inevitably declined. Landings of *O. edulis* in English and Welsh waters decreased from 3,500 tonnes in 1887, to < 500 tonnes in 1947 (Laing et al. 2006).

This decline in the native oyster is reflected in the Solent, the 5,506 hectare waterway that separates the Isle of Wight from the UK mainland and encompasses sheltered waters of multiple harbour and estuarine environments. Described in detail by Key & Davidson (1981), oyster growing activity within the Solent occurred from 1866 onwards, with small scale removal and relocation taking place in the early 20th century (Anon 1912-1940 in Key & Davidson 1981). Throughout the 1970s and early 80s, the Solent was one of the larger remaining *O. edulis* fisheries in Europe. For example in 1978 the fishery involved 450 commercial vessels between Weymouth and Chichester and supported at least 700 workers (Key & Davidson 1981). During 1979-80, 650 - 850 tonnes of *O. edulis* were landed, and seabed densities of 32 / m^2 recorded (Key & Davidson 1981). Continued unstainable extraction led to chronic decline (Davidson 1976; Key & Davidson 1981; Tubbs 1999; Vanstaen & Palmer 2009). At the turn of the 21st century annual stocks decreased rapidly from 200 to 20 tonnes by 2011 mirrored in the decline of fishing licences issued, from 77 (2002/3) to 22 (2009/10) (Kamphausen 2012). The Southern Inshore Fisheries and Conservation Authority (IFCA) closed the wider Solent completely 2013-2015 due to a failure of stocks to recover from a population crash in 2007 (Southern IFCA 2014 in Gravestock et al. 2014). Due to the complex lifestyle (Fig. 1), sporadic reproduction and relative accessibility of their habitat, a range of anthropogenic pressures and over-extraction has repeatedly exceeded the biological production of *O. edulis* within the Solent.

The distribution of *O. edulis* across the UK and Europe is a fraction of historic levels, predominantly subtidal and completely absent in many areas of the North Sea (Laing et al. 2005, 2006, Culloty & Mulcahy 2007). Globally, approximately 85 % of oyster reef habitat has been lost (Beck et al. 2011), resulting in ecological declines (Cranfield et al. 1999) Carbines et al. 2004). The impact of overfishing is further compounded by multiple detrimental factors summarised in Fig. 2.

The disease Bonamiosis has severely impacted *O. edulis* populations. Caused by the intrahaemocytic protozoan parasite *Bonamia ostreae* introduced into Europe via transplanted *O. edulis* seed from Californian hatcheries (MacKenzie et al. 1997), it has spread across Europe (Grizel et al. 1988, Lynch et al. 2005, Culloty & Mulcahy 2007, Lallias et al. 2008) causing mass mortalities of up to 90% of localised populations (Figueras 1991, Cigarria et al. 1995, Laing et al. 2005). The parasite becomes systemic within the host oyster, inducing physiological disorders that eventually become overwhelming causing death (Grizel et al. 1988). Some potential resistance can arise through breeding strategies (Baud et al. 1997, Culloty et al. 2001, Lallias et al. 2009).

The presence of the invasive gastropod *Crepidula fornicata* is a concern in the Solent. The species was accidently introduced with imports of *Crassostrea virginica* (Dodd 1893, McMillan 1938, Hoagland 1985, Utting & Spencer 1992, Minchin et al. 1995) and *Magallana gigas* (Blanchard 1997) to Liverpool in the 1880's (Moore 1880 in McMillan 1938), eastern coast and Thames estuary in the 1890's and early 1900's (Crouch 1893, Cole 1915). Despite claims that *C. fornicata* may increase macrozoobenthic communities in muddy sediments (de Montaudouin & Sauriau 2017), its rapid expansion throughout many areas of the UK (Orton 1950, Chipperfield 1951, Cole & Baird 1953, Barnes et al. 1973, Minchin et al. 1995) and Europe (Blanchard 1997, 2009, Davis & Thompson 2000, Thieltges et al. 2003), including rapid colonisation of oyster beds (Crouch 1893), has serious ecological and economic impacts (Blanchard 1997). *C. fornicata* has been shown to be detrimental to habitat suitability for juvenile fish (Le Pape et al. 2004), suprabenthic biodiversity (Vallet et al. 2001), shell growth and survival of *Mytilus edulis* (Thieltges 2005) and is also attributed to habitat modification, through the production of mucous pseudofaeces. Benthic substrata changes from predominantly sandy to muddy with a high organic content that rapidly becomes anoxic and unsuitable for other species (Streftaris & Zenetos 2006). This includes the native oysters through a reduction in suitable substrata available for larval settlement (Blanchard 1997), inducing difficulties with recruitment and therefore oyster restoration efforts on the seabed.

The shift towards a habitat dominated by *C. fornicata*, due to the decline of *O. edulis* and its accompanying biogenic habitat, is of concern in part because of the loss of associated socio-economic benefits (Grabowski et al. 2012) and ecosystem services that oysters provide (Coen et al. 2007). Increases in biodiversity (Wells 1961, Zimmerman et al. 1989, Smyth & Roberts 2010), habitat complexity (Bell et al. 1991) nekton biomass (Humphries & La Peyre 2015), non-oyster fishery stocks (Coen et al. 1999, Harding & Mann 200[illegible]terson et al. 2003, Tolley & Volety 2005) and nitrogen removal (Piehler & Smyth 2011, Kellogg et al. 2013, Smyth et al. 2013), as well as reduction in phytoplankton and seston biomass (Grizzle et al. 2008) are all examples of the beneficial impacts. The ecological and economic importance of this species within coastal temperate environments is highlighted by its inclusion within the UK Biodiversity

Action Plan (UKBAP 1999, Gardner & Elliott 2001), which described the biological resources of the UK and provided detailed plans for conservation of these resources. To add, further legislation encompassing the Native Oyster Species Action Plan (NOSAP) (Hawkins et al. 2005) has been agreed. The NOSAP assesses the conservation status of species and their habitats, and outlines conservation priorities.

With the global decline of oyster reefs and populations, oyster restoration efforts are growing in momentum. Numerous restoration feasibility studies (Key & Davidson 1981; Kennedy & Roberts 1999; Laing *et al.* 2005; Shelmerdine & Leslie 2009; Woolmer *et al.* 2011; Vause 2010 in Gravestock *et al.* 2014) and restoration projects (Burton pers. comm.; Debney pers. comm.; Sanderson, pers. comm.; Roberts *et al.* 2005; Eagling 2012: cited in Gravestock *et al.* 2014; Harding *et al.* 2016) have been, and are currently being, conducted within the UK. Laing et al. (2005, p 65–81) outlines many of the known previous attempts globally with zu Ermgassen et al. (2016) outlining the management strategies for future efforts.

This study, provides baseline data on the distribution, abundance and demographic structure in the eastern Solent encompassing Portsmouth, Langstone and Chichester harbour populations of *Ostrea edulis*. The health and resilience of each population is assessed using condition index and screening for infection rates of *Bonamia ostreae*. The increase in abundance of *Crepidula fornicata* within the harbour populations is determined by comparing current and historical datasets and related to direct ecological changes caused by this species.

MATERIALS AND METHODS

The demographic population data from 2015 - 2017is derived from oysters captured by commissioned dredge fishing at the beginning of the open fishing season of the stated year's fishery, with no selection for minimum landing size. All oysters were collected using ladder dredges in accordance with the local byelaw conditions for Portsmouth and Langstone harbours (Southern Inshore Fisheries and Conservation Authority 2018) and Chichester Harbour (Sussex Inshore Fisheries and Conservation Authority 2018). Oysters were obtained from commercial fishery areas near the entrance of Portsmouth Harbour (Hamilton Bank and Spit Bank, H+S, Fig. 3A) within Chichester Harbour (Emsworth and Thorney Channels, E & T, Fig. 3A) during November 2015. Oysters from Langstone Harbour fishery (Sinah Lake and Langstone Channel, S & L, Fig. 3A) were obtained during November 2016. Oysters from Langstone (Sinah Lake and Langstone Channel, S & L, Fig. 3A) and Chichester (Emsworth Channel, E, Fig. 3A) harbours were obtained during 2017. Unfortunately the fishers mixed the 2 harbour populations sampled from Langstone & Chichester during 2017 on landing. Live oysters were cleaned to remove epibionts and blotted dry before measuring. Measurements (Fig. 4A) for the maximum shell length, maximum shell width, maximum shell depth and wet weight (g) were recorded for a minimum of 700 oysters from each harbour. Maximum shell depth was not recorded for the first 500 Chichester and Portsmouth oysters, however, this was recorded for the final 200.

