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# Oyster (*Ostrea edulis*) extirpation and ecosystem transformation in the Firth of Forth, Scotland

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ABSTRACT

Marine inshore communities, including biogenic habitats have undergone dramatic changes as a result of exploitation, pollution, land-use changes and introduced species. The Firth of Forth on the east coast of Scotland was once home to the most important oyster (*Ostrea edulis* Linnaeus, 1758) beds in Scotland. 19th and early 20th century fisheries scientists documented the degradation and loss of these beds, yet transformation of the wider benthic community has been little studied. We undertook archival searches, ecological surveys and shell community analysis using radioisotope dated sediment cores to investigate the history of decline of Forth oyster beds over the last 200 years and the changes to its wider biological communities. Quadrat analysis of the present day benthos reveal that soft-sediment communities dominate the Firth of Forth, with little remaining evidence of past oyster beds in places where abundant shell remains were picked up by a survey undertaken in 1895. Queen scallops (*Aequipecten opercularis* Linnaeus, 1758) and horse mussels (*Modiolus modiolus* Linnaeus, 1758) were once common within the Forth but have also markedly decreased compared to the earlier survey. Ouranalyses of shell remains suggest that overall mollusc biomass and species richness declined throughout the 19th century and early 20th century, suggesting broader-scale community change as human impacts increased and as habitats degraded. Inshore communities in the Firth of Forth today are less productive and less diverse compared to past states, with evidence suggesting that most of the damage was done by early bottom trawling and dredging activities. Given the pervasive nature of intensive trawling over the past 150 years, the kind of degradation we document for the Firth of Forth is likely to be commonplace within UK inshore communities.



## Introduction

Healthy biogenic habitats such as oyster (*Ostrea* spp., *Crassotrea* spp.), maerl (*Lithothamnion* spp.) and horse mussel (*Modiolus modiolus* Linnaeus, 1758) communities perform a variety of ecological functions including stabilisation of sediment, creation of feeding and nursery habitat for juvenile fish species, and water filtration (Holt et al. 1998). A reduction or loss of these organisms results in subsequent loss of ecosystem services (Jackson et al. 2001; Lotze et al. 2006; Roberts 2007). Yet many of these communities are under threat from a multitude of human impacts including destructive fishing methods, increased sediment loading, altered hydrodynamic regimes, disease and the introduction of non-native competitors and predators (Airoldi & Beck 2007; Hall-Spencer et al. 2003; Jackson et al. 2001; Lotze & Milewski 2004). Beck et al. (2011) estimated that globally, 85% of oyster reefs have been destroyed with many remaining beds degraded to the point where they have limited or no ecological function.

In many cases the long time-interval over which degradation has occurred makes it difficult to determine the original extent and/or nature of biogenic habitats prior to large-scale human influence and hence determine the true degree of degradation (Lotze et al. 2006; Robinson & Frid 2008). It is likely that many estuarine or coastal seas have suffered from the 'shifting baseline syndrome' (Dayton et al. 1998; Pauly 1995), where current generations (and consequently current management) underestimate the extent of changes to coastal areas and therefore fail to manage areas for recovery. Exceptions do exist; the San Francisco Estuary Institute is an initiative that aims to document and record past conditions and use the information to guide restoration management (Grossinger et al. 2005). However conservation-planning policies often make little or no reference to past conditions (Ban et al., in preparation).

Native oysters (*Ostrea edulis*) were once plentiful in open sea environments and inshore estuaries around the UK (Royal Commission 1885). Yet today few wild populations of native

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oysters exist (Hiscock et al. 2005); indeed, many oyster populations were severely degraded prior to 1900 (Royal Commission 1885). This is almost certainly the case for many other bottom-living communities, e.g. maerl and horse mussel reefs (Airoldi & Beck 2007; Hall-Spencer & Moore 2000), but their historical extent and distribution tends to be less well represented in the literature (Airoldi & Beck 2007) compared to oysters, which were a valuable fishery. Where archival information exists, historical research can help to infer previous baseline states for biogenic communities. However, using archival methods alone may limit our interpretation of change to the few species mentioned in historical documents. Hence, other methods must be employed to determine the past status of benthic communities as a whole and to verify timings and drivers of change. Edgar and Samson (2004) for example, used mollusc death assemblages and isotope dating techniques from sediment cores to describe changes in molluscan assemblages in Tasmania over a period of 120 years. Whilst the decline of scallops and oysters – the target of a commercial dredge fishery – had been well documented there, Edgar and Samson were able to show that the wider mollusc community had also declined over the same period, a decrease not previously reported in the fisheries literature.

Our study uses historical, ecological and radioisotope dating techniques to reconstruct the history of the benthic community of the Firth of Forth, including the now-extinct oyster population, and to determine the extent and drivers of change to the Forth's inshore environment over the course of the last two centuries. We qualitatively compare past habitat descriptions with present day field assessments of habitats using information sourced from 19th century Admiralty charts and past scientific surveys. Using mollusc shell remains taken from dated sections of sediment cores we analyse changes over time to the molluscan benthos. We argue that human activities, in particular destructive fishing methods and land-use changes, have transformed marine communities in the Firth of Forth to a much greater extent than is generally acknowledged today.

## Methods

### *Historical records search and field site location*

We searched local museums, university libraries, public archives and published government reports for literature on past Firth of Forth marine habitats. Two main sources of information: 19th century Admiralty charts and a report of a number of scientific dredge surveys performed in 1895 (Fulton 1896), were used to determine sites that used to contain extensive oyster beds, and hence were potentially suitable for comparative analysis. Older charts did not make reference to magnetic North, so we determined the location of past oyster fishing grounds by comparing the position of the marked ground in relation to at least two obvious landmarks present on the chart (e.g. a named rock or a headland). We then found the same landmarks on present charts and thus established the location of each site using triangulation. We determined the position of the dredged sites in the same way, but only selected locations for study that revealed high quantities of live oysters during the 1895 survey. We then further selected sites for analysis on the basis of their practical suitability for diving. Given that the Firth of Forth has a mean spring tidal range of 5.0 m and a mean neap tidal range of 2.5 m (Webb & Metcalfe 1987), with currents up to 1.5 knots, we excluded from consideration sites that were unsuitable due to factors such as depth, strong currents, high shipping traffic or distance from a launch site. Sites likely to have been substantially altered by navigational dredging were also discounted. In total, we undertook diving surveys at 11 sites between April and October 2010. Fig. 1 shows the location of each site and

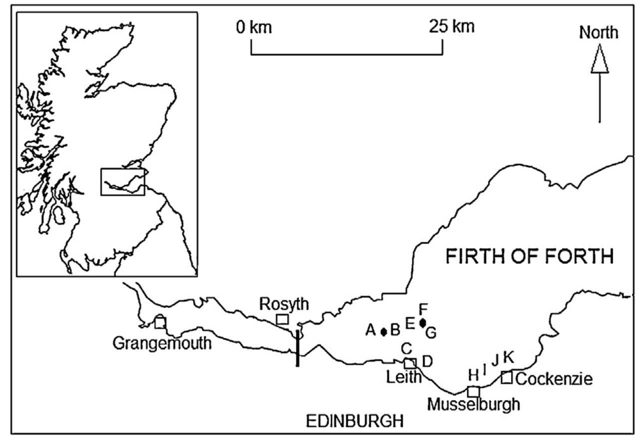


**Fig. 1.** Field sites in the Firth of Forth. Sites A–I were identified from Fulton's surveys in 1895 (Fulton 1896). Sites J and K were identified from an 1852-56 Firth of Forth Admiralty chart.

