Topical Issue - NORA 4 - Native Oyster Restoration Alliance 4th Conference

Research Article

Aquatic Living Resources Available online at: www.alr-journal.org

Open Ə Access

Population dynamics of the European native oyster in a Marine Conservation Zone exposed to unregulated harvesting

David Smyth^{1,*}, Rachel Millar², Annika Clements², Heidi McIvenny² and Maria Hayden-Hughes¹

¹ School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, Wales LL59 5AB, UK
 ² Ulster Wildlife, McClelland House, 10 Heron Road, Belfast BT3 9LE, UK

Received 29 June 2022 / Accepted 14 December 2022

Handling Editor: Tom C. Cameron

Abstract – The implementation of closed zones as fishery management tools have been shown to be successful in the augmentation of habitat restricted species. A concerted restoration effort is currently being focused on the European native oyster throughout its natural range. This has been accompanied by an increase in oyster prices. In 2018 a native oyster for restoration purposes cost 80 pence sterling by 2021 the price had increased to £3.50. It is likely that these price increases have led to harvesting pressure on established wild populations. A number of recovering *Ostrea edulis* assemblages in Strangford Lough Northern Ireland are located within a closed zone which has been in operation since 2008. This research investigated the effectiveness of this restricted area in regards to protecting *O. edulis* assemblages. The study revealed that within policed regions of the restricted area the population increased from an estimated 1000 oysters in 2004 to >88,000 in 2021. Furthermore, the age structure and population dynamics differed considerably from non-policed areas which still experienced harvesting. The research supports the use of closed zone legislation as a conservation tool with developing *O. edulis* populations. As newly restored populations become established, rising market prices will place these under increased harvesting pressure. The use of closed zones may offer a means of protecting these emergent populations.

Keywords: European oyster / Native oyster / Ostrea edulis / Strangford Lough / population dynamics

1 Introduction

Historically shellfish were one of the most readily exploited foods on the foreshore and were consumed in large quantities (McErlean et al., 2002). References to the European "Native Oyster" Ostrea edulis and its consumption abound the archives of libraries throughout the UK and Europe (Coles et al., 1971; Day and McWilliams, 1991; Murray, 2007; Sommerville et al., 2017). Archaeologists working throughout the oyster's natural range have unearthed shell middens containing O. edulis valves which can be dated as far back as the Mesolithic times and up to the post-Medieval period (Yonge, 1960; Magennis et al., 1983). Historical accounts relating to the harvesting of native oysters from the 1100 s to the early 1700s suggest its exploitation was carried out in a relatively sustainable manner as the bulk of effort was for personal consumption (Edwards, 1997; McErlean et al., 2002). However, as early as the mid-1700s native ovster fisheries were reporting alarming declines in landings and recruitment (Pazó and Camacho, 1987; Beck et al., 2011; Pogoda, 2019).

By the 19th Century the decrease in oyster numbers became a major concern for fishery managers with cause attributed to unsustainable fishing practices, unregulated harvesting and pollution (Went, 1962).

The small semi-enclosed sea lough of Strangford in Northern Ireland offers a classic example of the historical demise of a once prolific native oyster population (Fig. 1). Strangford had an extremely productive *O. edulis* fishery, the Montgomery Records of 1683 stated that, "The beds of Strangford are dredged of oysters in the deep water as well as being gathered on the Loughs foreshore in great numbers" (Montgomery, 1683). Quinn, in 1732, reported that "the oysters be good for eating both in summer and winter", while Harris, in 1744, noted that the oyster beds of Strangford were being commercially exploited by more than 20 small boats (Magennis et al., 1983).

However, oyster landings in the Lough declined rapidly by the mid-1800s following the scenario which was occurring throughout Europe (Day and McWilliams, 1991). Fishery managers and legislators throughout the native oyster's natural range attempted to halt the demise through a number of emergency actions (Steins, 1997; Helmer et al., 2019). In Ireland a country-wide official inquiry was conducted in 1877

^{*}Corresponding author: d.smyth@bangor.ac.uk

This is an Open Access article distributed under the terms of the Creative Commons Attribution License (https://creativecommons.org/licenses/by/4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.



Fig. 1. Strangford Lough situated on the north east coast of Northern Ireland. The loughs designated sea fishing exclusion zone falls within the T-bar demarcation area. Introduced in 2008 under the powers conferred by sections 19(1) and 124(1), (2) and (2A) of the Fisheries Act (Northern Ireland, 2002).

by the Inspector of Irish Fisheries, Mr. J.A. Blake. On account of the great reduction (90%) over the previous fifty-year period. It was decided to shorten the open season by a month and to prohibit the taking of juvenile oysters (Went, 1962). These methods seemed to have had little effect, as by the late 1800 s the oyster beds had all but disappeared. Went (1962) reported that commercial oyster fishing was no longer profitable in Ireland and had ceased before 1903.

