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50 years of estuarine cockles (*Cerastoderma edule L.*): Shifting cohorts, dwindling sizes and the impact of improved wastewater treatment

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ABSTRACT

Bivalve populations are prone to change due to sudden or gradual alteration in the natural environment and anthropogenic interference. Fisheries and environmental managers are therefore interested in long-term trends and disentangling natural and human influences, assisting them in conservation efforts and the management of bivalve stocks. Here, 64 monitoring reports covering a 50-year period from 1958 to 2009 of cockles *Cerastoderma edule* (Linnaeus, 1758) in South Wales, UK, were scrutinised for data on recruitment, growth and mortality. Changes in these population parameters were related to the modernisation of wastewater treatment in 1997, weather and climate variables (temperature, sun hours, air frost days, NAO) and numbers of cockles in the estuary. Recruitment as well as mortalities were high during the first and last decade of the study, and variation was significantly linked to the total number of cockles in the population. Cockle sizes of all cohorts as well as overall biomass declined in the late 1990s. Modernisation of wastewater treatment was significantly related with the downward trend, suggesting that the changed nutrient regime in the estuary may have resulted in reduced food provision for cockles. The average size of newly settled cockles was related to their mortality: the smaller the recruits the higher their mortality. The study indicated a link between the change in wastewater treatment in 1997 and diminishing sizes of cockle recruits that shortened their life span. Survey methods were profoundly changed after 2009, and it is recommended to develop conversion factors between the pre- and post-2009 survey methods. This would allow an extension of the timeline and deeper insight into the long-term impact of the change in wastewater treatment and the recovery of the cockle population.

1. Introduction

Intertidal bivalve populations are prone to dramatic fluctuations (Elliott and Ducrotoy, 1991; Beukema and Dekker, 2020). These are caused by diverse environmental, biological and anthropogenic factors, often with cumulative effects (De Montaudouin et al. 2010; Guillotreau et al. 2017). Seasonal changes in temperature and food availability were long established to be key external factors determining growth, reproductive activity and survival of marine bivalves , the age structure of a population and biomass (Bayne, 1976; Mann, 1979; Widdows et al. 1979). Bivalve density and position along the intertidal range affects recruitment success, growth and condition (De Montaudouin and Bachelet, 1996). Predation can lead to a decline in recruitment success of bivalves in intertidal sandflats, and de-eutrophication influences bivalve growth (Beukema and Dekker, 2005; Beukema et al. 2017).

Here, long-term (50 year) population dynamic of the commercially exploited European cockle *Cerastoderma edule* (Linnaeus, 1758) was explored. The bivalve is a suspension-feeder living in the upper centimetres of the sediment. Cockles occur in semi-sheltered marine and brackish systems with a wide geographical NE Atlantic distribution from the western region of the Barents Sea and the Baltic to the Iberian Peninsula, into the Mediterranean, the Black and Caspian Seas and south along the coast of West Africa to Senegal (Tebble, 1966). They link primary producers (phytoplankton, phytobenthos) and zooplankton to consumers such as crabs, shrimps, fish and birds (Reise, 1985). Generally, cockle populations are shaped by environmental factors such as temperature (Oertzen, 1973; Beukema and Dekker, 2005), immersion time (Jensen, 1992; De Montaudouin, 1996b; Kater et al., 2006), hydrodynamics (Kater et al., 2006) and sediment movement (Bouma et al., 2001), as well as biotic factors such as predation (Reise, 1985; McArthur, 1998; Beukema and Dekker, 2005), bioturbation (Goñi-Urriza et al., 1999), parasitism (De Montaudouin et al., 2000; Desclaux et al., 2004; Thieltges, 2006), and food availability (Iglesias and Navarro, 1990; Bos et al., 2006). Distribution and size of cockles is driven by access to food, site elevation and sediment properties (Callaway et al. 2014).

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Severe changes in bivalve populations are of particular concern to managers and fishers of commercially exploited species such as mussels (*Mytilus edulis*), cockles (*C. edule*) or oysters (*Magallana gigas*). These species may be persistently present at sites over time and thereby attract fisheries interests, but yields can be unpredictable. It is therefore of interest to understand factors impacting short and long-term development of these bivalve populations, and to disentangle natural and anthropogenic influences. For estuaries, Elliott and Quintino (2007) highlighted the 'Estuarine Paradox', saying that faunal communities are adapted to high spatial and temporal variability in naturally stressed areas, and that they have features very similar to those found in anthropogenically stressed environments. Therefore, it is difficult to detect anthropogenically induced stress in estuaries.

Cockles are commercially exploited, for example in the UK, The Netherlands and France and traded either fresh or canned (FAO, 2021). The investigated cockle population of the Burry Inlet, South Wales, UK, experienced dramatic short-term mortalities in the early 2000s (Callaway et al. 2013). Possible causes of the mortalities were studied at the time, and several coinciding factors weakening the population were established such as high density and parasite loading (Elliott et al. 2012). This study further explored if modernised wastewater treatment in the area in 1997 affected the cockle population.

Long-term studies of individual bivalve populations are uncommon, but there are detailed investigations of changes in sandflat communities studied over several decades in the western Wadden Sea of The Netherlands (Beukema et al. 2017) and a 50-year study of *Mercenaria mercenaria* (Henry and Nixon, 2008). Here, monitoring reports were analysed which had been produced by the UK fisheries agency CEFAS from 1958 to 2009, with the aim to understand long-term trends in the cockle population in terms of age-class structure, recruitment, mortalities and growth of cockles. Beyond improving our understanding of long-term variation in cockle populations, the study aimed to assess if there were earlier signs of change that may be linked to the mortalities in the 2000s.