Table S1 (see Appendix) provides location coordinates; transect bearings and depth of seabed at chart datum for these.

### *Fieldwork methods*

Fieldwork took place between April and October 2010. A team of four divers performed two dives at each site. One pair performed in situ quadrat analysis of the benthic habitat, while the second pair took a sediment core sample for shell community analysis. We used 50 m transects for benthic community analysis. Transects either followed the direction of dredge surveys conducted by Fulton (1896), or went between chart soundings (e.g. where the word 'oyster' was shown on the chart). Ten 1 $m^2$ quadrats were randomly selected on either side of the tape along the transect for in situ analysis. Site D had to be omitted from the analysis as no quadrat data were obtained due to strong currents and low visibility.

During the second dive, the two divers randomly selected a position to take a sediment core within 2 m of the start of the previously used transect. The core consisted of a 2 m long, 10 cm diameter PVC tube, with teeth cut into one end to facilitate penetration into the sediment. Our methodology for this procedure was based closely on Edgar and Samson (2004) and went as follows: the tube was held upright on the seabed using a long handled-clamp bolted together with wing nuts, once the tube was in position divers forced it into the sediment using a modified post-driver. Once driven into the sediment a sealed cap was placed on top of the core to allow it to be pulled out of the seabed with minimal loss of sediment. As soon as the corer was pulled out a second cap was secured on the base and a rope deployed allowing up-right recovery to the boat. The corer was kept upright until it was taken onto land where the seawater was siphoned off. The core was then extruded and split longitudinally using a thin metal wire to minimise contamination of sediment. One half of the core was used for isotopic dating analysis, the other for shell community analysis.

### *Benthic community analysis*

We analysed quadrats in situ and recorded the substrate type (e.g. percentage cover of mud, broken shell) and presence of live and dead shells (both percentage cover and number). Epifauna were identified to species or to family if further identification was not possible. For shell community analysis, each core was split into 5 cm-long sections and rinsed using a 1 mm sieve to leave only mollusc shells behind. These shells were then separated into those that were identifiable and those that were too fragmented to be positively identified. All shells in each 5 cm-long section were first weighed together to determine total shell biomass for that section. All identifiable shells from that section were then separated into species to determine minimum species richness (number of species present) for that section of core.

### Radiometric analysis

Nine sediment cores were analysed using facilities at the British Ocean Sediment Core Research Facility (National Oceanography Centre, Southampton, UK). Each core was first placed through a non-destructive Itrax micro-XRF scanner to provide down-core elemental profiles of heavy metals such as lead, zinc and copper. These elements increased in the Firth of Forth as industrial sites opened and introduced pollution into the estuary (SEPA 1998). Dramatic increases in copper and zinc are attributed to the opening of the Grangemouth oil refinery in 1924, although it is possible that increases in copper and zinc may have occurred earlier as human populations increased throughout the Firth of Forth catchment. We then split each core into 1 cm sections and freeze-dried these in preparation for radiometric dating analysis. We analysed nine cores for $^{137}$Cs, and seven of these cores for $^{210}$Pb. Each method used 10–15 sediment samples from various depths from each core.

$^{137}$Cs is an artificial radionuclide that was released in large quantities from 1954 onwards as a result of atmospheric nuclear weapons testing. Weapons testing, and therefore levels of $^{137}$Cs, peaked in 1963. Another, smaller peak as a result of the 1986 Chernobyl incident may also occur. However, the major source of $^{137}$Cs (post-1963) around the UK comes from the Sellafield Nuclear Reprocessing Facility in Cumbria (west coast of England). $^{137}$Cs derived from Sellafield emissions are known to have peaked in Forth sediments around 1978 (Bell et al. 1997). Hence peaks in activity throughout the core can be referenced to these dates (Bell et al. 1997) in order to derive rates of sediment accumulation. We determined $^{137}$Cs activity profiles by gamma spectrometry using Canberra HPGe well-type detectors. Errors were typically in the order of 8% ($2\sigma$).

$^{210}$Pb is a naturally occurring radioactive element produced during the decay sequence of $^{238}$U. Once on land or in water $^{210}$Pb becomes permanently fixed to sediment particles where over time its activity declines until it reaches equilibrium with background levels of $^{226}$Ra present in the sediment (Appleby 2004). This usually occurs after 5–6 half lives (110–130 years) but can be as little as 3 half lives (66 years) (Appleby 2004). Dating is based upon this excess $^{210}$Pb (i.e. $^{210}$Pb remaining above background levels), for which ages of sediment layers can be ascribed based upon the known decay-rate of $^{210}$Pb (Cundy et al. 2003). We determined $^{210}$Pb activity using the proxy method of alpha spectrometric measurement of $^{210}$Po activity (method based on Flynn 1968; Langdon et al. 2011). We estimated background rates of $^{210}$Pb as the point where total $^{210}$Pb activity levelled out (Appleby 2004). Rates of accumulation were then determined using the Constant Rate of Sedimentation (CRS) model, as this model is better suited for environments with varying rates of sediment deposition (Appleby 2004). Dates provided by the $^{210}$Pb activity profiles were verified using the independent $^{137}$Cs activity profiles and elemental compositions.

## Results

### Historical analysis

During the 1800s the Firth of Forth contained the most important oyster fishery in Scotland with oyster beds that extended 20 miles (Philpots 1891) and were up to 6 miles wide (Fulton 1896). At the beginning of the 19th century Forth oyster beds were so productive that one boat could frequently drag up 6000 oysters in one day (Fishery Board for Scotland 1890). Boats from Prestonpans on the south coast of the Firth of Forth would ship 30–40,000 oysters to Newcastle 3 or 4 times during the season (Sinclair's Statistical Account of Scotland, taken from Fishery Board for Scotland 1890). During the early 1800s exploitation of the Forth oyster beds increased as young oysters were taken to restock overexploited beds in England and Holland (Fulton 1896). Consumption of adult oysters also increased; from Newhaven alone it was estimated that an average of 19,900,000 oysters per year were exported during the period 1834–1836, whilst an estimated 1,700,000 oysters were sold in Edinburgh for local consumption (Fulton 1896). Information from local fishermen showed that from 1865 to 1870 the yield per boat amounted to 20–30,000 oysters per week (over 0.5 million oysters per week for all boats) during the season for boats from Prestonpans and Cockenzie on the south coast of the Firth of Forth (Fig. 1).

