# A switch in species dominance of a recovering pelagic ecosystem

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## Summary

Although many marine ecosystems have been adversely impacted by human activities[1], some are now recovering due to reductions in fishing pressure[2–4]. Here, we document the recovery of an ecosystem subjected to intense anthropogenic activity for over 200 years, the Clyde Sea[5]. This region once had productive fisheries for herring (*Clupea harengus*) and other fish, but these disappeared at the turn of the century[6,7]. Using acoustic surveys of the pelagic ecosystem, we found that the Clyde Sea supports 100 times as many forage fish as in the late 1980s. However, herring has now been replaced by sprat (*Sprattus sprattus*), despite virtually no fishing on herring for 20 years. A combination of a warming sea[6], bycatch of herring in the prawn (*Nephrops norvegicus*) fishery[8,9], and susceptibility of herring to poor recruitment may have contributed to this unexpected recovery. We compare this to similar unexpected 'recoveries' involving unforeseen ecosystem effects, such as: the return of hake (*Merluccius merluccius*) to the North Sea[10,11]; the recent expansion of the pelagic squat lobster, 'munida', (*Pleuroncodes monodon*) off Peru[12]; and the increase in scallop (*Placopecten magellanicus*) numbers on Georges Bank[13]. The lack of a current sprat fishery in the Clyde presents a unique opportunity to develop an alternative industry for its seafaring community: ecotourism. Charismatic megafauna (whales, dolphins and seabirds) that people will pay to see[14] will, in time - if not already[15,16] - be drawn in by the abundance of forage fish now present, further restoring the biodiversity of the region after centuries of overexploitation.

Keywords; marine ecology; forage fish; ecosystem recovery; anthropogenic impacts; fishery acoustics; geostatistics; fishery management

## Results

The Firth of Clyde, situated next to a major conurbation and industrial centre, is one of the most anthropogenically impacted marine environments in the world, and was a hub for shipping and ship building for over two centuries[17]. Historically, it supported important fisheries, both for demersal fish and, famously, for herring. However, overfishing throughout the latter half of the 20th century brought about the collapse of these traditional 'finfish' fisheries, and these have now been replaced with a fishery for prawns[5,18]. This is an example of fishing down the food web[19] and others have reported this as evidence of an ecological meltdown[5]. In contrast, there are also reports that the biomass of demersal fish remains high[7], but most of these are young and, as they grow, are then subjected to bycatch in the prawn fishery, which also operates on the seabed. Very little is known about the current state of the pelagic fish stocks.

We assessed the biomass and abundance of the two major pelagic forage fish species in the Clyde, herring and sprat. We conducted annual fisheries acoustic surveys from 2014-2016 and compared them with surveys from the late 1980's, which used very similar methods[20–25]. Acoustic data was collected with a calibrated Simrad EK60 multifrequency scientific echosounder (Figure 1A,B), and species composition of detected fish schools was determined by targeted trawling. This also provided biological samples to ascertain the species-specific length-frequency distributions, and weight-length relationships. Herring and sprat constituted 99.8% of all fish caught (by number) across all years. These two species, from the clupeid taxonomic family, are indistinguishable acoustically, so they were detected as "clupeids". Backscatter from clupeid fish schools was isolated from other targets, differentiating clupeids (Figure 1C) from dense euphausiid aggregations (Figure 1D)[16,26]. Extensive layers (several km in length, e.g. Figure 1C) and large schools of clupeids were detected in all years (Figure S1). Clupeid and euphausiid backscatter was integrated[27,28] over 1 km sampling units (Figure 2A-C), interpolated (Figure 2D) and (for clupeids) apportioned according to the species and length, statistical and spatial distributions (e.g. Figure 2E,F) to estimate species density.

Conditional geostatistical simulations of: i) backscatter from clupeid fish schools; ii) species proportions; and iii) fish lengths (Figure 2D-F), were combined to produce 1 million realisations of estimated biomass and abundance of herring and sprat in each year. This approach allowed for the uncertainty in the three data sources to be propagated into the final estimate as well as accounting for the spatial variability of the distributions underlying the data[29]. The resulting error calculated here (Figure 3), therefore, is higher than would normally be estimated from similar surveys, because typically only the error associated with the acoustic data component is considered. 500 realisations of estimated euphausiid biomass were similarly produced from geostatistical simulations of backscatter from euphausiid aggregations.

Mean estimates (and 95% confidence intervals) of sprat biomass (t) were 30,320 (18,180 – 45,660), 46,730 (26,710 – 73,090) and 70,100 (44,510 – 110,580) in 2014, 2015 and 2016, respectively, and for herring were 230 (140 – 350), 19,460 (9,770 – 35,400) and 6,160 (2,030 – 15,910) (Figure 3). Sprat abundance estimates were 19.02 (11.45 – 28.64) x $10^9$, 14.70 (8.46 – 22.77) x $10^9$ and 23.54 (14.95 – 36.38) x $10^9$ fish in 2014, 2015 and 2016, respectively. Herring abundance estimates were 0.026 (0.016 – 0.040) x $10^9$, 3.89 (1.95 – 6.93) x $10^9$, 0.31 (0.12 – 0.66) x $10^9$ fish. Sprat in 2016 was, therefore, 75 times more abundant than herring, with more than 10 times the biomass. The mean fish length, across all three years, was 11.1 cm (n = 3006, standard deviation (SD) = 3.2) for herring, and 8.3 cm (n = 6602, SD = 1.6) for sprat. Mean biomass estimates (t) for euphausiids were 64,900 (43,800 – 96,900) in 2014, 80,600 (71,400 – 92,400) in 2015, and 45,000 (42,000 – 48,500) in 2016.