The objectives of the study were to investigate the following aspects:

- Temporal trends in cockle recruitment and possible links with established cockle stocks and weather parameters.
- Mortality in all cohorts and assessment of links with environmental factors.
- Long-term trends in the size of cockles in each cohort.
- Relationship between the size of cockle recruits and their longevity
- Biomass of cockles >25 mm (commercial size)
- Changes in cockle population parameters after modernisation of wastewater treatment

2. Site description

The Burry Inlet and Loughor Estuary (South Wales, UK) is a macrotidal system with deep channels and tidal flats (Fig. 1). The estuary extends over 16 km from the mouth near Burry Port and Whiteford Point in the West to Pontardulais Road Bridge in the East and covers an area of approx. 45 km^2 at mean sea level (MSL). Tidal velocities at the mouth of the estuary are between 1.6 m s^{-1} (flood) and 1.9 m s^{-1} (ebb) (Robins et al., 2013), and the tidal range is approx. 5.5 m during neap tides and 9 m at spring tides. The main freshwater inputs derive from the rivers Loughor and Llan, but the freshwater input is low compared with the tidal prism, and so the estuary is vertically and laterally non-stratified in terms of salinity (Robins et al., 2013). The estuary was impacted by the grounding of the tanker "Sea Empress" at the entrance to Milford Haven in February 1996, releasing 72 000 t of Forties blend crude oil and 480 t of heavy fuel oil into the waters of southwest Wales (Lawa and Kelly, 2004), leading to mass mortalities of *C. edule*.

The water quality of the Burry Inlet can be impaired by nutrient loading from three primary sources: rivers (diffuse urban and diffuse agricultural sources), continuous discharges of wastewater from treatment works, and intermittent discharges of sewage from sewage pumping stations and combined sewage overflows (CSOs) (Metoc 2009 Report No. RN2020 unpublished). In 1997 the wastewater discharge regime was profoundly changed. Up until 1997 primary treated wastewater effluent was discharged into the estuary from seven sewage plants. This was modernised to two plants utilising treatment processes that includes activated sludge and ultraviolet disinfection (UV) of the final effluent and nitrogen removal. In response to sewerage improvements reductions in nutrient loads were in the range of 60–80% (Metoc 2009 Report No. RN2020 unpublished). Pre-1997 wastewater treatment plants contributed approximately 53% of the Dissolved Available Inorganic Nitrogen (DAIN) load, in 2008 it accounted for approximately 29%. Overall DAIN loads have fallen from 4360 kg day^{-1} during 1990–1997 to 2010 kg day^{-1} for 2005–2008. Dissolved Available

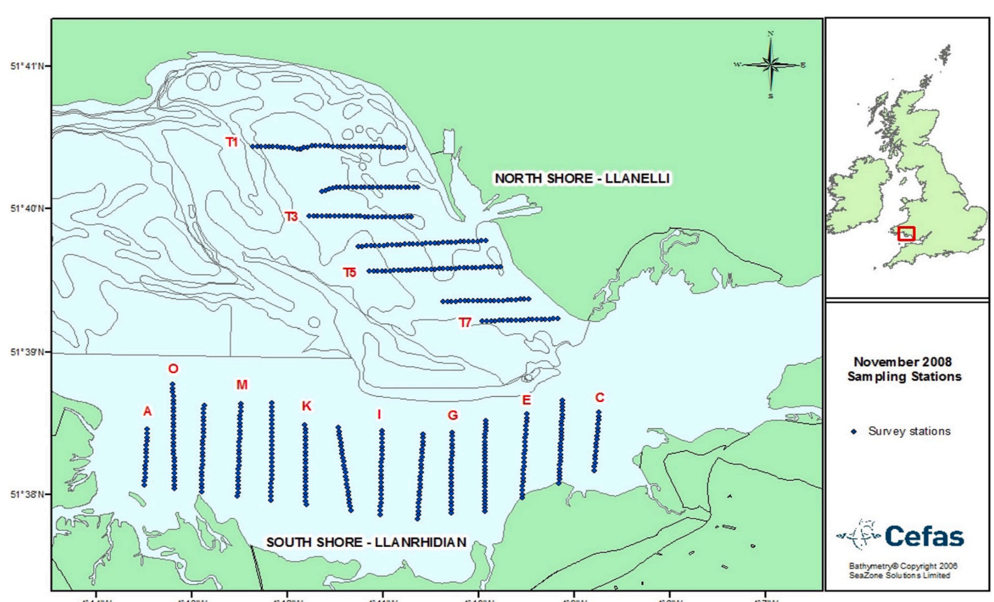

Fig. 1. Burry Inlet and Loughor Estuary (South Wales, UK). CEFAS cockle survey area showing transects and sampling positions. Figure from CEFAS monitoring report 2008.

Inorganic Phosphate (DAIP) loads to the estuary have also reduced significantly from 1990 to 1997 when water treatment plants contributed about 76%. In 2008 they still contributed the largest proportion of the load, approximately 73%. However, in absolute terms, total phosphorous load to the estuary has reduced from 476 kg day^{-1} during 1990–1997 to 174 kg day^{-1} during 2005–2008, an overall reduction of more than 64%. Bacterial loading stems mainly from tidally inundated grazed saltmarshes (Abu-Bakar et al. 2017). In 2001, routine testing for biotoxins returned atypical positive results for Diarrhetic Shellfish Poisoning (DSP) causing closures of the beds for long periods over two years, and considerable cockle mortalities were reported in 2005 and subsequent years (Elliott et al. 2012). Much of the northern edge of the inlet is fortified by flood defences and groynes to protect housing and infrastructure, but the shoreline is regarded as vulnerable (Denner et al. 2015). Cockles have been gathered in the estuary for centuries (Elliott et al. 2012). Until today they are harvested by 'rake and riddle', meaning a short-handled rake is employed to draw the cockles into piles, and they are then sieved through oblong mesh, the smaller dimension of which relates to the minimum legal size (MLS).

3. Methods

Altogether 64 cockle stock monitoring reports of surveys in the Burry Inlet and Loughor Estuary from 1958 to 2009 were studied. Initially the surveys were carried out by the Ministry of Agriculture, Fisheries and Food (MAFF), which later became the Centre for Environment, Fisheries and Aquaculture Science (CEFAS, Lowestoft, UK). The information was collected as part of a long-term study into trends in abundance and population structure of cockle stocks. However, the data was never collated into a continuous timeline but rather used for annual management of the fishery. Fieldwork was carried out by officers of MAFF/CEFAS in collaboration with the South Wales Sea Fisheries Committee.

Survey methods changed over time. From 1958 to 1972 transects on the South side of the estuary, called Llanrhidian shore, were sampled. In the 1970s this method was deemed too labour intensive and until 1979 surveys were reduced to walk-over observations with descriptive reports. No useful quantitative data could be obtained from those reports for this study. In 1979 surveys returned to a transect method. In 1982 the survey improved markedly with CEFAS establishing 15 fixed transect lines 400 m apart, which were sampled with standardised methods every 50 m along their length until May 2010. At the same time CEFAS started surveying 7 transects on the North side (Llanelli) in response to greater fishing interests in the area. Beyond the fixed transects, additional areas were temporarily surveyed in response to topographic changes and associated changes in cockle beds. Surveys were consistently carried out in October or November after cockle recruits had established, and in the 1960s and 2000s additional May surveys were carried out.