During the late 19th century oyster populations within the Forth began to decline. By 1889 Leith on the south coast of the Firth of Forth was the only port landing oysters commercially with landings having dwindled to just 315,000 oysters during the season (Fishery Board for Scotland 1890), a decline in landings of more than 99% over a 60-year period. By the 1890s there were no directed oyster fisheries left in the Forth; the only ones caught were obtained as by catch during fishing for queen scallops (*Aequipecten opercularis*) and mussels (*Mytilus edulis* Linnaeus, 1758) (Fulton 1896). In 1895 the Fishery Board for Scotland commissioned Fulton to research the current state of the Forth oyster population and the possibilities for improving the fishery. To do this Fulton carried out 233 dredge surveys in the Firth of Forth in 1895. On average the dredge was dragged for 600 yards (550 m). Once brought up the contents of the dredges were examined and numbers of live oysters, horse mussels, queen scallops and the number of shells were counted (Fulton 1896). Table 1 shows Fulton's findings from the sites that we surveyed. Fulton found just 317 living oysters in the 233 dredges although old oyster shells were present in the majority of hauls. In contrast, nearly 35,000 live queen scallops and 8,113 horse mussels were taken during the survey.

Fulton estimated that in 1895 in the Firth of Forth there was only one living oyster on every 660 square yards of bottom, or about 7.3 oysters to each acre (4046.9 $m^2$). He calculated that between 250,000 and 500,000 oysters were present in total in the Firth of Forth at this time, most likely closer to the lower estimate. However as oysters declined queen scallops became more plentiful (Fullarton 1889) and fisheries were increasingly directed towards catching this species as bait for line fisheries (Scottish Mussel and Bait Beds Commission 1889).

In his report Fulton stated,

> "*I am informed by fishermen that about twenty years ago, when oyster dredging, they generally took in a day's work some five or six hundred clams [queen scallops][...], while now fifteen times that number may be taken by a boat in a day. As one of them said – 'It used to be a case of picking out clams when dredging for oysters; now it is picking out an occasional oyster when dredging for clams'.*"

He concluded that the cause of decline was intensive fishing for oysters over the course of many decades. He attributed this to the trade in selling young oysters to English and Dutch private oyster fisheries, hence removing young oysters that would previously have been thrown back in the sea. After Fulton's survey the oyster beds of the Firth of Forth continued to decline. By the 1920s the oyster fishery no longer existed and in 1957 another survey was

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**Table 1**
Summary of Fulton's 1895 findings in the Firth of Forth for sites re-surveyed during this investigation.

| Site | Site number (Fulton 1896) | Description of dredge contents | *Ostrea edulis* | | *Aequipecten opercularis* | | *Modiolus modiolus* | |
|---|---|---|---|---|---|---|---|---|
| | | | Live | Dead | Live | Dead | Live | Dead |
| A | 32 | Hard. *Flustra* abundant, some stones | 2 | 564 | 1 | 36 | 16 | – |
| B | 174 | Some mud. *Solen*, *Mya*, and *Cyprina* shells | 3 | 258 | 24 | 20 | 7 | – |
| C | 48 | Clean | 4 | 415 | 276 | 500 | 7 | – |
| D | 70 | Clean. Much mussel seed | 2 | 340 | 87 | 150 | 2 | – |
| E | 41 | Shelly. *Laminaria*: *Carcinus* (1), *Alcyonium*: *Cribella* (1), *Ophioglypha*, *Ophiothrix*: *Hyas*: *Cyprina*: *Mya* | 3 | 162 | 181 | 300 | 53 | – |
| F | 107 | Clean. *S. endeca* (3) | 4 | 73 | 569 | 267 | 5 | – |
| G | 153 | Some mud. *Cribella* (1) | 6 | 60 | 6 | 22 | 139 | – |
| H | 229 | Slightly muddy | 7 | 48 | – | 120 | 31 | – |
| I | 117 | Clean. *Cribella* (1) | 7 | 42 | – | 240 | 68 | 12 |
| J[a] | 231 | Slightly muddy | 1 | 28 | 24 | 150 | 169 | – |
| K[a] | | No description | | | | | | |

Site J was chosen based Admiralty Chart 1852-6, however it lies close to a site dredged by Fulton. The data from this dredge is included.
[a] Taken from Admiralty Chart 1852-6.

**Table 2**
Results from Millar (1961) showing differences between standardised hauls between 1895 and 1957 in the Firth of Forth. Results show number of each species.

| Survey | *Asterias rubens* | *Solaster papposus* | *Aequipecten opercularis* | *Buccinum undatum* | *Modiolus modiolus* |
|---|---|---|---|---|---|
| 1895 | 19 | 1.1 | 150 | 6 | 35 |
| 1957 | 12 | 0.06 | 1.6 | 0.8 | 5.4 |
| Ratio 1895/1957 | 1.6:1 | 18.3:1 | 94:1 | 7.5:1 | 6.5:1 |

undertaken to once again assess the state of the oyster beds (Millar 1961). 65 hauls were taken, yet no living oysters were found. Only one 'clock' (a pair of valves still attached by the ligament, indicating a recently dead oyster) was found, with dead shells present in 48 of the 65 hauls. In 1961 Millar summarised the difference between his and Fulton's results for five principal species, standardised to the mean number of species found per standard 10-min haul (Table 2).

Millar (1961) concluded that as well as reductions in numbers of oysters as a result of overfishing other species had also reduced in abundance, particularly the queen scallop. Fulton (1896) stated that in the 20 or 30 years preceding the 1895 survey queen scallops had become much more abundant in the Firth of Forth and were popular as bait for line fisheries. By the time of the 1957 survey, queen scallops had declined in abundance by 99% and oysters were not to be found. Horse mussels had also declined by 85% compared to the 1895 survey (Table 2).

During the early 1970s the distribution of known populations of horse mussels in the southern area of the Forth was mapped and it was stated that horse mussels had taken over areas of the Firth that were once inhabited with oysters (Covill 1972). In 1979 a population of adult horse mussels was found off Cramond Island and large numbers of juveniles were found in the vicinity of the Forth bridges (Elliott & Kingston 1987). During the 1990s a study into the feasibility of restocking native oysters in the Firth of Forth was undertaken by Harding (1996) who used Van Veen grabs to characterise past oyster grounds. 34% of the sites examined contained remains of oyster shells and sites that used to support oyster beds largely consisted of semi-consolidated mud and fine sand. Harding (1996) stated it was unlikely that the underlying benthic substrate type had changed significantly since oyster beds were present, but that the decline of oyster and scallop shells decreased the suitability of the substrate for their juveniles. Hence, successful restocking was unlikely. During the 1957 survey queen scallops had declined but were still frequent, however, no trace of these beds occurred during the 1996 survey. This was attributed to the build-up in solid sewage sediments and mine waste residues (Howard et al. 1987). No horse mussels were found during this study although Harding (1996) stated that this may have been due to sampling inefficiency.

*Present-day communities*

We carried out quadrat analysis for each site with the exception of site D. The majority of the 11 sites analysed were primarily composed of fine, muddy sediment. Sites B, C, F, J and K were dominated by mud mixed with broken shell. Sites A, E, H and I were dominated by mud that was not obviously mixed with shell. Site G however, was dominated by live and dead horse mussels mixed with pieces of coal (Fig. 2).