In the late 1980s, acoustic surveys estimated a maximum total combined biomass of herring and sprat in the Clyde to be 20,400 t, and a maximum abundance of 0.23 x $10^9$ fish, over 100 times less than the abundance of sprat alone that we estimated in 2016. Another notable difference is the species dominance between these historical surveys and our recent ones: in the 1980's herring was clearly dominant, whereas now, sprat far outweighs herring (Figure 3). The mean sizes of fish caught in the historical surveys were also different: 25.0 cm and 12.1 cm for herring and sprat, respectively (the historical reports did not provide comparable estimates of uncertainty).

## Discussion

Here, we document the significant recovery of forage fish biomass in an historically overexploited marine ecosystem, to levels greatly exceeding those recorded 30 years ago. However, despite the collapse of the targeted fishery, and the imposition of strict management controls in the form of low catch limits, the previously dominant and commercially important species, herring, has not recovered. The pelagic fish assemblage is now dominated by a different, albeit ecologically related species, sprat. A high biomass of these forage fish was recorded in all three years of the recent surveys, to a maximum (in 2016) of almost 4 times higher than was reported in any of the last period of regular surveys (1985-1990). The abundance of forage fish was found to be up to two orders of magnitude higher, with the higher biomass of clupeids being made up of much smaller fish.

The change in species dominance, from a system dominated by herring to one dominated by sprat could be due to the focussed nature of the historical fishery (targeting herring only), favouring the unexploited species. However, since the increase in sprat biomass coincides with a period of minimal exploitation of the herring stock (zero landings since 2014)[30], and herring landings have been low for many years (<1000 t since 1999 and <500 t since 2010), the impacts of the differential fishing pressure exerted on the two species may not be significant. In the absence of biomass estimates for the two species in the years between survey periods, it is impossible to confirm causal links between variations in selective fishing pressure and the differing species biomass trends. Furthermore, sprat, in common with many common short-lived forage fish species, exhibit highly variable population dynamics[31,32]. The population increase recorded in the Clyde, however, appears to be in line with the population trends seen in neighbouring stocks. In the adjacent Irish sea, and the wider Celtic Sea, estimates of sprat biomass have been variable but increasing since 2010, and in the North Sea, the stock has been generally increasing, despite relatively consistent and high fishing mortality, since the late 1980s[33]. Further afield, the Baltic Sea stock has been decreasing from a peak in the mid-1990s, but this decline may be attributable to elevated local fishing pressure[34]. The variability in these population trajectories suggest that the causes of the increase in sprat biomass in the Clyde and elsewhere, are likely to be more complex than simply changes in local fishing pressure.

Other factors, such as warming water temperatures[6,35] or an alteration in the composition of the macrozooplankton assemblage, may have favoured sprat as the more generalist predator[36], which also prefers higher temperatures than herring[37]. Both of these factors were linked to previous changes in the distribution of North Sea herring[38]. It is also possible that while there has been limited fishing effort targeting herring in the past two decades, bycatch of larger herring in the *Nephrops* fishery may have contributed to the inhibition of the recovery of the herring stock. Herring is commonly bycaught and discarded by trawlers targeting *Nephrops*, whereas sprat is not[8,9]. Net mesh size is positively correlated with bycaught fish size, and sprat are likely too small to be retained by the nets used by the prawn fleet (70 mm average mesh size)[9]. This size selectivity may have been problematic for herring as it was primarily larger fish which were removed (e.g. Stratoudakis *et al*.[9] recorded a mean length of bycaught herring of 22.1 cm).

The susceptibility of Clyde herring to poor recruitment events may have placed the herring population at a further competitive disadvantage to sprat. Herring spawning is dependent on access to undisturbed gravel sediments[39–41], which, within the Clyde, historically occurred in just two small areas, Ballantrae Bank and south of Arran[40,41]. With such limited access to appropriate spawning areas and conditions, the Clyde herring stock was known to experience fluctuations in spawning success leading to great variability in year-class strength[5,18]. The intensity of trawling on the Clyde seabed may have further reduced the availability of the necessary spawning grounds. Catastrophic recruitment failures have been recorded previously[42], and the targeted fishing of the spawning component of the stock may have driven spawning numbers down sufficiently to impair spawning efficiency, preventing the emergence of a strong year-class[18]. Sprat, conversely, spawn over a longer period in open water[43,44], and so are less vulnerable to either such targeted exploitation, or such comprehensive failures of a specific spawning ‘event’. This imbalance may function in combination with the more rapid maturation of sprat relative to herring (a difference which has been found to be increasing the North Sea[45]), to have allowed sprat to increase in biomass while herring have shown no similar increase.

