Fisheries Research 266 (2023) 106780

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

A Baltic pelagic fish community revisited: Indications of profound changes in species composition in the Stockholm Archipelago

Henrik Svedäng[a,*,1], Gustaf Almqvist[b,2], Thomas Axenrot[c,3]

[a] Baltic Sea Centre, Stockholm University, SE-106 91 Stockholm, Sweden
[b] County Administrative Board of Stockholm, SE-104 22 Stockholm, Sweden
[c] Department of Aquatic Resources, Swedish University of Agricultural Sciences (SLU), Sweden

ARTICLE INFO

Handled by A.E. Punt

Keywords:
Acoustics
Baltic Sea
Herring
Inshore fish community
Three-spined stickleback

ABSTRACT

While the central Baltic herring (*Clupea harengus*) stock biomass is estimated to have been reduced by ~80 per cent since the 1970 s, the local effects of this decline remain unassessed. Coastal commercial fishermen have witnessed a widespread depletion at the spawning grounds and generally low herring abundance in inshore areas. We carried out hydroacoustic surveys, supported by midwater trawling in August 2021, to test whether herring abundance and recruitment have changed over time in the inshore areas. We used assessed recruitment success, measured as young-of-the-year (YOY) abundance, as a proxy for herring abundance in several areas of the southeast Stockholm Archipelago and compared the results with previous investigations in this area (hydroacoustics 2000–2001 and midwater trawling 2002–2004 monitoring). We found that the composition of the fish community had undergone significant changes. While acoustic backscattering (s_A) representing the whole fish community were similar to previous estimates, species composition was significantly changed. YOY herring, previously dominant, had declined from 55% to 4% in numbers, whereas three-spined stickleback (*Gasterosteus aculeatus*) increased from no representation to 76%. The observed changes makes it imperative that further investigation concerning herring population structure, biomass, and recruitment are conducted.

1. Introduction

1.1. General background

Species such as herring (*Clupea harengus*) and Atlantic cod (*Gadus morhua*) form mosaics of spawning units whose population structure and degree of connectivity still are unresolved issues (Smedbol and Stephenson, 2001; Han et al., 2021; Henriksson et al., 2023). Prolonged periods of intense exploitation in areas such as the Baltic Sea and Kattegat may seriously hamper future stock productivity (Svedäng and Bardon, 2003; Svedäng, Rolff, 2021; ICES, 2021). Depletion of the coastal herring population structure may also lead to shifts in species composition (Olin et al., 2022). But little is known on the nearshore spawning areas since most stock assessment relies on commercial fishing statistics and offshore monitoring survey data. Clearly, there is an urgent need to assess the developments in abundance and species compositions in coastal areas.

1.2. The central Baltic herring

In the Baltic Sea, herring and sprat (*Sprattus sprattus*) dominate the pelagic fish community (Sparholt, 1994), but three-spined stickleback (*Gasterosteus aculeatus*) may also be abundant (Jurvelius et al., 1996; Olsson et al., 2019). In inshore areas, European smelt (*Osmerus eperlanus*) may also be numerous. Spring spawning herring reproduce in sheltered coastal areas on sandy, stony, or vegetated grounds at 10–20 m depth (Aneer, 1989). A large part of the spawning can also occur at the outer skerries or on banks 5–10 km offshore (Hessle, 1925, 1937; Otterlind, 1976; Aneer, 1989). The spring spawning herring usually congregate outside the spawning areas during winter to early spring (from December to March; Parmanne et al., 1994).

In the studied coastal stretch of the Baltic Sea (the southern part of

* Corresponding author.
E-mail address: henrik.svedang@su.se (H. Svedäng).
[1] orcid 0000-0002-3639-7105
[2] orcid 0000-0003-0294-733X
[3] orcid 0000-0002-0647-9759

https://doi.org/10.1016/j.fishres.2023.106780
Received 19 April 2023; Received in revised form 17 June 2023; Accepted 19 June 2023
Available online 7 July 2023

the Stockholm Archipelago), the majority of herring spawn from the end of May to the beginning of July (Aneer, 1989), after which the adult fish migrate back to the open sea and intermingle with other substocks (Otterlind, 1976; Rajasilta et al., 1993; Parmanne et al., 1994). Local stocks also spawn inside the Swedish east coast archipelagos with a more restricted migration patterns (Hessle, 1937; Otterlind, 1976). Recently, many of these local populations have been identified as separate genetic subpopulations (Han et al., 2021).

Herring biomass is a vital part of the marine shelf ecosystem, populating the entire Baltic Sea. It forms an important food source and links nutrients, energy, and other substances between the plankton and benthic communities and the larger sea animals as well as between the inshore and the offshore (Rudstam et al., 1992; Arrhenius and Hansson, 1993). However, the central Baltic herring stock (CBH) has declined by about 80 per cent since the 1970 s (ICES, 2021). Thus, it remains to be evaluated how this reduction is reflected at different stretches of the coast where spawning herring are commonly found, including the risk of extirpations of herring subpopulations (Han et al., 2021). Indirect cascade effects on the coastal ecosystem due to declining coastal herring abundance have already been suggested (Eklöf et al., 2020).

1.3. Biomass extraction

The present herring fishing is entirely dominated by large-scale industrial midwater trawling, consisting of vessels over 24 m long, engine power over 450 KW, and trawls with a mesh size below 32 mm. This fishing occurs partly outside the trawling limit f(our nautical miles from the baseline that connects the outer islands and promontories), especially in the ICES statistical rectangle (47G9; Fig. 1), partly in area extensions inside the trawl limit (Fig. S1), i.e. near and within parts of the Stockholm archipelago. The trawl fishing for herring close to the archipelago areas takes place mainly from January to March, that is, during the period when herring concentrate close to their spawning grounds (Otterlind, 1976; Aneer, 1989).

Fishing has yielded higher catches in recent years; the annual Swedish landings are presently around 2000 tonnes, with a peak in 2018 when the catches amounted to approximately 7000 tonnes (Fig. S2). The total Swedish trawl catches increased by an average of 70 per cent during 2015 – 2021 compared to 2010 – 2014, while the catches close to the coast increased by an average of 218 per cent (Svedäng and Berkow, 2021). The proportion caught in the area close to the coast almost doubled, from 9 to 17 per cent, in 2015 – 2019 compared to the previous five-year period. The presence of multinational, large-scale trawlers fishing directly adjacent to the Stockholm archipelago in 2021 is a new phenomenon and contributes to increased fishing pressure.

1.4. Present status of herring in the coastal zone

The observations made by Stockholm County's remaining professional inshore fishermen testify that it has become increasingly difficult to get even very modest catches of herring, in sharp contrast to continuously high recorded catches from 1914 to the 1970 s (Sweden statistics, https://www.scb.se/en/). Additional important pieces of information on spawning stock biomass (SSB) for ICES subdivision (SD) 27 are provided in Axenrot and Hansson (2003) as a parameter when calculating future recruitment of herring (age class 2). The mean SSB in SD27 for 1985–2000 was 131.7×10^3 tons (lowest 41.1 and highest 208.6). The estimated SSB for 2019–21 was 20.6, 52.9, and 77.6×10^3 tonnes, respectively (Larson, 2020, 2021, 2022). Thus, the estimated spawning biomass for 2019–2021 increased over this period but was considerably smaller than in 1985–2000.

1.5. Methods for studying coastal herring abundance

Offshore acoustic surveys measuring the abundance of pelagic fish in the Baltic Sea, such as adult herring and sprat, are performed annually in October through internationally coordinated surveys, i.e. the Baltic International Acoustic Survey (BIAS; Axenrot and Hansson, 2003; Anonymous, 2022). Generally, the BIAS does not cover coastal or archipelago areas (Anonymous, 2022). Hydroacoustic estimates of herring shoaling outside spawning areas or during spawning in a specific area usually give uncertain results since spawning aggregations are scattered in patches and spawning takes place in "waves." Furthermore, it is difficult to calculate the number of fish in dense shoals and schools using hydroacoustic methods (Simmonds and MacLennan, 2005).

Alternatively, it is possible to estimate the importance of a coastal stretch as a spawning and nursery area, and the future recruitment to SSB, by assessing the abundance of young-of-the-year (YOY) herring. The first weeks after hatching, the yearlings pass through a larval stage, after which they metamorphose into fry. Younger herrings often remain in coastal, inshore areas over the summer before migrating to nearby offshore areas and, eventually, to the open Baltic Sea (Otterlind, 1976; Axenrot and Hansson, 2004). These ontogenic habitat shifts can be observed as a lack or low number of younger herrings in the offshore BIAS surveys (e.g. Anonymous, 2022). After metamorphosis, the fry develops a swim bladder that can be detected by hydroacoustics (echo sounding/sonar). Such methods are non-invasive and allow for the fast data collection on the occurrence of pelagic fish from just below the surface to close to the seafloor over extensive areas. Additional biological data, such as information on the relative distribution between YOY herring and other fish in the area, may be collected using short, representative midwater trawl hauls (Axenrot and Hansson, 2004).

There are many archipelago stakeholders, including various fishers (professional, recreational, and sports fishermen), who testifies that some traditional spawning grounds for herring are presently missing spawning fish. These disappearances coincide in time with an intensified large-scale trawling off the coast during winter (January-March).