Fig. 3 shows the average percentage cover of horse mussels (live and dead), bryozoa (not identified to species) and sea squirts (*Ascidiella aspersa* Müller, 1776) at each site. These made up the majority of the live benthic cover at each site. Other sessile species or shells present in small quantities included oyster shells (sites A, B and

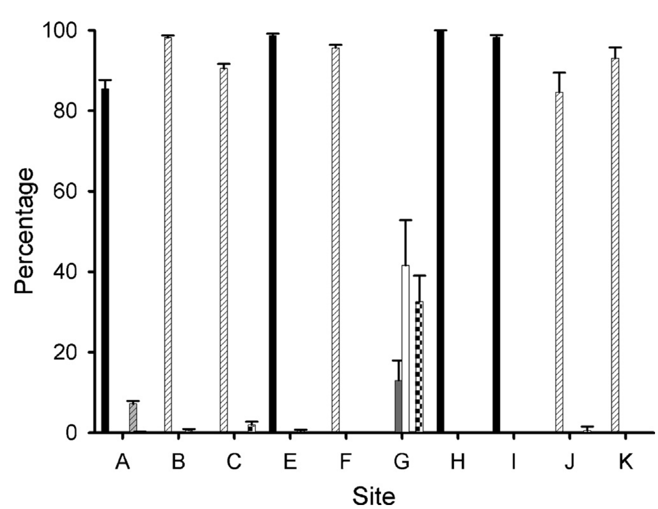


**Fig. 2.** Average percentage cover of major substrate types at each site in the Firth of Forth using ten 1 $m^2$ quadrats, with standard error. Black bars = mud; white patterned = mud and mixed unidentified shell; white = unidentified shell; grey = coal; grey patterned = oyster shell; white and black checked = horsemussel shell. Live benthos cover is not counted as it is included in Fig. 3, hence coverage does not always equal 100% for each site.

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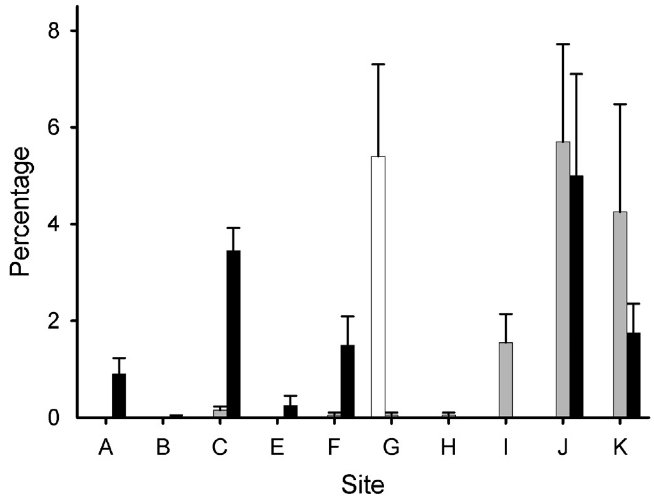


**Fig. 3.** Percentage cover of main species present at Forth sites, with standard error. White = live horsemussel; grey = seasquirts (*Ascidiella aspersa*); black = bryozoa spp.

E), razor shell remains (*Ensis* spp.), blue mussel and queen shell remains, horn wrack (another species of bryozoan, *Flustra foliacea* Linnaeus, 1758), plumose anemones (*Metridium senile* Linnaeus, 1761), burrowing anemones (*Sagartiogeton lacerates* Dalyell, 1848), phosphorescent seapens (*Pennatula phosphorea* Linnaeus, 1758, site H only), soft coral (*Alcyonium digitatum* Linnaeus, 1758) and dahlia anemones (*Urticina felina* Linnaeus, 1761). Mobile species weren't taken into account when calculating percentage cover but included sea mice (*Aphrodita aculeata* Linnaeus, 1758, site H only), sand gobies (*Pomatoschistus minutus* Pallas, 1770), common starfish (*Asterias rubens* Linnaeus, 1758) and small crabs (e.g. *Macropodia* spp.).

Fig. 4 shows the number of shells of live or dead queen scallops, horse mussels or oysters counted at each site within the ten quadrats. No live oysters and few live queen scallops were found. Site A had relatively high numbers of queen scallop shell and oyster shell remains, whilst site G contained a community of live horse mussels.

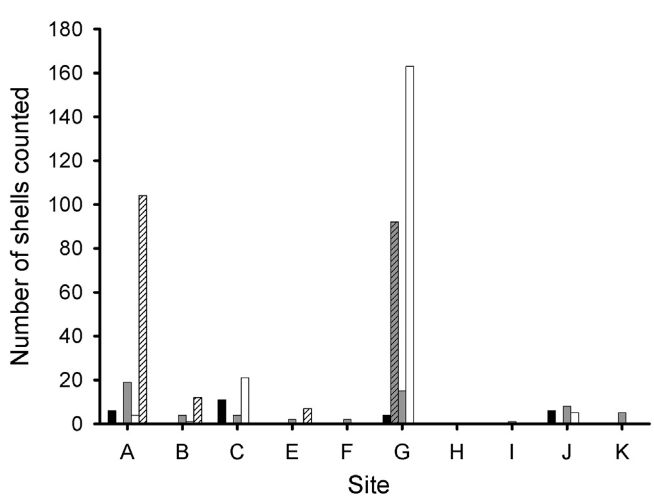


**Fig. 4.** Number of live shellfish and dead shells counted at each site within 10 1 $m^2$ quadrats in the Firth of Forth. Shell remains do not represent the number of individuals as most shells were found singly rather than in pairs. Black = live queen scallops; grey patterned = live horsemussels; grey = queen scallop shell; white = horsemussel shell; white patterned = oyster shell.

*Radioisotope and shell community analysis*

Seven cores were dated using all three methods (Itrax, $^{137}$Cs and $^{210}$Pb). Sediment accumulation rates could not be calculated for sites E and I, as measurable levels of $^{210}$Pb declined too quickly in the surface layers of the cores to form a reliable profile. $^{210}$Pb profiles could be established for the five cores from sites B, C, F, G and J. Fig. 5 shows excess $^{210}$Pb activity profiles with depth for the 5 core profiles able to be used. Due to the non-linear nature of the $^{210}$Pb profile, a Constant Rate of Supply (CRS) model was used to calculate rates of sediment accumulation (Appleby 2004). Independent dating methods ($^{210}$Pb, $^{137}$Cs and Itrax profiles) corresponded well at sites B, C and G, whereas site F $^{137}$Cs accumulation rates were lower than those suggested by $^{210}$Pb and Itrax profiles. $^{210}$Pb rates for site J were lower than $^{137}$Cs or elemental profile accumulation rates would suggest (Table S2, Appendix). This could be due to incorrect interpretation or because of inaccuracies in the $^{210}$Pb dating method.

No oyster shell remains were found in any of the ten cores, although oyster shell remains were observed partially buried or on the surface at sites A, B and E. The lack of oyster remains within cores could be due to sampling inefficiency, lack of preservation of buried shells or the removal of shells as they were dredged. No significant differences were found in species composition at different core depths, although some shell remains could not be identified because they were too fragmented. Therefore total shell biomass and species richness (as identified by intact shells) were used as proxy methods to identify changes to shell communities at different depths. Fig. 6 shows changes to species richness and shell biomass throughout the five dated cores (B, C, F, G and J), with estimated $^{210}$Pb reference dates applied. Estimation of dates prior to 1880 should be treated with caution because $^{210}$Pb dating accuracy diminishes beyond 5–6 half lives (approximately 110–130 years) (Appleby 2004).

