DTU Aqua
National Institute of Aquatic Resources

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Anders Nielsen, Bjarne Stage, Casper Berg, Christoffer M. Albertsen, Dorte Bekkevold, Eva Maria Pedersen, Henrik Mosegaard, Julie O. Davies, Kirsten B. Håkansson, Rebekka A. Rudolph, Sissel K. Bertelsen, Tommy Norin and Vanessa Trijoulet

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Colophon

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Preface

This report documents the results achieved in connection with the project Rebuilding Western Baltic spring spawning herring (acronym GENBYGSILD) funded under the European Maritime and Fisheries Fund (EMFF) with contract no. 33113-B-20-174. The project's work builds on results obtained in connection with the EMFF projects Pelagic Species (PELA) with contract no. 33113-B-19-154 and Distribution of Mackerel, Sprat, and Herring Stocks (MAKSIBRI) with contract no. 33113-B-16-065.

DTU Aqua was the project leader and received consultancy assistance from the Danish Pelagic Producers Organisation (DPPO) and the Danish Fishers Producers Organization (DFPO). The project also included collaboration with the Swedish University of Agricultural Sciences, SLU, in Lysekil, Sweden, and with the Thünen Institute of Baltic Sea Fisheries in Rostock, Germany. The report is partially written in Danish.

Silkeborg, December 2024

Dorte Bekkevold
Senior researcher, Project Leader

European Union
European Maritime and Fisheries Fund

HAV & FISK

Content

Summary

This report details results generated in connection with the European Marine Fisheries Fund funded project GENBYGSILD (English title: Rebuilding Western Baltic spring spawning herring). The aims of GENBYGSILD were to: Improve knowledge about biology (spawning timing, areas, distribution of biologically unique sub-stocks, sub-stock specific migrations, and potential drivers) of herring populations spawning in the Western Baltic Sea (Western Baltic Spring Spawning, abbreviated WBSS, herring) in the area spanning from the Skagerrak-Kattegat-Danish Belt Sea to the western parts of the Baltic Sea, perform quality control and critical evaluation of stock assessment models, and re-evaluate biological reference points, and develop management strategies that incorporate rebuilding plans for WBSS herring. DTU Aqua was the main project leader, with contributions from Danish Fishers Producers Organisation and Danish Pelagic Producers Organisation. The project also incorporated collaborations with international institutions Swedish University of Agricultural Sciences in Sweden and Thünen Institut für Ostseefischerei in Germany.

1. Knowledge base

1.1 Literature review

1.1.1 Introduction to assessment of WBSS herring

Many herring populations exhibit migratory behaviour, often gathering at shared feeding and wintering grounds, forming aggregations comprising individuals from various populations. Consequently, herring spawning groups maintain significant reproductive isolation, potentially influenced by selective differences in spawning and larval habitats (Limborg et al., 2012). The presence of genetic stratification is likely sustained through mechanisms such as natal homing, larval retention, and natural selection (Gaggiotti et al., 2009).

In the Western Baltic, tagging and genetic studies indicate the existence of three to four distinct stock components with well-defined characteristics. These components include Rügen herring (RH), local (autumn) spawning Fehmarn herring, herring from the Kattegat and Inner Danish waters, and potentially other Western Baltic herring stocks. Each of these stocks contributes differently to both the fishery and the ecosystem. Rügen herring is believed to comprise the majority of the Western Baltic Sea herring, particularly around the Geifswald Bay, with spawning occurring mainly from March to May, along with some autumn spawning (e.g., Nielsen et al., 2001; Bekkevold et al., 2007).

Other herring populations in the area are dispersed across various bays, including Kiel, Møn, Schlei, Flensburg, Fåborg, and Fehmarn, identified as spawning sites for these seemingly less abundant herring stocks. Consequently, the Western Baltic Spring Spawners (WBSS) stock is characterized by a complex mixture of different herring populations, predominantly spawning during spring but also featuring local spring, autumn, and winter spawning components. Although the precise proportions of these stocks remain unknown, their presence in the area is observed to some extent, suggesting their potential significance in the overall herring available for fisheries. These components mix and migrate during the year, but are all assessed and managed as one stock: the WBSS stock. Fishing activities targeting the WBSS are conducted in the eastern North Sea, specifically in Division 3.a, as well as in the Western Baltic. In the eastern North Sea and Division 3.a, the WBSS stock complex interacts with another significant herring stock complex known as the North Sea Autumn Spawners (NSAS). Despite the diverse local stocks, all spring-spawning herring in the eastern part of the North Sea (4.a & 4.b east), Skagerrak (Subdivision 20), Kattegat (Subdivision 21), and the Western Baltic (Subdivisions 22, 23, and 24) are collectively treated as a single stock.

Given the intermingling with the NSAS, the ICES Herring Assessment Working Group (HAWG) utilizes regularly collected biological samples to estimate the composition of the annual catches and assess the stock.

1.1.2 Stock splitting

The analysis of stock composition in commercial samples for stock assessment and management purposes of the herring populations in the North Sea and adjacent areas has been routine since the beginning of the 1990s.

The method for separation of the herring stock components in the catches has developed over the past decade. Prior to 1996, the splitting key between NSAS and WBSS herring used by ICES was calculated from a sample-based mean vertebral count. In the period from 1996 to 2001 splitting keys were constructed using information from a combination of vertebrae count and otolith microstructure (OM) methods. From 2001 and up to 2021, the splitting keys for division 3a and Danish catches in division 4a east have been constructed solely using the otolith microstructure method which uses visual inspection of season-specific daily increment patterns from the larval origin of the otolith supported by measurements of daily increment widths at predefined distances from the core (Mosegaard and Madsen, 1996; ICES, 2004; Clausen et al., 2007). With effect from the assessment in 2022, Denmark and Norway discontinued their previous sampling and data collection method in favour of stock classification with genetic markers.

1.2 Case studies (partly in Danish)

In connection with a request for advice on the status and fishing opportunities on herring in the Limfjord the following case study was produced.

The fact that Limfjord herring falls within the quota management area of the North Sea contradicts biological knowledge. The primarily spring-spawning Limfjord herring and the North Sea's autumn-spawning herring belong to distinct, reproductively separate populations with different population dynamics.

Additionally, it's concluded that the population dynamics of Limfjord herring differ from the majority of the total population of Western Baltic spring-spawning herring (to which Limfjord herring is closely related genetically) due to higher growth and delayed maturation. Limfjord herring indicates prolonged migrations to the northeast North Sea, primarily entering from the North Sea to spawn in the Limfjord in spring.

There's a possibility that the relatively high catches during 2004-2006 might have exceeded the biologically sustainable limit for the population, contributing to a decline and subsequent lower catches around 2010-2011.

Catches from 2012-2014 and 2016 were high but lower than the allocated Limfjord quota, possibly surpassing the population's carrying capacity during that period.

From 2017-2021, catches have been low, reflecting the ability under specific circumstances to move Individual Fishing Opportunities (IOKs) to fishing in the North Sea outside the Limfjord. However, the permitted catches in the Limfjord (as a percentage of the North Sea autumn-spawning herring quota), in relation to the population, were nominally high enough that equivalent yearly catches would likely have collapsed the population if taken (refer to Annual Catch > Spawning Stock Biomass in table 1.2.1).

Data for a quantitative analysis of the population development, especially post-2016, are lacking. However, the general situation for the Western Baltic Spring Spawning (WBSS) herring population is assessed to be far below the minimum reference point for spawning stock biomass (Blim). The declining proportion of herring from the sub-stock that spawns in Danish fjords (DK-herring) does not suggest that Limfjord herring is in a better condition than WBSS herring overall. Even after rebuilding, the linkage to the North Sea quota would allow a fishing pressure far exceeding what would correspond to sustainable catches (MSY) for the Limfjord population.

The assessment is that the current limited fishing in the Limfjord does not pose a risk to an existing population of about 5% of the total WBSS herring. It is emphasized that targeted monitoring would contribute to a more accurate determination of a sustainable herring fishery level in the Limfjord.

A detailed account of the underlying data and analyses underlying the advice follows here (in Danish):

Besvarelse

1. Det faktum at silden i Limfjorden er i kvoteforvaltningsområde med Nordsøen, er ikke i overensstemmelse med den biologiske viden, da den, primært forårsgydende, Limfjordssild og Nordsøens efterårsgydende sild (NSAS) tilhører to biologisk meget forskellige bestande, der er reproduktivt helt adskilte og heller ikke følger hinanden i bestandsdynamik.

2. Det samtidig også konkluderes at Limfjordssildens bestandsdynamik adskiller sig fra hovedparten af samle-bestanden af forårsgydende vestlige Østersøsild (WBSS, som Limfjordssilden er genetisk nært beslægtet med) gennem en højere vækst og senere kønsmodning. Limfjordssilden har indikationer på lange fødevandringer til den nordøstlige Nordsø og trækker formodentlig i overvejende grad ind fra Nordsøen for at gyde i Limfjorden om foråret.

3. Det kan ikke udelukkes at de relativt store fangstmængder i sildefiskeriet i Limfjorden fra 2004-2006 har oversteget hvad der var biologisk bæredygtigt for bestanden og var medvirkede til en bestandsnedgang og deraf følgende lavere fangster omkring 2010-2011.

4. Fangsterne fra 2012-2014 og i 2016 var høje, men lavere end hvad den afsatte kvote i Limfjorden tillod, og har muligvis oversteget bestandens bæreevne i perioden.

5. Fra 2017-2021 har fangsterne været lave og afspejlet muligheden for under særlige omstændigheder at flytte IOK'er til fiskeri i Nordsøen uden for Limfjorden. Derimod har de tilladte fangster i Limfjorden (som promille af NSAS kvoten), i forhold til

bestanden, nominelt været så høje at fangster svarende til årsmængder sandsynligvis ville have fået bestanden til at bryde sammen, hvis fangsterne var blevet taget. (se Års-Mgd.>SSB i tabel 1.2.1).

6. Der savnes data til en kvantitativ analyse af bestandsudviklingen især i årene efter 2016; men den generelle situation for den forårsgydende vestlige Østersøsild (WBSS) er en bestand som bedømmes til langt under minimum-referencepunktet for gydebiomasse (B_{lim}). De faldende andele sild fra den del-bestand, der gyder i de danske fjorde og bælter (DK-sild) tyder ikke på, at Limfjordsilden er i en bedre tilstand end WBSS-silden generelt. Selv efter genopbygning vil koblingen til Nordsøkvoten muliggøre et forhøjet fiskeritryk langt over, hvad der ville svare til langsigtet bæredygtige fangster (MSY) for Limfjordsbestanden.

7. Det er vurderingen, at det nuværende begrænsede fiskeri i Limfjorden ikke udgør en fare for en eksisterende bestand af størrelsesordenen 5% af den samlede WBSS-sild. Det påpeges, at en målrettet monitering vil bidrage til en sikrere fastsættelse af niveauet for et bæredygtigt sildefiskeri Limfjorden.

Metode

Til vurdering af Limfjordssildens tilstand og udvikling samt fiskerimulighederne på bestanden i Limfjorden er der blevet brugt litteratur, ICES rapporter og ICES rådgivning, Fiskeristyrelsens dynamiske tabeller og IOK-oversigter samt indsamlede biologiske data fra fiskeri og togter fra 1978-2021, samt ikke mindst information fra fiskere, om fiskeriets karakter og udvikling i Limfjorden. Biologiske data i form af størrelse, alder, modenhed, køn, hvirveltal og parasitter samt populationsgenetiske analyser af prøver holdt op mod basisprøver fra en lang række gydebestande er blevet anvendt.

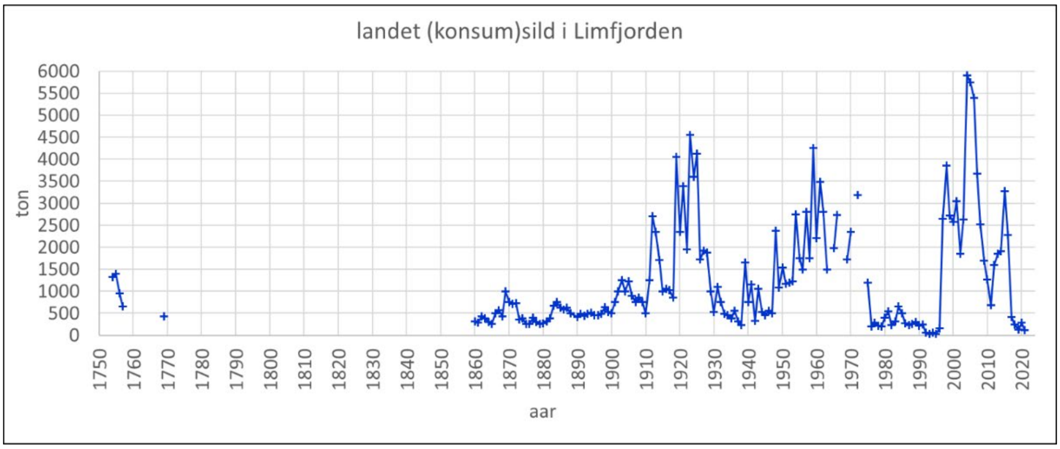
Baggrund

Fiskeri

Der har i århundreder foregået et vigtigt fiskeri efter sild i Limfjorden [10,15] hvor fangster har nået op til 6000 t årligt (figur 1.2.1). Fiskeriet var i tidligere tider reguleret lokalt, men Forvaltningsmæssigt henføres Ringkøbing Fjord, Nissum Fjord og Limfjorden nu til ICES-underområde IV b, der omfatter Nordsøen mellem 57°30' nordlig bredde og 53°30' nordlig bredde.

Der blev indført Individuelt overdragelige kvoteandele (IOK) for sild i 2003. Fra 2007 blev det muligt at overføre 25% af Limfjordskvoten til fiskeri uden for Limfjorden i Nordsøen. Fra 31. maj 2016 har det været muligt at overføre op til 100% af årsmængderne til fiskeri uden for Limfjorden i Nordsøen, for fartøjer hvor en fisker er ejer eller medejer af både det afgivende og det modtagende fartøj. 31. maj ligger senere end det typiske forårsfiskeri i Limfjorden.

Fiskeriet efter konsumsild i Limfjorden har varieret meget gennem tiden. Efter stoppet for sildefiskeri i Nordsøen 1977 var der kun lave fangster i en 20-årig periode, hvoraf en del sandsynligvis var forårsaget af et ødelagt marked med urentabelt fiskeri efter sildestoppet. Efter 1992 skete en stor ændring i fiskeriet efter bundlevende fisk bl.a. rødspætte hvor fangsterne reduceredes stærkt i forhold tidligere år, sammenfaldende med et regimeskift pga. de fysisk-kemiske forhold i fjorden [12,14]. Foruden et målrettet fiskeri til konsum tages også mindre mængder sild som bifangst i industrifiskeriet efter brisling i Limfjorden.



Figur 1.2.1 Landinger af konsumsild fra Limfjorden. Rekonstrueret fra [10, 12] og efter 2001 ud fra Fiskeristyrelsens dynamiske tabeller.

Fiskernes egne observationer

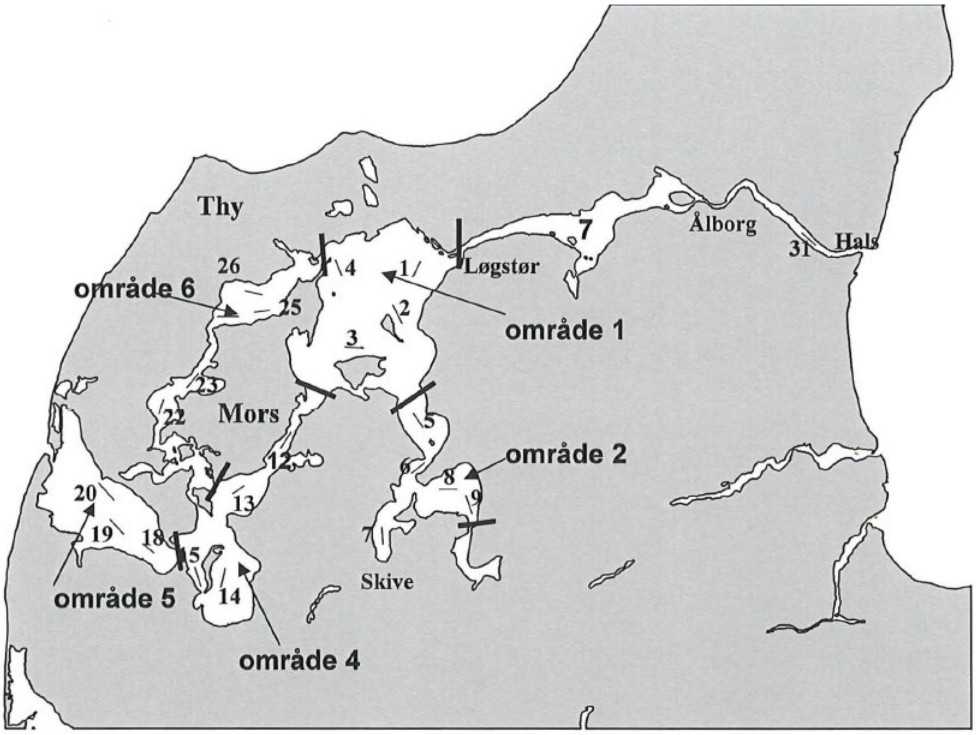
Gennem en konsultation med lokale fiskere er hovedtrækkene for de seneste tre årtiers fiskeri i Limfjorden sammenfattet. I slutningen af 1980'erne og begyndelsen 1990'erne blev et mindre sildefiskeri bedrevet med små trækuttere. I 1996 blev der genetableret et intensivt fiskeri af et antal oprustede partrawlere i 3-4 sjak, som ledte til historisk høje landinger de næste 20 år dog med et enkelt dyk fra 2006 til 2011. Yderligere blev sildefangsterne i 2013 landet som industrifisk pga. meget lave priser på konsumsild. Fiskeriet startede typisk kystnært i Nordsøen uden for Harboøre i januar, hvor silden på sin gydevandring samledes inden indtoget i Limfjorden. I marts og april kunne fiskerne derefter fange silden under vandringen stadig længere mod øst ind i fjorden. De fangede sild var store (180-200 g) og gydeklare, men forsvandt så snart gydningen var overstået. Der blev også fortalt om mindre sild som kom ind øst fra og ikke blandede sig med de vestligt indvandrede.

Fra 2017 og frem til i dag har de årlige landinger fra Limfjorden været lave, efter nogle fiskeres mening pga. af manglende indvandring af gydesild samt mindsket indsats pga. kompensationsmuligheden for overførsel af fangsterne til Nordsøen. Der blev f.eks. i 2021 overført 3.251.626 kg sild fra Limfjorden til Nordsøen. Fiskernes oplysninger tyder på at gydeklare sild vest for Løgstør formodentlig i overvejende grad trækker ind fra Nordsøen for at gyde i Limfjorden om foråret i marts og april.

Togter

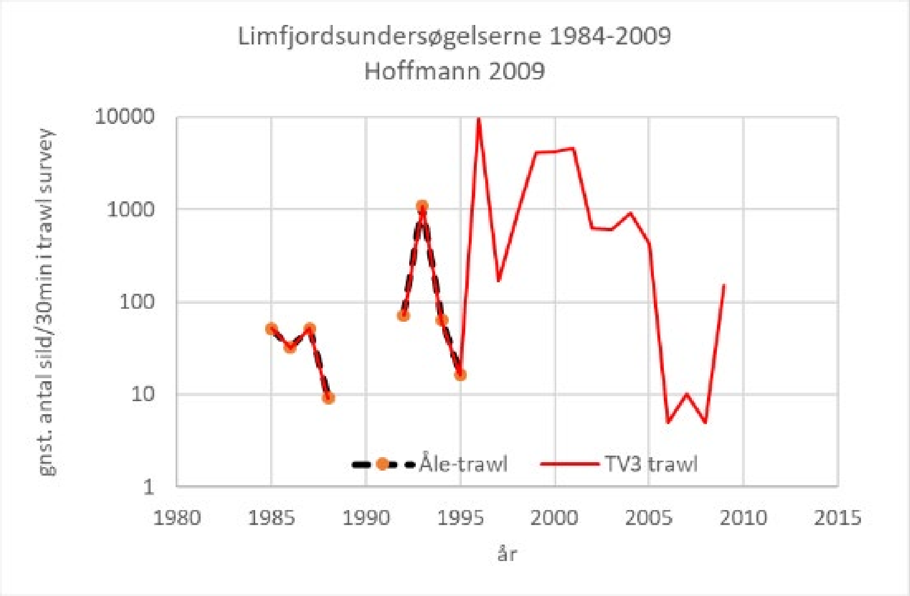
Der er i perioden 1984-2014 hvert efterår gennemført et trawltogt til monitering af de forskellige fiskebestande i Limfjorden, hvor også den juvenile sildebestands udbredelse og mængde er blevet kvantificeret [11,12,13]. Der blev i starten brugt et kommercielt Glyngøre åletrawl som i 1996 blev erstattet af TV3-trawlet, som er bedre til at fange pelagiske arter som sild og brisling. Figur 1.2.3 viser antal sild pr. 30 min træk med åletrawl 1984-1995 og

TV3-trawl 1996-2009. Det har ikke været muligt at estimere den relative effektivitetsøgning ved fiskeri efter 0-1 årig sild i Limfjorden efter overgang til TV3 trawl.



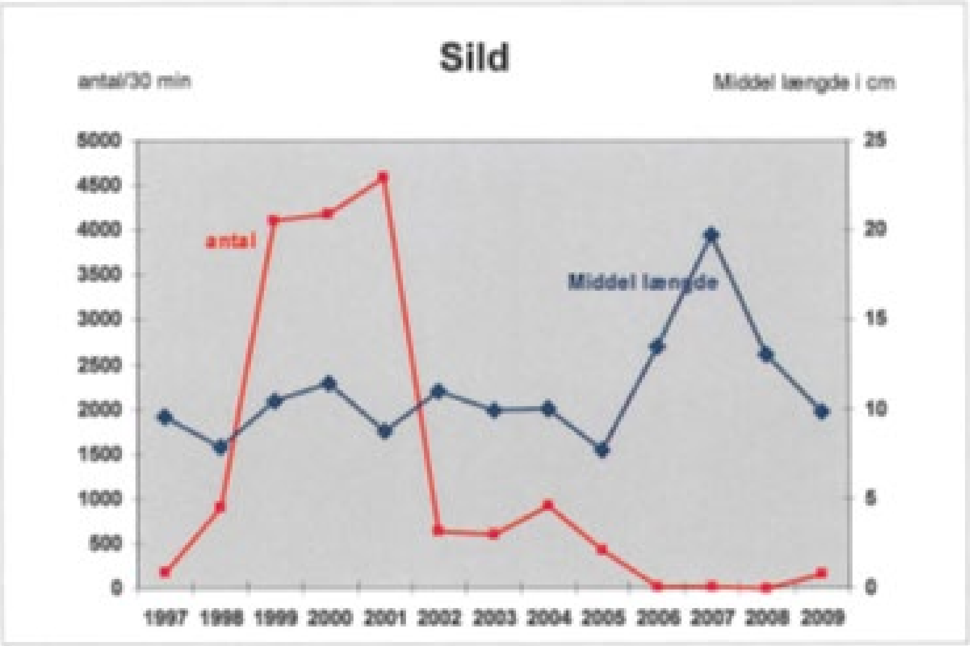
Figur 1. Standard-trawlstationer fra 1980 og frem samt områderne 1, 2, 4, 5, 6 og 7. Område 3 Hjarbæk Fjord med stationerne 10 og 11 benyttes ikke mere. Det samme gælder for en station nr. 17 nord for Jegindø samt st.nr.16 syd for station 14.

Figur 1.2.2. Kort over trawlstationerne i Limfjorden, efter [13].



Figur 1.2.3 Antal sild pr. 30 min træk (logaritmisk skala) med åletrawl 1984-1995 og TV3-trawl 1996-2009, efter [11,12,13].

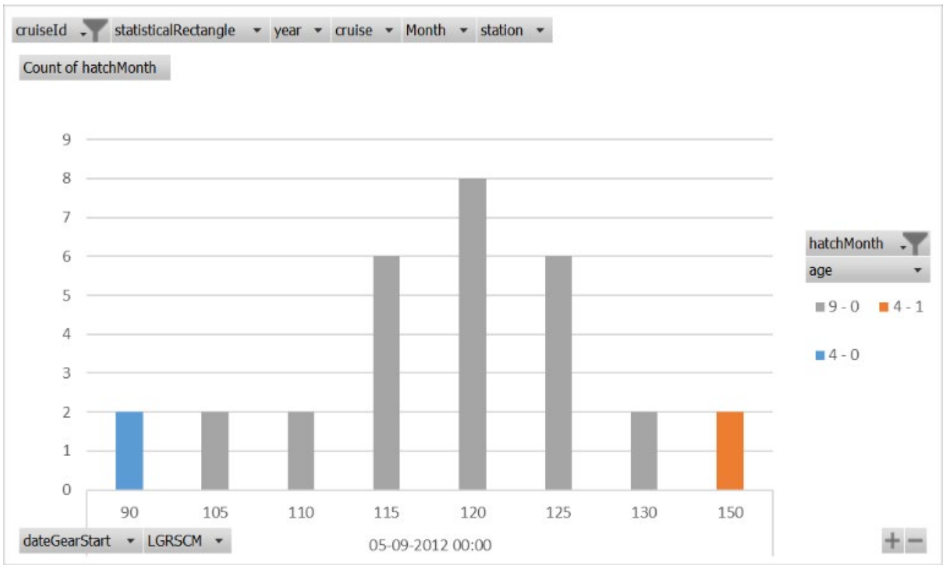
Hoffmann konkluderer i 2009 i en upubliceret rapport [13]; *"Der blev i september 2009 udtaget prøver af øresten (otolither) af sild fra en række stationer fordelt i fjorden. En analyse af ringstrukturen i ørestenene viste overraskende, at prøverne stammede fra både efterårs- og forårsgydende sild. Dette er nyt, idet det tidligere er antaget, at der kun forekommer forårsgydende sild i fjorden. De observerede efterårsgydere var alle mellem 10 og 14 cm, hvorimod alle sild mindre end 10 cm og større end 16 cm var forårsgydere. Forholdene undersøges fortsat, blandt andet ved at gennemgå ældre materiale indsamlet fra konsumfiskeriet efter sild. De efterårsgydende sild var i øvrigt karakteristiske ved at være mere blå hen over ryggen end de forårsgydende. Hvorvidt sildene er gydt inde i fjorden eller tilhører Nordsøens store stamme af efterårsgydende sild er uklart." … "Karakteristisk for forsøgsfiskeriet siden 2005 har været mangel på helt små sild i størrelsen 8 – 12 cm. dvs. årsyngel. Figur 1.2.4* (kopieret fra [13] ed.) *viser samlede fangster af sild pr. 30 min. samt middellængden af sild det pågældende år. Det fremgår med stor tydelighed, at der overvejende kun er fanget få, (men) store sild siden 2005, samtidig med at antallet af små sild er gået stærkt tilbage. Først i 2009 fanges der igen små sild. Efter det nu er påvist, at der i fjorden i september forekommer små sild, der er en blanding af forårs- og efterårsgydere, er det vanskeligt at udtale sig om årsagerne til nedgangen i småsild. Dog må det antages, at gydningen inde i fjorden (forår) har været mindre succesfuld, hvilket også hænger noget sammen med en samtidig manglende gyde-succes for silden i Nordsøen som helhed. Der er taget initiativer til at få disse forhold undersøgt grundigere, især da det har interesse i forhold til forvaltningen af sildefiskeriet i fjorden."*



Figur 4. Fangst af sild i forsøgsfiskeriet samt gennemsnitslængde 1997 – 2009.

Figur 1.2.4 Fangst af sild i forsøgsfiskeriet samt gennemsnitslængde 1997-2009

En analyse af en indsamling af prøver fra industrifiskeriet i 2012 viser resultater i samme retning som [13] med en stor andel juvenile fra en efterårsgydende bestand (figur 1.2.5).



Figur 1.2.5. Længdefordeling af juvenil sild i september 2012 fra såvel forårsklækkede 0 og 1-årige sild (4-0 blå og 4-1 orange) samt efterårsklækkede 0-årig sild (9-0 grå).

Ændringer af trawltype i 1996, stigende mængder forkastede trawl-træk efter år 2000 pga. gopler, og usikkerhed omkring gydetype for de juvenile leder til stor usikkerhed på selv de relative estimater af de juvenile årsklasser. Akustiske undersøgelser anses generelt for at give gode estimater af biomasse på sild [1]. Pedersen [10] estimerede biomassen for juvenil sild (0-1 år) i Limfjorden i september 1995 til 1500 tons. Der kan dog sættes spørgsmålstegn ved sikkerheden i aldersanalyserne eller gydetypen da gennemsnitslængden for 0-årig sild ved de akustiske undersøgelser var 11-11.5 cm hvorimod sild fra industrifiskeriet efteråret 1994 havde en medianlængde på 7.0 cm, hvilket er mere forventeligt i forhold sildens normale vækstkurve. Sammentaget med at årsklasserne ifølge trawl-togtet udviser større relative variationer end den samlede WBSS-bestand så kan både mængder og forskydningen ift. den senere gydebiomasse forventes.

Genetik

I den østlige Nordsø (øst for 4° Øst) samt i Skagerrak-Kattegat er fiskeri på sild typisk et fiskeri på blandede bestande; dvs. biologisk adskilte bestande der blander sig under opvækst og fødesøgning uden for gydetiden [1-3]. Op til gydningen vandrer de gydemodne sild tilbage til deres hjem-område, som det kendes fra de ofte massive indtræk i danske fjorde og bælter. Silden i Nordsøen, Skagerrak, Kattegat, de indre danske bælter og den vestlige Østersø tilhører en række genetisk adskilte bestande; hver med deres specifikke træk, som f.eks. inkluderer gydetidspunkt og arvelige tilpasninger til gydeområdet. Den genetiske kortlægning af sildebestandene er under stadig udvikling [4], og genetiske metoder til race-bestemmelse er i de seneste år enten blevet, eller er i proces med at blive, implementeret i rådgivningen i bl.a. Danmark [5], Norge og Sverige. Kortlægning af de sildebestande, der gyder i danske farvande, er pågående, f.eks. i forbindelse med nærværende EHFF-projekt *Genbygsild*, der specifikt adresserer muligheder for genopbygning af WBSS-silden, som er en samlebestand der inkluderer en række af de sildebestande der gyder i indre danske farvande, og som overordnet udviser en nedadgående trend i rekruttering og gydebiomasse under minimumreferencepunktet B_{lim} [7-8]. Pågående [5] og tidligere [3,9] genetiske analyser viser, at de sild der om foråret trækker ind og gyder i Limfjorden tilhører WBSS-samlebestanden. Det samme er gældende for alle andre til dato analyserede forårsgydende sildebestande fra indre danske farvande og bælter (f.eks. omkring Fyn og Sjælland), og herunder også i de vestjyske områder der afvander til selve Nordsøen (f.eks. Ho Bugt og Ringkøbing Fjord). Limfjordssilden er dermed ikke en biologisk del af Nordsø-bestanden, forstået som de sild der gyder om efteråret på bankerne i Nordsøen langs den britiske østkyst ('Banke-sild' og 'Orkney-Shetland-sild') og om vinteren i den Engelske Kanal ('Downs-sild'). Hvorvidt Limfjords-bestanden er genetisk adskilt (biologisk isoleret) fra andre danske bestande (f. eks. sild der gyder i naboområderne Ringkøbing Fjord og Randers fjord), et pt. under videnskabelig afklaring.

Graden af biologisk isolation har afledte konsekvenser for hvordan Limfjordssilden bør forvaltes. Hvis der er høj grad af isolation, vender Limfjordssilden altid tilbage til Limfjorden for at gyde (stærkt hjem-instinkt), og dermed kan bestanden overfiskes gennem et for højt fiskeritryk i Limfjorden, hvilket vil betyde at den i en længere årrække ikke vil være at finde i større mængder. Hvis Limfjordssilden derimod ikke er isoleret fra de øvrige danske fjordbestande, vil den kunne optræde som en lejlighedsvist optrædende gydeforekomst som bør forvaltes på samme måde som den øvrige bestand; en bestand som i lighed med den samlede vestlige Østersøbestand er under stærkt pres med dalende rekruttering og lav gydebiomasse.

Tidligere analyser af silden i Limfjorden [10-11] havde ikke adgang til genetiske metoder og var mindre sikre i deres henføring af enkelte fisk til de specifikke bestande. De tidligere analyser viser dog konsistens med nyere genetiske resultater idet der på grundlag af tællinger af ryghvirvler, der udviser gennemsnitlige bestandsforskelle mellem Nordsøsilden og WBSS silden, blev konkluderet, at sildene i Limfjorden primært var forårsgydende sild, der trak ind fra Kattegat i øst samt, i mindre antal fra Nordsøen i vest og hvor alle sild ældre end 1 år forlod Limfjorden igen efter gydeperioden. Hertil kom mindre bestanddele af Nordsø ung-sild, der trak ind og overvintrede, samt en mindre del der trak ind for at gyde om efteråret.

Der er ikke udført systematisk genetisk race-bestemmelse af sild fanget i Limfjorden uden for gydetiden om foråret, men det antages pga. fiskeriets koncentration til gydeperioden, at hovedparten af de sild, der fiskes i fjorden, tilhører den lokale forårsgydende Limfjordsbestand. Kun en enkelt prøve fra fiskeriet er blevet analyseret med genetiske metoder. Det drejer sig om 51 fisk fra en landing foretaget 28. maj 2021 (dvs. i slutningen af, eller lige efter gydetiden). Alle fisk blev genetisk analyseret og med høj statistisk sandsynlighed henført til den lokale bestand af Limfjordssild, hvilket dermed understøtter forventningen om, at det (primært) er den lokale stamme der fiskes i fjorden. DTU Aqua har ikke analyseret prøver af modne efterårsgydende sild fra Limfjorden, og ifølge fiskerne er forekomster af efterårsgydende sild kun sporadiske. Foreløbige genetiske analyser af tilsvarende efterårsgydende sild fra Ringkøbing Fjord tyder dog på, at disse sild også biologisk tilhører WBSS, og ikke f.eks. Nordsø-bankesild eller de andre bestande fra britiske farvande.

Bestandsanalyse

Der er ikke udført specifikke bestandsestimater af Limfjordssilden i nyere tid.

