Population dynamics of a commercially harvested, non-native bivalve in an area protected for shorebirds: *Ruditapes philippinarum* in Poole Harbour, UK.

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Abstract

The Manila clam *Ruditapes philippinarum* is one of the most commercially valuable bivalve species worldwide and its range is expanding, facilitated by aquaculture and fishing activities. In existing and new systems, the species may become commercially and ecologically important, supporting both local fishing activities and populations of shorebird predators of conservation importance. This study assessed potential fishing effects and population dynamics of *R. philippinarum* in Poole Harbour, a marine protected area on the south coast of the UK, where the species is important for oystercatcher *Haematopus ostralegus* as well as local fishers. Sampling was undertaken across three sites of different fishing intensities before and after the 2015 fishing season, which extends into the key overwintering period for shorebird populations. Significant differences in density, size and condition index are evident between sites, with the heavily dredged site supporting clams of poorer condition. Across the dredge season, clam densities in the heavily fished area were significantly reduced, with a harvesting efficiency of legally harvestable clams of up to 95% in this area. Despite occurring at significantly higher densities and growing faster under heavy fishing pressure, lower biomass and condition index of *R. philippinarum* in this area, coupled with the dramatic reduction in densities across the fishing season, may be of concern to managers who must consider the wider ecological interactions of harvesting with the interest of nature conservation and site integrity.

Introduction

The geographic range of the Manila clam *Ruditapes philippinarum* (Adams and Reeve, 1850) has been expanding since the early 20th century, facilitated by aquaculture and fishing activities due to its high food value (Humphreys et al., 2015; de Montaudouin et al., 2016a). In many European estuaries and lagoons the Manila clam has replaced the native clam *Ruditapes decussatus* (Bidegain and Juanes 2013) and represents a key target species for both recreational and commercial fishers (Bidegain and Juanes, 2013; Robert et al., 2013; Beck et al., 2015; Clarke et al., 2018). The species is now one of the most commercially valuable bivalves globally (Astorga 2014). In addition to its commercial value, the spread of the species outside of its native range has provided shorebird predators such as waders, waterfowl and gulls (Orders Anseriformes and Charadriiformes) with an additional food source, comprising a key overwinter prey item for some local populations (Ishii et al., 2001; Caldow et al., 2007).

Both fishing and shorebird predation represent non-random selective mortality in target species. In addition to eliciting wider impacts on marine ecosystems (Dayton et al., 1995; Collie et al., 2000; Kaiser et al., 2006), intensive fishing can cause phenotypic change and alter the abundance, size distribution and age structure of target populations of both finfish (Law, 2000; Conover et al., 2005; Hutchings, 2005; Walsh et al., 2006) and shellfish (Pombo and Escofet, 1996; Mannino and Thomas, 2001; Kido and Murray, 2003; Braje et al., 2007). Harvesting can preferentially remove the largest and most profitable avian food resources, particularly shellfish, with variability in the magnitude of impacts and subsequent recovery trends (Kaiser et al., 2006; Bowgen et al., 2013; Clarke et al., 2017). For molluscivorous shorebirds that consume invertebrate prey within discrete size ranges (Goss-Custard et al., 2006) such as Eurasian oystercatcher *Haematopus ostralegus*, common eider *Somateria mollissima* and red knot *Calidris canutus*, reductions in mean body size within a prey population may be of critical importance in determining survival overwinter and during onward migration to breeding areas (Bowgen et al., 2015). In intertidal areas there is therefore significant potential for the interests of nature conservation and commercial shellfishing to come into conflict (Smit et al., 1998; Atkinson et al., 2003; Verhulst et al., 2004), and in areas that receive designation for their conservation interests under international legislation (e.g. EU Habitats and Birds Directives), appropriate management of shellfish stocks for both economic and ecological interests is critical.

In the UK the Manila clam is approaching the northern edge of its range for naturalised populations (Humphreys et al., 2015). The species was introduced to Poole Harbour on the south coast of the UK for aquaculture purposes in 1988, and the population has since naturalised (Jensen et al., 2004). Manila clams are broadcast spawners, spawning in water temperatures between 18 and 26˚C (Solidoro et al., 2003) with larvae developing in the water column before settling approximately 12-15 days after spawning (Ishida et al., 2005; Ishii et al., 2005). Two separate recruitment events have been reported in Poole Harbour in June and September-October each year (Jensen et al., 2004; Humphreys et al., 2007). While the introduction of the manila clam has displaced the native *Ruditapes decussatus* in many areas throughout Europe (Bidegain and Juanes 2013), historic surveys prior to the introduction of *R. philippinarum* in Poole Harbour indicate that *R. decussatus* occurred at densities too low to be reliably sampled, if present at all (Warwick et al., 1989). Whilst unpublished survey data suggest that densities of other bivalves were higher in the 1970s (Humphreys et al., 2004), the decline of these species is generally considered to be as a result of tributyltin contamination within the harbour during the 1980s, prior to the manila clam's introduction (Langston and Burt, 1991). There is therefore little evidence that the introduction and naturalisation of *R. philippinarum* has displaced native bivalve species within the harbour, rather the species comprises a newly exploitable food item for molluscivorous bird predators (Hulscher, 1996; Caldow et al., 2007). The species now supports a significant local fishery, harvested along with the common cockle *Cerastoderma edule* from intertidal and shallow subtidal areas by a novel 'pump-scoop' dredge (Clarke et al., 2018), and provides an additional food source for the oystercatchers, reducing overwinter mortality within the harbour (Caldow et al., 2007), which is a protected area under the European Birds Directive.

A previous study reported a maximum size of 42mm in Manila clam in the harbour (Humphreys et al., 2007), in contrast to a maximum size of 60mm elsewhere in Europe (Beninger and Lucas, 1984; Mortensen et al., 2000; Colakoglu and Palaz, 2014) and South America (Ponurovskii, 2000). Other sites have however reported similar maximum sizes to those reported in Poole Harbour (Ohba, 1959; Bourne, 1982; Dang et al., 2010). A 75% harvesting efficiency of legal-size clams via pump-scoop dredging was reported (Humphreys et al., 2007) and it was suggested that the relatively lower maximum size of *R. philippinarum* in Poole may have been induced by intensive harvesting, as a 40mm minimum landing size (MLS) was enforced at the time of the study. The MLS has since been further reduced to 35mm (Lambourn & Le Berre, 2007).

The Manila clam continues to spread throughout Europe and along the UK coast (Humphreys et al., 2015; Chiesa et al., 2016), and so too are fisheries that target the species (Beck et al., 2015; Clarke et al., 2018). It is therefore important to understand the impacts of harvesting on the species outside of its natural range, as well as potential implications for shorebird populations that have come to depend on the species for overwinter survival. Given that the increase in densities of *R. philippinarum* since its introduction (Herbert et al., 2010) now appears to support the Poole Harbour oystercatcher population (Caldow et al., 2007), and the potential for fishing-induced changes to the clam population, this study focused on the impacts of commercial dredging on *R. philippinarum* in Poole Harbour. Potential implications for shorebird predators are also discussed. The main objectives of this study were to:

1. Assess how the open dredging season in Poole Harbour affects clam abundance, density and size distribution.

2. Investigate clam population dynamics (maximum size, recruitment, length at age, secondary productivity, condition index) across a gradient of fishing intensity.

3. Discuss the potential implications for sustainability of the fishery and shorebird predators.

Methods

Study Area

Poole Harbour (Lat 50˚42’44’’ N Lon 2˚03’30’’ W), in Dorset, UK (Figure 1), comprises extensive areas of intertidal mudflats, sandflats and saltmarsh. At high tide the harbour has an area of 36,000km^2 and has a tidal range of 1.8m on spring tides and 0.6m on neap tides. The harbour is designated for its conservation importance as a European Marine Site (EMS) (European Birds Directive 79/409/EEC) and Ramsar site to protect its important bird populations. Beginning in September, large numbers (> 25,000) of migratory waterfowl arrive in the harbour to feed and over-winter until March, when birds begin to leave the site for breeding grounds.

Sampling

We used a traditional pump-scoop dredge and a bespoke hand dredge to sample for *R. philippinarum* across three intertidal areas of Poole Harbour where clams are available to feeding shorebirds. Consultation with local fishermen and fishing sightings data obtained from the Southern Inshore Fisheries and Conservation Association (SIFCA) allowed the identification of significant shellfish beds throughout the harbour before sampling.

To investigate changes in densities and size of *R. philippinarum* across the fishing season, clams were sampled on 19th June 2015 and the 15th January 2016; before and after the commercial dredging season that runs from 1st July to 25th December each year. Sampling was carried out in calm conditions in three areas of different fishing effort (Holton Mere: high fishing effort, Wytch Lake: low fishing effort, Holes Bay: no fishing), as determined from routinely collected SIFCA fisheries sightings and consultation with local fishermen (Table 1; Figure 1).

Three dredge hauls were haphazardly undertaken across each site. A trailed pump-scoop dredge (dimensions 460mm x 460mm x 30mm) with a bar width spacing of 18mm was towed along the seabed for two minutes at a speed of 1.8 knots, then lifted aboard the vessel and the contents were emptied onto a sorting deck for counting and measuring. The dredge penetrates the sediment to a depth of a few centimetres (~ 5cm).

Given the relatively large mesh size of 18mm on the pump-scoop dredge, undersized and juvenile clams, including new recruits, are unlikely to be retained using this method. Therefore, on 10th February 2016, after the closure of the fishery, each area was revisited and samples were obtained using a bespoke hand-held naturalist's dredge in order to allow an estimate of juvenile settlement in each area. An aluminium frame with a 45˚ handle was used to drag the dredge, which is 30cm wide with a 1mm mesh, through the top layer of the sediment at a similar depth to the pump-scoop dredge, for 1m, covering an area of 0.3m^2. Six hand-held dredges were taken, located haphazardly across each site. Samples were sieved through a 2mm mesh sieve while on board the vessel before being preserved for further analysis in the laboratory.

