Defining Oyster Beds in the Blackwater Estuary

Developing a definition for oyster beds and habitats for potential management narratives for the Blackwater, Crouch, Roach and Colne Estuaries MCZ

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Further information

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Editorial statement

This submission was peer reviewed in an editorial capacity by the appointment of an independent Editor. However, the authorship of the work and the ideas and views presented are the sole work of the author.

Foreword

Natural England commission a range of reports from external contractors to provide evidence and advice to assist us in delivering our duties. The views in this report are those of the authors and do not necessarily represent those of Natural England.

Executive summary

The Blackwater Crouch, Roach and Colne Marine Conservation Zone (BCRC MCZ) was designated in 2013 to protect a number of habitats and species including native oysters (*Ostrea edulis*) and native oyster beds which are made up of aggregations of native oysters. These MCZs are assigned conservation objectives (either maintain or recover) depending on the condition of the feature. The condition of a feature is assessed based on specific attributes. For native oyster beds, this includes the density of oysters per square metre. The current conservation advice for minimum bed density is set using the OSPAR commission definition which states that a bed requires a minimum density of 5 oysters per square metre. However, many other factors may need to be considered when defining an oyster bed which could include but is not limited to associated species, the three-dimensional structure or shape of a habitat, its rugosity and ecosystem function such as nutrient cycling. The BCRC MCZ is protected for oyster beds, with a condition for recovery of both oyster populations and oyster "bed" habitats, because areas within the site have been identified to contain higher densities that meet the OSPAR definition of 5m^2. But the vast majority of the site has oyster aggregations well below this density threshold. There are local conditions in the BCRC MCZ that could mean that despite it hosting millions of adult oysters across 284km^2, and representing a stronghold for the species in the southern North sea, the presence of the Bonamia parasite, consistent low recruitment and high rates of sedimentation and disturbance, and high densities of non-native slipper limpets could mean a target for restoration of extensive areas of 5 oysters m^2 may be difficult to achieve without significant and ongoing management intervention.

As a result the author was asked by Natural England to undertake a review of the scientific and grey literature on what role oyster density may have on the persistence of oyster populations and the role of oyster density, spatial extent, sampling methods, associated species and associated ecosystem function in approaches to define an oyster "bed" habitat – given the local conditions of the BCRC MCZ. In approaching this great care has been taken to differentiate between what could be considered a minimum oyster density for an oyster population to persist and the higher densities that might be found in oyster beds, at which point the species has become habitat forming. This report concludes that oyster populations persist over large spatial and temporal extent at relatively low densities, helped by their longevity, with a minimum density to represent a viable population between 0.5 and 1 oyster per $^{m2.}$ A more complex and realistic approach is encouraged for defining an oyster bed habitat that is likely to be a spatially variable habitat with a mix of high and

low-density patches of oysters. In the context of the BCRC MCZ, where the current habitat sampling relies on 100m dredge tows, and therefore samples 120 m2 per tow, oyster bed habitats are likely to be found in areas where mean densities across the tow are exceeding 2 oysters per metre squared (20% dredge efficiency). Approaches to management with different emphasis on conservation objectives versus fishery recovery are used to demonstrate potential ways to work with complex but real bed definitions within a complex socio-ecological system.

Contents

Acronyms and Abbreviations

BCRC	Blackwater, Crouch, Roach and Colne Estuaries Marine Conservation Zone
CEFAS	Centre for Environment, Fisheries and Aquaculture Science
DEFRA	Department for the Environment, Food and Rural Affairs
IFCA	Inshore Fisheries Conservation Authority
MCZ	Marine Conservation Zone
NGO	Non-Governmental Organisation
OSPAR	Oslo Paris Agreement
SAC	Special Area of Conservation
SPA	Special Protection Area

Background

The European flat or edible oyster (*Ostrea edulis*) is a species of increasing contemporary conservation concern with remaining strongholds having only been identified in few areas (Allison *et al.*, 2020; Farinas-Franco *et al.*, 2018; Pogoda *et al.*, 2019), evidence of loss or decline from many areas (e.g. (Helmer *et al.*, 2019)) and found at low density in remnant populations throughout Europe with a current known range from north Africa to Scandinavia.

Throughout this extensive range the species is found across a range of habitats from rock faces and shelves (e.g.(Bergstrom *et al.*, 2021; Thorngren *et al.*, 2019)), rock, boulder and hard clay and gravel (e.g.(Millport, 2007)), sand and muddy sand coastal seas (e.g. wider North sea (Christianen *et al.*, 2018; Bennema, Engelhard and Lindeboom, 2020)) and mud and sandy muds on inshore or shallow seas and estuaries (e.g. southern North Sea and Northern France (Allison *et al.*, 2020; Pouvreau *et al.*, 2021)). Within this native range the species is also artificially cultivated in private beds using a range of methods and intensities and a number of positive and negative impacts of this cultivation on the dynamics of adjacent wild populations have been identified by stakeholders and researchers (e.g. *Bonamia* risks and spat donors – see further discussion below.

In the UK in the southern North sea and the channel, in contemporary time, extensive populations are known to have existed along inshore coasts and within estuaries including the Solent, the Thames and greater Thames Essex estuaries, the Alde and other Suffolk estuaries and more historically also the Wash (Bennema, Engelhard and Lindeboom, 2020). To the West of the Channel there are wild recruited low density populations in the Fal estuary (Jenkin *et al.*, 2018). Of these the remnant populations in the Solent and the

Essex estuaries are particularly well studied (Helmer *et al.*, 2019; Allison *et al.*, 2020; Cameron *et al.*, 2018; Lown *et al.*, 2020; Lown *et al.*, 2021; Key and Davison, 1981; SIFCA, 2017; Section, 1984; Preston *et al.*, 2020). These two populations (or spatially structured populations or metapopulations within each site) share several ecological features such as sediment load and high density of the American slipper limpet that make them particularly relevant to inform restoration of the European native oysters in the Essex population, an aim written into legislation by the creation of the Blackwater, Crouch, Roach and Colne Estuaries (BCRC) Marine Conservation Zone (MCZ) (DEFRA, 2013). This MCZ was designated in light of evidence submitted by the Essex Wildlife Trust to DEFRA, underpinned by research undertaken in collaboration with the University of Essex that identified a native oyster stronghold with four distinct populations in the Essex area (Allison *et al.*, 2020). Some of these sub-populations had features that approached or exceeded one definition of a native oyster "bed" (OSPAR, 2008). Across the Essex estuaries the highest densities of European oyster and most equitable size structures were found to be adjacent to areas of current or historical sea bed mariculture or known encouragement of the species (i.e. adjacent to areas where there had been some human management intervention) (Allison *et al.*, 2020).

Following designation there is now a "duty" assigned to the Inshore Fisheries and Conservation Authority (Kent & Essex IFCA) on behalf of the Secretary of State for the Environment to "restore" the native oyster populations and their habitats in the BCRC MCZ. Natural England is responsible for the conservation advice to underpin and steer the restoration, recovery and management of the protected features in the MCZ. A formal working group has been formed across a range of stakeholders to assist KEIFCA and the Secretary of State in this duty: the Essex Native Oyster Restoration Initiative.

Kent and Essex IFCA formally partnered with the University of Essex, and both informally partnered with the wider ENORI community, and undertook further research from 2014 to 2020 to determine the population sizes and dynamics of the native oysters in each of the four identified areas where oysters were most abundant within the MCZ, assess the range and extent of oyster densities present within each area and examine other features of interest in determining the status of habitats where native oysters are found. In addition, the University of Essex partnered with the Tollesbury and Mersea Oyster Company to undertake a similar set of studies in the largest and most productive native oyster sea-bed mariculture Several Order that sits legally separate to but within the BCRC MCZ (Cameron *et al.*, 2018; IFCA, 2019; SeaFisheriesOrderEngland, 2019). University of Essex research determined that the wider MCZ (284km^2) has a standing population of appx 5.1-5.8 Million native oysters in 2017/18 but these are predominantly in two areas - the river Blackwater mouth and the Ray Sand (Lown *et al.*, 2020). The active Several Order mariculture site - a substantially smaller area than the wider MCZ sitting inside the river Blackwater estuary was estimated to contain similarly significant numbers of oysters at that same time, and is a likely important source of reproduction activity that spills over into the wider public and protected MCZ (Cameron *et al.*, 2018).