The removal of oysters from Strangford during the 1800s was so complete that juvenile oysters were not reported in the Lough until the 1970s when aquaculture trials involving *O. edulis* were undertaken (Kennedy and Roberts, 2006). The trials of the 1970s demonstrated favourable growth of both the Pacific oyster, *Magallana gigas* and *O. edulis* (Briggs, 1978; Kennedy and Roberts, 1999). Although most of the resulting aquaculture concentrated on *M. gigas* production, commercial stocks of *O. edulis* were also maintained. Nunn (1994) provided the first viable reports in 1990 of small, concentrated assemblages of *O. edulis* juveniles in the Lough with their source attributed to spawning from the continuing aquaculture trials (Kennedy and Roberts, 2006).

By 1998, Strangford Lough held an estimated *O. edulis* culture stock of approximately 100,000 and had a small wild population of approximately 3000 (Kennedy and Roberts, 1999). In 2002, Smyth et al., (2009) estimated the wild stock at over 1 million and by 2003 the population had increased to >1.2 million, with all sites located in the northern sector. However, after an initial increase, oyster numbers rapidly declined to approximately 900,000 by 2004. The population decreased further with <600,000 reported in 2005 (Smyth et al., 2009).

The brood source for this rejuvenation of the wild population was always a point of debate with many fishermen believing an undiscovered settlement of subtidal oysters was responsible and that the Lough was once again self-sustaining and good to fish (Roberts et al., 2004). Smyth et al., (2016) ran a particle tracking model for an *O. edulis* pelagic larval phase using the location of the 1998 commercial stock at Ardmillan Bay as the designated source. The model output matched the newly settled native oyster sites recorded between 2002 and 2005 confirming that the 1998 spawning event from the 100,000 oysters at Ardmillan was most likely responsible for the restoration. Emphasising that the current population numbers could not yet be considered sufficient enough to open a fishery as a protected aquaculture stock source was no longer present (Smyth et al., 2016).

The decline of the newly established native oyster population of the 2000s in Strangford was initially thought to be a combination of detrimental environmental pulse events and parasitic infections from *Bonamia ostreae* (Kennedy and Roberts, 2006). However, the lack of empty oyster valves at sites where the most rapid decreases in numbers had been recorded did not concur with this theory (Smyth et al., 2009).

While monitoring the newly settled oysters between 2002 and 2005 observations were made of regular shellfish gathering suggesting that unregulated harvesting was a major contributor to the population decline (Smyth, 2008). The legislation related to the hand gathering of shellfish in Strangford Lough follows that set by authorities in the rest of the UK. Whereby, the gathering of shellfish is permitted if the harvest is in a class A watercourse and is for personal consumption and does not exceed 1.5 kg (https://www.gov.uk/ shellfish-harvesting-classification-ni). However, as the restoration of the wild O. edulis stocks was unexpected and not widely known harvesting practices were not monitored by the authorities. This resulted in a dramatic decrease in O. edulis numbers over a short three-year period in the 2000s (Roberts et al., 2005) reminiscent of the excessive exploitation of the 1800s indicating that personal consumption limits were not being adhered too. Indeed, subsequent surveys in the 2010s have shown small increases in oyster numbers at sites until they reach a commercial size (Kregting et al., 2020). However, the removal of these marketable size cohorts has been recorded for over a decade on low spring tides when shellfish gatherers have had easy access to the oysters (Smyth et al., 2020). Not all sites experienced this phenomena, safe havens from oyster harvesting on private land or on difficult to access sites showed signs of reaching a self-sustaining status (Guy et al., 2019).

Strangford Lough has benefited from being studied since the early 1960 s and is a designated Marine Conservation Zone (MCZ) and Marine Protected Area (MPA) with numerous Areas of Special Scientific Interest (ASSI) which accommo-

date Sites of Special Scientific Interest (SSSI) (Roberts et al., 2011). In the late 1990s intense trawling activity over Modiolus modiolus reefs was suspected of causing damage to highly diverse biotopes in the north of the lough (NIAO, 2015). As a result, local government introduced a closed fishing zone in 2008 in an attempt to initiate the natural recovery of the reefs (Roberts et al., 2011). The introduction of this closed zone increased the activities of government enforcement officers in the Loughs northern region where many of the remaining small assemblages of O. edulis were located particularly on the islands which could only be accessed by boats. As part of the legislative enforcement Fishery officers would regularly inspect small boats to check fishing was not being carried out and that vessels were legally registered (NIAO, 2015). It is thought that these actions deterred much of the unregulated harvesting of shellfish on the islands and as a result may have protected the remaining native oysters for more than 13 years. In an attempt to establish if the implementation and policing of the closed zone had an effect on the current status of O. edulis within Strangford Lough, a comparative population survey using 2004 data as a baseline was undertaken at sites where heavy and low intensity harvesting had been recorded.