Condition index (CI) and *Bonamia ostreae* prevalence:

Oysters sampled for CI and *B. ostreae* screening were immediately frozen and stored at - 20 °C. Condition index was performed to compare oyster populations from Chichester (n = 24) and Portsmouth (n = 24) according to the methodology conducted by Culloty et al. (2004, p 45) with modifications (105°C for 24 h). The calculation used by Walne & Mann (1975) and Lucas & Beninger (1985) (cited in Culloty et al. (2004) was used to determine condition index:

Condition index = *Dry Tissue Weight* / *Dry Shell Weight* x 100.

A minimum of 24 oysters randomly selected from the fishing landings. For each specimen, 5mm sections of gill tissue removed with sterile blade and genomic DNA extractions were performed on scalpel using DNeasy® Blood & Tissue kits (QIAGEN™ product 69504) following the tissue protocol provided by the manufacturer (Qiagen 2006). Quantification of the DNA extractions was conducted using a NanoDrop® 1000 Spectrophotometer (NanoDrop®, Thermo Fisher Scientific Inc., Wilmington, USA). Species specific primers Oe fw_1 / Oe rev_4 (Grecken & Schmidt 2014) were used to amplify the cytochrome c oxidase subunit I (COI) gene from the oyster DNA, as a positive control. Family and species specific primers (BO / BOAS (Cochennec et al. 2000) and CF / CR (Carnegie et al. 2000) were used to amplify fragments of the nearly complete small sub unit (SSU) of 18S rDNA from all microcell members of the family Haplosporidiidae and *Bonamia ostreae* specifically.

PCR amplifications were all conducted in a final volume of 25 µl, consisting of 12.5 µl 2 x DreamTaq™ PCR Master Mix (Thermo Fisher Scientific Inc.), 0.2 µM forward and reverse primers, 20 - 200 ng genomic DNA, and 6.5 – 10.5 µl molecular H2O. The PCR program ran in a G-STORM 482 - 48 Well Multi Block Thermal Cycler (Gene Technologies Ltd., Essex, England) as follows, for Oe fw_1 / Oe rev_4 primers, initial denaturation for 5 min at 94°C was followed by 35 cycles of denaturation at 94°C for 60 s, primer annealing at 45°C for 60 s, polymerase extension at 72°C for 60 s, and then by a final extension at 72°C for 10 min. For the BO / BOAS and CF / CR primers, initial denaturation for 5 min at 94°C was followed by 35 cycles of denaturation at 94°C for 60 s, primer annealing at 55°C for 60 s, polymerase extension at 72°C for 60 s, and then by a final extension step at 72°C for 10 min.

PCR products were visualised using 1 % agarose gels (Fisher Scientific, UK) composed of 100 ml 1X Tris-acetate-EDTA (TAE) buffer and 4 µl ethidium bromide (Sigma- Aldrich®). Electrophoresis was conducted at 95 - 100 V for 45 min - 1 h, following this the samples were visualised by ultraviolet (UV) transillumination in a 'VWR® Gel Documentation Smart Version system', products were initially compared against a GeneRuler™ 1kb DNA ladder (Thermo Fisher Scientific Inc.).

145 of the oysters collected from Langstone Harbour, were analysed by the Centre for Environment Fisheries and Aquaculture Science (CEFAS) with all individuals screened using traditional histological methods (OIE 2003), any samples that showed evidence of infection were confirmed using single round PCR. BO/BOAS and *Bonamia* duplex primers were used and any positive products were sequenced.

Ostrea edulis and _Crepidula fornicata_ benthic surveys, 1998 - 2017

The benthic surveys occurred before the opening of the 2017 oyster fishing season for areas actively fished. They were conducted during February in Langstone Harbour, April and October in Portsmouth Harbour and during October and December in Chichester Harbour. The 2017 active fishery area of Chichester Harbour (Emsworth Channel, E, Fig. 3A) was sampled before opening on the 1st November 2017, the other areas of the Harbour were sampled after this period as they were not active fishery areas, due to either oysters being unfit for human consumption with high recordings of *E. coli* or due to being voluntary broodstock protection areas under agreements with the local fishermen (Sussex Inshore Fisheries and Conservation Authority 2018).

Within each harbour 30 - 31 locations were chosen (Fig. 3B), three replicate samples were collected using a 0.1 m^2 Van-Veen grab. All material collected for each sample was passed through a 6 mm square mesh box sieve on board, to remove excess sediment, and was placed into individual plastic bags. Samples were then returned to the lab where they were rinsed and passed through a 6 mm square mesh box sieve for a second time to remove any remaining sediment and to easily observe live organisms. Total *Ostrea edulis* and *Crepidula fornicate* densities were recorded for each sample location. Geographical position was assessed with a precision of 2 m using a Lowrance ® Elite 7m GPS system. Distribution and abundance was successfully surveyed at 29 of the 31 proposed sites within Chichester Harbour (Farrell 1998), and the same sites were re-visited in the 2017 survey.

Data analysis

All statistical analysis was performed in IBM® SPSS® Statistics 22 (IBM Analytics).The data for all morphometric parameters (depth, weight, length, weight) were analysed using one-way ANOVA against year and site groups. Condition Index data were tested for homogeneity of variance using Levene's test and were found to be 'normal' ($F_{1,46} = 0.9$, $p > 0.05$) and analysed using a one-way ANOVA against location. 2017 benthic survey data for both oyster and limpet densities between all three harbours were tested for normality and square root transformed and analysed for each species using one-way ANOVA against abundance and harbour location, with Tukey's HSD pairwise post-hoc comparison tests. The comparison between oyster and limpet densities in all three harbours was analysed using paired student T-tests against total abundance for 2017 and 1998 benthic surveys. For comparisons between 1998 - 2017 benthic surveys, data for both oyster and limpet densities were tested for normality, and square root transformed and analysed for each species using one-way ANOVA against abundance and year, with Tukey's HSD pairwise post-hoc comparison tests. FAO-ICALARM stock assessment tools II (FiSat II) modal progression analysis of oyster length frequency distributions was used to identity distinct cohorts within each population. Minimum size class was specified at 15mm with 5mm size class intervals. Bhattacharya's method was used ~~for~~ to determine initial decompose composite length-frequency distributions and refined using NORMSEP.

The univariate and non-parametric multivariate techniques using ordination from Principle Coordinate Analysis (PCO) with data constrained in Bray Curtis similarity matrices were examined using PRIMER 6.1 (PrimerE Ltd: Plymouth Routines in Multivariate Ecological Research) to explore similarities with the relationship between the condition index, maximum shell length and infection occurrence. PCO analyses were used for visualizing the results as an ordination, constrained to linear combinations of the variables. Similarities of the condition index, maximum shell length and infection occurrences between localities were examined using PERMANOVA main tests and *post-hoc* pairwise tests.

RESULTS

Population demographics

The interquartile range, median and range of the populations are shown in Figs. 4B-4E with statistically significant populations distinguished by lettering. There were statistically significant differences between group means across site/years (Portsmouth 2015 vs Chichester 2015 vs Langstone 2016 vs Chichester & Langstone 2017) for all morphometric parameters;

length ($F_{3,2853}$ = 259, $p \leq 0.001$), width ($F_{3,2853}$ = 89.8, $p \leq 0.001$) depth ($F_{3,1853}$ = 305.9, $p \leq 0.001$) and weight ($F_{3,2853}$ = 329.4, $p \leq 0.001$). Tukey's HSD pairwise post-hoc tests were performed and significant differences are shown on Figs 4B-4E (a = ≤0.05). There was a significant difference in the mean maximum length, width, depth and weight between the oyster populations in Portsmouth and Chichester harbours in 2015. There is no significant difference in mean width or depth between the Chichester 2015 and Langstone 2016 populations. Mean length and width has decreased across sites and years since 2015; the Chichester and Langstone 2017 population has significantly smaller oysters than all previous year/site groups.

The Portsmouth 2015 population had a mean length 84.27 ± 0.44 mm, mean width 79 ± 0.48 mm, mean depth 33.1 ± 0.41 mm and mean weight 139 ±2.34 g (mean ± SE). The Chichester harbour 2015 population had a mean length 73.85 ± 0.45 mm, mean width 73.84 ± 0.39 mm, mean depth 20.29 ± 0.33 mm and mean weight 79.42 ± 1.54g (mean ± SE). The Langstone harbour 2016 population had a mean length 70.02 ± 0.36 mm, mean width 71.02 ± 0.34 mm, mean depth 23.03 ± 1.53 mm and mean weight 85.72 ± 1.52 g (mean ± SE). The combined Chichester and Langstone harbours 2017 population had a mean length 69.96 ± 0.38 mm, mean width 70.88 ± 0.36 mm, mean depth 23.13 ± 0.24 mm and mean weight 87.22 ± 2.46 g (mean ± SE).