To assess differences in population dynamics as an indication of potential longer-term changes due to fishing pressure, around 100 individuals of *R. philippinarum* were retained from both pump-scoop dredges and hand dredges taken from each area after the closure of the fishery in 2016 for ash-free dry mass (AFDM) and condition index calculations. It was ensured that these clams were representative of all size classes within the samples. Clams were stored at -80˚C before analysis was undertaken.

Analysis

Density and Size Frequency

Clams sampled using the pump-scoop dredge were counted and length measurements taken to the nearest mm while on board the vessel. Individual clams from hand dredge samples were counted in the laboratory and lengths taken to the nearest 0.01mm. Length measurements were taken by measuring each clam across the longest distance from the anterior end to the posterior end of the shell. Clam densities (individuals per square metre) were calculated by calculating the area covered by the vessel (1.8 kn = 0.5 m/s x 120 seconds = 111.12m) and the area of the dredge (0.21m^2). The area dredged during each individual sample was therefore calculated as 111.12 x 0.21 = 25.5m^2.

Differences in the density and size of clams between each site and across the fishing season were tested using a two-factorial ANOVA in the R statistical programming language (version 0.98.1062) (R Core Team, 2013). Site and sampling month were included as main effects, with an interaction term between the two included as an indication of whether the magnitude of change throughout the fishing season differed between sites.

Ash-Free Dry Mass and Condition Index

Ash-free dry mass (AFDM) of clams retained after the closure of the fishery and stored in the laboratory was calculated through loss-on-ignition (LOI). Clams were first dried for 24 hours at 105˚C before being burned to a constant weight at 560˚C for four hours. Dry flesh and dry shell weights (DSW) were recorded to five decimal places, and the difference between pre- and post-furnace flesh mass was taken as the ash-free dry mass AFDM in grams. The relationship between clam length and weight across sites was then modelled using a generalised linear model framework including site as a model effect and using the best-fitting error structure.

The following formula was used to calculate condition index (CI) (Sahin et al., 2006):

$$CI = (AFDM\ (g)\ /\ DSW(g)) * 100$$

A linear model was also used to test for differences in the condition index of clams between sites, including clam length as a covariate to identify differences in the slope of this relationship between sites.

Ageing and Cohort Analysis

The number of external concentric growth rings on the shell has been used in past studies to age individuals of marine bivalves (Jones, 1980; Breen et al., 1991; Ponurosvkii, 2000), although results of this method in *R. philippinarum* have been shown to be inaccurate (Ohba, 1959), and this proved the case with samples from this study. Therefore two different methods of aging were used to derive age estimates from the size frequency histograms.

Firstly, Bhattacharya's (1967) method was used within FiSAT II (Food Agriculture Organisation of the United Nations (FAO) http://www.fao.org/fishery/topic/16072/en) to analyse length frequency histograms from each study site. This method uses modal progression analysis to identify individual size cohorts as individual normal distributions within a composite distribution of multiple age groups, and is frequently used in the assessment of fish and shellfish stocks (Pauly & Morgan, 1987; Schmidt et al., 2008; Wrange et al., 2010). It was ensured that the separation index between modes was > 2 and whenever possible age groups were derived from at least three points consecutively (Gayanilo, 1997). Size classes of 2mm were used for this analysis as preliminary analyses using 5mm showed that additional modes in the data were lost using the larger size class.

Secondly, length-frequency histograms were analysed using the mixdist package in the R statistical programming language (version 0.98.1062). This method utilises maximum-likelihood estimation to fit finite mixture distribution models to length frequency histograms as normal distributions. Mixdist results estimate age distributions (π: the number of each age group present as a proportion of the population), mean length at age (μ) and standard deviations of length at age (σ). The mixdist method first requires values for π, μ and σ following visual examination of the length frequency histogram (Hoxmeier and Dieterman, 2011). These priors are then used to produce estimates of μ. Results were again used to establish the number of separate age cohorts present within the population and to validate those identified through Bhattacharya's method.

In both of these methods, age groups were derived from size cohorts based on a "known-age" reference group of age-0 (< 20mm). This is based on the reported average length of 15-20mm reached by spring recruits by the end of their first winter and previous work in Poole Harbour (Ohba, 1959; Harris, 2016). Given the inclusion of prior information in the mixdist analysis, results of this method were more accurate in identifying cohorts within the data. Therefore these results were carried forward when ageing individual clams. The mixing proportion of each cohort was then applied to the data to calculate the age of any given individual based on its shell length and the relative probabilities of each size cohort. These ages were then used for calculation of growth parameters as described below.

Growth Parameters

Growth parameters for length-at-age in clams from each area of the harbour were estimated using the Von Bertalanffy growth function in the R package FSA. The typical Von Bertalanffy growth curve is represented as:

$$E[L|t] = L_{\infty}(1 - e^{-K(t-to)})$$

where $E[L|t]$ is the predicted average length at age (or time *t*), L_{∞} is the asymptotic average length (i.e. the theoretical largest average length obtained by an individual in the population), *K* is the growth rate coefficient (yr^{-1}) and t_0 is the theoretical age at which length is zero (Beverton, 1954; Beverton and Holt, 1957). These parameters were then used to plot growth curves in length of clams as a function of age, allowing for comparison of growth in *R. philippinarum* at different sites around the harbour.

Results

Clam Densities and Size

No consistent effect of sampling month is evident on clam density although results show site differences ($F(2, 12) = 8.37$, $p < 0.01$) and a significant interaction term ($F(2, 12) = 12.22$, $p < 0.01$), indicating significant differences in the magnitude of change in densities between sites. The change in densities of *R. philippinarum* throughout the dredge season was greatest around Holton Mere, the heaviest dredged site (Table 2; Figure 2), where total clam densities (across all size classes) reduced by almost 75%, compared to 4% at Holes Bay, where no dredging occurred. Cohorts of juvenile (< 20mm) clams are evident at each site (Figure 3), indicating recruitment at all sites during the summer of 2015.

The changes in clam density following heavy fishing around Holton Mere are clearly evident (Figures 4 and 5), with ~95% of legally harvestable clams (> 35mm) and a large proportion of those between 30mm and 35mm extracted from this site throughout the 2015 dredging season. The proportional change in densities of harvestable clams was significantly greater at this site (ANOVA: $F(2,6) = 32.26$, $p < 0.001$) than the other two sites, between which no difference in the level of change in clam abundance is evident (Figure 4a). At Wytch Lake an increase in the density of harvestable clams is apparent despite this area being open to dredging July – October and subject to low fishing intensity. Neither of these changes is significant compared to pre-dredging conditions however (i.e. no overlap between 95% confidence interval and no effect). All 5mm size classes above 35mm show a significant reduction in density from pre-dredging conditions around Holton Mere (Figure 4b), providing strong indication of fishing pressure on larger clams.

A significant interaction term between site and month is also evident in the results of ANOVA performed on clam size data ($F(2, 2007) = 10.94$, $p < 0.001$), again indicating significant differences in the change in clam size across the season between sites. The reduction across the open season was greatest in Holes Bay and Holton Mere, with little change in Wytch Lake (Table 2).

Condition Index, Biomass and Length-Weight Relationships

Mean condition index of clams sampled in January was significantly different between sites ($F_{(2,276)} = 20.98$, $p < 0.001$), with clam condition lowest at Holton Mere and highest in Wytch Lake (Table 2). While clam length is a significant predictor of clam condition ($F_{(1,276)} = 74.81$, $p < 0.001$), no significant interaction term is present in the results, indicating that the relationship is consistent across all sites ($F_{(2, 276)} = 2.47$, $p = 0.09$). Mean clam AFDM recorded in January 2016 shows significant differences between sites (ANOVA: $F_{(2,279)} = 16.73$, $p < 0.001$), with mean clam biomass lowest at Holton Mere, significantly lower than at Wytch Lake and Holes Bay, between which there is no difference (Figure 5; Table 2).

The relationship between clam length and weight shows significant site differences, with results of a fitted GLM with a gamma error structure show that both the intercept (GLM: $p < 0.001$) and the fitted curve (GLM: $p < 0.001$) of the trend between clam length and weight is significantly different at Holton Mere compared to the other two sites (Figure 6). Overall clams at Holton Mere contain significantly more AFDM per mm of length than those at Wytch Lake or Holes Bay, while there is no difference in the slope between the latter two sites.

Cohort Analysis

Given the changes in clam densities evident through the 2015 dredge season only data from prior to the dredge season was included in the size cohort analysis (Table 3).

The size cohorts identified through the two analysis methods appear comparable, with a maximum difference of around 2mm in the estimates in the Wytch Lake data. Size cohorts identified from June 2015 data appear similar at Wytch Lake and Holes Bay, although the estimate of the first (1-year) size cohort is lower at Holton Mere than at these sites by approximately 5mm. However, the next estimates appear similar, with 2-year clams reaching around 35mm at all sites. As with our previous results it appears however that the larger cohorts in the Holton Mere population are smaller than those identified at the other two sites, where 3-year clams reach around 41mm in length compared to 37mm at Holton Mere.

Growth of R. philippinarum

Von Bertalanffy growth curves fitted to length-at-age data indicate differences in the asymptotic average length of clams in each site. The asymptote of the model fitted to data from clams at Holton Mere shows a model asymptote of 46.02mm, indicating that on average, clams from this site do not grow to larger than 46mm (Table 4; Figure 7). Clams achieve a larger size at Wytch Lake and Holes Bay, where the fitted growth models show clams to grow to an average maximum size of 57mm and 66mm respectively (Table 4; Figure 7). The inverse trend is apparent in K, the Brody growth coefficient, which is highest under heavy fishing pressure around Holton Mere and lowest in Holes Bay (Table 4).

