



From individual vital rates to population dynamics: An integral projection model for European native oysters in a marine protected area

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Abstract

1. Following an 85% decline in global oyster populations, there has been a recent resurgence in interest in the restoration of the European native oyster *Ostrea edulis*. Motivations for restoration from environmental stakeholders most often include recovering lost habitats and associated biodiversity and supporting ecosystem function. In coastal communities, another important justification is recovery of traditional and low-impact fisheries but this has received less attention.
2. Many restoration projects across Europe focus on the translocation of adult stocks, under the assumption that the limit to population growth and recovery is adult growth and survival. This may not necessarily be the case, especially where knowledge of large extant adult populations exists as in the Blackwater, Crouch, Roach and Colne Marine Conservation Zone in Essex, UK. Identifying what limits population growth for restoration and recovery is an important conservation tool.
3. Here, the first size-dependent survival, growth and fecundity data for free-living *O. edulis* from a novel field experiment are used to parameterize an Integral Projection Model that examines the sensitivity of a flat oyster population to variation in individual vital rates and to potential harvesting – an original objective of a coastal community-led restoration project.
4. Given the high adult fecundity in this species, population recovery is most sensitive to changes in recruitment success; however, elasticity (proportional sensitivity of the population) is more evenly spread across other parameters when recruitment is already high. Based on locally agreed management objectives, recovery to double the current stock biomass should take 16–66 years (mean = 30 years) without active intervention. At that point, harvest rates could be sustained below 5% of the harvestable adult size whilst ensuring λ_s remains above 1.

KEYWORDS

integral projection models, invertebrates, life histories, oysters, population dynamics

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1 | INTRODUCTION

Once a common species around all coastlines of the UK and widespread throughout Europe, the European native oyster, *Ostrea edulis*, has now been reduced to a few remaining strongholds, with oyster populations of all species thought to have declined by as much as 85% worldwide (Beck et al., 2011). In recent years, however, there has been a resurgence in European native oyster restoration across the historical range of this species (Pogoda, Brown, Hancock, & von Nordheim, 2017).

Many oyster restoration projects cite an ecosystem service as their primary motivation for restoration. These range from potential biodiversity benefits from the presence of flat oyster beds or reefs (Lown, 2019; Pogoda, 2019) to potential filtration benefits resulting in increased water quality (Rodriguez-Perez et al., 2019; Wilson, 1983). While not yet common in oyster restoration in Europe there is also a long history of restoration and conservation interventions for restoring traditional shellfish fisheries (Allison, Hardy, Hayward, Cameron, & Underwood, 2020).

Many European native oyster restoration projects are directed towards the translocation of adult stock (i.e. the movement of oysters from coastal areas of high/higher abundance to areas of low abundance), with population status largely assessed via estimated abundance or biomass of adults (Marine Management Organisation, 2019). This is in part due to the very low abundance or extinction of native oysters from many areas (Fariñas-Franco et al., 2018). However, this may not always be the most appropriate method to assess and restore *O. edulis* populations, especially in those areas where oysters already have significant local stocks (e.g. Scotland, Ireland, Essex) (Eagling, Ashton, & Eagle, 2015; Lown, 2019; McGonigle, Jordan, & Scott, 2016). It is also good conservation practice to *a priori* examine what life history stages are most likely to respond to restoration or management interventions, and thus affect population growth (Montero-Serra et al., 2018). Such comprehensive assessments of population status and sensitivity require real-time measurements of demographic parameters such as size structure, growth, survival and fecundity of individuals in the population (Caswell, 1989; Ellner & Rees, 2006; Merow et al., 2014). Once undertaken, these modelling approaches can determine if populations are likely to be influenced by changes to recruitment or survival, thus informing management. For example, increasing spat settlement and survival via manipulation of habitat may be a more appropriate restoration tool than translocating adult oysters, or halting their fishing in a given area.

Previous studies have monitored the growth rates and survival of various oyster species in aquaculture or laboratory settings in controlled environments, in bags at high density above the seabed or in cages. However, data in a useable format for modelling are rarely published (Katkansky, Dahlstrom, & Warner, 1969; Pogoda, Buck, & Hagen, 2011). In addition, no study to date has simultaneously monitored individual vital rates such as growth and survival of flat oysters at naturally occurring densities (Allison, 2017; Helmer et al., 2019; Lown, 2019), particularly on the sea bed

where smothering, predation risk and food resources may differ from conditions when raised above the benthos or in aquaculture settings (Sawusdee, 2015; Zwerschke, Emmerson, Roberts, & O'Connor, 2016). In order to appropriately monitor the success of restoration projects it is essential for these demographic data to be regularly estimated *in-situ* and incorporated into model predictions of responses to restoration activity.

A number of different types of population model are available to assess and make predictions on populations using vital rates such as growth, survival and fecundity. Individual based models follow every individual within a population to assess individual outcomes and consider individual-specific characteristics and dynamics, with population dynamics a sum of these outcomes. Conversely, distribution based models follow populations and their dynamics via population-level distributional changes (Picard & Liang, 2014). Subsequent differences between model types are largely due to the continuous or discrete nature in which age or size, time and/or reproduction are treated. Examples of these range from matrix based models whereby both time and size or age are discretized, to Ordinary Differential Equations or Physiologically Structured Population Models where time, reproduction and size are usually treated as continuous variables (de Roos & Persson, 2013; Picard & Liang, 2014).

Integral projection models (IPM) also use discretized time, calculating the dynamics of, and changes in, abundance and vital rate distributions of populations over fixed periods of time. Time segments can be set to any unit, e.g. 1 day, 1 month or 1 year, depending on the lifespan of the species under investigation (Merow et al., 2014). IPMs use a series of regression equations to parameterize growth, survival and reproduction rates to incorporate individual-based variation within the growth transition part of the model (Picard & Liang, 2014). IPMs use an integral equation called a kernel to describe changes of state of individuals from one timestep to another (e.g. their growth, survival and fecundity and how these are likely to change with each other throughout an individual's life; Merow et al., 2014; Rees, Childs, & Ellner, 2014). This means that IPMs are useful in situations where abundance estimates from census data are based on discrete timesteps whereas data on life stage-dependent vital rates have been collected as a continuous distribution, such as annual growth rates and survival. For this reason, an IPM of an *O. edulis* population and population dynamics is presented with how it can be used in restoration projects.

This study is of the native oyster populations in the Blackwater, Crouch, Roach and Colne Estuaries Marine Conservation Zone (BCRC MCZ) in Essex in the southern North Sea. The overall objective of the MCZ is to protect and recover native oysters and their habitats, with the population maintained in numbers which enable it to thrive (UK GOV, 2013). Undertaking active intervention is recognized as required to achieve this aim (Allison, 2017; Helmer et al., 2019). The Essex Estuaries have a long cultural history of oyster fishing, dating back to Roman times, with the Colne and Blackwater oyster fisheries listed in the Domesday Book (Benham, French, & Leather, 1993). Local oystermen are one of the biggest

champions of oyster restoration in Essex and have successfully restored the species over the last 35 years to about 8.27 km² of the 284 km² MCZ (i.e. the Tollesbury & Mersea private several order – Allison et al., 2020). The MCZ management group is charged with recovery of native oysters to 'good ecological status' throughout the rest of the MCZ and with an associated management aim of permitted sustainable harvesting of the oyster for local aquaculture once this status has been achieved (KEIFCA, 2019a; KEIFCA, 2019b). The statutory bodies responsible for the MCZ, Kent & Essex Inshore Fisheries and Conservation Authority, Natural England and stakeholders, have determined that in order for it to be considered in good status, the population of European native oysters must be 'thriving', amongst other factors such as the identity and abundance of associated species. One such measure that has been determined for what it would mean to be thriving is that the population would have to have continuous growth and have at least doubled from current stock size to reach a biomass of 800 t (KEIFCA, 2018).

The aim of this study is therefore to obtain locally relevant demographic information for native oysters in the BCRC MCZ and use this in an IPM modelling framework to assess how long recovery of the population may take under current growth, survival and reproduction rates and, subsequently, how a 'restored' population may respond to reintroduction of harvesting – one of several restoration objectives.

2 | METHODS

2.1 | The life cycle of *O. edulis*

The European native oyster is a protandric, sequentially hermaphroditic, slow growing bivalve. It spawns in the summer months (June to September) with offspring experiencing up to 10 days of brooding then up to 10 days of larval phase before settling as spat onto hard substrate (Helmer et al., 2019). Unlike the more widely studied *Crassostrea* spp., *O. edulis* is largely subtidal and is ovoviviparous. In addition, *O. edulis* are notoriously difficult to age, not exhibiting clear nacreous rings on the exterior of the shell. When these rings are visible, *O. edulis* may occasionally lay down multiple rings in a single growing season (Orton & Amirthalingam, 1927; Richardson, Collis, Ekaratnc, Dare, & Key, 1993). This means that IPMs incorporating age, as have been created with Eastern oysters (Moore, Lipcius, Puckett, & Schreiber, 2016; Moore, Puckett, & Schreiber, 2018), are not currently appropriate for this species.