Drawing on the research described above, a range of recent published peer-reviewed studies and guidance from statutory authorities (e.g. shellfish guidance from CEFAS), this summary report aims to address three main knowledge gaps required by Natural England to help form conservation and management guidance for the “recovery” of the oyster features of the BCRC MCZ. It will also serve to inform the successful partnership approach across Government, local oyster fisheries companies, NGOs, local authorities and academia to deliver an adaptive management plan and nationally unique Flexible Oyster Fishing Permit Byelaw (KEIFCA, 2019); which other authorities are now seeking to replicate as best practice to manage low to medium impact fishing activities in inshore protected areas.

Assessing bed density

The three questions agreed upon with Natural England are outlined below (Sections 1-3), and there is also a fourth question (Section 4) on the generality of the advice given on management approaches to the BCRC MCZ being applicable to other areas including "offshore" areas. This report refers to a shellfish "bed" where this is normally taken to mean a complex habitat that is providing an ecosystem function that is more than provided by a only a low density aggregation of shellfish (Ermgassen *et al.*, 2012; zu Ermgassen *et al.*, 2020a; zu Ermgassen *et al.*, 2020b). Lower density shellfish aggregations may provide ecosystem function but not to the extent that could be achieved with higher or restored densities. At all times in this report the purpose is to support contemporary advice for management objectives for the BCRC MCZ in its current state with the baseline being conditions determined from 2014-2020 and full consideration of a range of stakeholder views and the current legislative landscape as known to the author – with particular reference to the adaptive recovery and management plan aligned to the Flexible Oyster Fishing Permit Byelaw (KEIFCA, 2019).

1. What is the minimal density threshold that would be for a viable oyster bed to function within the context of the local *Bonamia* settings?

The review of what *Ostrea* oyster densities constitute a bed undertaken by OSPAR (i.e. Oslo and Paris Conventions on Protecting the North East Atlantic and its associated resources) concluded that a bed may occur when native oysters occur in densities of five or more oysters per m^2(OSPAR, 2008). This OSPAR definition cites a clear description of a marine habitat type "IMX.Ost" from the JNCC (Connor *et al.*, 2004), but this published marine habitat classification including potential associated species of "*Ostrea edulis* beds on shallow sublittoral muddy mixed sediment" has no further citations of where this density information comes from and no data records for this classification are assigned to define the biotope. While not stating where the information is from – the JNCC ref states that the "biotope description may need expansion to account for oyster beds in England".

A second source of scrutiny of a five per m^2 threshold is the historical nature of any data used to inform contemporary definitions of oyster beds due to the well documented effects of disease outbreaks of *Bonamia Ostreae* – a Haplosporidian protozoan parasite of *Ostrea* oysters that has caused significant mortality in recent decades. Disease induced mortalities have at times been recorded as significant in the Blackwater estuary (c1980s), where oysters could only be stocked at higher densities for short periods of time to prevent significant disease loss (Laing and Spencer, 2006); also TMO, personal communication). This is a similar narrative to what is one to manage the disease by producers in France – where stocking of very high densities of $50m^2$ can occur, but only for short periods of a year or two. It is likely – as well documented from several locations that *Bonamia* has not acted alone to affect native oyster losses in Essex with several stressors acting simultaneously including high sediment loads, pollution, heatwaves and disease (Laing and Spencer, 2006). In a post-*Bonamia* North Atlantic – this apparently fixed definition of an oyster bed minimum density of five oysters per m^2 may not be realistic, especially in the context of advice from statutory shellfish heath authorities to reduce densities of oysters in managed areas (e.g. max $10m^2$ only for short growing/fattening periods, CEFAS advice, 2015 – also (Laing *et al.*, 2004; Laing and Spencer, 2006)) and to minimise *Bonamia* outbreaks in wild/semi-wild populations may require densities to be at or lower than 1.26 m^2 (Doonan, Cranfield and Michael, 1999). OSPAR has engaged with this concern stating that in the UK densities may need to be decreased to manage disease risks (Haelters and Kerckhof, 2009). In Essex, oyster producers have experienced *Bonamia* outbreaks and state they may intervene when their oyster densities appear to be significantly above $1.26m^2$ as this figure from Doonan *et al*. (1999) is quoted to them by CEFAS (Essex oystermen various pers. Comm.). It must be noted this threshold density is a result from a single study to parameterise a model based on a different oyster-*Bonamia* species system based on an outbreak in 1985. It has been reported that since then the *Ostrea chilensis*-*Bonamia* dynamics of that fishery system have changed both spatially and through time (Michael, 2020). A request for further explanation of this statement has been made.

In recent years when *Bonamia* testing has been undertaken in or around the Blackwater it has been found positive in less than 5% of animals in most places in most years (e.g. 1 of 30 oysters sampled). This would be described by a low infection rate in the *O. chilensis* system, but with much higher sampling rates (e.g. over 1000 animals) (Michael, 2020). Oysters originating from hatcheries laid at low aquaculture density, $10m^2$, in the upper Blackwater in 1999/2000 were found to grow well to marketable size within three years and were found to withstand bacterial disease challenge (CEFAS project FC1121 (Laing *et al.*, 2004)). $10m^2$ would be considered a success in a fully mariculture wild-recruited system, or in the wider MCZ as a conservation objective as measured by dredge tows (see density estimation challenges section below). It is difficult to differentiate between snapshots of good news where native oysters appear to be doing well in *Bonamia* areas and to understand this is just a part of the character of this disease of intermittent outbreaks, or whether there has been a significant change in any oyster stock, such as for increased resistance or resilience (Michael, 2020; Egerton *et al.*, 2020; Flannery *et al.*, 2014; Holbrook *et al.*, 2021; Sas *et al.*, 2020). Other oyster producers from *Bonamia* infected areas such as Ireland and the Netherlands are stocking at very high oyster densities in order to be economical for oyster harvesting and do not see oyster recovery to higher densities problematic in a natural setting in the longer term (pers. comm.). Further scrutiny is required as this too may be referring to relaying for short periods of a single or few growing seasons. However, there is increased interest from producers and researchers in moving away from density management to living with *Bonamia* and exploring whether oysters would develop resilience to the disease when co-evolving (Ronza *et al.*, 2018; Holbrook *et al.*, 2021). That being said the results are so far mixed with one study comparing *Bonamia* naïve with long term (22 years) exposed oysters finding no difference in prevalence, intensity or seasonality in infection between the two groups over a 13 month period (Flannery *et al.*, 2014), and another study over 10 years finding low infection rates in an apparently naïve population in Loch Ryan Scotland associated with lower somatic growth rates (Egerton *et al.*, 2020). The current biomass of native oysters in the Blackwater and wider MCZ are largely believed to be from an original restocking in the 1980s from oysters bought in from the Solent and both the Solent and the Blackwater have been thought to be some of the longest exposed sites to *Bonamia* in the UK – as long as the probable introduction to the Fal in 1982 due to the frequent shipment of oysters between these three sites (Laing and Spencer, 2006). While research is ongoing to examine the genome of Blackwater and other Essex locality native oysters for evidence of resistance or resilience, it is timely to consider a research program to examine how susceptible to mortality local Blackwater and BCRC MCZ native oysters are to Bonamia in an experimental setting, as they may now be much less susceptible than they were in the past.

A greater understanding of whether any need for density considerations of native oysters in a *Bonamia* context is required given the research bias towards this problem from a fisheries and aquaculture basis. On one hand the BCRC MCZ is very closely linked to, indeed biologically coupled to, the success of the traditional native oyster mariculture methods from local oystermen who are concerned about *Bonamia* (Allison *et al.*, 2020). On the other hand, Natural England may wish to place more emphasis on "natural" processes and recovery of native oysters in the Marine Conservation Zone to higher densities. This would be despite any disease risk as this is entirely natural and will lead to peaks and troughs in oyster recruitment through time and space within the MCZ, with dead animals contributing to the much-needed shell budgets (zu Ermgassen *et al.*, 2020b; Lown *et al.*, 2021). More ideal still is that it may lead to a more resilient native oyster population in the longer term. It has also been highlighted that even if control of oyster densities can reduce *Bonamia* disease risks, it cannot reduce those risks to zero as many organisms including brittle stars , rock oysters and tunicates are carriers for this pathogen (Costello *et al.*, 2021; Sas *et al.*, 2020), and these are highly abundant in the Blackwater estuary and surrounding MCZ. This point about differences in risks of disease to mariculture, aquaculture or a fishery and the risks to conservation objectives of the MCZ shall be revisited below.