1.6. Study aims

Decreasing occurrence of herring may drastically change the functioning of the coastal ecosystem along the Swedish Baltic coast (e.g. Arrhenius and Hansson, 1993); better knowledge is thus needed concerning the development of the herring stocks along the western Baltic Coast. It is relevant to ask whether more profound changes in species abundance may occur within assessment units, such as the one for CBH, than is reflected in the overall view on the stock level based on commercial fishing statistics and offshore monitoring survey data (ICES, 2021).

Our study aims to test whether changes in herring abundance in a specific section of the Baltic coast have changed more than expected from the changes in the overall stock levels. We do this by comparing the results of the species composition and their relative abundance in 2021 with results from an older time series. Such times series are available from the southern part of the Stockholm Archipelago. In this area, Axenrot and Hansson (2003, 2004) investigated the seasonal dynamics of pelagic fish abundance during the herring recruitment period to estimate recruitment success for herring using the same methods as we used in 2021.

2. Material and methods

The surveys covered three areas - (*i*) Himmerfjärden (Fig. 2a), (*ii*) south of Himmerfjärden covering Svärdsfjärden, Krabbfjärden, Hållsfjärden and Hållsviken, hereafter referred to as Askö (Fig. 2b), and (*iii*) the Nämdö archipelago (Fig. 2c). For (*i*) and (*ii*), the survey design was partly based on previous surveys in the Himmerfjärden and Askö areas so that the hydroacoustic transects followed the transects of the old time series (Axenrot and Hansson, 2003; Axenrot and Hansson, 2004; Table S1). The Nämdö archipelago was included in our study to increase the areas surveyed even though that section was not surveyed by Axenrot and Hansson. Data collection in the field was carried out

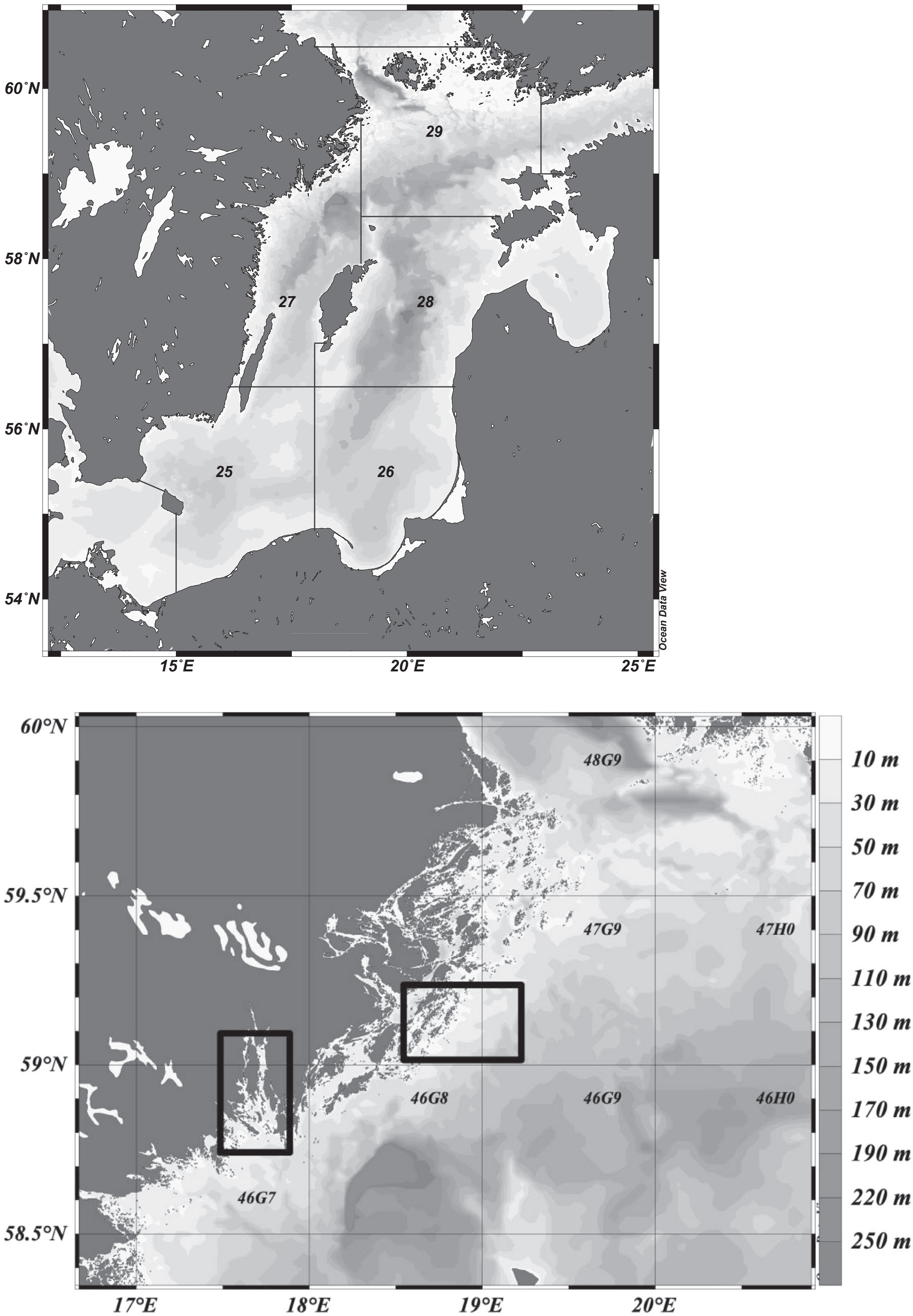

Fig. 1. a) The central Baltic Sea. ICES subdivisions are shown. b) The Stockholm Archipelago on the Swedish east coast. Study areas are framed by boxes. ICES statistical rectangles are annotated in their upper right corner. The distance between 59° N and 60° N is 60 nautical miles (111 km). The bathymetry is shown on a grey scale.

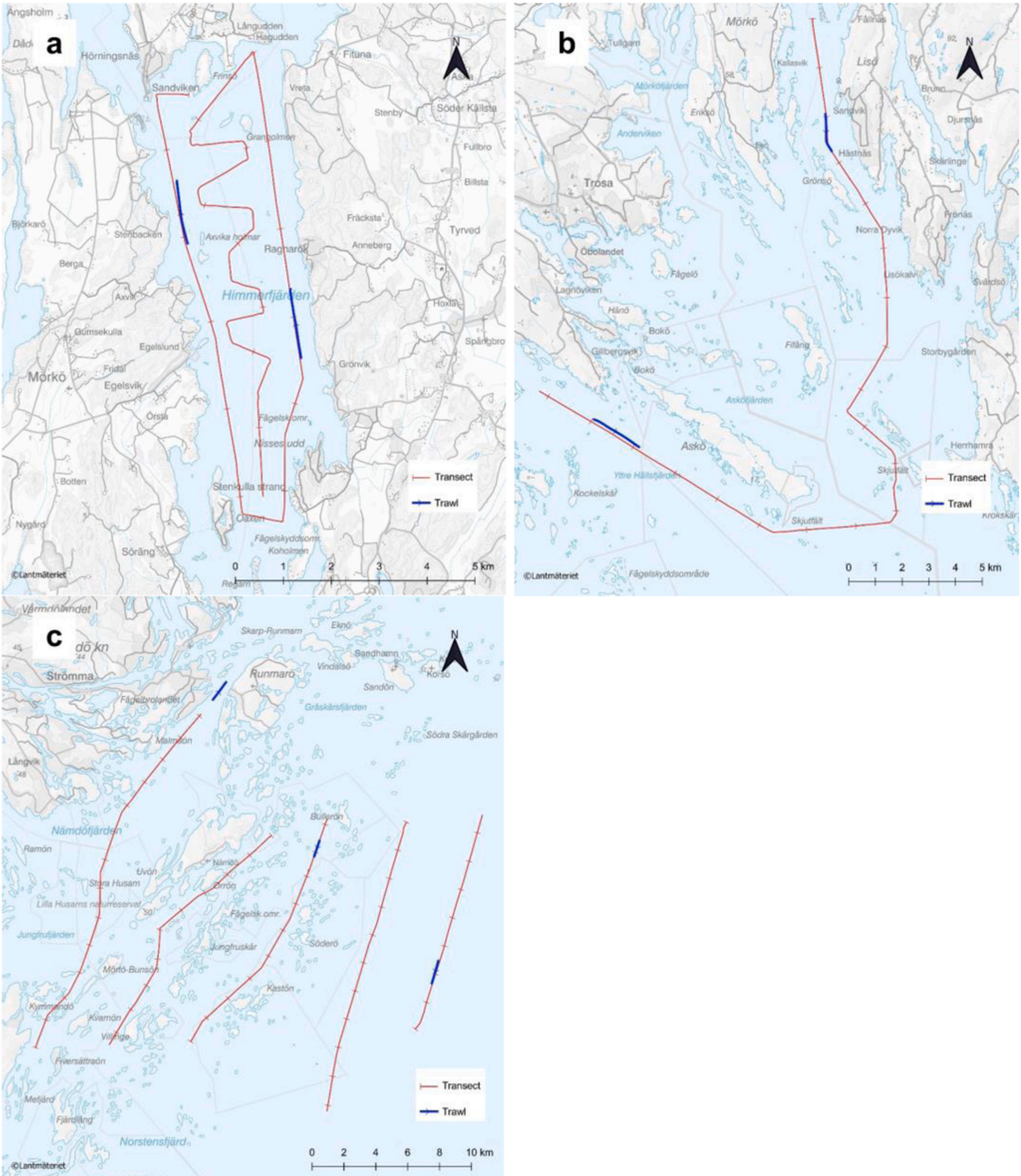

Fig. 2. Study areas: acoustic transects (red lines) and trawl hauls (blue lines) are shown. a. Himmerfjärden, b) Askö area, c) Nämdö area.

from 2 to 4 August 2021 at night, starting one hour after sunset and ending no later than one hour before sunrise. Corresponding data collection for the old time series was carried out at night between mid-August and early September (Axenrot and Hansson, 2003). Night-time surveys were chosen to avoid pelagic fish in the daytime standing close to the bottom, in dense aggregations, and at the small depths in coastal areas be more sensitive and show avoidance reactions (Fréon and Misund, 1999; Huse and Korneliussen, 2000).