Discussion

The results presented in this study add to the existing knowledge of the Manila clam as a commercially and ecologically important species as it increases its northern range, providing information on the species' population dynamics under exploitation at the edge of its range. We acknowledge the limitations to our sampling design, particularly the low replication (three dredge hauls per site) and a lack of spatial and temporal replication, although sampling was undertaken within strict project limitations. Furthermore, given that fisheries for this species are currently rare in the UK at the northernmost edge of the species' range, however, additional sites in which to replicate the study on dredging effects are not available. Whilst the effects of fishing across only one season are presented in this manuscript, discussions with local fishermen and the SIFCA indicate that the distribution of fishing effort throughout the harbour and across the sites sampled in this study is consistent between years.

Despite such limitations, our results nevertheless provide strong signals of fishing effects on the species in Poole Harbour and allow an assessment of potential implications for shorebird predators of the species in intertidal environments. The effects of the 2015 dredge season on the size and densities of *R. philippinarum* in Poole Harbour are clearly evident, particularly a dramatic decline in the density of legally harvestable clams in the heavily fished area around Holton Mere. Results show that legally sized clams may be harvested with up to 95% efficiency by pump-scoop dredging in this area (Figure 4a), which is higher than previous estimates in the harbour of up to 75% (Humphreys et al., 2007; Harris 2016). While catch and detailed logbook data are not available, fishing sightings demonstrate that fishing effort at Holton Mere was markedly higher than at other areas of the harbour, suggesting that these changes are indeed due to fishing pressure. At Wytch Lake an apparent increase in clam densities was observed across the dredging season, although the higher variability at this site may indicate patchiness of clams and/or fishing effort, as fishers moved into this area after depletion of other areas in the harbour.

Fishing across the harbour coincides with a period of increased mortality and competition in shorebirds for limited resources (Goss-Custard 1985; Whitfield 2003; Zwarts et al., 1996). When considering changes in prey availability for shorebirds, the changes in densities of each 5mm size class are particularly pertinent, given that birds consume bivalve prey within discrete size classes (Goss-Custard et al., 2006; Caldow et al., 2007). Oystercatchers within Poole Harbour consume clams between 16 and 50mm and ignore clams less than 15mm in length (Caldow et al., 2007), consistent with other estimates (Goss-Custard et al., 2006). Our data suggest that these clams represent individuals over one year old (Figure 7), which are present at all sites, although fishing appears to dramatically reduce the density of larger and thus more profitable prey for oystercatchers around Holton Mere. There is high variability in the change in abundance of the 30-35mm size class in this area, and inspection of Figure 2 suggests that this may be due to illegal removal of some clams below the 35mm MLS from this area. This area of the harbour has been heavily fished in past years and the pre-season mean size of clams here of 34.80mm is likely indicative of this, suggesting long-term impacts of heavy harvesting on local prey size and quality. This is a decline in the mean size from previous work (Humphreys et al., 2007), potentially as a result of the reduction in the MLS from 40mm to 35mm in 2007 (Lambourn & Le Berre 2007).

Condition indices of all clams across harbour are similar to those observed elsewhere in northern Europe (de Montaudouin et al., 2016b), although markedly higher than those recorded in the Marmara Sea, Turkey at the same time of year, (Colakoglu and Palaz, 2014). Mean body size, biomass and condition of *R. philippinarum* are significantly lower at the heavily exploited site at Holton Mere than at the other sites, however, which based on the availability of large, high quality prey alone, may therefore offer sub-optimal prey to oystercatchers, increasingly so as winter and the fishing season progress. Rather than targeting the most profitable individuals, however, oystercatchers target areas of highest prey density (O'Connor and Brown, 1977; Goss-Custard et al., 1991) and select smaller sub-optimal prey sizes in order to reduce bill damage, the prevalence of which is positively correlated with size of shellfish prey consumed and which can significantly reduce food intake rates (Rutten et al., 2006). Such feeding strategies may mean that oystercatchers preferentially target this heavily exploited area where higher clam densities occur, yet the impacts of fishing in the area at the critical overwintering period for shorebirds may be more complex than the intuitive assumption that removal of the largest individuals is of greatest concern. Despite the differences in clam densities between sites evident in our results, the available data on the distribution of oystercatchers across Poole Harbour (Frost et al., 2018) indicate similar densities in the three areas sampled in this study. However, these data were collected in the winter of 2004/2005 and may not be an accurate representation of oystercatcher distributions in recent years and in relation to contemporary fishing effort.

The asymptote of the Von Bertalanffy growth model for Holton Mere however is 46mm; higher than the mean size observed both before and after the dredging season at this site (Figure 9a; Table 4). This suggests that the short-term impacts of dredging in removing larger individuals may not be reflected in the population as a whole; despite higher dredging pressure reducing the mean length, individuals of *R. philippinarum* still achieve lengths markedly higher than the MLS at this site. This clearly is an important consideration for both fishery sustainability and shorebird prey resources. However, $L\infty$ is only relevant in populations where mortality is at sufficiently low levels that individuals can actually reach the age at which growth completely ceases (Francis 1988). Therefore, heavy fishing may remove clams before the theoretical age at which increases in length begin to slow down or stop is reached. It appears that at all sites *R. philippinarum* reaches the legally harvestable length of 35mm at between 2 and 3 years of age, although clams older than 3 years of age are only present in the data at Holes Bay, where no fishing occurs.

Elucidating fishing impacts from natural environmental variability is not straightforward, and the between-site differences in growth, weight and condition may be driven by factors other than fishing pressure. Such trends may be driven by environmental factors such as flow rates (Hadley and Manzi 1984), food availability (Norkko et al., 2005) and dissolved oxygen (Ferreira et al., 2007).

Furthermore, at higher densities intraspecific competition can limit individual growth and potentially survivorship, reducing flesh content (Fogarty and Murawski 1986), shell length (Peterson 1989; Olafsson 1986; Weinberg 1998) and shell width (Cerrato and Keith 1992). Such space-driven self-thinning (SST) (Frechette and Lefaivre 1990) has been described in many species of shellfish in response to high population densities. The densities within Poole Harbour are relatively low compared to other regions across Europe however; in the Venice Lagoon, Italy, densities of Manila clam reach up to 4000 m^{-2} and biomass of over 1 kg m^{-2} (Brusa et al., 2013).

Our results may further demonstrate the importance of areas closed to fishing, such as Holes Bay, in providing potential refuges of high quality bird prey when densities elsewhere are reduced due to fishing, as well as reproductive biomass and continued larval supply for the species elsewhere in the harbour. Clams in Holes Bay are significantly larger than in other areas of the harbour, and mean AFDM is significantly higher in both Holes Bay and Wytch Lake than in Holton Mere. Previous work of *R. philippinarum* larval dispersal in the harbour has indicated that Holes Bay does indeed act as an important larval source for the wider harbour and potentially other estuaries in the region. The most recently established Manila clam population in the UK in Southampton Water, which is yet to be licensed for commercial exploitation, is considered to have originated from Poole, whether through larval transport or deliberate introductions by fishers (Humphreys et al., 2015). Larvae notably remain in the Holton Mere area of the harbour > 12 days after spawning in Holes Bay (Herbert et al., 2012), with higher levels of spatfall contributing to higher densities in the area.

A single year of sampling does not allow for any assessment of between-year change in the population of *R. philippinarum* in Poole Harbour or recovery in response to fishing pressure, a key limitation in accurately assessing sustainability of the fishery, although densities of smaller (< 20mm) clams, representing new recruits to the population, remain higher at Holton Mere than at other sites in January despite the large reductions evident due to fishing (Figure 3). This is likely due to this larval supply and these sizes not being landed because of the enforced MLS or retained in dredges due to the mesh size. Peaks in recruitment elsewhere have been shown to occur from early summer into late autumn and early winter (Ruesink et al., 2014), consistent with our results. This continued recruitment may maintain both the current fishery, which appears sustainable, as well as a vital food supply for the area's oystercatcher population.

Despite providing clear indication of fishing-induced changes to clam size and density in Poole Harbour, this study highlights the complexities in accurately assessing the impacts of harvesting on wildlife populations in dynamic environments. Results will be of use to managers that aim to reconcile the interests of commercial fishing and nature conservation as the Manila clam continues to spread throughout Europe and the UK, although future studies should aim to provide further insight into the dynamics between harvesting activities and impacts to both economically and ecologically important shellfish and shorebird populations.

References

Adams A, Reeve L. The Zoology of the Voyage of HMS Samarang, Mollusca, London, 1850, pp. 87

Astorga M.P., 2014, Genetic considerations for mollusk production in aquaculture: current state of knowledge. Front. Genet. 5.

Atkinson P.W., Clark N.A., Bell M.C., Dare P.J., Clark J.A., Ireland P.L., 2003, Changes in commercially fished shellfish stocks and shorebird populations in the Wash, England. Biol Conserv 114, 127–141.

Beck F., Pezy J.-P., Baffreau A., Dauvin J.-C., 2015, Effects of clam rake harvesting on the intertidal *Ruditapes* habitat of the English Channel. ICES J Mar Sci 72, 2663–2673.

Beninger P.G., Lucas A., 1984, SEASONAL VARIATIONS IN CONDITION, REPRODUCTIVE ACTIVITY, AND GROSS BIOCHEMICAL COMPOSITION OF TWO SPECIES OF ADULT CLAM REARED IN A COMMON HABITAT: *TAPES DECUSSATUS*. J Exp Mar Biol Ecol 79, 19–37.

Beverton R.J., 1954, Notes on the use of theoretical models in the study of the dynamics of exploited fish populations. US Fishery Laboratory.