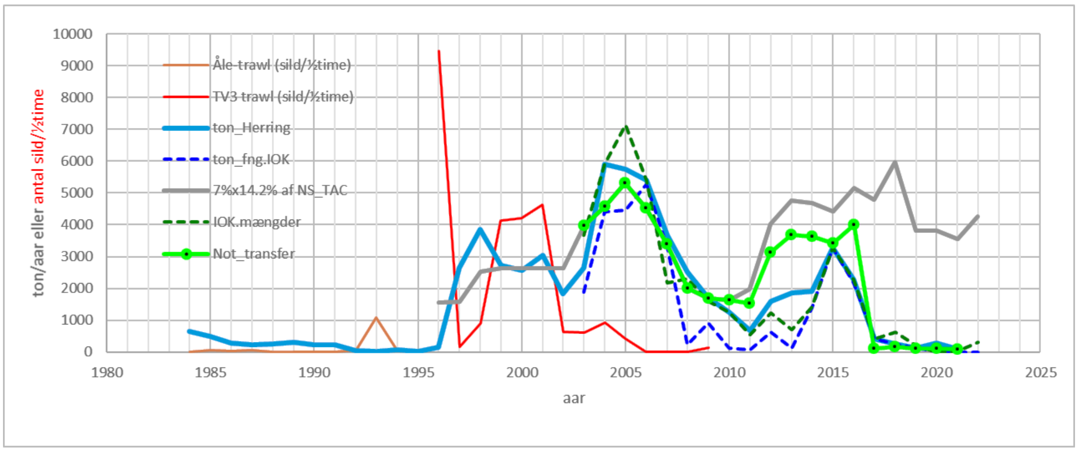
Da der mellem 2014 og 2021 ikke forefindes systematisk indsamlet information om sildebestanden i Limfjorden fra togter eller biologiske prøver fra fangster af gydesild i Limfjorden må en vurdering af bestandens udvikling og nuværende tilstand underbygges af mere indirekte evidens. Den information, som kan indgå, er:

1. Det fiskeri som har fundet sted i Limfjorden fra 1996 og frem til i dag under en række forskellige forvaltningsregimer.
    a. Dels det målrettede fiskeri efter konsumsild
    b. Dels bifangster af sild i industrifiskeriet.
2. Størrelse og alder af sild fra sporadiske indsamlinger fra fiskeriet.
3. Observationer fra fiskere om deres opfattelse af sildemængder som trækker ind i fjorden for at gyde.
4. Den generelle tilstand for de forårsgydende sild i farvandene omkring Limfjorden hvor bestanden biologisk tilhører komplekset af forårsgydende vestlig Østersøsild (WBSS).

(1a) Fiskeri og forvaltning

Figur 6 viser de af Fiskeristyrelsen registrerede landinger af konsumsild fra Limfjorden 1984-2021, samt årsmængder (2008-2021) og den estimerede kvoteandel af Nordsøsild afsat til Limfjorden. I mangel på data for Limfjordskvoten inden 2008, har vi udregnet tallene, som den andel Limfjordskvoten udgør af den totale Nordsøkvote, under antagelse af at den danske kvote pga. den relative stabilitet har været en konstant andel af Nordsøkvoten.

For at kunne sammenligne toppe i juvenile forekomster med efterfølgende kommercielle fangster af voksne sild er resultaterne fra trawltogter om efteråret (1984-2009) inkluderet i figur 1.2.6.

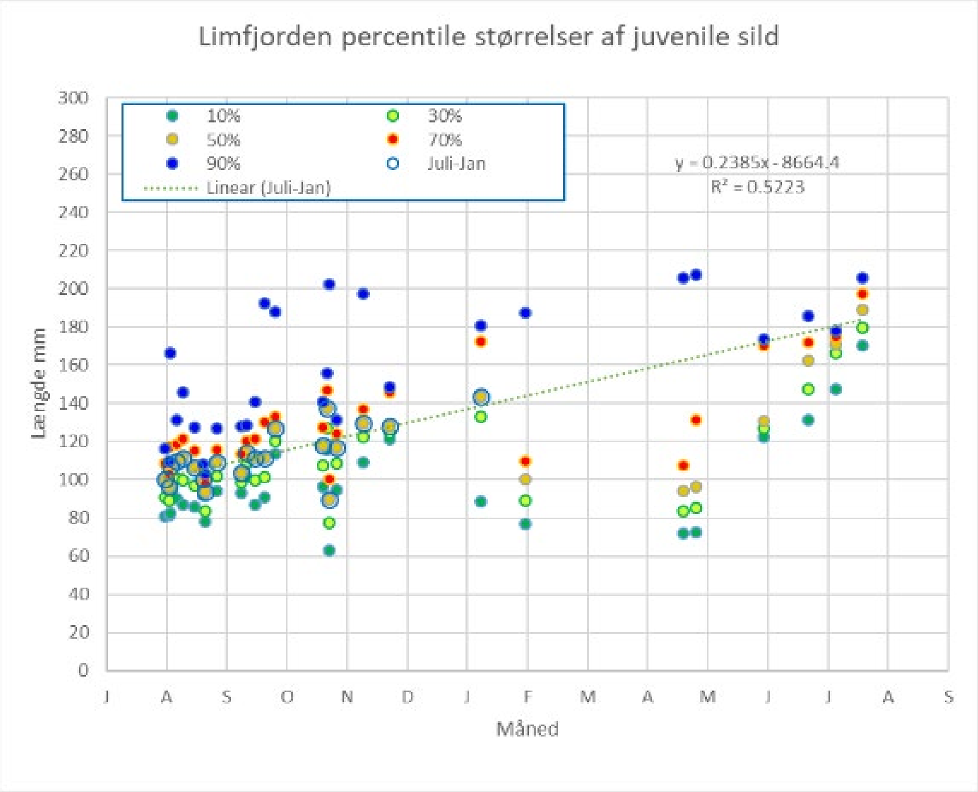


Figur 1.2.6. Rødlige linjer. Fangstrater (antal/30min) af 0-1 årig sild fra Limfjordsundersøgelsernes trawltogt (1984-2009, orange Åletrawl 1984-1995, optrukket rød TV3-trawl 1996-2009). Blå linje. Landinger af konsumsild fra Limfjorden – hovedsageligt marts-april (1984-2021). Stiplet mørkeblå linje fangst i Limfjorden per år for fartøjer på licens: 605 (individuel overdragelig kvoteandel af sild i ICES 4L Limfjorden.) Grå linje total kvote afsat til Limfjorden estimeret fra total Nordsø agreed TAC. Stiplet mørkegrøn linje angivne årlige mængder for fartøjer på licens: 605. Lys grøn linje m sorte prikker estimeret kvoteandel som kun må fanges i Limfjorden.

Mellem 1992 og 1996 lå fangsterne i Limfjorden på under 200 t om året, men i perioden 1997 til 2003 øgede de årlige fangster til mellem 2000 og 4000 t. Det kan konstateres at fiskeriet har betinget landinger på op til 6000 t i perioden 2004-2006, men at kurven for landinger følger kurven for den beregnede kvoteandel i Limfjorden (Figur 1.2.6). De juvenile årgange i 1999, 2000 og 2001 var tilsyneladende stærke og kan have ledt til en større mængde gydesild fra 2003-2005 og dermed øget fiskeriets fangster. Efter 2002 er mængden af juvenile sild tilsyneladende aftaget og den faldende rekruttering kan have medført en nedgang i gydebiomassen. Det er ikke muligt med det foreliggende materiale at afgøre, hvor stort fiskeritrykket har været på de gydende sild om foråret, men det ser dog ud til, at nedgangen frem til 2011 har været begrænset af kvoten. Det er dog sværere at tolke juvenile årsklasser ud fra togt-data fra perioden efter 2000 da øgende mængder gopler påvirkede validiteten af en stor del af trawltrækkene [12]. Fiskeriet i år 2016 er dog værd at notere, idet en opgang i kvoten ikke medførte et højere fiskeri, men derimod en reduktion i landingerne, hvilket uden anden forklaring kunne tages som et tegn på bestandsreduktion. Dette er under antagelsen, at fiskeriet på gydesild var overstået d. 31. maj 2016 hvor det blev tilladt at overføre hele Limfjords-IOK'en til fiskeri Nordsøen.

(1b) Fangst af juvenile sild fra forårs- og efterårsgydende bestandskomponenter
Da der kun foreligger begrænsede data på størrelse ved alder for juvenile sild i Limfjorden, og data på gydetype (dvs. om silden var en forårsgyder, som forventet for de lokale Limfjordssild) kun findes fra en enkelt prøve, blev samtlige længdefrekvenser i prøver fra perioden 1978-2014 analyseret. 28 prøver fra det kommercielle fiskeri med mere end 3 juvenile sild blev udtaget, hvorved i alt 3282 sild under 21.5 cm indgik i analysen. Størrelsen på sild ved 5 forskellige percentiler (10%, 30%, 50%, 70% og 90% af den kumulative længdefordeling) blev afbildet mod tidspunkt på året for fangst (Figur 1.2.7). Væksten fra først i april til først i december var 7mm pr. måned (median-længden øgede fra 97 mm i starten af april til 128 mm i starten af december). Af Figur 1.2.7 fremgår, at der visse år var en top af store juvenile (90% percentilen) som adskilte sig betydeligt fra den store gruppe små juvenile (<=70%).

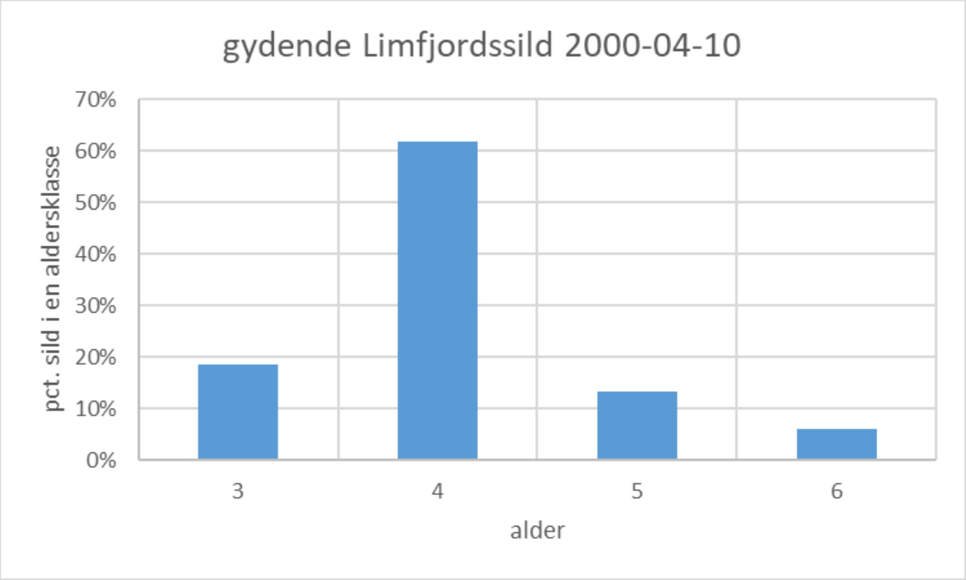
Når man ser på juvenile fanget fra maj til juli kunne disse godt tilhøre gruppen af små sild (<=70%) fra året før, hvorimod de store juvenile ser ud til at have forladt Limfjorden. Der er tre tilfælde af afvigende størrelsesfordelinger (meget små fisk) fanget i februar og april. Muligvis kan dette være efterårsklækkede sild som her optræder. Disse vil om foråret udgøre de mindste størrelser, men efter juli, når de fleste 1-årige sild har forladt Limfjorden og de nye forårs-klækkede sild er rekrutteret til fiskeriet, vil de udgøre sild i 90% percentilen. Med det lave antal prøver hvor der er overlap mellem de to grupper er det usikkert hvor stor en andel efterårsklækkede sild udgør af den juvenile bestand, men et groft estimat vil være at de visse år udgør mellem 10 og 30%, mens de andre år ikke optræder i fangsterne. Dette vil således være i overensstemmelse med observationer om, at efterårsgydning er mindre hyppig, eller endda kun sporadisk forekommende i Limfjorden. Det er imidlertid ikke muligt ud fra data at afgøre, om de efterårsklækkede sild stammer fra gydning i Limfjorden eller uden for i Nordsøen.



Figur 1.2.7. Størrelse ved 10%, 30%, 50%, 70% og 90% af den kumulative længdefordeling for juvenile sild under 215 mm.

(2) Størrelse, alder og gydemodenhed af sild

I år 2000 blev der udtaget en prøve på 97 gydende sild fra en fangst i Limfjorden, hvor de biologiske data viser at de indsamlede sild sandsynligvis er fra hurtigt voksende (vBtf: k=0.79, Loo=289 mm) delpopulation af WBSS-bestanden (gnst. hvirveltal 55.5). Aldersfordelingen er domineret af 4-årige (figur 1.2.8).



Figur 1.2.8 Procentandel pr. alder af gydende sild i april år 2000.

En indsamling i Limfjorden øst for Aalborg (57.063 N, 10.058 Ø) fra 22. maj 2003, dvs. noget efter toppen af gydeperioden i april, og med kun en gydeklar sild, viste følgende fordeling af potentiel modenhed:

prøve i Limfjorden 2003	potentielt gydemodne					
alder (WR)	**2**	**3**	**4**	**5**	**6**	**7**
totalt antal	37	36	13	9	3	2
% af modenheds-stadier 2,5,6 og 7	3%	11%	77%	89%	100%	100%
% med Anisakis	54%	56%	100%	100%	100%	100%

Analyserne af disse prøver udgør et spinkelt men indikativt grundlag for bedømmelse af bestandens karakteristika. Data på modenhed indikerer, at der i Limfjordsbestanden er en forskydning af gydemodenheden mod 1 år ældre ved første gydning, så ingen 2-årige og kun en mindre andel 3-årige er modne, hvilket passer godt med forholdet mellem 3- og 4-årige i prøven fra år 2000. Der er ligeledes i prøven fra 2003 få modne 3-årige og ikke fuld modenhed blandt 4-årige. I forbindelse med gydeperioden trækker der tilsyneladende yngre og umodne sild med ind i Limfjorden som her bliver udsat for et kommercielt fiskeri. Det er ikke muligt at konkludere om dette er et generelt fænomen da det ikke har været muligt at finde yderligere prøve-data fra kommercielle landinger i perioden.

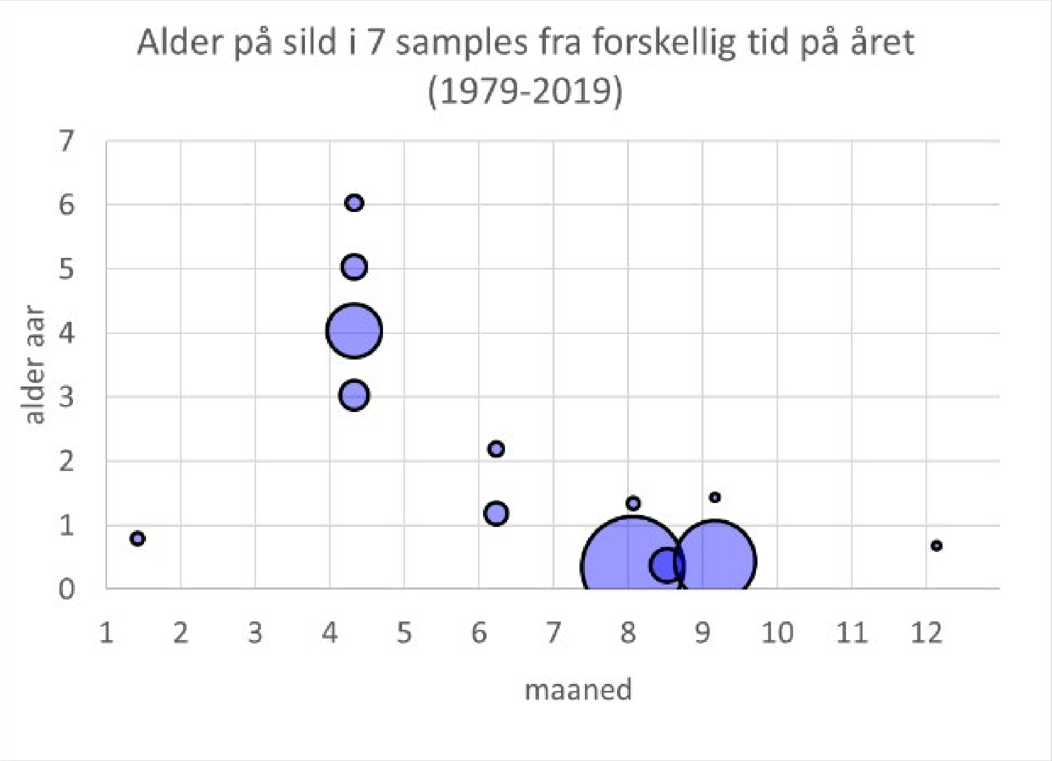
Det kan ikke udelukkes at prøverne fra 2000 og 2003 er taget fra to forskellige bestands-komponenter; en som vandrer ind fra Nordsøen i vest ved Thyborøn (2000) og en der vandrer ind fra Kattegat i øst ved Hals (2003). Antagelsen om, at Limfjordssilden gyder ca. et år senere end hvad man antager for den overordnede WBSS-bestand, ser dog ud til at gælde for begge typer. Det må desuden bemærkes at i prøven fra 2003 som blev analyseret for parasitter, var en stor andel af sildene inficeret med anisakis-parasitten, hvilket tyder på at de har vandret til nordligere farvande (Skagerrak og nordpå) hvor denne nematode forbindes med bl.a. kril; (Yderligere en prøve fra det kommercielle fiskeri i 2021 er ved at blive analyseret og vil kunne styrke antagelsen om modenhed).

Det må således konkluderes at de forårsgydende Limfjordssilds bestandsdynamik adskiller sig fra hovedparten af bestanden af forårsgydende vestlige Østersøsild (WBSS), gennem en højere vækst og senere kønsmodning. Limfjordssilden har yderligere indikationer på lange fødevandringer til den nordøstlige Nordsø.

Den samlede WBSS-sildebestand består af en lang række lokale stammer med hver deres gydeområde og vandringsmønster. Data til at estimere Limfjordssildens totale mængde og udbredelsesområde indenfor WBSS-bestanden er meget usikre pga. den forholdsvist store genetiske lighed med de andre WBSS-stammer (herunder bestande der gyder i de andre danske fjordsystemer), og på grund af den relativt lille andel Limfjordssilden tilsyneladende udgør af den totale WBSS-bestand.

DTU Aqua har ikke sikre data til at vurdere de konkrete udnyttelses-andele af Limfjordssilden i Nordsøen. Mindre prøver indsamlet under de årlige videnskabelige togter med DANA i den østlige Nordsø (område 4a-b) og analyseret med genetiske metoder, tyder dog på, at de danske sildebestande (DK-bestand) omkring 2000-2003 udgjorde mellem 15 og 9 % af den totale WBSS, og at DK-bestanden efter 2017 har udgjort 5% eller mindre af de voksne sild i området. Af denne andel vil kun en delmængde forventes at være

Limfjordssild. Fangster af konsumsild i Nordsøen og Skagerrak vil således typisk være spredt ud på fisk fra en række biologisk forskellige bestande (blandede bestande), mens tilsvarende fangster af konsumsild om foråret inde i Limfjorden forventes at være primært målrettet de lokale Limfjordssild (Se Figur 1.2.9).



Figur 1.2.9 Aldersfordeling af sild indsamlet på forskellige tider af året.

Fangster, årsmængder og fiskeridødelighed hos Limfjordssild er angivet i Tabel 1.2.1, under forskellige antagelser om Limfjordsildens andel af den totale WBSS-bestand. I perioden 2001-2016 udgjorde fangster taget i Limfjorden mellem 1.7% og 8% af den totale fangst af WBSS-sild inklusive fangst i Limfjorden. Fra 2017-2020 udgjorde de mellem 0.5% og 1.3%. Hvis man antager, at sild fra den genetiske komponent i de danske fjorde og bælter (DK-sild) frem t.o.m. 2017 udgjorde 10% af WBSS-bestanden og derefter 5%, samt i tre forskellige scenarier, hvor Limfjordsandelen udgjorde hhv. 100%, 75% og 50% af DK-sildene, så vil man få et konservativt estimat af, hvor høj fiskeridødeligheden under gydevandringen i perioden 2001-2020 kan have været (Tabel 1.2.1). Da Limfjordssild kun er en af flere bestande, udgør den mindre end 100% af DK-silden og dødeligheden under gydningen i Limfjorden i perioden 2021-2016 var formodentlig meget høj.

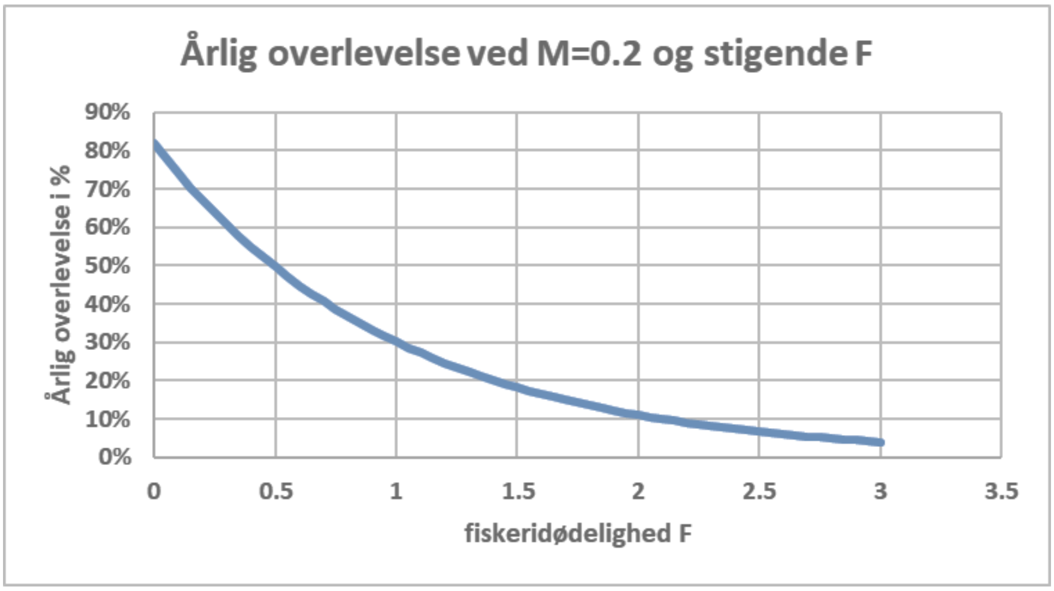
Overførsel af Limfjordskvoten til fangster i Nordsøen efter 2016 har med stor sandsynlighed medført, at det heraf affødte fiskeri har været koncentreret til Nordsøbestanden (NSAS) i det danske sildefiskeri vest for 4° Øst, og kun i mindre grad har udnyttet sildeforekomster i den østlige Nordsø med indblanding af Limfjordssild. Dette har dog ikke hindret, at Limfjordssilden er blevet fanget sammen med andre WBSS-sild under de lokale kvoter i Kattegat og Skagerrak samt under NSAS-kvoten i norsk farvand. De tilladte årsmængder i

Limfjorden er koblet til Nordsøkvoten, hvilket kan lede til meget kraftigt overfiskeri hvis årsmængderne tages i Limfjorden. Da silden desuden er udsat for yderligere dødelighed under sine vandringer (F uden for Limfjorden for 3-6 årige estimeret til 0.12 mellem 2008 og 2020), kan perioder med dårlig rekruttering i løbet af få år lede til drastiske reduktioner af gydebestanden.

I tabel 1.2.1 ses et kraftigt fald i gydebiomassen i Limfjorden fra 2017 til 2018. Dette skyldes nye tal i 2018 for den genetiske andel DK-sild i den samlede WBSS-bestand. Vi ved ikke med sikkerhed hvornår denne ændring er sket, men en del af forklaringen kan være det gode fiskeri i Limfjorden omkring 2015. Samlebestanden af de forårsgydende vestlige Østersøsild (WBSS) bedømmes til langt under minimum referencepunktet for gydebiomasse (B_{lim}). De faldende andele sild fra den genetiske komponent i de danske fjorde og bælter (DK-silden) tyder ikke på, at Limfjordsilden er i en bedre tilstand end WBSS-silden generelt. Selv efter en genopbygning af WBSS-bestanden vil koblingen af Limfjordskvoten til Nordsøkvoten muliggøre et forhøjet fiskeritryk langt over, hvad der ville svare til langsigtet bæredygtige fangster (MSY) for Limfjordsbestanden.

Tabel 1.2.1: Fangster og fiskeridødelighed (F) for Limfjordsbestanden ved forskellig andel af totalbestanden af WBSS i årene 2001-2020.

						Limfj. af DK-bestand	100%	75%	50%	100%	
år	WBSS-gydebiomasse (SSB)	DK bestande % af WBSS	SSB Limfj	Limfj fangst	Limfj fangst som % af WBSS-fangst	Limfj fangst som % af SSB	F	F	F	F ved Års-mgd svarende til 7% af Nordsø-TAC	Estimeret Årsmængde i Limfj svarende til 7% af Nordsø-TAC
2001	136051	10%	13605	3039	2.8%	*22%*	*0.25*	*0.35*	***0.59***	*0.22*	2634
2002	159982	10%	15998	1844	1.7%	*12%*	*0.12*	*0.17*	*0.26*	*0.18*	2634
2003	129160	10%	12916	2637	3.3%	*20%*	*0.23*	*0.32*	***0.52***	*0.37*	3976
2004	133609	10%	13361	5906	7.1%	*44%*	***0.58***	***0.89***	***2.15***	*0.42*	4572
2005	121380	10%	12138	5751	6.1%	*47%*	***0.64***	***1.00***	***2.95***	***0.58***	5318
2006	133027	10%	13303	5392	5.7%	*41%*	***0.52***	***0.78***	***1.66***	*0.42*	4523
2007	109135	10%	10914	3669	5.1%	*34%*	*0.41*	***0.59***	***1.12***	*0.37*	3390
2008	89005	10%	8901	2515	3.5%	28%	0.33	0.47	**0.83**	0.25	1998
2009	79609	10%	7961	1688	2.4%	21%	0.24	0.33	**0.55**	0.24	1700
2010	74031	10%	7403	1265	2.9%	17%	0.19	0.26	0.42	0.25	1630
2011	69532	10%	6953	677	2.4%	10%	0.10	0.14	0.22	0.34	1988
2012	72538	10%	7254	1587	**3.9%**	22%	0.25	0.34	**0.58**	***0.81***	4026
2013	80985	10%	8099	1852	**4.1%**	23%	0.26	0.36	**0.61**	***0.88***	4751
2014	83868	10%	8387	1913	**4.9%**	23%	0.26	0.36	**0.61**	***0.81***	4672
2015	84718	10%	8472	3273	**8.0%**	39%	0.49	**0.72**	**1.48**	***0.74***	4423
2016	80484	10%	8048	2282	**4.3%**	28%	0.33	0.47	**0.84**	***1.02***	5149
2017	73684	10%	7368	413	0.9%	6%	0.06	0.08	0.12	***1.05***	4787
2018	62561	5%	3128	246	0.6%	8%	0.08	0.11	0.17	***ÅrsMgd>SSB***	5970
2019	57841	5%	2892	132	0.5%	5%	0.05	0.06	0.10	***ÅrsMgd>SSB***	3827
2020	58434	5%	2922	290	1.3%	10%	0.10	0.14	0.22	***ÅrsMgd>SSB***	3827



Figur 1.2.1 Illustration af hvor stor en mængde sild der årligt overlever ved forskellige niveauer af F plus Naturlig dødelighed (M=0.2).

Vi har ingen nye data som kan indikere størrelsen på sildebestanden i Limfjorden, eller om der findes specifikke tiltag som kan sikre genopbygning af bestanden. Den nuværende fiskeriindsats i Limfjorden er relativt beskeden og selv sammenlagt med fiskeritrykket i 2021 uden for Limfjorden ligger det samlede fiskeritryk formodentlig under hvad F_{MSY} typisk ville være for en sildebestand. Det er vurderingen at de seneste års begrænsede fiskeri i Limfjorden på under 400 t heller ikke i de nærmeste år udgør en fare for en eksisterende bestand af størrelsesordenen 5% af den samlede WBSS-sild. Det må påpeges at denne vurdering afhænger af et fortsat begrænset fiskeritryk i Kattegat-Skagerrak og Nordsøens 4a-Øst. En målrettet moniteringsindsats ville give grundlag for en mere præcis vurdering af maksimale bæredygtige fangstmængder for Limfjorden.

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1.3 Data review

1.3.1 The N20 recruitment index

The primary factors influencing the survival of larval herring and the strength of year-class recruitment are believed to be associated with oceanographic dispersal, sea temperatures, and food availability during the crucial phase when larvae begin actively feeding. Nevertheless, research on the dynamics of larval herring survival suggests that the key variables may not only vary at the population level and by the region of spawning but also by the developmental stage of the larvae. As the Western Baltic Spring Spawners (WBSS) herring relies on inshore, transitional waters for spawning and larval retention, the set of environmental variables driving reproductive success may differ from other North Atlantic stocks that recruit from coastal shelf spawning areas. Ongoing research is dedicated to understanding the suite of variables influencing early ontogenetic development and major survival bottlenecks.

Time-series analyses of larval herring growth and survival dynamics reveal that distinct hatching cohorts contribute differently to the number of recruits with one winter ring (1+wr) in the overall western Baltic Sea. The abundances of the earliest larval stage (5–9 mm TL) explain 62% of the variability in later stage larval abundance and 61% of the variability in surviving (1+ group) juveniles. This suggests significant pre-hatching survival bottlenecks associated with spawning and egg development. Additionally, findings indicate that hatching cohorts occurring later in the spawning season contribute the most to the surviving year class, while earlier hatching cohorts do not result in significant growth and survival, possibly due to limited food supply at hatching before spring plankton blooms.

While the availability of suitable prey after yolk consumption is generally considered the primary survival bottleneck in larval fish ecology, analyses of zooplankton prey abundance in strong vs. weak year classes did not reveal significant food limitation in the eutrophic waters of Greifswald Bay. However, apart from prey abundance, larval growth and survival may also be influenced by the nutritional quality of prey. Comparative results on essential fatty acid contents of larvae and prey from two different spawning grounds showed no significant differences in larval growth conditions in Kiel Canal and Greifswald Bay, but the food quality was found to be generally important for larval growth. Hence, even when prey availability is abundant in mixed, natural feeding conditions, larval growth is affected by the nutritional value of prey.

Transitional waters, such as bays, lagoons, and estuaries along the inshore–offshore gradients of Western Baltic watersheds, appear to play a significant role in herring reproduction as important spawning grounds and retention areas for early developmental stages. Quantifying the role of small-scale drivers and stressors for overall recruitment strength remains a major challenge. The hypothesis of cascading scale effects is supported by current WBSS recruitment time-series and the relationship of indices derived on differing spatial scales. The consistent correspondence of the regional larval index with recruitment patterns of the WBSS stock implies a connection between larger-scale recruitment success and regional survival bottlenecks. Conversely, the N20 time-series provides a solid foundation to test the magnitudes of regional effects on the overall WBSS stock. There has declining trend in the N20 index since the onset of the assessment in 1991.

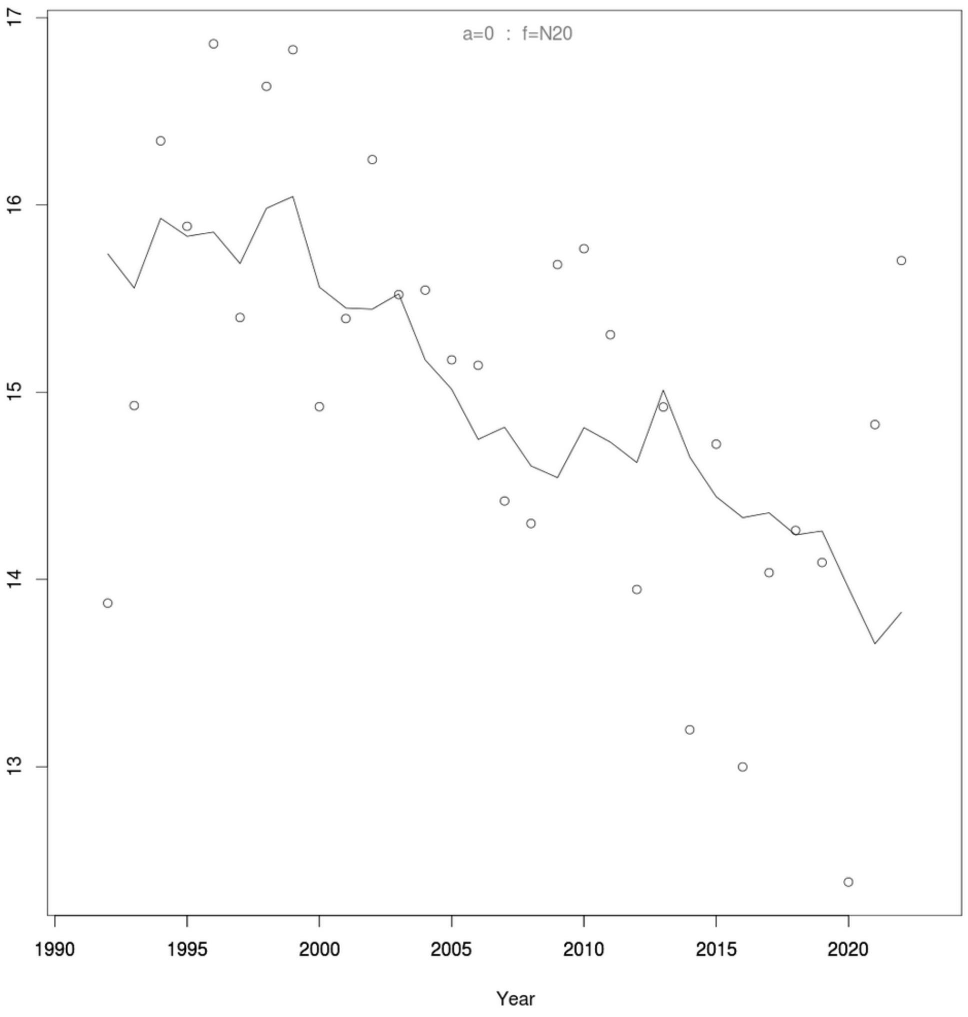


Figure 1.3.1. N20 recruitment index from the 2023 assessment (points) and the SAM assessment model fit (line).

1.4 Development of models for survey data

1.4.1 Integration of trawl surveys

The assessment model for WBSS originally only included acoustic survey data (the HERAS and GERAS surveys). However, two bottom trawl surveys each cover about half of the assessment area, namely the NS-IBTS survey, which covers the Northern part, and BITS which covers the Southern part. Although a pelagic species, herring are found near the bottom during the day and substantial amounts are caught in the bottom trawl surveys. The NS-IBTS survey data are already used for the assessment of North Sea autumn spawning herring, and samples of sub-components have been collected since 2002 (to filter out the WBSS component). However, to get a representative sample of the entire stock component, the NS-IBTS and the BITS survey data need to be combined. This poses several problems since herring found the in BITS survey have never been sampled for age nor sub-component. In addition, the two surveys use distinct types of trawls. The

NS-IBTS uses the GOV trawl whereas the TVS trawl is used in the BITS survey in this area.