To revisit what might be considered a minimum density for a native oyster "bed" to function we can first re-examine how the OSPAR estimate to define a bed came about – which is not clearly explained in the main OSPAR background document of beds report for *Ostrea edulis* (Haelters and Kerckhof, 2009; OSPAR, 2008). OSPAR's review found that a range of oyster densities from 1-9 oysters m^2 could be considered to be "beds" from evidence of densities of extant aggregations of this species (NE (Rob Whitely) & OSPAR pers. comm.). Five oysters per m^2 is no more than the median of this range. It is not clear whether OSPAR considered that lower densities were not functioning beds at the time of their publication (e.g. 1-4m^2), but they do state in their bed definition report that a bed is five oysters per m^2 or more. This is an important question as it could be considered that aggregation of oysters at very low densities are still evidence of native oyster habitat – but not "habitat forming" functionality. So large areas of low native oyster densities (0-1 m^2) may well be evidence of a *viable* oyster population, but not evidence of a functional native oyster "bed". Likewise, there may well be elements of ecosystem function that are found in areas where native oysters are found in low to moderate density (1-4m^2), but these functions are minimal or reduced. This point will be brought into consideration below in the conclusion.

There is a range of emerging evidence from historical records with some limited opportunities for reconstruction of abundance of oysters around the UK in sites like the Essex estuaries. But reconstruction of bed densities is challenging and as this work is currently underway, not complete and the author has a good understanding of the scope of that work – it will not be further considered here in estimating densities and density ranges of oysters in the BCRC MCZ.

We have information at least nationally or internationally, but also locally relevant studies that allow us to draw upon evidence to define the minimum density that could be considered a functioning *Ostrea edulis* bed or habitat in the soft sediment coastal seas of the BCRC MCZ. This information includes links between oyster densities and reproductive success, associated species richness and consideration of the range of observed densities in the BCRC MCZ (also see answers to Q2 below). Other factors that might help contribute to an understanding of minimum densities to allow ecosystem function such as *Ostrea* shell budget renewal, carbon sequestration, loss or storage, and denitrification will not be addressed as the evidence base for these functions is not robust enough at present to make any reliable conclusions of minimum densities for these functions. Shell budget renewal could be considered but it is not necessarily a density-dependent process. Instead shell half-life estimates (equivalent to losses of -plok,m0.05% mass per day) suggest oysters would have to contribute their shell mass via surviving offspring within 10-20 years to maintain existing budgets (Waldbusser, Steenson and Green, 2011). At this time it is not possible to assess what replacement rates would be required to guarantee that oyster beds persist in light of other pressures including burial from shifting sediments other than to say that the higher density areas with lower sedimentation rate are likely to persist for longer (Sander *et al.*, 2021). It is also reasonable to assume that the minimum density which delivers one function such as recruitment may not deliver other functions such as associated species richness or denitrification. Finally on shell budget, many other native and non-native species contribute shell budget to the BCRC MCZ, independently of native oyster densities, and these shall be discussed further below.

When discussing density, it must be realised that we are often dealing with observed or estimated density of oysters on the sea floor. This is an approximation or estimate of the real density. How these estimates are ascertained shall be tackled by Question 3 below but must also be noted here. Some studies referred to may have experimentally determined oyster density whereas others will have measured or estimated density in a more natural/wilder setting. Estimating oyster densities requires a range of assumptions about the method used such as its efficiency and scale. For that reason, when a study is mentioned in the text that follows, how density is presented will be stated.

When presenting discussions of contemporary estimates of oyster densities in the BCRC MCZ below, these are presented as average density m^2 from a minimum 100m ladder dredge sample. These estimates already consider dredge efficiency, and this will be discussed further below.

1.1. Fecundity

Maximum inter-individual distance to promote greater fertilisation success and brood success was determined to be 1.5 m among native oysters wild recruiting at a low intertidal site (Guy, Smyth and Roberts, 2019). Addressing a very important question of how low oyster density can become before an Alee effect occurs, the authors determined oyster density by hand in plots at the lowest spring tides and are likely to be measuring the "true" density. Understanding the link between inter-individual distances, reported to be influencing fecundity, and oyster density from this work is difficult as the two sets of data were measured on different occasions (Guy and Smyth, pers. comm.). There is also the potential reliance of the statistical significance of distance of fecundity on the single value of fecundity at 1.4 oysters m^2, and this should be taken into account (Figure 2 and 3 in (Guy, Smyth and Roberts, 2019)). It is not stated why in the manuscript, but the authors then split their data into those where inter-individual distance was greater or less than 1.5m in order to ask whether these pooled distance categories influenced fecundity. These new above/below 1.5m categories are pooled in a different way to the analysis that determines whether there are differences in mean inter-individual distance as judged by the different denominator degrees of freedom: 37 vs 164. It could be considered that the relationships presented of oyster density and fecundity (Figure 2 (Guy, Smyth and Roberts, 2019)) and between density and % of the population that is fecund (Figure 3) show a threshold of 1 oyster m^2 only below which fecundity can be seen to take very low values. My concern with this interpretation is that there is an unavoidable sampling bias towards sites with lower oyster densities that could explain this same relationship.

From the range of densities observed in this study, e.g. 0.2-1.4 oysters m^2 (Guy, Smyth and Roberts, 2019), it is not possible to exclude that other fecundity thresholds exist across the BCRC MCZ or other sites in Scotland, Sweden or France where *O. edulis* is known to reach much higher densities in both wild and cultured semi-wild populations (Table 1 this report). If 1.5m is a legitimate and repeatable distance threshold below which fecundity declines, we can conclude that a minimum oyster density that does not decline below a 1.5m average inter-individual difference lies somewhere between 0.5 oysters m^2 and closer to 1 oyster m^2 where in a uniform distribution oysters will always be less than 1.5m from their nearest neighbour. This is confirmed by the authors, saying that sites did have "oysters as low as $0.5m^2$ in the 1.5m distance" categories (Guy & Smyth, pers. comm.). The authors are trying to track down the original data so that it can be explored further by request.

Recruitment of juvenile oysters is an ecosystem function, and so we might say that the minimum oyster density required for successful recruitment could be as low as $0.5m^2$ or perhaps more conservatively $1m^2$. However, the link between oyster density and reproductive capacity is perhaps more akin to a definition for a minimum viable population than what is meant by a native oyster "bed". This will have to be addressed by Natural England when considering what is oyster habitat vs an oyster "bed" habitat.

1.2. Existing density data for southern North Sea coasts

Well-established but unmanaged contemporary populations of *O. edulis* in the southern North Sea are rare. A summary of density estimates for contemporary populations from several locations and whether they are likely to be fully wild or assisted populations can be found in Table 1. It is very important to remember that all contemporary data provided from the southern North Sea range are from a *Bonamia* positive period. These data may not reflect what densities might be achieved by restoration if *Bonamia* resilience in these populations has developed. Populations that are similar to the habitats found in the BCRC MCZ would be dominated by subtidal mud, subtidal sandy muds or subtidal mixed sediments (Allison *et al.*, 2020; DEFRA, 2013) and associated conservation advice from NE.

Coastal and estuary sites from the Norfolk Wash down through Suffolk, Essex and Kent and around the south to the channel estuary sites in the Solent are known to have had extensive oyster beds at least in former decades (e.g. Norfolk, (White, 1836)). Of these sites, rudimentary populations are known to have been present in Suffolk and north Essex sites such as Hamford water, the Orwell and the Alde sometime in the last 30 years but no current survey data exists (Essex oystermen pers. comm.). The same is likely to be true for many sites. Native oysters are known to be present in the Thames estuary from landings, fisheries interviews and stocks now held in aquaculture (i.e. Barrow deep) but again no formal surveys have taken place (J. Green and R. Hayward pers. comm. but see (Walker, 2016)). Native oysters are found in managed laying's as well as in wild recruited beds in northern France across a range of estuary and coastal habitat types (Table 1). In St Malo/Cancale the arrival of the non-native slipper limpet *Crepidula fornicata* has been referenced as a feature of the current system that differs from its historical state (Blanchard, 2009), as it has in the Essex estuaries, the Thames and the Solent.