2.2 | The IPM

An IPM maps the distribution of some form of vital rate that changes over an individual's life, such as size or age at time t , to the distribution of that same vital rate at time $t + 1$ (Merow et al., 2014). For the model of *O. edulis* in Essex, the main vital rate used to predict changes in the population was body size, data that is collected by most

fisheries and restoration programmes globally. Area of the oyster (mm²) was used as a proxy for body size assuming each oyster to have an elliptical shape [i.e. area = (height/2)(length/2) π]. This was deemed most appropriate owing to the nature of oyster growth, with some oysters growing in length rather than shell height (Lown, 2019). This model was developed following the collection of three primary types of data. These data were growth and survival data from an individual-based monitoring experiment (hereafter referred to as the string experiment), census data from multi-year extensive dredge surveys, and finally, reproduction and fecundity data from a literature review and assessment of the prevalence of fecund females during the breeding season. All field data were collected from within the BCRC MCZ between 2014 and 2019, during which time no harvesting of oysters was permitted to occur.

2.3 | Dredge surveys: population census data

Extensive dredge surveys were carried out between 2014 and 2019 using a 1.2 m width ladder dredge, with a 22 mm spaced ladder blade and 40 mm diameter mesh, towed at a ground speed of 2 knots for approx. 100 m. The initial survey in 2014 consisted of 235 dredge samples with a single initial dredge per 0.5' latitude and 1' longitude gridsquare. If oysters were present, a further four samples were taken in each of the north-west, north-east, south-west and south-east areas of the gridsquare. A reduced number of sites where *O. edulis* were found in 2014 were sampled in 2015 ($n = 67$ total dredges). From 2016 onwards, only areas where either *O. edulis* or *C. gigas* were found were sampled, including the five replicates per station where possible, avoiding land or extremely shallow water depths over 21 stations. This resulted in 393 dredge samples in March surveys between 2016 and 2019 across the 284 km² Marine Conservation Zone (99 sites per survey with only 96 in 2016 owing to boat constraints). Between 2016 and 2019 each oyster was measured for shell height (i.e. hinge to tip), length (longest point perpendicular to the length) and width (depth of both sides of oyster shell at the widest point) using Vernier callipers to assess the size distribution of the oyster population. Prior to this (i.e. 2014–2015), oysters were only measured for height. Whilst every effort was made to assess spat in this survey, the large sample sizes associated with dredge surveys and dredge ring size of 40 mm may have resulted in lower detection of smaller size classes, see parameter estimation and equation 1 for how this was accounted for within the model. For more information regarding dredge survey methods see Lown (2019). Total population size was estimated using inverse distance weighting (IDW) of the raster matrix using weighted averaging in ArcMap version 10.6.1, ArcMap, 2018) (Chen et al., 2016; McGonigle & Scott, 2012), constrained by individual oyster beds, outside of which oysters were not observed in extensive surveys performed in 2014 (for more information regarding bed boundaries see Lown, 2019). IDW works by calculating unknown values through interpolation within a specified area, weighted by the value of points closest to those being estimated

(Chen et al., 2016). A power value of 2 was used with five points used to calculate each interpolated cell owing to the five-point sampling design of the census survey and to give higher power of influence of near sites over more distant ones. An output cell size of 10×10 m was used to speed processing whilst maintaining a high-level detail within the calculation. Data from post-winter (March) surveys were used for the IPM census data.

2.4 | String experiment: individual-based data

To monitor growth and survival rates of individual oysters, an *in situ* experiment was designed. This was largely based around tile-, plate- or frame-based monitoring of individual oysters in studies such as Garland and Kimbro (2015) and Zwerschke et al. (2016). In comparison with these methods, where oysters were attached at high densities above the seafloor on tiles or frames, the method used in this study used oysters attached to strings at a lower density of 2 oysters m^{-2} ; this represents a common density observed in the dredge survey when assessed at the $100 m^2$ scale. Here, two oysters attached to 15 cm offshoots from a central string at 1 m intervals allowed oysters to be monitored between March 2017 and March 2018 in low, naturally occurring densities and, most importantly, on the seafloor where mortality from smothering and or predators more closely mirrored natural conditions (Figure 1). Each string had 20 oysters attached, with three strings per site. A further three strings were set at each site

in September 2017 to September 2018; however, these data are not used in this model with the model based on March census data only. Some strings were lost in storms during the study period, resulting in a total of 177 oysters used for analysis.

Three sites within the BCRC MCZ area were selected, based around existing distributions of native oyster observed within the dredge surveys (1, Blackwater estuary mouth, south of Mersea Island; 2, Ray sand; and 3, Crouch estuary mouth). Oysters monitored on strings at each site were collected during dredge census surveys from close proximity to the redeployment site to account for any local adaptation the oysters may represent for individual areas within the BCRC MCZ. These oysters consisted of a range of sizes reflecting the local size distribution, to assess the growth and survival rates of all sizes of oysters present.

Oysters were attached to the strings close to the hinge on the left valve, where natural attachment to substrate would occur. Milliput® (Dolgellau, UK) was used as the adhesive to attach oysters to the strings. The Milliput was marked using indentations and individual offshoots tagged using cable ties to identify individual oysters and left to cure overnight. Strings were then deployed the following day.

To monitor growth and survival, strings were hauled every 3 months (June, September, December and March); however, March 2017 to March 2018 data only were used for IPM analysis to provide annual growth and survival rates based on a pre-reproductive census. During this time, individual oysters were measured for height and length using Vernier callipers. In addition, any mortalities or newly settled oysters were recorded. Strings and marker buoys were cleaned of any debris and algal growth to maintain the experiment at each monitoring event.

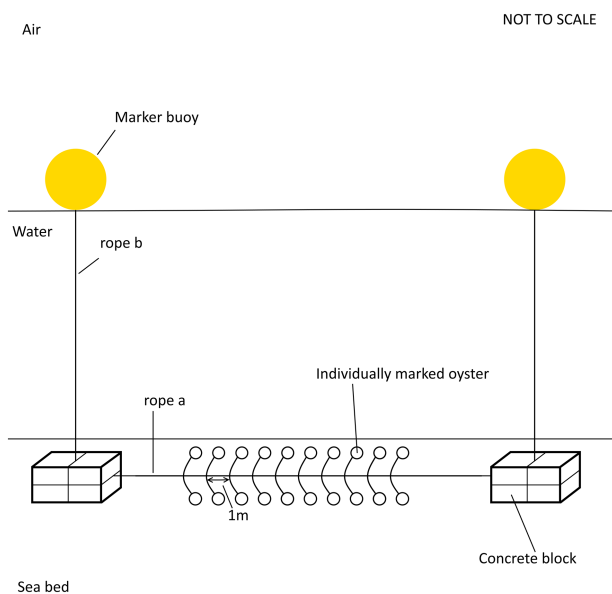


FIGURE 1 Schematic of the experimental design for the string-based growth and survival experiment. The concrete blocks act as anchors, marked using buoys/fenders and oysters are directly attached to rope using Milliput adhesive. Two types of rope were used: a 5 mm polypropylene rope (rope b) was used to attach marker buoys and a 2.5 mm polyester rope used to tether the oysters (rope a) (Lown, 2019)

2.5 | Parameter estimation

Oysters monitored in the string experiment described above between March 2017 and March 2018 were used for parameter estimation ($n = 177$), with the initial IPM model aiming to capture the dynamics of an annual pre-reproductive census in the following year(s). In order to capture how vital rates vary with size (area, mm^2), a series of General Linear Models were built: a binomial error distribution (logit link) for the survival data; a Gaussian error distribution for growth increases from time t to $t + 1$; and Poisson error distribution (log link) for the size-based fecundity regression. Owing to the lack of data available to assess new recruit size, a mean size of 750 ± 500 (SD) mm^2 was used for new recruit size from the previous breeding season (~ 30 mm height). Owing to the long breeding season when new recruits may be able to grow a substantial amount between the start and the end of the season (e.g. an oyster settled in May will be larger than an oyster settled in September by the following March), a large standard deviation for recruit size was deemed necessary to incorporate the wide range of sizes of new recruits. Initial starting size distribution of the population was estimated from measurements of all oysters observed in the census dredge surveys, adjusted to the total estimated population size estimated as described above using IDW,

assuming that oysters of all sizes had equal probability of being landed. To take into account the discreteness of sites within the overall population, parameters for each site were estimated individually and combined under a weighted average, weighted by the numbers present in each site in the March 2017 census. This resulted in a single IPM representing the whole BCRC MCZ area that takes account of the variation between the main sub-sites.