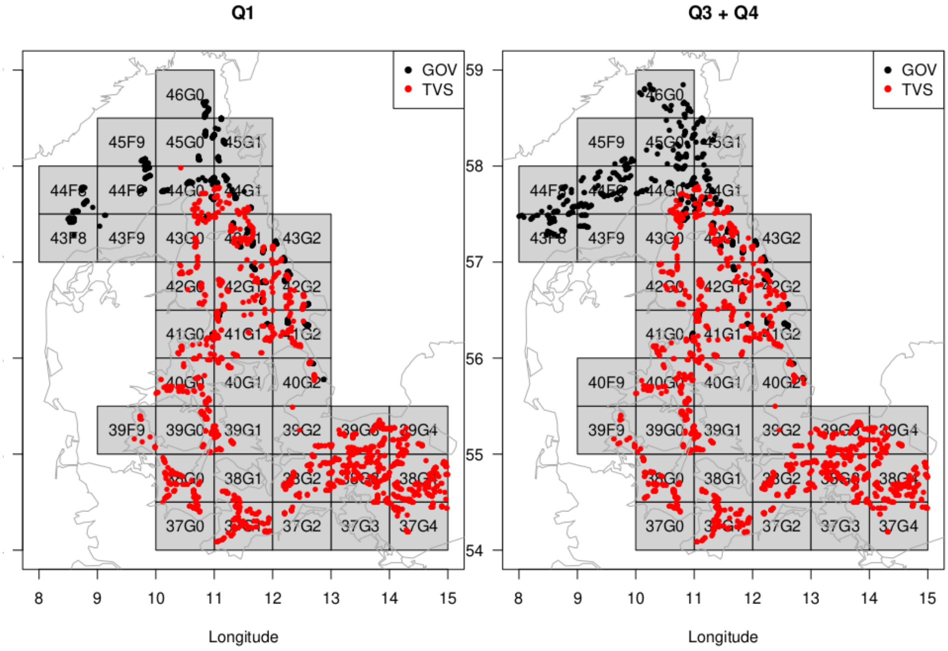


Figure 1.4.1. Trawling positions from the NS-IBTS using GOV trawl and from the BITS using TVS by quarter.

To combine the data from these two surveys into a single index of abundance of WBSS herring, it is thus necessary to build statistical models that can estimate the proportion of WBSS herring in the BITS survey samples from the NS-IBTS samples, as well as estimate the gear effect, I.e. the conversion factor from GOV to TVS with respect to catch efficiency of herring.

Such models were first developed in connection the benchmark workshop WKPELA in 2018 and refined and developed further during this project.

The procedure to estimate the WBSS trawl survey indices is as follows:

Fit a multinomial model to predict probability of WBSS given time, position, and length using individual samples of stock from NS-IBTS.

Multiply observed length distributions by haul with predicted stock probabilities to filter out all but WBSS.

Fit a multinomial model to predict probability of WBSS given same data and predictors as in step 1, but also include age and cohort.

Fit age-length keys (ALK) using aged individuals, but weight each age sample with probability of being WBSS using the model from step 3.

Apply ALK to WBSS specific length distributions from step 2.

Fit survey index standardization model for numbers-at-age by age and quarter, which estimates the conversion factor between TVS and GOV gears.

Select a fixed and fine-meshed grid of haul positions

Predict abundance on grid by year (using reference vessel, time-of-day etc).

Calculate index as the sum of grid points.
Steps 1 and 2 splits the length distributions by haul into WBSS / non-WBSS. Step 3 and 4 splits the individual age samples into WBSS / non-WBSS. This is gives us the stock-specific age-length key, which we can use to convert the split length distributions from steps 1 & 2 into numbers-at-age by haul.

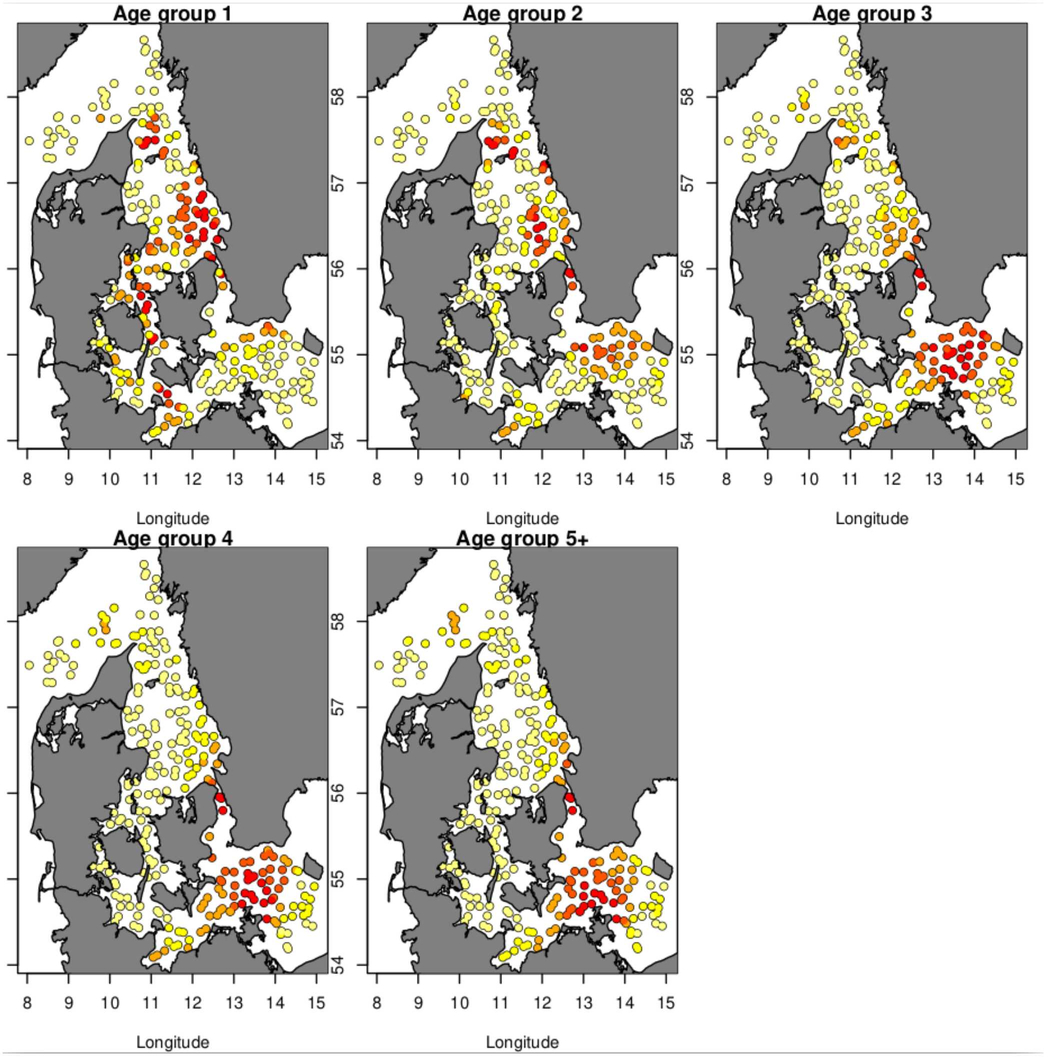


Figure 1.4.2. Average distribution map of WBSS herring from the combined trawl surveys in quarter 1 (using data up to 2023). Red colors indicate high abundance.

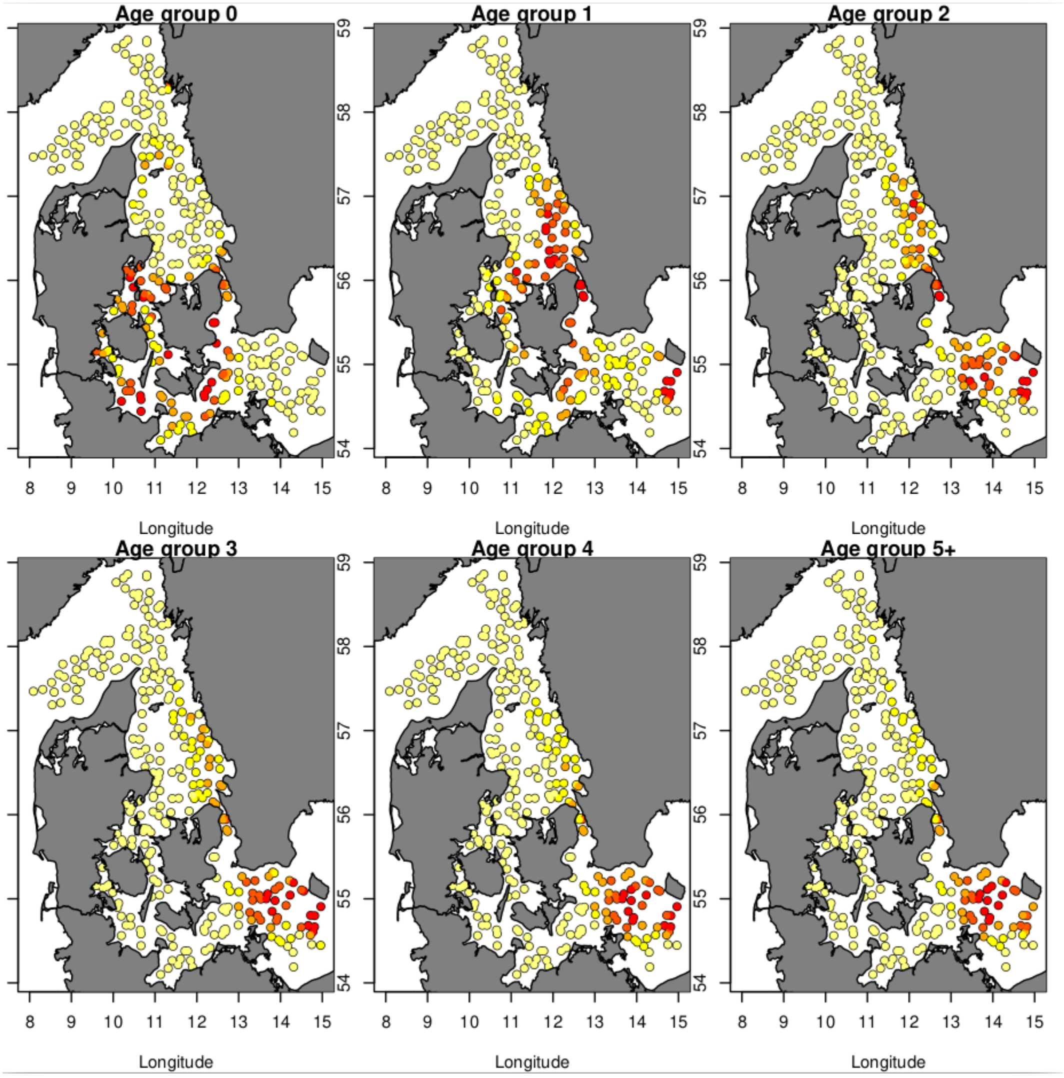


Figure 1.4.3. Average distribution map of WBSS herring from the combined trawl surveys in quarters 3 and 4 (using data up to 2023). Red colors indicate high abundance.

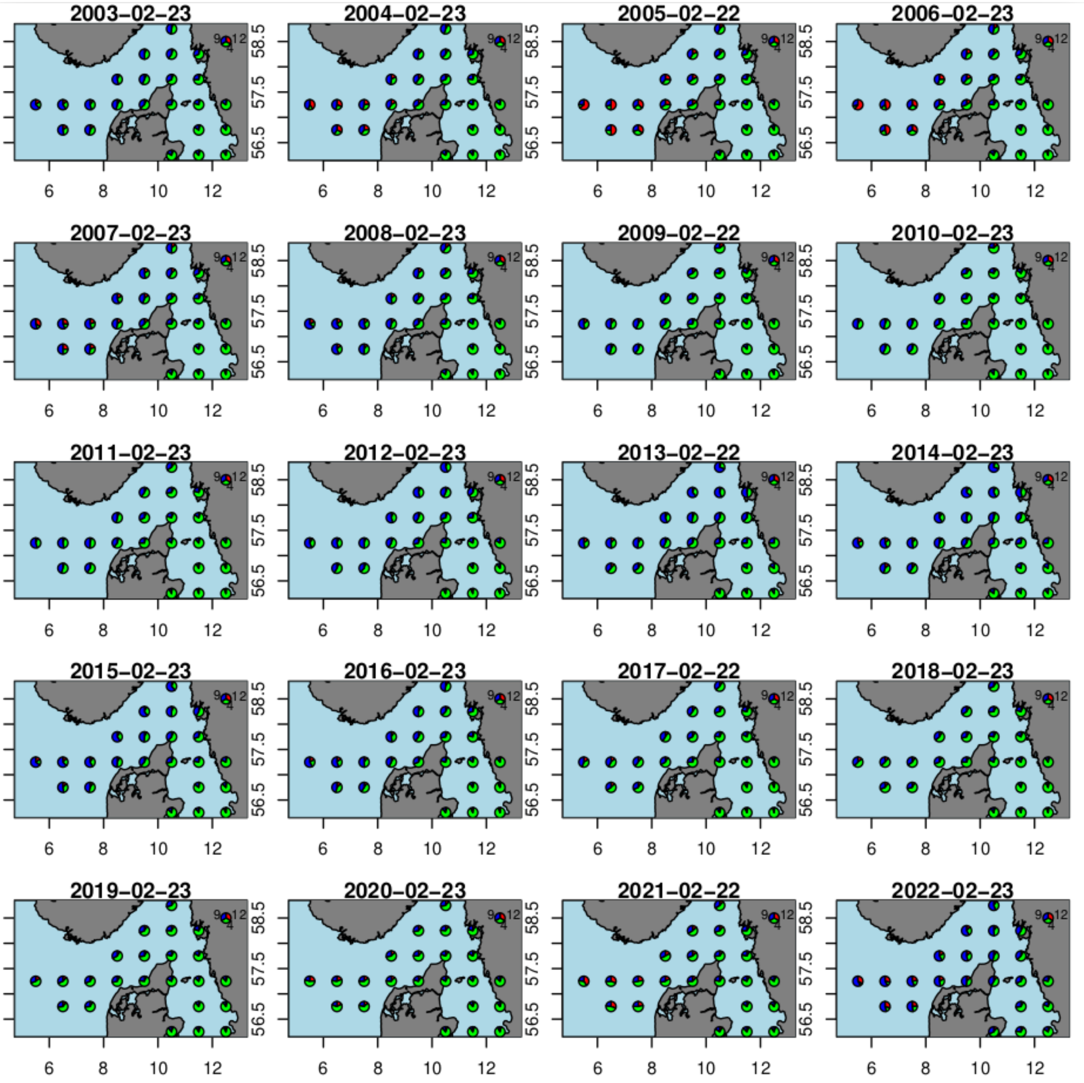


Figure 1.4.4. Estimated proportions of spring (green), autumn (blue), and winter spawners (red) in quarter 1.

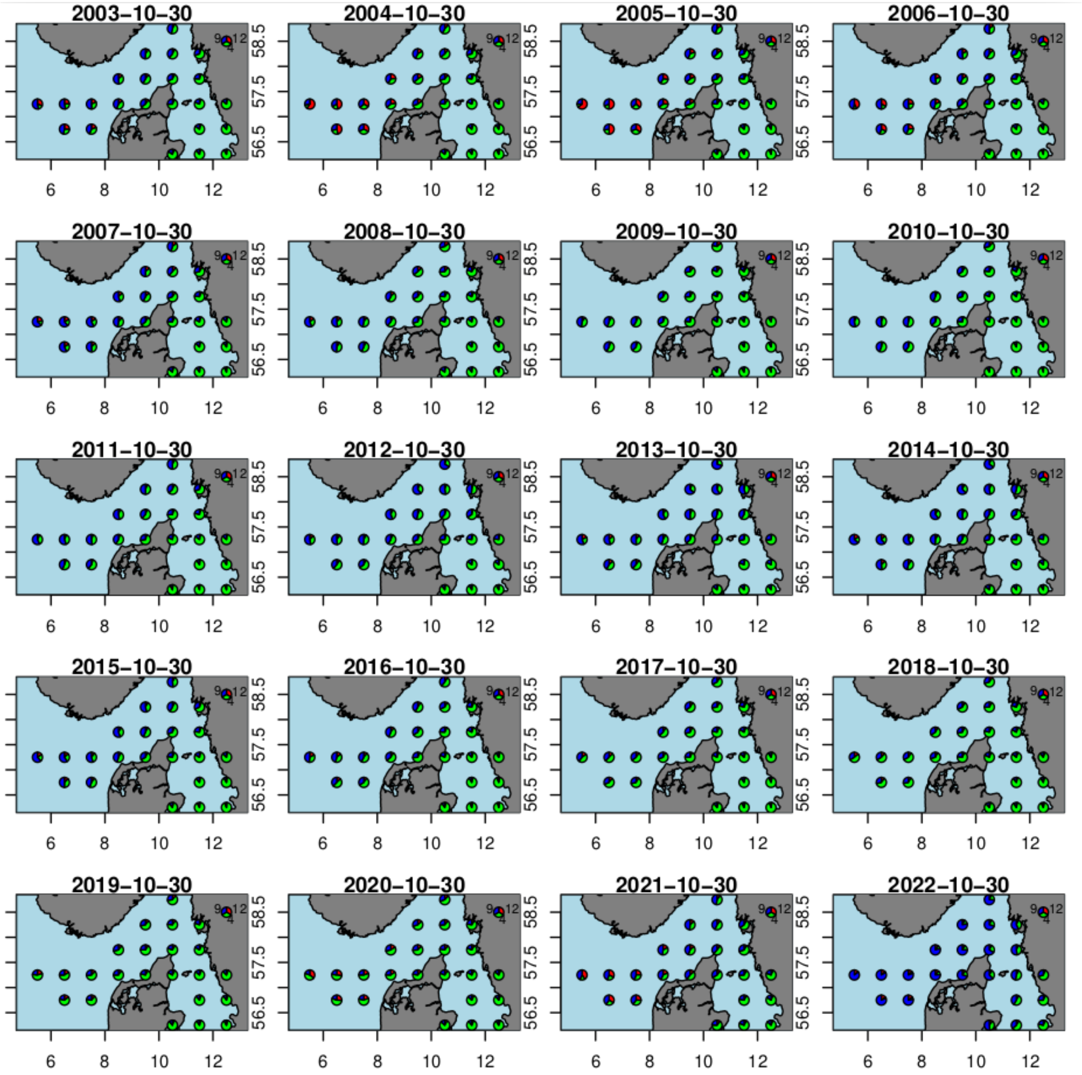


Figure 1.4.5. Estimated proportions of spring (green), autumn (blue), and winter spawners (red) in quarter 3/4.

The results show that the youngest (immature) age groups are distributed in Kattegat and the Danish Belts, whereas older herring are more predominant in the Sound (Øresund) and the Arcona Basin in the south-east. The distributions are similar in both quarters, although a slightly more north-eastern distribution in Q3 and Q4 compared to Q1. The internal and external consistencies (a measure between 0 and 1 of how well we can "follow the cohorts" within and between surveys under the assumption of constant mortality) are fairly good up to and including age 3, but poor hereafter. This is not surprising considering that the older age groups are mainly distributed in the area south of Kattegat where there are no age samples.

The standardized time series was finally assessed by calculating the correlation between the estimates from year to year, the so-called internal consistency measure, where a high correlation indicates a good survey index. Relatively high correlations were found for the youngest age groups, especially ages 2 and 3, but little correlations for the oldest age groups. On that background, it was decided to only use the time series for ages 1 to 3 from the first quarter and ages 2 to 3 for quarter 3+4 in the stock assessment model for WBSS. The lack of correlation for the oldest age groups may be due to the fact that age samples or random samples of mixing proportions are not collected that between central Baltic herring and WBSS in the BITS survey, which is the only survey carried out in the Arkona basin, where the older age groups are primarily found.

1.4.2 Sub-stock components

For the assessment of herring stocks in Subarea 4 and Divisions 3.a and 7.d, autumn spawners (NSAS; North Sea, Skagerrak and Kattegat, eastern English Channel; her.27.3a47d) and in Subdivisions 20–24, spring spawners (WBSS; Skagerrak, Kattegat, and western Baltic, her.27.20-24) catch data and survey estimates have routinely been split between these two stocks in Division 3.a (Skagerrak, Kattegat) and in the so-called ‘Transfer area’ in the southeastern part of Subarea 4 (Fig. 1.4.6). For the HERAS, however, catches from the entire eastern part of Subarea 4.a (4aE) have been split. Any mixing outside these areas has been considered negligible. Likewise, the abundance of other stocks in the assessment areas has been considered negligible.

Historically, the approach for splitting in the ‘Transfer area’ was by vertebral counts in Norwegian samples, whereas splitting in Division 3.a was based on otolith microstructure in Danish and Swedish data. The microstructure readings were supplemented by otolith shape analysis to increase sample sizes. In 2021, Denmark and Norway discontinued the previous sampling methods in favour of genetic marker based stock classification (hereafter ‘genetics’).

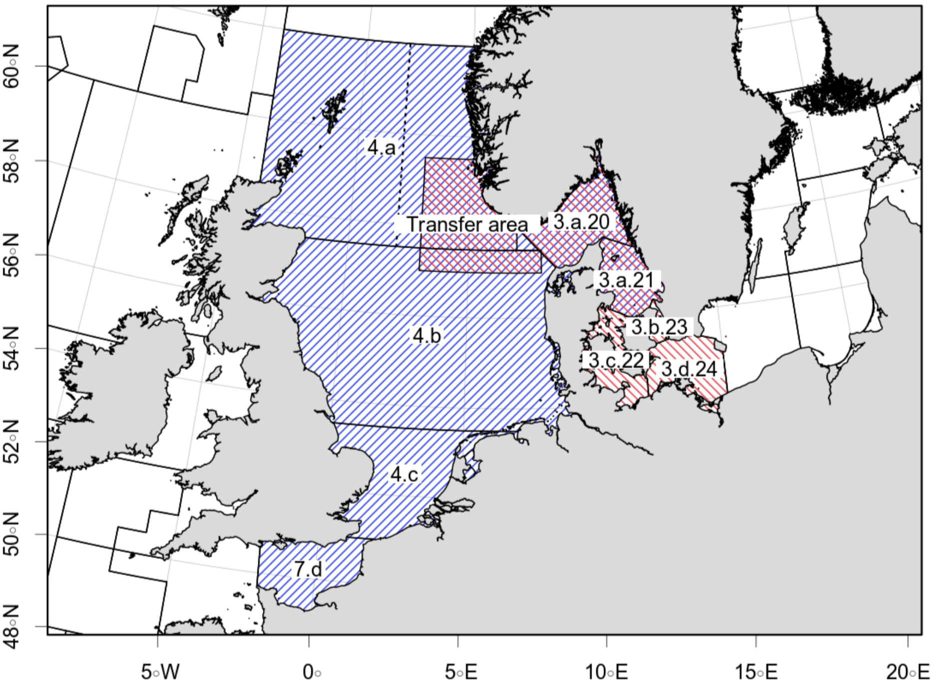


Figure 1.4.6. ICES Divisions for the her.27.3a47d (blue hatched area) and her.27.20-24 (red hatched area) assessments. The stocks are split in the ‘Transfer area’ and Division 3.a (3.a.20 and 3.a.21). The dashed black line in Subarea 4.a indicates the separation between 4.a east and 4.a west.

Previously, herring in Division 3.a were mainly split based on otolith microstructure and supplemented by otolith shape analysis (Danish and Swedish data), whereas herring in the ‘Transfer area’ were split based on mean vertebral counts (VS; Norwegian data).

Using otolith microstructure, it is possible to identify the hatching season of herring, thus fish classified as autumn spawners were assigned as North Sea autumn spawners (NSAS), whereas herring hatched in spring were assigned as western Baltic spring spawners (WBSS). For Danish samples, fish classified as winter spawners were assumed to be Downs herring and assigned as NSAS. In contrast, fish classified as winter spawners from Swedish samples were assumed to be from local coastal populations. Therefore, these were assigned as WBSS.

Using VS, the proportion of NSAS vs. WBSS were estimated per sample assuming that the VS of NSAS = 56.5 and of WBSS = 55.8.

These two splitting methods were adjusted to split NSAS and WBSS, whereas observations of other stocks (for example Norwegian spring spawning herring (NSS)) have been noted but not taken into consideration until recently.

Stock compositions were estimated by age (represented by the number of winter rings, wr), quarter, and area. Due to limited samples available, information was ‘borrowed’ between estimation groups by combining them to ensure at least 10 individuals per age specific estimate, through expert judgement and data patterns. Further, samples from surveys were included to increase the sample sizes. In Division 3.a, stock compositions were estimated for Danish and Swedish commercial catches. In turn, the country-wise estimates were combined to total Division 3.a composition estimates by a weighted average per age and area. The average was weighted by the relevant catches in numbers.

From 2021, genetic methods have been applied by Denmark and Norway replacing the two previously used methods, thereby allowing for a more detailed and precise stock assignment of herring. Likewise, Sweden has discontinued the use of otolith microstructure from 2022 in favor of genetic methods.

A detailed description of the applied genetic stock identification method is presented in Bekkevold et al. (2023). This method has been applied with similar sets of single nucleotide polymorphism (SNP) markers using almost the identical baseline samples across laboratories for Danish and Norwegian data. Thus, genetic assignments among different countries are clearly comparable. In contrast to the previous splitting methods, the genetics allow for a much more detailed small-scale population identification resulting in eight genetically distinct populations used here (Table 1.4.2).

The shift to a more high-resolution population identification raised several data issues for the transition from previous methods to genetic assignments in the 2022 update assessments of her.27.3a47d and her.27.20-24. The new genetic information revealed that more herring stocks are present in the assessment areas than previously accounted for. Further, all stocks are found in larger parts of the assessment areas than currently modelled.

Two options were considered for transitioning from the meristic/morphometric methods to genetics as the basis for estimating stock compositions.

The first option, which is preferable in the long term, was to split catch and survey samples directly by genetic information into genetic NSAS-Downs, genetic WBSS, and other genetic stocks. In the short term, however, that would make the 2021 data incompatible with previous years, which are based on spawning season and vertebrae counts. For example, genetic WBSS is only a subset of spring spawners present in the area. Moreover, this option would either result in parts of the catches not being allocated to one of the two assessed stocks (her.273a47d or her.27.20-24) or they would be allocated to their original assessed stock which would require changes to herring assessments in several working groups. Finally, Danish samples (split by genetics) would be incompatible with data from Swedish samples from 2021, as the latter were classified using otolith microstructure. The Danish and Swedish samples are used in combination for stock composition estimates in Division 3.a.

Ideally, future work can move the assessments towards corresponding to the biological populations, reflecting the relevant reproductive units. However, such changes would require corrections of data back in time, and close coordination between the assessments of all herring stocks that are part of the regional mixture. This was determined to be outside the scope of an update assessment and should be subject to the thorough peer-review of a benchmark. Instead, it was decided to keep the update assessment as consistent as possible with the procedure decided at the last benchmark (ICES 2018). The NSAS assessment later went through an inter-benchmark that did not change the stock composition estimation (ICES 2021). To be consistent with previous assessments, genetic stock identification was converted to the assignments that would be expected from the previous methods (Table 1.4.1). For microstructure, predominantly spring spawning genetic stocks were converted to WBSS while predominantly autumn and winter spawning stocks were converted to NSAS. For vertebral counts, genetic stocks with VS lower than 56.15 (midpoint between mean VS of NSAS and WBSS) were converted to WBSS while stocks with higher VS were converted to NSAS.

We note that this conversion does not fully correspond to what would be obtained with the previous methods. In the previous methods, otolith microstructure (and otolith shape) assignments were made at an individual level. However, in the transformation from genetic assignments (Table 1.4.1), all individuals from the same genetic stock are transformed to the same expected microstructure assignment, Therefore, differences resulting from inter-stock variability and the risk of misclassification is not accounted for. Likewise, the new method maps genetic stock to NSAS/WBSS based on the mean vertebral count of the stock. For example, all genetic Norwegian spring spawners (NSS) are assigned to NSAS in the new method (Mean VS: 57.1). However, roughly 10% of NSS herring have a VS of 56 or below. In the previous method, these would drag the estimated proportion (slightly) towards WBSS. The remaining 90% would drag the proportion towards NSAS. The impact on the proportions would depend on the individual VS and amount of NSS in each sample. Again, the difference resulting from inter-stock variability is not accounted for.

Table 1.4.1. Overview of genetically assigned distinct populations. Mean vertebral counts (VS) for each genetic populations were estimated based in Norwegian catches in 2021, total number of assigned individuals are presented. For consistency in the assessment, fish were assigned to either North Sea autumn spawners (NSAS) or western Baltic spring spawners (WBSS) based on expected outcome from previously used splitting methods. Norwegian data was split by mean vertebral counts, whereas Danish data was split by otolith microstructure into different hatching season. Mismatch between assigned stocks based on Norwegian and Danish data is presented in italic.

Genetic population	**VS**	**Hatching season**	**Stock assigned**	
			Norwegian data	**Danish data**
North Sea autumn spawners	56.5 (n = 530)	Autumn	NSAS	NSAS
Downs	56.5 (n = 782)	Winter	NSAS	NSAS
Western Baltic spring spawners	55.7 (n = 206)	Spring	WBSS	WBSS
WBSS-Skagerrak	56.8 (n = 172)	Spring	*NSAS*	*WBSS*
Norwegian spring spawners	57.1 (n = 194)	Spring	*NSAS*	*WBSS*
North East Atlantic (Faroes, Iceland)	56.3 (n = 6)	Autumn	NSAS	NSAS
Central Baltic herring	55.6 (n = 54)	Spring	WBSS	WBSS
Baltic autumn spawning herring	55.6 (n = 23)	Autumn	*WBSS*	*NSAS*

The further details of this work is described in Berg et al (2022).

With effect from the 2022 update assessments of NSAS and WBSS, Denmark and Norway discontinued the sampling of otolith microstructure and vertebral counts in favor of genetics. Therefore, it was necessary to update the stock splitting procedure. For the update assessment, a minimally disruptive update was chosen to remain consistent with previous years. Changes to the stock splitting that fully utilize the additional information from genetic samples were deferred to a future benchmark.

The updated method consists of a procedure for converting genetic assignments to the expected assignments of otolith microstructure and vertebral counts, respectively. Further, borrowing of information between ages, areas, and cruises was implemented in a model with less reliance on expert judgment than previously. The model was compared to the previous procedure in a re-analysis of data from 2020. The new implementation was found to give stock composition estimates that were overall consistent with the previous method.

Genetic analyses have revealed that more herring stocks mix in larger areas of the region than previously accounted for in the assessments. Therefore, it is appropriate to modify the currently applied two-stock procedure into a proper stock-specific composition procedure. Further, neither the previous nor present method accounts for differences in stock weight-at-age in the splitting. Stock compositions are estimated by numbers and used to split the CANUM calculated from average weights. Instead, an integrated model should be used to calculate stock composition, stock-wise catch weights, stock-wise age distributions and stock-wise CANUM. However, such improvements should be part of a benchmark process to ensure that they are thoroughly peer-reviewed, and the assessment models are built on the best available science. Further, it would require that age samples as well as genotyped samples and baselines are shared between countries, preferably in a standardized format such a GENEPOP (4.0) and with standardized locus names.

1.5 Assessment model development

1.5.1 Multi-fleet stock assessment model

When results from a stock assessment analysis are to be translated into concrete management, there are often practical and political considerations and circumstances that mean that it may be necessary to divide the catch quota among the various fleets. In order to assess the population consequences of such scenarios, it is necessary to base on a fleet-specific model rather than a single fleet and total catches. This project contributed to the further development, implementation and validation of a fleet-specific version of the SAM assessment model.

The details of the multi-fleet stock assessment model are described in Nielsen et al. (2021).

The model has been accepted at ICES benchmarks and are now being used for the official assessment of WBSS.

During this project, the multi-fleet version of the SAM model was merged with the single fleet version and a special “components” branch used for the assessment of NSAS herring.

This important merging ensures that all the latest options in SAM is available for the multi-fleet version and ensures its continued maintenance.

1.5.2 Forecasting

Several small extensions were made to the SAM to allow multi-fleet forecasting. For example, the average fishing mortality is calculated as the mean fishing mortality over a selected group of the most important ages. An option to set distinct groups for each fleet has been implemented. Another example is the option to provide fleet specific observation variances. Such extensions of the model enabled the analyses of WBSS stock rebuilding described in work package 5.

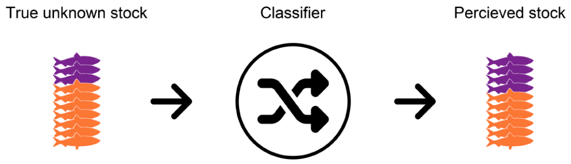
1.6 Stock component sampling and analysis

1.6.1 Implementation of stock identification for assessments - Statistical challenges

Introduction

The increasing collection of genetic samples and classification of herring opens many possible applications. However, there are also challenges to consider when using individual classifications. The presentation discussed two potential pitfalls when using individual classifications to infer stock compositions and how to avoid those using integrated models. This was followed by considerations on sampling strategies for mixed samples. Finally, three applications of genetic samples in integrated models was presented.

When using individual classifications to estimate stock composition, the risk of misclassification must be accounted for. If not, the resulting stock composition estimates will be biased. By construction, misclassification will move individuals to the wrong category in an asymmetric way, thereby giving a biased perception of the stock composition. This issue is independent of the type of classifier and data source used as long as there is a risk of misclassification.