The population structure of the herring stock in the Clyde is also important to consider in understanding the observed lack of recovery. In the recent surveys, the mean size of herring caught was <12 cm, in stark contrast with the historical surveys where the mean size was ~25 cm. This increased proportion of immature herring in the Clyde will further reduce the likelihood of strong recruitment years, contributing to the stock's lack of recovery. The reasons for the absence of large, mature herring remain unclear (possibly including e.g. emigration, predation or bycatch), although there is historical evidence of adult herring moving in and out of the Clyde[18] intra-annually. It is possible that surveys conducted at other times of year may record more large herring, but the survey timing was chosen in consultation with local fisherman who indicated that this was the best time to catch the larger herring.

The changes seen in this region - recovery of overall forage fish biomass but not of a commercially important species - are an example of the problems faced by managers aiming to recover commercial fish stocks to their former states. The central tenet of fisheries management is that a reduction in fishing mortality will lead to an increase in the abundance and biomass of the stock in question, but the present work provides a further example of how more complex ecosystem dynamics can mean that this is not always the case. Cod in the Northwest Atlantic is an infamous example of several collapsed fish stocks which have struggled to recover following closure of the targeted fishery[13,46,47]. In the case of Georges Bank, on the north eastern seaboard of the USA, managers attempted to recover cod by introducing area closures to protect cod spawning[13]. However, an unexpected consequence of this approach was the 14-fold increase in scallop biomass, which now supports one of the most valuable fisheries in the world (>$570 million in 2019)[13,48]. Another example of the unexpected consequences of good-intentioned management is seen in the rebuilding plan for Northern hake[49], which implemented significant reductions in fishing pressure, resulting in a huge increase in hake biomass. This caused a problematic situation to emerge as the stock massively expanded its range into unexpected areas, such as the North Sea, with low historical quotas for hake, set when the species was significantly less abundant. Huge quantities of hake discards ensued, with the potential for hake to act as a choke species in the mixed demersal fishery in the face of the European discard ban[10].

Environmental factors can also drive ecological processes which may result in significant changes to an ecosystem or fish stock, even in the absence of a change in management strategy. An important example of this is the recent explosion in biomass of the pelagic squat lobster or 'munida', in the waters off Peru[12]. Recent expansion of the cold-water range[50] of munida has led to a significant spatial and niche overlap with anchoveta (*Engraulis ringens)*, which supports the world's largest mono-specific fishery. The emergence of munida as a novel competitor of anchoveta may have implications for the future trajectory of the stock[12]. While the biomass of both species has been increasing since the 1990s[12,51], if the recent trend of high productivity is reversed, negative competitive interactions may have adverse effects on one or both populations, and in turn the associated anchoveta fishery.

It is important, therefore, that similar ecological interactions be considered when planning management interventions or forecasting the population trajectories of depleted or recovering stocks, where possible. Additionally, relying on fishery catch data as an indicator of the current state of a wider ecosystem, may lead to an inaccurate perspective over the health or function of an exploited ecosystem. As part of the present study, for example, as well as high forage fish biomass, we estimated significant quantities of euphausiids (primarily *Meganyctiphanes norvegica*) (Figure 1D), and detected relatively high concentrations of harbour porpoises (*Phocoena phocoena),* in all years[16]. This further debunks the 'ecological meltdown'[5] touted to have occurred in this region, and suggests that the pelagic ecosystem, with large biomass present across various trophic levels and functional groups, is in better health than previously suggested.

The resurgence of the pelagic ecosystem in this area over the last 30 years, and particularly the substantial increase in sprat biomass reported here, affords management options for the future of this region. One obvious option[33] is the establishment of a fishery for sprat in the Clyde, although the distributional overlap with juvenile herring is an issue which has precluded sprat fisheries in eastern Scotland. The increased forage fish biomass may have additional significant consequences for other components of the ecosystem, however, potentially creating the opportunity for an alternative livelihood for the local seafaring community. These forage fish comprise a large proportion of the diet of a wide range of charismatic megafauna[52–58] (e.g. marine mammals and seabirds), and the large biomass now present in the Clyde presents a significant food source which will attract these predators to this area. Indeed, as far back as the 19th century, accounts were written of the many cetaceans and seabirds which preyed on the Clyde's famous herring stocks[59]. However, while high densities of harbour porpoises[15,16] have been recorded in the area recently, other cetacean species have not been seen frequently for some time[60]. The recovery of forage fish in the area may now, however, precipitate the return of more of these charismatic species, which people will pay to see, paving the way for the development of a new industry for the region's seafaring community – ecotourism. One management option, therefore, is that the large biomass of sprat now found in the area be left unexploited, such that in time, the ecotourism industry could develop. Ecotourism can be to the detriment of the animals on which it relies[61–65], however, and so the implications of additional stressors on recovering megafaunal populations must be carefully considered. Any new development should, therefore, be in accordance with current industry best-practice guidance to ensure the economic benefits come at minimal cost to the animals the industry is built on[66–68]. This option would contribute to the ongoing recovery of the ecosystem, reversing the decline in biodiversity that the region has endured for over two centuries, paving the way for other systems to follow suit.