2.1. Hydroacoustics

2.1.1. Survey 2021

The investigations were carried out with the research vessel R/V Asterix, which has two scientific echo sounders (Simrad EK80 split-beam for 38 and 120 kHz), as well as the possibility of trawling and other types of sampling (Internet reference 1). The sonars were calibrated according to Foote et al. (1987) and recommendations from the manufacturer (Simrad AS).

Hydroacoustic data were collected along the pre-planned transects in each area (Fig. 2a,b,c) from about 3 m depth to about 0.5 m above the bottom. Both acoustic sensors (transducers) had an exit angle of 7°, positioned to cover the same volume of water for outgoing sound pulses (ping). The pulse length was set to 0.512 ms for both echo sounders. Both frequencies could thus be used equally for comparison with hydroacoustic data from the older time series. The target strength (TS) threshold for echoes from individual fish was set to − 60 dB to include small and young-of-the-year (YOY) fish. For the transformation of fish length (total length) to TS, the equation presented for herring and sprat in the Baltic Sea by Didrikas and Hansson (2004) was used. For the Nämdö archipelago area that was not surveyed in the past, we calculated a sufficient degree of coverage for the hydroacoustic surveys according to Aglen (1983).

The results were reported as s_A-values (nautical area scattering coefficient), representing reflected echo energy without interpretation and evaluation of, e.g. trawl results and fish density calculated from hydroacoustic size distribution (single echo detections).

2.1.2. Older time series

Simrad sonar EY/M for 70 kHz single-beam, 11°, was used during 1985–96, and Simrad sonar EY500 for 70 kHz split-beam, 11°, from 1997 to 2000 (Axenrot and Hansson, 2003). According to Rudstam et al. (1999), these two systems may show good agreement. Pulse length was set to 0.6 ms). Previous analyses of 38, 70, and 120 kHz results have shown comparable results (Guillard et al., 2014; Mouget et al., 2019).

2.2. Trawling

2.2.1. Survey in 2021

In conjunction with the hydroacoustic data collection in each sub-area, pelagic trawling was carried out at night to assign fish species and size composition to the hydroacoustic data. The minimum mesh size in the trawl codend was 5 mm, which permitted the capture of small fish and yearlings. The trawl opened 5 × 12 m. Two hauls were made in the Himmerfjärden at 15–20 m depth (Fig. 2a) and Askö at 5–10 and 10–15 m depth (Fig. 2b). At Nämdö, three trawl hauls were made from west to east, i.e. from sheltered inshore areas to the offshore, at 10–15, 15–20, and 10–15 m depth (Fig. 2c). Each trawl lasted 20 min at a speed of 2–3 knots. Fish caught in the trawl hauls were measured in length and weight. In the case of larger quantities of fish caught, random sub-samples were used for the analyses. Data from the trawl hauls were compiled separately for each sub-area.

2.2.2. Surveys in 2002–2004

The trawl hauls were carried out in Himmerfjärden with the same type of trawl described above, i.e. with the 5 mm smallest mesh in the codend and 5 m vertical opening. The trawling was performed at night on August 26, 27, and 23, respectively, in 2002–2004 (Table S1). Three trawl hauls were carried out each year at depths of 10–15, 15–20, and 20–25 m, using R/V Ancylus. The trawls lasted 30 min at 2.5 knots (Jensen et al., 2011). No estimates of abundances or biomasses for 2002–2004 based on acoustics are presented in this study.

2.3. Analysis of hydroacoustic data

Previous surveys were performed during mid-August through early September when young herring had metamorphosed, and maximum densities were recorded (Rudstam et al., 1992; Hansson, 1993; Axenrot and Hansson, 2004). At this time of the year, this coastal area was found entirely dominated by YOY herring (Rudstam et al., 1988, 1992; Hansson and Rudstam, 1995). The YOY abundance data was estimated from echo-integration values (integration threshold-80 dB) and the size distribution of single fish echoes larger than − 60 dB (herring larger than 30 mm, Rudstam et al., 1988).

Axenrot and Hansson (2003) used hydroacoustic fish density (abundance) as an inshore YOY herring density index in Himmerfjärden and Askö. At this time of the year, the pelagic fish community was strongly dominated by the YOY of herring (Rudstam et al., 1988, 1992; Hansson and Rudstam, 1995). This YOY herring density index was suggested to work as a predictor of the recruitment of herring to age class 2.

For the data collected in 2000–2001, the target strength threshold for echoes from individual fish (TS, target strength) was set to − 60 dB to include small fish and yearlings. A threshold value for total acoustic reflection (backscatter, S_v) was set to − 80 dB. To transform fish length (total length) to TS, the equation presented for herring and sprat in the Baltic Sea by Didrikas and Hansson (2004) was used:

(1) $TS = 20 \log_{10} L - 67.8$

where TS is the target strength and L is the total fish length in cm.

For the hydroacoustic results in 2021, we used the same threshold (−60 dB) for echoes of individual fish (TS). Normally, the threshold for total acoustic reflection (S_v) is set to include what can be judged to come from fish in accordance with CEN Comité Européen de Normalisation European Committee for Standardization (2014). However, to make the 2021 results analogous to the old time series, we rerun the analyses with total acoustic reflection set to − 80 dB for both 38 and 120 kHz acoustic data. As the 120 kHz sonar detected more weak echoes than the 38 kHz (Figs. S5 and S6), comparisons with the old time series were made with 120 kHz results from 2021. For calculating densities and biomass, classification trees were used to partition the trawl data into species and size groups (TL; e.g. Yule et al., 2013). Biomass was summed from the average of each species/discrete size groups within species based on the individual weight in the trawl catches.

The data from 2021 were analysed with settings consistent with the analysis of the old time series (Axenrot and Hansson, 2003, 2004). Hydroacoustic results in the old time series, collected at 70 kHz, on fish abundance (s_A) and fish density (numbers per km^2) were compared with the corresponding results from 2021 for 120 kHz (Figs. S3 and S4).

2.4. Statistical analysis

We tested changes in the proportions of pelagic fish species catches between the two study periods 2002–2004 and 2021 for all trawl hauls made in the Himmerfjärden and Askö (Table S1) after arcsine transformations of the proportion values (Sokal and Rohlf, 1981) by analysis of multivariance (MANOVA) (available in the r-script "MANOVA.RM" package, version 0.5.3; Friedrich et al., 2022). The hauls in the Himmerfjärden-Askö area were made at various depths and considered to represent the pelagic fish community. Four species/ size classes with sufficient representation were selected for the analysis, based either on the high abundance in one of the study periods or representation in most hauls in both periods: herring YOY, herring > 0 +, sprat, smelt, and sticklebacks (combined sample of three-spined stickleback and nine-spine stickleback (*Pungitius pungitius*). For resampling method, we used a Wild bootstrap approach, where the number of iterations was set to 10,000.

Differences in the herring size distribution between samples were tested with a two-sample Kolmogorov–Smirnov (KS) test (available in the r-script "dgof" package version 1.4 (Arnold and Emerson, 2022).

2.5. Miscellaneous

Data were collected for temperature (air, surface, and depth profiles) and oxygen conditions (depth profiles) to determine the presence of thermo- and haloclines.

3. Results

The results from the present study in 2021 are summarised regarding trawling and hydroacoustics in Table 1 and Table 2, respectively. For comparison reasons, the previous surveys in 2002–2004 are included (Axenrot and Hansson, 2004; Jensen et al., 2011). Detailed haul and catch information for previous and present studies are shown in Table S1.

3.1. Results of 2021 surveys by area

3.1.1. Himmerfjärden and Askö

The hydroacoustic transects' distance was 66 km, distributed approximately half in each area. The estimated abundance of all species in each area is reported in Table 3. In Himmerfjärden, three-spined stickleback was the most numerous species (Table 1 and Fig. 3). However, the biomass was dominated by herring > 0 + (Fig. 4), which judging from the size distribution, mainly consisted of one-year-old herring (Fig. 5a,b).

Also, three-spined stickleback dominated in the northern, more sheltered part of the Askö area, while sprat and herring were more frequent in the southern, more open part (Fig. 6). For the whole Askö area, herring > 0 + dominated the biomass (Fig. 4). The size distribution of herring in the trawl hauls in the Askö area showed that YOY herring were similar to the size distribution in Himmerfjärden (KS-test: not significant, statistics not shown). Herring > 0 + were, similar to Himmerfjärden, dominated by one-year herring (Fig. 5a).