Beverton R.J., Holt S.J., 1957, On the dynamics of exploited fish populations, Fishery Investigations Series II, Vol. XIX, Ministry of Agriculture. Fisheries and Food 1, 957.

Bhattacharya C.G., 1967, A Simple Method of Resolution of a Distribution into Gaussian Components. Biometrics 23, 115–135.

Bidegain G., Juanes J.A., 2013, Does expansion of the introduced Manila clam *Ruditapes philippinarum* cause competitive displacement of the European native clam *Ruditapes decussatus*? J Exp Mar Biol Ecol 445, 44–52.

Bourne N (1982) Distribution, reproduction, and growth of the Manila clam, Tapes philippinarum (Adams and Reeves), in British Columbia. J Shellfish Res 2:47-54

Borisov V.M., 1978, The selective effect of fishing on the population structure of species with a long life cycle. J Icthyol 18, 896–904.

Bowering W.R., Brodie W.B., 1991, Distribution of commercial flatfishes in the Newfoundland-Labrador region of the Canadian Northwest Atlantic and changes in certain biological parameters since exploitation. Netherlands Journal of Sea Research, Proceedings of the First International Symposium on Flatfish Ecology 27, 407–422.

Bowgen K.M., Stillman R.A., Herbert R.J.H., 2015, Predicting the effect of invertebrate regime shifts on wading birds: Insights from Poole Harbour, UK. Biol Conserv 186, 60–68.

Braje T.J., Kennett D.J., Erlandson J.M. and Culleton B.J., 2007, Human impacts on nearshore shellfish taxa: a 7,000 year record from Santa Rosa Island, California. American Antiquity, 72(4), 735-756.

Breen P.A., Gabriel C., Tyson T., 1991, Preliminary estimates of age, mortality, growth, and reproduction in the hiatellid clam *Panopea zelandica* in New Zealand. N Z J Mar Freshw Res 25, 231–237.

Brusà R.B., Cacciatore F., Ponis E., Molin E., Delaney E., 2013, Clam culture in the Venice lagoon: stock assessment of Manila clam (*Venerupis philippinarum*) populations at a nursery site and management proposals to increase clam farming sustainability. Aquat Living Resour 26, 1–10.

Caldow R.W.., Stillman R.A., Durell S.E.A. l. V. d., West A.D., McGrorty S., Goss-Custard J.D., Wood P.J., Humphreys J., 2007, Benefits to shorebirds from invasion of a non-native shellfish. Proc R Soc Biol Sci Ser B 274, 1449–1455.

Cerrato R.M., Keith D.L., 1992, Age structure, growth, and morphometric variations in the Atlantic surf clam, *Spisula solidissima*, from estuarine and inshore waters. Mar Biol 114, 581–593.

Chiesa S., Lucentini L., Freitas R., Nonnis Marzano F., Breda S., Figueira E., Caill-Milly N., Herbert R.J.H., Soares A.M.V.M., Argese E., 2017, A history of invasion: COI phylogeny of Manila clam *Ruditapes philippinarum* in Europe. Fish Res 186, 25–35.

Clarke L.J., Esteves L.S., Stillman R.A., Herbert R.J.H., 2018, Impacts of a novel shellfishing gear on macrobenthos in a marine protected area: pump-scoop dredging in Poole Harbour, UK. Aquat Living Resour 31, 5.

Clarke L.J., Hughes K.M., Esteves L.S., Herbert R.J.H., Stillman R.A., 2017, Intertidal invertebrate harvesting: a meta-analysis of impacts and recovery in an important waterbird prey resource. Mar Ecol Prog Ser 584, 229–244.

Collie J.S., Hall S.J., Kaiser M.J., Poiner I.R., 2000, Journal of Animal A quantitative analysis of fishing impacts on shelf-sea. J Anim Ecol 69, 785–798.

Conover D.O., Arnott S.A., Walsh M.R., Munch S.B., 2005, Darwinian fishery science: lessons from the Atlantic silverside (*Menidia menidia*). Can J Fish Aquat Sci. 62, 730–737.

Dang C, de Montaudouin X, Gam M, Paroissin C, Caill-Milly N (2010) The Manila clam population in Arcachon Bay (SW France): can it be kept sustainable? J Sea Res 63:108-118

Dayton P.K., Thrush S.F., Agardy M.T., Hofman R.J., 1995, Environmental effects of marine fishing. Aquat Conserv: Mar Freshw Ecosyst 5, 205–232.

Dixon C.D., Day R.W., 2004, GROWTH RESPONSES IN EMERGENT GREENLIP ABALONE TO DENSITY REDUCTIONS AND TRANSLOCATIONS. J Shellfish Res 23, 1223–1228.

Ferreira J.G., Hawkins A.J.S., Bricker S.B., 2007, Management of productivity, environmental effects and profitability of shellfish aquaculture — the Farm Aquaculture Resource Management (FARM) model. Aquaculture 264, 160–174.

Fogarty M.J., Murawski S.A., 1986, Population dynamics and assessment of exploited invertebrate stocks. In: North Pacific Workshop on Stock Assessment and Management of Invertebrates. Can Spec Publ Fish Aquat Sci. pp. 228–244.

Francis R.I.C.C., 1988, Are Growth Parameters Estimated from Tagging and Age–Length Data Comparable? Can J Fish Aquat Sci 45, 936–942.

Frechette M., Lefaivre D., 1990, Discriminating between food and space limitation in benthic suspension feeders using self-thinning relationships. Mar Ecol Prog Ser 65, 9.

Frost, T.M., Austin, G.E., Calbrade, N.A., Mellan, H.J., Hearn, R.D., Stroud, D.A., Wotton, S.R. and Balmer, D.E., 2018, Waterbirds in the UK 2016/17: The Wetland Bird Survey. BTO/RSPB/JNCC. Thetford. Available Online at https://app.bto.org/webs-reporting/?tab=lowtide. Last Accessed 10/10/2018.

Gayanilo F.C., 1997, Fisat: Fao-Iclarm Stock Assessment Tools, Reference Manuals. Food & Agriculture Organisation.

Goss-Custard J.D., 1985, Foraging behavior of wading birds and the carrying capacity of estuaries.

Goss-Custard J.D., Warwick R.M., Kirby R., McGrorty S., Clarke R.T., Pearson B., Rispin W.E., Durell S.E.A.L.V.D., Rose R.J., 1991, Towards Predicting Wading Bird Densities from Predicted Prey Densities in a Post-Barrage Severn Estuary. J App Ecol 28, 1004–1026.

Goss-Custard J.D., West A.D., Yates M.G., Caldow R.W.G., Stillman R.A., Bardsley L., Castilla J., Castro M., Dierschke V., Durell S.E.A., Eichhorn G., Ens B.J., Exo K.-M., Udayangani-Fernando P.U., Ferns P.N., Hockey P.A.R., Gill J.A., Johnstone I., Kalejta-Summers B., Masero J.A., Moreira F., Nagarajan R.V., Owens I.P.F., Pacheco C., Perez-Hurtado A., Rogers D., Scheiffarth G., Sitters H., Sutherland W.J., Triplet P., Worrall D.H., Zharikov Y., Zwarts L., Pettifor R.A., 2007, Intake rates and the functional response in shorebirds (Charadriiformes) eating macro-invertebrates. Biol Rev 81, 501–529.

Hadley N.H., Manzi J.J., 1984, Growth of seed clams, *Mercenaria mercenaria*, at various densities in a commercial scale nursery system. Aquaculture 36, 369–378.

Harris M.R., Cragg S., Humphreys J., 2016, A study of the naturalisation and dispersal of a non-native bivalve, the Manila clam, *Ruditapes philippinarum* (Adams and Reeve 1850) in estuaries along the South coast of England. Unpublished PhD Thesis 279.

Haug T., Tjemsland J., 1986, Changes in size- and age-distributions and age at sexual maturity in atlantic halibut, *Hippoglossus hippoglossus*, caught in North Norwegian waters. Fisheries Res, 4, 145–155.

Herbert R.J.H., Willis J., Jones E., Ross K., Hübner R., Humphreys J., Jensen A., Baugh J., 2012, Invasion in tidal zones on complex coastlines: modelling larvae of the non-native Manila clam, *Ruditapes philippinarum*, in the UK: Invasions in tidal zones on complex coastlines. J Biogeogr 39, 585–599.

Hoxmeier R.J.H., Dieterman D.J., 2011, Application Of Mixture Models For Estimating Age And Growth Of Stream Dwelling Brook Trout 13.

Humphreys J., Caldow R.W.G., McGrorty S., West A.D., Jensen A.C., 2007, Population dynamics of naturalised Manila clams *Ruditapes philippinarum* in British coastal waters. Mar Biol 151, 2255–2270.

Humphreys J., Harris M., Herbert R.J.H., Farrell P., Jensen A., Cragg S., 2015, Introduction, dispersal and naturalisation of the Manila clam *Ruditapes philippinarum* in British estuaries, 1980-2010. J Mar Biol Assoc UK 95, 1163–1172.

Hutchings J.A., 2005, Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 62, 824–832.

Ishida M. (Aichi-ken F.R.I., Ogasawara M., Murakami C., Momoi M., Ichikawa T., Suzuki T., 2005, Changes in behavioral characteristics, in relation to salinity selection and vertical movement at different growth stages of the planktonic larvae of the Japanese littleneck clam, *Ruditapes philippinarum*. Bulletin of the Japanese Society of Fisheries Oceanography (Japan).

Ishii R., Sekiguchi H., Nakahara Y., Jinnai Y., 2001, Larval recruitment of the manila clam *Ruditapes philippinarum* in Ariake Sound, southern Japan. Fish Sci 67, 579–591.