This leaves two areas with similar mud-based coastal habitats that are known to have contemporary populations of native oysters that range from heavily managed to free living and share a similar history of arrival and spread of the non-native slipper limpet and *Bonamia*: the Essex BCRC MCZ and the Solent estuaries complex. Both these regions are well studied, representing some of the largest coastal shell fisheries in their time, with managed wild fisheries and aquaculture of *Ostrea edulis* throughout contemporary time. For this reason surveys by statutory authorities have taken place in addition to surveys conducted by research institutions or via collaborations between authorities and research institutions (e.g. Association IFCAs and Universities). There is no intention to give a full review of all surveys but to draw upon some of the most recent population size estimates to give an idea of what minimum densities might sustain a viable oyster bed.

1.3. Existing density data for Solent coasts

The wider Solent consists of several semi-isolated harbours and estuaries and is known as a site of incredible historical abundance of native European oysters. In recent decades this has not consisted of several orders or private fisheries, but a public fishery has existed in the past. This is not an exhaustive review but a chance to compare estimates of the range of densities that are observed in the wider Solent.

Surveys carried out by Southern IFCA from 2014-2017 are the most similar to surveys carried out in Essex (SIFCA, 2017). These surveys were by ladder dredge and standardised to short 100-200m tows with estimates of oyster density undertaken considering dredge efficiency. The dredge efficiency used was 5% so as “not to underestimate density estimates” (SIFCA, 2017). In future years SIFCA dropped dredge efficiency altogether, switching to CPUE citing dredge efficiency concerns and a potential range of 3-32%. This will be important in comparing to Essex estimates that use a similar method but have assumed a 20% dredge efficiency via consultation and a review of literature on dredge efficiencies with Natural England and to avoid overestimation of bed densities.

SIFCA dredge surveys in 2017 largely follow surveys in previous years and find similar results with non-uniform densities ranging from 0.01-0.33m^2 in the eastern Solent, 0.01-0.06 m^2 western, and 0.04-0.4 m^2 in the harbours. Excluding those samples with no oysters present improved the density estimates where sites with 0.3-0.5 oysters per m^2 became more common. No site appears to achieve densities greater than 0.56 oysters per m2 and this is rare with average densities well below this. Noting the dredge efficiency rates of 5% chosen for this analysis, to compare to the Essex estuaries these values may have to be divided by four.

Dredge efficiency issues in density estimation can be avoided by using alternative sampling methods including grab. Grab samples have been used in many historical surveys and are generally less damaging to the marine environment, especially in sensitive or protected sites. However the grab method is recommended for use when oyster densities are much higher (up to 32 oysters m^2 (Key and Davison, 1981)). If working in areas where densities are at or lower than 1 oyster m^2 then replicates of at least 10 grab samples per sub site will be required to capture density accurately (assuming survey grabs of approximately 0.1 -0.125m^2). This assumes a uniform or random distribution as when oysters are clumped across areas giving the impression of a lower density – they may be missed by even 10 grabs.

Grab surveys were deployed to repeat a finer scale survey of oyster densities within the three Solent harbours in 2017 (Helmer *et al.*, 2019). Three replicate 0.1m2 grabs were deployed at each of 90 locations. Given the aforementioned estimated densities and dredge efficiencies used from the SIFCA surveys (SIFCA, 2017), it is highly unlikely this method can differentiate between sites of zero and 1 oyster m^2. Across c90 grab samples 3 live oysters were found, which may be more reflective of the low replication at that grab area* oyster density combination than there being no oysters present across each harbour. But taken together the SIFCA survey and the Helmer et al. (2019), study point to very low densities of oysters that have declined even since 1998 where harbour densities ranged from 0-88m^2 with an average density of 8m^2.

Table 1: Short summary of densities from other large contemporary populations with reference to similarity to BCRC MCZ via sediments; shaded = considered similar. [b] = *Bonamia* positive sites

Location	Status	Substrate	Density (oyster m^2)	Methods	Reference & (Survey date)
Loch Ryan Scotland	Actively managed	Oysters associated with “moderately soft ground (silty, shelly, sand)”	mean 1.65 m^2; SD 0.5-3.5 m^2; range 0-20m^2	Multi-level quadrats using SCUBA / Snorkel Envision –video	University Marine Biological Station Millport. 2007 (2004)
Koster Archipelago	Wild recruited	Rock shelves and gravel	mean m2; max 31.6 m2; ≥1m^2 in 21-27% oyster present sites	Video sled	Bergstrom et al 2021
Penthièvre, France[b]	Wild recruitment	Sands, Gravel, Shell debris	0-30 adults m^2	Dive or low tide survey	Pouvreau et al. (2021)
Penfouilic, France	Wild recruitment	Mud, Sand, Shell debris	0-30 adults m^2	Dive or low tide survey	Pouvreau et al. (2021)
Odet river, France[b]	Wild recruitment	Mud, Gravel, Stones, Rock	0-20 adults m^2	Dive or low tide survey	Pouvreau et al. (2021)
Daoulas bay, France[b]	Wild recruitment	Mud, Maerl, Shell debris	0-10 adults m^2	Dive or low tide survey	Pouvreau et al. (2021)
Penzé river, France[b]	Wild recruitment	Mud, Sand, Shell debris	0-5 adults m^2	Dive or low tide survey	Pouvreau et al. (2021)
Lancieux bay, France[b]	Wild recruitment	sand, Rock, Shell debris	0-5 adults m^2	Dive or low tide survey	Pouvreau et al. (2021)

Location	Status	Substrate	Density (oyster m^2)	Methods	Reference & (Survey date)
Solent[b]	Formerly fished/dredged – no active management	Mud, sandy mud and mixed sediments inc. *Crepidula*	mean 0.01 m^2 mean c0.01m^2; range 0-0.56m^2	0.125m^2 grab Ladder dredge	Helmer et al 2019 SIFCA 2017
Fal [b]	Fished/dredged - no active management	Mud, sandy mud and mixed sediments inc. *Crepidula*	Mean m2; range 0.1-1m^2	Ladder dredge – 34mm rings, 45mm mesh	IFCA 2018(2015-2018)
BCRC MCZ [b]	Not managed for at least 1 decade – variable and low recruitment	Mud, sandy mud and mixed sediments inc. *Crepidula*	0-4.1 m^2 (greater than 35mm)	Minimum 100m Ladder dredge tow – 34mm rings, 45mm mesh	Lown (2015-2018)
Blackwater Several Order[b]	Actively managed	Mud, sandy mud and mixed sediments inc. *Crepidula*	0-4.6 m^2 (greater than 35mm)	Minimum 100m Ladder dredge tow – 34mm rings, 45mm mesh	Cameron et al., 2018 (2018)

1.4. The Blackwater, Crouch, Roach and Colne Estuaries MCZ

Between 2008 and 2012 and then again between 2014 and 2018 1.2m ladder dredge surveys for native oysters have been undertaken by the University of Essex in collaboration with Tollesbury and Mersea Oyster Company, the Essex Wildlife Trust and the Kent and Essex IFCA. Allison et al reported 1-150 oysters per 100m dredge across four surveyed sites (or subpopulations) but applying the later adopted 20% dredge efficiency this represents a mean oyster density ranging from 0.4 to 1.25 oysters m^2, with some samples estimating >6 oysters m^2 (Allison *et al.*, 2020). Kent and Essex IFCA began ladder dredge surveys for native oysters in 2014 starting with an extensive survey to assess the oyster presence and density across entire BCRC MCZ. In subsequent years to 2018 only those sites with positive oysters present were surveyed. Again, applying a dredge efficiency of 20% oyster density estimates ranged from 0-4.1 oysters m^2 (0-96 oysters per 100m dredge; (Lown *et al.*, 2020; Lown *et al.*, 2021)). The vast majority of surveyed sites were at low density below 1 m^2 with 95% of samples less than 2.5 oysters m^2 (Lown *et al.*, 2021). Despite the skewed distribution of density estimates with many samples from dredge tows being of low density (0-2 $m^{2)}$ – these surveys also identified higher density areas (2<x<4..1m^2) at the Ray Sand and in the outer Blackwater estuary (Cameron *et al.*, 2018; Lown *et al.*, 2020; Lown *et al.*, 2021). Note the range of densities are not dissimilar to peak densities in both the upper (100-200 oysters per 3 minutes baird trawl south of Osea island in 1961) and outer estuary (11->50 oysters per 3 minute baird dredge on Tollesbury side of Blackwater downstream of Thirslet creek in 1981; (Section, 1984)). Across the 1960s, 80s (inside Blackwater estuary only) and present (inside estuaries and the wider MCZ) the vast majority of sampling found the seabed to have from <1 to 10-25 oysters per dredge haul – that is from 0.04 through 0.4-1.04 oysters m2 assuming the same dredge efficiency and dredge distances as in Lown et al., (2020, 2021).

