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RESEARCH ARTICLE

The sound of resilience? Exploring trophic cascades and positive feedbacks between cod and eelgrass in a trawl-free ecosystem

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Abstract This study examines The Sound, a strait between Denmark and Sweden protected by a trawl ban since 1932. Consistent with previous research, we show that the area supports greater densities, sizes, and landings of Atlantic cod (*Gadus morhua*) than adjacent trawled waters. Simulations from a bespoke food web model indicate that predation from the cod can suppress mesopredators, thus reducing filamentous algal growth through a trophic cascade, which benefits eelgrass (*Zostera marina*). In line with this, monitoring data show lower mesopredator densities and more extensive eelgrass meadows in The Sound compared with nearby trawled areas, although salinity and hydrodynamic conditions could also contribute. However, despite the trawl ban, adult cod densities are currently at their lowest levels since monitoring started, raising concerns about the ecosystem's long-term resilience. Model results further demonstrate how preserving eelgrass meadows benefits cod, illustrating feedback mechanisms that highlight the importance of integrated fisheries and conservation management.

Keywords Coastal food webs · Ecosystem modelling · Food web simulations · Gear restrictions · Seagrass · Trophic cascade

INTRODUCTION

In the face of growing anthropogenic pressure, many species are facing population declines and range contractions, and biodiversity is becoming increasingly eroded (IPBES 2019). In response, several ambitious international initiatives have been launched, including the global target of the Kunming–Montreal Global Biodiversity Framework and the European Nature Restoration Law (EU/2024/1991). Together, these initiatives call for protecting at least 30 per cent of land and sea areas by 2030, and for restoring 30 per cent of degraded habitats. Of the protected areas, one third should have strict protection, meaning that they exclude all destructive human activities. While these areal targets represent crucial political commitments, their measure of success ultimately lies in the achieved outcomes in terms of recovery of ecosystem functioning and resilience, which requires effective, targeted measures rather than undirected, blanket protection (Arneth et al. 2023). Certain species and functional groups play disproportionately large roles in maintaining these ecosystem functions. For example, keystone predators regulate community composition by top-down control and foundation species provide critical habitats for other species (Paine 1969; Dayton 1972). Hence, focusing conservation and restoration efforts on such species can yield disproportional benefits and may also enhance possibilities for sustainable coexistence with human activities, such as fishing (Gurney et al. 2021).

One rare example of such a well-functioning ecosystem coexisting with intensive human activity is The Sound, a strait in the transition zone between the brackish Baltic Sea and the North Sea, bordered by Denmark and Sweden. Despite being situated in a densely populated region with extensive shipping, sand mining, wind power, and tourism

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(Berglund et al. 2018), this area has sustained a population of Atlantic cod (*Gadus morhua*) with significantly higher densities and a healthier age and size structure compared to neighbouring sea basins (Svedäng 2010; Sundelöf et al. 2013; Svedäng and Hornborg 2017), where cod stocks are heavily depleted (ICES 2023, 2024a). It also harbours extensive eelgrass (*Zostera marina*) meadows (Berglund et al. 2018), in contrast to widespread declines in adjacent regions (Moksnes and Bergström 2025).

Cod and eelgrass in The Sound likely benefit from inherently good physical and ecological conditions, where strong currents can both support productivity and prevent the accumulation of organic materials on eelgrass meadows (van Deurs et al. 2016; Timmermann et al. 2023), the latter a mechanism that can otherwise suffocate eelgrass under enhanced nutrient conditions (Baden et al. 2003). However, the good status of cod and eelgrass in The Sound has also been ascribed to a long-standing trawl ban (Lindegren et al. 2010; Svedäng 2010; Krause-Jensen et al. 2021). This was introduced in 1932 for maritime safety reasons (Anonymous 1932), and prohibits all towed fishing gear in The Sound, except for in a wedge in the north covering 1.6% of the area. Partial regulations on seine fishing in The Sound were introduced already in the early 1900s (Ravanis et al. 2021). The fishery has instead been dominated by commercial gillnetting and recreational fishing with hand-held gear (Berglund et al. 2018). Both these methods are more selective than trawling, this limiting bycatches of undersized fish and leaving a greater proportion of large cod (Lindegren et al. 2013), although the fishery still selectively targets larger individuals (Sande et al. 2025). Furthermore, unlike bottom-trawling, this type of fishery does not have any destructive impact on the seabed (Pitcher et al. 2022), which is likely to result in more productive feeding habitat for the cod. The absence of trawling may also benefit eelgrass by minimising sediment resuspension and mechanical disturbance (Krause-Jensen et al. 2021).

In addition, eelgrass in The Sound may also benefit indirectly from the trawl ban through top-down control exerted by the cod. Studies from nearby areas (the Kattegat and Skagerrak, north of The Sound) that have historically been more heavily fished, suggest that cod in sufficient densities can suppress the abundance of coastal mesopredators, such as gobies, wrasses, sticklebacks and shore crab (*Carcinus maenas*), thereby reducing predation pressure on the prey of mesopredators, like idoteids, gammarids, amphipods and snails (Moksnes et al. 2008; Baden et al. 2010, 2012; Eriksson et al. 2011). This allows for higher grazing rates on filamentous algae, preventing algal overgrowth, which otherwise can have large negative impacts on eelgrass (Baden et al. 2003). In the Kattegat, a collapse of the cod stock due to overfishing (Cardinale and Svedäng 2004) has been suggested as a major driver of a large-scale decline of eelgrass, together with eutrophication, as both these mechanisms promote the growth of filamentous algae (Moksnes et al. 2008; Baden et al. 2012). Meta-analyses suggest that these two mechanisms—top-down and bottom-up control—have effects of similar magnitudes (Burkepile and Hay 2006; Östman et al. 2016). As The Sound is similarly affected by eutrophication, top-down control exerted by cod could thus be key to the maintenance of extensive eelgrass meadows in the area, although this has not been explicitly investigated. At the same time, the eelgrass meadows provide nursery and feeding grounds for cod (Pihl et al. 2006; Lilley and Unsworth 2014), which could boost cod recruitment, resulting in a positive feedback loop (Warren et al. 2010; Dunlop et al. 2022).

The Sound may thus provide an interesting case where the coexistence of human activities and a healthy ecosystem is enabled by the exclusion of trawling, which globally has large negative impacts on aquatic environments (Pitcher et al. 2022). This is likely to have resulted in preserved ecosystem functioning, supporting important ecosystem services. For cod, these include both its regulating role in the ecosystem, as described above, and its contribution to thriving small-scale commercial and recreational fisheries (Jervelund et al. 2018), while eelgrass meadows contribute to carbon sequestration, erosion protection and nutrient retention, and provide habitat for numerous fish and invertebrate species (Cole and Moksnes 2016).

In recent years, however, there have been mixed reports regarding the state of cod in The Sound. The poor status of the Western Baltic cod stock, which includes The Sound (together with the Arkona Sea and the Belt Sea; Fig. 1), has prompted frequent adjustments to fisheries regulations, including changes in allowable sizes and seasonal restrictions (ICES 2023) and a complete ban on all targeted fishing since 2024, with the exception of a small bycatch quota for the commercial fishery (EU Regulation 2024/0213). Yet, as the cod in The Sound appears at least partly isolated from the rest of the stock (Lundgreen et al. 2023), it is uncertain to what extent these alarming reports also reflect the state of cod in this sub-area. Recent reports of declines in size and condition (Sande et al. 2025), and diminishing catches prior to the complete ban on targeted fishing (Jervelund et al. 2018), suggest that there may be an ongoing shift in the population in The Sound too.