Jensen A.C., Humphreys J., Caldow R.W.G., Grisley C., Dyrynda P.E.J., 2004, Naturalization of the Manila clam (*Tapes philippinarum*), an alien species, and establishment of a clam fishery within Poole Harbour, Dorset. J Mar Biol Assoc UK 84, 1069–1073.

Jones D.S., 1980, Annual Cycle of Shell Growth Increment Formation in Two Continental Shelf Bivalves and its Paleoecologic Significance. Paleobiology 6, 331–340.

Kaiser M., Clarke K., Hinz H., Austen M., Somerfield P., Karakassis I., 2006, Global analysis of response and recovery of benthic biota to fishing. Mar Ecol Prog Ser 311, 1–14.

Kido J. S., and Murray S. N., 2003. Variation in owl limpet *Lottia gigantean* population structures, growth rates, and gonadal production on southern California rocky shores. Mar Ecol Prog Ser 257, 111–124.

Law R., 2000, Fishing, selection, and phenotypic evolution. ICES J Mar Sci 57, 659–668.

Mannino M. A. and Thomas K. D., 2001. Intensive Mesolithic exploitation of coastal resources? Evidence from a shell deposit on the Isle of Portland (Southern England) for the impact of human foraging on populations of intertidal rocky shore molluscs. J Arch Sci 28, 1101-1114.

Melville-Smith R., de Lestang S., 2006, Spatial and temporal variation in the size at maturity of the western rock lobster *Panulirus cygnus* George. Mar Biol 150, 183–195.

Millner R.S., Whiting C.L., 1996, Long-term changes in growth and population abundance of sole in the North Sea from 1940 to the present. ICES J Mar Sci 53, 1185–1195.

de Montaudouin X., Arzul I., Caill-Milly N., Khayati A., Labrousse J.-M., Lafitte C., Paillard C., Soudant P., Goulletquer P., 2016a, Asari clam (*Ruditapes philippinarum*) in France: history of an exotic species 1972-2015. B Jpn Fish Res Educ Agency 42, 35-42

de Montaudouin X., Lucia M., Binias C., Lassudrie M., Baudrimont M., Legeay A., Raymond N., Jude-Lemeilleur F., Lambert C., Le Goïc N., Garabétian F., Gonzalez P., Hégaret H., Lassus P., Mehdioub W., Bourasseau L., Daffe G., Paul-Pont I., Plus M., Do V.T., Meisterhans G., Mesmer-Dudons N., Caill-Milly N., Sanchez F., Soudant P., 2016b, Why is Asari (=Manila) clam *Ruditapes philippinarum* fitness poor in Arcachon Bay: A meta-analysis to answer? Estuar Coast Shelf S 179, 226-235

Moura P, Vasconcelos P, Pereira F, Chainho P, Costa JL, Gaspar MB (2018) Reproductive cycle of the Manila clam (Ruditapes philippinarum): an intensively harvested invasive species in the Tagus Estuary (Portugal). J Mar Biol Assoc UK 98:1645-1657

Mortensen S.H., Strand Ø., Høisœter T., 2000, Releases and recaptures of Manila clams (*Ruditapes philippinarum*) introduced to Norway. Sarsia 85, 87–91.

Norkko J., Pilditch C.A., Thrush S.F., Wells R.M.G., 2005, Effects of food availability and hypoxia on bivalves: the value of using multiple parameters to measure bivalve condition in environmental studies. Mar Ecol Prog Ser 298, 205–218.

O'Connor R.J., Brown R.A., 1977, Prey depletion and foraging strategy in the Oystercatcher *Haematopus ostralegus*. Oecologia 27, 75–92.

Ohba S., 1959, Ecological studies in the natural population of a clam, *Tapes japonica*, with special reference to seasonal variations in the size and structure of the population and to individual growth. Biol. J. Okayama Univ. 5, 13–42.

Olafsson E.B., 1986, Density Dependence in Suspension-Feeding and Deposit-Feeding Populations of the Bivalve *Macoma balthica*: A Field Experiment. J Anim Ecol 55, 517–526.

Pauly D., Morgan G.R., 1987, Length-based Methods in Fisheries Research. WorldFish.

Peterson C.H., Beal B.F., 1989, Bivalve Growth and Higher Order Interactions: Importance of Density, Site, and Time. Ecology 70, 1390–1404.

Pombo O. A. and Escofet A., 1996. Effect of exploitation on the limpet *Lottia gigantea*: a field study in Baja California (Mexico) and California (U.S.A.). Pac Sci 50, 393–403.

Ponurovskii S.K., 2000, Size and age structures of the bivalve mollusk *Ruditapes philippinarum* population in the shallow waters of South Primor'e. Oceanology 40, 693–699.

R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Robert R., Sánchez J.L., Pérez-Parallé L., Ponis E., Kamermans P., O'Mahoney M., 2013, A glimpse on the mollusc industry in Europe. Aquaculture Europe 38, 5–11.

Rose K.A., Cowan J.H., Winemiller K.O., Myers R.A., Hilborn R., 2001, Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. Fish and Fisheries 2, 293–327.

Ruesink J.L., van Raay K., Witt A., Herrold S., Freshley N., Sarich A., Trimble A.C., 2014, Spatio-temporal recruitment variability of naturalized Manila clams (*Ruditapes philippinarum*) in Willapa Bay, Washington, USA. Fishery Res 151,199-204

Rutten A.L., Oosterbeek K., Ens B.J., Verhulst S., 2006, Optimal foraging on perilous prey: risk of bill damage reduces optimal prey size in oystercatchers. Behavioral Ecology 17, 297–302.

Sahin C., Düzgüne E., 2006, Seasonal Variations in Condition Index and Gonadal Development of the Introduced Blood Cockle *Anadara inaequivalvis* (Bruguiere, 1789) in the Southeastern Black Sea Coast. Turkish J Fish Aquat Sci 6, 155–163.

Schmidt A., Wehrmann A., Dittmann S., 2008, Population dynamics of the invasive Pacific oyster *Crassostrea gigas* during the early stages of an outbreak in the Wadden Sea (Germany). Helgol Mar Res 62, 367.

Smit C.J., Dankers N., Ens B.J., Meijboom A., 1998, Birds, mussels, cockles and shellfish fishery in the Dutch Wadden Sea: How to deal with low food stocks for eiders and oystercatchers? Senckenbergiana maritima 29, 141–153.

Solidoro C., Melaku Canu D., Rossi R., 2003, Ecological and economic considerations on fishing and rearing of *Tapes phillipinarum* in the lagoon of Venice. Ecological Modelling, ISEM The third European Ecological Modelling Conference 170, 303–318.

Verhulst S., Oosterbeek K., Rutten A.L., Ens B.J., 2004, Shellfish Fishery Severely Reduces Condition and Survival of Oystercatchers Despite Creation of Large Marine Protected Areas. Ecol Soc 9.

Walsh M.R., Munch S.B., Chiba S., Conover D.O., 2006, Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. Ecol Lett 9, 142–148.

Weinberg J.R., 1998, Density-dependent growth in the Atlantic surfclam, *Spisula solidissima*, off the coast of the Delmarva Peninsula, USA. Mar Biol 130, 621–630.

Whitfield D.P., 2003, Redshank *Tringa totanus* flocking behaviour, distance from cover and vulnerability to sparrowhawk Accipiter nisus predation. J Avian Biol 34, 163–169.

Wrange A.-L., Valero J., Harkestad L.S., Strand Ø., Lindegarth S., Christensen H.T., Dolmer P., Kristensen P.S., Mortensen S., 2010, Massive settlements of the Pacific oyster, *Crassostrea gigas*, in Scandinavia. Biol Invasions 12, 1145–1152.

Zwarts L., Hulscher J.B., Koopman K., Piersma T., Zegersi P.M., 1996, SEASONAL AND ANNUAL VARIATION IN BODY WEIGHT, NUTRIENT STORES AND MORTALITY OF OYSTERCATCHERS. Ardea 84, 31.