2 Site selection

In order to obtain comparable data for population dynamics and density modelling, site locations were selected from a 2004 survey (Smyth, 2008). The 2004 data was considered to be of most value as harvesting was repeatedly taking place throughout the northern region. The survey consisted of 24 intertidal onshore sites and 14 intertidal island sites (Figs. 2–4). Sites were categorised as being intertidal if they were accessible during low tide from the shore; island sites could only be accessed by boat. Sites were allocated a regional description of 1. North, 2. East and 3. West to match the population modelling parameters used in Kennedy and Roberts (1999) and Smyth (2008).

3 Methods

3.1 Survey techniques

Surveys were undertaken at low tides of <0.5 m below chart datum. At each site oyster densities were established using counts in replicated quadrats and in timed searches. Quadrat surveys followed a 100 m belt transect recording oysters in a (50×50 cm) quadrat every 5 m on either side of the transect line. At sites where the terrain could not facilitate transect line surveys a timed search methodology was employed. This involved recording oysters in two 10 min searches in a site-specific plot size equal to a 100 m transect. Density estimates using both techniques showed a highly significant positive relationship ($r^2=0.999$; p < 0.0001).

During the surveys, substratum composition was recorded for each location. Digital stills of transect substrate types were taken to allow the relative percentage coverage of different substrata to be determined. To establish the population dynamics of *O. edulis*, live oysters were measured *in situ* at each site using a Vernier[©] calliper to 0.25 cm.

Table 1. Dimensions of survey regions, surface area and allocatedsubstratum correction factor (c.f.) (Kennedy, 1999; Smyth, 2008).Model outputs for population estimates will be expressed regionallyand as an overall total.

Region	Intertidal area m^{-2} (×10 ⁶)	Subtidal area m^{-2} (×10 ⁶)	Total area m^{-2} (×10 ⁶)
1. North	19.644 c.f. 0.056	26.816 c.f .0.234	46.460
2. East	4.509 c.f. 0.0236	32.318 c.f .0.236	36.828
3. West	5.438 c.f. 0.027	9.789 c.f. 0.019	15.227
Total	29.592	68.954	98.516

3.2 In situ site density

Site density was recorded for both quadrat and timed search methodologies with *n*. number of oysters per 100 m length of shore. Data was then converted into *n*. number of oysters per m^2 so that a direct comparison could be made between the current *O. edulis* densities and those presented in 2004 (Smyth, 2008). The statistical package PAST vr3.2[®] (Hammer et al., 2001) was employed for all statistical analysis throughout. Differences in oyster density/m² per site and year of survey was investigated using PERMANOVA analysis.

3.3 Population modelling estimates

A Gunderson population model was used to estimate the abundance of oysters at a site, based on the available total area of suitable substratum at each site. This modelling approach has proved extremely accurate when assessing sessile or regionally limited fishery stocks (Kennedy and Roberts, 1999; Smyth et al., 2009). For each site, the proportion of total area accommodating the settlement substrate was determined by examining biotope classifications of Phase 3 EUNIS biotope coding in combination with digital *in situ* imagery of the survey sites. This information allowed for the application of a correction factor, restricting abundance estimates to only the area within each survey site that possessed substrates suitable for the settlement of oysters.

Gunderson model formula

The total number of potential *O. edulis* was estimated using the following formula which was adapted from Gunderson (1993):

$$P = \sum_{i=1}^{h} (R_i \cdot F/a) C_i,$$

whereby P=total population resident in full survey area; R_i =area of region in m²; a=area sampled within a single sampling unit; F=correction factor estimating substratum types; C_i =Mean number of oysters observed per sampling unit in region *i* based on, samples; h=Number of regions composing the survey.

The surface area, ' R_i ', for the regions are estimated using scaled images of Strangford Lough from Global Lab image analysis software (Tab. 1). A proportionally weighted correction factor, 'F', was applied to ' R_i ' to account for the amount of suitable oyster settlement substratum present in the region. The correction factor was derived from survey results as per Kennedy and Roberts (1999) and Smyth et al. (2009).

4 Results

4.1 O. edulis in situ site density

In 2021, a total of 24 intertidal sites were surveyed (Fig. 2), 16 of these showed a decline in oyster density since 2004. These 16 sites were considered easy access with sporadic bouts of oyster harvesting recorded over the 17-year period between surveys (Tab. 3). Seven sites experienced an increase in densities; Nendrum S, Rignell, Millar's Corner, Pig Island SW, N and NW and Kircubbin. Regular harvesting was not recorded at these sites with the exception of Kircubbin. The western intertidal site of Killyleagh remained unchanged between 2004 and 2021 with no oyster assemblages recorded.