In this study, we assess the current state of cod in The Sound relative to adjacent, trawled areas, namely the Kattegat, the Belt Sea, and the Arkona Sea (Fig. 1) by comparing time series of densities, size structure and fisheries landings. We complement this with monitoring data on mesopredators and eelgrass from The Sound as well as the Kattegat, an area where the local cod stock is

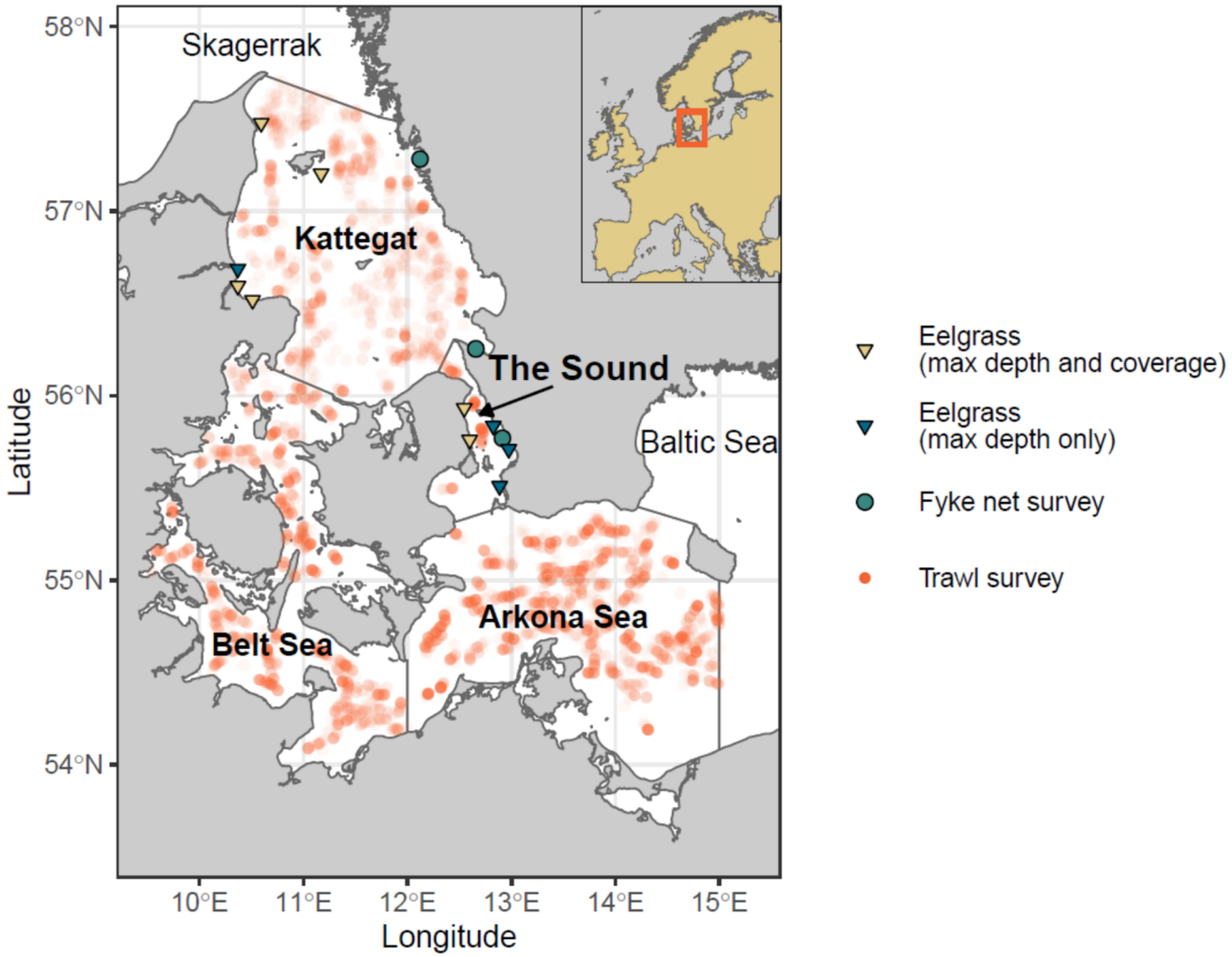

Fig. 1 Location of The Sound (ICES subdivision 23) and the study's reference areas the Kattegat (subdivision 21), the Belt Sea (subdivision 22) and the Arkona Sea (subdivision 24). Lines show ICES subdivisions. The cod in The Sound, the Belt Sea and the Arkona Sea together make up the Western Baltic cod stock, while the Kattegat stock is managed separately, though mixing likely occurs (Lundgreen et al. 2023). Symbols show the sites for eelgrass monitoring, fyke net surveys used for estimating mesopredator densities and trawl surveys used to estimate cod densities and size structure. The inset shows the location of the study area within northern Europe

severely depleted (ICES 2024a), to evaluate whether differences in cod densities correspond to contrasting trophic structures. In line with the trophic cascade described above, we expect that The Sound will host lower mesopredator densities and more extensive eelgrass meadows (unfortunately, intermediate trophic levels are not consistently monitored). To assess the potential strength of top-down control exerted by cod on lower trophic levels, we develop a locally parameterised food web model and use it to evaluate potential cascading effects of increased cod mortality rates. We also simulate the impact of changes in the amount of available eelgrass habitat and the destruction rate of eelgrass on other parts of the system. This allows us to compare bottom-up and top-down effects and evaluate the impact of conservation and restoration measures targeting cod and eelgrass, respectively.

MATERIALS AND METHODS

Time series of cod, mesopredators and eelgrass

Cod densities and size

To compare trends in cod densities and size structure between areas, we analysed data from the Baltic International Trawl Survey (BITS), which has followed a standardised protocol since 2001. Surveys using TV-3 bottom trawls with 30-min tows are conducted in February–March (Quarter 1), which overlaps with the spawning season when the cod resides in deeper water, and in October–November (Quarter 4), when the cod occupy more shallow waters (see Funk et al. 2020). Data were available as standardised catch per unit effort (CPUE; individuals

caught per hour) per length class and ICES subdivision (SD) calculated using depth-weighted means, with conversion factors applied to make hauls using smaller and larger trawls comparable. The data were downloaded from datras.ices.dk [2025-04-16].

For the analyses, we excluded data points based on fewer than three hauls (only affecting The Sound; see Table S5; resulting in N_{Sound} = 95 and 84, N_{Kattegat} = 598 and 577, $N_{\text{Belt Sea}}$ = 835 and 766, $N_{\text{Arkona Sea}}$ = 1231 and 1113 for Quarter 1 and 4, respectively). We converted the CPUE data to biomass per unit effort (BPUE) using a length–weight relationship for Western Baltic cod from the R-package *rfishbase* (Boettiger et al. 2012). We analysed three metrics: BPUE of juveniles ($\leq$ 25 cm), BPUE of adults ($>$ 25 cm) and the 95th percentile of the total length (L_{95}). 25 cm is broadly representative of the length at which 50% have reached maturation in recent years in The Sound (Sande et al. 2025). To test for differences between SDs, we fitted generalised linear mixed models using the R-package glmmTMB (Brooks et al. 2017), with SD as a factor and year as a random effect. For the BPUE models we assumed a negative binomial distribution where variance increases quadratically, and for the L_{95} model a gamma distribution. Since there were signs of heteroscedasticity, dispersion was allowed to vary between SDs. We used the R-package DHARMa (Hartig 2022) to assess model fit, both here and for models described below.

Cod landings

To compare commercial landings between areas, we used data from ICES (2023), covering 1965–2023. To enable comparisons across areas, we divided the landings in each SD by its fishable area (depth $>$ 3 m; Funk et al. 2021). For Denmark, we also used reported landings available since 1888 for The Sound and the Kattegat, based on annual fishery reports up until 1977 and later on data collected by the Danish Fisheries Agency (see Thomassen et al. 2024). These were also standardised by fishable area.

Danish recreational catches were available as estimates based on online surveys of licensed anglers and recreational fishers using passive gear (response rate around 30–45%) (ICES 2019). For the Western Baltic, these estimates are corrected based on results from on-site surveys on tour boats in The Sound, while this is not done for the Kattegat. Furthermore, the Western Baltic estimates include both kept and released cod, assuming an 11.2% post-release mortality, while Kattegat estimates only include kept cod. Data were available for all areas from 2010 to 2023. Swedish recreational catches are estimated from a questionnaire targeting Swedish residents aged 16–80 (SCB 2024), with data available for the Kattegat, The Sound and SD 24–25 (the Arkona Sea plus parts of the south-eastern Swedish coastline). Here, we used estimates pooled across 2014–2023 due to low numbers of responses per year (total N_{Sound} = 199, N_{Kattegat} = 93, $N_{\text{SD 24–25}}$ = 38). To account for the fact that the areas differ in size, we standardised catches in relation to coastline length for each SD. As recreational catch estimates are uncertain, we focus on relative cross-area comparisons rather than absolute values.

The data on commercial and recreational landings were used to describe human use of cod as a resource, noting that changes over time are not only linked to the state of the cod stock, but also, for example, to fishing regulations and technological advancements.