Figures

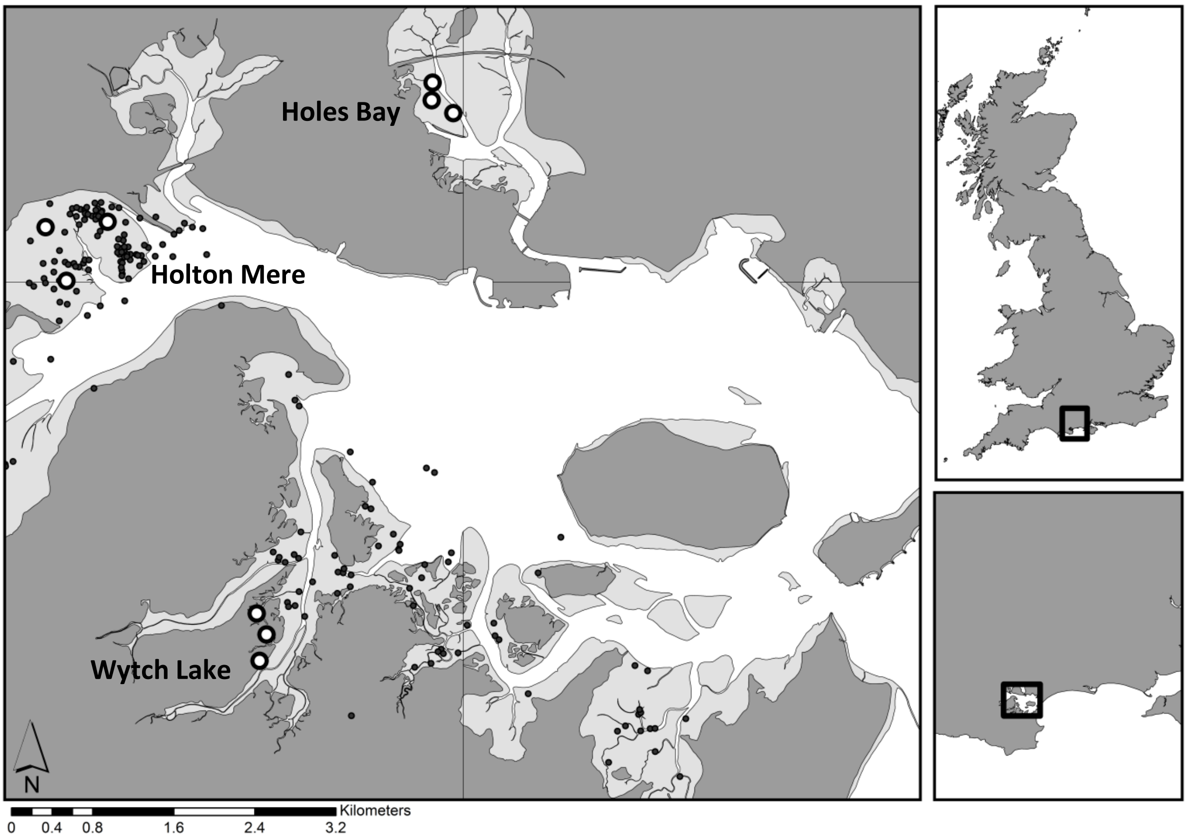

Figure 1. Approximate locations sampled by pump-scoop dredge for the clam stock assessment in June 2015 and revisited in January 2016 (white circles). The northern-most site is Holes Bay (closed site), the westerly site is the area around Holton Mere (high intensity fishing), and the southerly site is Wytch Lake (low intensity fishing). The small black circles indicate SIFCA fishing sightings during 2015. Sampling locations in Wytch Lake are within the intertidal. The locations in the UK and on the UK's south coast are inset.

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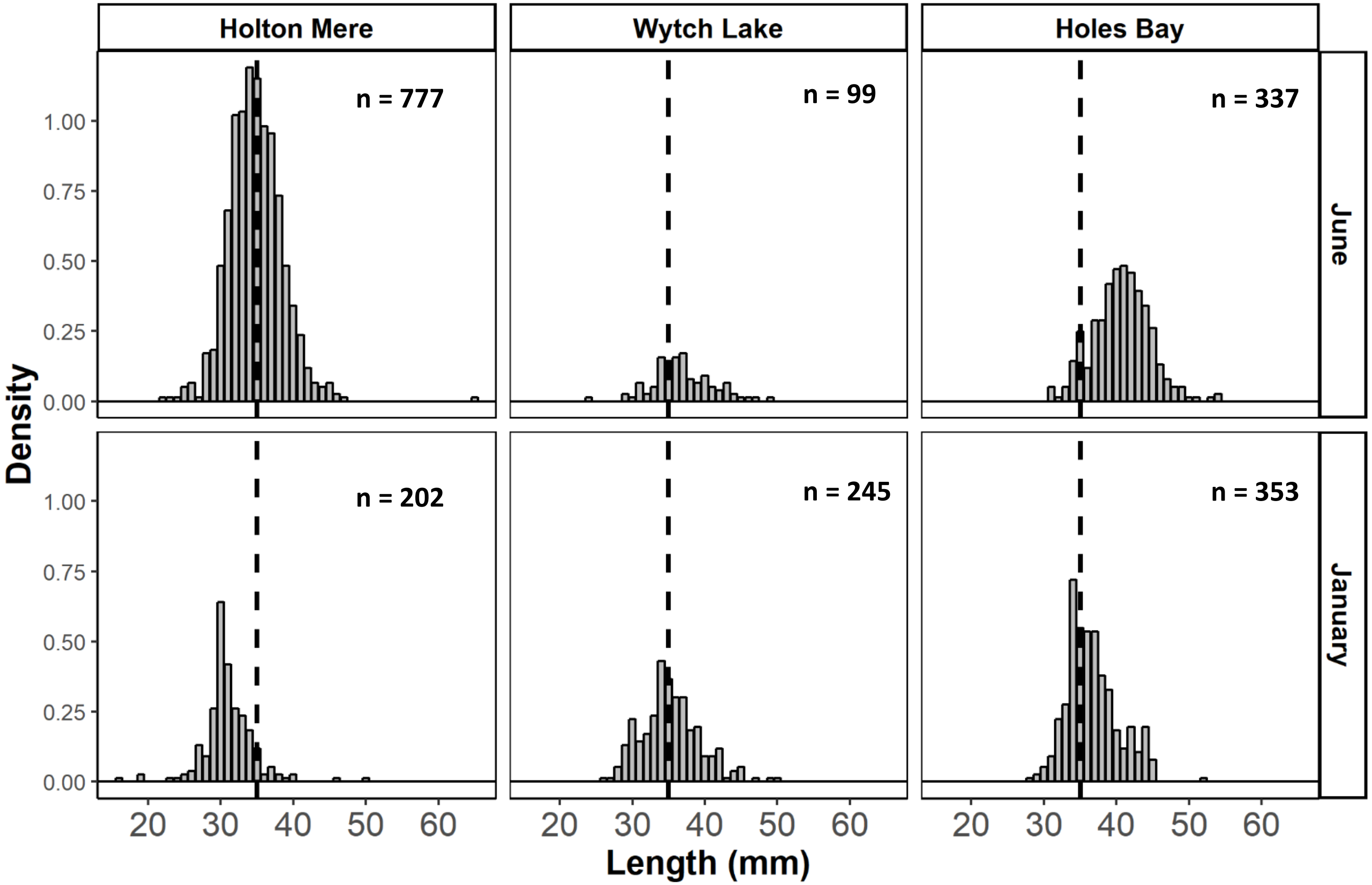

Figure 2. Density (ind. per m^2) of each 1mm size class of *R. philippinarum* sampled by pump-scoop dredging before (June 2015) and after (January 2016) the 2015 fishing season at each site (Holton Mere: high intensity fishing; Wytch Lake: low intensity fishing; Holes Bay: closed site). The dashed black line in each plot indicates the minimum legal landing size of 35mm. Data are from three dredges pooled.

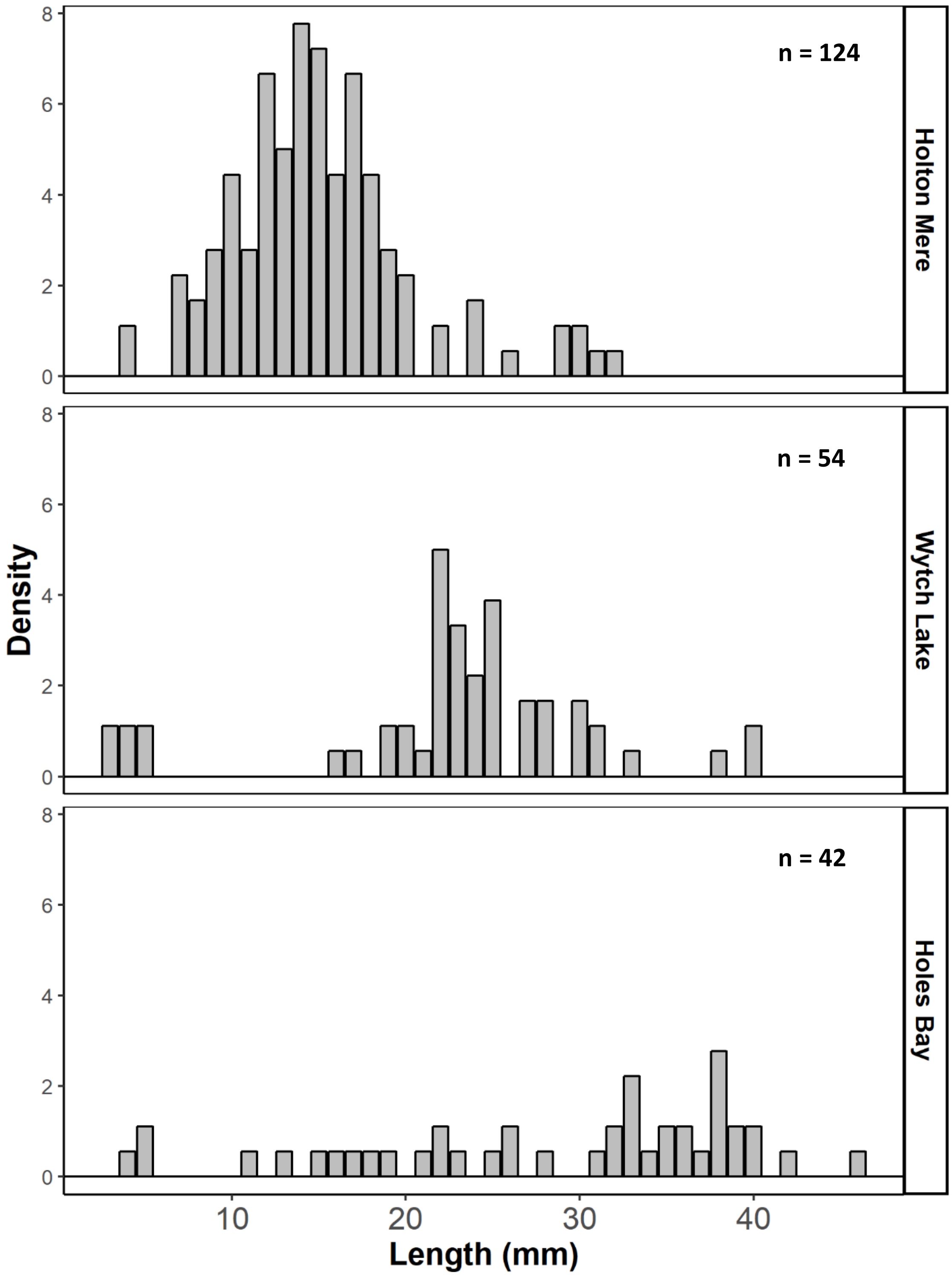

Figure 3. . Density (ind. per m^2) of each 1mm size class of *R. philippinarum* sampled by pump-scoop dredging after (January 2016) the 2015 fishing season at each site (Holton Mere: high intensity fishing; Wytch Lake: low intensity fishing; Holes Bay: closed site). Data are from six dredges pooled.