With *O. edulis* known to change sex after each breeding event, sex ratios and the percentage of the population likely to be a fecund female may vary between years. Size-based fecundity of oysters was estimated using egg counts extracted from Cole (1941) with a linear regression used to calculate height-based fecundity of ripe oysters. Owing to the potential for some oysters not to reproduce or to only reproduce as males, the percentage of fecund females within the population (i.e. females with white, grey or black 'sick') was estimated by sacrificing 149 oysters collected from the Blackwater estuary and Ray Sand within the BCRC MCZ between 22 June and 2 July 2018 to assess size-based likelihood of reproduction (mean = 73.26 ± 0.99 mm). Oysters were measured, wet-weighted and opened to check for the presence of white, grey or black 'sick' to indicate the presence of unfertilized, fertilized and developing, or near ripe eggs within the female mantle cavity (Younge, 1960). The percentage of mature females in the adult population was then included within the model as the probability of reproduction parameter or P_{rep} .

As with many species which include a cryptic life stage (e.g. larval stage or dormant seed stage), a common technique to overcome this 'unknown' is to implement a 'black box' called the establishment probability (P_{estab}). This method was used in this model owing to the larval stage of *O. edulis* lifecycle (Merow et al., 2014). P_{estab} was calculated using equation 1 for 2015–2019 (estimation for 2014 was not possible as an estimate of the previous year of adult population is required to estimate the probability of recruitment).

$$P_{estab} = \frac{J_{t+1}T_{t+1}}{A_t T_t f_{eggst}} * 4.34 \quad (1)$$

Here, J_{t+1} is the ratio of the measured population under 30 mm height at time $t + 1$ and T_{t+1} is the total census estimated population calculated through IDW. A_t is the ratio of the measured population 40 mm height or greater at time t (i.e. sexually mature adults), with T_t the total estimated population at time t and f_{eggst} the size-based fecundity for the average height adult at time t (i.e. the average height of an adult in the year for which reproduction is being calculated), incorporating a P_{rep} (i.e. 13.4% of the population likely to be fecund females) to individual fecundity estimates owing to sex ratios described previously with different numbers of females and males within the population in any one year owing to the sequential hermaphroditism exhibited in *O. edulis*. This, therefore, assumes that the same proportion of the population is fecund females each year. The value calculated was then multiplied up by 4.34. This was viewed as a detection coefficient and resulted in standardized establishment probability between settlement observed

on the string experiment in 2018 vs. recruitment observed in census surveys. It is recognized that this detection coefficient only results in scaled-up estimates of *O. edulis* spat settled on oyster shell and may not be incorporating oysters settled on other shell types. Owing to strings being more thoroughly checked over than the often-large dredge samples, detection of smaller sized oysters will have been reduced in census surveys despite shell substrate being available to assess.

2.6 | The IPM

The integral kernel used to create the IPM and map the size distribution at time t to the distribution at $t + 1$ (1 year later) was taken from (Merow et al., 2014):

$$N_{t+1}(z') = \int_{\Omega} K(z', z) n_t(z) dz \quad (2)$$

$$N_{t+1}(z') = \int_{\Omega} [P(z', z) + F(z', z)] n_t(z) dz \quad (3)$$

where z is the area in mm^2 of the oyster at time t and z' is the area in mm^2 at time $t + 1$. $n_t(z)$ is the size distribution of the population at time t and Ω denotes the possible range of sizes of the population. K is the full kernel, comprising P and F . P is the growth and survival kernel calculated to be:

$$P(z', z) = s(z)g(z', z) \quad (4)$$

Where $s(z)$ is the size (area of oyster) based annual survival from time t to time $t + 1$. $g(z'|z)$ describes the probability density of size (z') that an individual of size (z) can grow in a single time step, conditioned on it having survived. $F(z', z)$ is the fecundity kernel where:

$$F(z', z) = p_{rep}(z) f_{eggs}(z) P_{estab} R \quad (5)$$

with $p_{rep}(z)$ the size-based probability of reproducing (assuming oysters under $1,200 \text{ mm}^2$ do not reproduce), $f_{eggs}(z)$ is the size-based fecundity, P_{estab} the probability of an egg establishing and surviving 1 year (equation 1) and R the size distribution of 1-year-old recruits (Merow et al., 2014).

Eviction was assessed using methods described in Williams, Miller, Ellner, and Doak (2012), integrating the growth function over the bounds of the model. Initial models indicated a high probability of eviction of the largest oysters (0.3608 with error 8.6×10^{-8}). The maximum size was therefore increased from 1.2 times the maximum observed size ($11,000 \text{ mm}^2$) to 1.8 times the maximum observed size ($16,334 \text{ mm}^2$). This new limit equates approximately to a height of 14.5 cm assuming equal height and length. This size of oysters has occasionally been observed in shell records, with the largest *O. edulis* in the UK measuring 17.8 cm with other oysters observed above 14 cm in the Solent (Helmer et al., 2019; NAFC Marine Centre, 2009).

This size range therefore remains within the natural limits of this species. Following recalibration of maximum sizes, the eviction rate of the largest oysters was <0.06 with error 6×10^{-5} , with smaller sizes a fraction of a per cent. Therefore, no further measures were taken to account for eviction of oysters from the model.

Lambda values (λ) (i.e. the population rate of change) were calculated from the first eigenvector of K (Merow et al., 2014) and subsequent abundance estimates from model calculations were compared with total population estimates calculated from dredge survey data and IDW calculations. Confidence intervals on λ were calculated by jackknife resampling of the initial data set and recalculating λ 1,000 times.

2.7 | Model validation

To validate the model, population size distribution data were projected forward by 1 year from March 2017 to March 2018 and mapped onto the measured size and abundance distributions from 2018 dredge survey data. The output distribution from this model (i.e. the model estimated size distribution for March 2018) was subsequently projected forward an additional year and mapped onto the measured size and abundance distributions from March 2019 dredge surveys, maintaining the parameter estimates from the 2017–2018 period. Owing to the high level of noise between the small bins associated with the raw measured size distribution data, smoothed mean density distributions calculated from 999 bootstrap permutations were extracted from the measured size distribution dredge survey data and compared with the density distribution for the output of the IPM model to assess model fit. These density distributions were then compared using two sample Kolmogorov–Smirnov tests to assess differences in patterns between the IPM predicted distributions and the measured distributions from dredge survey data, in addition means were compared using t -tests. Owing to poor estimates in projecting forward 2 years, two potential causes for this were addressed:

Scenario 1: An undetected recruitment event in 2017 resulting in underestimation of the 2019 observations.

To induce a large recruitment event, otherwise termed spatfall in oysters (scenario 1), all coefficients were kept constant as previously described; however, P_{estab} was altered to 8.0×10^{-6} for 2017–2018 alone, estimated from repeated stepwise simulations.

Scenario 2: High summer spat-of-year growth rates in 2018 resulting in measured size distribution of 2019.

To induce scenario 2 the size of new recruits was changed from $750 \pm 500 \text{ mm}^2$, to $2,100 \pm 700 \text{ mm}^2$ (estimated through repeated stepwise simulations) when projecting forward from the predicted distribution of 2018 to 2019. P_{estab} for this year was estimated using equation 1, assuming that any oysters observed under $2,800 \text{ mm}^2$ were new recruits observed in the 2019 survey

(with P_{estab} calculated as 3.63×10^{-6} using equation 1). All other parameters remained constant.

2.8 | Parameter-based sensitivity and elasticity

In order to pinpoint which parameters are most sensitive to changes in λ , parameter sensitivity (how sensitive λ is to changes in this parameter) and elasticity (proportional sensitivity) by finite difference analysis was performed on the IPM using the initial coefficients assuming a low recruitment event (i.e. $P_{estab} = 5.13 \times 10^{-7}$) and assuming high recruitment (i.e. $P_{estab} = 8.0 \times 10^{-6}$ – estimated under scenario 1 above to induce high recruitment). Here, each underlying regression parameter to the IPM kernel was perturbed at random within a set threshold (0.0001) to assess how λ is influenced by changes in these parameters as presented in Griffith (2017).

Sensitivity and elasticity of λ for the model assuming low recruitment (i.e. $P_{estab} = 5.13 \times 10^{-7}$) and assuming high recruitment (i.e. $P_{estab} = 8.0 \times 10^{-6}$), with all other parameters the same, were calculated to determine how small changes to each parameter leads to proportional changes in λ and to investigate how these change between high and low recruitment years.