## Author contributions

J.L. wrote the main text, processed and analysed the acoustic data, and assisted with data collection. P.F. conceived the manuscript, wrote the summary, provided guidance on data processing and analysis, and edited the many versions of the manuscript.

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## Declaration of interests

The authors declare no competing interests.

<u>Main text figures</u>

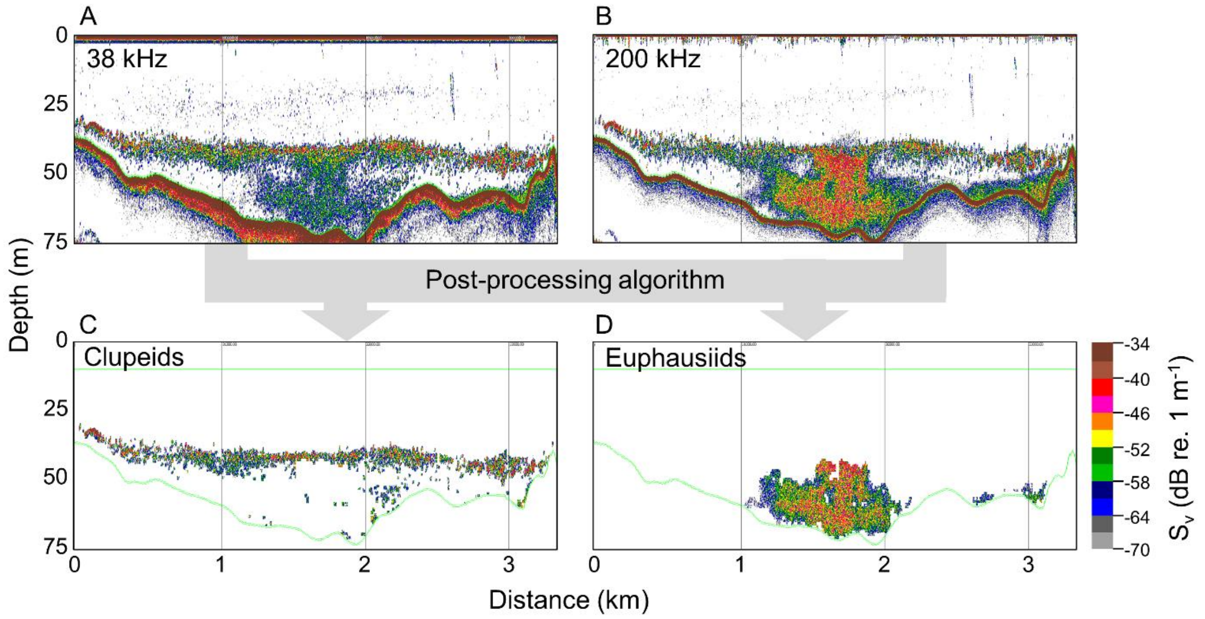

**Figure 1. Differentiating clupeid and euphausiid aggregations from raw acoustic data.**

*Figure 1. Raw (A,B) and processed (C,D) acoustic data, from the Clyde Sea taken in November 2014. Schematic demonstrates the application of a post-processing algorithm to raw data (volume backscattering strengths,* $S_v$*) collected at A) 38 kHz and B) 200 kHz, to distinguish backscatter from C) clupeid fish schools and D) euphausiid aggregations. The green lines on the lower plots are the seabed (with a 0.5 m offset) and a 10 m offset from the sea surface; only data between these two lines were used.*