3.1.2. Nämdö

The distance for the hydroacoustic transects was 91 km, distributed over five transects. In contrast to Himmerfjärden-Askö, sprat were the most numerous (Table 1), while herring > 0 + dominated the biomass (Table 3; Figs. 3 and 4). A gradual change in the pelagic fish community was also noted, with decreasing three-spined stickleback abundance from the inshore sub-area west of Nämdö via the archipelago east of Nämdö to the offshore area further to the east (Fig. 7). The share of three-spined stickleback decreased from 64 per cent to 16 per cent, while herring and sprat 0 + increased.

3.2. Results of 2021 surveys by species

3.2.1. Herring

The density of YOY herring was highest in the southern Askö area, followed by the northern part of the same area and the eastern offshore area at Nämdö (Figs. 3, 6, and 7; Table 3). The corresponding density was significantly lower in Himmerfjärden and at the inshore west of Nämdö (Figs. 3 and 7). The size distribution indicated that the YOY herring were similar in all studied areas (Fig. 5b; two-sample KS-test not significant; statistics not shown).

The biomass (kg per km^2) of herring > 0 + dominated all investigated areas (Fig. 4). The size distribution in the trawl hauls indicated that herring in size of one-year-old were most common in the areas of Himmerfjärden, Askö, and west of Nämdö, whereas larger – and thus probably older than 1-year-old individuals – were most common in the offshore east of Nämdö (Fig. 5a,b).

3.2.2. Three-spined stickleback

Three-spined stickleback dominated numbers (density per km^2) at the inshore areas (Figs. 3, 6, and 7; Table 2). We recorded the lowest

Table 2
Hydroacoustic backscattering (s_A per km^2) and estimated total fish density (numbers*10^6 per km^2) from night-time surveys in Himmerfjärden (south of Södertälje, Sweden) from years 2000, 2001 and 2021 (this study). Date is given for the start of each survey.

Date	s_A	SE	Fish density	sd
2000–05–30	94	10	0.280	nd
2000–06–05	42	3	0.129	nd
2000–06–19	29	1	0.086	nd
2000–07–04	26	1	0.092	nd
2000–07–18	75	4	0.429	nd
2000–08–01	139	6	1.127	nd
2000–08–15	208	8	1.206	nd
2000–08–30	180	11	0.805	nd
2000–09–13	146	6	0.595	nd
2000–09–27	118	3	0.557	nd
2000–10–19	101	7	0.443	nd
2000–11–14	115	4	0.412	nd
2001–05–08	27	1	0.082	nd
2001–05–22	28	1	0.089	nd
2001–06–06	30	1	0.095	nd
2001–06–20	22	2	0.040	nd
2001–07–04	45	1	0.120	nd
2001–07–18	82	3	0.427	nd
2001–07–31	218	8	0.861	nd
2001–08–14	303	13	1.104	nd
2001–08–28	222	10	0.516	nd
2001–09–12	198	14	0.449	nd
2021–08–02	343	19	1.688	0.486

Table 1
Summarised trawl catches in numbers per fish species in the Himmerfjärden from August 26, 27, and 23 in 2002–2004, respectively, and in the Himmerfjärden, Askö, and Nämdö August 2–4 in 2021. In 2002–2004, three hauls were made per year, and in 2021, two in the Himmerfjärden and Askö, respectively, and three hauls at Nämdö (Table S1).

	2002–2004			2021					
Species*	Himmer-fjärden Numbers	sd	Rel. Freq. (%)	Himmer-fjärden Numbers	Askö	Nämdö	Himmer-fjärden Rel. Freq. (%)	Askö	Nämdö
Herring 0 +	7356	1189	55	524	338	189	3	8	< 1
Herring > 0 +	1972	424	15	1111	356	425	6	9	2
Sprat	3812	1170	29	616	1925	25553	4	46	88
Three-spined stickleback	0	0	0	14646	1533	2631	85	37	9
Ruffe	56	32	< 1	1	0	0	< 1	< 1	0
Pikeperch	48	9	< 1	0	0	0	0	0	0
Smelt > 0 +	56	32	< 1	81	3	0	< 1	< 1	0
European flounder	0	0	0	0	1	0	0	< 1	0
Ninespined stickleback	0	0	0	177	17	11	1	< 1	< 1
Goby	0	0	0	4	2	1	< 1	< 1	< 1
Eelpout	0	0	0	2	0	0	< 1	0	0
Broadnosed pipefish	0	0	0	0	5	1	0	< 1	< 1
Fourhorned sculpin	0	0	0	0	0	1	0	0	< 1
SUM	13299			17162	4180	28812			

* Herring (*Clupea harengus*), sprat (*Sprattus sprattus*), three-spined stickleback (*Gasterosteus aculeatus*), ruffe (*Gymnocephalus cernua*), pikeperch (*Sander lucioperca*), smelt (*Osmerus eperlanus*), European flounder (*Platichthys flesus*), ninespined stickleback (*Pungitius pungitius*), goby (*Pomatoschistus minutus*), eelpout (*Zoarces viviparous*), broadnosed pipefish (*Syngnathus typhle*), fourhorned sculpin (Myoxocephalus quadricornis).

Table 3
Estimated fish densities (in millions per km^2) from hydroacoustics and assigned trawling data in Himmerfjärden, Askö, and Nämdö August 2–3, 2021, August 3–4, 2021 and August 4–6, 2021, respectively.

Species	Himmerfjärden Mean	±sd	Askö Mean	±sd	Nämdö Mean	±sd
Herring YOY	3.828E-02	1.760E-02	2.245E-01	1.115E-01	6.226E-02	1.496E-02
Herring > 0 +	4.891E-01	1.606E-01	3.311E-01	8.920E-02	5.030E-01	8.651E-02
Sprat 0 +	0.000E+ 00	0.000E+ 00	0.000E+ 00	0.000E+ 00	7.358E-02	1.391E-02
Sprat > 0 +	1.330E-01	4.600E-02	3.544E-01	7.628E-02	3.693E-01	5.314E-02
Three-spined stickleback	9.579E-01	2.726E-01	8.027E-01	1.943E-01	8.776E-01	1.630E-01
Ruffe	1.332E-03	5.200E-04	0.000E+ 00	0.000E+ 00	0.000E+ 00	0.000E+ 00
Smelt > 0 +	2.900E-02	9.261E-03	2.591E-03	4.600E-04	0.000E+ 00	0.000E+ 00
European flounder	0.000E+ 00	0.000E+ 00	2.792E-03	7.640E-04	0.000E+ 00	0.000E+ 00
Nine-spined stickleback	4.090E-02	1.273E-02	1.024E-02	3.274E-03	7.322E-03	2.032E-03
Goby	8.920E-04	2.760E-04	9.520E-04	1.490E-04	2.120E-04	7.900E-05
Eelpout	2.070E-03	5.510E-04	0.000E+ 00	0.000E+ 00	0.000E+ 00	0.000E+ 00
Broadnosed pipefish	0.000E+ 00	0.000E+ 00	1.137E-02	3.090E-03	9.000E-06	3.000E-06
Fourhorn sculpin	0.000E+ 00	0.000E+ 00	0.000E+ 00	0.000E+ 00	2.493E-03	9.080E-04

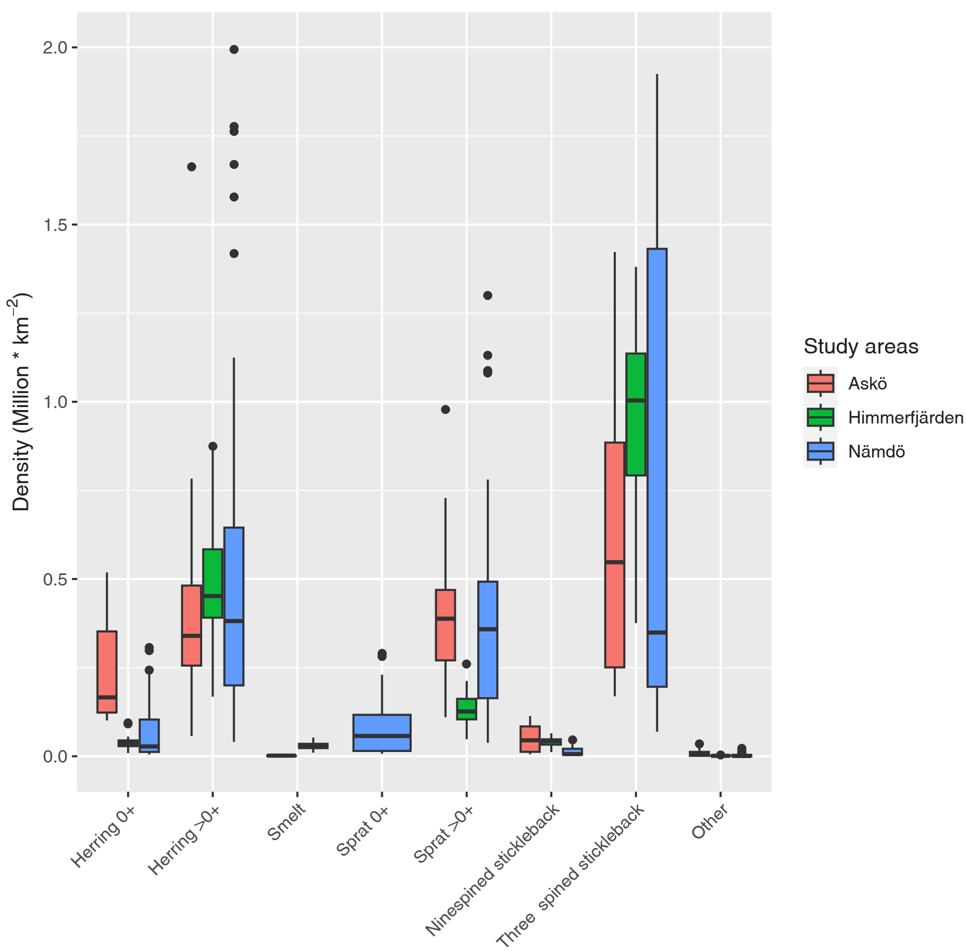

Fig. 3. Boxplots of fish density (number per km^2) by fish species, estimated from hydroacoustics surveys for the study areas of Himmerfjärden, Askö, and Nämdö, August 4–6 2021. Boxplots show median, interquartile ranges (box), ranges (vertical lines) and outliers (points).