The most frequent length size class recorded from the Portsmouth 2015 population was 81-90 mm (36%) in contrast to 61-70mm (33.86%) in the Chichester population. The latter was also the most frequent size class in the Langstone 2016 (40.57%) and Chichester & Langstone 2017 samples (40.69%) suggesting connectivity between the oyster populations in Langstone and Chichester harbours. The most frequent maximum shell width size class was 71-80 mm in Portsmouth 2015 (30.43%) Chichester 2015 (30.43%) and Langstone 2016 (37%) populations and 61-70 mm in the Langstone & Chichester 2017 (43.85%) combined population. The demographic structure is narrower within the 2016 and 2017 populations' sampled (Fig. 5). The NORMSEP modal progression analysis confirmed the narrowing demographic structure and lack of recruitment cohorts (Table 1). There is an almost complete lack of recruitment across all harbours and years; Portsmouth's smallest cohort (n = 652) modal mean + SD was 84.57 ± 9.67 mm. The 2017 Langstone & Chichester combined population structure is dominated almost entirely by a single cohort (n = 743) with a modal mean + SD of 71.20 ± 8.78 mm.

Condition index & Prevalence of *Bonamia ostreae:*

There was no significant difference between the condition index of the Chichester population 3.3 ± 0.5 g dry wt (mean ± SE) and the Portsmouth population 3.97 ± 0.5 g dry wt (mean ± SE) ($F_{1,46} = 0.9$, $p \geq 0.05$). The PCR provided 91 positive amplifications of the Oe fw_1 / Oe rev_4 positive control, those that did not provide positive amplifications were discarded from the results. Those that provided positive amplifications showed that 46.8 % of the Chichester oysters and 80.0 % of the Portsmouth oysters, were not infected with microcell Haplosporidians or *Bonamia ostreae*. Of the 53.2 % Chichester oysters that were infected, 32.0 % were positive for a microcell Haplosporidian other than *B. ostreae* and 21.3 % were positive for *B. ostreae*. In comparison to this, the 20.0 % of the Portsmouth oysters that were infected showed only positive amplifications for microcell Haplosporidians, with 0.0 % positive for *B. ostreae*.

Incidences of bonamiosis within the Chichester population occurred across a range of different sized oysters, however the majority (n = 6 / 9) occurred in oysters < 82 mm in length, all with a dry tissue weight of < 2 g. Incidences of infection with microcell Haplosporidians, other than *B. ostreae*, within the Chichester population occurred in oysters < 87 mm in length, all with a dry tissue weight of < 4 g. In comparison, the incidences of infection with microcell Haplosporidians, other than *B. ostreae*, within the Portsmouth population occurred in oysters between 70 - 100 mm in length, with a dry tissue weights of 2 - 11 g. No relationship was observed between condition index, maximum shell length and infection with *B. ostreae* ($F_{2,21}$ = 0.6, $p \geq 0.05$).

4.1 % of the sample population from Langstone Harbour showed positive products and were sequenced, showing 100 % homology to *B. ostreae* (KY296102.1) with those infected showing light to moderate levels.

2017 densities of *Ostrea edulis* and *Crepidula fornicata*

During the survey, no oysters were found in Portsmouth Harbour, two were sampled in Langstone Harbour and one in Chichester Harbour giving a mean harbour value of 0.2 ±0.2 oysters / m^2 (mean ±SE). and 0.1 ±0.1 oysters / m^2 (mean ±SE) (Fig. 6A) respectively. No significant difference was found between the harbours ($F_{2, 273}$ = 1, $p \geq 0.05$).

In contrast, *C. fornicata* was abundant in many areas, the highest density samples were 900.0 ±375.0, 926.7 ±487.0, 4043.3 ±2374.2 limpets / m^2 (mean ±SE) within Portsmouth, Langstone and Chichester harbours, respectively. The mean harbour densities were 84.1 ±24.5, 174.3 ±34.5 and 306.0 ±106.0 limpets / m^2 (mean ±SE) for Portsmouth, Langstone and Chichester, respectively (Fig. 6B). Both Langstone and Chichester harbours contained significantly more individuals than Portsmouth Harbour, despite Chichester containing more limpets / m^2 than Langstone there was no significant difference between these harbours ($F_{2, 273}$ = 4.1, $p \geq 0.05$). Significantly more *C. fornicata*, 189.0 ±39.0 limpets / m^2 (mean ±SE), were found across all three harbours compared with *Ostrea edulis*, 0.1 ±0.1 oysters / m^2 (mean ±SE) (t-value = 4.9, $p \leq 0.001$).

1998 densities of *Ostrea edulis* and *Crepidula fornicata* in Chichester Harbour

O. edulis was present in many areas of Chichester Harbour surveyed in 1998, with 14 out of 29 sites providing positive hauls. Mean densities per sample site ranged from 0 to 88 oysters / m^2 and the mean harbour density was 8.0 ±2.7 oysters / m^2 (mean ±SE) (Fig. 7A). *C. fornicata* was also present in many areas of the harbour, 19 of the 29 sites. Mean densities per sample site ranged from 0 to 1224 limpets / m^2 and the mean harbour density was 181.2 ±40.7 limpets / m^2 (mean ±SE) (Fig. 7C). There were significantly more *C. fornicata* than *O. edulis* (t-value = 4.9, p ≤ 0.001).

Long term data comparison of *O. edulis* and *C. fornicata* densities, before and after the complete collapse of the fishery in Chichester Harbour

A significant decrease in *O. edulis* from 8.0 ±2.7 to 0.1 ±0.1 oysters / m^2 (mean ±SE) was observed between 1998 and 2017 ($F_{1,172} = 19.3$, $p < 0.001$) (Fig. 7B). In comparison, an increase from 181.2 ±40.7 to 306.0 ±106.0 limpets / m^2 was observed for *C. fornicata* between 1998 and 2017, however this was not significant due to the large variation between sample sites ($F_{1,75} = 0.7$, $p > 0.05$) (Fig. 7D).

DISCUSSION

A comprehensive stock assessment was essential to determine the current baseline status of the three fishery areas of Portsmouth, Langstone and Chichester Harbours. The data collected provides essential information that can be used to determine the future success of restoration activities proposed in the Solent (Harding et al. 2016). The significant decrease in the abundance of the ecosystem engineer, *Ostrea edulis*, within Chichester Harbour observed over a 19 year period, the exceptionally low densities 2017 of *O. edulis* in Langstone harbour and absence of *O. edulis* in Portsmouth Harbour demonstrates the seabed population of *O.edulis* is not recovering, recruiting or present in reproductively relevant densities.

The long-term removal of *O. edulis* standing stock in the Solent from chronic overfishing, combined with pollution, disease and habitat destruction has facilitated the invasive gastropod, *Crepidula fornicata* to occupy a benthic ecological niche which appears now to maintain a stable and persistent competitive exclusion of *O. edulis*. The absence of this ecologically and economically important native benthic species will likely have a profound negative impact on biodiversity (Tolley & Volety 2005, Smyth & Roberts 2010), trophic pathways (Peterson et al. 2003) and water quality (Jackson et al. 2001) within the three harbours. The phase shift described in this study from a presumed historic three-dimensional hard substratum biogenic oyster dominated ecosystem (Korringa 1946) to a *C. fornicata* dominated silty mud benthos (Barnes et al. 1973, Erhold et al. 1998, Thouzeau et al. 2003, Streftaris & Zenetos 2006) has likely resulted in the severe loss of ecosystem function with detrimental implications for benthic community structure in these sheltered inshore habitats (Lenihan 1999). Furthermore, in contrast to the carbon sequestration provide by oyster growth, *C. fornicata* is source of carbon and influences the partial pressure of CO_2 in the water column, favouring efflux to the atmosphere (Martin et al. 2006, 2007).