Mesopredator densities

For mesopredators, we used fyke net survey data from the Swedish programme for coastal fish monitoring (Leonardsson et al. 2016), downloaded from Swedish University of Agricultural Sciences' database (KUL 2025) on 2025-07-15. This programme uses standardised fyke nets (55 cm high, with semi-circular opening, and a mesh size of 11 mm bar length in the cod-end), which are deployed at dusk and emptied the next day. Data were available from 2002 from one location in The Sound (split into 6 sub-locations) and two locations in the Kattegat, in some cases covering both a warmer (April) and a colder (October or April) season (see Table S6 for details). To make sure data were comparable across years and locations, we only included data from stations between 1.5 and 5.6 m depth and from the first night of fishing for each station. As there was a substantial revision in the stations fished in 2021, we restricted our statistical comparison (see below) to data from up until 2020. From the catches of the fyke-net surveys, we focused on goldsinny wrasse (*Ctenolabrus rupestris*), black goby (*Gobius niger*), and shore crab (*Carcinus maenas*) (Moksnes et al. 2008; Eriksson et al. 2011; Baden et al. 2012). Two-spotted gobies (*Gobius flavescens*) and three-spined stickleback (*Gasterosteus aculeatus*) are also important mesopredators in this ecosystem but were excluded due to low catch rates in the applied gear.

We assessed differences between The Sound and the Kattegat using generalised additive mixed models fitted with the R-package mgcv (Wood 2017) with SD as a factor, and CPUE (individuals per paired fyke net) as a response variable, assuming a negative binomial distribution ($N_{\text{The Sound}}$ = 429, N_{Kattegat} = 1852; Table S7). As temperature affects catchability, and as several of these species show seasonal patterns in activity and habitat use (Pihl and Rosenberg 1982), we included temperature as a linear effect and day of the year as a nonlinear effect. Year and location/sub-location were included as random effects.

Eelgrass meadows

For eelgrass, we used available data from standardised long-term monitoring in Sweden and Denmark. In Denmark, eelgrass has been monitored since 1989 as part of the National Monitoring Programme. Transects, all placed where environmental conditions support eelgrass growth, are surveyed using videos recorded from a boat-towed sled, and sometimes by diving or wading (Bruhn et al. 2022). Data were downloaded from kemidata.miljoeportal.dk [2000–2022 on 2023-03-22; 2023–2024 on 2025-05-22]. We used two types of data: (1) maximum depth of the main eelgrass meadow (> 10% coverage), and (2) point estimates of eelgrass coverage along transects (i.e. the percentage coverage of eelgrass in sampled squares along the transect). To make the data as comparable as possible across The Sound and the Kattegat, we excluded data from fjords and enclosed bays, which are only found in the Kattegat and are less hydrodynamically active, which may affect habitat conditions for the eelgrass as well as epiphytic growth. Hence, for both areas, we only include data from open coastal stretches. We only included data collected from year 2000 onwards and from areas monitored $\geq$ 10 times over a 15-year period. On the Swedish side of The Sound, eelgrass is monitored by divers, with comparable data from three stations available for 2003–2020 (Lundgren and Ljungdahl 2020). The maximum depth of eelgrass meadows with > 10% coverage has been recorded as in Denmark. Eelgrass coverage is also recorded, but the methods used are not comparable across nations. Therefore, we included both Swedish and Danish data on maximum eelgrass depth in our analyses, but only used the Danish data for our analyses on eelgrass coverage.

For the analyses, we first compared the maximum depth of the eelgrass between The Sound (data from Denmark and Sweden, N = 209 transects) and the Kattegat (Denmark only, N = 221 transects). Second, we compared eelgrass coverage between The Sound (2917 point estimates) and the Kattegat (9376 point estimates) using the Danish monitoring data. For comparability between areas, we only included data collected at 1–6 m from transects where the maximum sampled depth was $\geq$ 6 m. Differences between The Sound and the Kattegat were tested using generalised linear mixed models with glmmTMB. Eelgrass depth was modelled with a normal distribution, using SD and water body (as defined within the EU Water Framework Directive; for Sweden we used the three sampling sites) as fixed effects, transect as a random effect, and varying dispersion by water body. Coverage was fitted assuming a zero-inflated beta distribution, using SD and depth as predictors, with transect and a nested transect: year effect as random effects, to account for transects comprising a large and variable number of point estimates. In the model, the zero-inflated part models the probability of transect points containing eelgrass, whereas the beta part models the proportional bottom coverage of eelgrass in the sampling square, provided that the transect point contains eelgrass. This thus gives two ways to look at changes in coverage given available data. The water body effect was necessary to achieve a good fit in the depth model, but not in the coverage model.

Food web model

To explore the dynamics of trophic interactions in eelgrass meadows in The Sound, we developed a food web model based on a set of coupled differential equations. The state variables correspond to the abundances of key groups, chosen based on interactions described in Moksnes et al. (2008) and Baden et al. (2012), including adult cod $C_2(t)$ (> 25 cm); juvenile cod $C_1(t)$ ($\leq$ 25 cm); mesopredators (shore crabs, gobiids, stickleback, wrasses) $P(t)$; mesoherbivores (idotheids and gammarids) $H(t)$; eelgrass $E(t)$; and filamentous algae $A(t)$, with t denoting the time scale, set to years. We refer to these groups as 'trophic levels' throughout the text, although we note that eelgrass and algae represent the same trophic level, and that cod is the dominant, but not the only, predatory fish species in The Sound. The unit of all the variables is tonnes km^{-2}, except for eelgrass, which is in km^2 (Table S1). The differential equations all follow the same generic form:

$$\frac{\mathrm{d}J}{\mathrm{d}t} = \underbrace{g_J(t, J; \ldots)}_{\text{increase}} - \underbrace{h_J(t, J; \ldots)}_{\text{decrease}} \quad (1)$$

with $J \geq 0$ for $J \in \{C_2, C_1, P, H, E, A\}$. The equations capture all interactions depicted in Fig. 2, as well as the processes of natural mortality, fishing mortality of cod, competition, cod consumption of herring (*Clupea harengus*), anthropogenic destruction of eelgrass, limitation in the area of suitable eelgrass habitat, and the impact of nutrients on the growth of eelgrass and algae (assuming a constant nutrient concentration representative of the area). Herring was included as an external food source, since it constitutes an important prey item for the cod during its seasonal migration through The Sound (van Deurs et al. 2016). The processes included in the model were chosen to reflect the current state of knowledge regarding key mechanisms, while keeping a reasonable level of model complexity. The full model is described in the SI. For parameterisation, we used ecologically meaningful values for The Sound (Table S1). When such were not available, values were set to be a reasonable order of magnitude in relation to other parameters.

To assess the role of both cod and eelgrass in the ecosystem, several simulations were carried out, initialised