Of the fourteen island sites surveyed, 11 experienced significant increases in *O. edulis* densities (Fig. 2, sites: 23,24,25,26,28,29,30,31,32,33,34) with the remainder unchanged. The data revealed oyster densities and sizes characteristic of a brood stock source at the island sites in region 2. In 2004 intense harvesting was witnessed throughout the islands (Smyth et al., 2009). The present data suggests that harvesting has been limited over the last 17 years, and absent on some islands as oysters of >110 mm in shell length, approximately 8–12 years of age (Richardson et al., 1993) were found at several sites in concentrated assemblages.

PERMANOVA analysis showed *O. edulis* site density/m² between survey years (F = 93.33, p = 0.0001) to be significantly different. Likewise, density/m² at harvested and non-harvested sites between years was also significantly different (F = 50.48, p = 0.0001). A pairwise post-hoc test identified the highest density intertidal sites as 1. Ballyreagh and 2. Ballyreagh west from the 2004 survey as significantly different (p < 0.005) from the remainder. Similarly, the 2021 highest density island sites 23. Sheelah Island and 34. Skart Rock were significantly different (p < 0.05).

Harvesting activity witnessed at specific sites over the past 17 years matches a number of locations were declines and increases in oyster numbers have been recorded (Tab. 3). However, the actual quantity of oysters being removed by gatherers is difficult to quantify as witnesses did not always see the number or size of gather bags being used by harvesters.

4.2 Modelled population

In situ 2021 native oyster site densities/ m^2 were subjected to the Gunderson (1993) population model which estimates total oyster densities based on available suitable substratum for larval settlement.

The Gunderson model output showed a decrease of >814,000 O. edulis in the total population between 2004 and 2021. The model also revealed a shift in regionality with sites in region 2. East now accounting for the majority of the Lough's oysters in 2021 compared to the north region 1. in 2004. These findings indicate a shift in population dynamics which concurs with the recorded regional harvesting pressures.

Region 2. east experienced intense harvesting pressure in the early to mid-2000 s (Smyth et al., 2009) whereas presently it is region 1. North which is being exploited by shellfish gathers.

4.3 Population dynamics

Investigations into *Ostrea edulis* population dynamics within Strangford Lough in 2021 were based on *in situ* size density data which were categorised into five cohorts which could be approximated into age classes as per Walne (1974) and Richardson et al. (1993).

Individual site locations were divided into intertidal or Island. All *in situ* data were pooled and assigned a size cohort in mm; 1–30, 31–60, 61–90, 91–120 and 121–150.

The 2021 intertidal population of native oysters in Strangford Lough could be considered in a state of poor conservational health. The oyster assemblages were dominated with oysters ranging in the 31–60 mm size cohort, approximately years 1–3 with a low potential larval output (Walne, 1974).

The fecundity of these intertidal sites is also likely to be reduced when we consider that the average *in situ* densities dropped from $3.36/m^2$ in 2004 to $0.44/m^2$ in 2021. Guy et al. (2019) showed that fragmentation of oyster densities/m² to this degree does not correspond to successful spawning and settlement in the wild.

The island population was predominantly made up of oysters in the 4–7-year age categories (61–90 mm size cohort) (Walne, 1974). Oysters of this size can produce maximal larval outputs under suitable conditions. The fecundity of the island oysters has the potential to be high as the density $/m^2$ was considerably more concentrated than that found on the more expansive areas of the intertidal. Indeed, the morphometric and density data for the island population are characteristic of a brood stock source.

5 Discussion

The unsustainable exploitation of the native oyster has been an issue throughout its geographical range since the mid-1700 s (Laing et al., 2005). Indeed, the harvesting of oysters during the 1800 s, was so intense that many sites which were historically renowned as prolific remain absent of *O. edulis* more than 200 years after the event (Thurstan et al., 2013; Pogoda et al., 2019). In Strangford Lough this was the situation for the native oyster for more than a century, until the unexpected larval release from the commercial stock of 1998 (Kennedy and Roberts, 2006). The recovery of the Lough's native oysters was short-lived as unregulated harvesting removed 60% of the population within three years (Smyth et al., 2020).

This state of affairs whereby a threatened species with a market value becomes re-established after a management intervention, only to be returned to a state of poor conservational state through over-exploitation is common within many fisheries (Murawski et al., 2000; Bartley et al., 2008). In an attempt to counter these non-sustainable, species-enhancement scenarios, private stakeholders, habitat managers and fishery departments have introduced species-specific closed zones (Beukers-Stewart et al., 2005; Gray, 2016). The