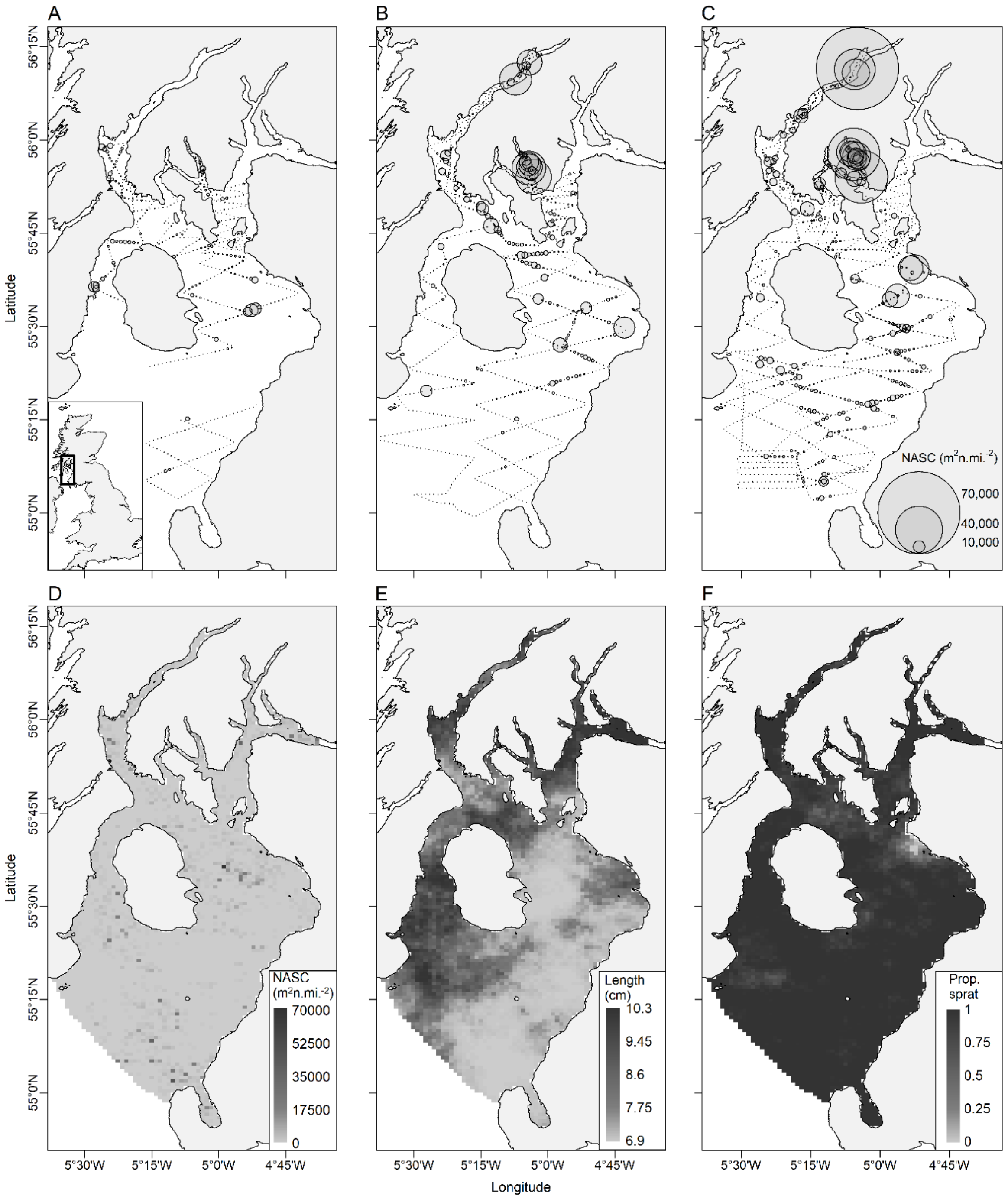

**Figure 2. Fish acoustic backscatter and example geostatistical simulations.**

*Figure 2. Maps of the Clyde Sea, showing integrated backscatter from clupeid fish schools in (A) 2014, (B) 2015 and (C) 2016, and a single realisation of the geostatistical simulations of (D) acoustic backscatter from clupeids, (E) sprat lengths and (F) proportion of backscatter attributable to sprat (all from 2016). Grey circle diameter in (A-C) is proportional to Nautical Area Scattering Coefficients (NASCs, m$^2$n.mi.$^{-2}$) for 1 km sampling units. Inset in (A) shows study area location in the UK (black rectangle).*