Because

In general:

$$\underbrace{\hat{p}}_{\text{Percieved stock}} = \overbrace{C}^{\text{Confusion matrix}} \cdot \underbrace{\pi}_{\text{True stock}}$$

For two stocks:

$$\begin{pmatrix} \hat{p}_{\color{purple}\bullet} \\ \hat{p}_{\color{orange}\bullet} \end{pmatrix} = \begin{pmatrix} P({\color{purple}\bullet} \to {\color{purple}\bullet}) & P({\color{orange}\bullet} \to {\color{purple}\bullet}) \\ P({\color{purple}\bullet} \to {\color{orange}\bullet}) & P({\color{orange}\bullet} \to {\color{orange}\bullet}) \end{pmatrix} \cdot \begin{pmatrix} \pi_{\color{purple}\bullet} \\ \pi_{\color{orange}\bullet} \end{pmatrix}$$

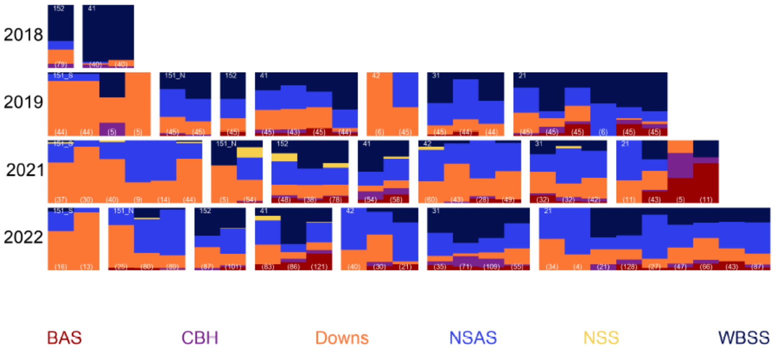
For example:

$$\begin{pmatrix} 0.38 \\ 0.62 \end{pmatrix} = \begin{pmatrix} 0.8 & 0.2 \\ 0.2 & 0.8 \end{pmatrix} \cdot \begin{pmatrix} 0.3 \\ 0.7 \end{pmatrix}$$

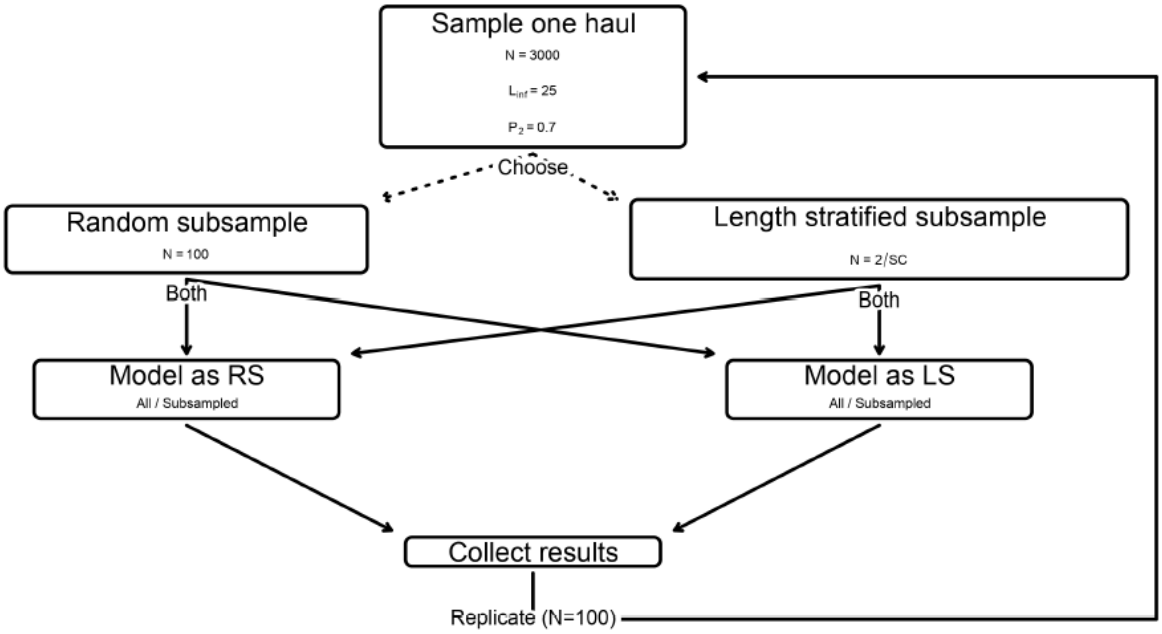
Solution:

- Back-correction
- Combined model

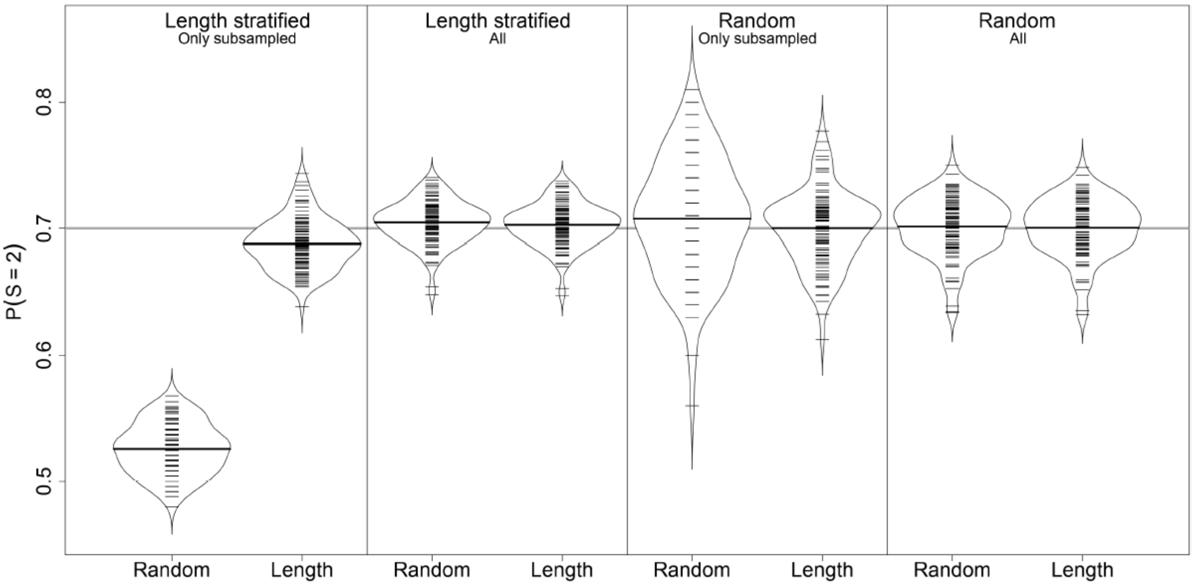
Further, fish caught together are often more similar than fish collected in different hauls. This is seen for length, age, and stock compositions. This must also be accounted for to give proper weight to different hauls in the analysis. In essence, 1000 fish from one haul will most often not be as informative as 1000 fish collected with 100 fish in each of 10 hauls.



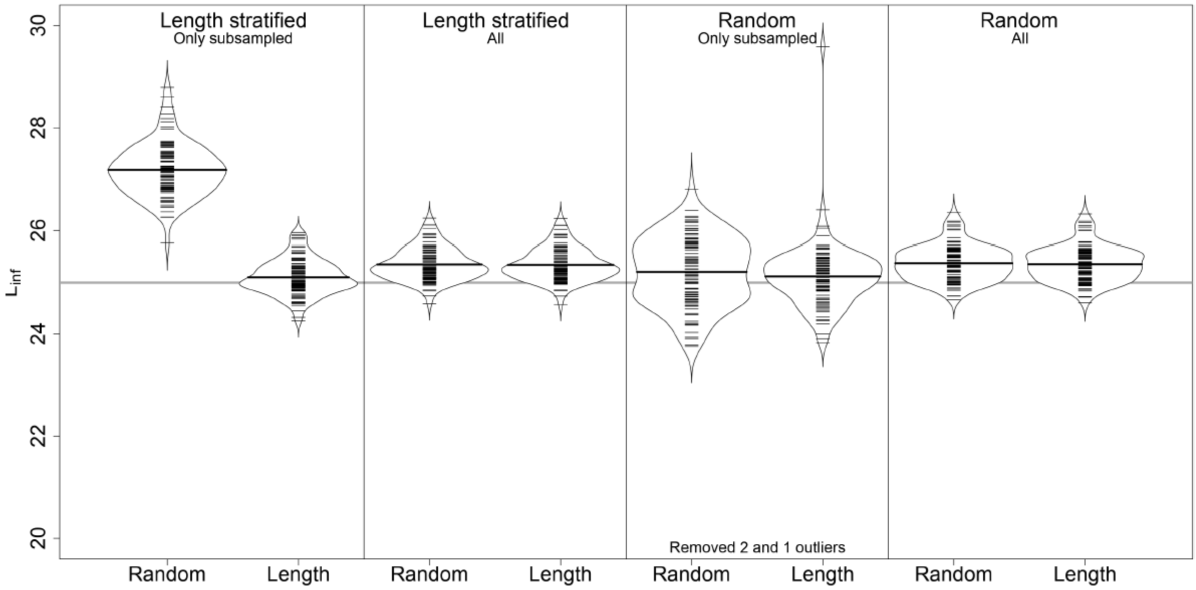
Besides the risk of misclassification and intra-haul similarity, data collection strategies can influence the estimation of stock compositions. A simulation study was presented to illustrate the difference between length stratified and random sampling of stock origin.



The study illustrated the potential bias that arises if length stratified sampling is not accounted for. In this case, the stock composition was estimated to be 55%-45% instead of the true 70%-30%.



In contrast, assuming randomly sampled observations arose from a length stratified program is less problematic and gave unbiased results, similar to the scenarios accounting for the sampling procedure.



However, finding an optimal sampling strategy will be case specific and depend on the subsequent method of analysis, the degree of intra-haul similarity, as well as practical and financial considerations.

- Optimal sampling strategy is case specific
  - Difficult to fully simulate data generating system and strategies
  - Depends on subsequent method for analysis
  - Depends on degree of intra-haul similarity
  - Competes with practical (and financial) concerns
- Should be Transparent, Available, and Fully documented (TAF)
- Can be accounted for in integrated models (becomes less important than for step-wise methods)
- Don’t rock the boat (unless there is a life vest)
- Ensure overlap when changing sampling scheme
- Design for the future

Three examples of using genetic samples in integrated models were presented.

The first example calculated catch numbers-at-age. Often, catch numbers are derived from a combination of total catch weight, length distribution samples, and age-length samples and - when relevant - subsequently split into stocks using stock keys or age-stock keys.

1. Convert total catch weight to numbers-at-age using mean weight-at-age
2. Classify individuals to stocks
3. Calculate stock composition (e.g., per age)
4. Split numbers-at-age per stock

Issue:

Different length-at-age and weight-at-age (or -length) between stocks can lead to mismatches when numbers go into assessments

As an alternative to the step-wise procedure, the example presented an integrated model estimating stock-wise catch numbers-at-age. The integrated model included age, length, weight, and genotype observations. Individual weight was modelled as a function of stock and length, length was modelled as a function of age and stock, age was modelled as a function of stock, and genotype was modelled as a function of stock.

- Inspired by split of catches in the transfer area
- (ignored length stratified sampling and intra-haul similarity)

CANUM:

$$C_{a,s} = N_T \cdot P(Age = a|Stock = s) \cdot P(Stock = s)$$

$$N_T = \frac{W_T}{\sum_s W_{a,s} \cdot P(Stock = s) \cdot P(Age = a|Stock = s)}$$

$$W_T = 3000\text{t}$$

Combined model outline

Individuals:

$$\begin{aligned} P(A_i, L_i, W_i, G_i) &= \sum_s P(A_i, L_i, W_i, G_i \mid S_i = s)P(S_i = s) \\ &= \sum_s P(W_i \mid L_i, S_i = s)P(L_i \mid A_i, S_i = s)P(A_i \mid S_i = s)P(G_i \mid S_i = s)P(S_i = s) \end{aligned}$$

- Weight-at-length: log-normal, log-log linear
- Length-at-age: log-normal, von Bertalanffy
- Age: categorical distribution
- Genotype: multinomial distribution
- Could have included length-stratified sampling here
- Could have included otolith shape, vertebrae count, microstructure, hatch month, etc.
- For baseline, don't sum over stocks
- Genotypes were simulated based on classified stock

We can calculate: $P(S_i = s|A_i, L_i, W_i, G_i)$ using Bayes' theorem.

Data: Individuals by stock and Age

Age \ Stock	BAS	CBH	Downs	NSAS	NSS	WBSS	NA
1	0	0	5	16	1	0	45
2	2	0	18	26	12	9	24
3	2	0	5	2	1	18	9
4	2	0	2	5	0	19	2
5	0	2	1	0	0	13	0
6	0	1	0	1	0	8	0
7	0	0	0	1	0	3	0
8	0	0	0	0	0	3	0
9	0	0	0	0	0	1	0
NA	0	0	0	0	0	0	48

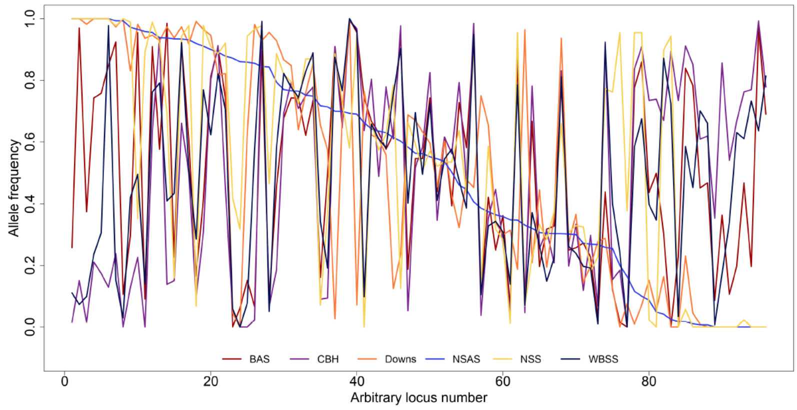
In the fitting, missing observations were accounted for. As a result, catch numbers-at-age could be calculated from total weight and estimated stock-wise weight-at-age and age compositions.

Result: Individual classifications

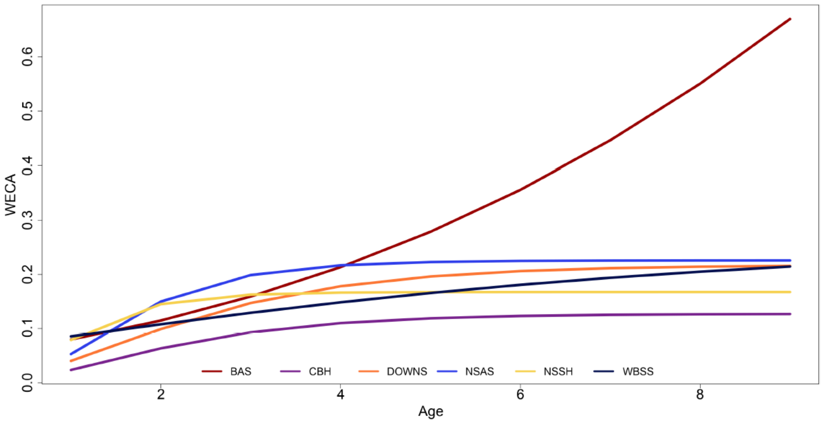
Observed \ Estimated	BAS	CBH	Downs	NSAS	NSS	WBSS
BAS	6	0	0	0	0	0
CBH	0	3	0	0	0	0
Downs	0	0	31	0	0	0
NSAS	0	0	0	51	0	0
NSS	0	0	0	0	14	0
WBSS	0	0	0	0	0	74
NA	25	0	34	28	7	34

The results affected both the estimated age and stock compositions compared to a step-wise approach. This was partly because the step-wise approach did not sufficiently account for stock-wise differences in length- and weight-at-age.

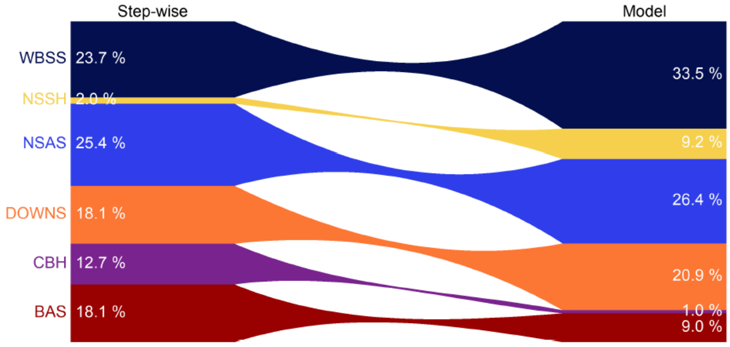
Result: Allele frequencies



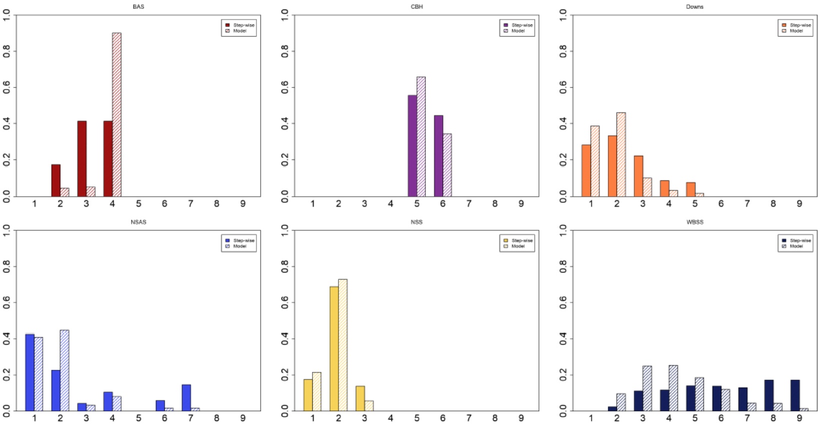
Result: WECA



Result: Stock composition (numbers)



Result: Age composition



The second example presented, illustrated a conversion of otolith based hatch month to genetic stock. Until recently, stock origin in, e.g., the HERAS survey was determined from otolith microstructure readings giving a hatch month classification, 4 four spring spawners, 9 for autumn spawners, and 12 for winter spawners. In the example, Danish samples from HERAS in subdivision 3.a.20 was used. In 2019, both genetic and hatch month classifications were available, while only hatch months were collected in 2020. The aim was to use the 2019 data to convert 2020 hatch months to genetic stock origin, Baltic Autumn Spawners, Downs winter spawners, North Sea Autumn spawners, or Western Baltic Spring Spawners. For simplicity, 5 Central Baltic herring were converted to 'unknown'. Further, Norwegian Spring spawners were not accounted for because there were not encountered in the 2019 data. The model was similar to the model in the previous example, but also included the probability of observing a given hatch month classification given the true stock origin.

Can hatch month be converted to genetic stock?

Data:

- Danish samples from HERAS, 2019-2020, Subdivision 3.a.20
- Hatch month classification in 2019 and 2020 (4, 9, 12)
- Genetic classification in 2019 (BAS, Downs, NSAS, WBSS)
- (No NSS observed. Convert 5 CBH to unobserved)

Goal:

- Use overlap in 2019 to estimate genetic stock composition in 2020

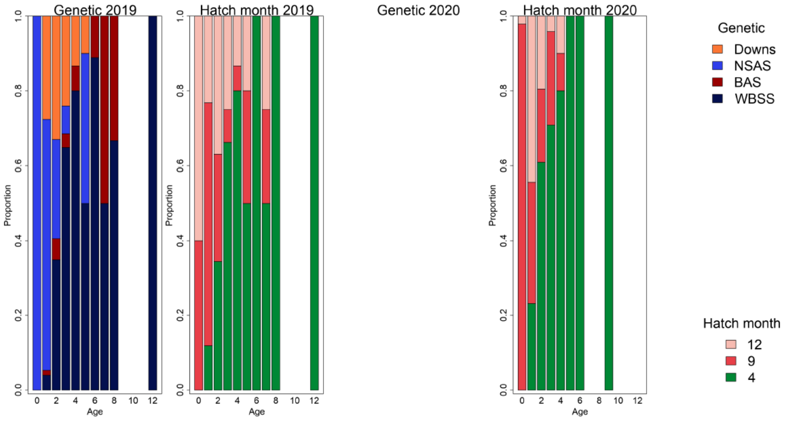
Approach:

- Basically same model as in previous slides
- Include $P(HM_i = h \mid S_i = s)$
- Hope that partial information is enough
- (ignored length stratified sampling and intra-haul similarity)

Data

Genetic \ Hatch	4	9	12	NA
BAS	4	4	4	3
Downs	12	8	55	18
NSAS	6	82	10	41
WBSS	84	1	3	21
NA	155	217	159	1793

Data: Simple proportions-at-age



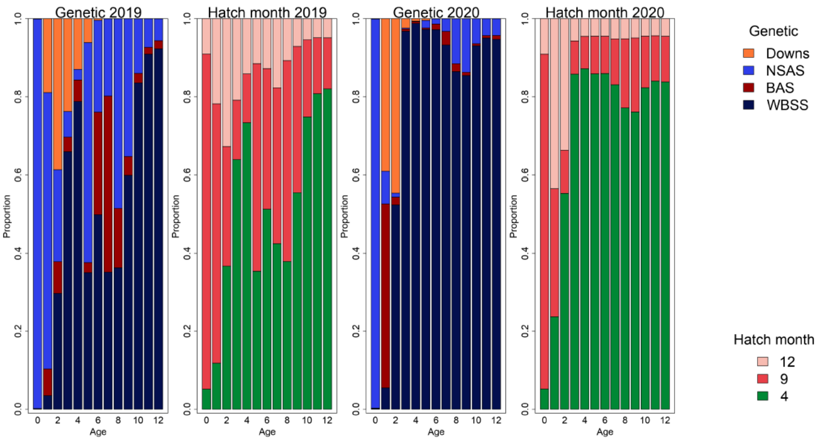
The model provided reasonable estimates of genetic stock origin using the partial observations available. Further, the model estimated a confusion matrix for hatch month classifications.

Result: Estimated confusion matrix

Genetic \ Hatch	4	9	12
BAS	0.23	0.44	0.32
Downs	0.19	0.11	0.69
NSAS	0.05	0.86	0.09
WBSS	0.88	0.08	0.04

True Western Baltic Spring spawners were estimated to have 88% probability of being correctly classified as hatch month 4, North Sea Autumn spawners had an 86% probability of being classified as hatch month 9, Downs winter spawners had a 69% probability of being classified as hatch month 12, while Baltic autumn spawners had 44% probability of being classified as hatch month 9.

Result: Estimated proportions-at-age



The third example presented extended the models from the two first examples to split acoustic survey data into stocks. Building on the two previous examples, an integrated model of nautical area scattering coefficients (NASC), trawl catch compositions, and spatio-temporal stock/species abundance was developed with the aim of estimating a smooth split of NASC values into species and stocks, while accounting for differences in growth, length distribution, and spatial abundance.

Integrated model for splitting NASC

Data:

- Danish HERAS samples in 2019
- 6 herring stocks, 13 other species
- Species composition data per haul (wt)
- Length composition data per species and haul (n)
- Biological samples from HER and SPR
- Genetic and hatch month classifications
- Spatial NASC measurements

Note:

- Only for illustration
- Some results don't seem quite right
- No samples of NSS

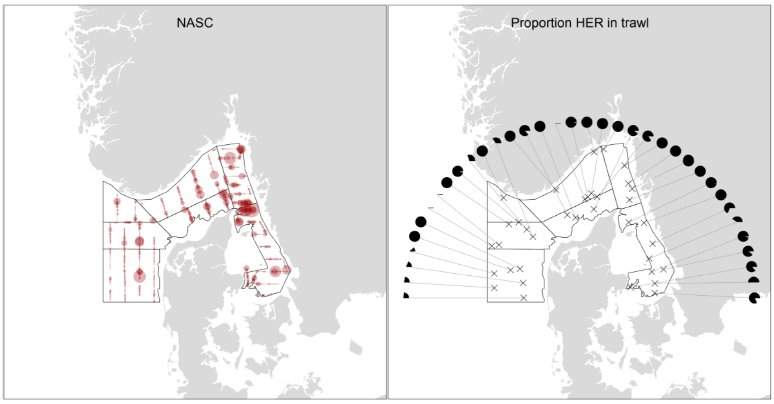
Approach:

- Basically same model as before
- Random effects: Spatial logN per stock/species
- Species / Length composition: zero inflated Dirichlet
- Tried to estimate retention in trawl
- NASC: log-normal with detection limit
- Ignored length stratified sampling and intra-haul similarity

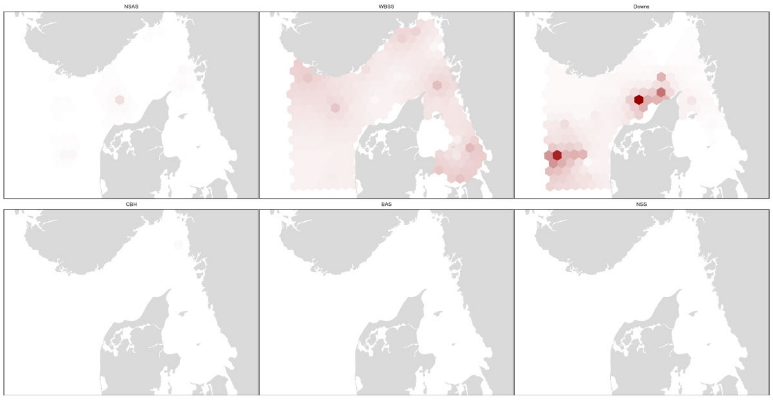
Goal:

- Smooth split of NASC values
- Alternative to step-wise approaches
- Account for different size-at-age when estimating stock abundance
- Use this for evaluating sampling strategies at some point

Data



Result: Total abundance



Result: Genetic-Hatch confusion

Genetic \ Hatch	4	9	12
NSAS	0.07	0.79	0.14
WBSS	0.88	0.04	0.08
Downs	0.37	0.24	0.40
CBH	0.74	0.09	0.17
BAS	0.24	0.52	0.24
NSS	0.33	0.33	0.33

Summary

- Account for misclassification risk
- Partial information is still information
- What you see is what you model
- Integrated models solves (almost) all problems (but creates a few new)

2. Spawning Stock Mapping

Mapping of spawning locations and populations of Western Baltic Spring Spawning (WBSS) herring

The Western Baltic Spring Spawning herring stock constitutes a mixture of biologically distinct populations spawning in the North Sea-Baltic Sea transitional waters. A part from one of the main stock components, the 'Rügen' population, that mainly spawns in the German Greifswald Bay and in neighbouring estuaries and sounds, there is scarce knowledge about the individual biological components making up the WBSS stock. A main objective was to explore WBSS spawning in Danish waters; to map spawning areas and to determine the biological relationships among herring spawning at different locations, by means of population genetic analyses. In order to determine biological relationships from local to regional geographical scales, the work included knowledge and sample exchange with international collaborators engaging in WBSS stock assessment, in Sweden, Germany and Norway.

2.1 Construction of a DNA database for herring populations

In collaboration with international partners, DTU Aqua has generated and curates a genotype database for herring populations in the North Sea-Baltic Sea region. Samples represent local spawning units (adults in full spawning condition and in some cases newly hatched larvae) that have been genotyped using a panel of 96 SNP (Single Nucleotide Polymorphism) markers (Bekkevold et al. 2023), selected from whole-genome screening analyses (Han et al. 2020) to enable accurate classification of individual fish to population (their reproductive unit). To date, the database comprises more than 80 individual collections and more than 2000 individual herring genotypes (Figure 2.1.1). The database is used as a baseline for genetically assigning (classifying) mixed-stock catches of herring in compliance with the EU Data Collection Framework as of 2021.

For more than a century, it has been assumed that herring in Danish waters perform homing to natal spawning locations (Jensen 1946). Moreover, individual herring populations tend to spawn either in spring or autumn/winter with spawning time fidelity (i.e. spawning time switching being rare).

In spring, herring on spawning run (ripening and ripe adults) can be encountered in most Danish coastal and fjord areas and are often seen in large densities when migrating though narrow straits and manmade locks into estuaries and fjords. Autumn spawning herring appear to be less predictable in their occurrence in local Danish waters in general but are encountered in several spawning areas. Spawning bed monitoring is routinely undertaken in the Rügen herring's main spawning area in the Greifswald Bay in Germany but there are no published records for spawning areas in Danish waters, and the timing, occurrences and densities are generally poorly described.

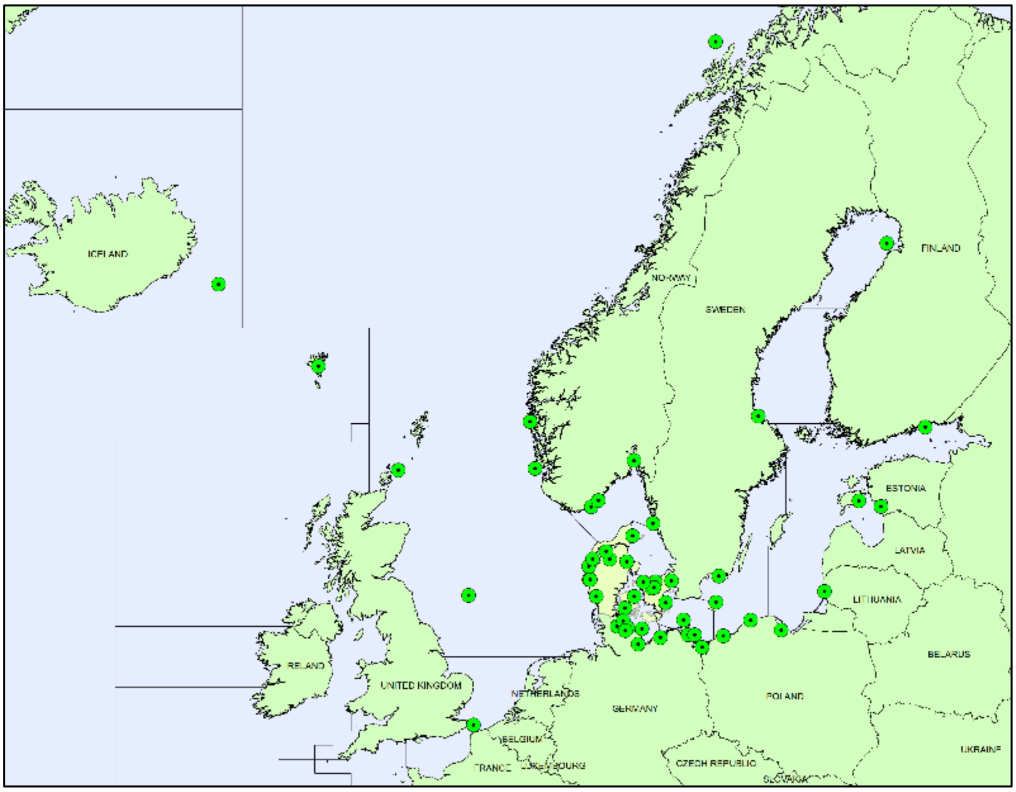


Figure 2.1.1. Sampled spawning locations for Atlantic herring in DTU-Aqua's DNA database (green symbols).

Prior to genetic determination of population origins, demographically distinct herring population units were classified based on differences in morphological traits including numbers of vertebrae, otolith growth patterns, growth rates, and parasite infestations (ICES 2022). Based on previous morphological marker (e.g. vertebral counts) studies, Jensen (1946) listed separate populations spawning in (§ indicates locations that were sampled for genetic analyses in this study):

1. Limfjorden ('Aalborg-herring') migrating into the fjord from east (Kattegat) to spawn in Nibe, Løgstør, Lovns and Skive Bredning in spring §
2. Limfjorden ('Thyland-herring') migrating into the fjord from west (North Sea, via the Thyborøn Kanal) to spawn in Nissum and Thisted Bredning in spring §
3. Limfjorden ('West-Jutland autumn herring') migrating into the fjord from west (North Sea, via the Thyborøn Kanal) to spawn in Nissum Bredning in autumn
4. Herring spawning on banks in the southern Kattegat in spring (no specific spawning localities were documented)
5. Wadden Sea herring entering from the North Sea to spawn in spring §
6. Ringkøbing and Nissum Fjord herring entering from the North Sea to spawn in spring §
7. Jammerbugt (part of the Skagerrak) spring spawning herring (no specific spawning localities were documented in Jensen 1946)
8. Aalbæk Bay and Anholt (Northern Kattegat) spawning in spring
9. Aalborg Bay (Southern Kattegat) spawning in spring §

10. Mariager Fjord entering from Southern Kattegat in spring (neighbouring Randers Fjord was sampled here §)
11. North Sjælland (Southern Kattegat) spawning in spring §
12. Great Belt Sea ('Storebælt') spring spawning §
13. Great Belt Sea ('Storebælt') autumn spawning
14. Holbæk-Roskilde-Isefjord (entering from Southern Kattegat) spring spawning §
15. Little Belt Sea ('Lillebælt') and Western Baltic Sea spring spawning §
16. North Sea offshore ('Jyske Rev-silden') autumn spawning herring; spilling over from (British waters) spawning banks in the western North Sea
17. North Sea inshore ('Thyborøn-herring') spawning in autumn off the west coast of Jutland at Thyborøn (§)
18. Kattegat ('Kobbergrund-herring') autumn spawners spawning on banks in the central Kattegat Sea
19. The Sound ('Øresund-herring') and Møn autumn spawners §
20. Southern Belt Sea spawning in autumn in the Western Baltic Sea §
21. Bornholm island spawning in autumn in the Western Baltic Sea §

However, few of all these listed populations have been formally characterized or analysed with population genetic methods, and it is unexplored to which extent this list is comprehensive and founded on biologically sound knowledge. An aim of the current study hence was to collect and genetically characterize ripe-and-running herring from across this geographical distribution to gain a better understanding of their spawning distributions in Danish waters. The study also included samples from neighboring WBSS spawning areas focusing mainly on German, Swedish and Norwegian waters, but also included genetically more strongly differentiated populations spawning in British, Faroese, Icelandic, Greenland, Polish, Latvian, Estonian and Finnish waters.

2.1.1 Herring population genetic baseline (spawning herring database)

Spawning locations and population affiliations of WBSS herring, with special focus on Danish spawning sites, were examined by sampling a select number of known (or presumed) spawning locations. Targeted locations represented semi-enclosed areas (fjords, estuaries, lagoons) known to attract herring on spawning run. Collections included 1) adult, ripe-and-running fish expected to represent the local spawning units, and 2) recently spawned live embryos, representing the locally produced fish expected to eventually recruit into that locality (see Section 2.2).

Adult fish were collected by netting and angling during peak spawning time in spring or autumn 2021-2023. To identify local spawning grounds in the Inner Danish Waters, around 90 recreational fishermen distributed throughout Denmark's coastal areas and registered as "Key Fishers" were encouraged to report and collect spawning herring (see Section 2.3).

A total of 14 locations were successfully sampled during the project; some of them repeatedly over time (Table 2.1.1; Figure 2.1.2). Upon capture, fish were euthanized, measured for length and weight, their maturity stage was recorded by visual inspection of gonads and a pectoral fin clip was preserved in 96% ethanol for subsequent genetic analyses. Otoliths were extracted, and age and hatching season (season in which the fish was born) was estimated from otolith growth patterns (Clausen et al. 2007). In some instances, samples were obtained from recreational and commercial fishers and only subsets of biological data were available.