CEFAS stopped their cockle surveys in 2010 when first Environment Agency Wales (EAW) and later Natural Resources Wales (NRW) took over the shellfish monitoring and management of the estuary. Methods were radically changed from transect to grid-based surveys and results are not easily comparable. It would need a dedicated project to establish conversion factors.

Since the purpose of this study was to understand long-term trends in the cockle populations, analysis concentrated on information from the autumn surveys of the South side (Llanrhidian sands), because of the considerably longer timeline since 1958. All other surveys were consulted to underpin confidence in observed trends.

3.1. Field survey methods

Detailed descriptions of field methods were reported since 1982. At each sampling station a single sample was collected using a 0.1 m^2 quadrat. The quadrat was driven into the substrate to a depth of 6 cm. Substrate was removed using a rake and fingers and sieved through a 4 mm mesh sieve. All cockles taken were counted and aged immediately. Ages were recorded as 'spat', which are the new recruits before their first winter, '1 ring' and '2 ring and older'; *C.edule* develop growth rings in winter, facilitating the determination of cohorts in populations. On each transect, two to four samples were retained for more detailed ageing and length measurement to the nearest millimetre below. Sub-samples of approx. 20 cockles of each 1 mm length group were weighed in bulk on an electronic balance to the nearest 0.1 g to allow an overall length-weight relationship to be determined.

The number of cockles in the area represented by an individual transect was calculated as the product of transect area and average cockle density within that area. The estimate for the year-class strength on the whole bed was the sum of the individual transect estimates, and the total abundance estimate was the sum of the individual year-class estimates. A length-frequency distribution of cockles within a survey area was found by combining all length measures from the samples. Stock biomass was calculated from fitted length-weight relationships for cockles from regression of log-transformed weight and length data. Biomass was reported as total biomass and separately for cockles >25 mm; the latter was seen as an indication of commercially exploitable stocks. Detailed information about the equations used are given in Appendix 2.

3.2. Database construction

The total number of cockles at the South side of the estuary was reported from 1958 to 2009 and could be collated in a database. This number was split into the cohorts Year 0 (referred to as 'spat' in reports), Year 1 (1-ring) and ≥ Year 2 (2+ rings). From 1989 onwards the average size of cockles within cohorts was reported, and from 1991 onwards information about size-weight measures was added, which allowed calculating the biomass of the total cockle stock.

3.3. Data analysis

Mortality rates for individual cohorts at the South side of the estuary were calculated from 1958 to 2009 as annual change from one November survey to the next. For example, Year 0 (Y0) mortality was calculated as the change of numbers of Y0 in one autumn survey to numbers of Y1 the following November.

The relationship of cockle size, mortality and recruitment success with the change in wastewater treatment, weather and climate parameters was tested with linear multiple regression analysis. The factor 'site' (South and North side of estuary) was tested for cockle size as data was available for years since 1989. Further, the relationship of size of cockle recruits with their mortality was tested (linear regression).

Change in wastewater treatment was added as a categorical factor as before (0) and after (1) 1997 when the treatment works were modernised. Weather data were obtained from the Met Office for Aberporth (Wales, UK). They were geographically closest to the study site spanning back 50 years (https://www.metoffice.gov.uk/research/climate/maps-and-data/historic-station-data). Weather data consisted of mean daily maximum temperature (tmax), mean daily minimum temperature (tmin), days of air frost (af), total rainfall (rain) and total sunshine duration (sun). Winter conditions were calculated as averages from November–March each year and total number of air frost days, summer conditions were calculated as averages from April–August. The relationship of climate variation with cockle population parameters was explored using NAO data obtained from the National Centres for Environmental Information. Linear regression analysis was also used to test for the relationship of the total numbers of cockles in the estuary with recruitment success, % mortality, and cockle sizes. Numbers of Year 0 cockles were compared with adults of the same year as well as numbers of Year 1 and older cockles of the previous year to assess a lag effect.

All factors were tested for normality (Shapiro-Wilk test and

Kolmogorov-Smirnov test), and they were $\sqrt{}$-transformed if their data distribution failed the tests. Factors not complying with normality after transformation were removed from the analysis, as well as factors with high collinearity ($R > 0.8$).

4. Results

For the past 50 years the cockle population of the Burry Inlet consisted of 3–5 cohorts: newly settled Year 0 recruits (Y0), Year 1 cockles with one winter growth ring (Y1), Year 2 cockles with two rings (Y2), few Year 3 cockles (Y3), and very occasionally Year 4 cockles (Y4). Until the 1980s numbers for Y2 and older cockles were grouped in surveys and therefore this study focuses on three age groups: Y0, Y1, ≥Y2.

The relative proportion of age groups within the entire cockle population varied dramatically over time (Fig. 2). From 1958 to 2009 Y0 was on average the largest cohort with a proportion of 65 ± 23% (mean ± sd), Y1 19 ± 18% and ≥Y2 15 ± 13%. However, in some years Y1 was the numerically strongest cohort, with 1964 being an exceptional year with 93% Y1 cockles. From 2004 to 2010 over 90% of all cockles were Y0.

4.1. Recruitment (Year 0)

The number of annual cockle recruits from 1958 to 2009 was 2062 ± 2195 million (M) (median ± sd) on the South side of the Burry Inlet (Fig. 3). There were two discrete phases of above average recruitment: before 1970 and after 1995; recruitment was below average during the 1980s. Exceptionally successful Y0 cohorts were recorded in 1963 and 2004, and exceptionally poor recruitment in 1964 and 1990.

Multiple regression testing 15 factors indicated only one significant relationship: the number of established cockles in the sands (≥Year 1) with the magnitude of recruitment (Fig. 4, $R^2 = 0.15$, $p = 0.017$, $n = 36$); the larger the number of ≥Year 1 cockles the lower recruitment. Change in wastewater treatment, weather, or large climatic variation (NAO) showed no significant relationships with recruitment success. There was also no significant relationship between the number of cockles of the previous year and the number of new recruits, meaning the size of spawning cohorts was not significantly related to the number of next year's recruits.