densities of three-spined stickleback for the more open areas Askö South (Hållsfjärden) and the east of Nämdö, adjacent to the open Baltic Sea. It was observed that the low densities of YOY herring were found in areas where three-spined stickleback showed high densities.

3.2.3. Sprat

No YOY sprat were caught in Himmerfjärden or the Askö areas (Fig. 3). In the Nämdö area, YOY sprat increased east towards the offshore (Fig. 7). In Himmerfjärden, the density of sprat > 0 + was low compared to other areas (Table 2).

3.3. Comparison between 2021 results and 2002–04 results

A comparison of trawl catches in the Askö-Himmerfjärden area showed significant differences in the species composition between the two periods 2002–2004 and 2021 (Table 4: MANOVA results). The abundance of herring YOY and older herring had decreased, while sticklebacks, absent in 2002–2004, had become numerous. The strongest term was the interactions between species and time.

The results for 2021 showed higher sA value and fish density (Table S1, Figs. S4, and S5). Even the total fish density in Himmerfjärden

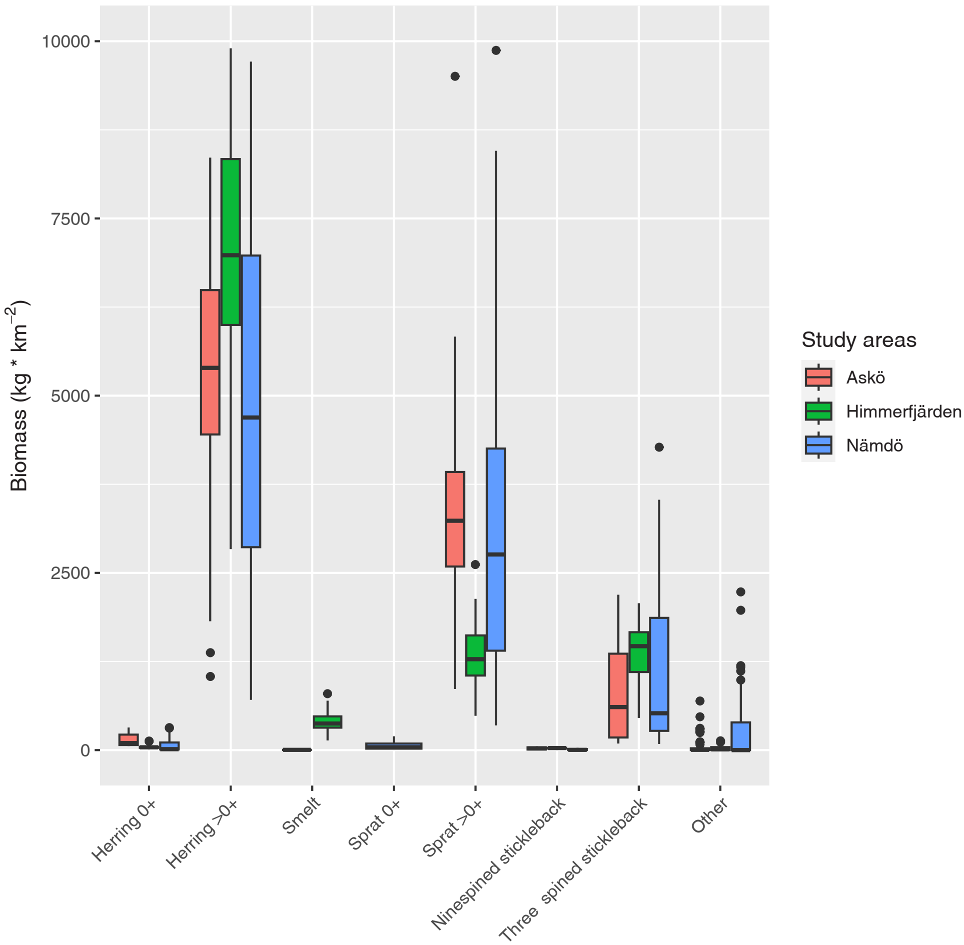

Fig. 4. Boxplots of biomass (kg per km^2) by fish species, estimated from hydroacoustics surveys for the study areas of Himmerfjärden, Askö, and Nämdö, August 4–6, 2021. Boxplots show median, interquartile ranges (box), ranges (vertical lines) and outliers (points).

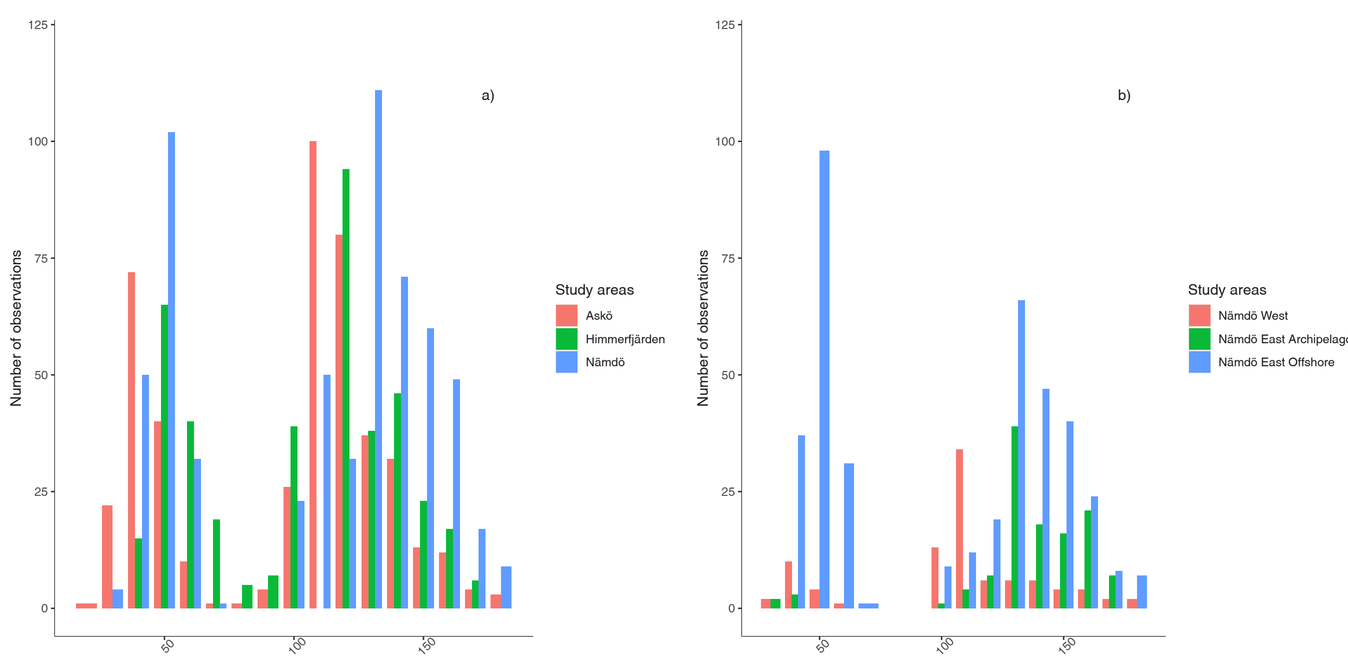

Fig. 5. a) Size distribution of herring in trawl hauls by study area: Askö, Himmerfjärden and Nämdö, August 4–6, 2021, b) size distribution of herring in trawl hauls in different parts of the Nämdö area, August 4–6, 2021.