First sighted in oyster ponds in Bosham, 'Portsmouth Bay' during 1913, and later in the wider Solent in 1930, *Crepidula fornicata* spread west during the 1940s (Blanchard, 1997). By the 1970s the Solent was almost characterised *C. fornicata* dominated associated macrofauna. However *O. edulis* still occurred with a 19% frequency on average, greater in the West (45%)

than the East Solent (9%), (Barnes et al 1973). This persistent and increasing dominance of *C. fornicata* since the 1970s is of serious concern for the natural recovery of *O. edulis,* particularly the extremely high densities of over 4000 m^2 within Chichester harbour which demonstrates the ecological carrying capacity of inshore waters for this invasive species. The diet of *C. fornicata* has been shown to be non-selective for particle size and to overlap with that of the oyster species, *Magallana gigas* and *O. edulis* (Beninger et al. 2007, Decottignies et al. 2007, Nielsen et al. 2017) with an efficient particle retention (Jørgensen et al. 1984) superior to that of *M. gigas* (Barillé et al. 2006). The high densities of mature *C. fornicata* in the Solent are likely to exert extreme competition stress on *O. edulis* for both habitat and food resource ~~partitioning~~.

The presence of *C. fornicata* not only negatively impacts the broodstock oyster population but *O. edulis* larvae could also be subject to substantial predation (Korringa 1951 in Pechenik et al. 2004) and competition. Oyster larvae attempting to settle will suffer competition for food and space from high *Crepidula* densities (Fitzgerald, 2007) which form a cohesive shelly mud where they become dominant in contrast to hard substrate preferred by oyster larvae (Smyth et al 2018). The reduced availability of suitable settlement substrate for *O. edulis* larvae due to both the levels of mucus pseudofaeces (Blanchard 1997) generated by such high densities of *C. fornicata* and the lack of conspecific shell substrate is a serious concern. This reduction in preferential substrata will be further compounded by competition for food arising during the overlapping breeding periods of both species, with *C. fornicata* spawning two to four times between February and September (Richard et al. 2006) and *O. edulis* typically spawning once between May and August (Hayward *et al.* 1996). The reproduction reproduct~~ive~~ ~~stage~~ of the *O. edulis* lifecycle is also relatively complex in relation to other oyster species and that of *C. fornicata* which is sexually mature within 2 months (Richard et al. 2006). In comparison, *O. edulis* is not usually mature until individuals reach 3 years old (Roberts *et al.* 2010).

The remaining natural populations of mature oysters, within the Solent, have decreased significantly in size and abundance over a short time frame. This smaller, less mature and narrowed demographic population will negatively impact spawning potential. For example, a decrease in mean size from 80 mm to 70 mm, similar to the decline observed from 2015 - 2017, would result in a reduced output of 260,000 larvae per reproductive female (Walne 1974). When applied to a fishery with skewed sex ratio (6:1 male:female sex ratio (Kamphausen et al. 2011)), reproductive and recruitment success will be severely impacted. This is of great concern as at a conservative estimate, 85% of the Langstone & Chichester 2017 population will be above the minimum landing size for the 2018/19 fishing season and therefore at high risk of being extracted to the point of functional extinction (Beck et al. 2011). To put this in context, in 1973 only 22% of *O.edulis* population in Stanswood Bay were of marketable size >70mm (Barnes et al, 1973), and it was this population that feed the boom of the Solent fishery in the late 1970s and 1980s.

This risk of extirpation at current fishing levels seems particularly high as there is no sign of recruitment cohorts. The last successful recruitment, estimated from size (Richardson et al. 1993), was approximately 5-6 years ago in 2012 for the Langstone & Chichester Populations. The Portsmouth 2015 smallest cohort with a mean maximum length of 84 mm suggests this is the aged remnant population from a successful spatfall 8-10 years ago, approximately 2008. The morphometric data reveals a disjunct population structure over microgeographic scales within the Solent, particularly between the Portsmouth and Chichester harbours in 2015. This could be attributed to the re-stocking that took place as part of a small scale restoration project in

Chichester during November 2010 (Vause 2010, Eagling 2012 cited in Gravestock et al. 2014, MEDIN 2016), which aligns with the estimate from the demographic cohorts. This disparity suggests there is a barrier to larval exchange between the two harbours despite their connectivity, although this could be a density dependent phenomenon. However, of huge concern is that the demographic data showed lack of recruitment to the seabed in all three harbours despite a previous two year of fishery closure and reduced fishing season since 2015.

? Less emotive

Disease control is of utmost importance when planning and managing restoration projects. The prevalence of *Bonamia ostreae* within the Chichester population has increased in this study, from previous years (1993 - 2007 average 12.1 % (Laing et al. 2014)). The results obtain in this study are in agreement with the findings of Eagling (2012) citied in Gravestock et al. (2014), who reported prevalence of between 25 - 35 %. This rise in prevalence of *B. ostreae* could be attributable to the increase in mortality of many of the re-laid oysters within the harbour observed by Jensen (pers. comm. with Gravestock et al. 2014) and indicate that this area may possibly be susceptible to mass mortality events in the future.

disease

In contrast to this, the parasite was completely absent within the Portsmouth sample population decreasing from an average of 5.6 % (1993 - 2007 (Laing et al. 2014)). This result is encouraging with the apparent absence of *B. ostreae* from a population previously exposed and subject to the parasite and could be indicative of resistance. Again, in contrast to the increase within Chichester, a lower prevalence was recorded within the Langstone population compared with previous years (9.1 % mean 1993 - 2007 (Laing et al. 2014)). This suggests that although the three harbours are all interconnected the hydrodynamics of the area appear to prevent dispersal of the parasite in a westerly direction either in the water column or via larval transmission (Flannery et al. 2016) and is supported by the distinct demographic structure of the

Portsmouth population. However, given the exceptionally low population numbers this could be a density dependent phenomenon.

On a final note, water quality is also of concern: all three harbours are classified as Nitrate Vulnerable Zones (NVZ) and designated as both Sensitive area (Eutrophic) and Polluted Water (Eutrophic). Portsmouth Harbour is currently hypernutrified in regard to nitrogen levels, Langstone has improved but remains elevated along with Chichester Harbour. (Environment Agency 2016). Alongside the ecosystem services for biodiversity, the biogeochemical cycles that are maintained by oysters and their associated epibionts, are highly efficient at nitrogen cycling and removal (Kellogg et al. 2013). Restoration of the native oyster habitat *O. edulis* to these harbours has the potential to exert natural eutrophication control (Officer et al. 1982, Dame 1996), improve water clarity (Newell 2004) and decrease suspended sediment. In turn this could facilitate seagrass growth (Newell & Koch 2004) with the associated multi-trophic benefits of restoring both seagrasses and oyster beds. The dramatic change in ecosystem, from one stable state to another is known as a regime or phase shift (Scheffer et al. 2001, Barange et al. 2008), such as those often seen on Caribbean coral reefs (Hughes 1994, Mumby 2009) with declines in fish and invertebrate biomass (Cheal et al. 2010). Without significant intervention or disturbance, it appears the *Crepidula fornicata* dominanted benthos in the Solent is excluding the return of the native oyster *O. edulis* and the biogenic habitat and associated biodiversity it provides.

CONCLUSION

The low standing stock of *Ostrea edulis*, a benthos dominated by high densities of *Crepidula fornicata*, the presence of *Bonamia ostreae* and ongoing fishing pressure are significant barriers to self-sustaining native oyster populations within the Solent. Based on the status of *O. edulis* in the commercially fished areas of the Solent presented here, active management of the seabed is recommended to 1) control the extent and spread of *Crepidula fornicata*, 2) provide suitable settlement substrate for *O. edulis* larval recruitment and 3) establish a protected *O. edulis* broodstock population in all commercially fished Solent harbours.

This paper highlights the importance of understanding local population structures and disease prevelance over relatively small geographic scales and reinforces the need for relevant and comprehensive baseline data to underpin *O. edulis* restoration practices. For biosecurity reasons, it is strongly recommended that there is no transfer of oysters from Langstone or Chichester Harbours to the wider Solent to diminish spread of infection.

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Figure 1

Lifecycle of *Ostrea edulis*.

Arrows with glow effect indicate stages that occur internally within the female oyster pallial (mantle) cavity, plain arrows indicate stages that occur externally. Approximate sizes and timings are based upon information from Hu *et al.* (1993), Acarli & Lok (2009), FAO (2016) and, Loosanoff *et al.* (1966), Pascual (1972) and Tanaka (1981), cited within Hu *et al.* (1993). Images of life stages are not to scale.