4.2. Mortality of Year 0 and Year 1 cockles

The average annual mortality of Year 0 cockles since 1959 was 73.2 ± 16.8% (mean ± sd, $n = 37$) and the mortality of Year 1 cockles was

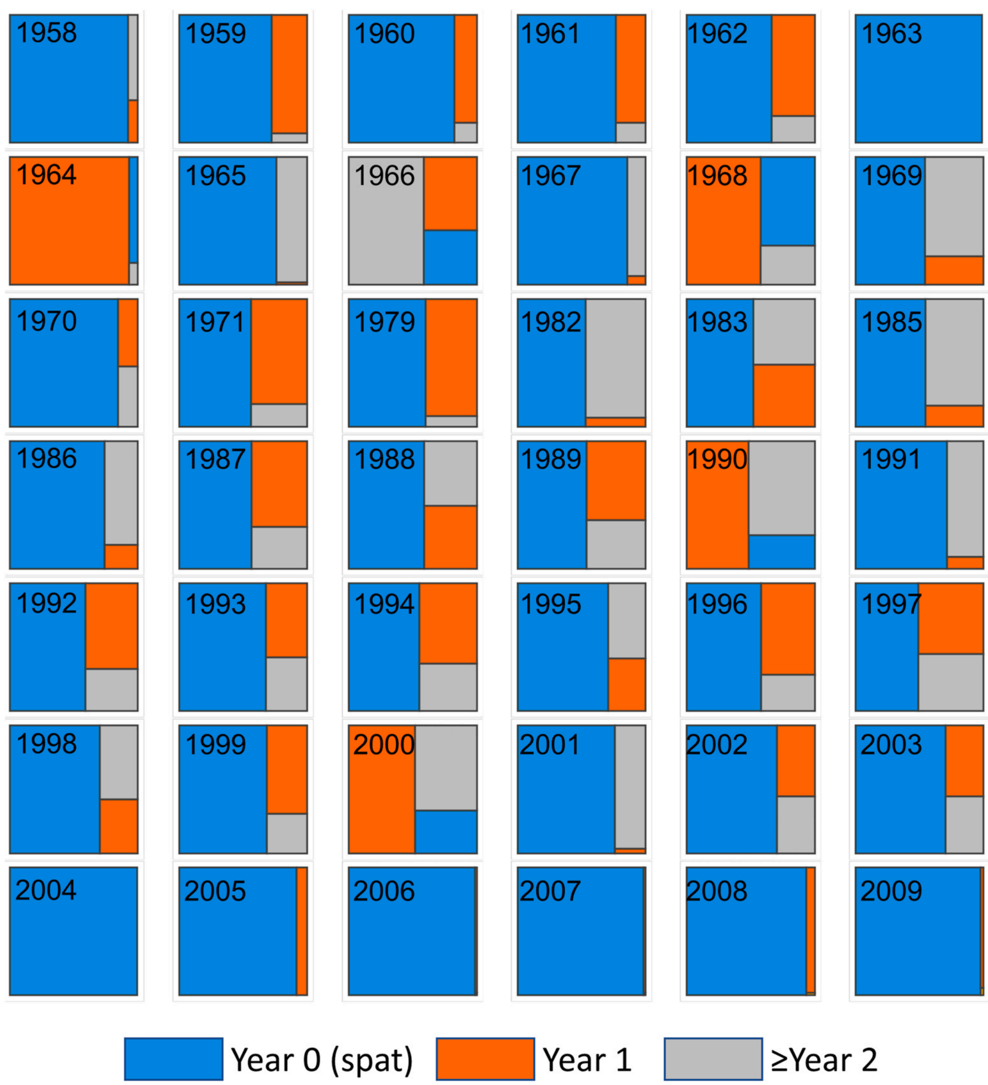

Fig. 2. Relative proportion of cohorts of a cockle population in the Burry Inlet, South Wale (UK) from 1958 to 2009. Treemaps showing new recruits (Year 0), Year 1 and combined ≥2 year cockles.

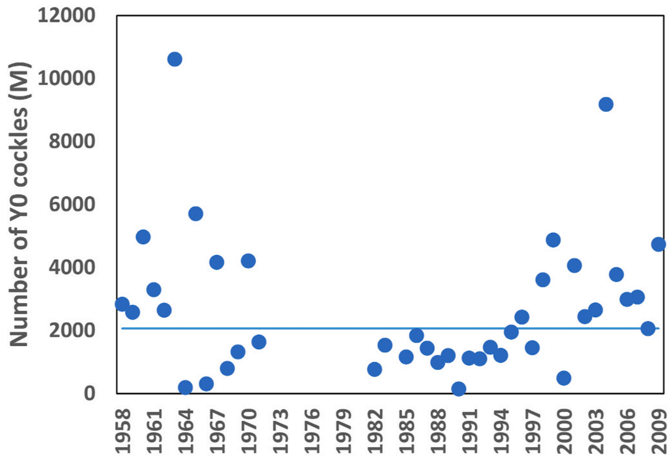

Fig. 3. Total number of cockle recruits (Year 0) at the South side of the Burry Inlet (in millions). Horizontal line shows the median number of Year 0 cockles between 1958 and 2009.

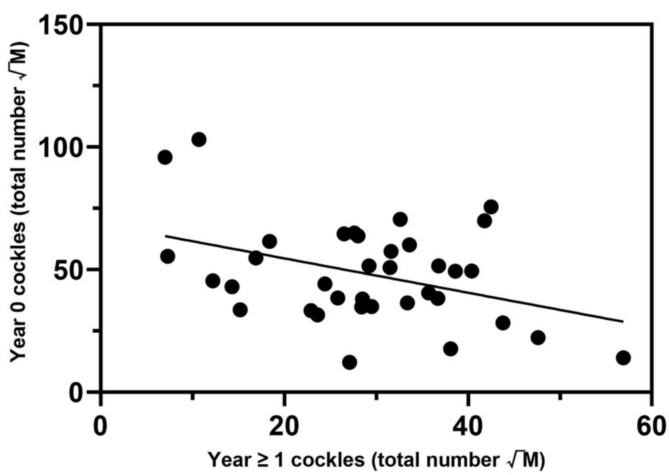

Fig. 4. Relationship between established cockle cohorts (≥ Year 1) and total number of recruits (Year 0) at the South side of the Burry Inlet ($R^2 = 0.15$, $p = 0.017$, $n = 36$).