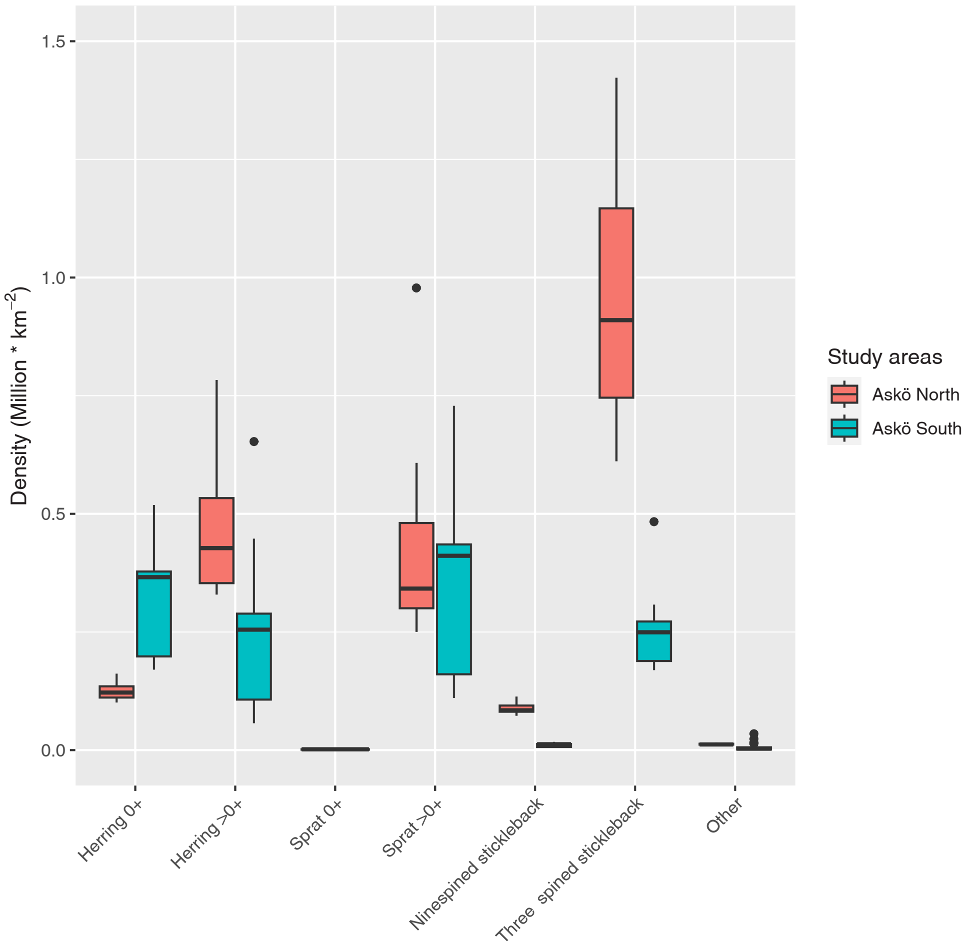

Fig. 6. Comparison of fish density (number per km^2), estimated from hydroacoustics surveys, between the northern, more sheltered, part and the southern, more open part of the Askö area in 2021 (see Fig. 2b). Boxplots show median, interquartile ranges (box), ranges (vertical lines) and outliers (points).

in 2021, calculated with trawl data and more up-to-date stringent settings for analyses, was higher than the estimated fish density in early August for 2000 and 2001 (Table 2). The size of the YOY herring in Himmerfjärden varied between 42 and 89 mm in August 2021 (Fig. 5a), corresponding to the period when they occurred in large numbers during the study period 2000–2001 (Fig. S3).

In spite of the observed changes in the species composition, the observed sA-value (nautical area scattering coefficient), representing the pelagic fish abundance, was in line with previous estimates at this time of the year (Table 2). In Axenrot and Hansson (2004), the seasonal dynamics in Himmerfjärden were followed from late May to November in 2000 and early May to mid-September in 2001; the highest values for fish abundance in both years were recorded in mid-August. We, therefore, chose to investigate the pelagic fish community in August in order to maximise the probability of encounter high YOY herring abundances. The corresponding s_A-value (average, 95 per cent confidence intervals) from the 2021 data (120 kHz) has been inserted into the diagram from Axenrot and Hansson (2004) for comparison reasons, showing similarity in sA-values (Fig. S3). In Axenrot and Hansson (2004), the results also presented fish densities calculated from sA-values and the size distribution of hydroacoustic single echo detections. The corresponding fish density (average, 95 per cent confidence intervals) from the 2021 data (120 kHz) has been inserted into the graph from Axenrot and Hansson (2004) for comparison reasons (Fig. S4).

The mean fish density (number per km^2) for the Himmerfjärden and Askö areas in mid-August through early September between 1985 and 2000 was estimated to be 1.045 million, with minimum and maximum densities at 0.280 and 2.198 million, respectively (Axenrot and Hansson, 2003). In 2021, the corresponding total fish density in early August was estimated at 1.707 million, according to hydroacoustic results with assigned trawl data. However, in this calculation, YOY herring accounted just for 0.158 million per km^2 (9.3 per cent), while three-spined stickleback accounted for 0.918 million per km^2 (53.8 per cent). Thus, corresponding figures for YOY herring during the peak period between 1985 and 2000 were, on average, ten times higher, whereas no sticklebacks were caught.

3.4. Temperature profiles

The temperature profile from each area is reported in appendix 1. The stratification of the water masses is usually strongest in July-September and is important for structuring the fish community. For example, YOY herring and sticklebacks occupy the upper warm water layer for fast growth and food resources.

4. Discussion

4.1. Changes in the fish community

Comparing the trawling results in 2002–04 and 2021 indicated two very different fish communities in the study areas (Table 1). In the Himmerfjärden-Askö area in 2021, three-spined stickleback strongly dominated in numbers. Sprat was more abundant in Askö S, closer to the offshore than in other areas. While YOY herring constituted 55 per cent of the trawl catches performed in 2002–2004 in the Himmerfjärden-Askö area, YOY herring only constituted 9.3 per cent of the pelagic fish

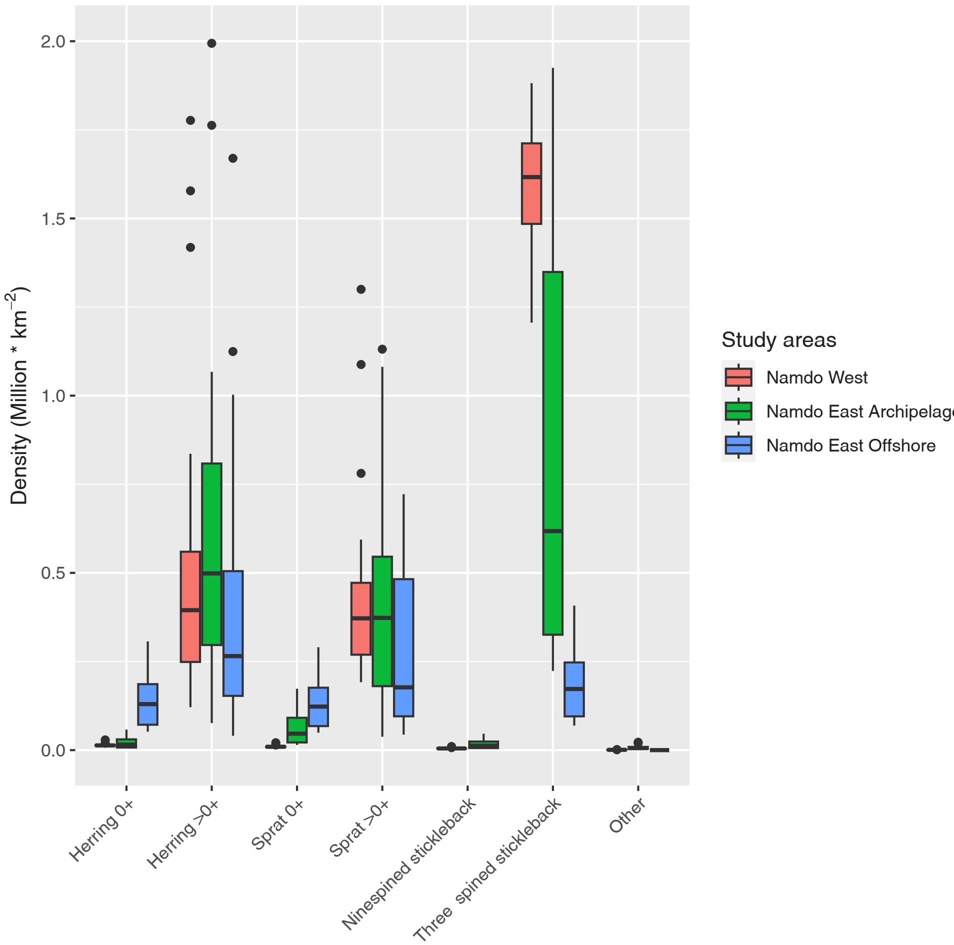

Fig. 7. Comparison fish density (number per km^2), estimated from hydroacoustics surveys, in the Nämdö area (Fig. 2c), August 4–6, 2021.

community in 2021.

We do not have the time series data to know when this change may have taken place. As presented in Axenrot and Hansson (2003), the year-class strength of the YOY herring can show variation between years. However, it is unlikely that the notable increase in population size of three-spined stickleback between 2003 and 04 and 2021 could have happened from one year to another. According to Olsson et al. (2019), there was a sharp increase in three-spined stickleback during 2011–14 in ICES subdivision 27 (SD 27), in which the areas Himmerfjärden and Askö are included. Furthermore, the fishing pressure on herring offshore the studied areas has increased sharply in recent years (Svedäng and Berkow, 2021).