All samples were analysed and genotyped using the standardized method detailed in Bekkevold et al. (2023). Briefly, the method entails genotyping 59 Single Nucleotide Polymorphism (SNP) markers selected to maximize genetic resolution among populations in the North Sea-Baltic Sea area. The resulting spawning database included tissue samples from 2005 individual herring spawning across the Northeast Atlantic, of which 553 were collected in Danish waters and 258 were collected in German waters and analysed in connection with the present study. Opportunistic sampling was employed in a few cases, where scientific cruises came across herring assemblages in (or close to) spawning condition (Table 2.1.1).

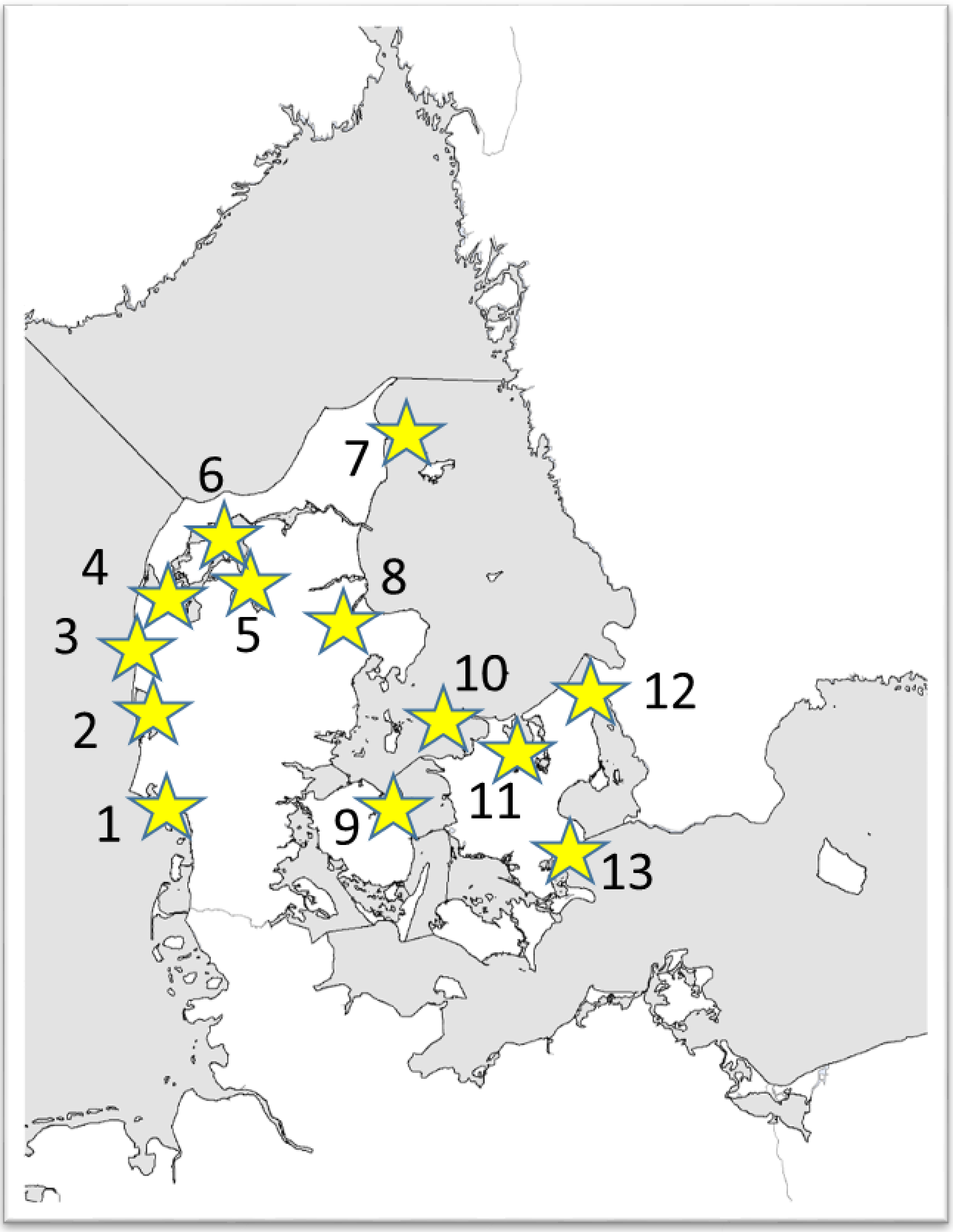


Figure 2.1.2. Danish locations for new collections of spawning herring and embryos obtained 2021-2023. Location number codes and further details are found in Table 2.1.1.

Genetic structure in herring sampled on spawning locations

Although population genetic analyses based on a subset of 59 SNP markers are unlikely to fully reflect and distinguish evolutionary trajectories that can be assessed with whole-genome analyses (Han et al. 2020), analyses are still expected to yield important insights into the relative similarities and differences among collections from different geographical areas.

Genetic clustering analyses of SNP data (using a Discriminant Analysis of Principal Components) typed in new collections of herring analysed together with previously obtained data corroborated that the selected SNP panel was able to distinguish among major stock components in the Northeast Atlantic, as well as among WBSS populations (Bekkevold et al. 2023; Figure 2.1.3). Temporal replicates within location showed close genetic relationships (estimated using pairwise F_{st}) in all cases, supporting that they belonged to the same locally spawning population. An exception to this was found within the Danish Isefjord (see below). Overall, all new WBSS samples could be genetically assigned to one of the four geographically separated WBSS populations identified in Bekkevold et al. (2023): WBSS-Skagerrak (spawning along the Norwegian-Swedish Skagerrak coast), WBSS-IDW (Inner Danish Waters, including fjord systems flowing into the North Sea and Wadden Sea), WBSS-W. Baltic (German Western Baltic Sea fjords in SD22), and WBSS-Rügen (with its main spawning site in the Greifswald Bay and extending to neighbouring spawning locations in SD24).

Table 2.1.1. Atlantic herring samples from Danish waters used in genetic analysis of population origin. # indicates locations tested for spawning beds in spring 2023. ł indicates samples that were tested for hatching season using otolith microstructure analysis. Sampling years for samples collected in connection with the current study are underlined.

Region (SD)	Locality (no. in Figure 2.1.2)	Life stage	Number fish sampled	Spawning season	Genetic origin (population)	Collection years	Area no. corresponding with Jensen's (1946) list above
North Sea (Wadden Sea)	Ho Bay Esbjerg ł (1)	Adults	57	spring	WBSS-IDW	2021	5
North Sea	Ringkøbing Fjord ł (2)	Adults, embryos	106	spring	WBSS-IDW	2009,2021, 2022,2023	6
North Sea	Ringkøbing Fjord ł, €	Adults	34	autumn	Mixed WBSS-IDW, BAS, NSAS	2021	(17)
North Sea	Nissum Fjord# (3)	Adults	20	spring	WBSS-IDW	2023	6
North Sea	Nissum Bredning Limfjord# (4)	Adults	39	spring	WBSS-IDW	2009	2
Kattegat	Hjarbæk Fjord Limfjord# ł (5)	Adults, embryos	50	spring	WBSS-IDW	2021,2022, 2023	1
Kattegat	Fur Limfjord (6)	Adults	51	spring	WBSS-IDW	2021	1
Kattegat	Sæby Aalborg Bay (7)	Adults	10	spring	WBSS-IDW	2011,2022	9
Kattegat	Randers Fjord# ł (8)	Adults, embryos	58	spring	WBSS-IDW	2021,2023	10
Kattegat	Holbæk-Isefjord ł (11)	Adults	76	spring	Mixed WBSS-IDW, BAS and hybrids	2003,2009, 2021,2023	14
Kattegat	Holbæk-Isefjord ł	Adults	38	autumn	Mixed WBSS-IDW and BAS	2021,2022, 2023	N.A.
Kattegat	Sejerø ¤ (10)	Adults	4	spring	WBSS-IDW	2021	11
Storebælt	Kerteminde Fjord ł (9)	Adults	56	spring	WBSS-IDW	2021,2023	12
Øresund (the Sound)	Øresund § (12)	Adults	20	autumn	Mix of BAS, NSAS and hybrid genotypes	2021	19
Øresund (the Sound)	Fakse Bay Rødby ł (13)	Adults	30	spring	WBSS-IDW	2021,2023	15
Baltic Sea	Bornholm Basin	Larvae	52	autumn	BAS	2016,2017, 2018	21

€) Samples from carcasses only; no maturity estimation possible; §) opportunistic sampling of near-ripe fish; ¤) not included in analyses due to low sample size (<10 fish).

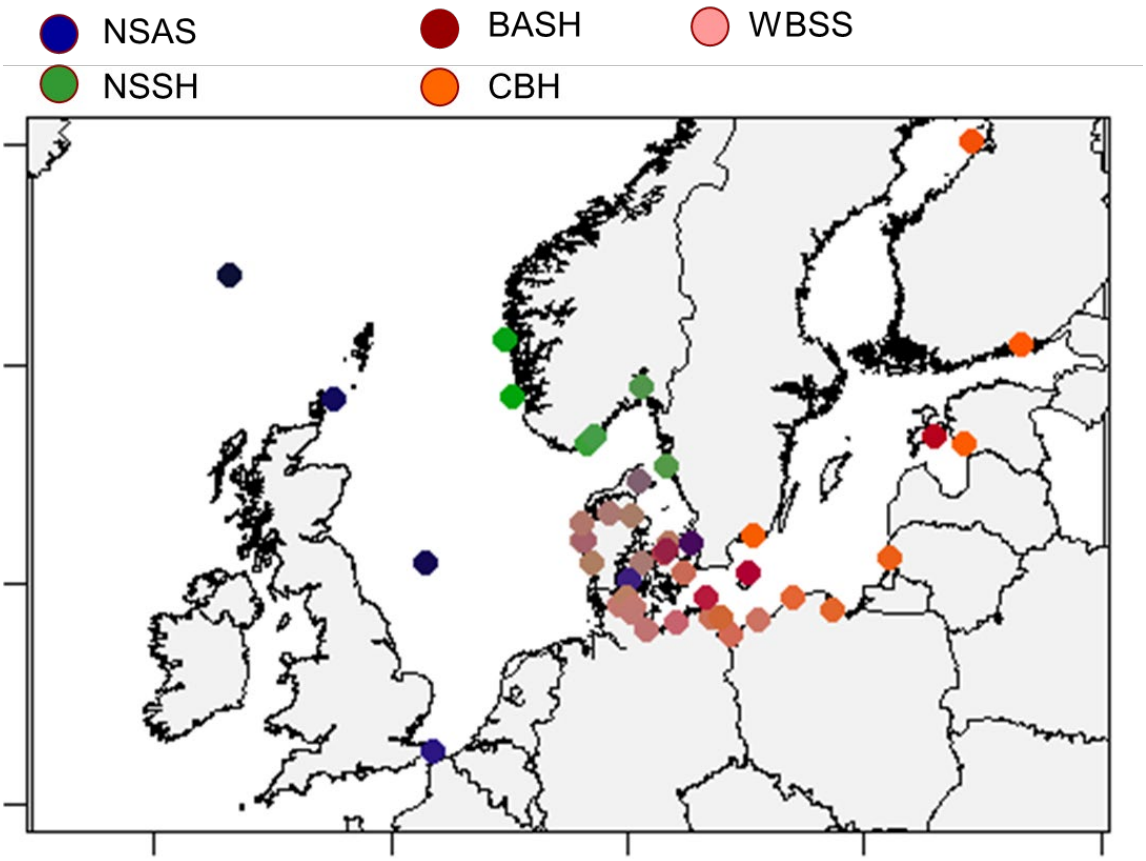


Figure 2.1.3. Collections of herring from spawning locations included in the DNA baseline, where symbol colours identify genetic relationships among collections determined using DAPC analysis. The first three Discriminant Axes (DA) are reflected in colour grading along the red, green, and blue spectra, respectively (i.e. genetically more similar collections show more similar colour shades and vice versa). The legend shows the correspondence between collection colours and overall stock afiliation.

Spring spawning herring populations in the North Sea-Baltic Sea transition zone

When the SNP genotype dataset was filtered to only include all WBSS herring (i.e. also from the Skagerrak), a DAPC clustering analysis corroborated the strong differentiation between genetic profiles of herring spawning in Norwegian-Swedish Skagerrak waters (green symbols in figure 2.1.4 left panel) and all other WBSS herring (red symbol shades in Figure 2.1.4 left panel). The genetic sub-structure among WBSS spawning locations south of the Skagerrak was also clearly illustrated in Figure 2.1.4 (right panel), when extracting variance explained by DA 1 (mainly explained by SNPs associated with salinity) and focussing on information for DA 2-4. Here, it was evident that genetic differentiation between neighbouring populations was not always abrubt (e.g. the collection from the Warnow area showed genetic relatedness to both the Rügen and the W. Baltic Sea population) but also that in most cases local collections could be clearly grouped into specific populations.

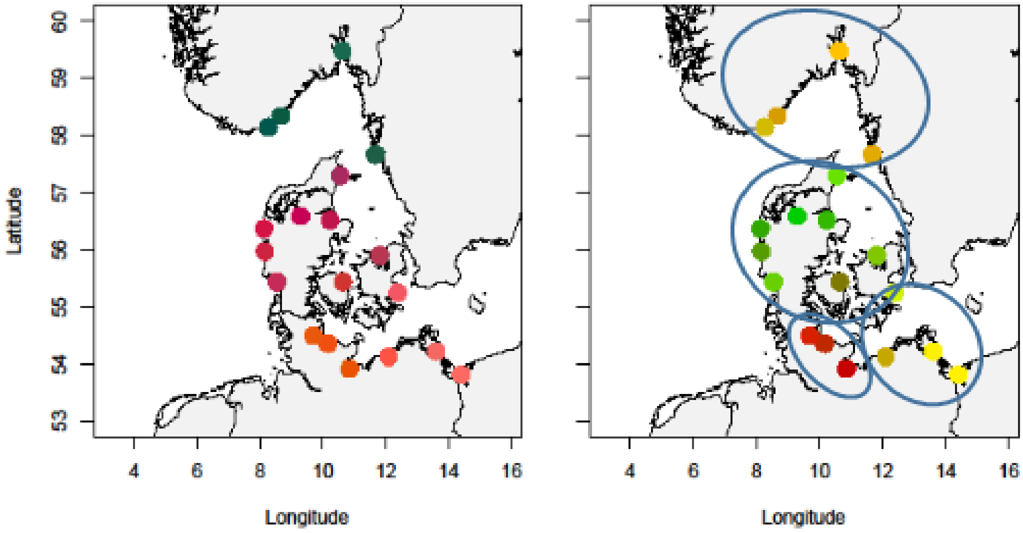


Figure 2.1.4. Collections of WBSS herring in the DNA baseline where symbol colours identify genetic relationships among collections determined using DAPC analysis. Left panel: the first three discriminant axes (DAs) are reflected in colour grading along the red, green, and blue spectra, respectively (i.e. genetically more similar collections show more similar colour shades and vice versa). Here, main differences are found between Skagerrak (northern; in green shades) and Western Baltic (southern; in red shades) populations. Right panel: depicts the same data as in the left panel but colour grading only reflects the DAs 2-4 (i.e. removing inference for DA 1 which is mainly associated with spawning site salinity). The approximate geographical delimitation of the four WBSS populations is shown by ellipses.

When the SNP genotype dataset was filtered to only include brackish water collections from the Baltic Sea and the Western Baltic Sea (i.e. excluding collections from the Skagerrak), a DAPC clustering analysis again reflected differentiation among these populations (Figure 2.1.5) and that genetic differences displayed a gradual change that to a large extent reflected geographical location along the transect from the Kattegat (represented by the sample from Sæby) in northwest to the Bothnian Bay in northeast (compare the two panels in Figure 2.1.5). The variations in genetic profiles are thus consistent with the area’s environmental variance.

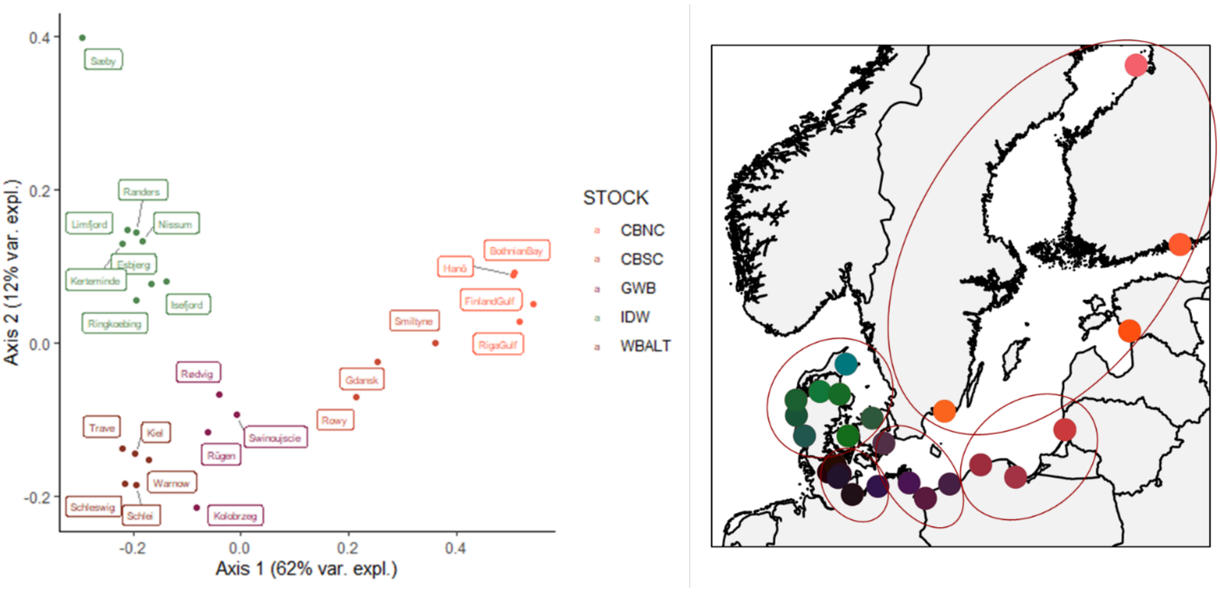


Figure 2.1.5. Principal component analysis showing genetic relationships among collections of spring spawning herring in the greater Baltic Sea area (i.e. including both Central Baltic Sea and WBSS populations from brackish waters) as assessed using 59 SNP markers. Individual collections are shown by spawning location name in the PCA on the left and colored by population. The map to the right shows collection locations coloured by degrees of genetic differentiation along the first three PCs. Ellipses delimit the approximate geographical distribution of populations WBSS-IDW, WBSS-W. Baltic, WBSS-Rügen (GWB), CBSC and CBNC (from left to right).

Limfjord, Ringkøbing and Nissum Fjord spring spawning herring

Three of the sampled spawning locations, Limfjord, Ringkøbing and Nissum Fjord, represent brackish fjord systems flowing into the eastern North Sea on the Jutland west coast. Their herring populations are currently managed as part of the North Sea stock (IVb) (also see case study in Section 1.2). The genetic analyses however, clearly demonstrated that herring spawning in all these locations, together with herring from the Wadden Sea, belong to the WBSS-IDW population and are genetically highly distinct from the NSAS herring spawning in the fully saline North Sea. In the Limfjord, Jensen (1946) listed two different populations and both areas were sampled for this project. However, there was no evidence from the SNP data that the two locations (respectively in the western and central part of the fjord) represented different populations. Although analyses including a larger number of genetic markers may be needed to map fine scale population structure within the fjord, a pilot analysis of samples from the Limfjord and Ringkøbing fjord using more than 4000 SNPs spanning the herring genome did not identify population differentiation (D. Bekkevold, unpublished data). Current evidence hence points to lack of demographic structure among spring-spawning herring in Danish fjords, including both fjords in the North Sea and western Baltic Sea areas.

Autumn spawning herring in the North Sea-Baltic Sea transition zone

The North Sea-Baltic Sea transition zone is an area typically associated with spring spawning herring populations, and autumn spawning herring populations have been less studied as they are considered overall less prominent in the area. However, the medieval herring fisheries of the area was mainly based on autumn spawning populations (Atmore et al. 2024) and in the Baltic proper, it is suggested that Baltic autumn spawning herring are increasing in importance in recent years (Ojaveer et al. 2024).

We carried out genetic analyses of opportunistic samples of autumn spawning herring at three locations: Holbæk-Isefjord and the Sound in the Baltic-North Sea transition zone, and in Ringkøbing Fjord bordering the North Sea.

Øresund autumn spawning herring

An opportunistic sample was obtained from the Øresund (SD 23) by the German *MS Solea* autumn cruise on the 20th October 2021 (Table 2.1.1). The expectation is that the area constitutes the wintering site for WBSS herring that will eventually migrate to Rügen/Greifswald Bay to spawn the subsequent spring (e.g. Miethe et al. 2013). As many of the samples constituted mature fish, there was interest in determining their population origin. A total of 18 ripe and running herring were genotyped using the standard method and genotypes were compared with the DNA database. In a genetic admixture analysis with the software STRUCTURE (Pritchard et al. 2000) the majority (N=15) of these samples represented neither 'pure' BAS nor 'pure' NSAS genotypes, but rather admixed genotypes, i.e. fish that to varying degrees harboured a mixture of NSAS- and BAS-specific gene variants (Figure 2.1.6). A genetic clustering analysis (using PCA) with other autumn and winter spawning populations (Figure 2.1.7) supported that the genotypes of several of these fish did not correspond with an origin in either a NSAS or a BAS population. The biological significance of this, presumed divergent, group of herring, including where they would have spawned, remains to be elucidated with extended sampling campaigns. It could be hypothesized that the fish belong to what Jensen (1946) termed the 'Øresund autumn spawners' (see Table 2.1.1). Interestingly, one of the gene variants that showed hybrid behavior was a SNP associated with adaptation to (low) salinity, which is near-fixed for one variant in the brackish Baltic Sea and for another variant in the saline North Sea (Figure 2.1.8). However, in the Øresund sample, a large proportion of the fish showed both types. It could be hypothesized that these 'hybrid' fish perform optimally under local environmental conditions with intermediate salinity levels.

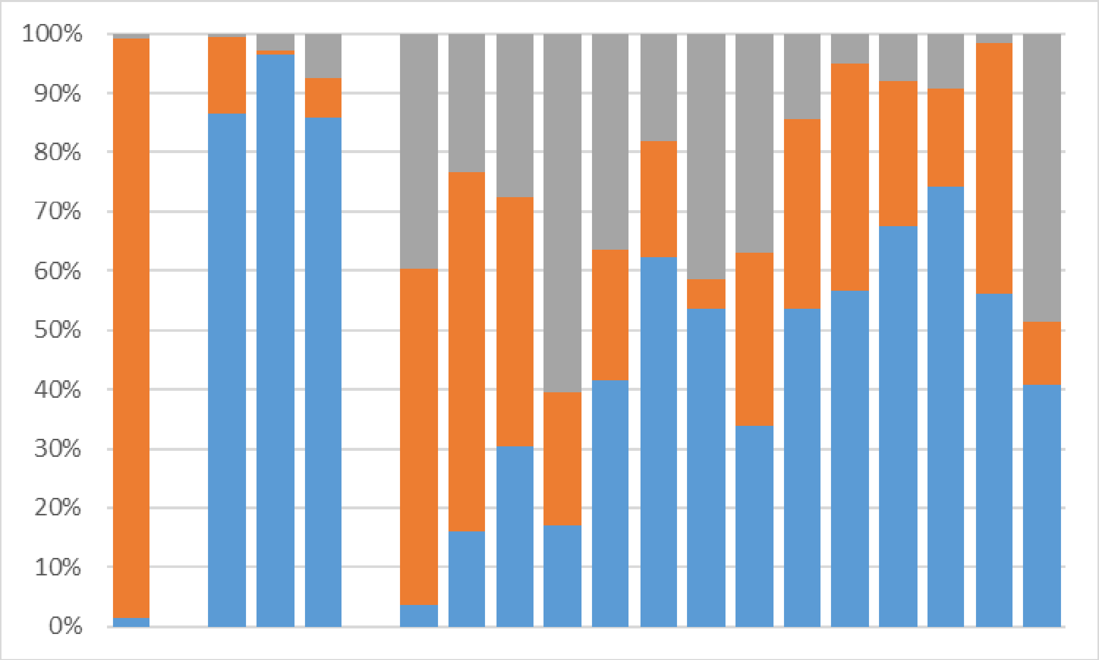


Figure 2.1.6. Genetic admixture estimated with STRUCTURE for 18 fully mature autumn spawning herring sampled in Øresund (SD23) in October 2021. Each bar represents the genotype of an individual and the colour indicates the estimated proportion of the genotype that originated from either NSAS (orange), Downs (gray), or BAS (blue). The first fish from left assigned to NSAS, the second to fourth to BAS, whereas the remaining 14 fish showed admixed genotypes.

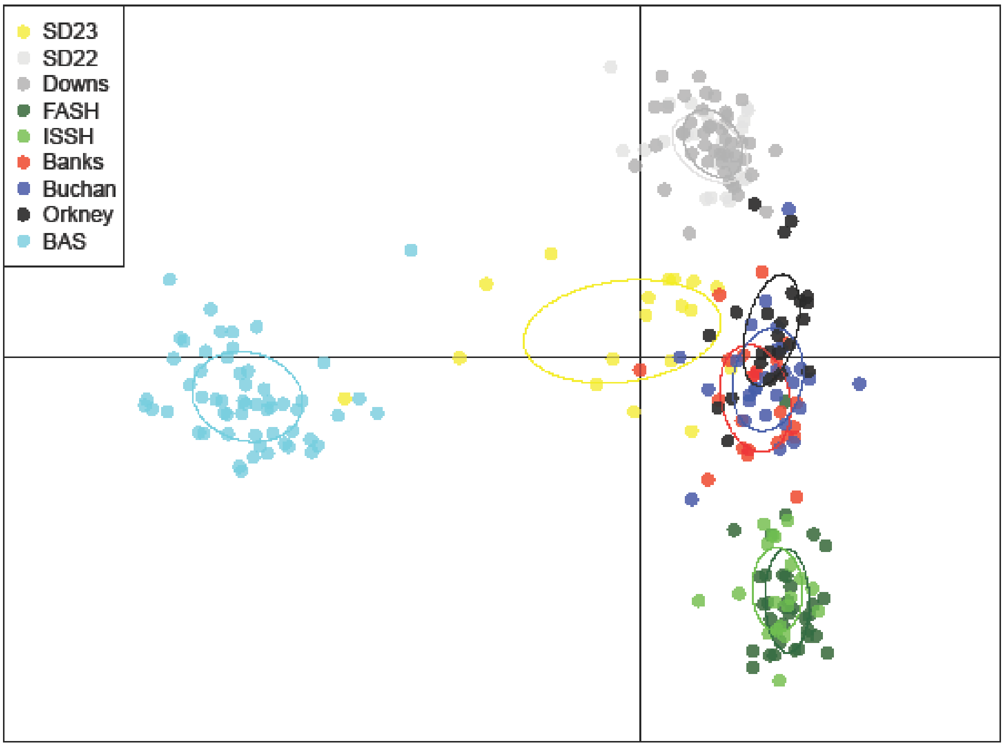


Figure 2.1.7. Genetic clustering of herring samples from summer/autumn and winter spawning populations analysed with 59 SNPs, showing the first two axes in a principal component analysis (axis1 explains 58.53% and axis2 explains 33.67% of the variance). Samples are coloured by population or collection site, where 'SD23' represents 20 fully mature herring spawning in the Øresund (SD 23) and 'SD22' represents a sample of maturing winter spawned herring collected in Lillebelt (SD22). Results show clear clustering among 1) Baltic autumn spawning herring (BAS), 2) North Sea autumn spawners (NSAS: Banks, Buchan, Orkney), 3) Downs winter spawners, and 4) Northeast Atlantic autumn/summer spawners (FASH, ISSH), with no differentiation between the latter two stocks. The SD22 sample clusters with Downs. The SD23 sample clusters with neither BAS nor NSAS.

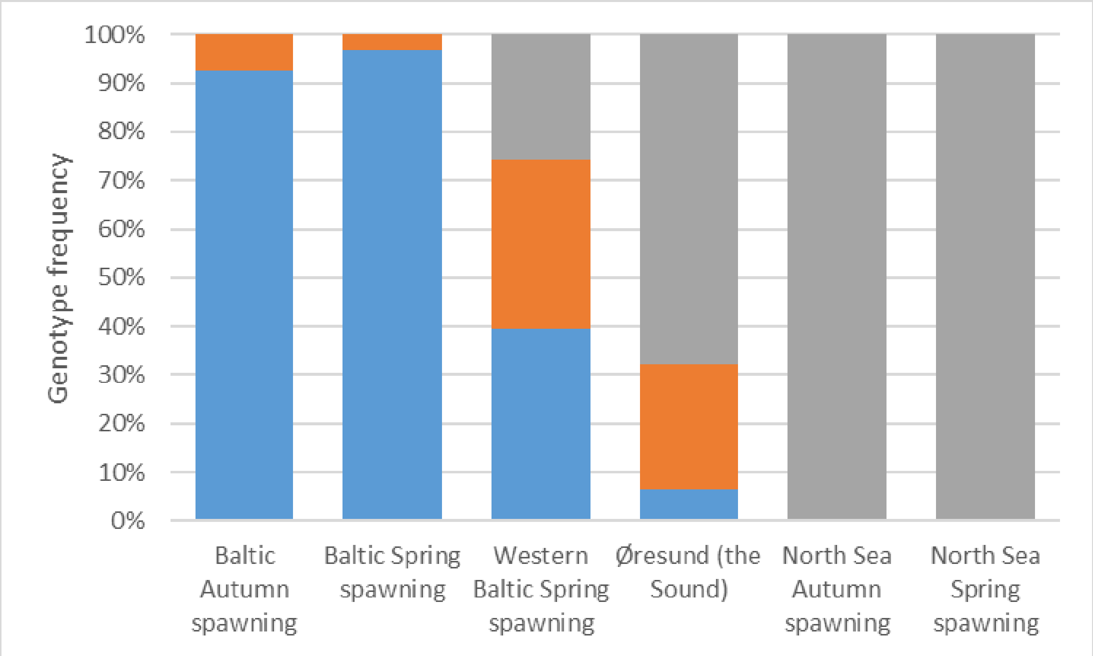


Figure 2.1.8. Variant (genotype) frequencies of a SNP marker associated with salinity adaptation, shown for population samples representing both spring and autumn spawning populations in the Baltic Sea (left, spawning at low salinity) and in the North Sea (right, spawning at high salinity), in comparison with spring spawning populations from the salinity-variant Western Baltic Sea and the Øresund sample of autumn spawning herring. Bar colours indicate the relative frequencies of the homozygote 1 (blue: fish with two copies of the low-salinity variant), the heterozygote (orange: fish with one copy of the low-, and one copy of the high -salinity variant), and homozygote 2 (gray: fish with two copies of the high-salinity variant).

Isefjord autumn spawning herring

Spring spawning herring are commonly observed in the Ise-/Holbæk/Roskilde Fjord system in northern Zealand. The fjord system is a brackish water body flowing into the southern Kattegat (SD21) and previous genetic studies have shown that the local spring spawning population belongs to WBSS. The coastal area bordering the fjord is listed as a spawning location for autumn spawning herring (Clausen et al. 2015), but samples and genetic testing have not been undertaken. Samples included in the present study targeted both autumn and spring spawning herring collected by recreational netting operations and by angling inside Isefjord and Holbæk Fjord. Otolith based assessment of hatching season was available for a subset of the collections (Table 2.1.2), allowing comparison between inferred spawning time based on maturity stage at capture, assigned genetic population, and estimated hatching season of individual fish. Results are shown in figure 2.1.9. The majority (68%) of 68 samples of ripe herring collected from the fjord in spring 2021-2023 assigned to the WBSS-IDW population. However, 22 herring had genotypes suggestive of either being of BAS or hybrid background. Subsets of BAS & hybrid fish were tested for hatching time (see below) and they showed evidence of hatching in either autumn or winter, i.e. there was overall correspondence between spawning time predicted from genetic and morphological data.

In 38 samples of ripe herring collected in the Holbæk-Isefjord system in autumn 2021-2022, 58% had a BAS genetic profile, and respectively 2% (one fish), 6%, and 34% clustered with NSAS, hybrid genotypes, and WBSS. It was thus clear that the fjord system constitutes a mixing area for herring with different genetic backgrounds and different spawning types (spring/autumn) potentially also with hybridisation. Time series data are needed to determine the temporal dynamics of the mixing, but it was suggested that the area supports (mainly) WBSS-IDW herring spawning in spring and (mainly) BAS spawning in autumn, intermixed with (smaller proportions of) hybrid genotypes.

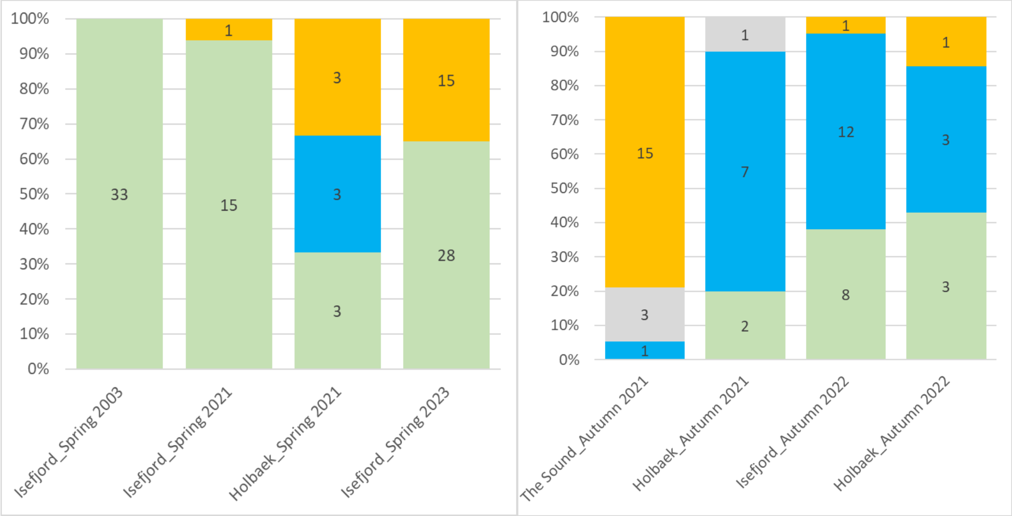


Figure 2.1.9. Genetic clustering of herring samples from spring (left panel) and autumn (right panel) spawning herring from the Holbaek-Isefjord. Numbers of fish genetically assigning to either, WBSS (light green bars), BAS (blue bars), NSAS (gray bars) or with hybrid genotypes (orange bars) are indicated by collection location and year. NB. In the left panel, contemporary samples are shown together with a sample from 2003 for comparison. In the right panel the Øresund (the Sound) autumn spawning herring are included for comparison.