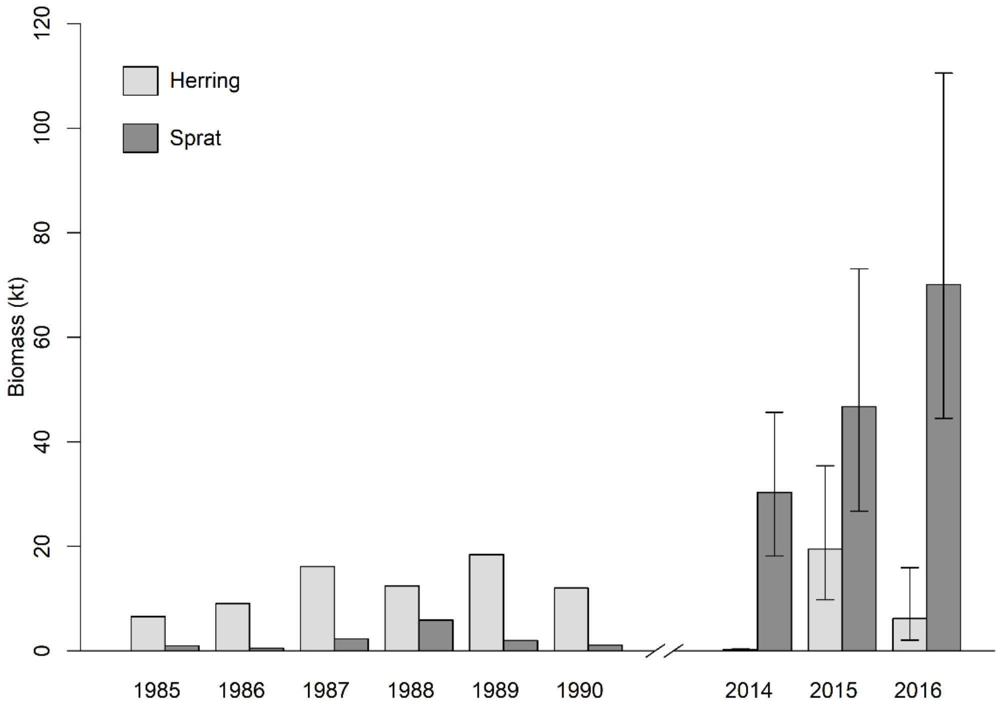

**Figure 3. Herring and sprat biomass estimate time series.**

*Figure 3. Biomass estimates for herring and sprat in the Clyde Sea in the historical surveys (1985-1990) and the present study (2014-2016). Error bars on the recent estimates are 95% confidence intervals, derived from the $10^6$ realisations of biomass produced through the geostatistical simulation procedure. Note, the 2014 herring estimate & confidence intervals are indistinguishable due to their extreme low values.*

## STAR Methods

## Resource availability

**Lead Contact:**

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Joshua Lawrence (joshua.lawrence1@abdn.ac.uk).

**Materials availability:**

This study did not generate new unique reagents.

**Data and code availability:**

All data (integrated acoustic data, mean fish lengths and species proportions) and R code to replicate these analyses are available at:

https://github.com/joshua-lawrence1/CurrentBiology_Lawrence_Fernandes2021.git

## Experimental model and subject details

We collected acoustic data in the Clyde Sea, Scotland, as part of the Scottish Government's series of acoustic surveys in this area. Biological samples from significant aggregations identified from the acoustic data, were collected using a pelagic trawl. These samples consisted almost entirely (>99% by number) of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*).

## Method details

Data collection was carried out aboard the *MRV Alba na Mara*, the Scottish government's inshore research vessel, in the Clyde Sea and surrounding sea lochs. The surveys were conducted in three consecutive years, utilizing the same data collection techniques in each year; the surveyed periods were 5th – 12th November 2014, 26th October – 2nd November 2015 and 15th – 26th October 2016, and data were collected only during daylight hours (approx. 07:00 – 17:00). The survey was scheduled in autumn following a consultation with local fishermen indicating this was the best time of year to catch herring, the primary focus of the survey series. A systematic zig-zag survey pattern was used due to the confined nature of the northern part of the survey region, and surveying was carried out at a steady speed of 7.5 knots ( ~3.9 $m.s^{-1}$). 541, 891, and 1,331 km of survey transect was carried out in 2014, 2015 and 2016, respectively, in an area of 3,600 $km^2$.

A Simrad EK60 scientific echosounder collected active acoustic data, with three split-beam transducers operating at 38, 120 and 200 kHz. The echosounder was configured to transmit at all frequencies simultaneously at a rate of 1 Hz, with a pulse duration of 1.024 ms. The raw data were recorded as time-stamped digitized volume backscattering strengths (VBS, $S_v$; dB re. 1 $m^{-1}$), saved as *.raw files along with detected bottom depth and the vessel's GPS location for each ping. Surveying was interrupted to carry out sampling with pelagic trawls on any significant echotraces detected (Figure S1), to provide information on species composition and fish size distribution data, in accordance with standard fisheries acoustic survey protocols[69]. 5, 9 and 19 trawls were completed in the 2014, 2015 and 2016 surveys, respectively. The echosounder was calibrated using standard techniques[70] at anchor in Lamlash Bay on the 29th October 2015, and the 20th October 2016. Poor weather prevented a calibration in 2014, but the 2015 and 2016 calibrations showed the equipment to be relatively stable (a difference of just 0.2dB gain for the 120 kHz transducer). During these calibrations, a 38.1 mm diameter tungsten-carbide sphere was suspended beneath each transducer to calibrate the on-axis gains ($G_0$), filter attenuation correction factors ($s_a$ correction), and beam patterns for each transducer.

Active acoustic data were processed with the software Echoview v5.4[71]. Algorithms were developed for the isolation of echotraces from schools of swim-bladdered fish and aggregations of macrozooplankton from 38, 120 and 200 kHz data. Standard active acoustic data processing steps (bottom line correction and removal of off-transect data) were carried out prior to the implementation of the fish and macrozooplankton isolation algorithms.

Swim-bladdered fish, as geometric scatters, are readily distinguishable from other targets encountered, scattering sound strongly and relatively equally at the 3 frequencies used. To isolate backscatter from swim-bladdered fish schools, a modification of the workflow described by Fernandes[26] was used. The echograms at all three frequencies were summed, and a -180 dB threshold was applied to the resulting echogram. This is an adjustment of the -226 dB threshold used by Fernandes[26], to account for the use of just 3 frequencies.  A 3x3 pixel median filter was then applied to remove isolated scatters, followed by a 5x5 pixel dilation filter to ensure the edges of fish schools were captured. The Fernandes[26] algorithm was further extended through the addition of a dB-differencing component, which examined the difference between the returns at 38 and 200 kHz, excluding regions where the return at 200 kHz was >2dB stronger than at 38 kHz, to ensure very dense zooplankton aggregations were not included. This was not an issue for Fernandes[26], since such dense zooplankton aggregations were not encountered during their data collection, and the use of the 18 kHz transducer would further reduce the chance of any Rayleigh scatters being mistaken for fish. Echoview's 'school detection' facility was used to delineate regions around all areas of backscatter retained by the algorithm, and the regions were masked onto the raw 120 kHz data (thresholded at -70 dB) to produce the final fish echogram.