2.9 | Understanding the consequences of increased oyster recruitment: establishment probability (P_{estab})

To understand impacts of recruitment, the measured abundance and size distribution of the population of *O. edulis* in the BCRC MCZ in March 2017 was projected forward by 100 years, selecting P_{estab} values calculated using equation 1 only at random (stochastic run 1, i.e. establishment probabilities of 5.13×10^{-7} , 2.22×10^{-6} and 3.79×10^{-7} calculated using equation 1 from the settlement of juvenile oysters in census surveys in previous years) and secondly, using an increased level of establishment probability, estimated when correcting model validations to predict the population size distribution in 2019 below (here termed stochastic run 2, i.e. using establishment probabilities of 5.13×10^{-7} , 8.0×10^{-6} , 3.79×10^{-7} and 2.22×10^{-6} selected at random each year). The mean of log population size was assessed to investigate long-term changes with stochastic lambda (λ_s) calculated as described in (Metcalf et al., 2015) using:

$$\log \lambda_s = \lim_{t \rightarrow \infty} \frac{1}{t} \log \|K_t \dots K_0 n_0\| \quad (6)$$

with $\|\bullet\|$ denoting total population size calculated in each year, as also used in Metcalf et al. (2015). The population size distribution measured in the March 2017 survey, scaled to the full estimated population, was used as the starting population distribution (n_0). Confidence intervals for λ_s were calculated by calculating λ_s for each stochastic run and extracting the 95% confidence intervals on these values.

2.10 | Understanding the consequences of decreased oyster survival: harvesting

With fishery stock size commonly estimated using biomass as outlined above, and the current IPM model calculating population abundance, to assess fishery impacts on the European native oyster population it was necessary to convert predicted size-based population estimates to biomass estimates. Methods regarding this process and caveats associated with it are described in Supporting Information Part 2.

Using stochastic projections of the higher recruitment success needed to capture 2017–18 recruitment, i.e. stochastic run 2, the population structure from the model for the year where the average log population size surpasses 800 t was extracted (i.e. where the red line on Figure 6b surpasses 800 t). Specifically the population size structure for the individual run that produced a stock biomass closest to, but above, 800 t was extracted. This new population size distribution was then used as a starting distribution to represent a 'restored' population of 800 tonnes of native oysters in the MCZ for introducing experimental harvesting to our stochastic models. Continuing with the establishment values used in stochastic run 2 (i.e. 5.13×10^{-7} , 8.0×10^{-6} , 3.79×10^{-7} and 2.22×10^{-6}), the model was projected forward from this point to estimate the response of the oyster population to different harvest rates and rules.

To induce harvesting mortality on the landable-sized oysters if an oyster was above 3,760 mm² [i.e. an oyster of shell height 70 mm, the minimum landing size in Essex, with average height to length ratio dimensions in Lown (2019) of 1.0236:1], a mortality parameter of 'harvest probability' was subtracted from 1 and multiplied to the existing function for mortality, such that a harvest parameter of 1 would result in all adult oysters being harvested (i.e. the survival of adult oysters would be 0). This new model with a new starting population size structure was projected forwards 100 years but with introduced annual harvest mortality of 0, 1, 2.5, 5 and 10%. Estimates of λ_s and corresponding confidence intervals were undertaken as described above.

All GIS analysis was performed using ArcMap 10.6.1 (ESRI, 2017) and statistical analysis performed in RStudio 1.1.456, R-3.5.1 (R Core Team, 2018; RStudio Team, 2018).

3 | RESULTS

Size frequency distributions of measured oysters observed in census surveys are shown in Figure 2 along with corresponding population size estimates calculated through IDW, assuming a 20% dredge efficiency (for corresponding analysis of dredge efficiency assumptions see Lown, 2019). Oysters were commonly larger than the largest oysters estimated in growth rates for previous studies indicating differences between historical and current populations (maximum size observed = 119 mm shell height vs. ~100 mm shell height) (Richardson et al., 1993); however, growth rates were

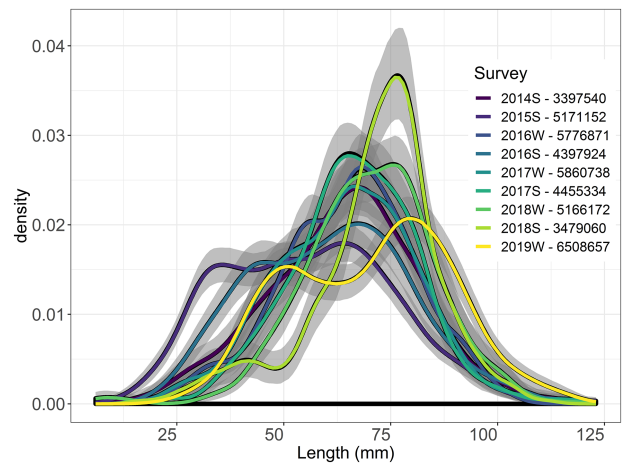


FIGURE 2 Height density plot for all oysters measured in dredge surveys between 2014 and 2019. Year_season indicates survey with W representing surveys completed in March to April and S surveys in August to September with corresponding population shown estimated assuming a 20% dredge efficiency and inverse distance weighting. The 95% confidence intervals were calculated using 999 bootstrap permutations. Density is not relative, so higher peaks do not necessarily mean higher numbers comparing between years

lower than those estimated in the same study. Here, it was estimated to take 4–5 years to reach 70 mm shell height vs. 2–3 years in Richardson et al. (1993).

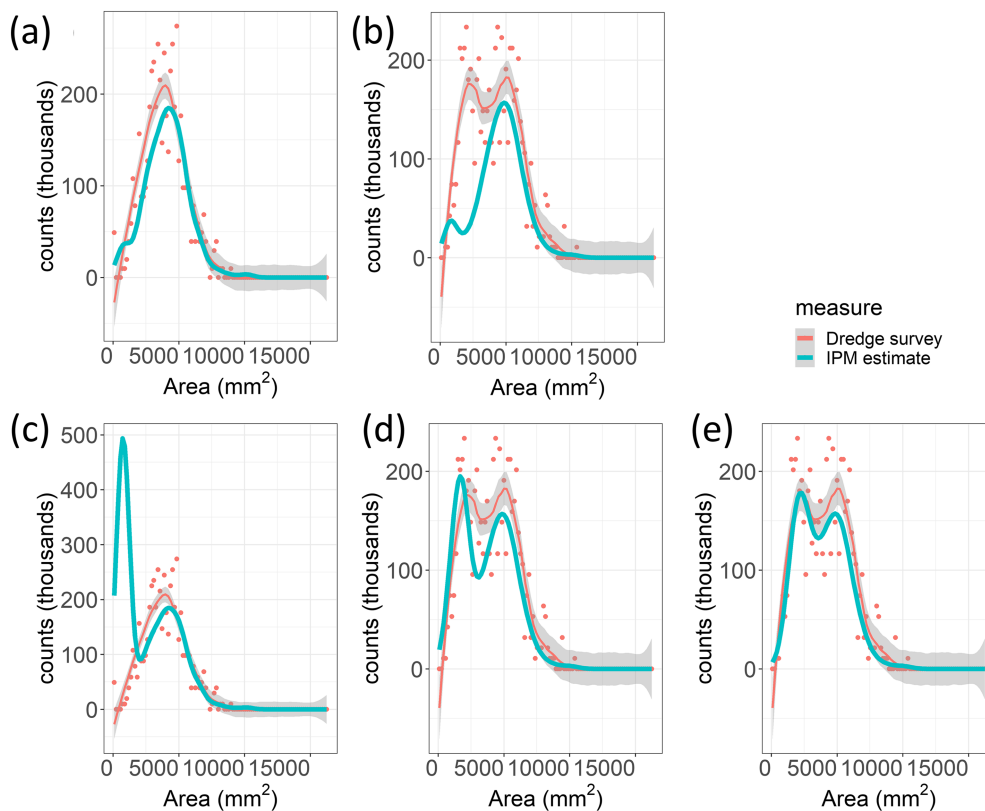
Coefficients extracted from regression equations to parameterize the IPM along with establishment probability estimates calculated using equation 1 can be found in Table 1 with kernel plots found in Supporting Information Part 1.