In core B species richness gradually declined over time, whilst shell biomass declined 20-fold over the course of the late 19th and 20th century. Species richness showed a more stable pattern in core C, with increases in the latter half of the 20th century. However, shell biomass throughout C was more variable with increases in recent years (mid-late 20th century), whilst earlier data suggest a dramatic decrease (50–76%) during the 19th century. Trends in shell biomass and mollusc species richness at site F also suggest that declines occurred before the onset of the 20th century and continued until the mid-20th century, at which point increases in both richness and biomass occurred. Site G shows a decline in shell biomass prior to 1900. Species richness shows a slight decline overall but remains more stable than shell biomass. The core from site J shows a different pattern to the other cores, in that shell biomass and richness were lower in earlier years with increases seen during the late 20th century.

## Discussion

Prior to the early 19th century the Firth of Forth contained rich, extensive biogenic habitat dominated by oysters (Fulton 1896 and references therein; Royal Commission 1885). These sustained a hugely productive fishery and consolidated large areas of seabed with diverse, three-dimensionally complex habitat. By the late 19th century oysters were still present but in much reduced abundance, most likely as a consequence of intense overexploitation and the collateral damage done by bottom trawlers and dredgers as they penetrated areas of the Forth for the first time (Fulton 1896). By the first half of the 20th century Firth of Forth oysters had declined to the point of extirpation (Millar 1961). Sustained, intensive exploitation undoubtedly played a large role in their decline. However,

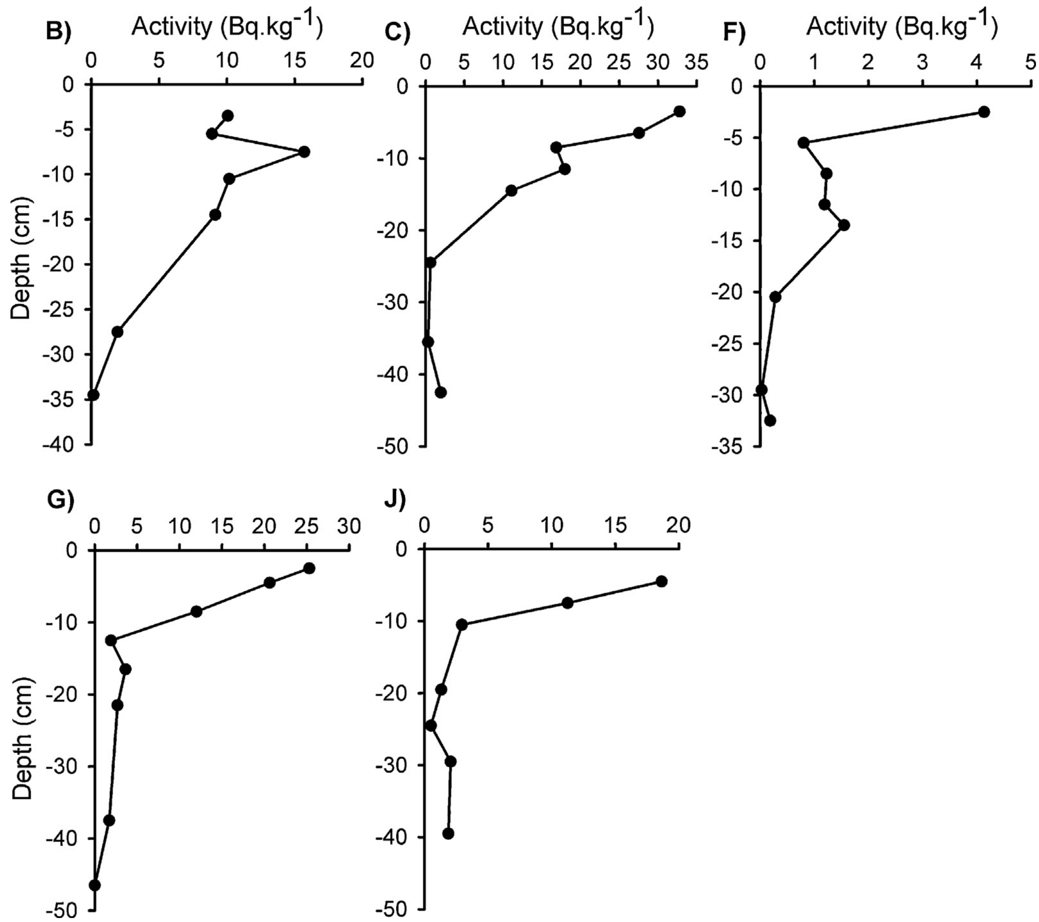


**Fig. 5.** Excess $^{210}$Pb (Bq kg$^{-1}$) at various depths for sites B, C, F, G and J.

their much reduced population meant that remaining oysters in the Forth were likely to have been less resilient to disease, competition and predation by non-native species and had undergone years of failed recruitment. As oyster abundance declined in the Forth queen scallops increased in number, sustaining fisher livelihoods in the Firth of Forth as they began to target scallops for bait for line fisheries. However as exploitation for scallops intensified, this secondary community also declined and much of the Firth of Forth (with the exception of a few sites that still contained horse mussels beds) was converted to less diverse, soft-sediment dominated communities.

Our study used two independent methods to document timings of change to the oyster fishery and other benthic communities within the Forth. Qualitative analyses of dredge surveys undertaken in 1895 versus in situ surveys during 2010 showed that benthic communities have altered substantially since the late 19th century. Since 1895, live oysters have completely disappeared while queen scallops and horse mussel populations have declined. Starfish and brittlestars still occur in some quantity, but in general we saw few crustaceans or live bivalves during the survey work. By contrast, the presence of phosphorescent seapens at site H and the presence of horse mussels at site G suggests that in recent times at least, these sites have been relatively undisturbed. Except for site G, few hard substrates were present, and no trace of oysters or layers of hard shell matrix were found in the sediment cores. In 1895 Fulton described grounds as slightly muddy, clean or shelly (Table 1). However, in general we found thick black mud that could only support soft sediment organisms. A quote in 1883 by W. Hunnam, a fisherman from Cockenzie on the south coast of the Firth of Forth suggests that this thick mud was already present in the Forth then, but that prior to intensive fishing activities oysters and other benthic organisms living at the surface had built a consolidated matrix over the top of it,

> "*[The beam trawlers] have taken away the upper crust of the ground. And, mark you, it is the upper crust that the scallops and clams live amongst. [...] [The crust] is just a ground made up of broken shells, and all the like of these sort of things; and underneath that is mud. If we give our dredge half a fathom too much rope, she goes down altogether into the mud.*" (Royal Commission 1885)

By 1885 the oyster fishery was almost non-existent, and it would appear that this shell matrix was also fast disappearing. This hard substrate would have provided a habitat for the settlement of young oysters and other species, with contemporary studies citing the loss of shell matrix as a major cause of recruitment failure (Gutiérrez et al. 2003; Mann & Powell 2007; Meyer & Townsend 2000). Communities described in the area today are low diversity, soft-sediment communities. While some species we found are similar to those from Fulton's descriptions; e.g. *Flustra* was commonly seen by him, his descriptions of horsemussels and queen scallop communities no longer exist where we surveyed (with the exception of site G).