A picture is emerging that a thriving wild recruited native oyster population is likely to consist of relatively more area that are characterised by low oyster densities interspersed with areas of higher density. That is what is found in the BCRC MCZ, Loch Ryan and also in the studies of more extensive sites such as the Koster archipelago in Sweden (Table 1, e.g. (Bergstrom *et al.*, 2021)) and also in a more extensive study of the Swedish coast (Thorngren *et al.*, 2019). It is also what is found in most of the natural recruitment sites surveyed at the low intertidal in France (Table 1), where the mean density across larger areas is not informative as native oysters are found in clumps on what little hard rock substrate there is across a landscape of fine muds (S. Pouvreau pers. comm.; (Pouvreau *et al.*, 2021)). Therefore, in terms of what is a minimum oyster density that could characterise a “bed”, a habitat-forming “bed” is more likely to be found in these less common high oyster density areas whereas more common lower oyster density areas could be said to be oyster “habitat”, but not a “bed”. In the BCRC MCZ in the context of *Bonamia* and based on the assumptions of sampling methods, dredge efficiencies, sampling scale (e.g., 100m+ sample) the densities most likely to be associated with “beds” at above 2 oysters m^2. The population of native oysters may well be secure in the long terms as long as they can be found over large areas at greater densities of 0.5-1 oyster m^2, but this may not be considered as a minimum “bed” density with associated highly functional ecosystem functions/services.

As per the discussion on sampling methods and oyster distributions below, future research objectives should include identification of higher oyster density aggregations in the BCRC using smaller scale sampling methods as soon as possible to help inform our biological understanding of the system and your conservation advice about minimum densities for “beds”.

1.4.1. Biodiversity: Associated Species Richness

Native oysters are described as habitat engineers such that when they aggregate as live oysters and contribute to the immediately surrounding environment their dead shells, over time this creates a matrix of shelly gritty hardening of surrounding soft sediments that provides settlement substrates and refugia for a range of other species that would not otherwise be found there in such densities or abundance (zu Ermgassen *et al.*, 2020a; zu Ermgassen *et al.*, 2020b). Having said this – there is little published peer reviewed research from contemporary populations in a natural subtidal setting to confirm this claim – albeit that it would be expected from semi-permanent aggregations of bed forming shellfish (zu Ermgassen *et al.*, 2020b). In a recent review of knowledge gaps on the ecosystem service provision of shellfish habitats, many of those gaps existed for *Ostrea* spp. oysters, but links between native oysters and cultural biodiversity services are described as strongly evidenced (zu Ermgassen *et al.*, 2020b). Of the studies reviewed to support this claim, several were historical qualitative observations that oyster beds were thought to be particularly diverse, three noted that shells of oysters can host many other species and one reported that *Ostrea angasi* beds could host three times the faunal abundance and different species composition than surrounding softer sediments (Crawford *et al.*, 2020). Part of the reason for limited research is the challenge of working with extensive subtidal habitats in what can be limited visibility and one response to that is to undertake experimental approaches to manipulating oyster presence and density, or where native oysters are found in the more accessible lower intertidal. Zwerschke et al., (2016) experimentally manipulated native flat oysters and non-native oyster (*Crassostrea gigas*) presence at a single density in experimental sites in the intertidal and subtidal in Strangford Lough, Northern Ireland (Zwerschke *et al.*, 2016). Small hatchery reared juvenile oysters were used (14-15mm), at a high density of 444 juvenile oysters m^2 (2D surface density) presented in a 3D cage matrix which the authors state is a suitable density for this life history stage at this site. All else being equal, and after 12 months, the authors found a total of 181 associated species but there was no difference in the diversity and structure of the ecological communities growing on the two oyster species (Zwerschke *et al.*, 2016). Two further pieces of work by this same team found that from observation surveys and when at low density – there was no difference in intertidal biodiversity associated with the two species (Zwerschke *et al.*, 2018), and no significant differences in nutrient cycling or associated biodiversity between the two species across an experimental gradient of densities at the same sites (Zwerschke *et al.*, 2020). Epibiont species richness associated with native flat oysters was examined in intertidal living animals in Strangford Lough, Northern Ireland (Smyth and Roberts, 2010). Seventy-five oysters were examined from each of two sites that ranged in size from less than 30 to greater than 60mm (reported as shell length). Epibiont species richness increased with size (i.e. age) and was 15-21 species at max in the largest size class across both sites (Smyth and Roberts, 2010). No information was provided on density of the oysters or surrounding hard shell to differentiate the two sites, but native oysters hosted more epibiont diversity than surrounding rocks.

Guy et al., (2018) also examined associated species with native oysters but also non-native rock oysters in Strangford Lough, Northern Ireland and again in the intertidal.

Animal were selected from 0.5m below chart datum along a transect, but only 17 animals of each species were selected and again no information about variation in densities was included in this study. Greater per capita species richness was found on *O. edulis* than *C. gigas* (12.6 vs 8.4 species respectively), but the best selected model to explain this included age as flat oysters were on average two years older than rock oysters at this site, and as a collective sample there was no difference between the total species found between the two oysters (48 vs 51 respectively). There was a statistically significant difference between the identity of the ecological communities found on the two oyster species, however the majority of this was explained by two species found exclusively on *O.edulis* (Guy *et al.*, 2018). In the discussion four species are emphasised as being particularly dominant on flat but not rock oysters and the authors suggest the main reason for this is the orientation of flat oysters at the site being more exposed to water flow that prevents sedimentation. With such a low sample size (n=17 animals) it is likely stochastic sampling bias and low statistical power for the multivariate analysis has influenced the results of this study as there were a relatively large number of epibiont species abundance/presence samples for each oyster that were often exclusively found on one species but not the other (e.g. 33 species found on *C. gigas* not found on *O. edulis* at the same site). It is not stated in the study, but it is likely these zero values – 60+ in total – were excluded from the multivariate analysis otherwise even greater dissimilarity values would have been estimated albeit erroneously.

Christianen *et al.*, (2018) examined a subtidal mixed species oyster reef in the North Sea in the Netherlands that consisted predominantly of native flat oysters colonising an existing rock oyster and blue mussel reef. The native flat oyster density across the reef was 6.8m^2, over a matric of predominantly rock oysters of a density of 19.4 oysters m^2. Due to the co-occurrence of native, rock oysters, blue mussel and rocks that authors state they could not differentiate between associated species to the substrate level – but that the shellfish reef habitat contained 60% more surface associated species than surrounding mud/sand (14.9 vs 9.3 species respectively; (Christianen *et al.*, 2018)).

Across all four of these experimental or observation approaches (Zwerschke *et al.,* 2016; Smyth and Roberts, 2010; Guy *et al*., 2018' Christianen *et al.,* 2018), a picture emerges that on their own oysters of various species provide relatively similar benefits to biodiversity, in that species richness increases relative to soft or non-shellfish habitat. All four also share a property of not being able to assess if there is a minimum density below which biodiversity benefits do not accrue or more generally how biodiversity responds to the density of shellfish in a given area.