3.1 | Model validation

The initial model using coefficients listed in Table 1 resulted in an estimated λ for the whole MCZ site between March 2017 and March 2018 of 0.9911 (lower and upper 95% CI = 0.9910 and 0.9912 respectively). In the March-based survey for 2017, the population for the whole of the MCZ was estimated to be 5,860,737 assuming a dredge efficiency of 20% through IDW calculations (Lown, 2019). Applying a λ of 0.9911 resulted in a predicted 2018 population of 5,808,576 through projecting the population forward by 1 year. In the March 2018 survey, the MCZ population was estimated to be 5,166,172 through IDW calculations, therefore indicating a slight overestimation of the model prediction. Projecting forward 1 year from the measured size distribution of March 2017 to March 2018 resulted in the size distribution shown in Figure 3a. There was a statistically significant difference between the smoothed size distribution from the census survey in March 2018 and the IPM predicted size distribution (KS-test, $D = 0.19417$, $P = 0.04116$) but no difference in the mean sizes

TABLE 1 Individualbased site coefficients and coefficients for the Blackwater, Crouch, Roach and Colne Estuaries Marine Conservation Zone (BCRC MCZ) combined under a weighted average

Coefficient		Blackwater	Crouch	Ray Sand	MCZ _{coeff}
Survival intercept	SI	$8.70 \cdot 10^1$	$1.18 \cdot 10^1$	$3.38 \cdot 10^1$	$3.22 \cdot 10^1$
Survival slope	SS	$2.92 \cdot 10^4$	$4.05 \cdot 10^4$	$4.55 \cdot 10^4$	$4.19 \cdot 10^4$
Growth intercept	GI	$1.28 \cdot 10^3$	$1.07 \cdot 10^3$	$8.27 \cdot 10^2$	$9.62 \cdot 10^2$
Growth slope	GS	$8.17 \cdot 10^1$	$8.30 \cdot 10^1$	$9.55 \cdot 10^1$	$8.96 \cdot 10^1$
Growth standard deviation	GSD	$4.16 \cdot 10^2$	$4.97 \cdot 10^2$	$5.01 \cdot 10^2$	$4.90 \cdot 10^2$
Fecundity intercept	FI	$1.15E \cdot 10^1$	$1.17 \cdot 10^1$	$1.20 \cdot 10^1$	$1.18 \cdot 10^1$
Fecundity slope	FS	$5.39 \cdot 10^4$	$4.45 \cdot 10^4$	$3.75 \cdot 10^4$	$4.18 \cdot 10^4$
Recruit size mean	RM	$7.50 \cdot 10^2$	$7.50 \cdot 10^2$	$7.50 \cdot 10^2$	$7.50 \cdot 10^2$
Recruit size standard deviation	RMSD	$5.00 \cdot 10^2$	$5.00 \cdot 10^2$	$5.00 \cdot 10^2$	$5.00 \cdot 10^2$
Establishment probability	EP _{st}				$5.13 \cdot 10^7$

**FIGURE 3** (a) Estimated size distribution of *Ostrea edulis* population in the Blackwater, Crouch, Roach and Colne Estuaries Marine conservation zone dredge surveys in March 2018 (blue) compared with measured size distribution of *O. edulis* in the March 2018 census surveys with loess smoother added (red); $\lambda = 0.9765625$. (b) Estimated size distribution of *O. edulis* population in the Blackwater, Crouch, Roach and Colne Estuaries Marine Conservation Zone dredge surveys in March 2019 (blue) compared with measured size distribution of *O. edulis* in the March 2019 census surveys with loess smoother added (red) after projecting model a forward for 2 years; $\lambda = 0.9765625$. (c) Estimated size distribution of *O. edulis* population in the Blackwater, Crouch, Roach and Colne Estuaries Marine Conservation Zone dredge surveys in March 2018 (blue) compared with measured size distribution of *O. edulis* in the March 2018 census surveys with loess smoother added (red) assuming a high, undetected recruitment event occurred in March 2017 (scenario 1). (d) Estimated size distribution of *O. edulis* population in the Blackwater, Crouch, Roach and Colne Estuaries Marine Conservation Zone dredge surveys in March 2019 (blue) compared with measured size distribution of *O. edulis* in the March 2019 census surveys with loess smoother added (red) assuming that a high, undetected recruitment event occurred in March 2017 (scenario 1). (e) Estimated size distribution of *O. edulis* population in the Blackwater, Crouch, Roach and Colne Estuaries Marine Conservation Zone dredge surveys in March 2019 (blue) compared with measured size distribution of *O. edulis* in the March 2019 census surveys with loess smoother added (red) assuming high growth rates of juvenile oysters between 2018 and 2019 (scenario 2)

between the observed and predicted groups (two-sample *t*-test, $t = 0.75802$, d.f. = 201.94, $P = 0.4493$). This difference in distribution is largely associated with an underestimation of smaller-size class frequencies within the IPM model (Figure 3a). Projecting forward 2 years from the measured size distribution of March 2017 to March 2019 resulted in the size distribution shown in Figure 3b. A clear difference between distributions is observed (KS-test, $D = 0.27184$, $P < 0.001$) with a difference between the means (two-sample *t*-test, $t = 2.168$, d.f. = 198.64, $P = 0.0313$).

3.2 | Using model scenarios to find missing juvenile oysters

3.2.1 | Scenario 1: an undetected recruitment event in 2017 resulting in underestimation of the 2019 observations

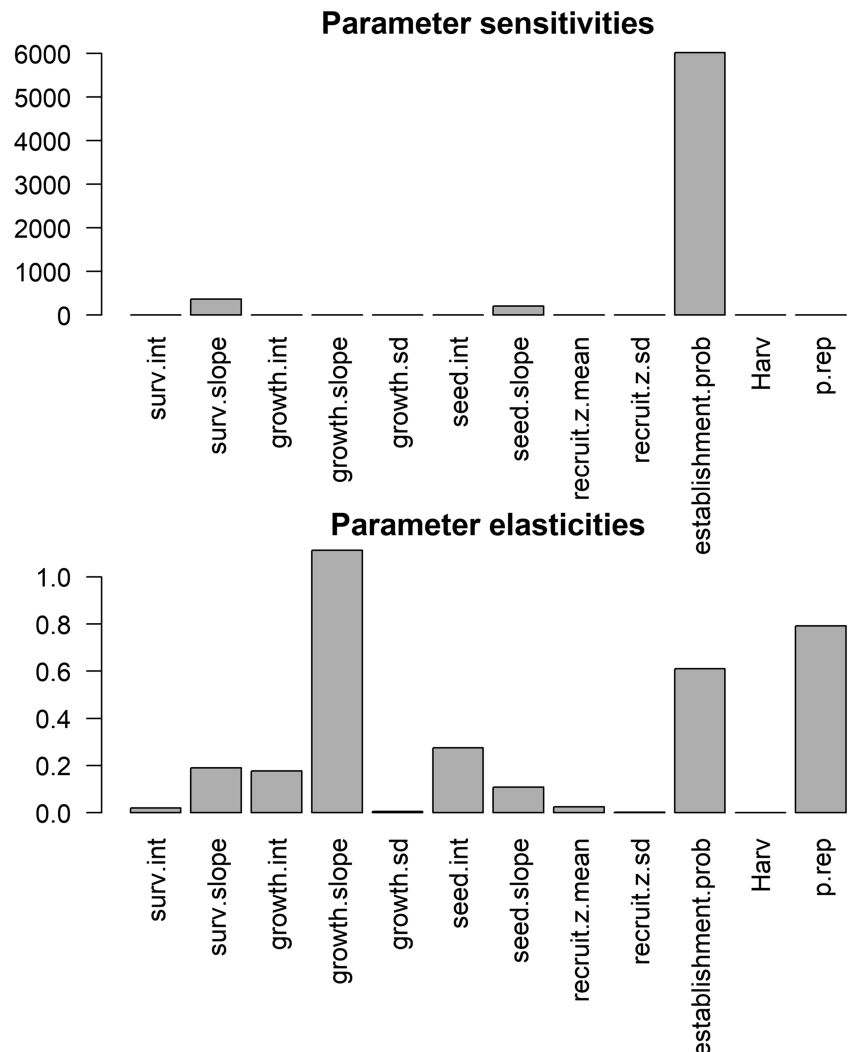
The increased recruitment pulse is shown in Figure 3c with subsequent 2019 distribution in Figure 3d. A significant difference

between the measured and predicted distribution in 2019 is still observed (KS-test, $D = 0.2524$, $P = 0.0028$), with no statistical difference now observed between means (two-sided *t*-test, $t = 0.9616$, d.f. = 195.14, $P = 0.3375$). This resulted in $\lambda = 1.11437$ (upper and lower 95% CI = 1.11448 and 1.11426) between 2017 and 2018. This resulted in the model predicting a total of 7,910,449 oysters in 2018 compared with 4,303,992 if recruitment was 0 (Figure 3c).

3.2.2 | Scenario 2: high summer spat-of-year growth rates in 2018 resulting in measured size distribution of 2019

No differences were made to the 2018 model for this scenario with the only differences observed in 2019. There is a statistical difference in the overall distribution between the model output and measured distribution in 2019 (KS-test, $D = 0.2524$, $P = 0.0028$) with no difference between means (two-sided *t*-test, $t = 1.0572$, d.f. = 194.02, $P = 0.2917$).