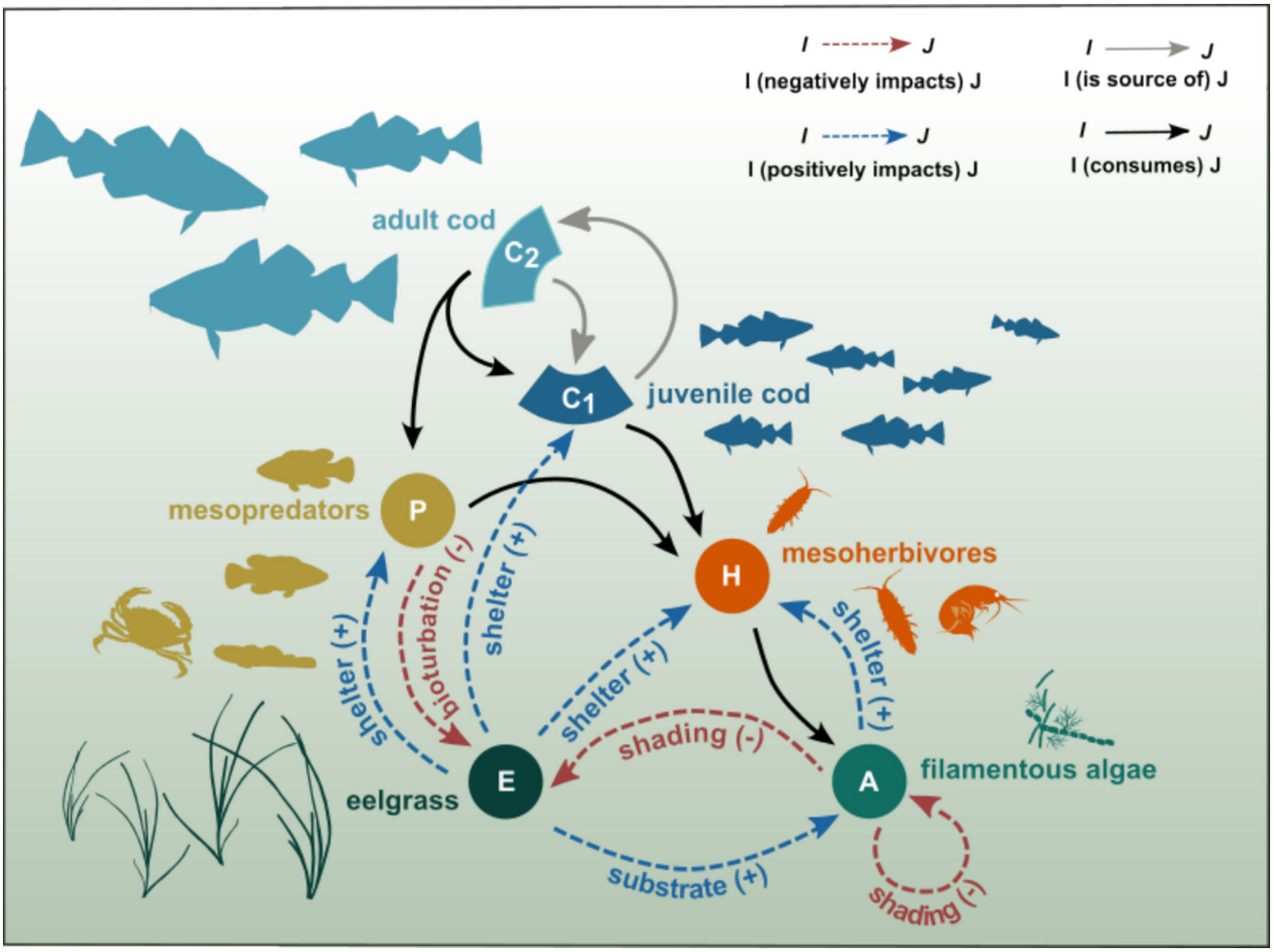

Fig. 2 Illustration of the interactions between trophic levels included in the food web model: adult cod (C2), juvenile cod (C1), mesopredators (P), mesograzers (H), filamentous algae (A), and eelgrass (E). Solid black arrows denote predator–prey (consumptive) interactions, whereas dashed blue and red arrows denote positive and negative non-consumptive interactions, respectively. The full model description and its parameter values are provided in the SI

with values derived from the literature, see Table S1. In the simulations, we varied the natural mortality of juvenile (ν_{C1}) and adult (ν_{C2}) cod, the fishing mortality of adult cod (η_{C2}—the fishing mortality of juveniles η_{C1} was assumed change in proportion based on relative estimated fishing mortalities from the stock assessment, see ICES 2023), the eelgrass destruction rate (η_E), and the area of suitable habitat for eelgrass (ω_E). Fishing mortality of cod was modelled separately from natural mortality to account for fishing mortality being higher for adults than for juveniles, while the opposite is the case for natural mortality. Simulations were carried out as follows:

(1) Two parameters were varied at a time, and simulations ran for 75 years. Areal coverage (eelgrass) and density (all other groups), collectively referred to as "abundances", were averaged over this time period and visualised as phase diagrams. If abundances went below a critical threshold (see Table S4), this average was set to zero. To better understand effects on the full system, we also calculated a structural presence-abundance index (I_{PA}) quantifying the combined presence and abundance of each trophic level (Sect. "Presence-abundance index, I_{PA}" in the SI), and applied this to (i) all trophic levels, and (ii) cod and eelgrass only.
(2) As in (1), but visualised across a single parameter.
(3) Simulations were run until cod abundances reached below a critical threshold (see Table S4), and the effects of fishing mortality and eelgrass destruction rate on the number of years until collapse were explored.
(4) Simulations incorporating environmental stochasticity in the natural mortality rates of cod were performed to evaluate how this affected the impact of different fishing mortality rates and eelgrass destruction rates on the cod (see Sect. "Stochastic

dynamics: simulating the impact of environmental noise in cod natural death rates" in the SI).

(5) To account for uncertainties in parameter values, we performed a sensitivity analysis assessing the robustness of the results from (1) (see Sect. "Sensitivity analysis using Monte Carlo" in the SI).

RESULTS

Time series of cod, mesopredators and eelgrass

Cod densities and size

Based on the fisheries-independent trawl surveys, cod were generally more abundant and larger in The Sound than in the surrounding areas (Fig. 3a–c; Table S8). Specifically, in Quarter 1 (Q1), adult and juvenile BPUEs as well as the 95th percentile of total length (L_{95}) were higher than in all other areas ($p < 0.01$, except for juvenile BPUE in the Arkona Sea where $p = 0.02$). In Quarter 4 (Q4), L_{95} was higher in The Sound than in all other areas ($p < 0.001$), while adult BPUE was higher than in the Kattegat and the Belt Sea ($p < 0.001$), but not than in the Arkona Sea ($p = 0.2$) (Fig. S2; Table S8). Juvenile BPUE in The Sound in Q4 did not differ from the Belt Sea ($p = 0.6$) or the Kattegat ($p = 0.5$) and was lower than in the Arkona Sea ($p < 0.001$).

From ca. 2015, adult cod BPUE increased in The Sound in both Q1 and Q4 (Fig. 3b; Fig. S2). An expansion of the survey design in 2016, with new haul sites added in The Sound, may partially explain this rise for Q4, but not Q1, based on separate analyses excluding the new stations (Fig. S3). Following this increase, BPUE decreased again (Fig. 3b; Fig. S2). In the last data point included, Q1 of 2025, both adult cod BPUE and L_{95} in The Sound were the lowest since the beginning of the time series.

Cod landings

Commercial landings of cod per unit area were largest in the Belt Sea until the mid-1980s, and at similar levels in the other areas (Fig. 3d). However, since the early 1990s, The Sound has had the largest landings per unit area almost every year. Landings in the Kattegat have been low since the early 2000s. The overall trends in landings over time reflect changes in quotas (Fig. S4), which have been close to zero in recent years (ICES 2024a, 2025).

Over a longer time scale, the Danish data starting in 1888 show that landings in the Kattegat increased consistently until a peak in 1974, after which they declined (Fig. 3e). Landings per unit area have consistently been higher in The Sound, except for in the 1960s and the 1970s, when they were more similar.

Recreational catches per km of coastline in Denmark during 2009–2023 were on average 15 times higher in The Sound than in the Kattegat, 25 times higher than in the Belt Sea and 9 times higher than in the Arkona Sea (Fig. 3f). In Sweden, corresponding values during 2014–2023 were on average 16 times higher in The Sound than in the Kattegat, and 49 times higher than in the Arkona Sea (Fig. 3g).

Mesopredator densities

The CPUE of mesopredators was significantly lower in The Sound compared to the Kattegat for shore crab ($p < 0.001$) and goldsinny wrasse ($p = 0.04$), but not for black goby ($p = 0.4$) (Table S9; Fig. 4a). For goldsinny wrasse and shore crab, values were more similar between areas in the later years of the time series.

Eelgrass meadows

The eelgrass extended deeper in The Sound than in the Kattegat ($p < 0.001$) (Fig. 4b). The maximum depth for eelgrass meadows was just above 6 m in The Sound and around 2 or 5 m in the Kattegat, depending on the location. However, higher values (up to 7.5 m) have been noted in the Kattegat in recent years. While the probability of transect points containing eelgrass was higher in The Sound than in the Kattegat, especially for deeper transect points, the bottom coverage of eelgrass when present was similar between areas and may even be higher in the Kattegat in recent years (Fig. 4b; Fig. S7). The probability of a transect point containing eelgrass has declined in the last couple of years in The Sound (Fig. 4b, Fig. S7).

Food web model

In the model simulations, increasing either the natural mortality (v_{C1}, v_{C2}; Fig. 5a) or the fishing mortality of cod η_{C2} (Fig. S15) generally resulted in decreased cod abundances, higher abundances of mesopredators and filamentous algae, and lower abundances of mesoherbivores and eelgrass. These dynamics are associated with reduced top-down control exerted by cod on mesopredators, leading to a cascade that ultimately affects eelgrass. Generally, when cod mortality was low, the modelled ecosystem persisted by means of self-sustained fluctuations (Fig. S9) and the time taken until the simulations resulted in a collapse of cod increased (Fig. S17).