Macrozooplankton (here, euphausiids), as Rayleigh scatterers in the frequency range used, scatter sound more strongly as the frequency increases[72]. Consequently, a similar method to that which has been widely used to isolate echoes from other macrozooplankton species (in particular Antarctic krill, *Euphausia superba*) could be used [73–78] to isolate euphausiids, relying upon the dB-difference between the received returns at 38 and 120 kHz. These two echograms were resampled (3 pings x 1 m), and a dB-difference echogram (120-38 kHz) was created. Only regions of scattering where the dB-difference was in the 2-12 dB range [73,75,77,78] which was masked onto the resampled 120 kHz data. A 3x3 median filter was used to remove isolated scatters, and areas identified as backscatter from fish by the fish school algorithm were removed to avoid double-counting. School detection was then carried out to delineate regions around all areas of retained backscatter, and the resulting regions were masked onto the 120 kHz data (thresholded at -100 dB) to produce a final euphausiid echogram.

Both final echograms (for fish and euphausiids) were integrated between 10 m below the surface to 0.5 m above the seabed to give Nautical Area Scattering Coefficients (NASCs, $m^2$ $n.mi.^{-2}$) for 1 km sections of acoustic transect.

A fault with the 38 kHz transducer used during the surveys meant integration of the active acoustic data was carried out on the data from the 120 kHz transducer (as opposed to the more normal 38 kHz). This meant that the published target strength-length (TS-L) relationships (of the form $TS = 20.\log_{10}(L) + b_{20}$) could not be used, as they are frequency-dependent (specifically the $b_{20}$ parameter). Instead, the standard TS-L relationship ($20.\log_{10}(L) - 71.2$) was adjusted using data collected as part of an acoustic survey in the North Sea using data collected from fish schools confirmed as herring via pelagic trawl. The adjustment procedure involved manipulating the $b_{20}$ parameter to optimise the new TS-L relationship to minimise the difference between fish density calculated using the 38 kHz data with the standard TS-L relationship and fish density calculated using the 120 kHz data with the new TS-L relationship. This yielded the relationship $TS = 20.\log_{10}(L) - 71.67$, which was used when calculating fish abundances from fish NASCs. Predictably, there was little difference from the standard relationship, as expected given the geometric scattering of fish at these frequencies.

### Quantification and statistical analyses

To convert from clupeid NASC to species specific biomass, knowledge of the proportion of acoustic backscatter attributable to each species is required (in addition to the length-frequency distribution for calculation of TS). For each trawl, these proportions were calculated as:

$$p_x = \frac{\sum_{j=L_{min}}^{L_{max}} n_{xj}\,.\sigma_{bs_j}}{\sum_{i=1}^{s}\sum_{j=L_{min}}^{L_{max}} n_{ij}\,.\sigma_{bs_j}} \qquad \text{(Equation 1)}$$

where $p_x$ is the proportion of acoustic backscatter attributable for species of interest $x$, $s$ is the number of species caught, $n_{ij}$ is the number of fish caught of species $i$ in length-class $j$¸ $L_{max}$ and $L_{min}$ are the maximum and minimum length-classes caught, and $\sigma_{bs_j}$ is the backscattering cross-section of the length-class $j$, calculated as:

$$\sigma_{bs_j} = 10^{\frac{20.\log_{10} L_j - 71.67}{10}} \qquad \text{(Equation 2)}$$

where $L_j$ is the midpoint (cm) of length-class $j$. Here, the proportion of sprat was calculated for each haul, and the proportion of herring (as the only other species caught) was the remainder.

In order to estimate the uncertainty around biomass estimates produced from several variables (in this case: acoustic data, fish lengths and species proportions), geostatistical simulations of each variable were generated and combined so that their associated uncertainties could be propagated through to the final estimates. This process was carried out using the *RGeostats* package for the statistical software R.

For the conditional simulations to be reliable, it is necessary that the data are approximately Gaussian, cf. the highly positively skewed distribution of the raw data, and so a transformation is required[29,79]. A Gaussian anamorphosis was used to transform the raw variables to approximately normal, and a Gibbs sampler was used to redistribute the excess zeroes into the left-hand tail of the distribution[29,80]. Conditional simulations were produced using the transformed data and the variogram models created from each dataset, generating simulated values for each variable across a 1 x 1 km grid covering the entire survey region (3710 km$^2$).