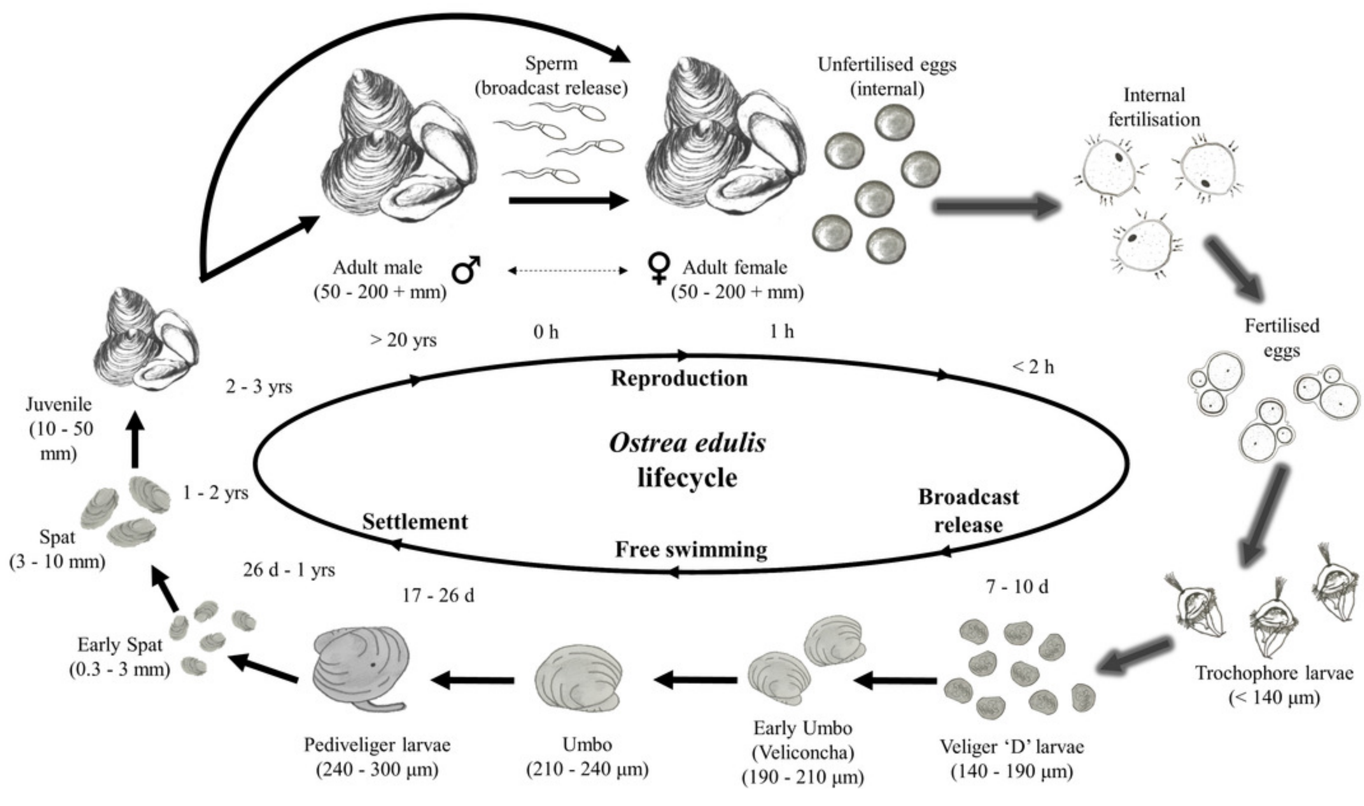


Figure 2

Interactive effects adversely affecting *Ostrea edulis*

The factors that are known to be adversely affecting *Ostrea edulis* populations within the Solent and their interconnecting relationships. Examples of the factors are shown where necessary.

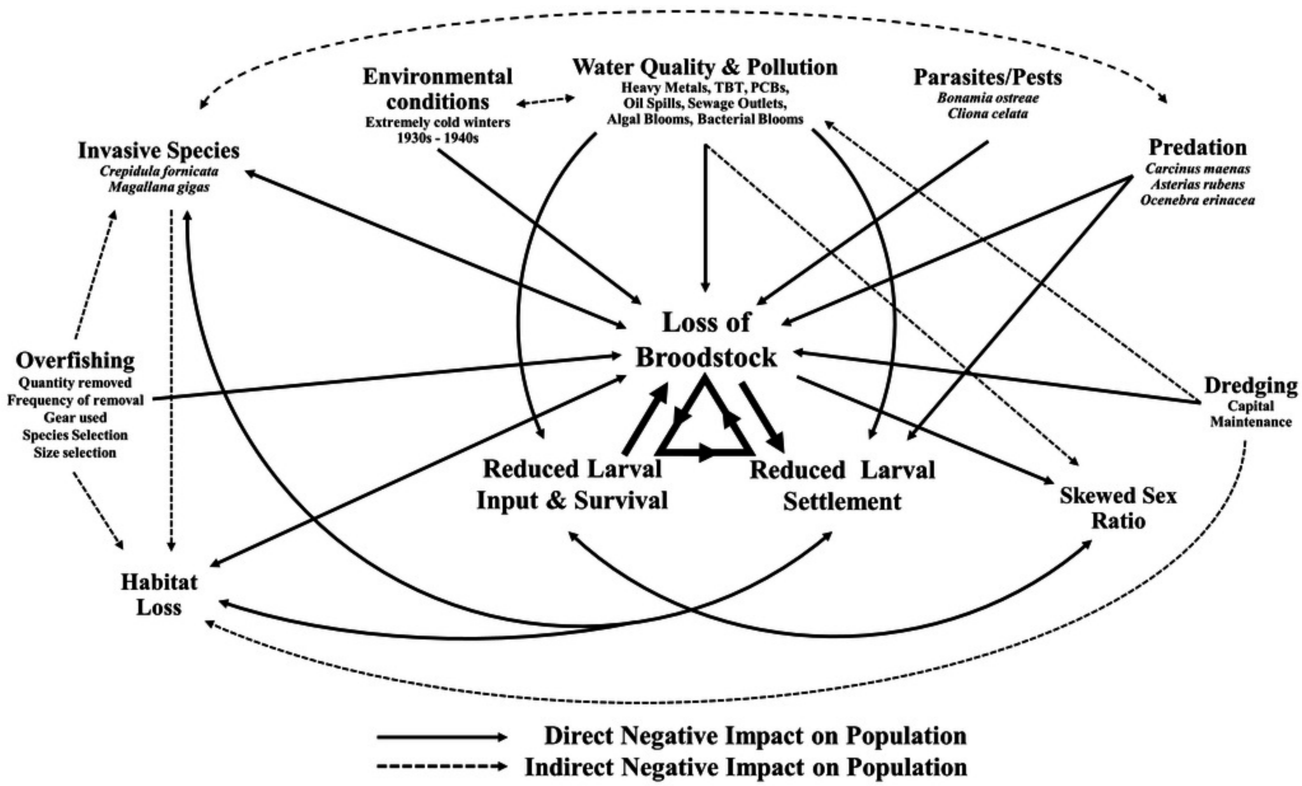


Figure 3

Overview of Solent sampling locations.

Figure 3. The wider Solent, showing the three harbours under investigation with locations of sample collection. (H+S) Hamilton Bank and Spit Bank, (S) Sinah Lake, (L) Langstone Channel, (E) Emsworth Channel, (T) Thorney Channel (A). Benthic sample locations within Portsmouth, Langstone and Chichester harbours for the 2017 survey, three 0.1 m^2 samples were retrieved from each area marked by a ○ with areas selected to cover the maximum amount of each harbour within reason (B). Maps created using ArcMap software.

**Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.*

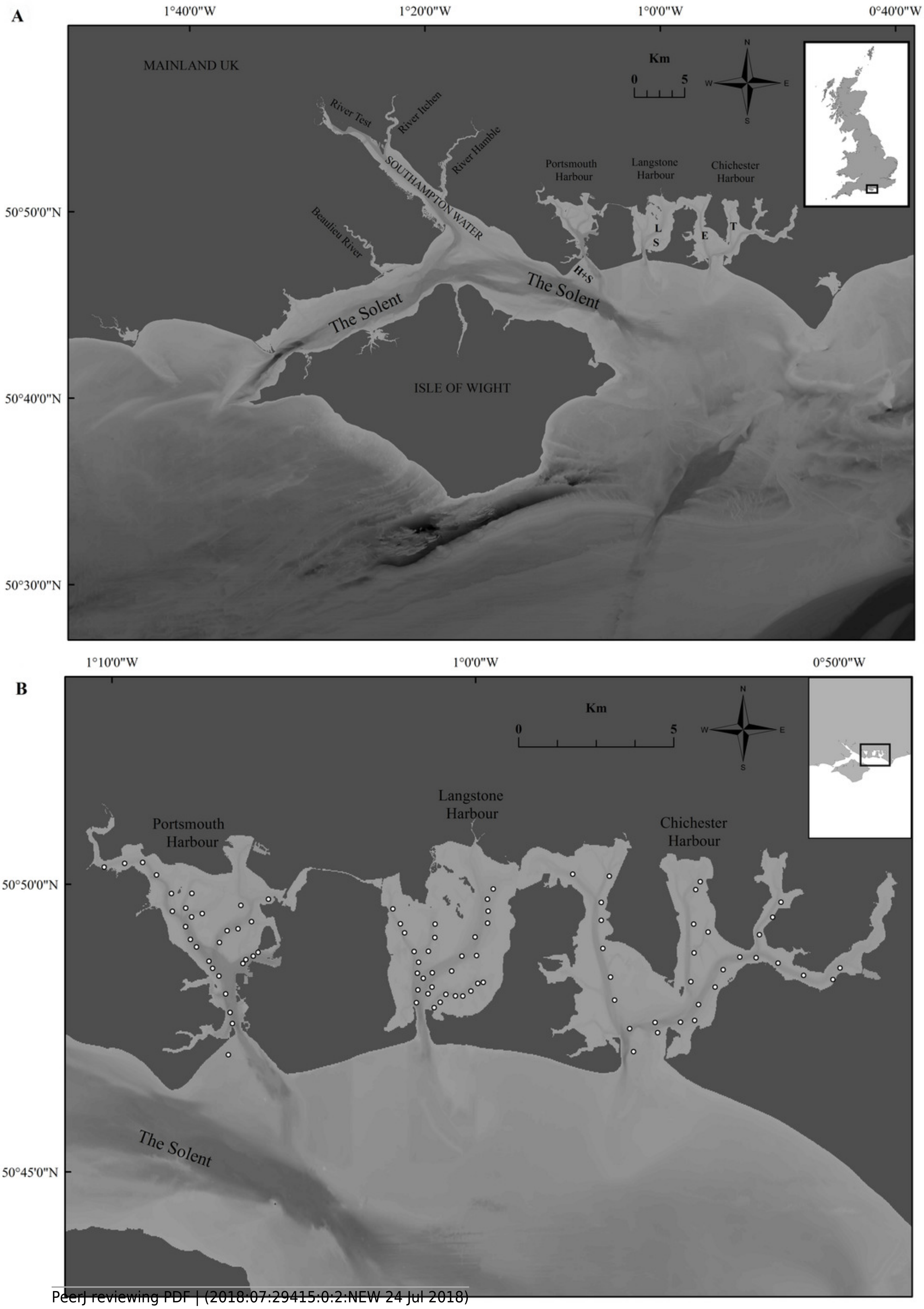

A
1°40'0"W
1°20'0"W
1°0'0"W
0°40'0"W
MAINLAND UK
Km
0
5
N
S
E
W
River Test
River Itchen
River Hamble
SOUTHAMPTON WATER
Beaulieu River
Portsmouth Harbour
Langstone Harbour
Chichester Harbour
L
S
E
T
H+S
The Solent
The Solent
ISLE OF WIGHT
50°50'0"N
50°40'0"N
50°30'0"N
B
1°10'0"W
1°0'0"W
0°50'0"W
Km
0
5
Portsmouth Harbour
Langstone Harbour
Chichester Harbour
The Solent
50°50'0"N
50°45'0"N

Figure 4

Morphometric measurements of Solent oysters

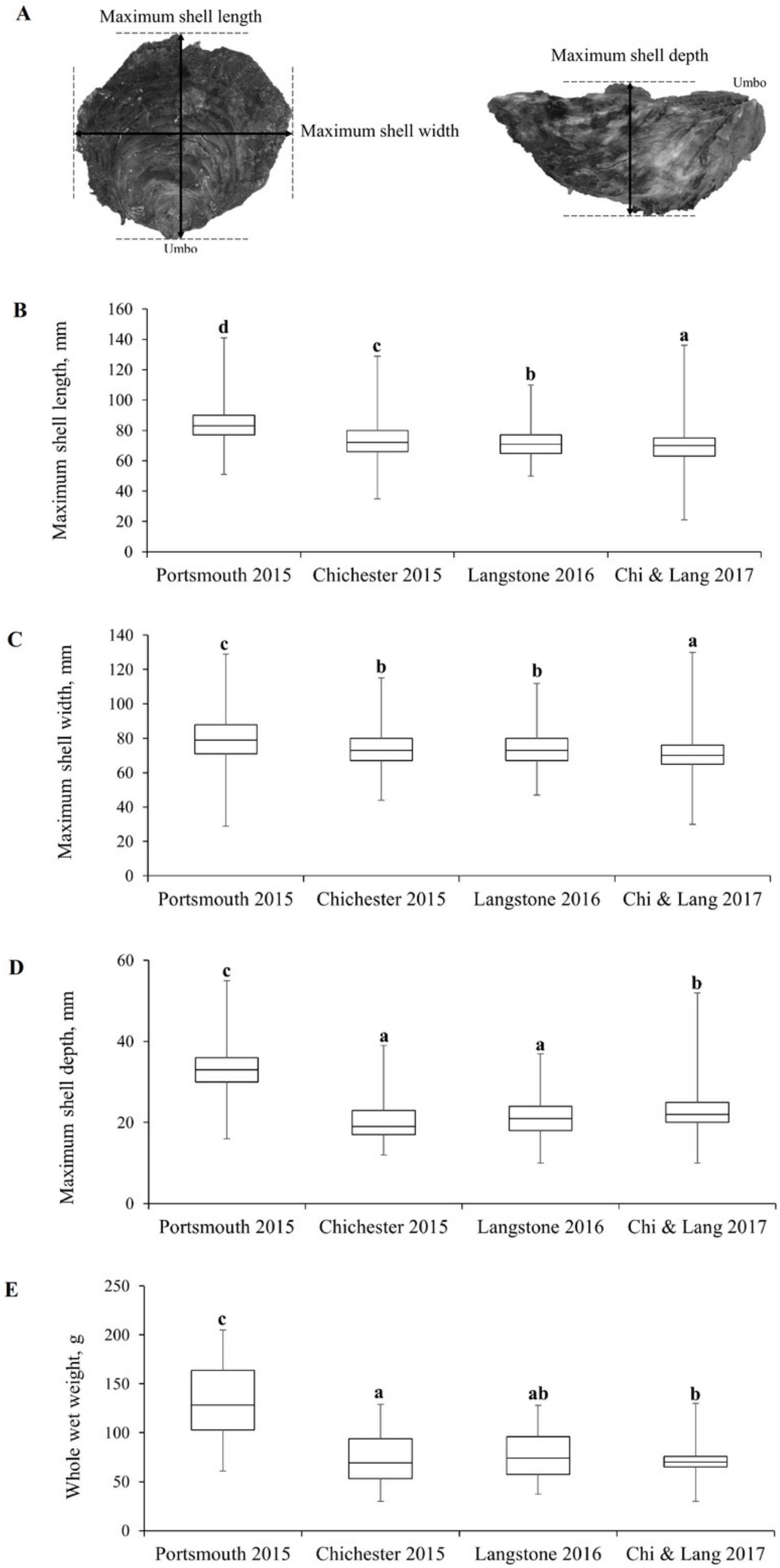

A
Maximum shell length
Maximum shell width
Umbo
Maximum shell depth
Umbo
B
Maximum shell length, mm
d
c
b
a
Portsmouth 2015
Chichester 2015
Langstone 2016
Chi & Lang 2017
C
Maximum shell width, mm
c
b
b
a
Portsmouth 2015
Chichester 2015
Langstone 2016
Chi & Lang 2017
D
Maximum shell depth, mm
c
a
a
b
Portsmouth 2015
Chichester 2015
Langstone 2016
Chi & Lang 2017
E
Whole wet weight, g
c
a
ab
b
Portsmouth 2015
Chichester 2015
Langstone 2016
Chi & Lang 2017

Table 1(on next page)

Native oyster population demographics.

Maximum mean length percentage frequency (with 5mm intervals) of *Ostrea edulis* populations (n = 700 minimum) from East Solent harbours.