Increasing eelgrass destruction rate η_E or reducing the amount of available area for eelgrass ω_E resulted in scenarios with low abundances of cod and eelgrass and high abundances of mesopredators and algae (Fig. 5b;

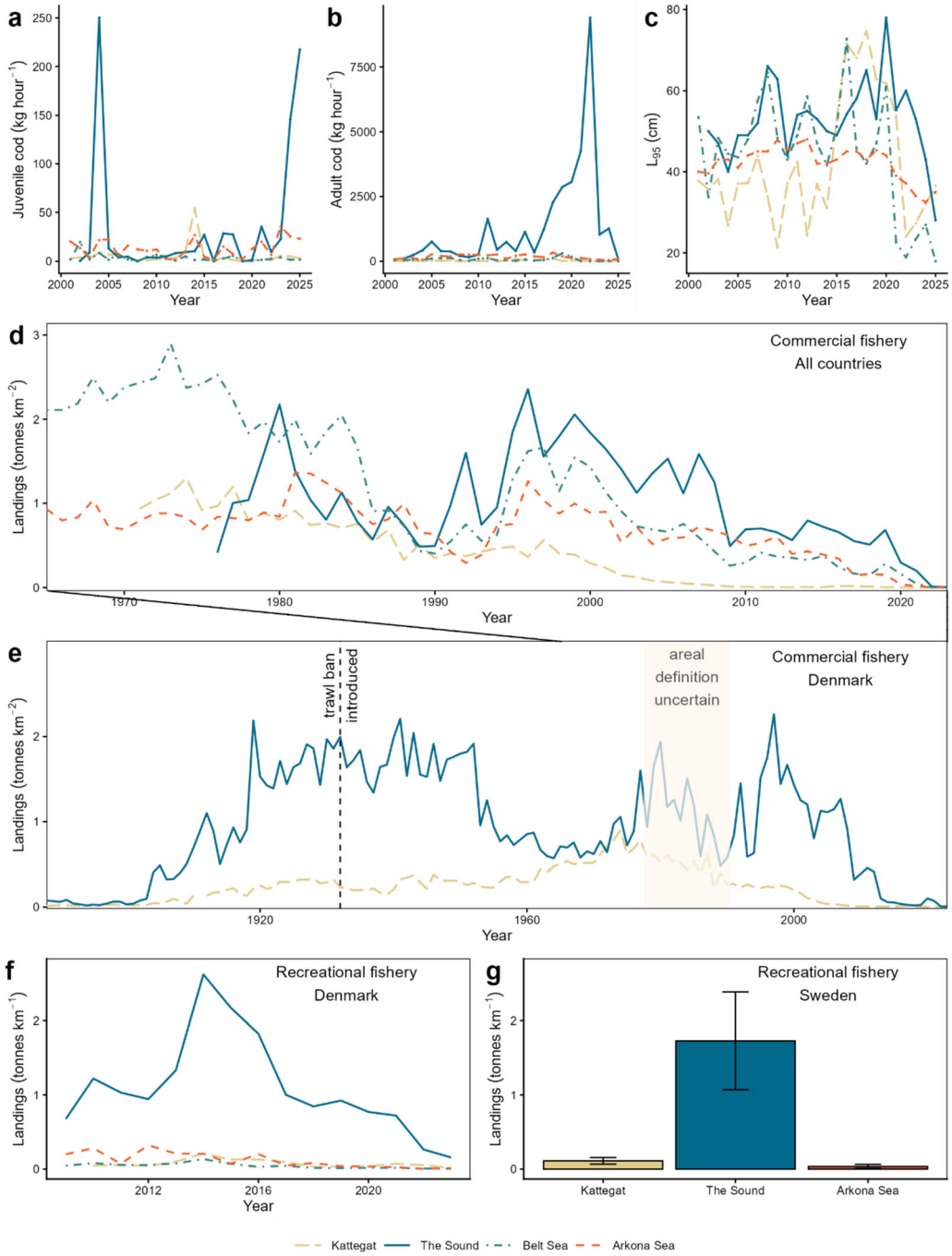

Fig. 3 Time series of cod biomass and size (**a**–**c**), commercial landings (**d**–**e**) and recreational landings (**f**–**g**) in The Sound and adjacent areas. The upper panel shows biomass per unit effort (BPUE; an index of population density) of **a** juvenile ($\leq$ 25 cm) and **b** adult ($>$ 25 cm) cod, and **c** the 95th percentile of total length of cod (L_{95}) based on fisheries-independent trawl surveys in The Sound, the Kattegat, the Belt Sea and the Arkona Sea in Quarter 1. For corresponding plots for Quarter 4 see Fig. S2. Other panels show: **d** Commercial cod landings combined for all countries in tonnes per fishable km^2 ($>$ 3 m depth) in The Sound, the Kattegat, the Belt Sea and the Arkona Sea, see Fig. S4 for corresponding trend in total allowable catches; **e** Danish commercial cod landings in tonnes per fishable km^2 ($>$ 3 m depth) in The Sound and the Kattegat. Note that at some point between 1978 and 1990 (precise year unknown), the spatial definitions used for data reporting were altered for The Sound and the Kattegat (see Fig. 3; Thomassen et al. 2024). When calculating landings per unit fishable area, we used the older spatial definitions for years prior to 1978, the newer ones from 1991 onwards, and an average of the two for the uncertain period. **f** Danish recreational cod landings per km coastline per year in The Sound, the Kattegat, the Belt Sea and the Arkona Sea. **g** Swedish recreational cod landings per km of coastline per year in The Sound, the Kattegat and the Arkona Sea (including also ICES subdivision 25), averaged over the years 2014–2023. Error bars represent 95% confidence intervals