Lown *et al.,* (2021) assessed the richness and composition of faunal diversity associated with variation in density of native oysters, weight of other dead shell and live biomass of the non-native slipper limpet *Crepidula fornicata* across the BCRC MCZ. The study was undertaken using 100m tows of a 1.2m ladder dredge with 40mm diameter ring mesh resulting in 396 samples across 2016-17, with oyster densities varying between 0-4.1m^2, and a total of 39 macrofauna species included in the analysis. The benefit of this approach is the large number of samples retrieved at a scale and method appropriate to estimate seabed density of oysters and other potential explanatory variables such as hard shell and slipper limpets. The costs are that many small-bodied animals (e.g., dogwhelks), juvenile fishes and soft bodied organisms (e.g., larger anemones) are not retained by the dredge and no data was collected on algae and seaweed diversity. Once accounting for the relatively small but significant positive effect of dead shell weight on species richness and the relatively large negative effect of high slipper limpet biomass on species richness there remained a very large *predicted* effect of increasing oyster density on associated species richness (+87% richness at highest densities of oysters (4-5m^2) at lowest biomass of slipper limpets; Lown *et al.,* 2021). There are three important points to take from this study, first as described below the vast majority of observed native oyster densities were between 0.01-2.5 oysters m^2, densities above this are rare and will have had a disproportional effect on the predictions of the model. Secondly, one of the strongest effects observed is between those areas with exceptionally low oyster density (0-0.1 oysters m^2) and those with 1 oyster m^2 (as measured over 120 m^2) with an uplift of an additional 1-2 species was found on average between these oyster densities. Notably above this density of 1 oyster m^2, and in the current condition of the BCRC MCZ with very high biomass of slipper limpets, achieving those high oyster density:high richness gains will be challenging. In addition to richness, community composition was also related to oyster densities, and this included spatial correlations between higher densities of native oysters and species of commercial interest such as Edible crab (Lown *et al.,* 2021). To summarise – in the current conditions of the BCRC MCZ with high slipper limpet biomass and at the spatial and taxonomic scales and methods used in this dredge-based survey – species richness will be relatively unresponsive to changes in oyster density above 0.5-1m^2 but does decline below this density threshold (perhaps lower, Figure 2 Lown *et al.,* 2021). Finally, there are also methodological shortcomings in examining density in this study – as the measured density is an estimate based on a 100m long dredge tow with a dredge efficiency applied. While the research suggests that increased species richness is associated with increased oyster density, how this mechanism is delivered is unclear as the oyster distribution on the seabed is unknown.

1.5. Conclusion on minimum density

Based on the only study to measure fecundity effects being highest at densities equivalent to or above 0.5 m^2 (Guy *et al.,* 2018; but see pers. comm.), and accepting that across multiple sites around the UK self-recruitment and persistence are traits that can be attributed to sites dominated by densities of 0.5-1.5m^2 (where most (70%+) areas of the sites have these densities or lower) – it would appear that **minimum density for a viable oyster population based on fecundity and self-recruitment alone could be as low as 0.5-1m^2.** But this is not the same as estimating the properties of an oyster “bed” or estimating the density above which native oysters are “habitat-forming”.

Despite a significant body of work that demonstrates the role of shellfish aggregation in increased marine biodiversity, where it can be concluded that in their lower subtidal and subtidal habitats native oysters will be supporting colonisation of other species and at higher densities this uplift in associated species richness can be substantial (e.g., 60-80% compared soft sediments/sand, less so compared to other non-live but hard rock habitat). The only study of species associations with native oysters in the southern North Sea to attempt to examine the role of oyster density was conducted in an environment with high *Crepidula* densities and using methods that may not capture the true density of oysters on the seabed (Lown *et al.,* 2021). It found that ecosystem function gains in terms of supporting increased species richness are currently maximised in areas where oyster densities are 0.5-1m^2 or higher measured over 120 m^2 area, but there was potential for much higher gains. These higher gains were predicted when native oysters were at higher densities (1-5 oysters m^2 and in the absence or reduction of *Crepidula*. Density studies are limited by the maximum measured density observed already being 4-5 oysters m^2 and, even while accepting that the highest dredge estimated densities are likely to include what is oyster “bed” habitat, further work may be necessary to confirm this. Crucially, none of the study sites or surveys discussed above can preclude that successful oyster recruitment across the entire site is maintained by the fewer high-density sites. Likewise, Lown *et al.,* (2021) cannot exclude that the positive relationship between oyster aggregations and species richness is maintained mostly by higher oyster density areas or by non-uniform distributions of oysters at higher density aggregations than was possible to measure (i.e., at lower spatial scales than 100m dredge tows).

Given the review above it seems the simplest minimum density definition below which an oyster population cannot function is somewhere 0.5-1m^2; a precautionary density would say 1 oyster m^2. Therefore, if intervention for fishing or extraction or disease risks – advice would be that densities should not be reduced below this level**.** But a minimum density above which we might consider the oysters to be “habitat forming” and become “bed” would be higher than this and certainly to be found where the highest dredge obtained densities of 2-5 oysters m^2 are located in the BCRC MCZ. These habitat forming densities are not supporting biodiversity on their own, but in a complex of live shellfish, dead shell, gravel and rocks as would be the case in other shellfish “bed” or “reef” formed habitat. The nature of the contemporary highly modified BCRC MCZ has some important caveats to consider in this regard as one could envisage many areas that have 2-5 live oysters m^2 but the surrounding cover is provided by live slipper limpets at higher densities and several studies has now shown this will limit the biodiversity potential of the formed habitat.

Therefore, given the very many confounding variables discussed above it may be when seeking to define an oyster habitat, a “bed” is only one component of that habitat. This is the same as thinking about any population that has areas of higher and low density. Collectively all individuals contribute to the demographic structure of the population, and instead of thinking about minimum density, it may be important to consider a more complex definition of oyster populations and habitats that includes scale of an area and hosts a range of densities – for example:

An area of not less than 0.5 km^2 with a patchy native oyster population with an average oyster density not less than 0.5m^2 (of oyster present sites only) but where 20% or more oyster present samples are ≥ 0.5m^2 and 2% are ≥3m^2

This figure is presented as an example of what could be agreed. A more useful and detailed definition would require further review and stakeholder engagement and a greater understanding of how this definition would aid good policy or management decisions.

2. Range densities

The second question this paper aims to answer addresses range density. If a bed is self-sustaining between X (the minimum for self-sustaining bed) and Y (the point at which Bonamia becomes a problem), it can be managed for Y. If the bed drops below Y (but not as far as X) an opportunity exists for management intervention before the bed drops to a very low density that cannot be self-sustaining.

Areas that contain native oyster should not be described by their mean densities alone (Table 1 and above discussion). This has also been recommended by Pouvreau *et al.* (2021) who finds that based on shoreline and dive surveys wild recruited oysters are found in patchy distributions where clumps of 10 or more oysters can be found on a rock or rock aggregation but are otherwise surrounded in oyster-less soft-sediment landscapes (pers. comm). As covered above in Question 1 and relating to Question 3 below, native oysters can be found at a broad range of densities at any one site and are known to form complex non-uniform spatial distributions (Table 1). Focussing now on the density range and the areas over which native oysters are found in the wider BCRC MCZ – we have addressed above that a minimum density for a viable population may be a “large” area where the native oyster density does not drop below 0.5 or 1 oyster m^2 (of adults or individuals ≥35mm height – umbo to outer edge; NB. new monitoring guide suggests minimum size to include in monitoring of adults is 35mm). It has also been raised above in Question 1 that a more complex definition may be appropriate – but still focussed on oyster densities. However, the evidence reviewed suggests that a minimum density for a viable population is not the same as a minimum density for a minimum native oyster “bed” that provides high levels of biodiversity and socio-ecological services.

Likewise, based on the methods and scale over which the data above have been collected, 100m dredge samples, greater than 95% of samples of oyster present areas constitute densities of no more than 2.5 oysters m^2 and most are much lower density (Lown *et al.,* 2021). In a managed several order within the BCRC MCZ in river Blackwater near West Mersea – not included in any density estimates for the main MCZ mentioned above or in Table 1 – similar density ranges to the main MCZ were found in a subset of samples undertaken in 2017 (0.54–4.6 oysters m^2; Lown et al., 2021) and in an extensive survey in 2018 (0-4 oysters m^2; Cameron *et al.,* 2018). However, the vast majority of cultivated oyster bed habitat was of 1-3 oysters m^2 (Cameron *et al.,* 2018).