Herring entering the Ringkøbing Fjord in autumn

The brackish Ringkøbing Fjord on the Jutland west coast (flowing into the North Sea) mainly constitutes spawning grounds for local spring spawning herring belonging to the WBSS-IDW population. However, autumn spawning is also reported from the fjord and a sample of 34 herring attempting to enter the fjord in October 2022 were included in genetic analyses to test the hypothesis that the fjord supports a local brackish autumn spawning population related to the 'Thyborøn' autumn spawning population reported in Jensen (1946). Samples were caught by recreational anglers upon entry through the lock at Hvide Sande. Only carcasses were available and the maturity stages of individual fish were therefore not available. Genetic assignment analyses showed that the fish constituted a mixture of the spring-spawning WBSS-IDW (N=28), autumn-spawning NSAS (N=1) and BAS (N=2), as well as BAS-NSAS hybrid genotypes (N=3). Subsamples of 16 otoliths were analysed to determine the hatching season of these fish. The results showed that there was some agreement between otolith and genetic data in the sense that the majority (8 of 10) of fish hatched in spring assigned to WBSS-IDW, although they were, presumably, entering spawning locations in autumn, suggestive of spawning time switching. Conversely, only half of six fish hatched in autumn (Table 2.1.2) belonged to either a BAS or NSAS population and instead also represented the local spring spawning population. In conclusion, it remains unknown whether the fjord has a discreet local autumn spawning population but the majority of the sampled individuals entering the fjord from the open sea represent the local spring spawning population, and not an autumn spawning population.

Comparing otolith growth based and genetic assignment data

Comparisons of genetic assignment, observed spawning season and hatching month estimated from otolith growth patterns in 89 herring showed differing results for different locations (Table 2.1.2). Although tested numbers of fish were moderate (53 fish), there was overall a tendency for herring caught in full spawning condition in spring to also having been spawned in spring, and to belong genetically to the WBSS-IDW population (85%). The remainder were fully ripe (would have spawned) in spring but had BAS genotypes and had hatched in autumn. In 36 herring spawning in autumn, 56% hatched in autumn and belonged genetically to an autumn spawning population (either BAS or NSAS). The remainder were either spring-spawned WBSS that displayed autumn spawning (39%) or spring-spawned (hatched) BAS that displayed autumn spawning, as expected from their genotype (6%). There was generally good correspondence between otolith based hatching season classification and expected spawning time from genetic population classification, i.e. herring genetically assigning to BAS and NSAS were generally hatched in autumn, and herring genetically assigning to WBSS were generally hatched in spring (see "% Match genotype and hatching season" in Table 2.1.2). However, there were also locations where fully ripe fish displayed a mixture of genetic origins and hatching times, e.g. in Holbæk and Ringkøbing Fjord. In Ringkøbing Fjord, the majority of the fish entering the fjord for spawning in autumn were born in spring and belonged to the WBSS-IDW population, i.e. exhibited spawning time shift.

Table 2.1.2. Comparison between genetic classification and otolith growth based hatching season classification (HM4=spring, HM9=autumn, HM4/12=uncertain whether hatched in spring or winter) for 89 mature herring sampled in Danish waters 2021-2023. Underlined numbers identify fish with a match between their observed spawning season, genetic background and hatching season.

Year	Location and spawning season	HM4 genetic WBSS	HM4 genetic BAS	HM9 genetic BAS	HM9 genetic NSAS	HM4/12 genetic BAS	% Match btw genotype and spawning season	% Match btw genotype and hatching season
2021	Ho Bay spring	10					100	100
2021	Holbæk autumn	2	2	4	1		75	67
2021-23	Holbæk spring	4		3	1	**2**	40	100
2022	Isefjord autumn	2		10			83	100
2021-23	Isefjord spring	5					100	100
2021	Kerteminde spring	3		1		**1**	75	100
2021	Limfjord spring	8					100	100
2021	Randers spring	10					100	100
2021	Ringkøbing spring	5					100	100
2021	Ringkøbing autumn	10		3	2		33	100

2.2 Mapping of spawning locations for WBSS herring in selected Inner Danish Waters

Presence/absence of spawned eggs (embryos) was assessed by fishing in five fjord spawning areas; Hjarbæk Fjord and Nissum Bredning in the Limfjord, Nissum Fjord, Randers Fjord, and Ringkøbing Fjord (Figure 2.2.1; Table 2.2.1). These spawning areas were also represented by samples of ripe adult spawning fish in the DNA database (Table 2.1.1), allowing for a test of genetic similarity between embryos and previously collected adult spawning fish. Test fishing for live embryos was done by boat and macrophyte (spawning substrate) sampling. Here, a network of shallow water stations were sampled from each fjord, using prerecorded information about the presence of macrophyte cover and depths from 1 to ten meters (the maximal reach of the applied macrophyte sampler and an approximation of the expected depths of deposits of WBSS herring eggs, Kotterba et al. 2017). The sampling device entailed an anchor used to drag across the sea floor to rake up macrophytes that were then visually inspected for attached embryos. Numbers of stations sampled per fjord varied due to differences in vegetation cover and practical sampling opportunities. All locations were sampled once during the peak spawning season in April-May 2023. For each sampling station latitude-longitude coordinates, water temperature, depth, detected macrophyte species and egg density (none, or below or above 10 eggs per 100 cm^2 leaf-surface) were recorded, and all embryos were subsampled by placing them in tubes with 96% Ethanol for subsequent genetic analysis. Embryos were stored by macrophyte sample (i.e. keeping a record of embryos attached to the same vegetation segment) in order to test for sib-ship relationships (i.e. whether embryo samples from the same spawning event represent brothers and sisters) within and among potentially separate spawning events. For genetic analyses, subsets of embryos were selected and DNA was extracted using a standard kit extraction (DNeasy Blood & Tissue Kit, Qiagen).

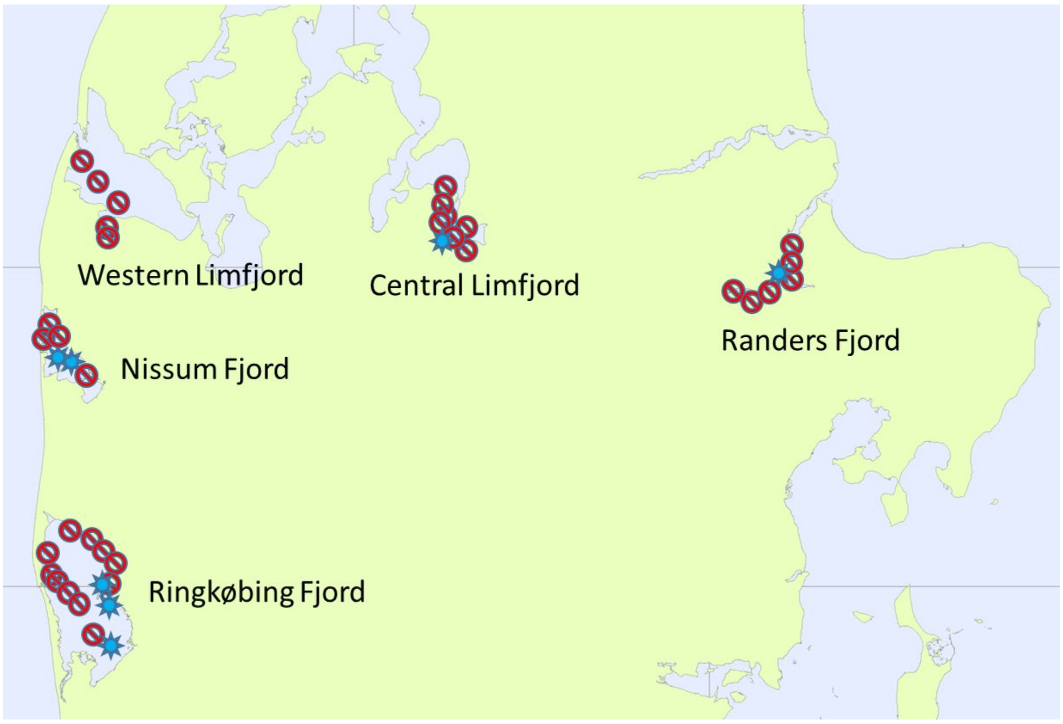


Figure 2.2.1. Approximate positions for test fishing for herring spawning beds (presence of embryos) in Midt- and Vestjylland in April-May 2023. See Table 2.2.1 for details. Red crosses and blue stars indicate, respectively, absence and presence of embryos at the station.

Table 2.2.1. Spawning location mapping by test fishing for embryos in Danish fjords in spring 2023.

Location	No. stations examined	No. stations with detected embryos	Collection date	Water temperature degrees C	Avr. depth (m) all stations	Avr. depth (m) of successful stations	Lat (avr.)	Lon (avr.)	Density of embryos (stations, st., with *below* or *above* 10 eggs per 100 cm^2 leaf-surface)
Randers Fjord	13	1	26.04.2023	10.0	3.7	6	56.49	10.17	1 st. below
Hjarbæk Fjord (Limfjord)	29	2	27.04.2023	7.3-8.9	2.3	2.5	56.58	9.29	1 st. above, 1 st. below
Ringkøbing Fjord	21	5	28.04.2023	8.0-8.2	1.9	2.6	56.03	8.21	3 st. above, 2 st. below
Nissum Fjord	17	2	03.05.2023	8.1-9.0	1.9	2.1	56.37	8.17	2 st. below
Nissum bredning (Limfjord)	6	0	04.05.2023	8.4	4.5	-	56.60	8.28	-

For testing of population affiliation of the sampled embryos, 96 SNP markers were analysed using the procedure detailed in Bekkevold et al. (2023). Samples consisted of 11 embryos from Randers, 12 from Limfjord, 3 from Nissum Fjord and 13 from Ringkøbing Fjord (Table 2.2.1). For testing of sib-ship relationships, a total of nine microsatellite markers were analysed using the approach detailed in Bekkevold et al. (2005) in subsets of embryo samples (Table 2.2.2). These data were used to test for sib-ship relationships with the maximum-likelihood approach in the software COLONY 2.0 (Wang 2004). Briefly, the probability of individual pairs of embryos being full- or half-sibs was estimated from genotype probabilities, using information about all tested offspring (embryo) genotypes, as no parental candidates were available. The success rate of correctly identifying sib-ships using that given set of nine loci was *a priori* expected to be low, as typing of relatively few loci resulted in low exclusion rates and high expected rates of spurious identification of sib-ships. Thus, analyses were only expected to yield approximate estimates of sibships. To exert some control of spurious detection of sib-ships, analyses were restricted to only classify sibs, if the associated P-value was consistent with either a 'relaxed' ($P > 0.85$) or a 'strict' ($P > 0.95$) sib-ship assignment criterion.

Results showed that live embryos were detected at a total of ten out of 86 tested sampling stations (Table 2.2.1). At all locations, embryos were detected at a minimum of one station. The exception was Nissum Bredning where no embryos were detected at the six tested stations. Perhaps significantly, there was also no recreational fishing activity detected in the local (Oddesund) area at the time of test fishing. Embryos were found on *Fucus vesiculosus* (brown algae, 'blæretang'), *Zostera marina* (eelgrass, 'ålegræs'), *Stuckenia pectinate* (sago pondweed, 'børstebladet vandaks'), and not on the, otherwise commonly observed, *Ulva lactuca* (sea lettuce, 'søsalat'). All embryos were detected at depths below two meters. In comparison, spawning beds are concentrated at ~1 meter in the Greifswald Bay, (Kotterba et al. 2017). Embryos were visually (using a dissection microscope) assessed to be 1-5 days old. No further age estimation was performed. Embryo densities were in all cases relatively low compared to reports from Greifswald Bay (e.g. Kotterba et al. 2017) but no formal assessment was made to estimate total numbers per site and location.

Genetic analyses showed that all tested embryos showed close genetic relationships with samples of adult fish from the same locations signifying that they belonged to the local populations from which they were sampled. Sib-ship analyses returned a total of one full-sib pair (estimated at P=0.952), identified from the same piece of vegetation, and six half-sib pairs (none of which had P > 0.88). Among suggested half-sib pairs, only one pair was identified from the same piece of vegetation, two pairs were identified within the same sampling station but from different pieces of vegetation (Table 2.2.2). The remaining three detected half-sib pairs were identified between different locations, suggesting the results were suffering from a high ratio of false positives. It is thus suggested to be most probable that the single full-sib pair detected from embryos attached to the same piece of vegetation were produced by the same male-female pair in a single spawning. However, it remains unknown whether the detected half-sib pairs were in fact results of polygamous spawning events, e.g., a female releasing eggs in a mass spawning with multiple male sires. Resolving this would require increased sampling efforts (per vegetation piece) and increased numbers of genetic markers to allow unambiguous sib-in-/exclusion analyses. The main inference from the sib-ship analysis is that full-sibs were gauged to be relatively rare, suggesting that multiple males and females contributed gametes to both specific locations and to specific targeted (macroalgae) spawning substrate. However, larger sample sizes are needed for more precise quantitative estimates of numbers of spawners per spawning event.

Table 2.2.2. Genetic sib-ship analyses and results by location (fjord area), station and vegetation piece.

Location	Station no.	vegetation piece no.	No. embryos analysed	No. full-sib pairs within vegetation piece	No. half-sib pairs within vegetation piece	No. half-sib pairs within location and between vegetation pieces
Hjarbæk Fjord	HJ4	9	2	-	-	-
(Limfjord)		10	6	1 (P=0.952)	-	-
		11	13	-	-	1 (P=0.862)
		13	5	-	-	-
	HJ15	12	10	-	-	1 (P=0.871)
Nissum Fjord	NI6	6	3	-	-	-
Ringkøbing Fjord	RI12	14	7	-	-	-
	RI15	1	1	-	-	-
		2	1	-	-	-
	RI16	1	1	-	-	-
		2	1	-	-	-
		3	1	-	-	-
		4	1	-	-	-
Randers Fjord	RA9	1	8	-	-	-
		3	8	-	1 (P=0.877)	-
		4	8	-	-	-
		6	9	-	-	-

In conclusion, spawning bed test fishing corroborated the presence of embryos in locations where spawning was inferred from presence of mature adults during the same periods. Multiple males and females were inferred to contribute to spawning in all sampled sites. The detected number of sampling stations containing embryos was limited and embryos were found on slightly deeper water than reported in a study of WBSS herring from Greifswald Bay. It is unknown if the extent of detected spawning beds reflected actual spawning activity. It is also unknown, but considered unlikely, that test fishing failed to locate actual large spawning beds that would have better represented local spawning effort and contributions to larval recruitment. Extended analyses targeting the same areas are required to provide further insights into the relative importance of local spawning areas for WBSS population dynamics.

2.3 Sampling via key fishers

To identify local spawning grounds in the Inner Danish Waters, around 90 recreational fishermen distributed throughout Denmark's coastal areas and registered as “Key Fishers” were encouraged to report and collect spawning herring. There was positive feedback about observations of spring spawning herring from Gershøj in Roskilde Fjord, Holbæk Fjord (Isefjorden), Præstø Fjord, outside Nysted in Femern Belt, around Sæby and from Sebbersund in the Limfjord. However, it was only possible to obtain samples from Sæby, Sebbersund and Holbæk Fjord. The recreational fisherman from Holbæk fjord collected annual samples of both spring and autumn spawning herring. To supplement these sample locations, further herring samples were collected from two commercial fishermen, one in Limfjorden and one in Kerteminde Fjord. In addition, DTU Aqua carried out experimental fishing at selected locations in week 15 & 16 2023 in Præstø Fjord, at Rødvig and in Isefjorden.

3. Pressure Factors for Spawning and Recruitment

3.1 Processes impacting WBSS recruitment

WBSS recruitment processes have been studied for decades, with main geographical focus on spawning and nursery areas in the Greifswald Bay and Kiel Canal, and knowledge and knowledge gaps were recently reviewed in a comprehensive study by Moyano et al. (2023). Regulating factors include both bottom-up (e.g. abiotic environmental condition) and top-down (e.g. predation rate) processes operating in a complex fashion. They state: *"Despite the significant advances in knowledge reported above on the ecology of WBSS herring and the potential drivers impacting the recruitment process, it is still difficult to precisely identify where the bottleneck lies. Furthermore, from a management standpoint, it remains challenging to translate the outcomes of existing research into a clear, unified set of equations/indicators useful for stock assessment and advice" (*Moyano et al. 2023). However, they also provide a prioritised list of the work needed to close the current knowledge gaps to provide science-based advice to management: research and data on 1) migration pathways, and 2) population structure. The current project has improved analysis tools and data on both accounts, but the data still have to be expanded and applied. A third, potentially highly important issue, is related to the prediction of climate induced environmental changes on WBSS recruitment. This was addressed experimentally in the current project (section 3.2).

3.2 Can climate change-induced deviations from optimal egg developmental temperature explain the Western Baltic spring-spawning herring stock decline?

3.2.1 Summary

Over the past decades, the Western Baltic Spring Spawning (WBSS) stock of herring (*Clupea harengus*) has been in decline. Understanding if and how the climate change-driven warming of the oceans has contributed to the stock decline necessitates an understanding of the effects of temperature on the vulnerable early life stages of the species. This study aimed to determine the temperature optimum for the embryonic development of WBSS herring eggs from primarily the Greifswald Bay in Germany, the main spawning site of the stock, to evaluate if recent climate warming and more frequent heat waves could be causing a mismatch between ambient temperature during spawning and the optimal developmental temperature of the eggs. This was done by estimating the so-called energetic cost of development of the eggs, which is the product of egg metabolic rate and development time, as a function of temperature. Cost of development theory suggests that the energetic cost of developing from fertilisation to hatching follows a U-shaped pattern with temperature, with the lowest cost (the optimal developmental temperature) occurring at an intermediate temperature, which should coincide with the ambient temperature a species has historically been adapted to. Thus, herring eggs were incubated at six temperatures (5, 8, 11, 14, 17, and 18.5^{o}C) and their metabolic rates quantified as oxygen consumption rates at these temperatures. Metabolic rate in the first few days of development showed a significant positive relationship with temperature, however, only the 5°C treatment group reached the hatching stage, due to issues with fungal infection on the eggs at higher temperatures. At 5°C, metabolic rate was measured multiple times during egg development, showing a significant increase across the incubation period. Due to lack of data at all temperatures, egg development time was estimated using an equation derived by Peck et al. (2012). Using these estimated development times, the cost of development was found to decrease linearly with temperature, with the lowest cost of development observed at the highest incubation temperature of 18.5°C. However, a slight increase in metabolic rate over time in the eggs incubated at 5°C indicated that the cost of development might have been underestimated at the higher temperatures, where the metabolic rate was only measured in the first few days of development. This could explain why a temperature optimum at an intermediate temperature closer to the historic ambient temperature during peak herring spawning, in accordance with the development cost theory, was not observed in this study. We conclude that, with the limited amount of data obtained in the study, the results are inconclusive, and further studies are needed to improve our understanding of how temperature effects the early life stages of WBSS herring.

3.2.2 Introduction

The Western Baltic herring is an important species for the ecosystem dynamics of the Baltic Sea and has been an important species for commercial fisheries for many decades (Sparholt, 1994). However, the Western Baltic Spring Spawning (WBSS) herring stock is in decline, and the underlying reasons are not yet understood (ICES, 2021). A potential reason for the decline of marine fish stocks could be elevated temperatures resulting from climate warming and more frequent heat waves (IPCC, 2014). As sensitivity to temperature change is believed to be highest for early embryonic life stages (eggs), compared to later life stages such as larvae and adults (Dahlke et al., 2020), deviations in environmental temperature away from optimal are expected to be particularly critical if they occur during early development.

Marshall et al. (2020) have recently suggested that ectotherms, such as fishes, have minimised their energetic cost of developing from fertilisation to hatching by evolving combinations of temperature dependencies of metabolic rate and development time that ensure the lowest cost of development across a small thermal window within their historic natural temperature range. This means that any recent and rapid warming resulting from climate change may present populations of ectotherms with environmental temperatures that are suboptimal for their development, thereby elevating development costs with negative consequences for performance and survival (Marshall et al., 2020).

The temperature-dependent cost of development for a given species can be obtained from measurements of the species' metabolic rate (usually measured as the rate of oxygen consumption, $\dot{M}_{O_2}$) and development time (Marshall et al., 2020). For most ectothermic species, the cost of development is highest at both the lower and upper limits of the temperature range they can tolerate (Marshall et al., 2020). This is because, at cooler temperatures, metabolic rate is lower but development time longer, whereas at warmer temperatures, development time is shorter but metabolic rate higher (Pettersen et al., 2019). The cost of development as a function of temperature, $C(T)$, can therefore be calculated as the product of development time, $D(T)$, and metabolic rate, $M(T)$ (Marshall et al., 2020):

$$C(T) = D(T) \times M(T) \quad (1)$$

The temperature-dependent development time can be expressed as the product of temperature (°C) and the time (days) from fertilisation to hatching, referred to as degree days. The WBSS stock of herring have a development time of ~100 degree-days (Peck et al., 2012).

The presumed largest WBSS spawning ground is in the Greifswald Bay in Rügen, Germany, an estuarine and semi-enclosed brackish water (Von Dorrien et al., 2013). Smaller WBSS herring spawning grounds can be found along German, Danish, Swedish, and Norwegian coastlines. The WBSS herring migrates seasonally between their spawning grounds and the feeding areas in Skagerrak, Kattegat, and the North Sea. The WBSS herring usually spawn from March to May, where the spawning initiates when temperatures exceed ~3.5 to 4.5°C (Polte et al., 2021). The reproductively mature herring (> 2 years) migrate to the spawning grounds for a short period (few days) where they complete the spawning (Von Dorrien et al., 2013). The eggs adhere to aquatic vegetation as well as each other, forming bundles of layered eggs. The herring eggs are often exposed to a wide range of temperatures during the spring months (Oeberst et al., 2009a).

This study used cost of development theory to investigate if recent climate-change-induced warming of WBSS herring spawning sites may have caused a mismatch between the optimal temperature for egg development and the environmental temperature at the time of herring spawning.

3.2.3 Materials and methods

Collection of spawning herring

Ripe specimens of the WBSS herring were wild caught at three different locations in the Western Baltic Sea using gill nets monitored regularly: Rügen (Greifswald Bay) in Germany and Rødvig and Kerteminde in Denmark (Fig. 3.2.1). The locations were chosen based on geographical information about the main herring spawning ground in the Western Baltic Sea (Greifswald Bay), as well as the availability of spawning herring and cooperation with fishermen in Denmark (Rødvig and Kerteminde).

Fig. 3.2.1. Map of the Western Baltic Sea surrounding Denmark and Germany, including the three geographical locations of the wild-caught herring used in the present study.

Multiple herring populations were targeted in the study in order to obtain a broad representation of the WBSS herring stock, as well as to identify any population specific variation. The herring from each location were caught approximately one week apart, with water temperatures at each location ranging from 6.1 to 7.4°C at the time of capture (Table 3.2.1). Immediately after capture, the herring were placed in an electrical cooler and transported to DTU Aqua in Lyngby, Denmark, where the experiments took place. The time from catch to fertilisation was ~2-5 hours (Table 3.2.1).

Table 3.2.1. Location-specific data on the dates of herring capture.

Location	Temperature (°C)	Salinity (ppt)	Time from catch to fertilization (hr)	Date
Greifswald Bay	6.1	7.5	2-3	14-04-2021
Kerteminde	6.9	20.0	4-5	22-04-2021
Rødvig	7.4	8.0	4-5	29-04-2021

Strip spawning and egg fertilisation

Upon arrival at DTU Aqua, the herring were sorted into males and females and strip spawned. The three populations of herring were strip spawned according to three different protocols: (1) for the Greifswald Bay population, sperm from eight males were mixed and used to fertilise eggs from eight females; (2) for the Kerteminde population, sperm from two males were mixed and used to fertilize eggs from five females; and (3) for the Rødvig population, sperm from 14 males were mixed in two containers (sperm from seven males in each) and each used to fertilise eggs from four females (eight females in total).

The sperm was mixed in a container of site-specific water, collected on the day of herring capture, and the eggs from the specimens were each divided into six petri dishes (one for each of the six temperature treatments). A thin plastic disc at the bottom of each petri dish served as egg substrate (for the eggs to adhere to). The petri dishes were then placed in the sperm-containing water for 15 minutes (Annegret Finke, personal communication). After fertilisation, the plastic discs from the petri dishes were moved to fresh site-specific water and rinsed for scales and other debris, after which the discs with eggs were placed in clean petri dishes. This was done to keep the eggs and the environment surrounding the eggs as clean as possible. The clean petri dishes with eggs were then placed in a container with water from the lab with salinity and temperature made according to the location of origin (cf. Table 3.2.1). When all petri dishes had gone through the procedure outlined above, the petri dishes were placed in 3 L plastic containers (two petri dishes in each container) with lab water and distributed to the temperature-controlled holding tank setup (Fig. 3.2.2) for the eggs to develop in, where the containers with eggs slowly reached the target treatment temperature of either 5, 8, 11, 14, 17, or 18.5°C.

Fungal treatmen*t*

To reduce fungal infections on the eggs, some of the eggs were treated with formalin (Rach et al., 1997). At the high temperatures (17 and 18.5°C), the eggs from the Greifswald Bay population became infected with fungus 3 days post-fertilisation. All eggs from this population were treated in a formalin bath with a concentration of 150 ppm (0.15 mL/L). The rest of the temperatures, except the 5°C treatment, still got infected, though at a slower rate. The eggs from the Kerteminde population were treated the same day as the fertilisation, as a preventative measure to avoid fungal infection, with an increased concentration of 1500 ppm (1.5 mL/L), however, the eggs did not develop. The eggs from Rødvig were therefore not treated, as it was uncertain if the formalin treatment had caused the eggs from Kerteminde to not develop.

Experimental setup for egg development

The setup for the egg incubation consisted of six separate temperature-controlled tank setups. Each tank- setup comprised of two tanks (Fig. 3.2.2): one small tank (tank 1, 30 L) for temperature control, with either a heating element placed in the tank or connected to a cooler, and one bigger tank (tank 2, 55 L) that could contain 16 of the 3 L plastic containers with eggs. Tank 2 was elevated above tank 1, enabling a circulation of water by passive flow from the outlet of tank 2 into tank 1 whilst receiving water by pump from tank 1. The salinity in the 3 L containers was set according to the locations of the collected herring (cf. Table 3.2.1). The water in the containers was aerated and renewed daily. The herring eggs were incubated at six different temperatures: 5, 8, 11, 14, 17, and 18.5 ° C (± 0.4 °C). The setup was made to accommodate two populations of herring eggs, with location specific salinity, simultaneously: 2 x 4 containers with two petri dishes with eggs in each, and 2 x 4 with new (fresh) water.

The Rødvig population of herring eggs were incubated directly in tank 2 according to the site-specific conditions. This was done in an attempt to prevent fungal infection by creating a larger volume of water around the eggs. A UV-filter was also added to the tank setup.

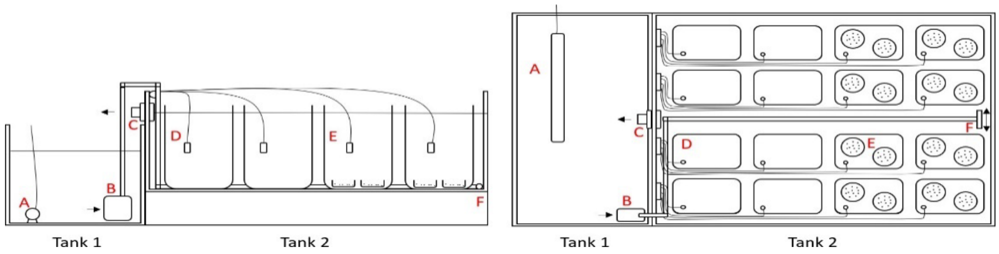


Fig. 3.2.2. Illustration of the holding setup for one temperature seen from a cross section (left) and from above (right). This setup could accommodate two populations of herring eggs, with eight petri dishes for each population. A: heating element; B: inflow pump; C: passive outflow from tank 2; D: container with new/fresh saltwater; E: container filled with saltwater, an air stone, and two petri dishes with eggs; and F: outflow from pump in tank 1.

Measuring metabolic rate

Metabolic rate of the herring eggs was measured as oxygen consumption rate using a state-of-the-art microplate respirometry system with associated MicroResp™ software (Loligo Systems; Viborg, Denmark). The respirometry system consisted of a glass microplate with 24 wells of 200 µL volume with optical oxygen sensors at the bottom of each well, an optical fluorescence oxygen reader, a thin non-permeable Parafilm layer to seal the wells in the microplate in association with a soft silicone gasket and a compression block to keep the Parafilm in place, and a water bath connected to a water heater/cooler (Fig. 3.2.3).

On the day of a respirometry trial, clusters of 2-10 eggs were cut from the plastic disc they were adhered to and placed in each of 20 of the wells in the respirometry plate, with each well containing water at the site-specific salinity and respective target temperature treatment. After placement of eggs, the wells were sealed with parafilm and the compression block with the intermediate silicone gasket, and oxygen recordings were initiated on the software. Each well represented one replicate. Five oxygen consumption rate measurements were made on eggs from four different females at a time, leaving room for four random blanks in the 24-well respirometry plate. These blanks recorded any background (microbial) oxygen respiration. Oxygen consumption rate was measured for a minimum oxygen decline of 5% air saturation (~0.5-1 hr). The temperature of the respirometry plate was kept constant, according to the treatment temperature, in a flow-through water bath connected to the water heater/cooler. After oxygen consumption rate measurements, the eggs and the plastic pieces were weighed and the developmental stages of the eggs documented under microscope (see Supplementary Fig. 3.2.10).

The eggs from the Rødvig and Kerteminde populations died shortly after fertilisation and the few measurements made on these populations were therefore not included in the study. Thus, all subsequent data and results are for eggs from the Greifswald Bay population.

For eggs from the Greifswald Bay population, the 5°C treatment was measured on the sixth day post-fertilisation and then every third day until hatching (N = 20 per measurement day). The treatments 8, 11, 17, and 18.5°C were measured only once during early development (N = 20 per temperature) due to fungal infections developing over time. The measurements were not taken on at specific degree day, though all were made in the beginning of the incubation period (degree day 30 to 44). The eggs from the 14°C treatment became infected with fungus before oxygen consumption rate measurements, and they were therefore discarded with no measurements. Eggs from one female (female 5, see Supplementary Fig. 3.2.9) had very little fertilisation success and were removed from the experiment.

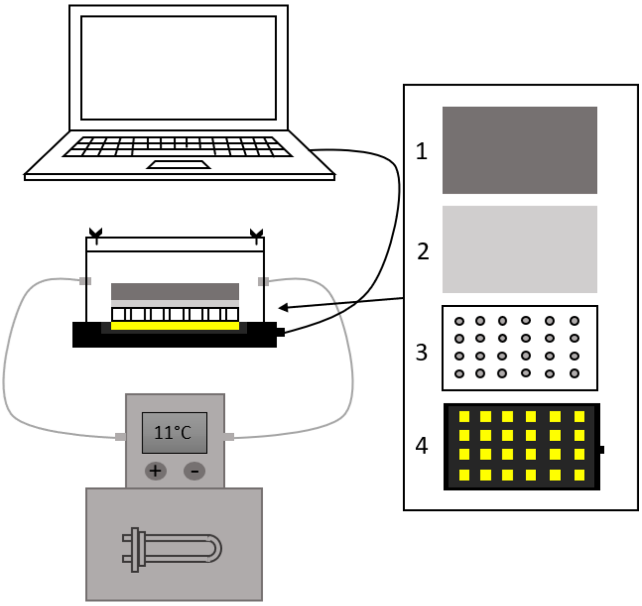


Fig. 3.2.3. Illustration of the microplate respirometry setup with water bath attached to a water heater/cooler. 1: compression block; 2: soft silicone gasket; 3: microplate with 24 wells and oxygen sensor spots; 4: optical oxygen reader connected to the computer software; 1-3 were inside the water bath. In-between 2 and 3 there was a thin non-permeable Parafilm layer sealing the wells in the microplate.

Data analysis and calculations

Raw metabolic rate (raw oxygen consumption rate; $\dot{M}_{O_2^*}$, µg O_2/hr) was automatically calculated from the measured decline in oxygen over time in each microplate well by the MicroResp™ software, as:

$$\dot{M}_{O_2^*} = a \times V_{\text{resp}} \qquad (2)$$

where *a* is the linear regression slope for the decline in oxygen over time (µg O_2/L/hr) and V_{resp} is the volume (200 µL) of each microplate well (V_{well}). This raw measure of metabolic rate did not account for the number of eggs (N_{egg}) in each well and the well water volume displaced by the eggs (including the plastic they were adhered to; V_{egg}). To account for this, the weight of the eggs was subtracted from the well volume, under the assumption of an egg density of 1 mg/µL. This was then divided by the number of eggs in each individual well, so the final metabolic rate ($\dot{M}_{O_2}$) per egg was calculated as:

$$\dot{M}_{O_2} = \frac{((V_{well} - V_{egg})/V_{well}) \times \dot{M}_{O_2^*}}{N_{egg}} \qquad (3)$$

The temperature sensitivity coefficient, Q_{10}, which represents the fold change in a biological rate (here metabolic rate) with a 10°C change in temperature, was calculated both manually with the equation:

$$Q_{10} = \left(\frac{\dot{M}_{O_{2,2}}}{\dot{M}_{O_{2,1}}}\right)^{\left(\frac{10}{T_2 - T_1}\right)} \quad (4),$$

where $\dot{M}_{O_{2,1}}$ and $\dot{M}_{O_{2,2}}$ is the metabolic rates at temperatures T_1 and T_2, respectively, and by using the slope (*b*) from the linear regression of the log-transformed metabolic rate as a function of temperature:

$$Q_{10} = e^{10 \times b} \quad (5)$$

The eggs from the 8, 11, 17, and 18.5°C treatments did not reach the hatching stage due to fungal infections developing during the experiment. The development time, $D(T)$, for eggs from each temperature (except 5°C) was therefore estimated based on the study by Peck et al. (2012), who derived an equation for the peak hatch time as a function of temperature (T) for WBSS herring from Kiel Bight in Germany:

$$D(T) = 4461.9 \times T^{-1.232} \quad (6)$$

The cost of development, $C(T)$, was then calculated as the product of this estimated development time and the metabolic rate measured at each temperature, $M(T)$, according to Equation 1.

Statistical analysis

Statistical analyses were performed in R v. 4.0.3 (R Core Team, 2020). Due to the issues with fungal infection previously mentioned, the data were split into two datasets: Dataset 1 had one estimate of metabolic rate early in development (before the fungal infection) at each of the different temperatures (5, 8, 11, 17, and 18.5°C, but not 14°C where fungus had developed before metabolic rate measurements), while Dataset 2 had several (five) measurements of metabolic rate across the full developmental period from fertilisation to hatch, but only at the coldest temperature of 5°C.