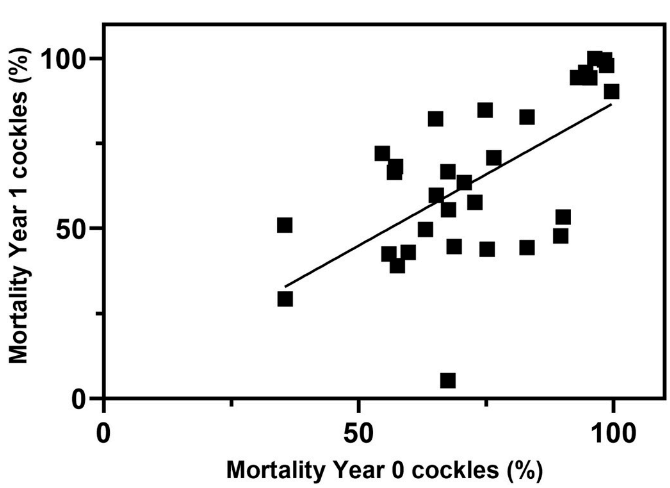

Fig. 5. Relationship between mortality of cockle cohorts: Year 0 (recruits) and Year 1 cockles ($n = 31$). Mortality calculated as annual % change from one November survey to the next ($R^2 = 0.39$, $p < 0.001$, $n = 31$).

64.4 ± 23.6% (mean ± sd, n = 31). The annual % mortality of Y0 and Y1 cockles was significantly correlated ($R^2 = 0.39$, $p < 0.001$, $n = 31$) (Fig. 5). Mortality of older cockles could not be reliably calculated due to inconsistent records of Year 2 and older cockles.

Mortality was below average during the 1990s and above average during the 2000s (Fig. 6). From 2004 to 2009 mortality was over 90% for Year 0 and Year 1 cockles. Multiple regression testing 12 factors indicated that mortalities were significantly linked with the total number of cockles, meaning the larger the population the higher mortalities (Fig. 7, $R^2 = 0.25$, $p = 0.002$, $n = 34$). None of the other factors linked to the change in wastewater treatment, weather or large climatic variation (NAO) showed significant relationships with cockle mortalities.

4.3. Size of cockles

The size of cockles was reported since 1989 for both the South and North side of the Burry Inlet. From 1989 to 2008 the average size of cockles declined significantly in all age classes (Fig. 8, Table 1). Within this 20-year period cockle sizes in each cohort were below average from about 1999 onwards.

There was a significant relationship between the change in wastewater treatment in 1997 and the size of cockles in all cohorts (n = 40; Y0: $R^2 = 0.39$, $p < 0.0001$; Y1: $R^2 = 0.47$, $p < 0.0001$; Y2: $R^2 = 0.57$, $p < 0.0001$). Further, there was a significant relationship between the numbers of cockles and the average size in the cohorts Year 0 and 2, meaning the larger the population the smaller the cockles (n = 40; Y0: $R^2 = 0.21$, $p < 0.0032$; Y1: $R^2 = 0.10$, $p < 0.054$; Y2: $R^2 = 0.16$, $p < 0.017$).

The size of cockle recruits (Y0) was significantly linked with their longevity (Fig. 9). By the time of the autumn surveys the mean size of cockle recruits was between 8 and 16 mm on the South and North side of the Burry Inlet. After one year 35.6–99.9% of the recruits had died, and after two years between 74.2 and 100%. The larger the average size of the cockle recruits, the lower was their mortality after their first and second year (size vs mortality after 1 year, $R^2 = 0.15$, $n = 40$, $p < 0.0134$; size vs mortality after 2 years, $R^2 = 0.20$, $n = 40$, $p < 0.0037$).

There was no significant difference between the South and the North side of the estuary, and none of the long-term weather parameters had a significant link with the size of cockles in any year class.

4.4. Biomass

The average cockle biomass in the Burry Inlet was 6288 ± 3158 tonnes on the South side and 4571 ± 2508 tonnes on the North Side (mean ± sd, n = 18, 1991–2009 Oct/Nov surveys). Highest recorded biomass in the entire estuary was 18400 tonnes in 1997. Lowest biomass was recorded in 2008 with 2608 tonnes.

Biomass of cockles >25 mm, which are of particular interest to the fishing industry, varied dramatically between 1991 and 2009 (Fig. 10). On average it was 2383 ± 1822 tonnes on the South side and 1892 ± 1779 tonnes on the North side. Biomass of >25 mm cockles collapsed in 1999 to <2000 tonnes in the entire estuary. After a short phase of recovery in 2000–2003, cockles >25 mm disappeared from the records. No recovery was noted to the final report in 2009. The absence of cockles >25 mm since 2004 led to low average biomass in the estuary of <4000 tonnes from 2004 to 2009.

5. Discussion

Monitoring reports of the cockle population in the Burry Inlet, South Wales, UK, indicated profound variation in growth rates, mortalities, and recruitment of *C.edule* over a 50-year period from 1958 to 2009. Recruitment and mortalities were high during the first and last decade of the study, and growth rates as well as overall cockle biomass declined in the late 1990s.

Shifts in cockle populations influenced by biotic (e.g. parasites) and

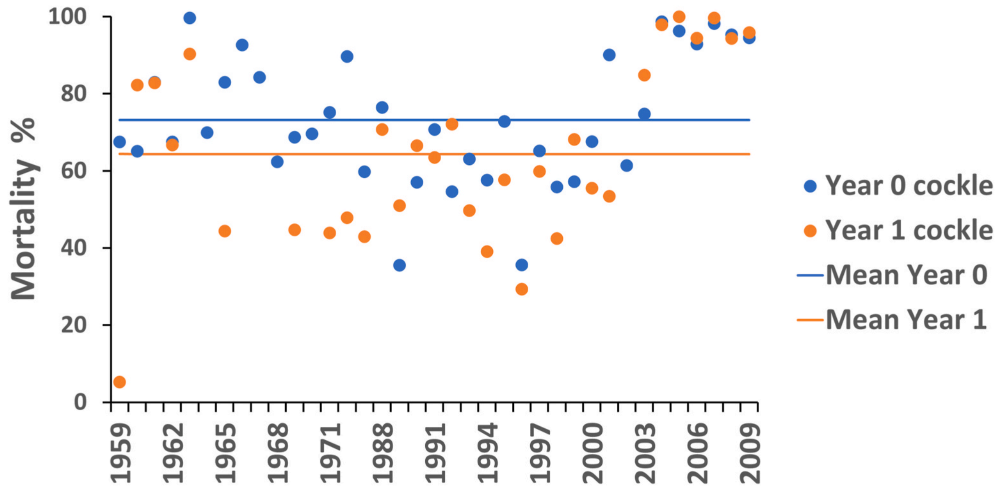

Fig. 6. Mortality of new cockle recruits (Year 0) and Year 1 cockles. Mortality calculated as annual change from one November survey to the next.