Previous investigations showed a dominance of YOY herring in the coastal fish community (Rudstam et al., 1988, 1992; Hansson and Rudstam, 1995). The results from August trawling in Himmerfjärden 2002–04 showed that YOY herring made up over 50 per cent of the total number of fish (average for three years; Table 1), and according to Jensen et al. (2011), about 90 per cent could be assigned as fish < 90 mm. Thus, we may assume that the increase in hydroacoustic response and fish density, as reported in Axenrot and Hansson (2003, 2004), was related to the abundance of YOY herring. However, due to the significant change in the composition of the fish community between 2004 and 2021, the assumptions about the fish community made by Axenrot and Hansson (2003) concerning YOY herring abundance no longer hold. Hydroacoustic fish density as an index for coastal herring fry in the current areas (Axenrot and Hansson, 2003) has thus ceased to match the pelagic fish community in 2021.

In comparison of trawling catches, it should be noticed that the trawling in this study was conducted in early August, in contrast to previous studies, which were made from mid-August through September. However, in the previous studies sticklebacks were absent, and the abundance of YOY herring through August and September is influenced by counteracting factors such as mortality induced by predation, migration towards the offshore and the inflow of YOY herring as they become metamorphosised from larvae to juveniles.

Axenrot and Hansson (2003) estimated stock spawning biomass (SSB) in ICES SD 27 from 1985 to 2000 to an average of 130 693 tonnes. A similar estimation would suggest that SSB may have varied between 20 612 and 77 607 tonnes between 2019 and 2021. The decline in YOY herring in the present study could thus signal an ongoing erosion of the population structure (c.f. Smedbol and Stephenson, 2001). Herring is a species with a stock consisting of many spawning subpopulations (Sinclair, 1988). Han et al. (2021) have identified a high degree of genetic diversity connected to population richness within the Baltic Sea, partly confirming the previous identification of local and offshore herring spawning populations (Hessle, 1925, 1937; Otterlind, 1976; Rajasilta et al., 1993).

Sprat juveniles were only found close to the offshore and were absent in inshore areas. Since sprat reproduction in the northern Baltic Proper occurs in the pelagic and towards the Gulf of Finland, this pattern could be expected (Ojaveer and Kalejs, 2010).

4.2. Research needs

This study shows the need for regular monitoring; if carried out earlier, the change in the fish community could have been detected, planning management actions. Such monitoring is the prerequisite for understanding the reasons for (*i*) the observed change in which three-

Table 4
Summary of multivariate analysis of variance (MANOVA) model for arcsine transformed proportion of species (for herring divided between age = 0 + and age>0 +) per haul, *Prop,* with the period of sampling (*Time*) and *Species* as fixed factors: *Prop* ~*Time* + *Time*:*Species*. The number of iterations was set to 10,000. *p*-values are based on modified ANOVA-type statistics (MATS) for multivariate designs with metric data, and Wald-Type statistics (WTS) are shown for comparison reasons (see Friedrich and Pauly, 2018; Friedrich et al., 2021). *Time*: past (2002–2004) and present (2021). *Species*: Herring YOY, herring > 0 + , sprat, and stickleback (combined three-spined stand nine-spined stickleback).

Time	Species	n	Mean
Past	Herring > 0 +	9	0.051
Past	Herring YOY	9	0.213
Past	Sprat	9	0.077
Past	Stickleback	9	0.000
Present	Herring > 0 +	4	0.028
Present	Herring YOY	4	0.038
Present	Sprat	4	0.125
Present	Stickleback	4	0.321
Wald-Type Statistic (WTS):			
	Test statistic	df	p-value
Time	1.173	1	0.279
Species	10.3	3	0.016
Time:Species	17.59	3	0.001
Modified ANOVA-Type Statistic (MATS):			
Test statistic			
Time	1.173		
Species	10.300		
Time:Species	17.590		
p-values resampling:			
WildBS(WTS)		WildBS(MATS)	
Time	0.285		0.285
Species	0.062		0.062
Time:Species	0.002		0.002

spined stickleback – in terms of numbers – strongly dominate areas that were previously dominated by YOY herring, (*ii*) when, how, and why this change took place, as well as (*iii*) how does this affect today's recruitment of herring, e.g. through predation by three-spined stickleback on eggs and yearlings of herring (Kotterba et al., 2014, 2017).

Ongoing research also suggests that larger herring (>18 cm) consume three-spined stickleback – increasingly with increasing body size. Thus, a decline in larger-sized herring may also be a factor in the observed increase of three-spined stickleback (Olin et al., 2022).

5. Conclusions

Our study suggests that a severe decline in local/regional herring abundance has occurred within the stock unit area for CBH in parallel with a change in the fish community, which is in line with the coastal fishermeńs experiences. This decline deviates from the general understanding on the stock unit level. It is confirmed that such abundance reductions may result in shifts in dominance between fish species.

The signal of changes in the coastal fish community merits further investigations and monitoring, including studies on population structure.

CRediT authorship contribution statement

Authors' contributions. H.S., and G.A. coordinated the study, G.A., H.S., and T.A. designed the research; T.A. acquired and analysed the acoustic and trawling data; T.A., and H.S, analysed the data, all authors wrote the paper. All authors gave their final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial, interests or personal relationships that could have appeared to influence, the work reported in this paper. No conflict of interest has been identified.

Data Availability

Data will be made available on request. Older fishery data have been collected from referenced publications. Time series used in this study are available upon request to the corresponding author.

Acknowledgement

This study was partly financed by Nordic Environment Finance Corporation as fund manager with the respect to the HELCOM BSAP fund (BSAP-2021-142), and partly by the Swedish Agency for Marine and Water Management (SWAM). Project managers: Gustaf Almqvist, Stockholm County Administrative Board, and Henrik Svedäng, Stockholm University. Project leader Thomas Axenrot, Swedish University of Agricultural Sciences. The survey in 2021 was carried out on U/F Asterix. We are indebted to the personnel from SLU Aqua: Lars-Erik Wiberg (skipper), Olavi Kaljuste (field planning, hydroacoustics), Magnus Larsson and Rikard Yngwe (trawl, sorting of catch), Helena Strömberg and Malin Hällbom (field planning, sorting of catch), Lovisa Wennerström, (planning). We thank the participants from Stockholm University: Agnes Karlsson (planning) and John Taylor (sorting and analysis of yearlings of herring and sprat). We thank Niklas Larson (SLU Aqua) for data from BIAS 2021 and Magnus Larsson for producing the maps showing the acoustic transects and trawl hauls. We thank the two anonymous reviewers for their helpful comments.

Animal welfare

All experimental fishing were carried out according to the animal welfare regulations of SLU and EU directive for animal experiments. Ethical permit from the Swedish Animal Ethics Committee covered all experiments reported here, diary number 5.8.18–10169/2019.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2023.106780.

References

Aglen, A., 1983. Random errors of acoustic fish abundance estimates in relation to the survey grid density applied. FAO Fish. Rep. 300, 293–297.
Aneer, G., 1989. Herring (*Clupea harengus* L.) spawning and spawning ground characteristics in the Baltic Sea. Fish. Res. 8, 169–195. https://doi.org/10.1016/0165-7836(89)90030-1.
Anonymous. 2022. Baltic International Acoustic Survey, October 2021 – R/V Svea, Sweden, 23p. Report 2022:18. ISBN: 978–91-576–9995-4.
Arnold, T.B., Emerson, J.W., 2022. Discrete goodness-of-fit tests. (Version 1.4) R Core Team. 〈https://cran.r-project.org/〉.
Arrhenius, F., Hansson, S., 1993. Food consumption of larval, young and adult herring and sprat in the Baltic Sea. Mar. Ecol. Prog. Ser. 96, 125–137. 〈https://www.jstor.org/stable/24833538〉.
Axenrot, T., Hansson, S., 2003. Predicting herring recruitment from young-of-the-year densities, spawning stock biomass, and climate. Limnol. Oceanogr. 48, 1716–1720. https://doi.org/10.4319/lo.2003.48.4.1716.
Axenrot, T., Hansson, S., 2004. Seasonal dynamics in pelagic fish abundance in a Baltic Sea coastal area. Estuar. Coast. Shelf Sci. 60, 541–547. https://doi.org/10.1016/j.ecss.2004.02.004.
CEN [Comité Européen de Normalisation (European Committee for Standardization)]. 2014. Water quality – Guidance on the estimation of fish abundance with mobile hydroacoustic methods. EN 15910.
Didrikas, T., Hansson, S., 2004. In situ target strength of the Baltic Sea herring and sprat. ICES J. Mar. Sci. 61, 378–382. https://doi.org/10.1016/j.icesjms.2003.08.003.
Eklöf, J., Sundblad, G., Erlandsson, M., Donadi, S., 2020. A spatial regime shift from predator to prey dominance in a large coastal ecosystem. Commun. Biol. 3, 459. https://doi.org/10.1038/s42003-020-01180-0.
Foote, K.G., Knudsen, H.P., Vestnes, G., MacLennan, D.N., Simmonds, E.J., 1987. Calibration of acoustic instruments for fish density estimation: a practical guide. ICES Coop. Res. Rep. 144, 57.