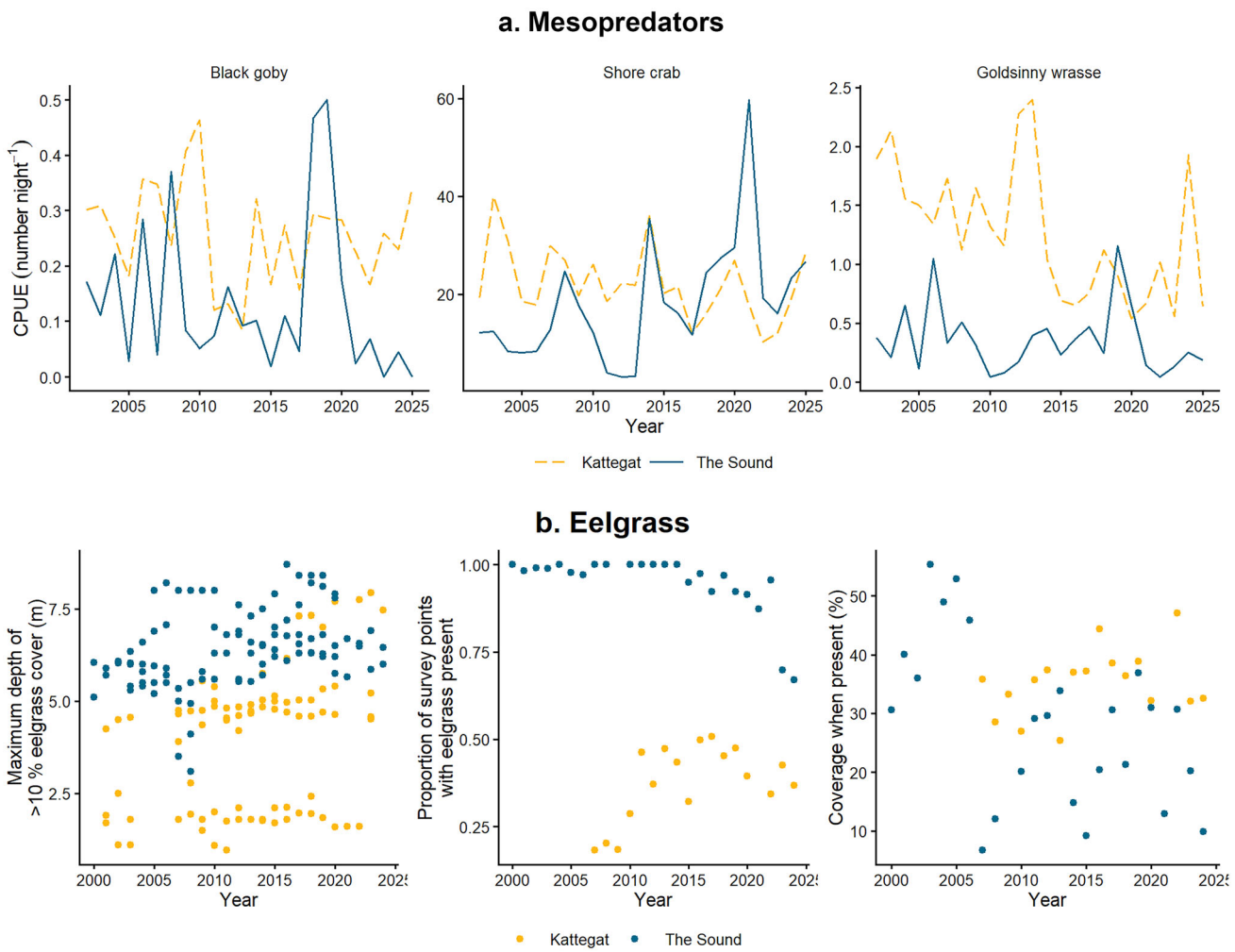

Fig. 4 **a** Yearly average CPUE of black goby, shore crab, and goldsinny wrasse caught with fyke nets along the Swedish coast in The Sound and the Kattegat, respectively. Data are shown for the August sampling period, which is the season when the focal species are expected to be most active (see Fig. S5 for corresponding figures for other sampling periods, note also that the statistical comparison includes data from all seasons). **b** Yearly average maximum depth of eelgrass meadows with coverage > 10%, proportion of survey points with eelgrass present, and eelgrass coverage in survey points when present, in The Sound and the Kattegat, respectively. For maximum depth, each point represents a water body, while for the other plots they represent averages across SDs. As these values are depth-dependent (Fig. S6), data are shown for depths 3–5 m, where most data are collected (see Fig. S7 for patterns at other depths)

Figs. S11–S13). Further, it made cod more prone to collapse (Fig. S14) and more sensitive to fishing, i.e. to maintain the same abundance of cod, the fishing mortality needs to decrease if disturbance to the eelgrass increases (Fig. S15). Increasing eelgrass destruction rate also led to a reduced ability of cod to exert top-down control on the system (Fig. S10).

When applied to eelgrass and cod only, the highest values of our structural presence-abundance index, which quantifies the combined presence and abundance of each trophic level, occurred in conditions with very low mortality of cod. Furthermore, under high eelgrass destruction rates ($\eta_E = 0.85$), the parameter space with high index values was drastically reduced (Fig. 5c; see also Sect. 3.2 in the SI). When the index was instead applied to all trophic levels, the highest values occurred in parameter spaces with low natural mortality of juvenile cod, and intermediate levels of natural mortality of adult cod (Fig. 5d), which means that the index does not reach its highest values where cod mortality is minimised, as one might expect. This is, at least partly, a result of dynamics emerging from the model, where the filamentous algae disappear if cod abundances are high, due to the strong top-down control, which in turn results in a collapse of mesoherbivores, which rely on the algae for food and shelter (note grey areas in Fig. 5 and see Fig. S14). If simulations are run for longer than the 75 years presented here, the mesopredators eventually collapse too. However, while this dynamic emerges from the model, it is unlikely to occur in nature. This discrepancy could result from

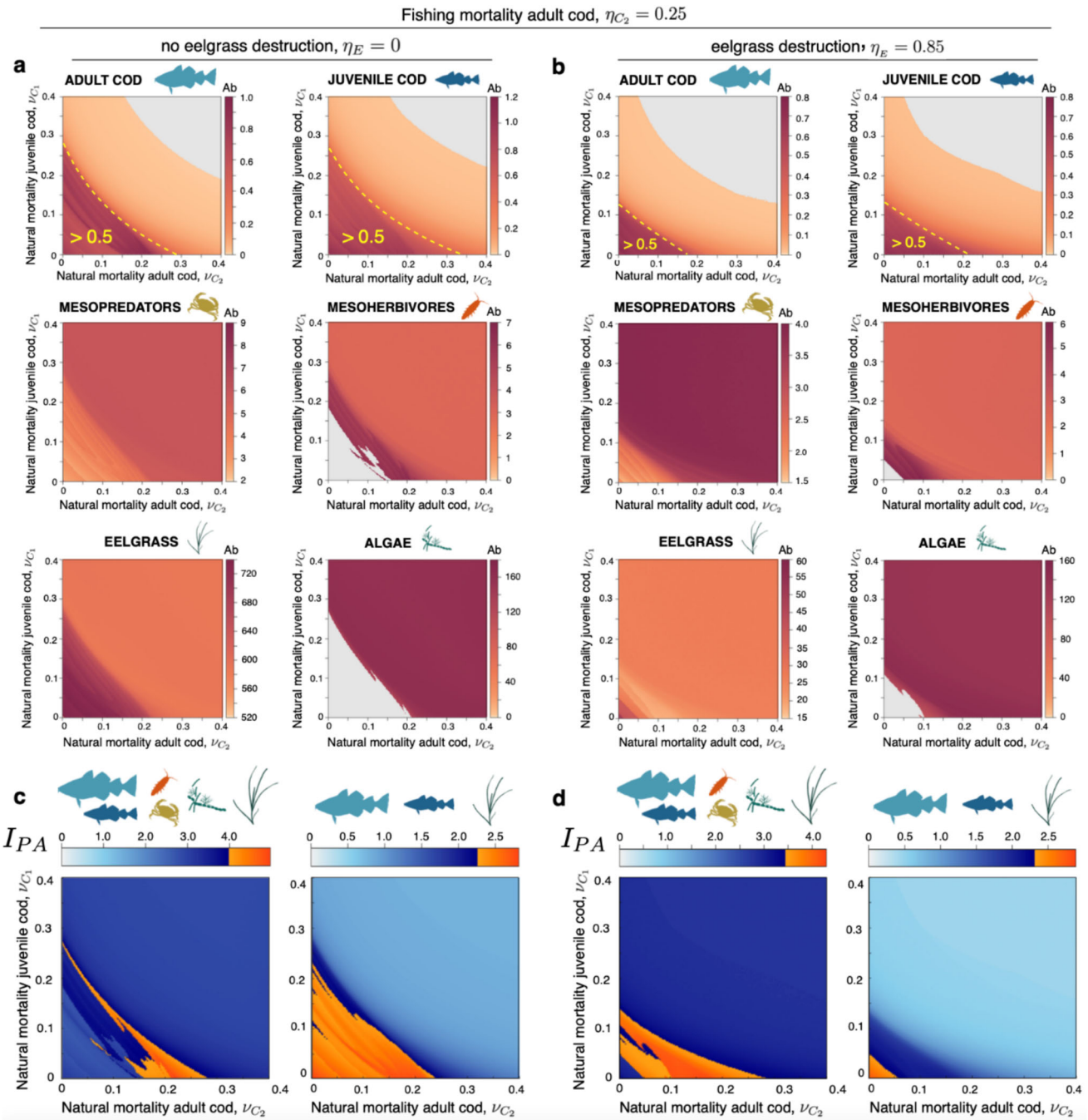

Fig. 5 The upper panels **a** and **b** show the effects of increasing the natural mortality of adult cod (horizontal axes) and juvenile cod (vertical axes) on the simulated abundance of each trophic level (Ab, colour scale shown on the right-hand side of each plot). Two different scenarios for eelgrass destruction are shown: (**a**) no and (**b**) high destruction rate (η_E = 0 and 0.85, respectively). Mean abundances in the (ν_{C1}, ν_{C2}) parameter space were computed by averaging the estimated abundances over 75-year simulations with cod fishing mortality (η_{C2}) set to 0.25 to allow for persistent cod abundances. Note that colour scales are not standardised across the two scenarios due to large differences in values. For cod, the dashed lines mark the parameter space where abundances are equal to or higher than 0.5 tonnes km^{-2}, at which point a clear shift occurs. The lower panels **c** and **d** show the corresponding effects on the structural presence-abundance index (I_{PA}), computed (**c**) for all trophic levels and (**d**) and for eelgrass and cod, respectively (see Sect. "Presence-abundance index, I_{PA}" in the SI). The orange areas indicate values within the top 20%. In all the simulations we used ω_E = 1. See SI for details on how the plots were generated

uncertainties in the model parameterisation or from the fact that the model does not capture the full range of mechanisms present in the actual ecosystem.

Importantly, the impact on the system was often nonlinear, both when changing the level of cod mortality, and when changing the level of eelgrass destruction rate or the

amount of available eelgrass habitat. In the model, although eelgrass area decreases linearly with increased rates of eelgrass destruction, cod abundances decrease nonlinearly following an inverted sigmoidal function (Fig. 6a; Sect. 3.1.1 in the SI). The abundance of filamentous algae also increases sharply (Fig. S14). An increase in the fishing mortality of adult cod causes a nonlinear decrease of both eelgrass and cod (Fig. 6b; Fig. S15). Further, filamentous algae exhibited a threshold-like response to changes in cod mortality (e.g. Fig. 5a and b), with simulations showing either low or high biomass states and limited intermediate values. This behaviour may arise from the combination of rapid algal growth, saturated rates of grazing, and reinforced feedbacks with eelgrass. The decline of cod abundances is more abrupt when fishing mortality is increased than when the eelgrass destruction rate is increased, and the time taken until cod collapses also decreases faster (Figs. S16 and S17).