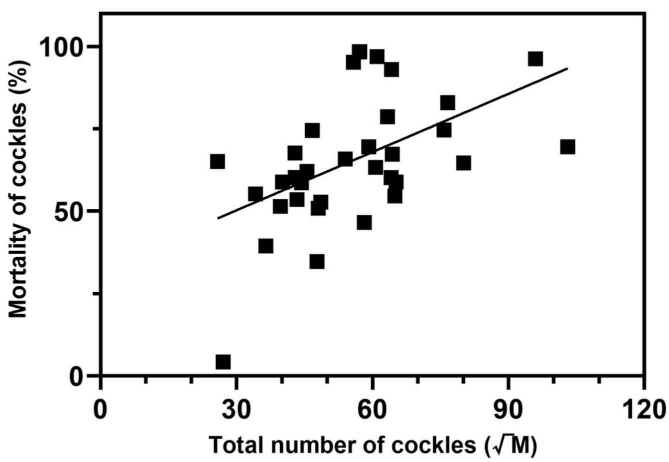

Fig. 7. Relationship between the size of the cockle population (total number of cockles) and mortality ($R^2 = 0.25$, $p = 0.002$, $n = 34$).

abiotic factors (e.g. temperature, harvesting) are well documented, and at a global scale by climate (AMO Index) (Mahony et al. 2020). Long-term studies from estuarine environments evidenced striking regime shifts and recoveries in benthic communities, including bivalves, similar to those in this study, for example changes in *Mytilus edulis*, *Magallana gigas*, *Mya arenaria* and *C.edule* (Beukema et al. 2017; Van der Meer et al. 2019). Beukema et al. (2017) showed three distinctive phases, with elevated growth rates between 1991 and 2005. It was

Table 1
Size of cockles from 1989 to 2008 at the South and North side of the Burry Inlet. Linear regression analysis results of changes in average cockle size over time; statistically significant reductions are marked in bold. Y0: Year 0 cockle recruits, Y1: Year 1 cockles, Y2: Year 2 cockles.

	Y0	Y1	Y2
Mean size ± sd (mm)	12.0 ± 2.1	20.6 ± 2.3	24.1 ± 3.1
Minimum size (mm)	8.0	15.7	17.8
Maximum size (mm)	16.0	25.4	28.6
R^2	0.25	0.41	0.56
n	40	39	36
F	12.54	26.20	42.82
p	**0.0011**	< **0.0001**	< **0.0001**

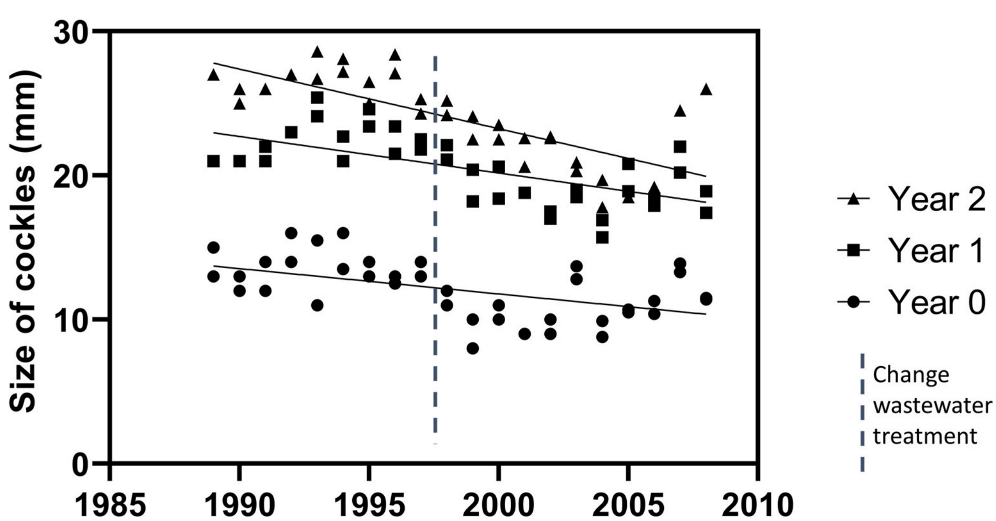

Fig. 8. Mean size of cockles of each cohort over time (for regression analysis results see Table 1). Measures taken during autumn surveys at the South and North side of the Burry Inlet; after 2006 the Year 2 cohort was almost absent from the site and mean cockle sizes were based on very few individuals. A dashed vertical line indicates the beginning of a new wastewater treatment regime in 1997.

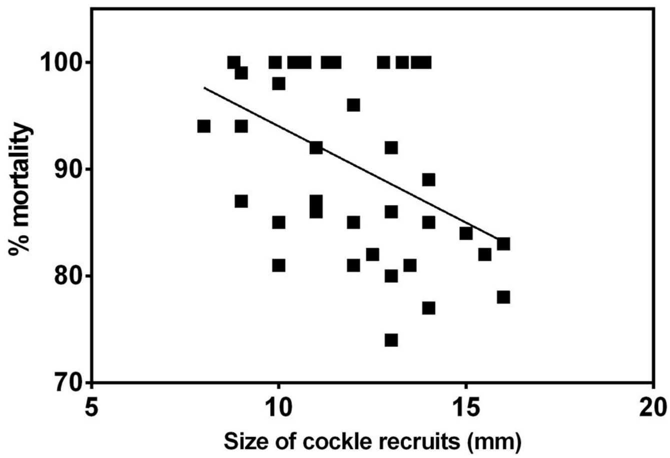

Fig. 9. Relationship between size of cockle recruits and their mortality. Size of recruits during autumn surveys at North and South side of the Burry Inlet 1989–2008 (n = 40). Mortalities after two years; $R^2 = 0.20$, $p < 0.0037$.

concluded that the regime shifts were triggered by short-term natural and anthropogenic events. A combination of storms and intensive fishery removed all mussel beds from tidal flats and thereby reduced their food demand, which led to faster growth of the remaining bivalves for more than a decade (Beukema and Cadée, 1996). Bivalve populations decimated by fishing can recover naturally, but it may take years or decades (Van der Meer et al. 2019). In this study the impact of the cockle fishery could not be assessed since the monitoring reports did not quantify landings, TACs and maximum or minimum landing sizes, and other long-term harvesting statistics were haphazard. Fishing cannot be ruled out as a factor contributing to variation in the cockle population.