To produce fish biomass estimates, 100 simulations of acoustic backscatter, fish length (by species), and species proportion were generated and combined to give 1,000,000 realisations of fish abundance, as:

$$N_{ij} = \frac{s_{A_i}.p_{ij}}{4\pi.1.852^2.\sigma_{bs_{ij}}}.A_i \qquad \text{(Equation 3)}$$

where $N_{ij}$ is the abundance of species $j$ in grid square $i$, $s_{A_i}$ is simulated acoustic backscatter (NASC) from clupeids in grid square $i$, $p_{ij}$ is the simulated proportion of acoustic backscatter attributable to species $j$ in grid square $i$, $A_i$ is the area of grid square $i$ (for most grid squares this was 1 km$^2$, but <1 where the grid meets the coast) and $\sigma_{bs_{ij}}$ is the backscattering cross-section for the simulated mean length for species *j* in grid square *i*, calculated as in equation 2. Fish abundances were converted to biomass according to weight-length relationships of the form

$$B_{ij} = N_{ij}.\left(a.{L_{ij}}^{b}\right) \qquad \text{(Equation 4)}$$

where $B_{ij}$ is the biomass (g) of species *j* in grid square *i*, and the parameters *a* and *b* were derived from catch data and were year- and species-specific.

500 simulations of acoustic backscatter from euphausiids were generated using the same methods, and were converted to biomass using a TS-biomass relationship, (TS of 1 kg of euphausiids (or krill) = -38.77 dB[75]), such that

$$B_{ij} = \frac{s_{A_i}}{4\pi.1.852^2.10^{\frac{-38.77}{10}}}.A_i \qquad \text{(Equation 5)}$$

where $B_i$ is the biomass (kg) of euphausiids in grid square *i*, $s_{A_i}$ is simulated acoustic backscatter (NASC) from euphausiids in grid square *i*, and $A_i$ is the area of grid square *i*.

Biomass estimates were summed across the simulation grid to give total biomass for each realisation, and mean and 95% confidence limits (as the 2.5th and 97.5th percentile when estimates were sorted in ascending order) were calculated for each species (herring, sprat and euphausiids) for each year, as given in the Results.

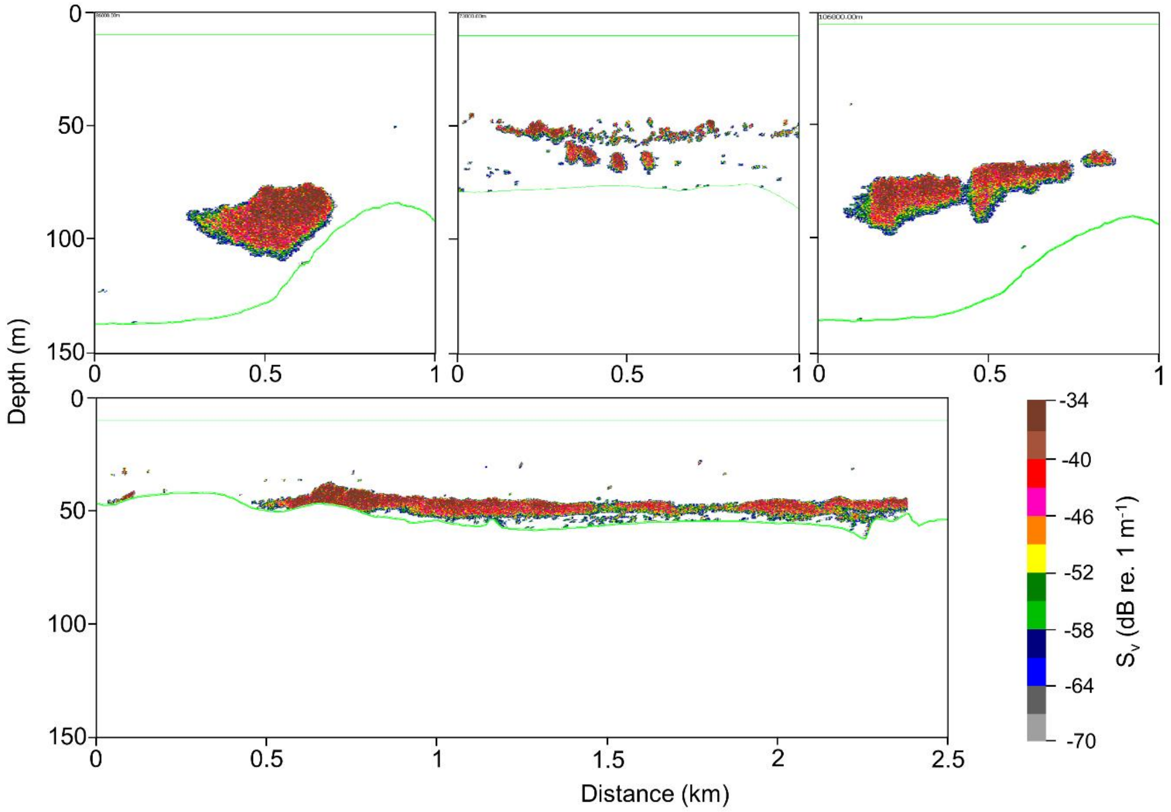

**Figure S1. Example echograms of large fish schools.**

*Figure S1. Echograms of a range of examples of significant acoustic targets which were subject to trawling for the collection of biological samples. These echograms have been post-processed to remove the near-field and the seabed (upper and lower green lines, respectively) and to isolate backscatter from swim-bladdered fish. All echograms show data collected at 120 kHz.*

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