FIGURE 4 Parameter sensitivity (above) and elasticity (proportional sensitivity) of the basic IPM with zero harvesting and low establishments probability. Parameters are: surv.int (survival intercept), surv.slope (survival slope), growth.int (growth intercept), growth.sd (growth standard deviation), seed.int (fecundity intercept), seed.slope (fecundity slope), recruit.z.mean (recruit size mean), recruit.z.sd (recruit size standard deviation), establishment.prob (establishment probability, here set to 5.13×10^{-7}), Harv (probability of harvest of adult oysters – here set to 0), p.rep (probability of being a fecund female – here set to 0.135 i.e. 13.5%)



3.3 | Parameter sensitivity

The sensitivity and elasticity of the current population is shown in Figure 4 assuming a small recruitment event in 2017. Figure 5 shows the sensitivity and elasticity of this same population if there was a large recruitment event in 2017 (i.e. establishment probability = 8.0×10^{-6}). Both models incorporate the same growth and survival parameters. In both scenarios sensitivity is primarily associated with changes in parameters associated with recruitment (i.e. the establishment probability of larvae). In years of lower recruitment, the population is elastically sensitive to adult growth, the establishment of new recruits and the proportion of population that are fecund females. Elasticity analysis in years of high recruitment switches to show lower elasticity levels for the establishment of new recruits and the proportion of the population that are fecund females, whilst increasingly sensitivity to the seed intercept (i.e. fecundity of smaller sized oysters), the fecundity of adult oysters and the growth and survival of adult oysters.

3.4 | Understanding the consequences of increased oyster recruitment: establishment probability (*P.establish*)

Initial stochastic models (stochastic run 1), varying *P.establish* at random from those calculated from dredge data between 2016 and 2018 and assuming no large recruitment event in 2017 results in the *O. edulis* population increasing slowly over time with $\lambda_s = 1.001927$ (upper and lower 95% CI = 1.002218 and 1.001636 respectively; Figure 6a). However, following discussions with local oyster growers and local experts, it was deemed that scenario 1 was the most likely to have occurred and that an initially undetected large recruitment event occurred in 2017 with *P.establish* potentially as high as 8.0×10^{-6} . Therefore, a second forward projection model was run including this measurement as well. This resulted in a forward projection shown in Figure 6b (stochastic run 2) with equal probability of *P.establish* being 8.0×10^{-6} , 3.79×10^{-7} , 2.22×10^{-6} and 5.13×10^{-7} , resulting in a λ_s value of 1.039455 (upper and lower 95% CI = 1.040117 and 1.038792 respectively), i.e. 1 in 4 years of very high establishment, 1 in 4 of high and 2 in 4 of low (Figure 6b).

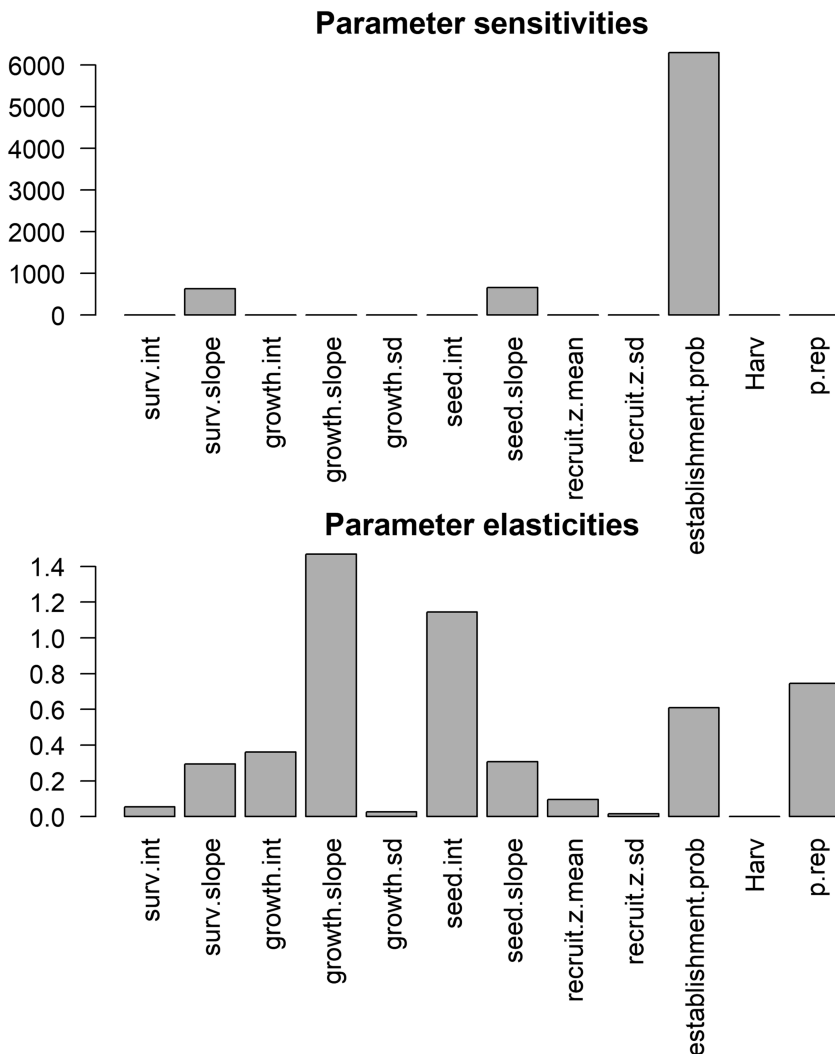


FIGURE 5 Parameter sensitivity (above) and elasticity (proportional sensitivity) of the basic integral projection models (IPM) with zero harvesting and high establishment probability. Parameters are: surv.int (survival intercept), surv.slope (survival slope), growth.int (growth intercept), growth.sd (growth standard deviation), seed.int (fecundity intercept), seed.slope (fecundity slope), recruit.z.mean (recruit size mean), recruit.z.sd (recruit size standard deviation), establishment.prob (establishment probability, here set to 8.0×10^{-6}); Harv, probability of harvest of adult oysters - here set to 0; p.rep, probability of being a fecund female - here set to 0.135, i.e. 13.5%

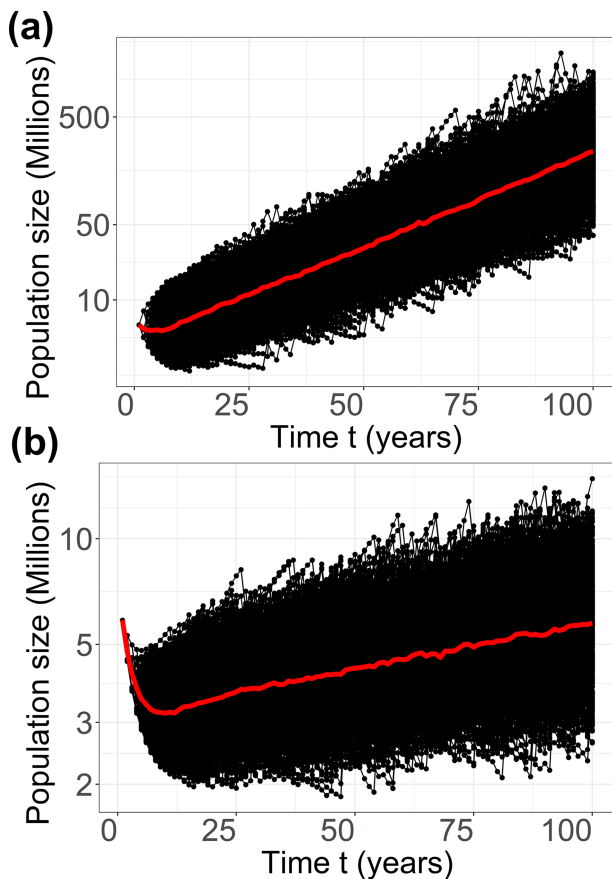


FIGURE 6 (a) Stochastic forward projection of 500 runs, projecting forward for 100 years from March 2017 changing establishment probability at random within estimated measured values between 2016 and 2018, not assuming a large recruitment event in 2018; λ_s value = 1.0032. The red line highlights mean log population size for all model runs with black lines representing individual model runs. (b) Stochastic forward projection of 500 runs, projecting forward 100 years assuming an unobserved recruitment event in 2017 and subsequently changing establishment probability at random between 5.13×10^{-7} , 8.0×10^{-6} , 3.79×10^{-7} and 2.22×10^{-6} ; λ_s value = 1.0211. The red line highlights mean log population size for all model runs with black lines representing individual model runs

When converted to biomass, the mean log stochastic projection of the BCRC MCZ oyster populations (i.e. the stochastic model shown in Figure 6b) reaches 800 t in 30 years (range 16–66 years). Note this analysis excludes oyster populations in the four main rivers (Lown, 2019) and is based on estimations of current recruitment and survival without any management intervention.