The effect of temperature on metabolic rate ($\dot{M}_{O_2}$) was evaluated from Dataset 1 using linear mixed-effects regression in the package lme4 (Bates et al., 2015). The linear mixed-effects model had log- transformed metabolic rate as the response variable, and temperature, developmental time, female ID, and log-transformed egg weight (egg mass) as predictor variables (fixed effects). Female ID, nested within temperature, was included as a random effect to account for eggs from the same female being distributed across the different temperatures. Metabolic rate was log-transformed under the assumption of an exponential increase in metabolic rate with temperature. Likewise, egg mass was also log-transformed, since the relationship between metabolic rate and mass theoretically is a power function.

To identify the best-fit model, non-significant predictor variables were excluded one at a time, starting with the variable with the highest P-value, and the model re-run at each step. Due to known issues with P-values (Boos and Stefanski, 2011; Halsey et al., 2015; Halsey, 2019), these were treated as continuous measures providing an approximate level of evidence against the null hypothesis, and variables that were borderline significant at the traditional P = 0.05 level were therefore kept in the model. Sequential models were compared using likelihood ratio tests and the more complex model retained if the likelihood ratio test was significant. Model assumptions (non-multicollinearity of predictor variables, normality of residuals, homoscedasticity, variance homogeneity, and normality of random effects) were checked with the package performance (Lüdecke et al., 2021).

The effect of developmental stage on metabolic rate was evaluated from Dataset 2 using linear mixed- effects regression, similar to the effect of temperature on metabolic rate. Log-transformed metabolic rate was again used as the response variable, while development time, female ID, and log-transformed egg mass were predictor variables, and female ID nested within developmental stage was a random effect. Metabolic rate and egg mass were again log-transformed. The model was also checked for non-significant predictor variables and reduced if non-significant.

Finally, the effect of temperature on the cost of development was evaluated, similar to the two other models, with a mixed-effects regression. Cost of development was the response variable, temperature, female ID, and log-transformed egg mass were predictor variables, and female ID nested within temperature was a random effect.

3.2.4 Results

Effect of temperature on metabolic rate

The first measurement of egg metabolic rate made at each treatment (Dataset 1) showed a significant positive relationship between metabolic rate and temperature (Fig. 4). The mixed-effects regression model analysing the effect of temperature, development time (degree days), egg mass, and female ID showed that only temperature had a significant influence on metabolic rate (P = 0.002), while female ID had a borderline significant effect (P = 0.096) (see Supplementary Fig. 9 for metabolic rates categorised by female ID).

The temperature sensitivity coefficient (Q_{10}) calculated from the modelled effect of temperature (Equation 5) was 1.41, meaning that egg metabolic rate increased 1.41-fold with a 10°C increase in temperature. The manually calculated Q_{10} (Equation 6) showed a slightly higher value of 1.55, which was not surprising, since the mean metabolic rates fluctuated around the average regression line (Fig. 3.2.4).

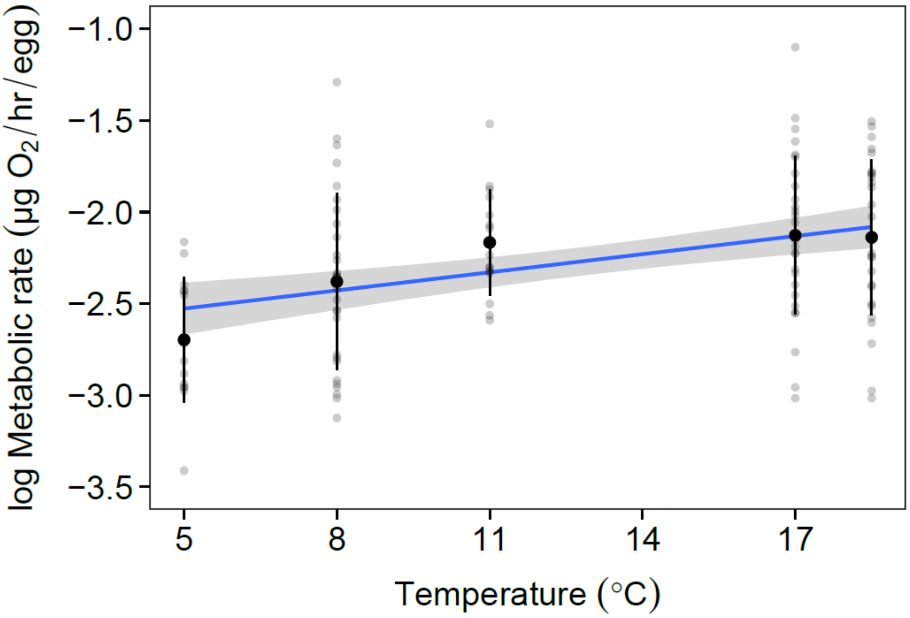


Fig. 3.2.4. Log-transformed metabolic rate as a function of temperature for eggs from the Greifswalder Bay WBSS herring population at degree day 30 to 44 (the first measurement of metabolic rate). Small dots in translucent black represent individual eggs (measured in clusters of 2-10 eggs; N = 20 per temperature), while larger black dots with error bars represent mean metabolic rates and their standard deviations. The grey shaded area around the fitted linear regression line is the 95% confidence interval.

Effect of development time on metabolic rate

The 5°C treatment reached hatching on day 18, with peak hatch on day 19. Metabolic rate for the 5°C treatment group increased significantly with the time it took to development from fertilisation to hatching (P = 0.027) (Fig. 3.2.5), with a significant effect of female ID on development time (P = 0.009). Egg mass had no significant effect on development time (P = 0.280).

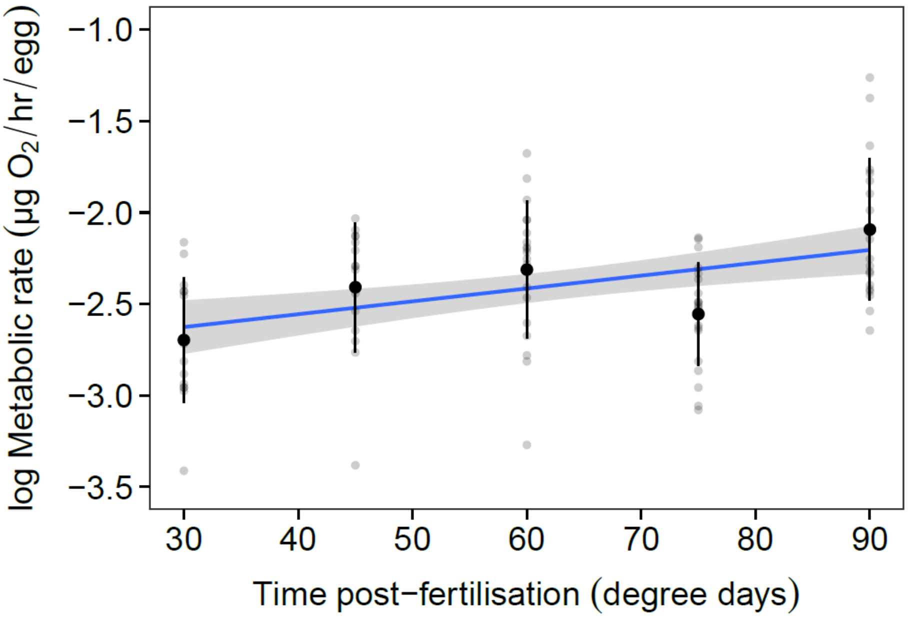


Fig. 3.2.5. Log-transformed metabolic rate as a function of development time (time from fertilisation to hatching in degree days) for eggs from the Greifswalder Bay WBSS herring population at 5°C. Small dots in translucent black represent individual eggs (measured in clusters of 2-10 eggs; N = 20 per temperature), while larger black dots with error bars represent mean metabolic rates and their standard deviations. The grey shaded area around the fitted linear regression line is the 95% confidence interval.

Estimated cost of development

The estimated cost of development – the product of metabolic rate measured here early in development (cf. Fig. 3.2.4) and development time estimated from Peck et al. (2012) – decreased significantly with temperature from 5 to 18.5°C ($P < 0.0001$) but did not show the theoretical U-shape with an intermediate optimum (lowest cost of development) within the temperature range used here (Fig. 3.2.6).

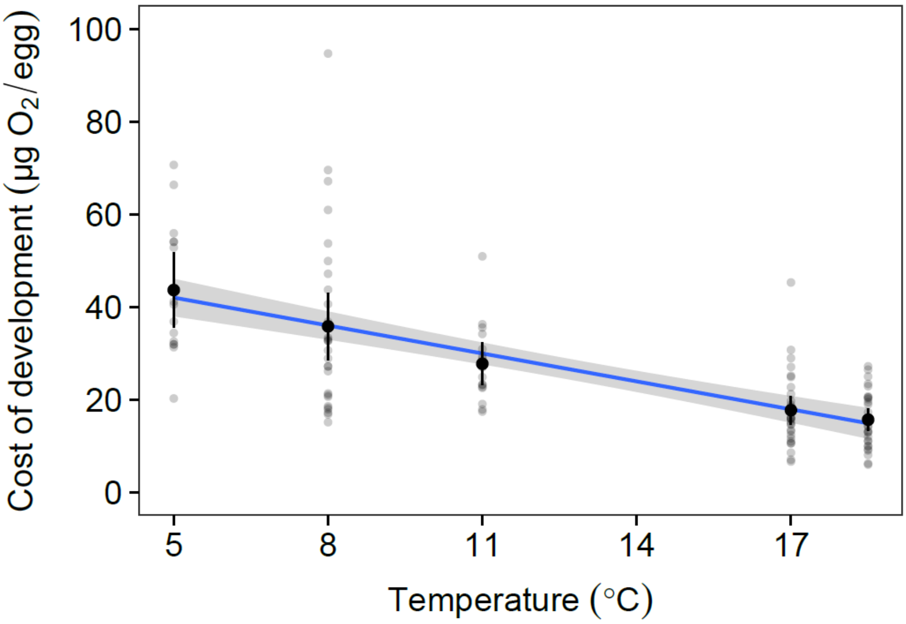


Fig. 3.2.6. Cost of development as a function of temperature for eggs from the Greifswald Bay WBSS herring population. Cost of development was calculated as the product of the metabolic rates measured at 5, 8, 11, 17 and 18.5°C (Fig. 4) and the development time from fertilisation to hatching estimated from the equation in Peck et al. (2012). Small dots in translucent black represent individual eggs (measured in clusters of 2-10 eggs; N = 20 per temperature), while larger black dots with error bars represent mean costs of development and their standard deviations. The grey shaded area around the fitted linear regression line is the 95% confidence interval.

3.2.5 Discussion

The WBSS herring, like other marine fish species, are sensitive to temperature changes during early life stages (Peck et al., 2012). Based on developmental cost theory (cf. Marshall et al., 2020), this study explored if elevated temperatures during egg development negatively affected (increased) the energetic cost of developing from fertilisation to hatch, a metric that has been shown to correlate tightly with survival and the environmental temperature a species is historically adapted to (Marshall et al., 2020).

We hypothesised that the cost of development would be minimised at the historical environmental temperature at the time of WBSS herring spawning, so that elevated temperatures resulting from recent climate warming would have increased the cost of development, possibly explaining the decline in the WBSS herring stock due to a mismatch between environmental temperature at the time of spawning and optimal egg developmental temperature.

Cost of development

The estimated cost of development found in this study was at its lowest at the highest temperature of 18.5°C. The WBSS herring usually initiate spawning on their main spawning grounds in the Greifswald Bay when temperatures reach 3-4°C (Klinkhardt, 1996) and, for the present study, were collected at a water temperature of 6.1°C (Table 3.2.1). Based on developmental cost theory, which implies that selection has resulted in a minimised (optimal) cost of development close to the environmental temperature a species is historically adapted to, an optimal developmental temperature closer to the ambient spawning temperature was expected. In other words, a minimised (optimal) cost of development at the highest temperature of 18.5° C used here appears unrealistic given cost of development theory (Marshall et al., 2020). This unrealistically high optimal development temperature of 18.5°C could be caused by several issues surrounding the present study, in particular that development time was estimated from a previous study (Peck et al., 2012) because of issues with fungal infections on the eggs in the present study, meaning that all eggs kept at temperatures above 5°C did not develop all the way to hatching. Cost of development was therefore calculated not only from an estimated development time from another study, but also from an initial measurement of metabolic rates during early egg development only (30-44 degree days post-fertilisation; cf. Fig. 3.2.4), before fungal infections, rather than an average metabolic rate across multiple different egg development stages. Metabolic rates across developmental stages were only successfully collected for eggs at 5°C that did not become infected with fungus and reached hatching. As metabolic rate in these eggs at 5°C increased significantly across development, from 30 to 90 degree days post-fertilisation (Fig. 3.2.5), using only an initial measurement of metabolic rate to calculate cost of development likely resulted in an underestimation of the cost of development at the higher temperatures, providing a likely explanation for why a continually decreasing cost of development with warming was found.

The use of the development time equation by Peck et al. (2012) may also be questioned in light of a previous study (Hempel and Blaxter, 1961), which found that herring development time was shorter at 5-11°C than at 14°C. Moreover, based on the equation by Peck et al. (2012), development time at 5°C was expected to be ~125 degree days (25 days), whereas the observed peak hatch in the present study was 95 degree days (19 days), indicating that the Peck et al. (2012) equation did not provide a good approximation of development time for the herring from the Greifswald Bay population used here. Other studies have found that the Western Baltic herring hatched 96-118 degree days after fertilisation (see Peck et al., 2012), Gulf of Riga herring after 66-75 degree days (Ojaveer, 1981), Gulf of Gdansk herring after 97-128 degree days (Herra, 1986), and Gulf of Finland herring after 130-160 degree days (Laine and Rajasilta, 1999). The differences in hatching time may be due to differences in the studies, specifically temperature ranges, as Peck et al. (2012) found no systematic relationships between these development times and salinity. Moreover, development time, although expressed in degree days, may not be completely independent of temperature, in which case degree day findings in different studies are difficult to compare (Peck et al., 2012).

Alternative impacts of climate change

Climate change affects aquatic organisms directly through the effects of rising temperatures on physiological functions, such as metabolic rate (Rubalcaba et al., 2020). However, climate change may also affect organisms through its impact on other elements of the ecosystem such as predators and prey. Several studies have evaluated the effect of climate change on the Baltic herring populations by assessing the impact of temperature on various parameters. For example, a study found that, in cooler winters, temperature is the presiding factor controlling the abundance of larvae, whereas in warmer winters the spawning stock biomass determines the strength of the year class (Ojaveer et al., 2011). Moreover, the relationship between temperature and recruitment can be connected to several different processes: Rajasilta et al. (1993) found that higher temperatures can decrease egg development time, the effect of which was mediated through the decreased time the eggs would be susceptible to predation. On the other hand, higher temperatures have also been found to increase egg oxygen demand and can disrupt reproduction by causing deformities during the embryonic development (Raid, 1991). In addition, bacterial and fungal infections can be more frequent at higher temperatures (Rajasilta et al., 1993; Cardinale et al., 2009). Peck et al. (2012) also found that the size of the larvae, which is strongly correlated with their chances of survival (Sogard, 1997), decreased with increasing temperature. The variation in larval size at hatch at different temperatures may be due to the efficiency of converting yolk into growth being affected by temperature (Peck et al., 2012). Another reason could be that hatching may take place at different developmental stages (Geffen, 2002). Additionally, Blaxter and Hempel (1963) evaluated the maternal investment in eggs, which plays an important role for the eggs' chances of survival. The primary function of maternal investment is to provide the offspring with adequate resources to reach the developmental stage of nutritional independence (where the offspring can feed itself) (Pettersen et al., 2019). The maternal investment is often temperature dependent. At cooler temperatures, maternal investment tends to make some offspring larger, whereas at warmer temperatures offspring are often smaller (Pettersen et al., 2019), though the specific maternal alterations of the embryos for different temperature tolerances are unknown (Peck et al., 2012).

All the studies mentioned above are consistent with development cost theory. For instance, the findings of Ojaveer et al. (2011) that temperature is the determining factor for the strength of the year classes in cold winters may reflect that, as the gap between ambient temperature and the temperature optimum closes, the year class strengthens. This does not reveal the exact temperature optimum, but as spawning stock biomass is determining the strength of the year class in warmer winters, it could be expected that the optimum temperature for cost of development lies within the temperature range of a warm winter.

Egg size

The body size and fat content of the adult herring can induce production of larger eggs with a higher chance of survival (Cardinale et al., 2009). Blaxter and Hempel (1963) found that the size of eggs strongly correlated with their survival rate and with larval body size. In the present study, egg mass decreased with development time (see Supplementary Fig. 3.2.8). Prior to hatching, the embryos depend solely on internal resources from the yolk sac, of which only about half is converted into growth, whereas the rest is used for metabolism (Von Dorrien et al., 2013). This may explain the observed decrease in egg mass over time in the present study, although no correlation between metabolic rate and egg mass was observed for measurements taken early in development (degree days 30-44 post-fertilisation; see Supplementary Fig. 3.2.7).

In theory, larger eggs would have a better chance of survival due to a larger food reserve, though at cooler temperatures development time is longer. At higher temperatures, the eggs and larvae grow faster, though the time that the larvae can survive without an external source of food decreases (Von Dorrien et al., 2013). The point at which the larvae's yolk reserve is used up and the larvae are too weak to feed themselves has been found to happen at ~100 degree days post-hatching (Blaxter and Hempel, 1963). This point of no return occurs at different rates for different herring populations. Larvae hatched in the beginning of spring and late autumn have longer time to begin feeding whereas, in the early and late summer, the larvae only have a few days before reaching the critical point of no return (Peck et al., 2012). Still, hatchlings from late spring have a high survival and growth rate (Oeberst et al., 2009b). In terms of the effects of climate change on recruitment, these findings are inconclusive, as on one hand it seems that warmer winter will lower maternal investment, while on the other hand it may reduce the time span from hatching to the critical point of no return.

Other potential effects on recruitment success

While the present study investigated the effect of temperature on the cost of development, other environmental factors may play a role in the recruitment success of the WBSS herring, as discussed below.

Oxygen availability: Another fundamental factor concerning the effects of climate change on aquatic organisms is oxygen availability, which may limit metabolic functions (Rubalcaba et al., 2020). When the WBSS herring spawn, the eggs stick together in bundles, creating multiple layers of eggs (Von Dorrien et al., 2013). This layering of eggs might cause low oxygen conditions in the middle or bottom layers of the egg bundle, possibly affecting development and increasing mortality (Klinkhardt and Biester, 1984). This was observed by a previous study (Hempel and Shubert, 1969) that found both deformities and increased mortality in the bottom of egg bundles. Understanding the oxygen diffusion though layers of eggs and how this is affected by different temperatures could add to the understanding of the mechanisms driving the population dynamics of early life stages of WBSS herring.

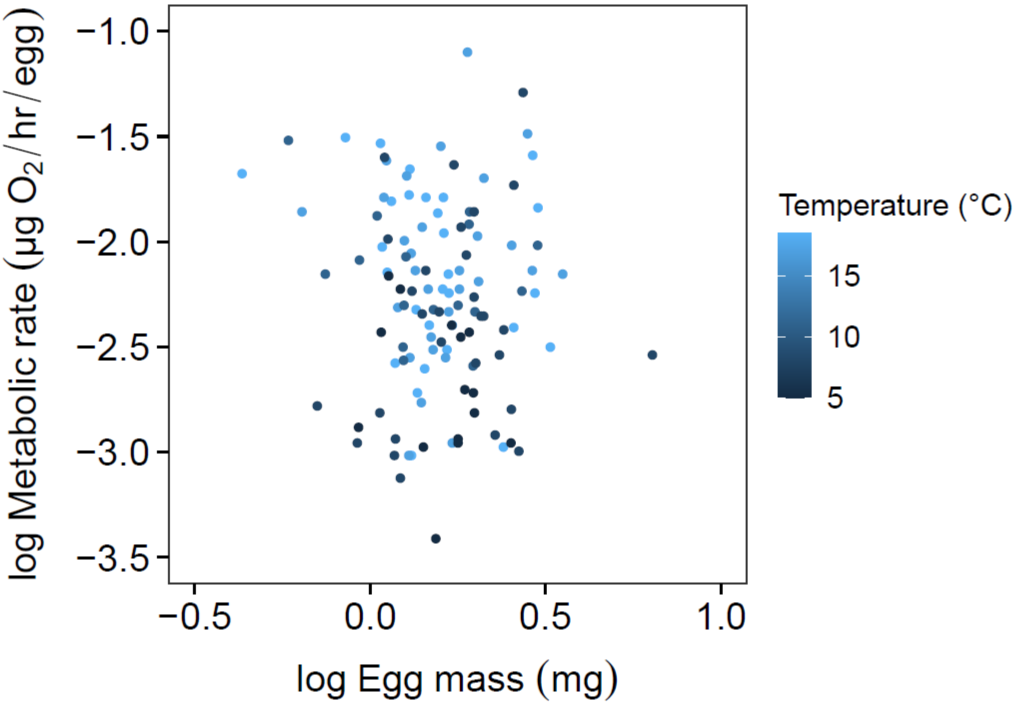
Another consideration is that the larger herring, which have higher fecundity and produce more and larger eggs than smaller herring, arrive earlier to the spawning sites than younger herring (Von Dorrien et al., 2013). The younger herring thus lay their eggs on top of those from the larger herring, which may cause oxygen depletion in the bottom layers of eggs, that initially had a better chance of survival. In addition, the eggs might suffer from accumulating excretory products (Von Dorrien et al., 2013). A study by Klinkhardt (1986) found that the eggs laid early when temperature was still low had a lower mortality, compared to smaller eggs laid later in the spawning season, when the temperatures had risen (Von Dorrien et al., 2013, and references within).

Spawning substrate and disturbance: The WBSS herring mainly spawn on aquatic vegetation, making the reproduction success highly vulnerable to anthropogenic activities such as nutrients runoff, coastal modifications for infrastructure and climate adaptation, as well as habitat tampering (Von Dorrien et al., 2013), which all impact the extent of aquatic vegetation. Turbidity due to construction or other human induced disturbance near the spawning grounds, such as the powerplant construction on the coast of Greifswald Bay and gas pipelines across the spawning ground, might also have a negative impact on the spawning success. Turbidity furthermore restricts the photic zone, consequently limiting the aquatic vegetation that is necessary for the herring to reproduce (Von Dorrien et al., 2013). Moreover, introduction of suspended matter and fine material poses at risk of increased nutrient load, as well as direct harm on the embryos by impaired gas exchange (Braum, 1973). The Baltic Sea is very vulnerable to eutrophication, due to the surrounding agriculture and low exchange of water. A study in the Southwest of Finland found a negative correlation between herring landings and nutrient load, however, the reduction in nutrient input to the Baltic Sea over the past two decades (HELCOM, 2020) have not (yet) resulted in an increase in the herring population.

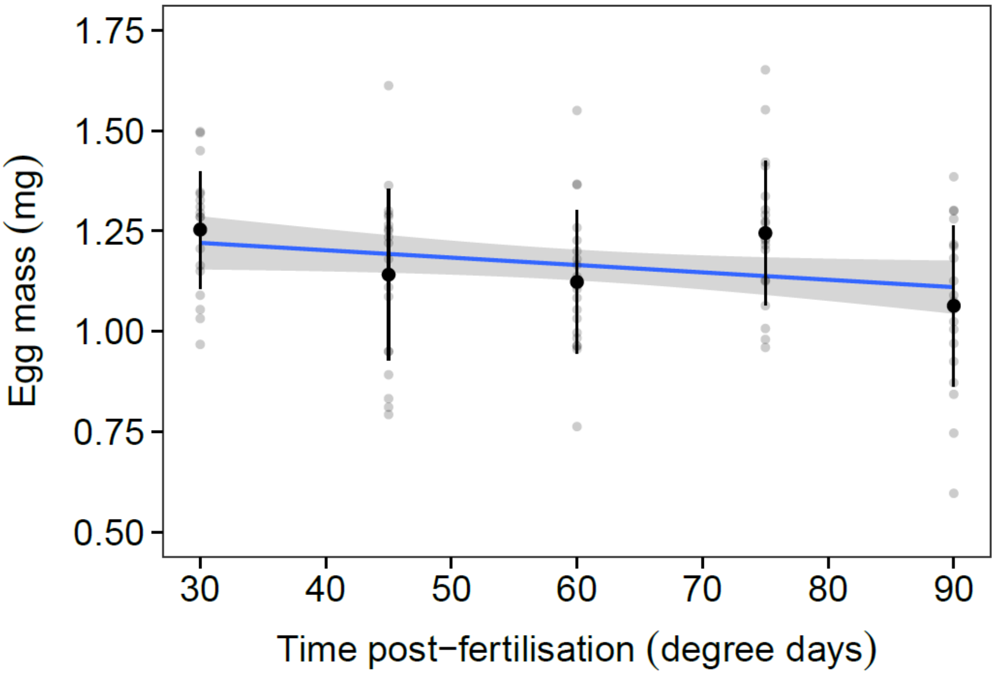
3.2.6 Conclusion

Based on the results obtained in this study, the cost of development decreased linearly with temperature, with the lowest estimated cost at 18.5^{o}C. This seemingly very high "optimal" developmental temperature is, however, not consistent with developmental cost theory, which implies that the temperature optimum (where the cost of development is lowest) should fall within a relatively narrow thermal window within the natural (historic) temperature range of a species (Marshall et al., 2020). An optimal temperature for WBSS herring development closer to their ambient spawning temperature (cf. Table 3.2.1) was therefore expected but not found. Although an intermediate temperature optimum for the cost development could not be determined, the increase in egg metabolic rate with temperature could indicate an energetic sensitivity to climate change that should be further explored. Overall, the validity of the results from the study is questionable due to issues with fungal infections and the resulting need to estimate cost of development from a limited amount of data and findings from other studies.

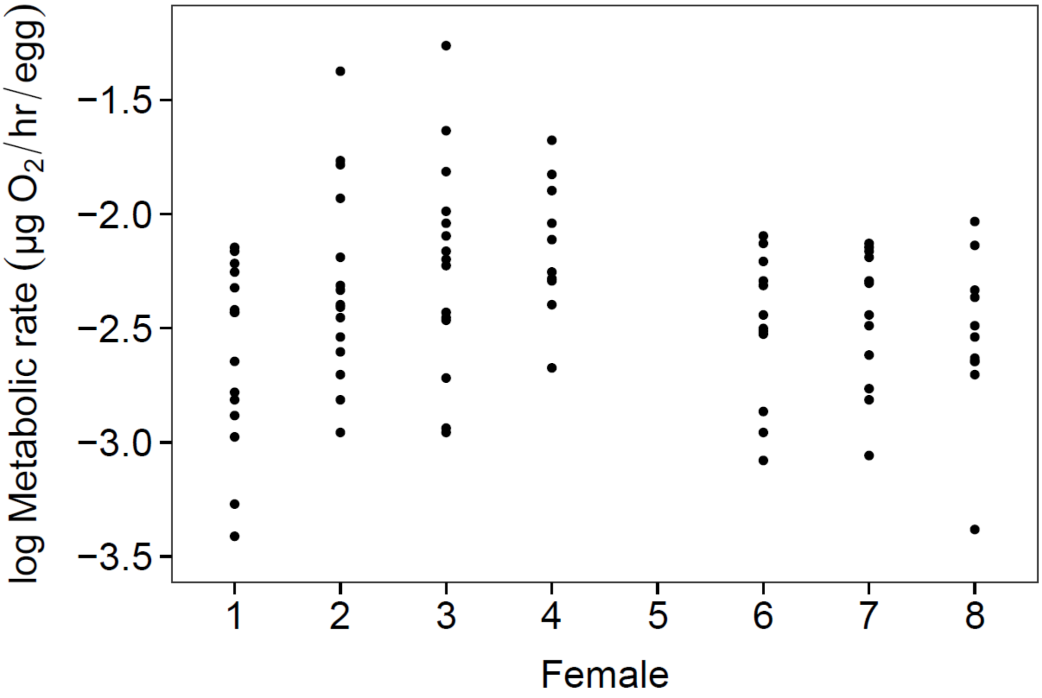
Supplementary material



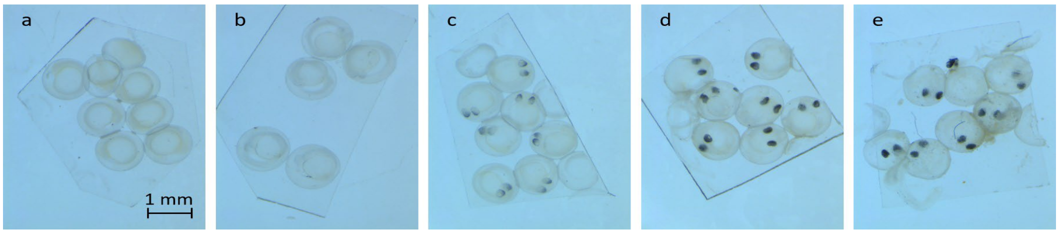
Supplementary Fig. 3.2.7. Log-log transformed plot of metabolic rate as a function of egg mass for eggs from seven female herring from Greifswalder Bay at the first measurement of egg metabolic rate (degree days 30-44) across treatment temperatures.



Supplementary Fig. 3.2.8. Egg mass from the 5ºC treatment from the Greifswalder Bay herring population as a function of development time (time after fertilisation in degree days).



Supplementary Fig. 3.2.9. Log-transformed metabolic rate categorised by herring females from the 5°C treatment of the Greifswalder Bay population.



Supplementary Fig. 3.2.10. Photos of the temporal development of Greifswalder Bay herring eggs from the 5°C treatment. a: day 6; b: day 9; c: day 12; d: day 15; and e: day 18 (start of hatching).

4. Stock Distribution during Migration and Catches

Migration behaviour in WBSS herring

Genetic split data were compiled across different data sources and used to assess population specific migrations in time and space. Data comprised collections by DTU Aqua individual fish from both scientific surveys and commercial catches, all of which had been typed for a suite of biological traits as well as assigned to a 'stock' and a population following Bekkevold et al. (2023). As commercial catches and scientific surveys sample feeding and migrating herring in different areas at different times of the year it was not possible to obtain detailed information about the migration behaviours of all populations through a full year and a full life cycle. Yet, to maximize biological inference from the data at hand, data were combined temporally and spatially, as follows. Catch data are spatially resolved by latitude-longitude, by ICES square and by ICES fisheries area and subdivision. Here, the analyses were done by ICES fisheries area/subdivision. To address annual differences associated with population specific feeding and spawning migrations, data were reduced from specific collection dates to analyses per annual quarter (Q1-4). In some cases (see below), data were combined across collection years. To track life stage specific differences in migration behavior, data were in some analyses (see below) separated between juveniles (fish with 0-2 winter rings) and adults (≥3 winter rings) when otolith age data were available. The analyses assessed migration behaviours in all assigned stocks, with special focus on WBSS and populations commonly occurring in Danish waters.

4.1 Data from genetic splits of commercial catches

Data on genetic stock affiliation for commercial catches were limited as few commercial catches were landed in Danish ports during the study period. A total of 1247 herring representing 35 fishing trips were genotyped under the Data Collection Framework and assigned to stock (1-114 fish analysed per trip, with 35 fish on average per trip). Estimated stock proportions shown here are not necessarily representative of total catches. Yet, in the data trends emerged on which stocks were present in the fishery where and when. First, as expected, NSAS (light gray pies in Figure 4.1.1), Downs (dark gray) and WBSS (dark blue) made up considerable proportions in most areas in most quarters (Figure 4.1.1). Across all genotyped samples, these three main population groups together made up 82% (again, note that the catches were not indexed to total catches and the figure only reflects the fish sampled from the catches). NSAS and Downs winter spawners were near-absent south of Kattegat (SD21) in catches in the Western Baltic Sea's SD22 and 24. In the analysed samples, there was a trend for larger proportions of WBSS herring in catches in Skagerrak-Kattegat than in catches in the North Sea, where NSAS and Downs herring were dominating. Herring assigning to NSAS were, however, also prevalent across the nine catches (trips) available from the Skagerrak and Kattegat, where they made up ~32% on average (range 0-70%).

Catches in Danish waters in the 2nd quarter (i.e. during WBSS spawning time) mainly contained WBSS (88.4% in total, Figure 4.1.1 Q2). BAS (shown in red pies in Figure 4.1.1) were captured in all examined fishing areas, except in one catch from inside the Limfjord in Q2, which represented the local spring spawning population. BAS were relatively most prevalent in catches from the Kattegat and the western Baltic Sea's SD24. All BAS assigned to the Western Baltic Sea population. This supports that BAS from eastern and northern parts of the Baltic Sea do not emigrate out of the Baltic Sea for feeding, in contrast to BAS from the western Baltic area.

Central Baltic Sea spring spawning herring (shown in yellow pies in Figure 4.1.1) comprised both individuals from the Northern Component, CBNC, and from the Southern Component, CBSC. CBSC made up 73% of these fish and CBNC herring were only identified in the western Baltic Sea's area 24 (where they made up 31% of Central Baltic spring spawners; not shown). This supports the observation that CBNC herring are less prone to feed outside the Baltic proper in contrast to CBSC, which are repeatedly identified in catches from the Kattegat, Skagerrak and the North Sea (Bekkevold et al. 2023).

Extracting data only for WBSS herring and examining their affiliation to specific substocks (populations) by area and quarter (Figure 4.1.2) corroborated previous notions about their spatial distributions (Bekkevold et al. 2023). For instance, the Skagerrak population (WBSS herring spawning in spring along the Swedish and Norwegian Skagerrak-Kattegat coasts) was only detected in Kattegat, Skagerrak and the eastern North Sea and not in Baltic Sea (SD24) catches. The 'Inner Danish waters' population was also scarce in the Baltic Sea (SD24) catches. The Rügen population was contributing major proportions to most samples, except to the collection from the North Sea where only few WBSS were identified (14 WBSS out of 271 sampled herring). Also, the Limfjord sample taken during spawning time, showed little impact of Rügen herring and mainly contributions from the local 'Inner Danish waters' population. Finally, the 'Western Baltic' population was most prevalent in the Danish Belt Sea area (Lillebælt) north of its main identified spawning sites in German Schleswig-Holstein fjords.