Fig. 2. Survey site locations Strangford Lough: 1. Ballyreagh, 2. Ballyreagh W, 3. Ballyreagh E, 4. Ballyreagh N, 5. Millars Corner, 6. Pig Island SW, 7. Pig Island N, 8. Pig Island NW, 9. Kite Surf, 10. Cunningburn, 11. NSC N, 12. NSC S, 13. NSC E, 14. Chapel N, 15. Chapel Island W, 16. Peggy's Island, 17. Greyabbey 1, 18. Greyabbey fish trap, 19. Greyabbey fish trap 2, 20. Nendrum N, 21. Nendrum S, 22. Rignell, 23. Sheelah Island, 24. Eel Rock, 25. Dulsk Rock, 26. S Dougherty Rock, 27. Kircubbin, 28. North Bucky, 29. Bird Island, 30. Woman's Rock, 31. South Rock, 32. South Buckey, 33. West Rock, 34. Skart Rock, 35. Horse Island, 36. Inisharoan, 37. Inishanier, 38. Roe Island, 39. Killyleagh.

Intertidal area $m^{-2} (x10^6)$	Substratum correction factor*	Area suitable for settlement $m^{-2} (x10^6)^*$	Standing stock Oysters+ 2004	Standing stock Oysters+ 2021
29, 591	Region 1. North (0. 056)	11.000	964,000	58,212
	Region 2. East (0. 236)	1.064	1000	88,242
	Region 3. West (0. 027)	0.146	500	350
	Total	12.21	964,600	146,804

Table 2. Gunderson population model estimate comparisons for 2004 and 2021 for total suitable available substrate coverage at intertidal and island sites in Strangford Lough.

Table 3. Harvesting incidents witnessed and recorded between 2004 and 2022. Harvest site numbers are displayed in Figure 2. Harvesting scale refers to the gathered effort, if <5 kg considered personal if, >5 kg commercial (witnessed estimates). Oyster number decreases have been calculated from data cited in the reference list.

Date	Harvested sites	Harvesting scale	Oyster no. decrease	Witnessed by:	References
Sep-May 2004-05 Sep-May 2004-06	Island sites: 23,24,25,26,28, 29,30, 31,32,33,34 Ballyreagh sites: 1,2,3 and 4 NSC sites: 11,12 and 13 Greyabbey sites: 17,18 and 19	Commercial Commercial and Personal Commercial and Personal	≈100,000 >300,000 ≈50,000 ≈20,000	Dr. D. Smyth- Queen's University Belfast (QUB) Mr. S. Rogers- Cuan Marine Services Ltd. Dr. C. Guy- QUB Dr. L. Browne- Centre for Marine Research Portaferry. Mr. D. Rogers- Portaferry Marine Laboratory. Dr. Dai Roberts- QUB	Smyth, 2008 Roberts et al., 2005 Smyth et al., 2009
June-July 2006–07	Pig Island sites: 6,7 NSC sites: 11,12,13 Greyabbey sites: 18 and19	Commercial Personal Commercial	≈350 ≈500 ≈800	Dr. A. Mahon-QUB Members of general public	Kregting et al., 2020 Smyth et al., 2020
2008–2018	Sites: 5–21	Personal	≈15,000	Mr. D. Rogers- Portaferry Marine Laboratory. Newtownards RYA Members. North Down Kite Surfing Club.	Smyth et al., 2020
May-Mar 2019–2022	Sites: 5–19 Horse Island site:35	Commercial Commercial and Personal	≈10,000 ≈4,500	North Down Kite Surfing Club. Mr. S. Rogers-Cuan Marine Services Ltd. Dr. D. Smyth- Bangor University Wales. Dr. L. Lieber- QUB Dr. L. Kregting- QUB	Smyth et al., 2020

introduction of closed zone policies has proved to be an extremely useful management tool in regards to stock enhancement and species rejuvenation within threatened or depleted populations (Hart et al., 2006; Shester et al., 2021).

The findings of this research provide evidence that supports the implementation of closed zone policies in relation to *O. edulis* restoration. It must be emphasised that the restoration of *O. edulis* in Strangford Lough is from a passive perspective with no pro-active practices such as the addition of spat on shell, adult or juveniles, cultch laying or harrowing. This makes the increase in oyster numbers in region 2. east from circa 1000 in 2004 to 88,242 in 2021 (Tab. 2) remarkable. The increase in the region 2. east island oyster assemblages highlights the value of closed zone legislation and associated policing when attempting to restore a native oyster population. In contrast, the severe depletion of *O. edulis* numbers at the once densely populated intertidal sites in region 1. north from 964,000 to 58,212 (Tab. 2) over the same time-span emphasises how detrimental a non-protective policy can be when trying to restore a commercially valuable species.





Fig. 3. Intertidal sites in situ native oyster size umbo to outer rim (mm) densities and age per cohort in 2021.



Fig. 4. Island sites in situ native oyster size umbo to outer rim (mm) densities and age per cohort in 2021.