3.5 | Understanding the consequences of decreased oyster survival: harvesting

The starting size distribution for stochastic projections incorporating harvests is shown in Figure 7 when the population biomass

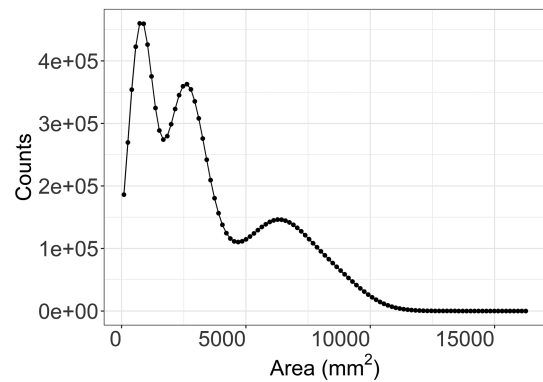


FIGURE 7 The starting size distribution of the population at time 0 with population 10,652,341 extracted from projecting the current population forward 34 years using establishment probability 5.13×10^{-7} , 8.0×10^{-6} , 3.79×10^{-7} and 2.22×10^{-6} and extracting the population where the converted size to weight ratios would result in a population being above, yet closest to 800 t. This population therefore has an estimated biomass of 800.99 t

approaches recovery at year 30 – and indicates a large influx of recruits and a large influx of oysters approaching 2 years old at this time, assuming 2-year-olds are $\sim 3,000$ mm². The total population count at this starting point is 15,060,795. Assuming a landing size (area) of 3,760 mm² (70 mm by 68.39 mm assuming a height to length ratio of 1.0236:1; Lown, 2019), there are 2,856,463 landable oysters. Converting this oyster population and size distribution to the estimated biomass would result in this population having a biomass of 800.99 t – a potential benchmark for recovery. This distribution was projected forward inducing 0, 1, 2.5, 5 and 10% harvest of landable oysters and resulted in λ_s values with 95% confidence intervals in brackets for the stochastic populations of 1.0439 (1.0421–1.0439), 1.0345 (1.0337–1.0355), 1.0215 (1.0206–1.0224), 1.0010 (1.0000–1.0018) and 0.9597 (0.9588–0.9606), respectively (Figure 8).

Assuming the same weight to area ratio as calculated above, a 2.5% harvest of the corresponding size distribution for adults only oysters would result in ~ 10.8 tonnes of oysters harvested by dredge in the model starting year under current stochastic prediction with a 5% harvest indicating a catch of 21.6 tonnes, whilst ensuring λ_s remains above 1. These models assume that stochastic scenario 1 is the most likely scenario, as discussed above.

4 | DISCUSSION

This study has incorporated extensive census data from 99 sites in a 284 km² MCZ across 4 years and individual-based growth and survival data measured from a novel string-based monitoring experiment to parameterize an IPM and make predictions on time to recovery, exploring the impacts of recruitment success and survival rates (i.e. establishment) and future harvesting scenarios for the European native oyster. This has resulted in projected distributions closely mirroring those observed in dredge census surveys for adult oysters;

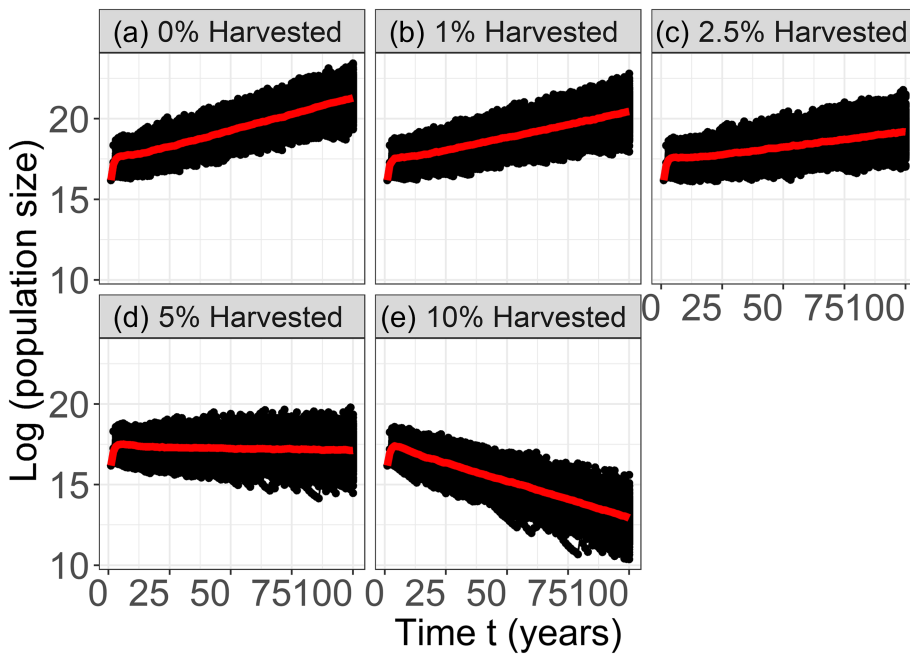


FIGURE 8 Forward stochastic projections projecting forward from the extracted 'recovered' population selecting establishment probability at random from 5.13×10^{-7} , 8.0×10^{-6} , 3.79×10^{-7} and 2.22×10^{-6} and inducing 0, 1, 2.5, 5 and 10% probability of mortality of landable sized oysters every year. The red line highlights mean log population size for all model runs with black lines representing individual model runs

however, our capture of the dynamics of smaller size classes requires improvement. While difficult to achieve, obtaining data on the smallest wild shellfish to parameterize this model will increase accuracy of future predictions.

Model coefficients were found to differ between sites. Whilst no simple experiment has yet been completed using oysters from these sites, differences in growth and survival rates between areas may be due to differences in habitat, e.g. Blackwater sites have high *Crepidula fornicata* populations and potentially increased input of larvae from the neighbouring Tollesbury and Mersea Several Order, whereas the Ray Sand is shallow with areas of softer mud and sand and the Crouch being an area of high *C. gigas* density with the presence of mixed shellfish beds (Lown, 2019). There was, however, no statistical difference in temperature between sites and all sites were fully saline (Lown, 2019).

4.1 | How sensitivity of the population changes with recruitment

Parameter-based sensitivity estimates highlight the sensitivity of the current population between 2017 and 2018 to recruitment, both in high- and low-recruitment years (Figures 4 and 5; Griffith, 2017). In years when recruitment is high, whilst sensitivity of the population is still primarily driven by recruitment and adult growth, elasticity of the population (i.e. the proportional sensitivity) becomes more evenly spread across various parameters such as growth and fecundity rates. This indicates that, when establishment of recruits is high and/or regular, the population may potentially be able to withstand changes to multiple other parameters, with population rate of change influenced more evenly by a range of demographic

processes as opposed to being driven by a single parameter. This has also been observed in a similar way in Californian mussels (*Mytilus californianus* and *M. galloprovincialis*), where elasticities of individual patches within a meta-population were most sensitive to juvenile and recruitment-based vital rates with individual patches most sensitive to demographic parameters than connectivity, strengthening as local retention of recruitment increased (Carson, Cook, López-duarte, & Levin, 2011; Figueira, 2009).

4.2 | Stochastic projections of recovery under interannual variation in recruitment

Stochastic projections have highlighted how the population may change under recruitment variation, assuming that vital rates such as growth and survival remain constant at the observed values of 2017. Whilst this scenario may be unrealistic in a real-world situation, only using a single year of growth, survival data and a single year calculation for proportion of the population found to be fecund females, these projections illustrate how incorporating variable processes such as recruitment into forward projections is essential for understanding longer-term population size distributions and abundance – thus managing expectations of all stakeholders. In addition, it illustrates that, when modelling species such as *O. edulis*, which is renowned for sporadic recruitment (Cole, 1949), conclusions require clear statements on predictive error or uncertainty for the predictions of population dynamics of future years. Historically, particularly large recruitment events in this species have occurred once every 7 years or less (Cole, 1949). Stochastic run 1 assumes no variation in growth and survival and incorporates estimated recruitment rates that assume a medium-sized recruitment event in 2017. This recruitment

subsequently re-occurs semi-sporadically at random, assuming that medium-sized recruitment events have the probability of occurring at a rate of 1 in 3 years, and two different levels of small events at a rate of 2 in 3 years. The revised model incorporating a large, undetected spatfall in 2017 (i.e. stochastic run 2) results in 1 in 4 high-recruitment years, 1 in 4 mid-level-recruitment events and 1 in 2 low-recruitment events. This second model results in the population of *O. edulis* in the BCRC MCZ increasing in abundance over time with a λ_s value of 1.039455 with growth and recruitment able to sustain mortality events.