The surveys undertaken by Fulton in 1895 did not document an unexploited habitat. By this time much of the damage to the oyster fishery had already occurred, and the shift to a secondary community dominated by queen scallops and to a lesser extent horse mussels was already underway. Results from our sediment cores are able to extend this picture of change further back in time, and tentatively suggest that declines in mollusc communities,

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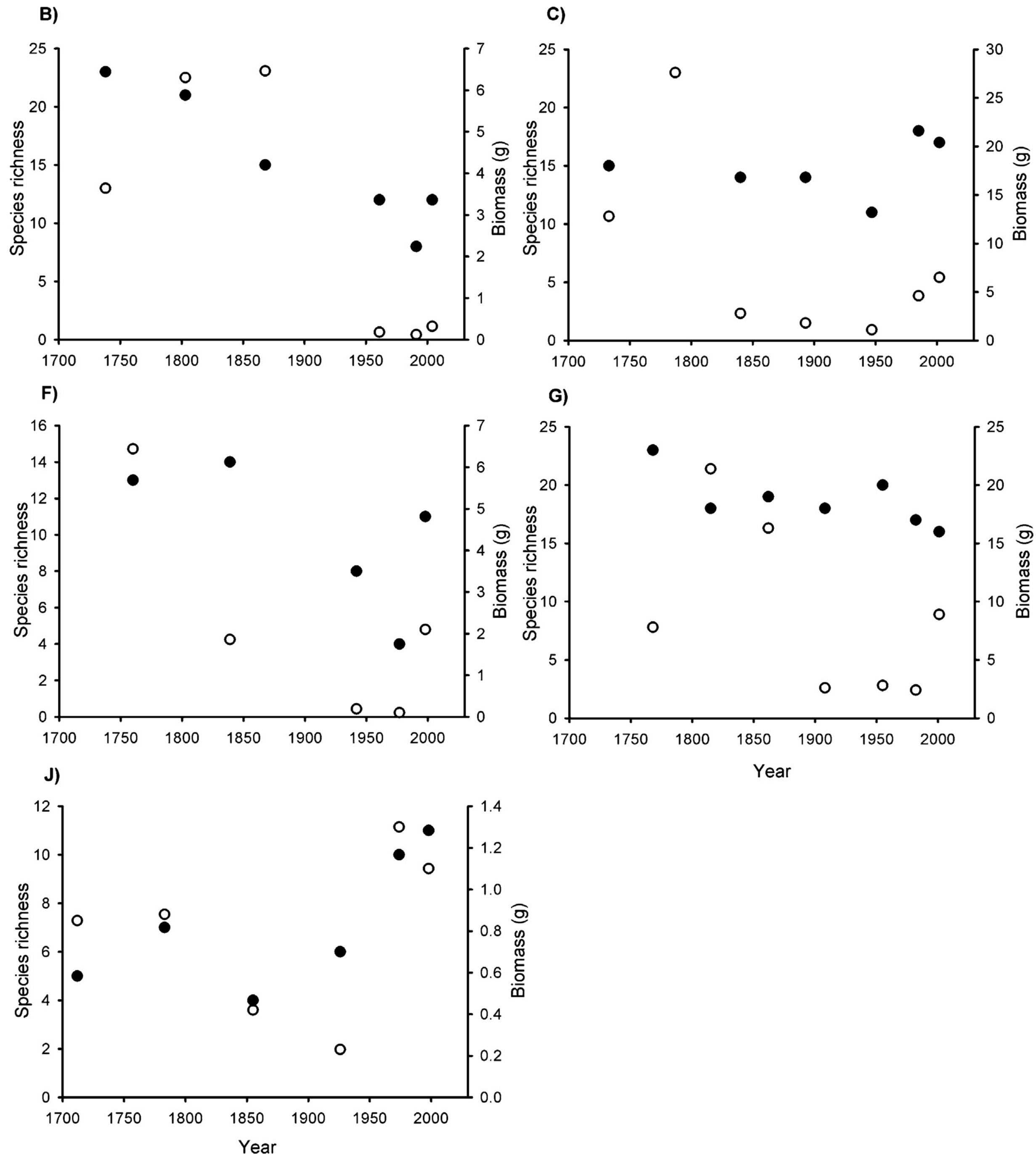


**Fig. 6.** Changes to mollusc species richness (filled circles) and shell biomass (open circles) per 5 cm core for sites B, C, F, G and J. Note the different scales on the axes.

particularly biomass, occurred throughout the 19th century, with increases in biomass and species richness seen from the mid-20th century onwards. Site J showed an increase in species richness and biomass throughout the 20th century. This site is close to the southern shore of the Firth so may have been subjected to heavy fishing activity and subsequently abandoned earlier than other sites. None of our 11 cores showed any evidence of an oyster shell base layer. This could have been removed as the oysters were depleted, subsequently reducing survival rates for juvenile oysters. Historical descriptions of the quantity of oysters removed from the Forth during the 19th century provides evidence that much of the oyster shell base was removed or destroyed, indeed, many oyster shells were not thrown back but ground up and used as building materials or spread upon crop fields (Royal Commission 1885).

Using mollusc shells to determine past community composition requires careful interpretation since post-mortem processes may result in shell assemblage remains that do not always reflect past realities (Kidwell & Bosence 1991). For example, the composition of the shell assemblage may be modified by differential preservation e.g. some shells break down more quickly than others due to size, shape or chemical composition. Assemblages from different periods might also have been mixed together (time-averaged) by physical or biological processes i.e. bioturbation (Kidwell & Bosence 1991). Differential preservation can reduce or skew past measures of species richness and/or biomass, whilst time averaging may increase perceived species richness as species from different layers of sediment become mixed together over time (Kidwell 2002). Despite these caveats, Kidwell and Bosence (1991) state that

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mollusc remains are generally considered to provide a good indication of the original rank order of these species and hence should provide a reasonable picture of changes over time.

The mixing of sediments within the Forth is a factor that may also significantly affect the reliability of radionuclide dating of sediments. Whilst mixing of sediments through physical processes (i.e. storms, fishing) may affect shell remains by moving them vertically through the sediment, another important process is the mixing of sediments by live bivalves, annelids and other invertebrates (Kidwell & Bosence 1991). Bioturbation processes have been shown to affect sediment chronologies in the Irish Sea and off the west coast of Scotland (Hughes et al. 1996), influencing the distribution of radionuclides over the upper few tens of centimetres of sediment (Kershaw et al. 1983) and at deeper depths (Kershaw 1986). Thoughout the inner Firth of Forth, infaunal communities were found to be dominated by burrowing bivalves such as *Venus* and *Abra* spp. (Elliott & Kingston 1987), both of which can burrow to depths of 40 cm (Allen 1983). Hence it is possible that bioturbation by infauna such as these influenced the distribution of radionuclides in the upper 40–50 cm of sediment, a process that must be acknowledged when attempting to date these sediments. It is also possible that the vertical distribution of mollusc shells is not just a function of time, but also related to the ecology of each species (Eleftheriou & Holme 1984) e.g. an organism's depth in the sediment may be related to preferred feeding behaviour or tolerance to oxygen-limited environments in life (Cardoso et al. 2010; Hines & Comtois 1985).