The results presented above have considered a deterministic model and have therefore neglected sources of noise. To incorporate environmental stochasticity, we introduced multiplicative Gaussian fluctuations in the natural mortality rates of juvenile and adult cod, which are likely to show large between-year variation. The results show that stochasticity can substantially modify cod persistence and trophic dynamics, with intermediate noise levels delaying a collapse of the cod and, in some cases, resulting in stable, low-density, populations (Fig. S18). The interplay between noise, fishing mortality, and eelgrass destruction further reveals that eelgrass habitat degradation and fishing can amplify destabilising effects of stochasticity and accelerate a collapse of the cod (Fig. S19). Indeed, despite this potential stabilising effect of stochasticity, the cod populations were found to be in a transient towards collapse in many of the simulations under the studied parameter values (see Figs. S9, S18–S19), in agreement with Figs. 3d and 3e.

Finally, our sensitivity analysis showed that, as in Fig. 5, the highest cod densities were still obtained at low rates of natural mortality, but the effect of increasing the eelgrass destruction rate on cod was not as clear (Figs. S20 and S21). Changes in line with the trophic cascade were partly visible, with high densities of cod being associated with low densities of mesopredators and algae. However, the responses of mesoherbivores and eelgrass were less clear, with the highest densities found in disparate areas of the

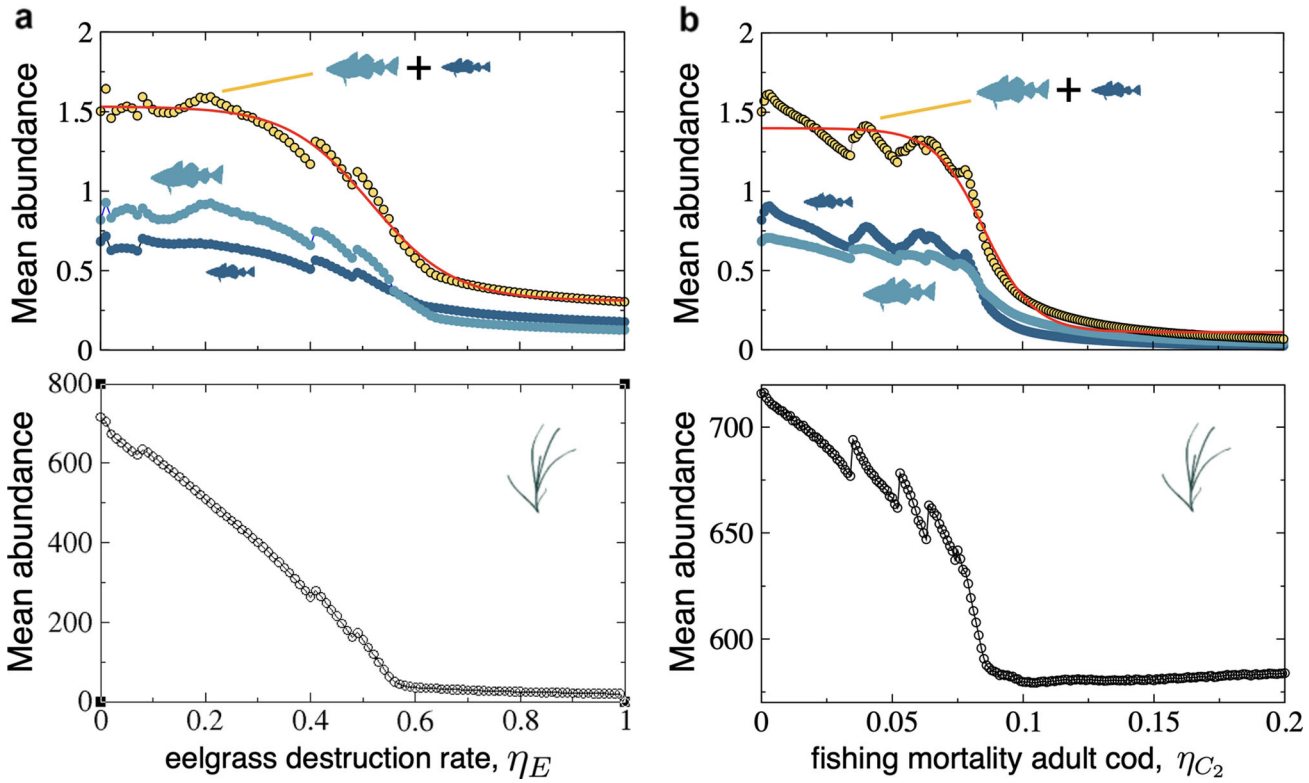

Fig. 6 Simulations of mean abundances of cod (upper panels) and eelgrass (lower panels) at **a** increasing eelgrass destruction rates η_E with zero fishing mortality η_{C2} and **b** increasing cod fishing mortality η_{C2} with no eelgrass destruction η_E. The simulations were run with the proportional area of available eelgrass habitat ω_E=1, natural mortality for juvenile cod ν_{C1} = 0.25 and adult cod ν_{C2} = 0.2, to allow for persistent cod abundances. The red solid lines show fits performed with a four-parameter logistic function (see Sect. "Two-parameter phase diagrams and dynamics" in the SI for further details)

parameter space (see Sect. "Sensitivity analysis using Monte Carlo" in the SI for further details).

DISCUSSION

Our study confirms consistently higher densities of adults and larger sizes of cod in The Sound than in adjacent trawled waters, in line with earlier work (Svedäng 2010; Svedäng and Hornborg 2017). Similarly, both commercial and recreational landings per unit area have been consistently higher in The Sound for a long time. However, despite strict fishery restrictions, including seasonal closures and bag limits within the recreational fishery over the past decade (ICES 2023) and a complete ban since 2024 (EU Regulation 2024/0213), adult cod densities in The Sound are currently at their lowest levels since the start of monitoring 25 years ago. The food web model showed that cod has the potential to exert strong top-down control, ultimately benefiting eelgrass, while extensive eelgrass meadows, in turn, also benefit cod. These outcomes align with monitoring data: compared with the Kattegat, where the cod stock has collapsed, The Sound has for an extended time hosted lower mesopredator densities, and a higher occurrence of eelgrass, which also extend deeper. However, additional drivers may also contribute to the observed patterns (discussed further below).

The stark difference in the density and landings of cod between The Sound and adjacent trawled waters reinforces previously established views that the long-standing trawl ban has played an important role in sustaining a productive cod population and a productive cod fishery in The Sound (Lindegren et al. 2010; Svedäng 2010). Based on the historical data from Denmark, landings per unit area have been higher in The Sound than in the Kattegat since the late 1800s. The only exception is a brief period in the 1960s and 1970s when they were at similar levels, which likely reflects both an increase in the Kattegat cod stock (Bartolino et al. 2012) and increased use and efficiency of active fishing gears such as trawls (see Hentati-Sundberg 2017). The latter subsequently contributed to a collapse and spatial contraction of cod in the Kattegat (Cardinale and Svedäng 2004; Bartolino et al. 2012), while the cod fishery in The Sound remained unaffected. Compared not only to the Kattegat, but also the Arkona Sea and the Belt Sea, landings per unit area by all countries combined have been higher in The Sound since the early 1990s. Estimated recreational catches in The Sound have been around 15 times higher per km of coastline compared to adjacent areas over the last 10–15 years, though recreational fishing in neighbouring basins was likely more extensive in the past (Andreas Sundelöf pers. comm.). In 2017, the total value generated by the commercial landings was estimated at around 26 million €, and revenues from the recreational fishery at around 52 million € (Jervelund et al. 2018).