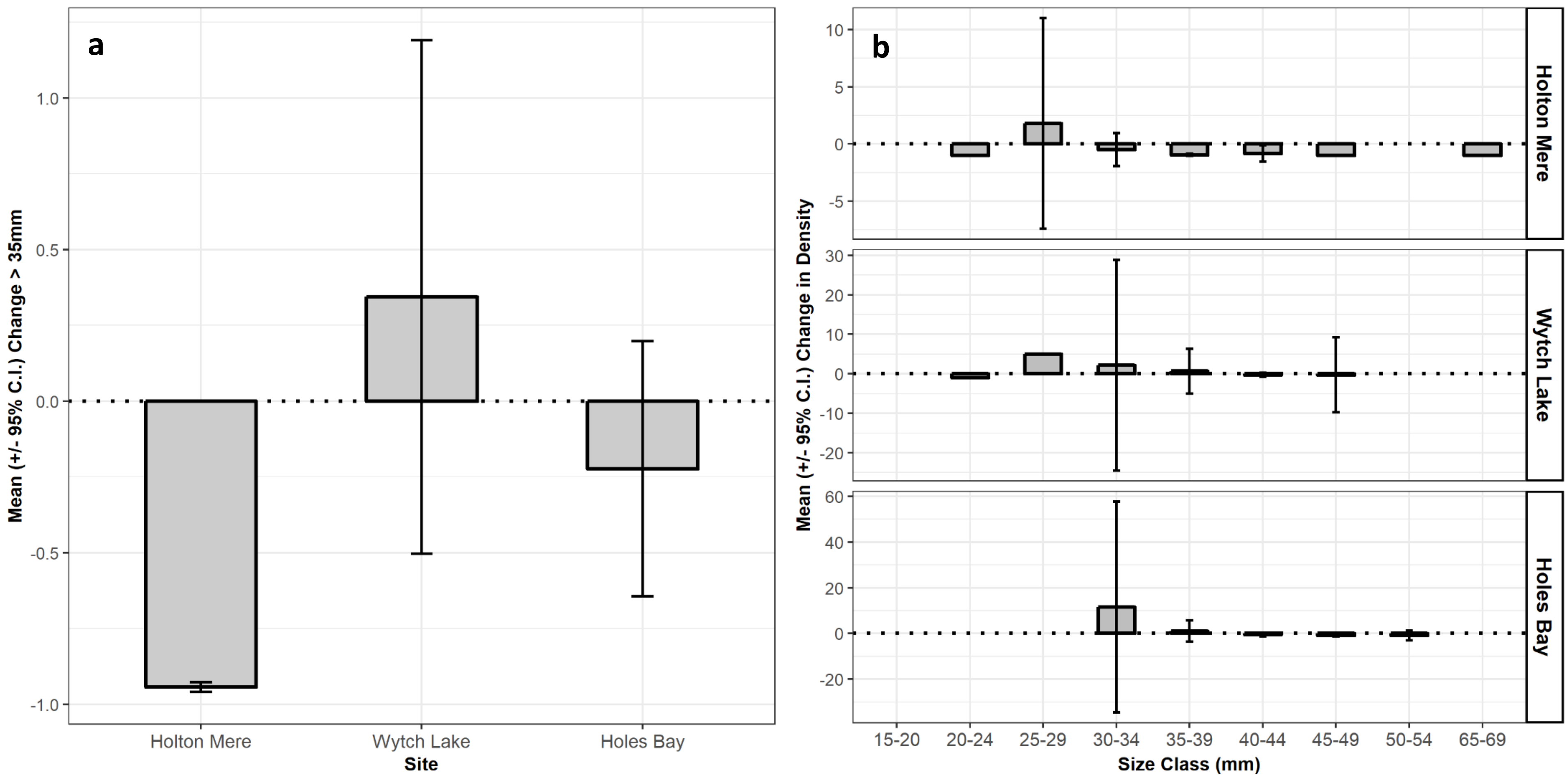

Figure 4. a) Mean (+/- 95% C.I.) proportional change in density of legally harvestable (>35mm) *R. philippinarum* at each site over the course of the 2015 dredging season. b) Mean (± 95% C.I.) proportional change in densities of *R. philippinarum* in each 5mm size class across (before vs after) the 2015 dredging season at each site sampled. (Holton Mere: high intensity fishing; Wytch Lake: low intensity fishing; Holes Bay: closed site).

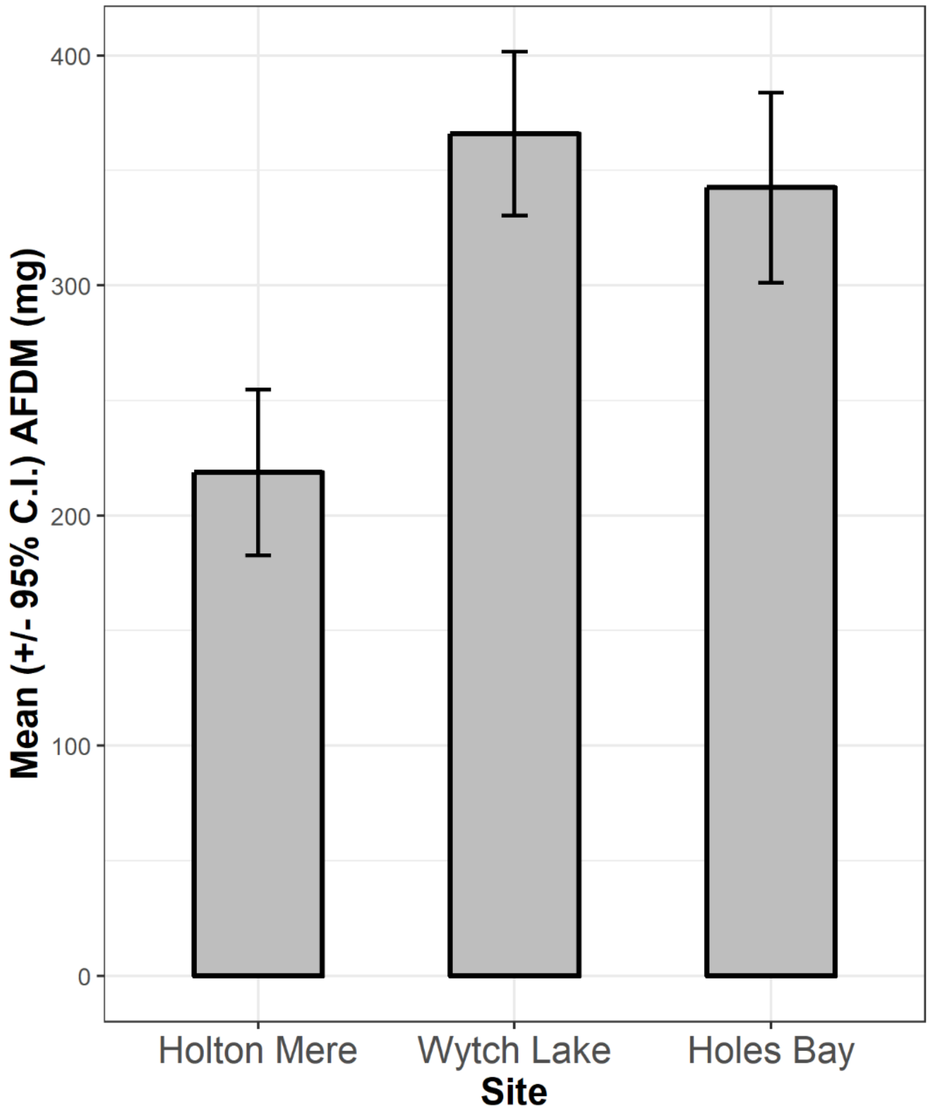

Figure 5. Mean (± 95% C.I.) ash-free dry mass (mg) of *R. philippinarum* sampled in each site after the 2015 fishing season in January 2016. (Holton Mere: high intensity fishing; Wytch Lake: low intensity fishing; Holes Bay: closed site).