While discussing interventions on an internationally important and sensitive marine site may cause alarm, there are only two management scenarios that need be considered: a small sustainable harvest to support the local heritage oyster fishery (KEIFCA 2019; Lown *et al.,* 2020) or a management intervention that could be combined with the former harvest scenario to reduce areas of high oyster density that might pose a disease risk.

There are several not mutually exclusive considerations in setting density thresholds for MCZ management intervention scenarios for native oysters at any site that consider the presence or potential presence of *Bonamia*:

Protection of the higher native oyster density areas (2.5-5 oysters m^2) as these could be having disproportionally positive contributions to the persistence of the population and the ecosystem functions and services habitats provide. This is a fundamentally important consideration as the conservation advice Natural England would wish to provide is about the BCRC Marine Conservation Zone and not primarily for the potential for a future managed heritage fishery within the MCZ or the current Several Order in the river Blackwater within the MCZ. As discussed in answer to Question 1 above it is increasingly recognised that as *Bonamia* is endemic at the site and likely at the regional scale, to try to manage it away is likely to fail and a better strategy is to manage for resilience to the parasite within the local oyster population (Holbrook *et al.*, 2021). Dead oysters are widely considered as much a part of high-density native flat oyster bed habitat, as they would on shellfish reef habitat formed by other species, so mortality of oysters in of itself is not counter to the conservation objectives of the BCRC MCZ. It may be entirely illogical then to promote the destruction of high density areas when we recognise they are so rare across a large site, may take a long time to form, provide exactly the ecosystem services that is providing social and cultural excitement about this “bed” habitat and are naturally ephemeral/ temporary (zu Ermgassen *et al.*, 2020a; Sander *et al.*, 2021).

Prioritise the utilisation of the highest native oyster areas (4+ oysters m^2) as these are most likely to cause the greatest opportunity for *Bonamia* outbreaks. It was previously recommended that the disease reduction risk density threshold be set at $6m^2$ (KEIFCA workshops). This was a compromise based on information at that time that the OSPAR definition of an oyster bed of five oysters m^2 was a fixed legal definition; when we had less knowledge on the current densities in Essex and the MCZ (KEIFCA, 2019); with recommendations from CEFAS that oysters in on-bed aquaculture should be kept at lower densities (below $10m^2$ for short term relay; below $1.26m^2$ longer term but see discussion elsewhere in report) to maximise survivorship from Bonamiosis (Doonan, Cranfield and Michael, 1994; Doonan, Cranfield and Michael, 1999; Laing *et al.*, 2004; Laing and Spencer, 2006). If such a threshold was required, the evidence would now suggest four oysters m^2 (as measured by dredge tows) as these are close to the peak densities observed in the MCZ and adjacent several orders, and given they are density estimates from 100m dredge tows these areas likely represent patches of much higher density. Targeting these areas would require less fishing effort to reach any quota and therefore reduce the footprint of fishing on any other features or species, however as discussed immediately above this approach would remove any “bed” habitat in that area and prevent any such areas ever developing in to “bed” habitat. Even if at a very low spatial scale this may be counter to the conservation objectives of the MCZ.

Prioritise utilisation of only moderate density areas (1-2.5 oysters m^2) as areas at this density are common providing many opportunities for adaptive spatial management of any interventions; therefore, protecting reference areas of the highest density.

Lower self-sustaining and ecosystem function threshold of 0.5-1 oyster m^2 where interventions should not be allowed to reduce densities below this value as it would threaten the population viability longer term.

2.1. **Density range thresholds for harvest**

Once the BCRC MCZ has attained double its 2017/18 population size (in biomass; a locally agreed threshold of recovery KEIFCA management plan), the population is predicted to sustain zero population growth at harvest rates up to 5% by biomass of the harvestable adult size, and still maintain positive growth at up to 2.5% annual harvest rates by biomass of harvestable adult size. Harvest rates substantially less than 2.5% are ample to support the local small scale heritage fishery with an annual landing of ~10tonnes or alternatively considered to provide scope for 40 vessel fishing days assuming the full catch allowance of 250kg is landed per vessel per day (KEIFCA, 2019; Lown *et al.,* 2020). Based on responses to the oyster fishing permit consultations, and the provision in the BCRC MCZ flexible fishing permit byelaw, this would more than meet the needs of the local heritage fishery.

Under this management scenario it would be recommended to have maximum flexibility on where to dredge, outside of any areas that are already deemed to be long term protected areas within the BCRC MCZ. To this end it would be advised to target fishing in areas where density is moderate 1.5-2.5 oysters m^2. This leaves higher density oyster areas permanently untouched (see next management scenario). By setting a lower density estimate of 1.2-1.5 oyster m^2 one could prevent harvesting pushing oyster densities below $1m^2$. If it were considered that a further objective of minimising dredging effort and area were to be applied in considering which areas to harvest, obviously targeting higher density areas may allow the same harvest to be obtained with less effort and footprint.

A research consideration to allow this management scenario to develop would be finer spatial scale mapping of high-density oyster areas in the BCRC MCZ to see where “bed” habitat is developing and at what scale.

2.2. Density range thresholds for disease risk intervention

While there is a lot of excitement about potential for disease tolerant or resilient native oysters likely to be existing in areas where they have coevolved for many generations – such as the BCRC MCZ, *Bonamia* is still considered the greatest threat to high oyster density beds and the “single greatest constraint to restoration” (CEFAS pers. comm 2017). Understanding the role of *Bonamia* in recovery has been highlighted as one of the most important questions in flat oyster restoration in Europe (zu Ermgassen *et al.*, 2020a), but this same review highlights that many knowledge gaps remain not least of which is when, where and to what extent *Bonamia* causes declines in contemporary flat oyster populations. To be more clear, documented evidence of specific “crashes” in oyster populations from *Bonamia* is difficult to find.

It is noticeable that many areas around the UK with *Bonamia* have average densities not much higher than 1 oyster m^2. However, it has already been well demonstrated above that such mean or average densities are not a good descriptor of a native oyster population and depending on how those estimates are obtained they may not represent the true densities in a non-uniform distribution within a population of oysters. From France, Northern Ireland, Holland, England and Scotland there is evidence that oyster producers are content to replay native oysters at high density in known *Bonamia* infected areas, but this is often only for a short time period. The short time period method of growing on oysters from hatcheries was studies in the river Blackwater by CEFAS and a lower density estimate of 10m^2 allowed high survival and growth rates whereas higher densities experienced density dependent effects and suppressed immunocompetence (Laing *et al.*, 2004; Laing and Spencer, 2006). Few on bed mariculture production specialists exist anymore but those in the BCRC MCZ consider long term growth and certainly summer periods at or above the OSPAR density of 5m^2 is too high to prevent *Bonamia* outbreaks and have lost stocks to this disease at these densities in the recent past (TMO pers. comm. 2021). Opinion is not unanimous however, with producers in Essex and around Europe communicating that they believe that losses to *Bonamia* are lower than they used to be and support an approach that manages for local stock resilience to *Bonamia* (various pers. comm. to T. Cameron and P. zu Ermgassen).

It is essential to remember that the conservation objectives of the BCRC MCZ are not the same aims as for aquaculture or a fishery. However, it would not be considered appropriate to manage the site in such a way that *Bonamia* outbreaks are encouraged in such a way or in such proximity that could influence local livelihoods, and without further research it is unclear whether investment in higher oyster densities would backfire on any recovery or restoration efforts. A conservative approach could be to accept that greater caution is required closer to any significant areas of production, i.e., the Blackwater several order while also supporting research that i) identifies is greater resilience to *Bonamia* infection now exists in the BCRC MCZ and surrounding areas than did in the past and ii) continuing with support of small-scale high-density restoration to document in-field survival over at least three years.

Until such evidence to the contrary exists (but see Table 1, France) it would be prudent to recommend continuation of *Bonamia* infection status surveys but increase the number of animals sampled and intervention of some kind to reduce very high densities of oysters that that are close to the mouth of river Blackwater MCZ if infection rates increase. Discussion on sampling effort and what is required to detect early increase of *Bonamia* infection status would be required. If intervention was to occur the oysters could be used to support restoration and recovery of native oysters across the MCZ where this intervention is not combined with a planned harvest under the Flexible Permit Bylaw (KEIFCA, 2019). But given the criteria suggested, the oysters should not be moved to other extant areas within the MCZ but perhaps to areas where a known flat oyster subpopulation has been known to go extinct (such as happened in Eagle bank).