Whilst our dating results must be interpreted with care, the profiles obtained from our sediment cores using several independent dating methods provide evidence for the existence of consistent temporal chronologies. Due to the limitations described above, we restricted our analyses to broader community patterns, i.e. biomass and species richness, and used these as a broad proxy for community changes over time. Our mollusc death assemblage data suggests that wider community species richness and biomass declined over the past 150–200 years. We do not show statistical analyses to evaluate spatial or temporal patterns in our data on Firth of Forth benthic communities and instead, our results are largely descriptive. Our reasons for this were driven by the differing nature of the substrate and species composition found during quadrat surveys of the 11 sites (Figs. 2–4), as well as the different temporal trends and species richness patterns evident throughout the 5 cores. Averaging across sites would lose much of the variance shown in our results, whilst the cores (as discussed above) have potential taphonomic issues. As a result, statistical trends would not aid our interpretation of historic baselines further.

In addition to the increased exploitation of oysters during the 19th century, other environmental changes took place within the Forth at this time as a result of increased pollution, coastal development and reclamation of land. From the 1750s areas of raised peat bog such as Flanders Moss were drained and excavated for use as agricultural land (Scottish Natural Heritage 2009). This resulted in large quantities of material being carried downstream and deposited in the Inner Firth as a thick black mud (Harding 1996). In addition coal and ash solids were regularly thrown overboard by steam trawlers during the late 19th and early 20th centuries whilst suspended solids discharged from coalmines posed a threat to benthic habitats by physical smothering (Harding 1996). The main source of industrial pollution to the Forth during the 19th century was from gas works, tanneries and dye works (Griffiths 1987). Today the Forth receives waste from sewage treatment works, petrochemical and oil refineries, coal-fired power stations, distilleries and yeast manufacturers. However, on balance it has been reported that pollutants have been substantially reduced since the late 1980s (Graham et al. 2001). Whilst earlier changes did not appear to reduce the productivity of the oyster fishery (i.e. catches continued to increase until the 1860s), cumulative impacts may have reduced the oyster population's ability to recover once population declines set in.

The approaches we used fill out a history of change in benthic communities that is missing from archival sources, which usually focus upon commercially important species (Airoldi & Beck 2007; Beck et al. 2011; Zu Ermgassen et al. 2012). Our research provides a cautionary tale that UK inshore marine communities were severely degraded long before present generations were born, and that to successfully unravel the true extent of these changes, multiple, interdisciplinary methods may be required. The changes we describe from the Forth and their drivers of change probably apply much more widely to oyster beds and other biogenic habitats throughout northeastern European waters (Laing et al. 2005; Shelmerdine & Leslie 2009). Today, the southern North Sea is largely made up of expanses of sand, mud and gravel, yet the Piscatorial Atlas of 1883, published just prior to the intensification of bottom trawling, shows large areas of oyster beds throughout much of the southern North Sea.

This dramatic and largely unappreciated transformation of nearshore, estuarine and continental shelf environments will likely have greatly altered the functioning of marine ecosystems as well as changed the habitat suitability for a host of associated species. In general, the restoration of severely degraded habitats and their associated fisheries requires a radical alteration to current environmental practise. One approach to aiding this process is to focus management efforts on first identifying and then promoting recovery of areas where biogenic habitats still exist. Our work has shown that even within a heavily impacted environment such as the Firth of Forth, communities with key biogenic species such as horse mussels do still occur, thus providing hope for their resilience and recovery given appropriate management. Within the UK many inshore pressures, for example, pollution, have successfully been reduced in recent years as a result of national and international legislation. However, multiple pressures still continue to impact inshore environments, hence sustained, coherent management of both land and sea-based impacts will continue to be required, and stepped up, if recovery is to be our goal.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jnc.2013.01.004.

## References

Airoldi, L., & Beck, M. W. (2007). Loss, status and trends for coastal marine habitats of Europe. *Oceanography and Marine Biology: An Annual Review*, *45*, 345–405.
Allen, P. L. (1983). Feeding behaviour of *Asterias rubens* (L.) on soft-bottom bivalves: A study in selective predation. *Journal of Experimental Marine Biology and Ecology*, *70*, 79–90.
Appleby, P. G. (2004). Chronostratigraphic techniques in recent sediments. In W. M. Last, & J. P. Smol (Eds.), *Tracking environmental change using lake sediments: Basin analysis, coring, and chronological techniques* (pp. 171–203). The Netherlands: Kluwer Academic Publishers.

Beck, M. W., Brumbaugh, R. D., Airoldi, L., Carranza, A., Coen, L. D., Crawford, C., et al. (2011). Oyster reefs at risk and recommendations for conservation, restoration, and management. *Bioscience*, *61*, 107–116.

Bell, F. G., Lindsay, P., & Hytiris, N. (1997). Contaminated ground and contaminated estuary sediment illustrated by two case studies. *Environmental Geology*, *32*, 191–202.

Cardoso, I., Granadeiro, J. P., & Cabral, H. (2010). Benthic macroinvertebrates' vertical distribution in the Tagus estuary (Portugal): The influence of tidal cycle. *Estuarine, Coastal and Shelf Science*, *86*, 580–586.

Covill, R. W. (1972). The quality of the Forth estuary (2). *Proceedings of the Royal Society of Edinburgh B*, *71*, 143–170.

Cundy, A. B., Croudace, I. W., Cearreta, A., & Irabien, M. J. (2003). Reconstructing historical trends in metal input in heavily disturbed, contaminated estuaries: Studies from Bilbao, Southampton Water and Sicily. *Applied Geochemistry*, *18*, 311–325.

Dayton, P. K., Tegner, M. J., Edwards, P. B., & Riser, K. L. (1998). Sliding baselines, ghosts and reduced expectations in kelp forest communities. *Ecological Applications*, *8*, 309–322.

Edgar, G. J., & Samson, C. R. (2004). Catastrophic decline in mollusc diversity in Eastern Tasmania and its concurrence with shellfish fisheries. *Conservation Biology*, *18*, 1579–1588.

Eleftheriou, A., & Holme, N. A. (1984). Macrofauna techniques. In N. A. Holme, & A. D. McIntyre (Eds.), *Methods for the study of marine benthos* (pp. 140–216). Oxford: Blackwell Scientific Publications.

Elliott, M., & Kingston, P. F. (1987). The sublittoral benthic fauna of the Estuary and Firth of Forth. *Proceedings of the Royal Society of Edinburgh B*, *93*, 449–465.

Fishery Board for Scotland. (1890). *Eighth annual report of the Fishery Board for Scotland, being for the year 1889. General report (Part I)*. Edinburgh: HMSO.

Flynn, W. W. (1968). Determination of low levels of polonium-210 in environmental materials. *Analytica Chimica Acta*, *43*, 221–227.

Fullarton, J. H. (1889). *On the habits of Pecten and on the clam beds of the Firth of Forth. Seventh annual report of the Fishery Board for Scotland being for the year 1888. Scientific Investigations (Part III)* Edinburgh: HMSO., 341–352.