Fréon, P., Misund, O.A., 1999. Dynamics of Pelagic Fish Distribution and Behaviour: Effects on Fisheries and Stock Assessment. Fishing News Books. Blackwell Science Ltd, Oxford, p. 348.
Friedrich, S., Pauly, M., 2018. MATS: Inference for potentially singular and heteroscedastic MANOVA. J. Multivar. Anal. 165, 166–179. https://doi.org/10.1016/j.jmva.2017.12.008.
Friedrich, S., Konietschke, F., Pauly, M., 2022. Resampling-based analysis of multivariate data and repeated measures designs. (Version 0.5.3) 〈https://github.com/smn74/MANOVA.RM〉.
Guillard, J., Lebourges-Daussy, A., Balk, H., Colon, M., Jóźwik, A., Godlewska, M., 2014. Comparing hydroacoustic fish stock estimates in the pelagic zone of temperate deep lakes using three sound frequencies (70, 120, 200 kHz). Inland Waters 4, 435–444 https://DOI.org/10.5268/IW-4.4.733.
Han, F., Jamsandekar, M., Pettersson, M.E., Su, L., Fuentes-Pardo, A.P., Davis, B.W., Bekkevold, D., Berg, F., Casini, M., Dahle, G., Farrell, E.D., Folkvord, A., Andersson, L., 2021. Ecological adaptation in Atlantic herring is associated with large shifts in allele frequencies at hundreds of loci. eLife 2020 (9), e61076. https://doi.org/10.7554/eLife.61076.
Hansson, S., 1993. Variation in hydroacoustic abundance of pelagic fish. Fish. Res. 16, 203–222. https://doi.org/10.1016/0165-7836(93)90094-N.
Hansson, S., Rudstam, L.G., 1995. Gillnet catches as an estimate of fish abundance: a comparison between vertical gillnet catches and hydroacoustic abundances of Baltic Sea herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). Can. J. Fish. Aquat. Sci. 52, 75–83. https://doi.org/10.1139/f95-007.
Hessle, C., 1925. The herrings along the Baltic coast of Sweden. Publ. Circ. Cons. Int. Explor. Mer. 89, 55.
Hessle, C., 1937. Undersökningar över strömmingen i Stockholms skärgård. Sven. Hydrogr. -Biol. Komm. Skr. Ser. Biol. 2 (2), 21 ([in Swedish]).
Huse, I., Korneliussen, R., 2000. Diel variation in acoustic density measurements of overwintering herring (*Clupea harengus* L.). ICES J. Mar. Sci. 57, 903–910. https://doi.org/10.1006/jmsc.2000.0577.
ICES, 2021. Baltic Fisheries Assessment Working Group (WGBFAS). ICES Sci. Rep. 3 (53), 717. https://doi.org/10.17895/ices.pub.8187.
Jensen, O.P., Hansson, S., Didrikas, T., Stockwell, J.D., Hrabik, T.R., Axenrot, T., Kitchell, J.F., 2011. Foraging, bioenergetic and predation constraints on diel vertical migration: field observations and modelling of reverse migration by young-of-the-year herring *Clupea harengus*. J. Fish. Biol. 78, 449–465. https://doi.org/10.1111/j.1095-8649.2010.02855.x.
Jurvelius, J., Leinikki, J., Mamylov, V., Pushkin, S., 1996. Stock assessment of pelagic three-spined stickleback (*Gasterosteus aculelatus*): a simultaneous up- and down-looking echo-sounding study. Fish. Res. 27, 227–241. https://doi.org/10.1016/0165-7836(95)00464-5.
Kotterba, P., Kuhn, C., Hammer, C., Polte, P., 2014. Predation of three-spined stickleback (*Gasterosteus aculeatus*) on eggs of Atlantic herring (*Clupea harengus*) in a Baltic Sea region. Limnol. Oceanogr. 59, 578–587. https://doi.org/10.4319/lo.2014.59.2.0578.
Kotterba, P., Moll, D., von Nordheim, L., Peck, M.A., Oesterwind, D., Polte, P., 2017. Predation on larval Atlantic herring (*Clupea harengus*) in inshore waters of the Baltic Sea. Estuar. Coast. Shelf Sci. 198, 1–11. https://doi.org/10.1016/j.ecss.2017.08.017.
Larson, N., 2020. Baltic International Acoustic Survey report, October 2019. Aqua reports2020:10 Swedish University of Agricultural Sciences, Lysekil, 20 pp.
Larson, N., 2021. Baltic International Acoustic Survey report, October 2020. Aqua reports 2021:21 Swedish University of Agricultural Sciences, Lysekil, 21 pp.
Larson, N., 2022. Baltic International Acoustic Survey report, October 2021. Aqua reports 2022:18. Swedish University of Agricultural Sciences, Lysekil, 21 pp.
Mouget, A., Goulon, C., Axenrot, T., Balk, H., Lebourges-Dhaussy, A., Godlewska, M., Guillard, J., 2019. Including 38 kHz in the standardization protocol for hydroacoustic fish surveys in temperate lakes. Remote Sens. Ecol. Conserv 5, 332–345. https://doi.org/10.1002/rse2.112.
Ojaveer, E., Kalejs, M., 2010. Ecology and long-term forecasting of sprat (*Sprattus sprattus balticus*) stock in the Baltic Sea: a review. Rev. Fish. Biol. Fish. 20, 203–217. https://doi.org/10.1007/s11160-009-9130-5.
Olin, A.B., Olsson, J., Eklöf, J.S., Eriksson, B.K., Kaljuste, O., Briekmane, L., Bergström, U., 2022. Increases of opportunistic species in response to ecosystem change: the case of the Baltic Sea three-spined stickleback. ICES J. Mar. Sci. 79, 1419–1434. https://doi.org/10.1093/icesjms/fsac073.
Olsson, J., Jakubavičiūtė, E., Kaljuste, O., Larsson, N., Bergström, U., Casini, M., Cardinale, M., Hjelm, J., Byström, P., 2019. The first large-scale assessment of three-spined stickleback (*Gasterosteus aculeatus*) biomass and spatial distribution in the Baltic Sea. ICES J. ICES J. Mar. Sci. 76, 1653–1665. https://doi.org/10.1093/icesjms/fsz078.
Otterlind, G., 1976. Fish stocks and fish migration in the Baltic Sea environment. Ambio Spec. Rep. 4, 89–101.
Parmanne, R., Rechlin, O., Sjöstrand, B., 1994. Status and future of herring and sprat stock in the Baltic Sea. DANA J. Fish. Mar. Res. 10, 29–59.
Rajasilta, M., Eklund, J., Hänninen, J., Kurkilahti, M., Kääriä, J., Rannikko, P., Soikkeli, M., 1993. Spawning of herring (*Clupea harengus membras* L.) in the Archipelago Sea. ICES J. Mar. Sci. 50, 233–246. https://doi.org/10.1006/jmsc.1993.1026.
Rudstam, L.G., Lindem, T., Hansson, S., 1988. Density and in situ target strength of herring and sprat: a comparison between two methods of analyzing single-beam sonar data. Fish. Res. 6, 305–315. https://doi.org/10.1016/0165-7836(88)90001-X.
Rudstam, L.G., Hansson, S., Johansson, S., Larsson, U., 1992. Dynamics of planktivory in a coastal area of the northern Baltic Sea. Mar. Ecol. Prog. Ser. 80, 159–173.
Rudstam, L.G., Hansson, S., Lindem, T., Einhouse, D.W., 1999. Comparison of target strength distributions and fish densities obtained with split and single beam echo sounders. Fish. Res. 42, 207–214. https://doi.org/10.1016/S0165-7836(99)00047-8.
Simmonds, J., MacLennan, D., 2005. Fisheries acoustics: theory and practice. Blackwell, Oxford.
Sinclair, M., 1988. Marine Populations: An Essay on Population Regulation and Speciation. University of Washington Press, Seattle.
Smedbol, R.K., Stephenson, R., 2001. The importance of managing within-species diversity in cod and herring fisheries of the north-western Atlantic. J. Fish. Biol. 59, 109–128. https://doi.org/10.1111/j.1095-8649.2001.tb01382.x.
Sokal, R.S., Rohlf, F.J., 1981. Biometry. W. H. Freeman, San Francisco.
Svedäng, H., Bardon, G., 2003. Spatial and temporal aspects of the decline in cod (*Gadus morhua* L.) abundance in the Kattegat and eastern Skagerrak. ICES J. Mar. Sci. 60, 32–37.
Svedäng, H., Rolff, C., 2021. Fisket i Stockholms skärgård under historisk tid. Havsmiljöinstitutets Rapport nr 2021:3 Havsmiljöinstitutet. 70 p. [in Swedish with English summery] 〈https://havsmiljoinstitutet.se/projekt/det-historiska-fisket-i-stockholms-skargard〉.
Svedäng, H., Berkow, C., 2021. Reduce coastal trawling to protect the Baltic herring. 2021–03-09. 4 p. Stockholm University: Stockholm 〈https://www.su.se/stockholm-university-baltic-sea-centre/policy-analysis/policy-briefs-and-fact-sheets/reduce-coastal-trawling-to-protect-the-baltic-herring-1.590918〉.
Yule, D.L., Adams, J.V., Hrabik, T.R., Vinson, M.R., Woiak, Z., Ahrenstorff, T.D., 2013. Use of classification trees to apportion single echo detections to species: application to the pelagic fish community of Lake Superior. Fish. Res. 140, 123–132. https://doi.org/10.1016/j.fishres.2012.12.012.