Whilst it is recognized that higher levels of recruitment have been induced to replicate an observed distribution of potentially 2-year-old recruits (i.e. scenario 1), higher levels of recruitment than those induced here have previously been observed in the Essex estuaries. A previous stock survey of the River Crouch showed 80% of the population as 1-year-old recruits (Shelbourne, 1957). This model indicates that a high recruitment event in 2017 would result in 7,910,449 oysters being present in 2018. Of that population, 3,606,457 are predicted to be ~1-year-old recruits. This represents 45.59% of the population. It may therefore be possible that high-recruitment years surpass the highest recruitment levels incorporated in this model. Conversely, other previous studies have indicated no recruitment in multiple years, highlighting that the reverse may also be true (Bromley, McGonigle, Ashton, & Roberts, 2015). Owing to climate warming, oyster growers in Essex now expect reasonable recruitment events to occur at least once a year, with particularly large recruitment events occurring on intermittent occasions (Essex oyster growers, KEIFCA stakeholder workshop July 2019), as has also been observed in scallops (Shephard, Beukers-Stewart, Hiddink, Brand, & Kaiser, 2010). In Essex, the grounds of the private oyster-growing areas are specifically managed to promote recruitment and it is therefore reasonable to expect recruitment rates within the public grounds (i.e. the grounds outside of the several orders and private fisheries) to be lower than those observed in the several order and private fishery grounds. Likewise, from this comparison with private managed areas, it is also reasonable to assume that management to improve recruitment success is feasible in the wider MCZ. This may include desilting or spatting substrate habitat improvement activities (Laing, Walker, & Areal, 2005).

Understanding cryptic life stages is highly problematic for population modelling. Cryptic life stages are found in species ranging from fin fish to plants and include any species with a larval stage, small seed dispersal phase or seed bank. This is commonly overcome with the use of a 'black box', described here as the probability of recruitment (Merow et al., 2014). Understanding how these cryptic life stages impact population change greatly assists in understanding best- and worst-case scenarios for future population predictions and allows those involved in restoration of species to understand the demographic uncertainty associated with the model (Nguyen, Buckley, Salguero-Gómez, & Wardle, 2019). With juvenile and larval stages often difficult to measure directly, they are often back-calculated, as has been performed here; therefore increased monitoring of larvae abundances and spat survival needs to be

developed in order to accurately understand bottlenecks within these vital life stages.

Current stochastic projections assume constant levels of growth and survival with recruitment and harvesting, the only two parameters that varied over time. It is highly likely that growth and survival of adult oysters will change owing to other internal or external forces, for example spawning events and climate change, or owing to damage close to dredge and or fishing sites (Rose, 1973). Previous studies have indicated that *C. gigas* experience increased post-spawning mortality owing to decreased energy reserves and increased stress associated with breeding (EFSA, 2010); this may also occur in *O. edulis*. It is therefore possible that adult growth and survival may be higher in areas where oysters are not putting as much energy reserves into reproducing, and lower in years when they do; however, data regarding these associations remain unclear. Further research into associations between growth, survival rates and spawning activity under different climate warming scenarios would aid model improvement and have wider benefits to aquaculture.

4.3 | Estimates of time to recovery

Under the Kent & Essex IFCA BCRC MCZ native oyster fishery flexible permit byelaw, it may be possible in the future for a small, local fishery to harvest native oysters from within the MCZ area (KEIFCA, 2019a). In order for a fishery to open in limited spatially restricted areas, a number of key conditions must have been met: a stock assessment will have been performed by KEIFCA by 30 April each year and if stock levels do not meet the specified criteria, a fishery will not open. These criteria are currently specified as 800 t and increasing or stable stock levels for the previous 3 years, and no further biosecurity considerations, e.g. disease outbreaks (KEIFCA, 2019b). In addition to other clauses and requirements, there must be sufficient evidence of successful reproduction occurring with the presence of juvenile oysters and any vessel may only catch a maximum of 250 kg in any single trip (KEIFCA, 2019b).

Under this model, 'time to recovery' is the time taken for the current native oyster population of the BCRC MCZ to reach the threshold of 800 t. This model predicts that, assuming growth and survival rates remain constant, under current conditions, the Essex population of *O. edulis* may take between 16 and 61 years to grow from ~300 to ~800 t without any active intervention (mean 30 years). With only a single year of growth and survival data for this area in the current model and high levels of variability regarding recruitment mean, this range is particularly large; however, we are already working on further data collection and model validation. Increasing data availability and accuracy will result in increased accuracy of mean time to recovery. Including greater variation in coefficients and assigning coefficients to 'blocks' of good or bad years, varying coefficients together stochastically to investigate long-term population change as a whole, may provide further insight as opposed to how vital rates vary together. This is in contrast to varying recruitment in isolation and may highlight interactive effects of coefficients that are currently unknown.

Ostrea edulis are notorious for highly fluctuating populations and a succession of chance low or high recruitment events will greatly alter the population size and extent, with fisheries often able to be sustained by one or two particularly large recruitment events for multiple years (Spärck, 1949). Historical oyster populations have taken in excess of 20 years to be deemed adequately restored for fishing to occur with several years of highly favourable recruitment required for populations to recover (Spärck, 1949). The estimate of 30 years to recover from ~300 to ~800 t may therefore seem appropriate given the extent of population growth required to open a sustainable fishery, noting that the increased frequency of warm summer months means that southern oyster populations are now experiencing spawning conditions in most years. It is possible that contemporary warming (up to some limit), a super-recruitment event and any active intervention could result in faster recovery times than are estimated here.

Whilst making predictions on the number of individuals is key for assessing the recovery of a population, understanding how other ecosystem services may benefit is also necessary to determine the long-term viability and benefit of a population. As with other species of oyster, *O. edulis* shells show higher species diversity than other non-living hard substrate (Smyth & Roberts, 2010). In addition, an increasing density of native oysters results in greater species richness, in the absence of the invasive slipper limpet *Crepidula fornicata* (Lown, 2019). These metrics, such as biodiversity benefits, are essential in fully determining a recovered ecosystem as a whole.

4.4 | Modelling harvest scenarios

Once recovered (i.e. once the population reaches 800 t or ~10 million oysters), λ_s values obtained inducing various levels of harvesting of adult populations indicate that a population of this size would result in ~3 million oysters of landable size. A 2.5% harvest or less of this population would result in ~75,000 oysters of a range of sizes able to be landed and would enable harvesting to occur whilst maintaining $\lambda_s > 1$. A 5% harvest would maintain λ_s close to 1 (1.0018) and result in 150,000 oysters. This equates to ~10 t of oysters per year for a 2.5% harvest and 20 t for a 5% harvest. Assuming that the maximum level of 250 kg native oysters is harvested on any one day, this would allow 40 boats to be granted a single day licence for the fishery for a 2.5% harvest rate (or 10 boats for 4 days assuming the full catch allowance is landed per day) (KEIFCA, 2019a). This is under the assumption that growth and survival rates do not decrease (or increase) and establishment of new recruits is not below an average of 2.53×10^{-6} over 4 years. This highlights that, if it is maintained at low levels within a growing, healthy population with regular recruitment, fishing within sustainable guidelines may be possible, provided there is sufficient habitat available to sustain the population. Further research, particularly in understanding habitat limitations, density dependence and drivers influencing the establishment probability of new recruits, is required in addition to increased years of data collection to further validate our model and improve its predictive power.

5 | CONCLUSION

If current estimates of growth, survival, fecundity and recruitment are accurate and do not improve further in the absence of active intervention recovery of the BCRC MCZ, the native oyster population is estimated to recover in 16–66 years with a mean of 30 years. Following recovery, this study has shown that it is reasonable for a sustainable fishery to be developed with harvest rates <5% that would meet local stakeholder needs such as sufficient catch allowance to justify a small fishery, whilst ensuring sustainability of the *O. edulis* population. However, to increase accuracy of forward projections, more data on spawning frequency, percentage of spawners in the population, spat abundance and recruitment success are required. Therefore, by repeating the growth and survival string experiment over a number of years, a fuller understanding of how variability in these parameters influences them year to year can improve accuracy of the model (i.e. how growth, survival and fecundity all change together). Only incorporating a single year of growth and survival data and assuming that these rates do not vary as recruitment varies may result in vast over- or underestimations of λ , and as has been shown here, may have contributed to our poorer prediction for the 2019 census. In addition, investigating density-dependent demographic responses on increasing or decreasing oyster density may be assessed by manipulating on-string densities of *O. edulis*. Post-reproduction mortalities have been observed in many species and increased recruitment may result in increased intraspecific competition (Menge & Sutherland, 1987; Taylor & Wilson, 2007); it is therefore clear that vital rates such as growth, reproduction and survival influence each other and only varying one parameter in isolation will not provide the full picture of how the population is responding as a whole. Further data gathering of life history information from free-living oysters in Essex and elsewhere is recommended to help improve this model for use in *O. edulis* restorative conservation and management. Future projections of this protected species in the current state appear hopeful, with λ values along with the 95% confidence intervals for both unharvested stochastic models remaining >1.

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AUTHOR CONTRIBUTIONS

The initial project ideas were generated by TCC, LAH and the Kent and Essex Inshore Fisheries and Conservation Authority (RD). All data collection from 2016 onwards was completed by AEL and Kent and Essex Inshore Fisheries Authority (RD). All analysis was completed by AL and TCC, with input on the written paper and content provided by all authors.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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