The data also show that even prior to the trawl ban in 1932, Danish landings per unit area were substantially higher in The Sound compared to the Kattegat. While these differences may not directly reflect differences in fish densities, as factors such as access to fishing grounds or fish demand may also contribute, and the historical data have large uncertainties, this could suggest that differences in underlying ecological conditions have also contributed to our observed patterns, in addition to the trawl ban. For example, cod growth in The Sound may be enhanced by favourable hydrodynamical conditions (Timmermann et al. 2023) and the aggregations of Western Baltic herring providing a lipid-rich food resource during its spawning migrations (van Deurs et al. 2016). Several factors have thus likely acted in conjunction to support the productive cod population in The Sound. Further, the notable decrease in large cod observed in trawl surveys in recent years, which aligns with fisher reports (Jervelund et al. 2018), as well as the smaller sizes observed (see also Sande et al. 2025), suggest that the trawl ban alone may not be sufficient for maintaining a productive population, or that the spatial extent of the ban is insufficient, as the cod may spend parts of its life outside The Sound. Recent work also suggests that the cod in The Sound are in poorer condition and mature at smaller sizes over the last couple of years (Sande et al. 2025). While it is not yet known whether low numbers in recent years represent a persistent decline or a temporary dip, possible explanations include increased predation from great cormorants *Phalacrocorax carbo* and seals (Berglund et al. 2018), changed prey availability due to a decline in the local herring stock (see ICES 2024b), and water temperatures increasingly often exceeding the preferred temperature for cod in The Sound (Dinesen et al. 2019). Problems with hypoxia constraining cod recruitment are however generally not an issue in The Sound as it is in the Baltic Proper (Hüssy 2011; Bergström et al. 2025). The Western Baltic stock has been continuously overfished in recent decades (ICES 2023; Froese et al. 2025), and while the drop in The Sound was observed after severe restrictions on fishing were introduced, size-selective harvesting over a longer time period has likely driven declines in size and size-at-maturation at the population level, potentially reducing the reproductive potential of the cod (Sande et al. 2025).

The simulations from our food web model showed that decreases in cod abundances generated cascading effects on lower trophic levels, with increases of mesopredators and algae, and decreases of mesograzers and eelgrass. In line with this, the monitoring data showed that mesopredators were generally less abundant in The Sound than in the Kattegat, where the cod stock has collapsed. This

also aligns with earlier studies using natural experiment-like field data in the same areas showing that higher densities of cod were associated with lower densities of mesopredators (e.g. Moksnes et al. 2008; Kraufvelin et al 2022; Nielsen et al. 2025). The density of shore crabs, which may have a negative effect on eelgrass not only via the trophic cascade but also through direct disturbance (e.g. Infantes et al. 2016), was lower in The Sound, at least up until the early 2010s. A lower salinity in The Sound than in the Kattegat may have contributed to the observed differences, as the goldsinny wrasse and shore crab are closer to their physiological salinity limit in The Sound. However, The Sound is still part of their normal distribution range (Fredriksson et al. 2021). Notably, mesopredator densities were more similar between The Sound and the Kattegat in recent years, suggesting that salinity is not a limiting factor in The Sound. No consistent time series on mesograzers or filamentous algae were available, but results from occasional surveys that have been carried out (Jephson et al. 2008; Emanuelsson et al. unpubl; data used in Baden et al. 2012) align with the model output, pointing to higher densities of mesograzers and lower densities of filamentous algae in The Sound compared to the Skagerrak (north of the Kattegat). Finally, the monitoring data showed that the probability of eelgrass being present in a location was higher in The Sound than in the Kattegat and that the meadows extended deeper. Other studies have suggested that, as the two areas have similar levels of turbidity (usually the main driver of the depth limit), the differences in depth limit could be linked to increased sediment resuspension and direct mechanical impact from trawling in the Kattegat (Krause-Jensen et al. 2021). A lower probability of eelgrass presence in the Kattegat could also be linked to higher wave exposure along the more open coastline, via increased physical disturbance to the eelgrass. In The Sound, on the other hand, filamentous algae can in some areas to a higher extent be swept away by the stronger currents. It is also possible that the higher densities of filamentous algae in the Kattegat further reduce eelgrass depth distribution via shading (see Krause-Jensen et al. 2005), and/or reduce the probability of eelgrass being present at shallower depths, where the negative effect of filamentous algae is likely to be larger (Moksnes and Bergström 2025). Shading by epiphytic algae has the potential to reduce eelgrass productivity (Hasegawa et al 2007), and the results of our simulations show that the impact on eelgrass via this mechanism alone can be substantial. In recent years, survey data showed a tendency towards decreasing probabilities of eelgrass presence in The Sound, which warrants close monitoring.

The model results showing that extensive eelgrass meadows benefit cod are so consistent with a wide range of empirical studies (Pihl et al. 2006; Warren et al. 2010; Lilley and Unsworth 2014), in addition to other habitat types such as mussel beds and stone reefs (e.g. Grabowski et al. 2018), and suggest that preserving and restoring eelgrass meadows may generate positive ecological feedbacks. In particular, the simulations show that a linear increase in eelgrass destruction can trigger a nonlinear collapse of cod populations together with a sharp increase in filamentous algae, highlighting the importance of avoiding critical ecological thresholds. Conversely, increasing cod fishing mortality can also lead to rapid declines in eelgrass meadows. These interacting processes generate threshold-like dynamics, in which relatively small changes in eelgrass destruction or cod mortality produce disproportionately large responses in ecosystem structure. These dynamics are consistent with the potential for regime shifts in shallow coastal ecosystems, where systems may alternate between eelgrass-dominated and algae-dominated states (Scheffer et al. 2001; Moksnes et al. 2018). Importantly, the transitions are not gradual but instead characterised by tipping points arising from reinforcing trophic feedbacks.

From a management perspective, these nonlinear relationships emphasise the importance of maintaining both cod populations and eelgrass meadows above a critical threshold. Importantly, a recovery process may also be nonlinear: rebuilding cod populations from low levels may not immediately result in eelgrass recovery if the system has shifted to an algae-dominated state. These findings highlight the importance of strategic, precautionary management that avoids predator depletion and considers both top-down (e.g. fisheries regulation) and bottom-up habitat protection and restoration processes to maintain or restore coastal ecosystem functioning.

While the model was carefully developed to capture key dynamics, and the parameter values were informed by local data and literature, models always represent a simplified reality. Our model also produced some unrealistic dynamics, including collapses of filamentous algae and mesoherbivores at low cod mortality levels, and rapid collapses of the cod at estimates of natural and fishing mortality from current stock assessments. The model results should therefore not be used as proof that certain processes are driving ecosystem development over time or to extract quantitative information (see Sect. 1.4 in the SI for a detailed discussion on model limitations). Still, the model results can be used to point to key mechanisms in the ecosystem and give an indication of their relative importance, and to explore nonlinear dynamics. Similarly, while the temporal developments in key species (cod, mesopredators, and eelgrass) in the empirical data are coherent with the model results, comparisons across geographical areas and national borders are subject to some uncertainties due to incoherent monitoring designs and data gaps for several variables. These bottlenecks ideally need

to be overcome to facilitate more harmonised evaluations in the future.

CONCLUSIONS

The Sound is subject to intense human activities but has maintained higher densities, larger sizes, and greater landings of cod than adjacent waters over long time periods, likely at least partly because of a long-term trawl ban. Our study expands on previous work by exploring how cod in The Sound influences the surrounding ecosystem. Results from our food web model and monitoring data both suggest that the cod population in The Sound has, for a long time, been at levels that exert top-down regulation of the local food web, ultimately benefitting the habitat-forming eelgrass. However, the density of large cod has declined markedly in recent years, and the modelling results suggest that the persistence of the cod population can be sensitive even to small perturbations. Further, observations over the last few years of higher densities of some mesopredator species and indications of reduced eelgrass coverage could indicate reduced top-down control and warrant close monitoring. Results from the food web model also suggest that extensive eelgrass meadows, in turn, likely benefit the cod population, pointing to the importance of both top-down and bottom-up processes for a resilient and productive food web. Together, these findings offer a compelling example of how the protection and restoration of key species can preserve ecosystem functioning and sustain the provisioning of essential ecosystem services.

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Author contributions Lena Bergström, Mikael van Deurs, Maria Eggertsen and Ulf Bergström contributed to study conception and design. Data collation and curation was performed by Agnes Olin, Mikael van Deurs and Hans Jakob Olesen. Data analyses were performed by Agnes Olin. The food web model was developed and analysed by Josep Sardanyés, Ceren Ekinci and Filip Ivančić. Visualisations were done by Agnes Olin, Josep Sardanyés and Maria Eggertsen. Agnes Olin led the writing of the manuscript. All authors contributed to the writing and approved the final manuscript.

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Data availability The code used to generate figures and tables relating to the time series analysis can be found at https://github.com/KLabMSP/MPA4S. The corresponding data are available at [link to be added when data are made available upon manuscript acceptance]. The code for the food web model and the data simulated from the model can be obtained upon request.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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