Fulton, T. W. (1896). *The past and present condition of the oyster beds in the Firth of Forth. Fourteenth Annual Report of the Fishery Board for Scotland, being for the year 1895. Scientific Investigations (Part III)* Edinburgh: HMSO., 244–293.

Graham, M. C., Eaves, M. A., Farmer, J. G., Dobson, J., & Fallick, A. E. (2001). A study of carbon and nitrogen stable isotope and elemental ratios as potential indicators of source and fate of organic matter in sediments of the Forth estuary, Scotland. *Estuarine Coastal and Shelf Science*, *52*, 375–380.

Griffiths, A. H. (1987). Water quality of the estuary and Firth of Forth, Scotland. *Proceedings of the Royal Society of Edinburgh B*, *93*, 303–314.

Grossinger, R. M., Askevold, R. A., & Collins, J. N. (2005). *T-sheet user guide: Application of the historical U.S Coast Survey Maps to environmental management in the San Francisco Bay area*. San Francisco: San Francisco Estuary Institute.

Gutiérrez, J. L., Jones, C. G., Strayer, D. L., & Iribarne, O. O. (2003). Mollusks as ecosystem engineers: The role of shell production in aquatic habitats. *Oikos*, *101*, 79–90.

Hall-Spencer, J. M., Grall, J., Moore, P. G., & Atkinson, R. J. A. (2003). Bivalve fishing and maerl-bed conservation in France and the UK – retrospect and prospect. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *13*, S33–S41.

Hall-Spencer, J. M., & Moore, P. G. (2000). Scallop dredging has profound, long-term impacts on maerl habitats. *ICES Journal of Marine Science*, *57*, 1407–1415.

Harding, T. (1996). *Reintroduction of the native oyster (Ostrea edulis) into the Firth of Forth, Scotland: A feasibility study*. MSc thesis, Napier University.

Hines, A. H., & Comtois, K. L. (1985). Vertical distribution of in fauna in sediments of a subestuary of central Chesapeake Bay. *Estuaries*, *8*, 296–304.

Hiscock, K., Sewell, J., & Oakley, J. (2005). *Marine health check 2005: A report to gauge the health of the UK's sea-life*. Godalming: WWF-UK.

Holt, T.J., Rees, E.I., Hawkins, S.J., & Seed, R. (1998). *Biogenic reefs (volume IX). An overview of dynamic and sensitivity characteristics for conservation management of marine SACs*. Scottish Association for Marine Science (UK Marine, SACs Project).

Howard, F. G., McKay, D. W., & Newton, A. W. (1987). Fisheries of the Forth Scotland. *Proceedings of the Royal Society of Edinburgh B*, *93*, 479–494.

Hughes, D. J., Ansell, A. D., & Atkinson, R. J. A. (1996). Sediment bioturbation by the echiuran worm *Maxmuelleria lankesteri* (Herdman) and its consequences for radionuclide dispersal in Irish Sea sediments. *Journal of Experimental Marine Biology and Ecology*, *195*, 203–220.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., et al. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science*, *293*, 629–638.

Kershaw, P. J. (1986). Radiocarbon dating of Irish Sea sediments. *Estuarine, Coastal and Shelf Science*, *23*, 295–303.

Kershaw, P. J., Swift, D. J., Pentreath, R. J., & Lovett, M. B. (1983). Plutonium redistribution by biological activity in Irish Sea sediments. *Nature*, *306*, 774–775.

Kidwell, S. M. (2002). Time-averaged molluscan death assemblages: Palimpsests of richness, snapshots of abundance. *Geology*, *30*, 803–806.

Kidwell, S. M., & Bosence, D. W. J. (1991). Taphonomy and time-averaging of marine shelly faunas. In P. A. Allison, & D. E. G. Briggs (Eds.), *Taphonomy, releasing the data locked in the fossil record* (pp. 115–209). New York: Plenum Press.

Laing, I., Walker, P., & Areal, F. (2005). *A feasibility study of native oyster (Ostrea edulis) stock regeneration in the United Kingdom*. Centre for Environment, Fisheries and Aquaculture Science, CARD Project FC1016.

Langdon, P. G., Caseldine, C. J., Croudace, I. W., Jarvis, S., Wastegård, S., & Crowford, T. C. (2011). A chironomid-based reconstruction of summer temperatures in NW Iceland since AD 1650. *Quaternary Research*, *75*, 451–460.

Lotze, H. K., Lenihan, H. S., Bourque, B. J., Bradbury, R. H., Cooke, R. G., Kay, M. C., et al. (2006). Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science*, *312*, 1806–1809.

Lotze, H. K., & Milewski, I. (2004). Two centuries of multiple human impacts and successive changes in a North Atlantic food web. *Ecological Applications*, *14*, 1428–1447.

Mann, R., & Powell, E. N. (2007). Why oyster restoration goals in the Chesapeake Bay are not and probably cannot be achieved. *Journal of Shellfish Research*, *26*, 905–917.

Meyer, D. L., & Townsend, E. C. (2000). Faunal utilisation of created intertidal eastern oyster (*Crassostrea virginica*) reefs in the southeastern United States. *Estuaries*, *23*, 34–45.

Millar, R. H. (1961). *Scottish oyster investigations 1946–1958*. Department of Agriculture and Fisheries for Scotland: Marine Research 3.

Pauly, D. (1995). Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology and Evolution*, *10*, 430.

Philpots, J. R. (1891). *Oysters and all about them*. London: John Richardson and Co.

Roberts, C. M. (2007). *The unnatural history of the sea*. Washington, DC: Island Press.

Robinson, L. A., & Frid, C. L. J. (2008). Historical marine ecology: Examining the role of fisheries in changes in North Sea benthos. *Ambio*, *37*, 362–371.

Royal Commission. (1885). *Report of the commissioners: Trawl net and beam trawl fishing with minutes of evidence and appendix*. London: Eyre and Spottiswoode.

Scottish Mussel Bait Beds Commission. (1889). *Report of the committee appointed by the Secretary for Scotland to inquire into the condition of the Scottish mussel and bait beds together with evidence and appendix*. London: Eyre and Spottiswoode.

Scottish Natural Heritage. (2009). *Scotland's National Nature Reserves: The story of Flanders Moss National Nature Reserve*. Scottish Natural Heritage: University of Stirling.

SEPA. (1998). *Trace metals in the Forth (1986–1996)*. Scottish Environment Protection Agency: SEPA East Region, Report No. TW 17/98.

Shelmerdine, R. L., & Leslie, B. (2009). *Restocking of the native oyster, Ostrea edulis, in Shetland: Habitat identification study*. Scottish Natural Heritage Commissioned Report No. 396.

Webb, A. J., & Metcalfe, A. P. (1987). Physical aspects, water movements and modelling studies of the Forth Estuary, Scotland. *Proceedings of the Royal Society Edinburgh B*, *93*, 259–272.

Zu Ermgassen, P. S. E., Spalding, M. D., Blake, B., Coen, L. D., Dumbauld, B., Geiger, S., et al. (2012). Historical ecology with real numbers: Past and present extent and biomass of an imperilled estuarine habitat. *Proceedings of the Royal Society B*, *279*, 3393–3400.