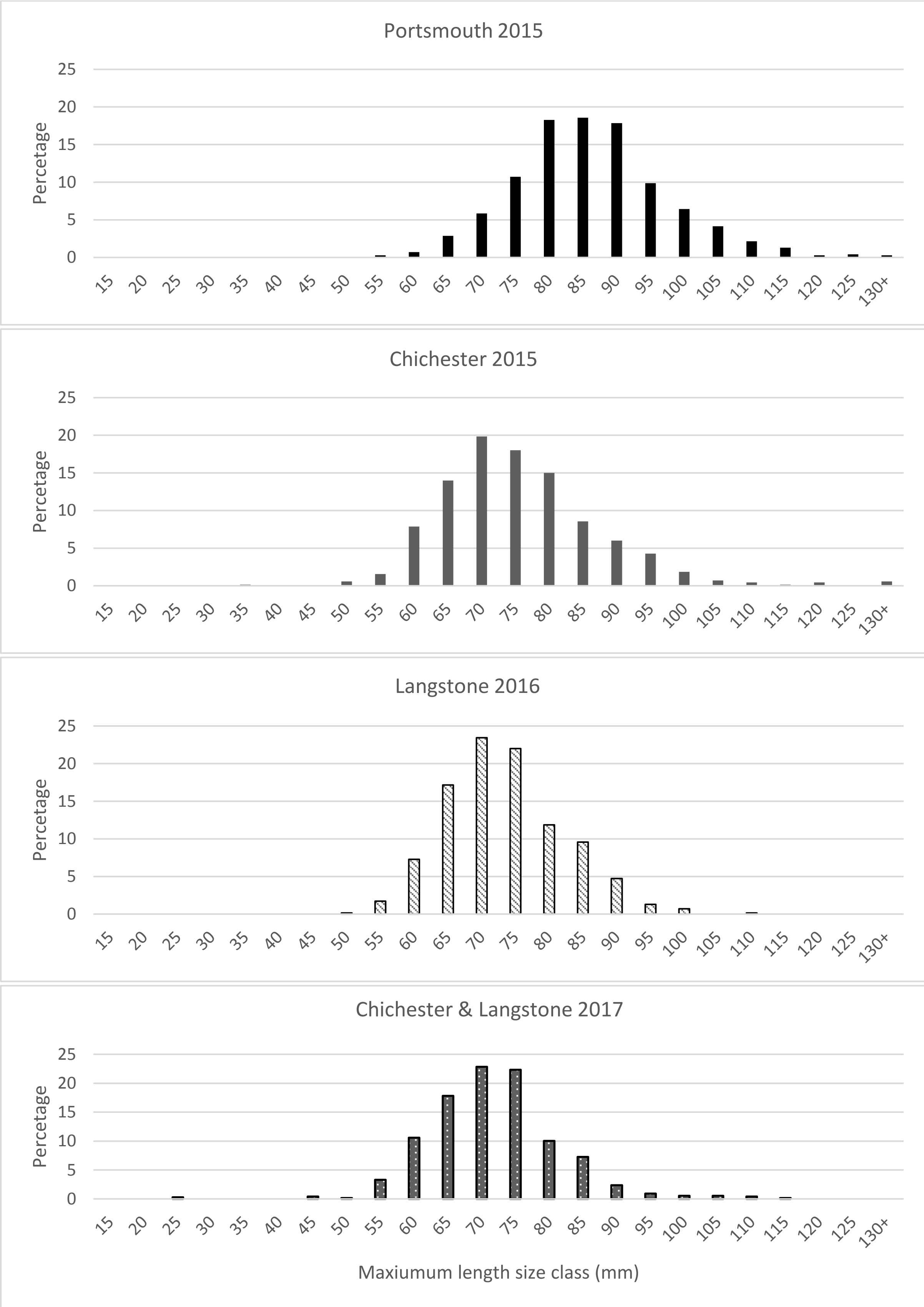


Figure 5: Maximum mean length demographic structure of *O. edulis* from East Solent harbours (with 5mm intervals).

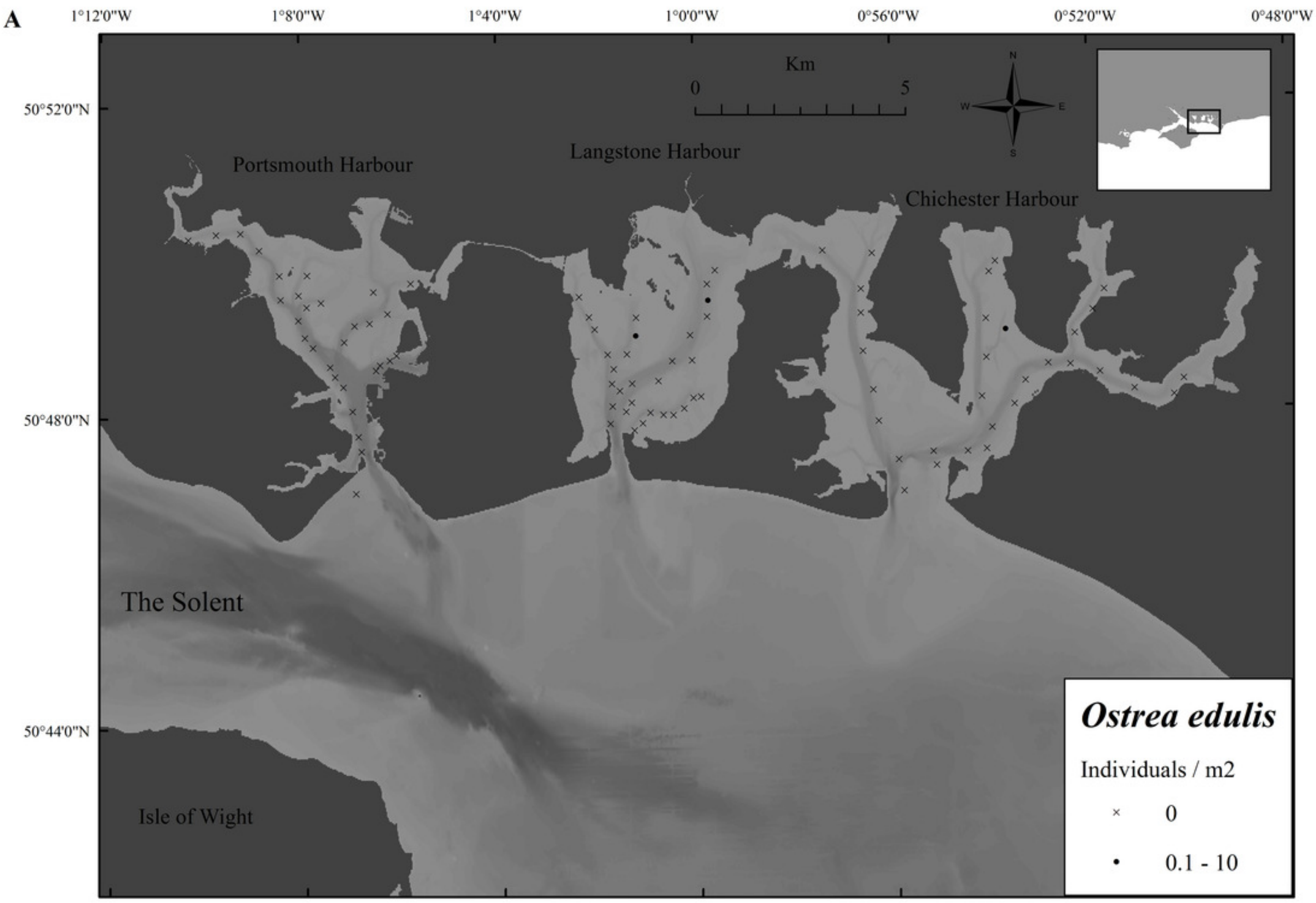
Figure 5

Native oyster and slipper limpet distributions within the Solent harbours during 2017

Mean densities of *Ostrea edulis* at the sampling locations in Portsmouth, Langstone and Chichester harbours, 2017 (A). Mean densities of *Crepidula fornicata* at the sampling locations in Portsmouth, Langstone and Chichester harbours, 2017 (B). Maps created using ArcMap software.

**Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.*

A


1°12'0"W
1°8'0"W
1°4'0"W
1°0'0"W
0°56'0"W
0°52'0"W
0°48'0"W
50°52'0"N
50°48'0"N
50°44'0"N
Km
0
5
Portsmouth Harbour
Langstone Harbour
Chichester Harbour
The Solent
Isle of Wight
Ostrea edulis
Individuals / m2
0
0.1 - 10

B

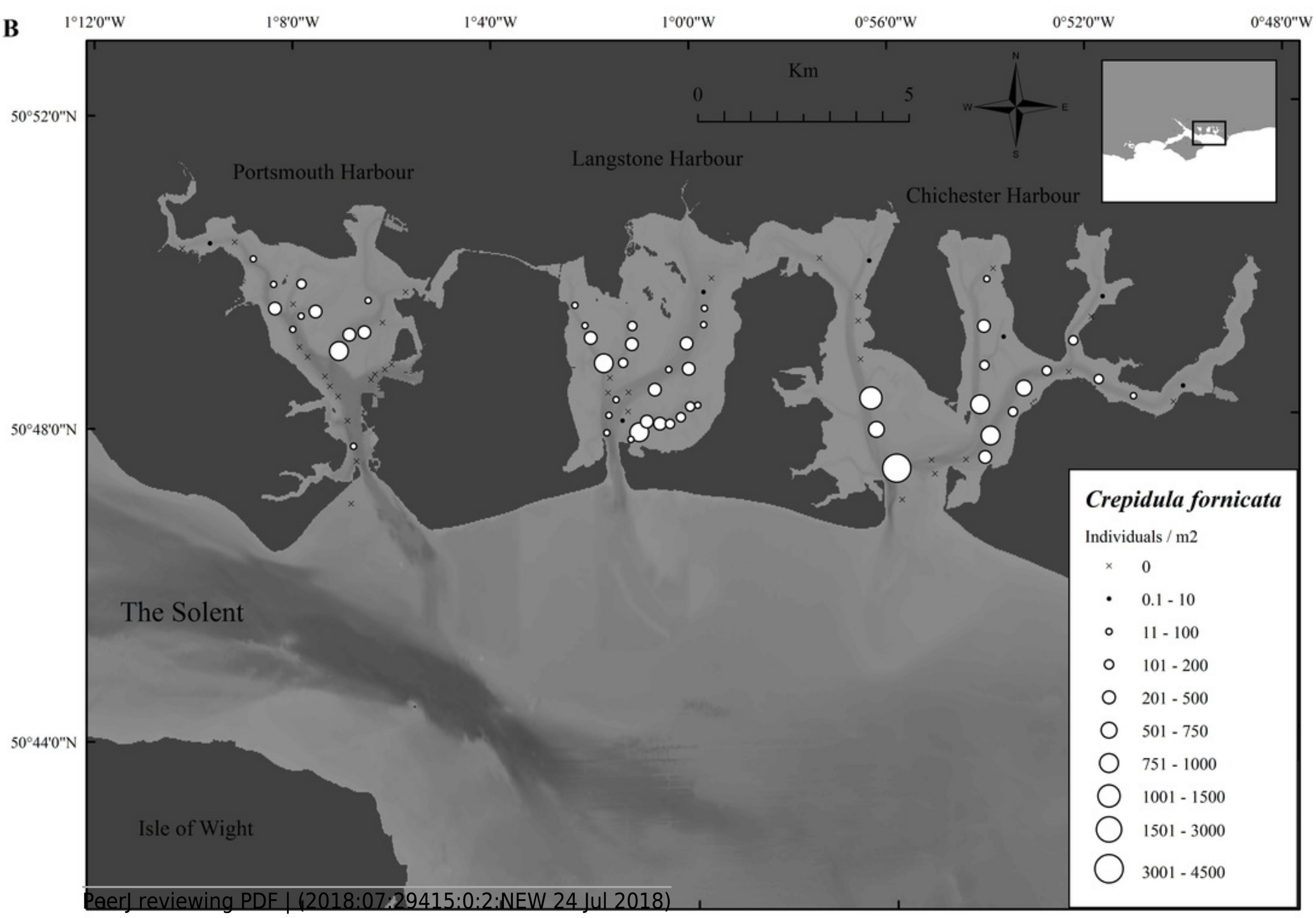

1°12'0"W
1°8'0"W
1°4'0"W
1°0'0"W
0°56'0"W
0°52'0"W
0°48'0"W
50°52'0"N
50°48'0"N
50°44'0"N
Km
0
5
Portsmouth Harbour
Langstone Harbour
Chichester Harbour
The Solent
Isle of Wight
Crepidula fornicata
Individuals / m2
0
0.1 - 10
11 - 100
101 - 200
201 - 500
501 - 750
751 - 1000
1001 - 1500
1501 - 3000
3001 - 4500

Figure 6

Temporal change in native oyster and slipper limpet distributions over 19 years.

Densities of *Ostrea edulis* in Chichester harbour, 1998 (A). Change in *Ostrea edulis* densities in Chichester Harbour from 1998 to 2017 (B). Densities of *Crepidula fornicata* in Chichester harbour, 1998 (C). Change in *Crepidula fornicata* densities in Chichester Harbour from 1998 to 2017 (D). Maps created using ArcMap software.

**Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.*

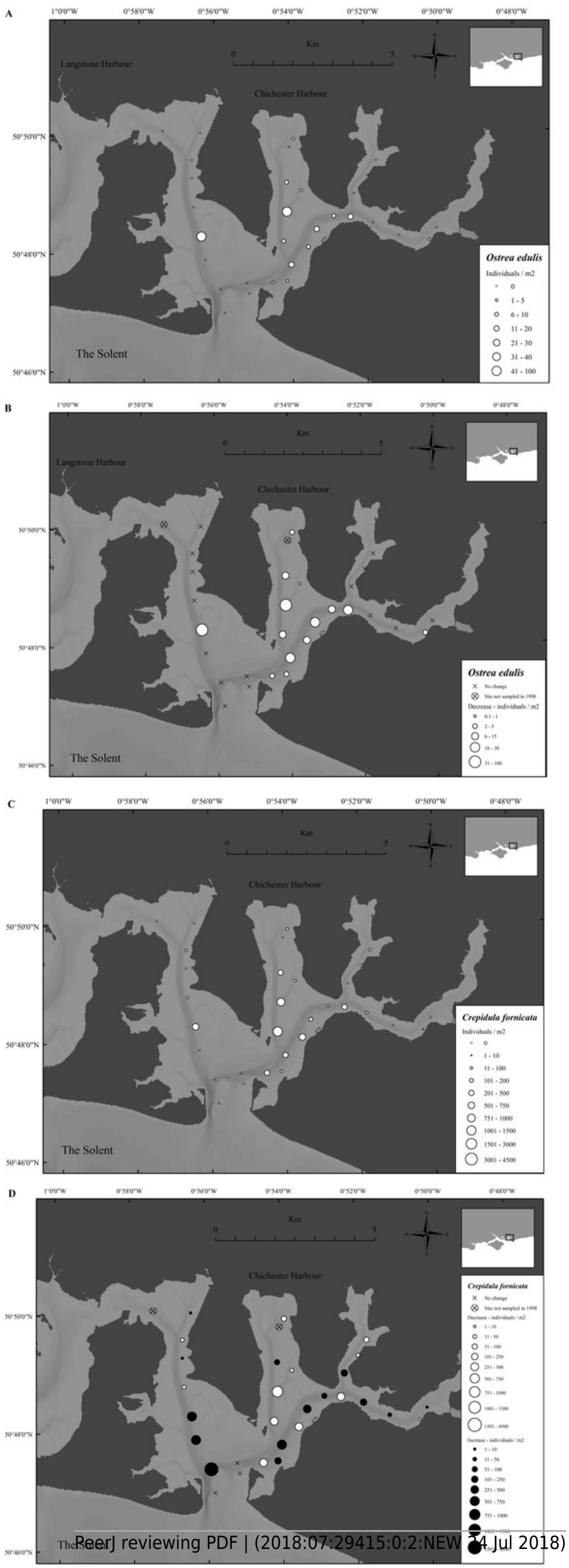

A
1°0'0"W
0°58'0"W
0°56'0"W
0°54'0"W
0°52'0"W
0°50'0"W
0°48'0"W
50°50'0"N
50°48'0"N
50°46'0"N
Km
0
5
Langstone Harbour
Chichester Harbour
The Solent
Ostrea edulis
Individuals / m2
0
1 - 5
6 - 10
11 - 20
21 - 30
31 - 40
41 - 100
B
Ostrea edulis
C
Crepidula fornicata
Individuals / m2
0
1 - 10
11 - 100
101 - 200
201 - 500
501 - 750
751 - 1000
1001 - 1500
1501 - 3000
3001 - 4500
D
Crepidula fornicata

Table 2(on next page)

Computed modal mean ± SD length (mm) cohort estimates from length frequency analysis of all samples. N = population.

Table X: Modal mean ± SD length (mm) estimates form length frequency analysis of all samples. N = population

	Port 2015		Chichester 2015		Langstone 2016		Langstone & Chichester 2017	
Cohort/age class	Mean ± SD	N	Mean ± SD	N	Mean ± SD	N	Mean ± SD	N
1	84.57 ± 9.67	652	71.73 ± 8.18	559	69.12 ± 6.18	400	71.20 ± 8.78	743
2	107.62 ± 6.26	43	89.35 ± 8.66	133	79.08± 8.76	300	103.33 ± 6.53	14
3	126.97 ± 2.65	5	124.19± 6.28	8				