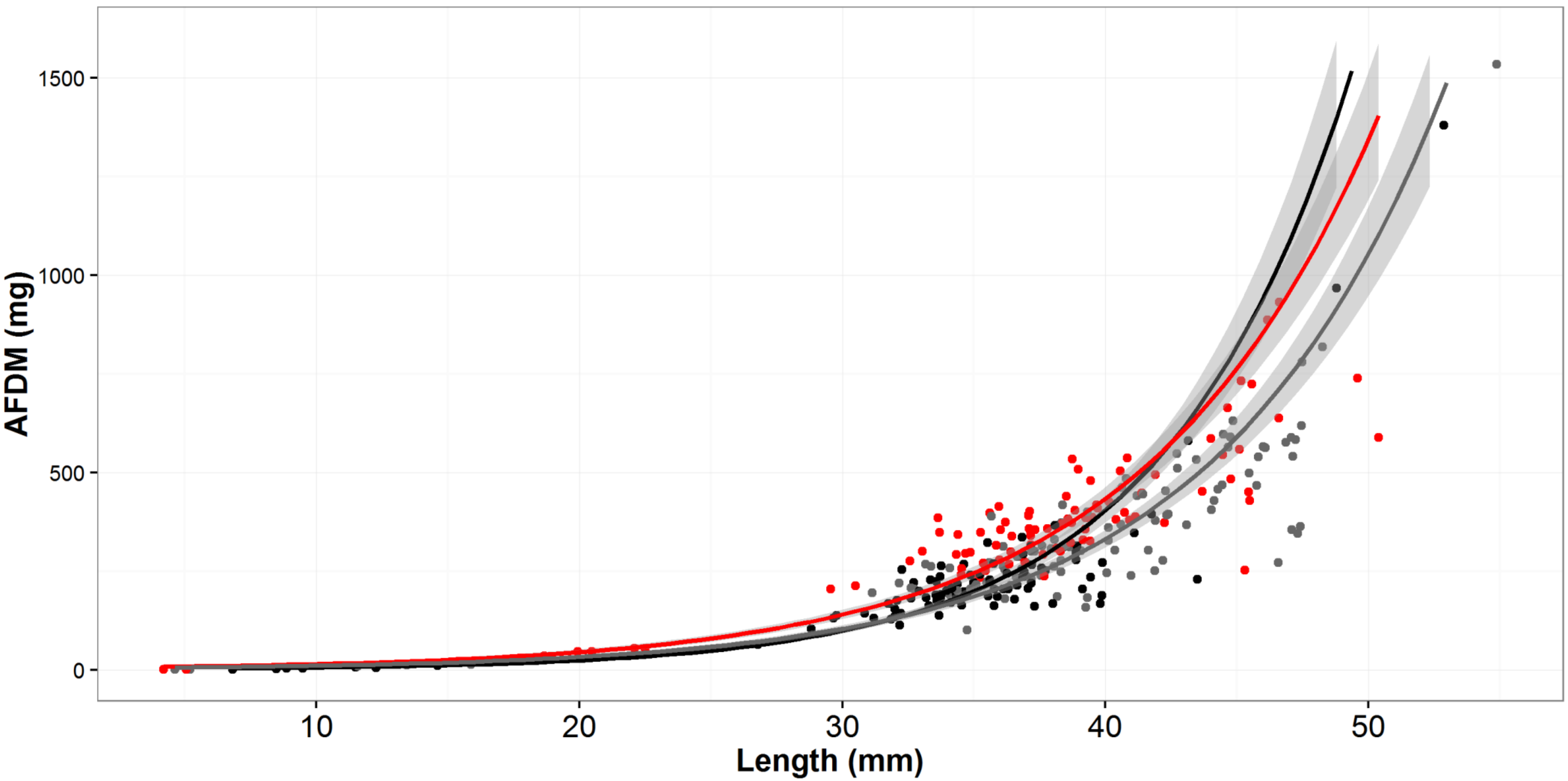

Figure 6. The relationship between length and weight (in mg AFDM) of *R. philippinarum* in areas of different fishing intensity within Poole Harbour. Black line = Holton Mere (heavy fishing); red line = Wytch Lake (low fishing); grey line = Holes Bay (closed).

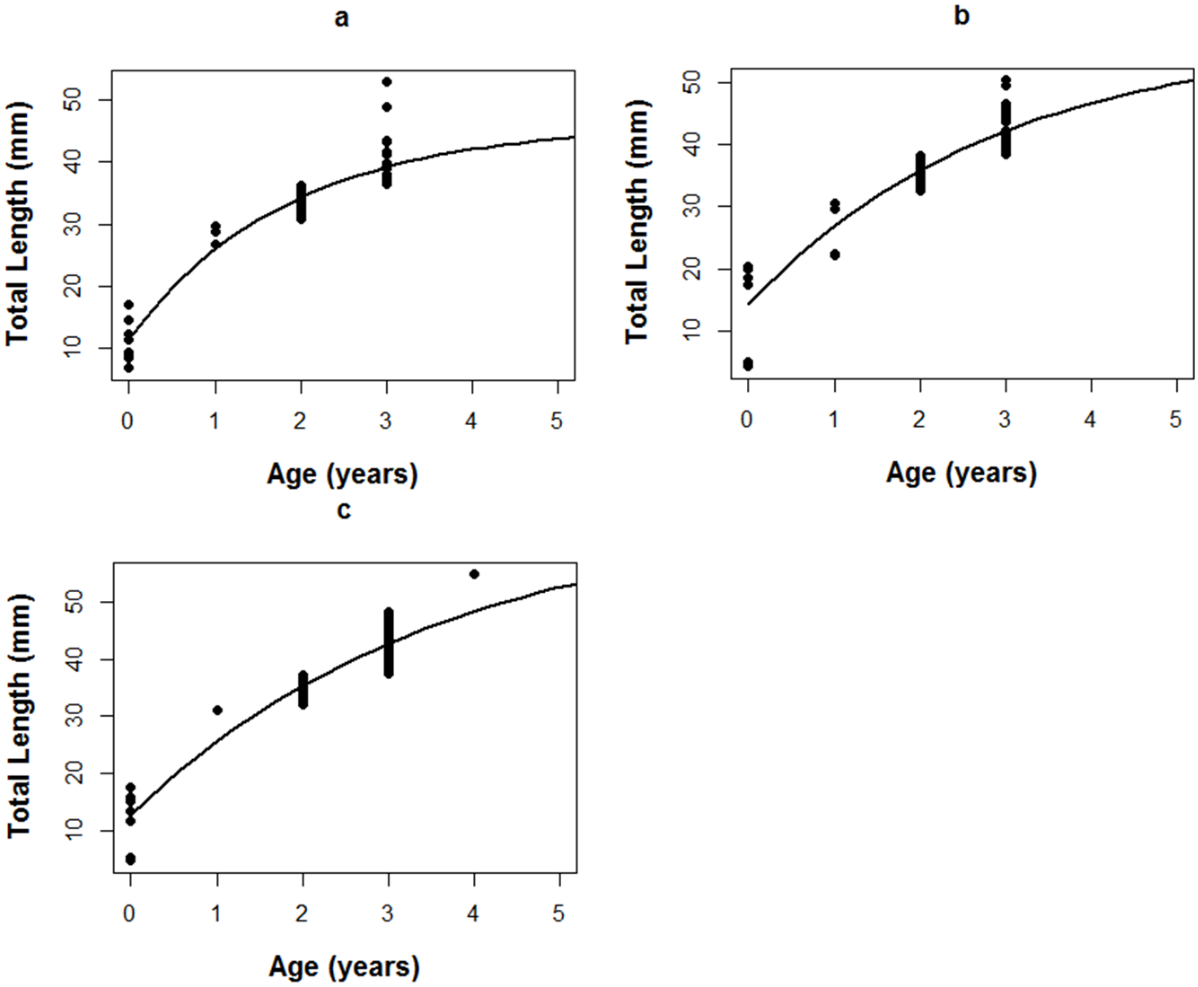

Figure 7. Von Bertalanffy growth curves fitted to length-at-age data of *R. philippinarum* from a) Holton Mere (heavy fishing); b) Wytch Lake (low fishing); c) Holes Bay (closed) in Poole Harbour, UK.

Tables

Table 1. Study sites in Poole Harbour, UK in which *R. philippinarum* was sampled in June 2015 and January 2016.

Site	Fishing Intensity	Fishing Sightings (July – December)
Holton Mere	High (open 1st July – December 25th)	81
Wytch Lake	Low (open 1st July – October 31st)	14
Holes Bay	None (closed)	0

Table 2. Mean (± S.E.) length, density and biomass of *R. philippinarum* across each site before (June 2015) and after (January 2016) the 2015 fishing season. (Holton Mere: high intensity fishing; Wytch Lake: low intensity fishing; Holes Bay: closed site).

Site	Month	Length (mm)	Density (ind. m$^{2\ -1}$)	Biomass (mg)	Condition Index
Holton Mere	June 2015	34.80 ± 0.13	10.15 ± 0.67	No data	No data
	January 2016	31.05 ± 0.25	2.64 ± 1.60	218.75 ± 18.15	3.60 ± 0.09
Wytch Lake	June 2015	36.89 ± 0.42	1.29 ± 0.67	No data	No data
	January 2016	35.35 ± 0.26	3.20 ± 0.46	365.88 ± 17.90	4.58 ± 0.10
Holes Bay	June 2015	40.66 ± 0.21	4.40 ± 0.84	No data	No data
	January 2016	36.70 ± 0.19	4.61 ± 1.35	342.54 ± 20.83	4.21 ± 0.10

Table 3. ***R. philippinarum*** **cohort estimates derived from Bhattacharya's method within FiSAT II and the mixdist package in R. (Holton Mere: high intensity fishing; Wytch Lake: low intensity fishing; Holes Bay: closed site).**

Site	Mean Cohort Size (mm)		Age Class
	Bhattacharya	mixdist	
Holton Mere	NA	NA	0
	25.00	24.20	1
	34.79	33.78	2
	NA	37.81	3
Wytch Lake	NA	NA	0
	30.00	31.80	1
	36.96	34.94	2
	42.96	40.65	3
	NA	NA	4
Holes Bay	NA	NA	0
	NA	NA	1
	34.30	34.27	2
	40.87	40.61	3
	54.01	53.13	4

Table 4. Parameter estimates of the Von Bertalanffy growth curves fitted to length-at-age data of *R. philippinarum* from each site sampled after the 2015 fishing season in January 2016. (Holton Mere: high intensity fishing; Wytch Lake: low intensity fishing; Holes Bay: closed site).

Site	L_{∞} +/- S.E.	K +/- S.E.	t_0 +/- S.E.
Holton Mere	46.02 +/- 2.47	0.54 +/- 0.08	-0.53 +/- 0.08
Wytch Lake	57.52 +/- 6.10	0.35 +/- 0.08	-0.81 +/- 0.16
Holes Bay	66.29 +/- 9.69	0.27 +/- 0.08	-0.77 +/- 0.15