5.1. Change of wastewater treatment, cockle size and mortalities

The change in wastewater treatment in the Burry Inlet in 1997 provides a plausible explanation for the reduction in cockle sizes over 20 years (1989–2008), with knock-on effects on total biomass. Significantly reduced shell sizes occurred in all cohorts after the modernisation of wastewater infrastructure. Environmental factors like temperature were not significantly linked with declining cockle sizes. De-eutrophication was also seen as a principal factor for reduced bivalve growth in the Dutch Wadden Sea (Beukema et al. 2017). There, declining growth rates were linked to a decline in chlorophyll concentration. In the Ems Dollard estuary in the eastern Wadden Sea, The Netherlands, de-eutrophication led to declining total biomass, and the introduction of two polychaete species shifted the benthic community from bivalve to polychaete domination (Compton et al. 2017).

The reduction in the quantity and quality of POM and nutrients may have directly affected food availability for cockles in the Burry Inlet; freshwater POM can contribute 50–60% of food intake of cockles (Jung et al. 2019). Changes in the nutrient regime may have also reduced the production of microphytobenthos (Underwood, 2010). The primary production of microphytobenthos can be 1–12 times that of plankton in shallow estuaries (Navarro et al. 1992).

Generally, locally produced organic matter such as microphytobenthos and phytoplankton determines growth rates, production and biomass of bivalves (Duggins et al. 1989; Ruckelshaud et al. 1993; Sauriau and Kang, 2000). The concentration of suspended food determines up to 87% of the variation in the growth of cockles (Navarro et al. 1992). Their digestive system is flexible to respond to varying quantities and quality of food (Prins et al. 1991; Ibarrola et al. 2000; Navarro et al. 2016). A preference of suspension-feeding bivalves for fresh microalgal has been well established (Kiørboe and Mohlenberg, 1981; Prins et al. 1991). Suspended microphytobenthos is a particularly important food source in tidal estuaries and contributes 24–44% of the food for *C.edule* (Daggers et al. 2020). The reduction in cockle sizes in the Burry Inlet therefore suggests a change in the accessibility to food.

This aligns with Dynamic Energy Budget theory (DEB) and growth models for cockles that found food quantity and quality to have the strongest positive effect on growth, while temperature is a secondary factor (Rueda et al. 2005; Van der Meer et al. 2014). However, it must be kept in mind that other environmental stressors such as highly varying salinity can compromise the physiology of cockles and reduce their consumption ability (Gonçalves et al., 2017). Although cockles tolerate brackish to hyper-haline waters with salinity ranging from 11 to 45, low salinities were found to be linked to high mortality populations (De Montaudouin et al., 2021). Extreme salinity, temperature, and acidity (pH) were found to trigger higher biochemical alterations in cockles (Magalhães et al., 2018).

Intraspecific competition may have also contributed to changes in food availability. In this study, the higher the number of cockles the smaller was their average size. High densities of cockles can lead to intraspecific competition for food and reduce the intake (Beukema et al. 2017). Substantial growth reduction in cockles due to food shortage by competition appears though to be a rare phenomenon (Beukema et al. 2017), and it was linked to densities exceeding 800-1000 m^{-2} (Jensen, 1993, Masski and Guillou, 1999). In the Dutch Wadden Sea two recently introduced suspension-feeding bivalve species are now becoming dominant, *Magallana gigas* and *Ensis directus* (Troost, 2010; Tulp et al.

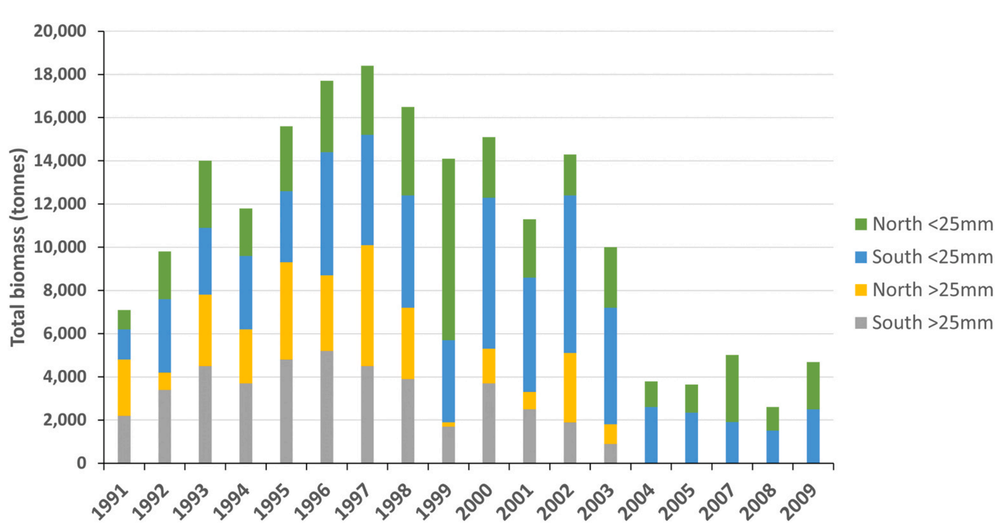

Fig. 10. Biomass of cockles in the Burry Inlet, separated in cockles smaller and larger 25 mm.

2010). Their food demand was seen as a possible cause for reduced growth in established bivalves (Beukema et al. 2017). In the Burry Inlet it is possible that mussels *Mytilus edulis* contributed to intraspecific competition for food. Dense aggregations developed temporarily in the early 2000s when mussel larvae used layers of empty cockle shells as foundation for mussel banks ('Surveys of cockle and mussel stocks in the Burry Inlet, 2005; 2006 & 2007', Moore 2009; unpublished report). It is therefore likely that the change in wastewater treatment, intraspecific competition through large numbers of recruits and interspecific competition by mussels affected food availability and cockle growth during the last decade of this study.