3. What would be deemed to be an appropriate scale over which density could be measured?

Ecology is the study of the distribution, abundance and structure of populations and how they interact with each other, other species and their environment. As a science ecology has been fascinated by the estimation of population density and abundance for over one hundred years and this continues today with the native fat oyster; largely because it is a challenging organism to obtain a true estimate of density at any reasonable scale and effort and especially so in the deep or expansive subtidal habitats from which it is most known.

The relative benefits of different survey methods for marine surveys are well described in the literature, the purpose of the following short review is to consider grab vs dredge surveys of subtidal flat oysters, with some reference to alternative methods. A key point to note with regards to any grab sampling has been made above in reference to the relationship of the grab sample area and the expected oyster density (Key and Davison, 1981; Helmer *et al.*, 2019). In short oyster densities would have to be minimum 1 oyster m^2 and at a near uniform density for standard effort grab sampling to be effective. Standard effort in this case is three to five grabs, each of an area 0.1-0.125 m^2 per point sample. Sampling by grab alone requires too much effort to be accurate across much of the MCZ (density 1-1.5 m2 or less) or indeed many sites where it is already being deployed by other research teams as the efforts used cannot differentiate between oyster present at less than $1m^2$ and zero oysters (Cameron *et al.,* 2018). As such, the recommendation to use grabs for native oyster sampling was in a report where average oyster densities were closer to 30 oysters m^2. That being said the shortcoming in using a grab can be overcome with uplift in effort, e.g., each replicate point sample is the average of ten $0.125m^2$ grabs. Grab samples are time consuming and a relatively dangerous piece of equipment, so the uplift in effort required to make grab samples worthwhile at a larger scale may not be possible due to time and cost limitations and potential safety risks. It is also a method that is considered harmful to the environment in the recently published Native Oyster Monitoring handbook, but also considered suitable if used at a site that has a large population with high enough densities such that any mortality does not threaten the population (Native Oyster Monitoring handbook, In Press). Therefore, grab sampling would be appropriate for refining the density estimate of a smaller area in the BCRC MCZ once it had been identified as being a candidate for a given density by dredge sampling.

Dredging, with good reason, is considered harmful to the marine environment for a range of different reasons but not least of which the physical damage it can cause to marine habitats, structures and organisms but also due to the disturbance it causes to ecological succession, including for example the formation of native flat oyster “bed” habitats. Therefore, it is recommended that is only suitable for certain sites and studies at an appropriate scale (Native Oyster Monitoring Handbook in Press). The BCRC MCZ is 284 km^2 and transect/grid-based dredge surveys are the only suitable way to survey this site at scale to provide an index of oyster presence and abundance. To give an example of a survey footprint from such a dredge-based survey – a 100m long tow of a standard ladder dredge at 1.2m wide is a $120m^2$ footprint taken within a 4-hectare plot (e.g., Cameron *et al.,* 2018), this represents $120m^2$ footprint in a 10000 m2 plot – 1.2%. If the main purpose of the survey is to estimate abundance than an annual survey, or less frequent, is unlikely to cause long term damage to native oyster population integrity. It is also the case that native oysters are rarely damaged by this dredge and can be returned to the same place they are sampled. This is evidenced by dredged oysters being placed on long- term string survival experiments (Lown *et al.*, 2020) or studied for survival in the lab over a period of three months post-dredging with zero mortalities in some treatments (T. Cameron unpublished).

Having considered the main negative features of dredge sampling we can consider the benefits. The main benefit is that for sampling extensive areas of low population density at or below 1 oyster m^2, a density that will make up most of a native oyster population by area, the dredge will provide a more accurate and efficient method for determining the presence of native oysters. This will mean the dredge will also give a reasonable estimation of the extent of any a population distribution at a site at a large site in a way that grab sampling or technological methods such as sonar will not be able to achieve. A secondary benefit is that depending on the mesh size in a dredge-based approach this can also provide similar information for species that will co-occur with native oysters and also be caught in the dredge (e.g., Lown *et al.,* 2021).

Unlike a grab, diver, video or camera or laser scanning sonar a dredge survey cannot easily provide an estimate of the true density of live native oysters on the seabed. The two reasons for this limitation are that the efficiency of the dredge to capture oysters is much less than 100% and unknown, and it is more difficult to tow dredge for a very short compared to longer tow e.g. 10m vs 50m or 100m tow.

Dredge efficiency rates matter as they are used to multiply the catch of oysters per dredge to give an idea of the total number of oysters on a particular area of ground. As discussed above in critique of the analysis of SIFCA surveys of the Solent that applied a very generous 5% dredge efficiency (SIFCA, 2017), a review of literature and evidence by the Essex Marine Team at Natural England suggested an efficiency of 20% was probably more appropriate and this has been used in Essex and Kent by KEIFCA and the University of Essex. Since then, and more recently (2021), experimental assessment of ladder dredge efficiency for native oysters has been commission by Natural England and the median value so far across three ground types, two densities and a uniform density using 50m tows is 15% (T. Cameron unpublished). This is similar to estimates of a similar 1.2 commercial dredge towed at similar speeds for the New Zealand *O. chilensis* fishery ~ 15-18% (Doonan, Cranfield and Michael, 1994).

At the scale of the BCRC MCZ and given the management challenges posed here by Natural England and the management and research challenges that have been raised by KEIFCA, ENORI and their members, both dredge and grab sampling have a role to play in the BCRC MCZ. While trials of other methods have occurred, such as diver and video surveys, they have not yet been successful. Further trials of these methods led by ENORI are ongoing. The scale in which these methods should be applied very much depends on the question being asked but it would **remain appropriate for basic annual (or less frequent) surveys to be undertaken at the largest scale (e.g., the 2014 or the 2015-2018 KEIFCA surveys) to occur by 100m dredge surveys** on the original 2014 survey grid. **But it would also be appropriate to supplement that work with a targeted grab survey** to examine the links between the dredge survey results, dredge efficiency and the distribution of the oysters which will more easily be determined by grabs. **A complementary research question to this is for some areas of the BCRC MCZ to assist in a varied tow length survey where sites known to have relatively high or low**

oyster density are surveys using dredges of variable length such as 10, 50 and 100m to see how this influences the estimation of realised oyster densities. These research objectives will assist NE and KEIFCA in identifying to a greater level of accuracy where oyster "bed" habitats are.

This review has mostly considered spatial scales, but temporal scales are also important. Some oyster habitats will be short lived, sink populations, or longer term and/or source populations. The frequency with which conduct surveys will help to understand these dynamics in the BCRC MCZ, but destructive sampling could also damage the sites and its features if it is done too often at too large a scale. That it has been some time since a full MCZ wide oyster survey has been recognised and was planned for 2020-2021. This was postponed due to the coronavirus outbreak. This survey, a repeat of the full MCZ survey not undertaken since 2014 is important as will give some ideas about whether sites where oysters were not discovered in 2014 have recovered or sites where they were discovered are declining. It is unclear whether beyond these annual surveys are required and a less frequent survey of the main sub populations of native oysters in the MCZ may well be sufficient to meet the conservation objectives of Natural England and the fishery permit byelaw obligations of KEIFCA – at least until we have seen significant recovery of the oyster stocks in the MCZ and at Ray Sand or in new sites. Note however that the experimental evaluation of ladder dredge efficiency will influence the 2014-2018 estimates of Native oyster population size.

4. Are there differences in this definition in an estuarine environment relative to the offshore?

Due to limited resources this section will not be considered in detail other than it is thought that the advice provided above in answers to all questions which includes the concerns about simple definitions of populations, habitat and beds is likely to be a universal set of concerns with both shared and site specific considerations, e.g. all oyster populations will have range of densities and some of these areas within a population may be habitat forming and others may not. The evidence that discusses the ecology and potential ecosystem services and management interventions shares properties with some sites, e.g., coastal high sediment load and relatively soft sediment estuaries. But it is also worth remembering that some of the features of the BCRC MCZ make it unique due to the close proximity and history of fisheries activity, imports of stock of shellfish from around the world over time and the resulting non-native species communities to be found there and the context of local pressures to consider *Bonamia* risks that might not apply at a site where there was no on-bed mariculture or aquaculture.

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