The *O. edulis* population of Strangford has been considered unique for the species as the majority of the population is found in the lower intertidal and not within the subtidal zone. However, the implementation of closed zones as a population rejuvenation tool with other subtidal molluscan species has been as equally effective as that experienced by the intertidal island sites at Strangford (Geist and Hawkins 2016). Beukers-Stewart et al. (2005) showed that a population of *Pecten maximus* in a closed zone off the Isle of Man, over a 14-year period was more than seven times higher than a fished area. The research also revealed a shift towards much older and larger scallops in the closed area with lower total mortalities, findings which mirror those recorded on the island sites during this research.

The scallop density at Georges Bank in New England USA increased 14-fold within closed areas between 1994 and 1998. In 1998, the total harvestable scallop biomass was nine times

denser, respectively, in the closed zone than in the adjacent open areas (Murawski et al., 2000). Puckett and Eggleston (2012) showed how effective closed zone implementation could be in regards to *Crassostrea virginica* restoration when they recorded average oyster recruitment and total density had increased 15- and fivefold, respectively over a two-year period. Concluding that their research unequivocally supported the efficacy of marine reserves and closed zones in rapidly increasing the density and age-size structure of the protected species.

The intertidal surveys during this research documented a confusing harvesting practice not seen before among gatherers in the Lough. Sites which were known to have low fragmented assemblages of under sized oysters and therefore deemed no longer economically viable as the Catch Per Unit Effort (CPUE) would be too low to warrant harvesting were still visited. Indeed, the reports of shell fish gathering incidents had increased since the peak of unregulated harvesting in the early 2000 s (Tab. 3).

Initially, this activity was difficult to explain, however, with a decrease in over 90% of O. edulis biotopes within the species natural range a concerted effort is now underway to restore these lost populations (Helmer et al., 2019). There are presently more than 20 O. edulis restoration programmes underway in Europe and the UK and this number is increasing annually (NORA, 2022). This in-turn has led to an increase in demand for O. edulis from suppliers and subsequently the market value of O. edulis has increased. In 2018 a native oyster for restoration purposes could be purchased at 80 pence sterling per oyster, in 2021 the price per oyster from the same supplier had increased to £3.50 (personal communication Conwy Mussels Ltd). It would appear that this increase in price has now made the once non-viable CPUE for wild native oysters now worthwhile. Inadvertently, putting evermore pressure on threatened wild populations. Indeed, this may go some way to explaining the increase in harvesting pressure on the low-density intertidal sites at Strangford witnessed during this 2021 survey. As O. edulis numbers start to rise within restoration project areas, newly established recruits may find themselves under the same harvesting pressure as the native oysters of Strangford Lough.

The restoration of a depleted commercial fishery species is an extremely challenging task and for success legislative protection must be in place (Puckett and Eggleston (2012). Instigating a change to the current fishery status of O. edulis in Europe and the UK could take years of governmental lobbying. So local and regional Government and Council bylaws may need to be considered to protect restored O. edulis populations. An excellent example of this is provided by the East Lothian Council in Scotland who have implemented a local byelaw specific to Aberlady Bay Local Nature Reserve and John Muir Country Park which makes: "The killing, taking or disturbing of any living animal within these areas an offence". Permits for fishing and hunting can be issued by the local authority and Council and as a consequence staff patrol the sites on a regular basis and prosecute rigorously anyone found breaking the law (ELC, 2020). With stringent policing this byelaw has proved extremely effective in countering incidents of wildlife crime including the illegal gathering of shellfish. Legislation like this may be needed in the coming years if the European native oyster is to truly return to a self-sustaining status.

6 Conclusion

The findings of the research presented here show that the implementation of a closed zone policy does aid the passive restoration of *O. edulis* populations within a heavily harvested region. Oyster numbers and densities increased in less accessible or more regularly patrolled regions compared to sites that were less well patrolled and more accessible and this is linked to harvesting pressure. As restoration programmes start to return wild populations of European native oyster within its natural range, the implementation of closed zone legislation should be considered as a management tool to protect this iconic bivalve from the trials and tribulations its

predecessors experienced in the past. However, international examples with other threatened molluscan species have shown that the legislation must be policed and managed to be effective.

Authors contribution statement

David Smyth: Concept, Data collection, Statistical analysis, Write up and Review. Rachel Millar: GIS and map creation, Manuscript edits. Annika Clements: Concept and Review. Heidi McIvenny: Concept and Review. Maria Hayden Hughes: GIS and map creation, Statistical analysis, Review, Manuscript edits.

Conflicts of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements. This work was supported by the Department of Agriculture, Environment and Rural Affairs (DAERA) as part of the Blue Carbon Challenge Fund. We are particularly grateful to Mr. Simon Rogers and all those at Cuan Marine Services Ltd. for their field-work assistance. We would also like to offer our thanks to the reviewers of this manuscript for their constructive suggestions.

Supplementary Material

The Supplementary Material is available at https://www.alr-journal.org/10.1051/alr/2022023/olm.