This study showed that the size of recruits was significantly linked with their mortality: smaller Year 0 recruits had shorter life spans. Similar results were reported for other estuaries, where the size of cockle recruits determined their longevity, and a low-mortality and high-mortality group could be distinguished (De Montaudouin et al. 2021). The authors evidenced that the shells of the Year 0 cohorts were larger in the low-mortality group in August and September, and smaller in the high-mortality group. It is therefore possible that reduced growth in Year 0 cockles in the Burry Inlet is linked to a shorter lifespan.

Weather parameters like temperature and climate variation (NAO) were unrelated to annual cockle mortality. This contrasts with studies indicating that high summer temperatures can trigger widespread cockle mortalities (Desprez et al. 1992). The only factor explaining part of the variation in mortalities over the 50-year period was the total number of cockles in the estuary: the higher the number the higher the percentage mortality. The data analysis should though be viewed with caution. One-off events like the exceptionally cold winter in 1962/63, the Sea Empress oil spill and fishing contributed to variation in mortality data (Burdon et al., 2014), but it would be impossible to disentangle all factors over a 50-year period.

The results of this study broadly agree with results of investigations into cockle mortalities in the early 2000s (Elliott et al. 2012). Cockle mortality of over 90% from 2004 to 2009 was considerably higher than in the 1990s and motivated comprehensive research into possible causes. The study concluded that it was unlikely for a single factor to have caused the high mortalities. The most plausible explanation was a combination of high density and high energy expenditure due to high reproductive output weakening the cockle population, which led to reduced tolerance to external stressors and parasites. Similar dramatic mortalities caused by a chain of coinciding negative factors were reported from cockle populations (*Austrovenus stutchburyi*) in New Zealand (Tricklebank et al. 2021). There, density and growth within a stable population suddenly declined, followed by mass mortalities (Tricklebank et al. 2021). The cause(s) of the regime shift remained speculative and only moderate recovery was observed. This study provides additional evidence that the change in wastewater treatment in 1997 reduced food availability for cockles, leading to diminishing growth of cockle recruits, which shortened their life span.

5.2. Recruitment of cockles (Year 0)

Variation in recruitment success was negatively correlated with numbers of individuals in the established cockle population, suggesting that competition for space or food at least partly controlled numbers of recruits. Similar patterns were found in other estuaries (Whitton et al., 2015), but adult population size does not necessarily influence recruitment (Magalhães et al., 2016). It is possible that predation by other species such as shore crabs may have contributed to variation in recruitment as they can diminish density of juvenile cockles by up to 85% (Masski and Guillou 1999).

Average or extreme temperatures and other weather parameters as well as climate fluctuations (NAO), or the local change in wastewater treatment, could not be directly linked with recruitment. In contrast, long-term changes in climate were related to declining cockle recruitment in the Wadden Sea (Beukema and Dekker, 2005, Philippart et al., 2014). In the Burry Inlet recruitment success varied among decades, and it was exceptionally high in more recent years. A key factor for recruitment is the supply of larvae, with cockle larvae being in the water column from March to September (Philippart et al. 2014). The length of the pelagic phase of these larvae is in the order of weeks, implying that multiple spawning events take place. Conditions independent from the Burry Inlet, outside the estuary, are likely to influence the number of cockle larvae reaching the site and determine recruitment success (Robins et al. 2013).

Movement of sediment may also have affected the settlement of cockle recruits (Bouma et al. 2001; Van der Heide et al. 2014). Throughout the 50-year monitoring period changes in the topography of the Burry Inlet were mentioned anecdotally in the monitoring reports (Appendix 1). The changes were due to natural hydrodynamic forces as well as a training wall crossing the estuary that breached in 1951 and 1965 and was not repaired (Elliott et al. 2012). This led to a variable pattern of accretion and erosion, but on balance accretion has led to significant increase in saltmarsh. Its area enlarged from 980 ha in 1876 to 1717 ha in 2000. The estuary is a long-term sink for sediment. It seems plausible that the continued accretion and overall increase in elevation in the estuary promotes cockle recruitment. However, individual growth rate declines with increasing tidal elevation as tide level is negatively correlated with immersion time (Jensen, 1992).

5.3. Biomass

The absence of cockles >25 mm from the Burry Inlet severely reduced the overall biomass of the species in the estuary during the last decade of the study. Studies from other European locations suggest that the production of cockle biomass is mostly supported by older cohorts with a size of 26–33-mm (74% of the total production) (Gam et al. 2010). Cockles under 10-mm shell length contributed little to the total somatic production. On the contrary, consequences of changes in annual bivalve growth were seen to be limited for the Wadden Sea ecosystem because the observed variability in both annual production as well as biomass was explained by their numerical abundance and the numbers of recruits rather than by their growth rates (Beukema et al. 2017). Similar patterns to the Burry Inlet in terms of biomass were found for the New Zealand cockle *Austrovenus stutchburyi*, where after a largely unexplained mass mortality event parts of the population showed slow recovery, but density and growth rates remained low, resulting in absence of larger cockles (Tricklebank et al. 2021). This study suggests that the reduction in growth of cockles in the Burry Inlet combined with diminishing older cohorts had a severe effect on biomass despite high recruitment.

6. Conclusions

One of the motivations for this study was to evaluate possible effects of improved wastewater treatment in 1997 on cockles. Smaller cockle sizes following the changes suggest that reduced nutrient loading in the estuary may have been responsible for reduced food availability, which could have led to a regime shift.

The longer-term development in the cockle population, subsequent to the data analysed here, would answer the question whether the new state persisted, or whether the population regains older individuals and age-classes. This time series was stopped because a different authority took over the surveys in 2009 and changed the monitoring method. So far it was not assessed how the post 2009 method compared with the previous one, which would be necessary to continue the timeline. Long-term studies often suffer from inconsistent data gathering, and the analysed reports indicated conflicting interests and pressures on authorities to adapt survey areas and methods due to change in topography or fishing interests (Appendix 1). It is recommended to a) determine conversion factors between the pre- and post 2009 methods and calculations, and b) combine old and new survey results. This would strengthen the confidence in emerging trends in the cockle population, deepen our understanding of the relationship between wastewater management and bivalves, and provide environmental and fisheries managers with invaluable information in case of exceptional events affecting the estuary in the future.

CRediT authorship contribution statement

Ruth Callaway: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing 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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2022.107834.

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