References

- Bartley DM, Bell JD. 2008. Restocking, stock enhancement, and sea ranching: arenas of progress. *Rev Fish Sci* 16: 357–365.
- Beck MW, Brumbaugh RD, Airoldi L, Carranza A, Coen LD, Crawford C, Defeo O, Edgar GJ, Hancock B, Kay MC, Lenihan HS, Luckenbach MW, Toropova CL, Zhang G, Guo X. 2011. Oyster reefs at risk and recommendations for conservation, restoration and management. *Bioscience* 61: 107–116.
- Beukers-Stewart BD, Vause BJ, Mosley MWJ, Rossetti HL, Brand AR. 2005. Benefits of closed area protection for a population of scallops. *Mar Ecol Progr Ser* 298: 189–204.
- Briggs RP. 1978. Aspects of oyster culture in Strangford Lough, Northern Ireland. Aquaculture 15: 307–318.
- Coles JM, Allo J, Candow RDM, Clegg TM, Cowles GS, Hibbert FA, Wilson G. (1971 December). The early settlement of Scotland: excavations at Morton, Fife1. *Proc Prehistoric Soc* 37: 284–366
- Day A, McWilliams P. 1991. Ordnance Survey Memoirs of Ireland, Parishes of County Down II 1832-4, 1837 North Down & The Ards. Belfast. The Royal Irish Academy, pp. 88–89.
- ELC.gov. 2020. East Lothian Council Shellfish Gathering bylaws 2020, https://www.eastlothian.gov.uk/homepage/10450/gather ing bivalve shellfish [Accessed 20 May 2021]

- Edwards ERIC. 1997. Molluscan Fisheries in Britain, p 85–99. In U. S. Department of Commerce, NOAA Technical Report NMFS 129.
- Geist J, Hawkins SJ. 2016. Habitat recovery and restoration in aquatic ecosystems: current progress and future challenges. *Aquat Conserv* 26: 942–962.
- Gray CA. 2016. Assessment of spatial fishing closures on beach clams. *Glob Ecol Conserv* 5: 108–117.
- Gunderson D. 1993. Surveys of fisheries resources. New York, Chichester, Brisbane, Toranto, Singapore. John Wiley and Sons, Inc.
- Guy C, Smyth D, Robert D. 2019. The importance of population density and inter-individual distance in conserving the European oyster Ostrea edulis. *J Mar Biol Assoc UK* 15: 1–7.
- Hammer Ø, Harper DAT, Ryan P. 2001. Past: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontolog Electr* 4: 9.
- Harris W. 1744. Ancient and present state of County Down. A. Reilly, Dublin.
- Helmer L, Farrell P, Hendy I, Harding S, Robertson M, Preston J. 2019. Active management is required to turn the tide for depleted Ostrea edulis stocks from the effects of overfishing, disease and invasive species. *PeerJ* 7: 6431.
- Kennedy R, Roberts D. 1999. A survey of the current status of the flat oyster Ostrea edulis in Strangford Lough, Northern Ireland, with a view to the restoration of its oyster beds. *Biol Environ Proc R Ir Acad* 99: 79–88.
- Kennedy R, Roberts D. 2006. Commercial oyster stocks as a potential source of larvae in the regeneration of Ostrea edulis in Strangford Lough, Northern Ireland. J Mar Biolog Assoc UK 86: 153–159.
- Kregting LT, Hayden-Hughes M, Millar RV, Joyce PWS, Smyth DM. 2020. A first record of intertidal Ostrea edulis 3D structural matrices in Strangford Lough Northern Ireland. An emergent reef? J Sea Res 163: 101927.
- Magennis BA, Gosling E, Wilkins NP. 1983. Irish oyster populations: an historical and genetic study. *Proc R Irish Acad* 83B: 291–299.
- McErlean T, McConkey R, Forsyth W. 2002. Strangford Lough: an archaeological survey of the maritime landscape. Belfast, Northern Ireland: Blackstaff Press, p. 689.

Montgomery H. 1683. The Montgomery Manuscripts. Belfast.

- Murawski SA, Brown R, Lai HL, Rago PJ, Hendrickson L. 2000. Large-scale closed areas as a fishery-management tool in temperate marine systems: the Georges Bank experience, *Bull Mar Sci* 66: 775–798.
- Murray E. 2007. Molluscs and middens: The archaeology of 'Ireland's early savage race'. *Environ Archaeol Ireland* 119–135.
- NIAO. 2015. Protecting Strangford Lough. A report by the auditor and controller of the Northern Ireland Audit Office, 31 March 2015, available at: https://www.niauditoffice.gov.uk/publications/ protecting-strangford-lough [accessed 13 January 2022].
- Northern Ireland. 2002. Section c.17 124 was substituted by the Fisheries Amendment 1966. Order 1981 (S.I. 1981/227 (N.I. 7)), Article 6 and amended by the Fisheries (Amendment) Act (Northern Ireland) 2001 c.4 (N.I.), section 1 and the Sea Fisheries Order 2002/S.I 2002/790, article 6(2) available: https://www.legislation.gov.uk/nisr/2012/441/ made [accessed 28 September 2022].
- NORA. 2022. Projects: Overview, Native Oyster Restoration Alliance, 16 January 2022, available at: https://noraeurope.eu/ restoration-projects/projects-overview/ [accessed 5 March 2022].

- Nunn J. 1994. The marine mollusca of Ireland 1. Strangford Lough. Bull Irish Biogeogr Soc 17: 23–282.
- Pogoda B, Brown J, Hancock B, Preston J, Pouvreau S, Kamermans P, Sanderson W, von Nordheim H. 2019. The Native Oyster Restoration Alliance (NORA) and the Berlin oyster recommendation: bringing back a key ecosystem engineer by developing and supporting best practice in Europe. *Aquat Liv Resourc* 32: 13–22.
- Puckett BJ, Eggleston DB. 2012. Oyster demographics in a network of no-take reserves: recruitment, growth, survival, and density dependence. *Mar Coast Fish* 4: 605–627.
- Richardson C, Collis SA, Ekaratne K, Dare P, Key D. 1993. The age determination and growth rate of the European flat oyster, *Ostrea edulis*, in British waters determined from acetate peels of umbo growth lines. International Committee for the Exploration of the Sea. J Mar Sci 59: 116–120.
- Roberts D, Davies C, Mitchell A, Moore H, Picton B, Portig A, Preston J, Service M, Smyth D, Strong D, Vize S. 2004. Strangford Lough Ecological Change Investigation (SLECI). Report to Environment and Heritage Service by the Queen's University, Belfast.
- Roberts D, Smyth D, Browne L. 2005. Native oyster (*Ostrea edulis*) fishery enhancement in Strangford Lough, Northern Ireland. *Shellfish News* 20: 5–6.
- Roberts D, Allcock AL, Fariñas-Franco JM, Gorman E, Maggs C, Mahon AM, Smyth D, Strain E, Wilson CD. 2011. Modiolus Restoration Research Project: Final Report and Recommendations Queen's University Belfast, Belfast.
- Shester GG, Enticknap B, Mecum B, Blacow-Draeger A, Brock T, Murray S. 2021. A win-win for deep-sea corals and fishing: increasing seafloor protections while restoring fishing opportunities off the United States West Coast. *Front Mar Sci* 7: 525619.
- Smyth D. 2008. Impacts of stock-enhancement strategies on *Ostrea* edulis in Strangford Lough.uk.bl.ethos.486199, available: https:// ethos.bl.uk/OrderDetails.do?uin=uk.bl.ethos.486199.
- Smyth D, Roberts D, Browne L. 2009. Impacts of unregulated harvesting on a recovering stock of native oysters (*Ostrea edulis*). *Mar Pollut Bull* 58: 916–922.
- Smyth D, Kregting L, Elsäßer B, Kennedy R, Roberts D. 2016. Using particle dispersal models to assist in the conservation and recovery of the overexploited native oyster (*Ostrea edulis*) in an enclosed sea lough. J Sea Res 108: 50–59.
- Smyth D, Millar R, Hayden-Hughes M, Joyce P, Royan E, Horne N, Kregting L. 2020. Wild gregarious settlements of *Ostrea edulis* in a semi-enclosed sea lough: a case study for unassisted restoration. *Restor Ecol* 28: 645–654.
- Steins NA. 1997. Ostrea edulis in crisis: The state of Europe's oyster fisheries and lessons from management systems in the Solent (UK). In 2nd Concerted Action Workshop "Northern Waters", organized by the European Social Science Fisheries Network (ESSFiN) Århus, pp. 29–31.
- Thurstan RH, Hawkins JP, Raby L, Roberts CM. 2013. Oyster (*Ostrea edulis*) extirpation and ecosystem transformation in the Firth of Forth, Scotland. *J Nat Conserv* 21: 253–261.
- Walne PR. 1974. Culture of Bivalve Molluscs: 50 years' experience at Conwy. Fishing News Books, Oxford.
- Went A. 1962. Historical notes on the oyster fisheries of Ireland. Proc Royal Irish Acad 62: 195–223.
- Yonge CM. 1960. Oysters. London: Collins Scientific Press. https:// www.gov.uk/shellfish-harvesting-classification-ni [accessed 03/ 10/2022]

Cite this article as: Smyth D, Millar R, Clements A, McIvenny H, Hayden-Hughes M. 2023. Population dynamics of the European native oyster in a Marine Conservation Zone exposed to unregulated harvesting. *Aquat. Living Resour.* 36: 3