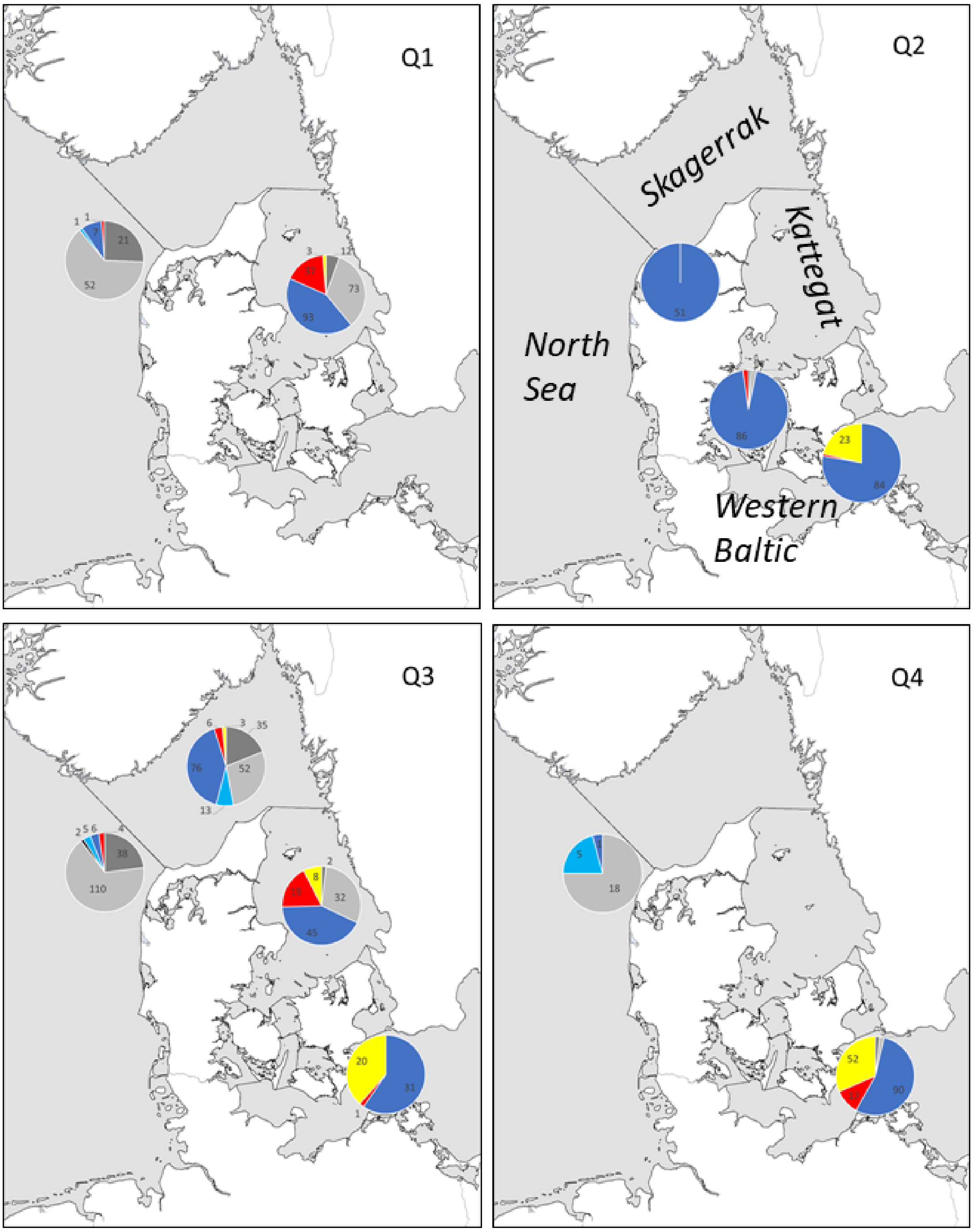


Figure 4.1.1. Genetic stock assignment of samples from commercial catches where data are combined across years 2021-2023 (including 1247 fish in total) and shown by quarter 1-4. Pie slice colours indicate stock affiliation as North Sea Autumn spawners (NSAS; light gray), Downs winter spawners (dark gray), Western Baltic Spring spawners (WBSS; dark blue), Norwegian Spring spawners (NSS; light blue), Baltic Autumn spawners (BAS; red), Faroese Autumn Spawners (FAS; black), and Central Baltic spring spawners (CB; yellow). Numbers of fish are shown by pie slice.

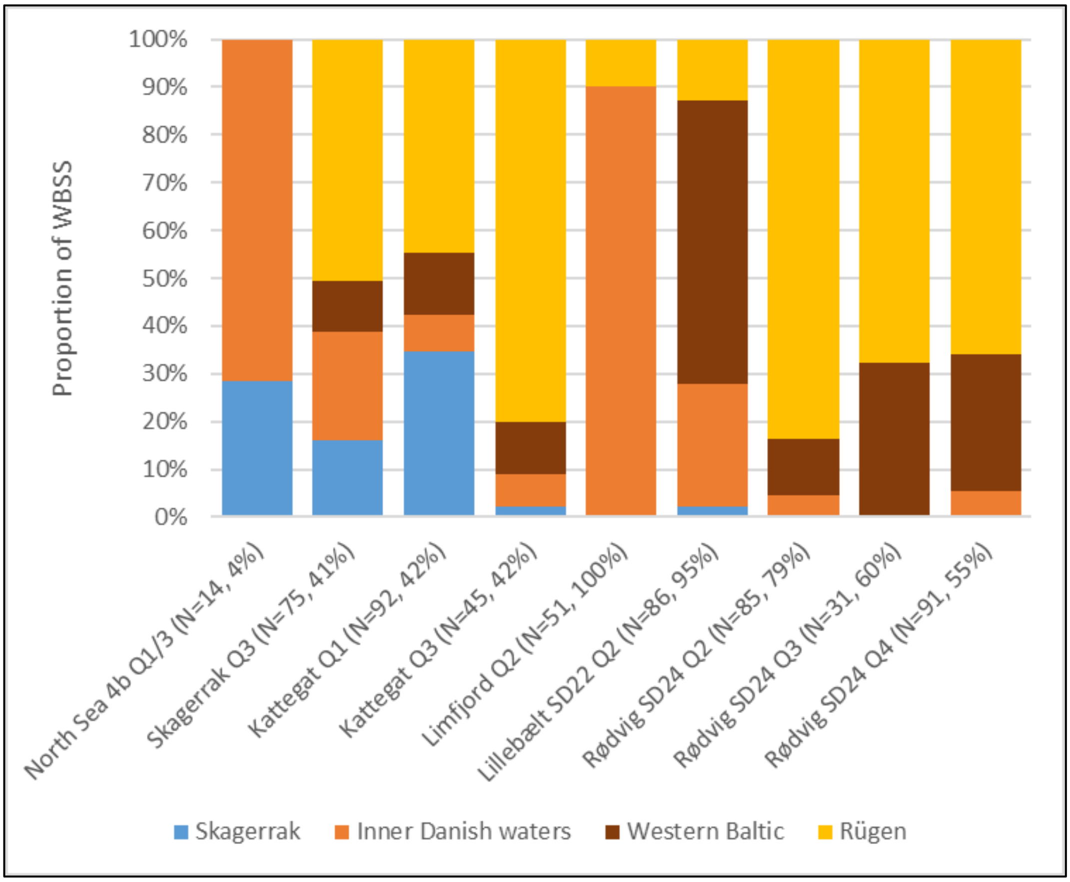


Figure 4.1.2. Commercial fishery samples showing the proportions of WBSS herring genetically assigning to, respectively the Skagerrak (blue), Inner Danish waters (tan), Western Baltic Sea (brown) and the Rügen (orange) population by area and quarter. Numbers in brackets indicate the N number of WBSS in the analysis, and the percentage of WBSS herring in the total trip sample.

4.2 Data from genetic population assignment of scientific survey catches

Data on genetic stock affiliation were extracted from data bases delivered under the Data Collection Framework and from other data sources held by DTU Aqua, such as survey data detailed in Bekkevold et al. (2023). The majority of data containing information about WBSS came from the Herring Acoustic Survey (HERAS). More scattered data were available for the Danish part of the International Bottom Trawl Survey.

A total of 5100 herring were extracted for analysis from HERAS data. These fish were captured from the North Sea, Skagerrak and Kattegat in 2002-2023 and were genetically assigned to stock and population (sub-stock), where applicable following (Bekkevold et al. 2023). Of these 5100 fish, age was estimated for 4754 (93%). Data varied among years and areas (Table 4.2.1) and were not necessarily representative for the total stock compositions at time and place, as different selection criteria by haul had been followed in different years (see Bekkevold et al. 2023). Briefly, selection criteria were directed at estimating stock compositions for all age classes in a haul (using either age estimated from otolith growth patterns, or total fish length, as proxies), rather than a randomized selection of the catch.

Table 4.2.3. Numbers of herring extracted from HERAS databases by area (basin and subdivision) and year. All fish were genetically assigned to a stock and, where appropriate, a population (sub-stock) following the method detailed in Bekkevold et al. (2023). Numbers of fish with age data are shown in brackets.

Area	**Year**	**No. fish (no. aged)**
Skagerrak (SD 20)	2002	133 (133)
	2003	178 (178)
	2018	92 (0)
	2019	356 (355)
	2021	338 (225)
	2022	740 (740)
	2023	617 (575)
Kattegat (SD 21)	2019	259 (256)
	2021	70 (69)
	2022	457 (457)
	2023	66 (66)
North Sea (IVa)	2002	45 (45)
	2003	45 (45)
	2008	40 (39)
	2019	37 (37)
	2021	164 (164)
	2022	188 (188)
	2023	459 (458)
North Sea (IVb)	2019	200 (200)
	2021	293 (232)
	2022	134 (134)
	2023	189 (158)

When split data were compiled across all ages it was clear that collections in all examined areas and years represented mixed stocks with fish originating in multiple populations (Figure 4.2.1). Time series were not equally representative across areas and years but nonetheless suggested shifts in the relative contributions of some of the populations. As many of the observed trends were associated with specific ages (juveniles versus adults), the results are further detailed in sections below.

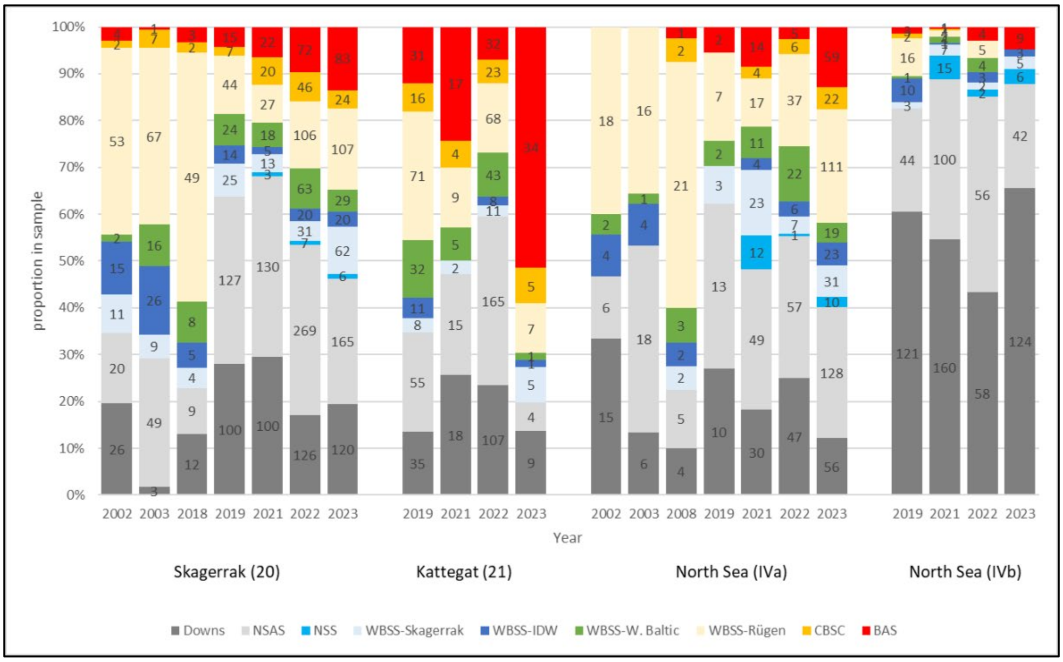


Figure 4.2.1. Time series of population assignment data from Danish HERAS cruise collections. Data are grouped by area and collection year and include all ages. Assignment proportions to specific stocks or populations are shown by colouring as indicated in the legend. Numbers of fish are shown inside bars.

4.2.1 Juvenile data

Filtering out time series data for juvenile fish (0-2 otolith winter rings) corroborated the expectation that the majority of juvenile fish originated in the populations NSAS and Downs (Figure 4.2.2). Thus, across all years and areas, 72% of the sampled juveniles belonged to one of these two populations. Overall, Downs juveniles were more prevalent than NSAS in the samples from North Sea's IVb compared to samples from IVa (making up, respectively, 67% and 42%), suggestive of a slightly more southerly main distribution of Downs juveniles compared to NSAS juvenile herring, as expected. There was no trend for temporal variation in their distributions. WBSS juveniles were encountered in all areas but were most commonly observed in the Kattegat (SD21). In collections from the North Sea, only 15% of all WBSS juveniles were 0-1 WR, indicating that it was mainly the 2y sub-adults that migrated into the North Sea. Samples from the Kattegat showed the strongest input from BAS juveniles, although BAS were commonly observed across all areas, with a trend for gradually increasing importance in recent years. Juveniles assigning to the CBSC were generally rare in the dataset and there was no indication of increased importance over time series, in contrast to the observation for adult fish (see below).

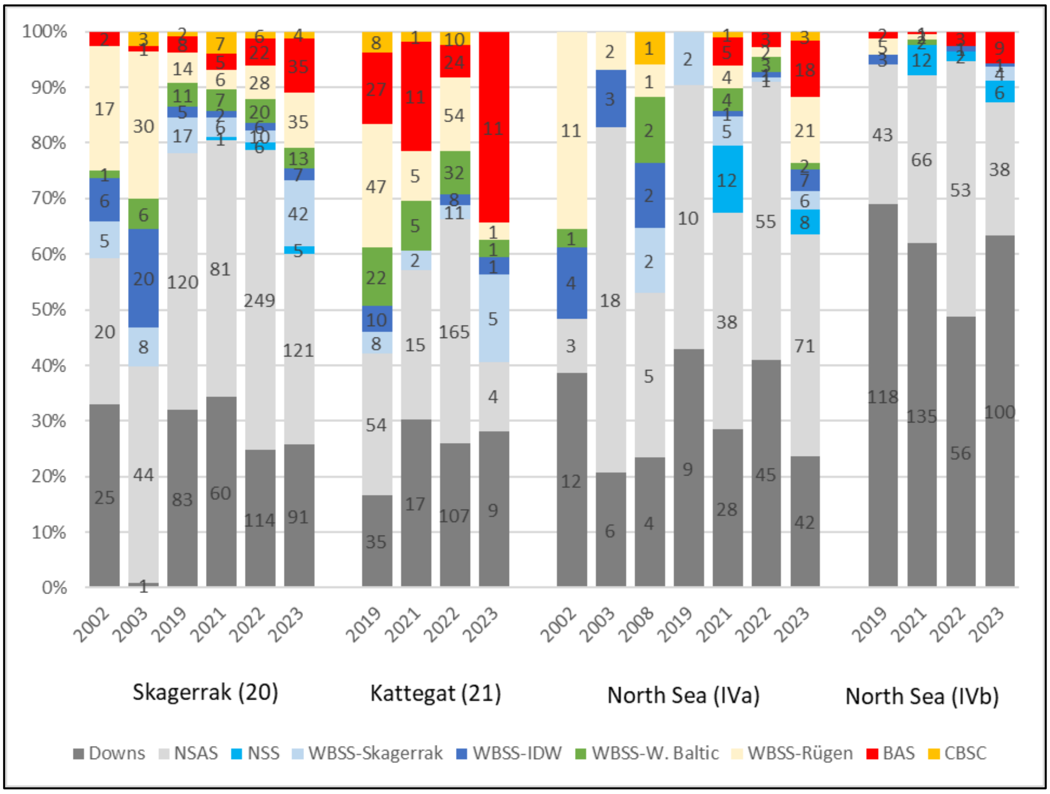


Figure 4.2.2. Juvenile herring time series of stock split data from Danish HERAS cruise collections from which genetically assigned herring were available. Data are grouped by area and collection year and only include fish with 0-2 otolith winter rings. Assignment proportions to specific populations are shown by colouring as indicated in the legend. Numbers of fish assigned are shown inside bars. NB. A single fish assigning to the Faroese Autumn spawning population, caught in the Skagerrak in 2023 was excluded from the analysis.

4.2.2 Adult data

Adult fish made up different proportions of the analysed catches in different areas. Thus, in the North Sea IVb, only 62 (8%) of 724 herring with age data were adult (≥3 WR). In North Sea IVa collections, 491 (44%) of 975 herring with age data were adult. In the Kattegat 138 (24%) of 848 analysed fish were adult. In the Skagerrak 767 (44%) of 2205 fish were adult. This meant that sample sizes by area and population were highly variable. When all populations contributing adult fish to hauls were compared over time series, there was nonetheless evidence of temporal trends in the relative contributions from different population (Figure 4.2.3). Adult NSAS and Downs were caught in highly variable proportions in the North Sea and Skagerrak but were not observed further south in the Kattegat. Also, in the North Sea and Skagerrak, the WBSS-Rügen population showed a slightly decreasing trend over time, while observations of BAS adult herring increased in the samples. For instance, the proportion of BAS in adult samples from the Kattegat increased from 9% to 68% over the five years from 2019-2023. Although sample sizes were modest (< 50 fish analysed in total per year) and data not scaled to total catch, the result indicates temporal changes in the importance of this population throughout the examined areas.

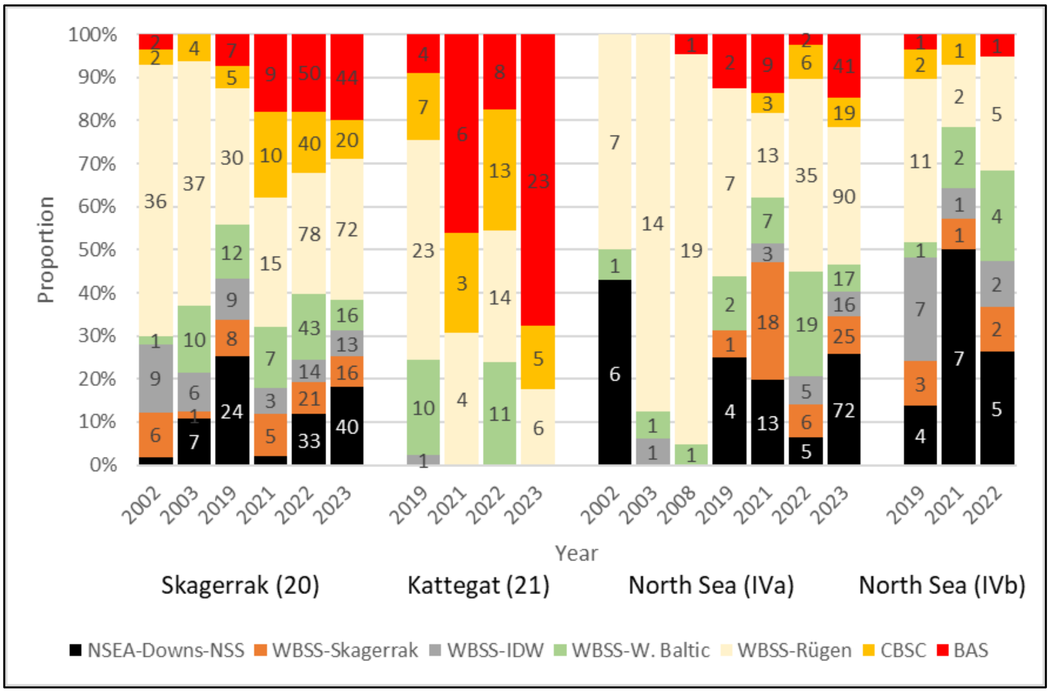


Figure 4.2.3. Adult herring time series of stock split data from Danish HERAS cruise collections from which genetically assigned herring were available. Data are grouped by area and collection year and only include fish with ≥3 otolith winter rings. Assignment proportions to specific populations are shown by colouring as indicated in the legend. Fish assigning to NSAS, Downs and NSS are combined and shown in black for improved visual inference about the WBSS and Baltic Sea populations. Numbers of fish assigned per population are shown inside bars.

Analyses on smaller spatial scales only including 1280 adult herring from data combined across recent years (2019-2023; where data were more consistently collected across areas compared to earlier years in the time series), again showed considerable stock mixing in all examined areas and strong presence of WBSS throughout all areas (Figure 4.2.4). Extracting data for genetically assigned Norwegian HERAS samples 2021-2022 supported consistent presence of WBSS further north along the Norwegian west coast. Adult NSAS and Downs herring were rarely encountered east of 10°E, which was in contrast to the more easterly distributions of those populations in juvenile herring, reaching into Kattegat (SD 21; Figure 4.2.2).

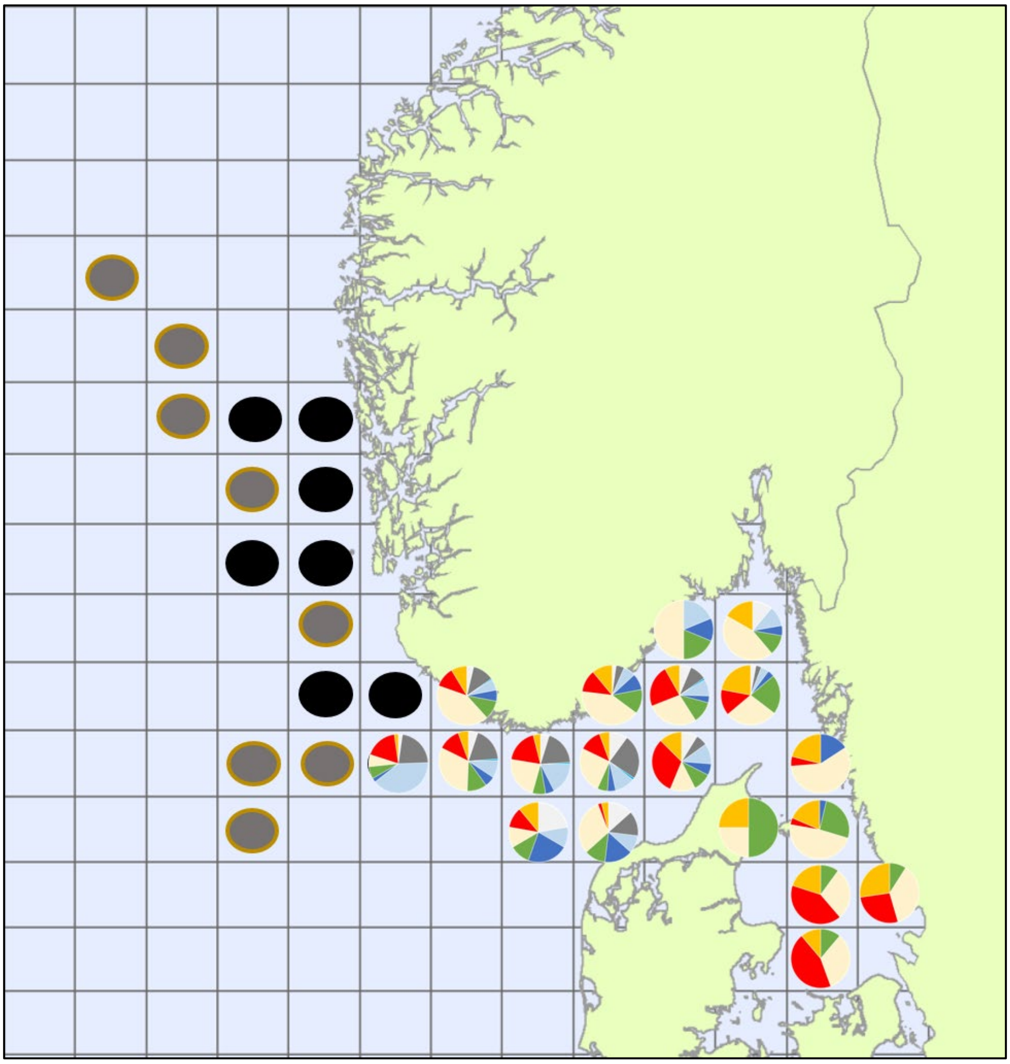


Figure 4.2.4. Stock composition of Danish HERAS collections of adult (≥3 otolith winter rings) herring for data combined across years 2018-2023 shown as pie diagrams by ICES square. Individual pies reflect data for 70 fish on average, range 10-236. Colours indicate population affiliation as Downs: light gray; NSAS: dark gray; NSS: turquoise; WBSS-Skagerrak: light blue; WBSS-Rügen: sand; WBSS-IDW: dark blue; WBSS-W. Baltic: green; BAS: red; CBSC: orange. ICES squares with black and dark gray ovals indicate where Norwegian HERAS data 2021-2022 identified, respectively, more than 15 WBSS, and 1-15 WBSS per sampled square.

To further examine the presence of individual WBSS populations during summer feeding migration, the data set was filtered to comprise only 1026 adult fish assigning to spring spawning populations in the western and central Baltic Sea areas (WBSS and CBSC). Although the resulting dataset was small and estimated proportions may not reflect true contributions to mixed-stock feeding schools per year and area, the data were suggestive of several differences in migration patterns among populations (Figure 4.2.5).

The Rügen population (sand coloured bars in Figure 4.2.5) was encountered throughout all examined areas. There was a trend for Rügen herring to make up smaller proportions in samples collected after 2019 in the North Sea (IVa,b), but this could be an effect of relatively low sample sizes for early years of the time series (2002-2008).

The genetically highly distinct WBSS-Skagerrak population (blue coloured bars in Figure 4.2.5) was not observed to be present in the Kattegat (i.e. south of the main spawning areas), but was consistently encountered in both the Skagerrak and in the North Sea, indicating that adult feeding migrations west into the North Sea are common in this population.

The spring spawning herring from the Baltic Sea all assigned to the population spawning in the southern Baltic Sea, CBSC. These CBSC (yellow bars in Figure 4.2.5) were encountered in all areas, with a trend for increasing numbers of observations after 2019, in comparison with earlier years. This indicates that feeding migrations out of the Baltic proper and northwest into the North Sea are common in this southern Baltic Sea population.

WBSS herring from both the Inner Danish waters (dark orange bars) and the Western Baltic (green bars) populations were also observed in most areas but were relatively more common in the Skagerrak and North Sea IVb, and less commonly observed in samples from the Kattegat and North Sea IVa. There was no trend in temporal changes for either population. This indicates that both populations perform long distance feeding migrations out of the Western Baltic area and the Inner Danish waters into the North Sea.

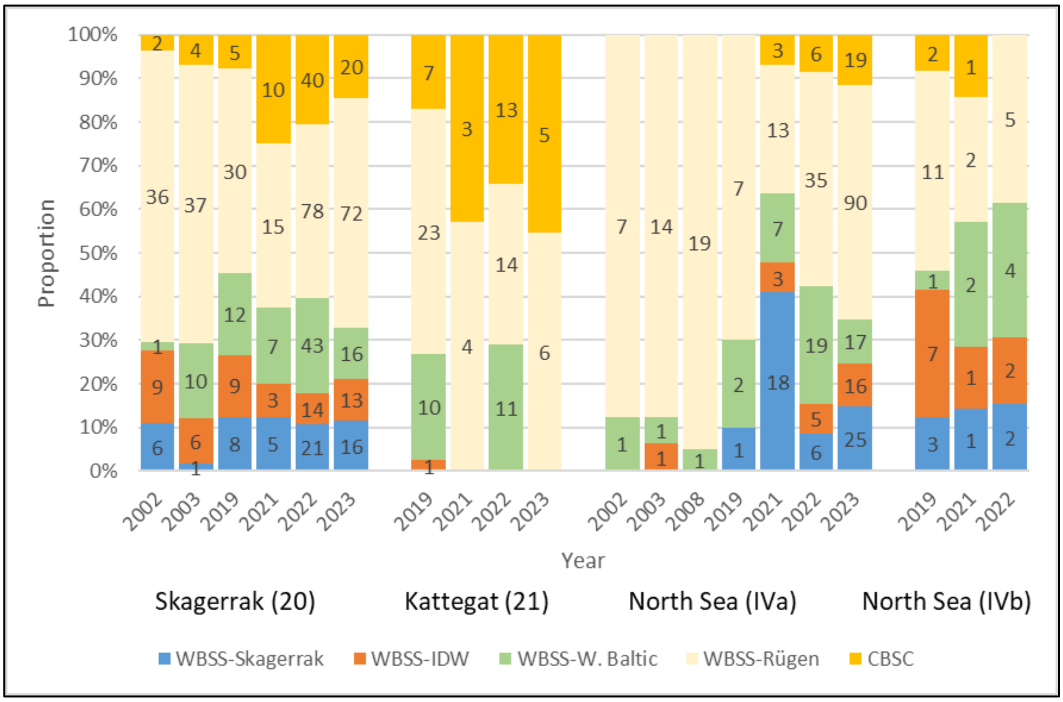


Figure 4.2.5. Adult herring time series of stock split data from Danish HERAS cruise collections, including only fish with ≥3 winter rings assigned to WBSS and CBSC. Data are grouped by area and collection year. Assignment proportions to specific populations are shown by colouring as indicated in the legend. Numbers of fish are shown inside bars by population.

4.3 Conclusions on WBSS and Baltic Sea herring migrations in the North Sea-Skagerrak-Kattegat

Genetic assignment analyses (‘stock-splits’) allows for monitoring the distributions and migration behaviours in the individual WBSS populations. At the stock complex level, analyses corroborated that WBSS occur throughout the examined North Sea areas, including north of 59.5°N, i.e., north of the so-called ‘Transfer Area’ in which data are split between the stocks WBSS and NSAS in input to current stock assessment models (ICES 2023). Based on combined information for the different collections of mixed feeding stocks, the following population specific characteristics and trends were observed.

- **WBSS-Skagerrak** adults and juveniles perform westbound migration into the Skagerrak and North Sea (IVa),but are in the data more rarely encountered in the more southerly areas Kattegat and the North Sea IVb in Q3. In Q1, commercial fishery samples from the Kattegat included immature WBSS-Skagerrak fish. No WBSS-Skagerrak herring were encountered in samples from the Western Baltic Sea (SD 24), suggesting that individuals from this population rarely migrate south of the Danish Belt Sea.
- Adult (≥3WR), sub-adult (2WR), and to a lesser extent juvenile, **WBSS-Rügen** herring perform migration north through the Danish Belt Sea and into the Kattegat-Skagerrak and North Sea.
- Adults and juveniles of WBSS spawning in **Inner Danish waters (WBSS-IDW)** migrate to the Skagerrak and North Sea. Juveniles (1WR) captured in the North Sea may originate from WBSS spawning locations in western Jutland fjords and estuaries flowing into the North Sea. Few WBSS-IDW herring were encountered in samples from the Kattegat (SD 21) in Q3, suggesting migration through and out of the Kattegat to take place prior to the summer months. In commercial fishery samples, WBSS-IDW adults are mainly encountered in the Kattegat and Inner Danish waters in Q1-2 (i.e. close to spawning time). Few WBSS-IDW herring were encountered in samples from the Western Baltic Sea (SD 24), suggesting that individuals from this population rarely migrate south of the Danish Belt Sea.
- Adults (and to a lower extent juveniles) of WBSS herring spawning in the fjords along the German Western Baltic Sea coast (**WBSS-W. Baltic**) migrate to the Kattegat, Skagerrak and into the North Sea. In commercial fishery samples they were most prevalent in Western Baltic Sea areas SD22 and SD24.
- There was no indication that populations within the WBSS stock complex display marked changes in relative strength over the examined 20-year period.
- Adults (but not juveniles) from the **Central Baltic Southern Component, CBSC,** of spring spawning herring migrate through the Inner Danish waters into the Kattegat-Skagerrak-North Sea areas and were inferred to increase in importance in time series from 2002-2023. This suggests changing distribution and/or stock strength.
- Finally, **Baltic Autumn Spawning (BAS)** herring adults and juveniles migrate through the Inner Danish waters into the Kattegat-Skagerrak-North Sea areas and were inferred to increase in importance in time series from 2002-2023, suggestive of changing distribution and/or stock strength.

5. Stock Rebuilding

5.1 Consequences of depensatory recruitment for rebuilding WBSS

5.1.1 Introduction

The recovery potential of populations at low abundances significantly affects their resilience and risk of extinction. Compensatory dynamics suggesting rapid growth at low abundances are countered by the Allee effect, linking per capita growth rate positively with abundance, reducing productivity at lower levels (Hutchings, 2012). The confusion surrounding Allee effects, their definition, and detection issues stem from limited empirical documentation due to sparse populations (Hutchings, 2012; Sugeno & Munch, 2013). Differentiating between strong and weak Allee effects based on population thresholds is highlighted (Hutchings, 2012). While Keith and Hutchings (2012) found variability among exploited fish stocks in their compensatory dynamics or evidence of Allee effects impacting recovery rates (Keith & Hutchings, 2012), harvested fish populations have shown limited recovery despite reduced fishing, suggesting non-compensatory dynamics (Hutchings, 2012; Perälä & Kuparinen, 2017). Detecting Allee effects in marine fishes has historically been challenging due to limited recruitment data and methodological limitations (Myers et al., 1995; Liermann and Hilborn, 1997; Frank and Brickman, 2000). Recent perceptions challenging the rarity of Allee effects in marine fishes are supported by meta-analyses, albeit with ongoing methodological limitations and data constraints at low abundances (Perälä & Kuparinen, 2017; Rogers et al., 2018). Rogers et al. (2018) emphasized the implications of the adopted migrant life history in pelagic marine fishes, highlighting social learning and recruitment dynamics among populations and their role in population collapse and recovery hindrance after crossing a tipping point (Rogers et al., 2018).

New analytical approaches were applied to 79 ICES stock recruitment data series, among which we highlight the specific differences of applying compensatory versus depensatory recruitment models to two herring stocks, North Sea Autumn Spawners and Western Baltic Spring Spawners. The full results are described in Albertsen et al. (2024).

5.1.2 Consequences of ignoring the possibility of depensatory recruitment for rebuilding times

Often, recruitment is modelled using compensatory models such as the Beverton-Holt, segmented regression/hockey stick or constant median. This is the case for ICES reference points. Compensatory models assumes that productivity increases as stock sizes decreases. However, when this is not the case, rebuilding potential from low stock sizes may be affected.

To investigate the effect of assuming compensatory recruitment in the presence of depensation, a simulation study was conducted. For each of 79 ICES stock assessments, a total of 20 recruitment models were fitted using a penalized maximum likelihood errors-in-variables approach, accounting for uncertainty in both recruitment and stock size. The recruitment models included the compensatory Beverton-Holt, Ricker, Deriso, and smoothed hockey stick models. Further, each of them was combined with four depensatory modifications. For each stock, the best fitting recruitment family was determined by

AIC and, within this family, the compensatory model was compared with the best fitting depensatory modification in terms of rebuilding time and probability of stochastic collapse. Further, three depensatory thresholds were calculated: (i) the biomass of maximum productivity, SMP, (ii) the biomass where the recruitment function changes from convex to concave, S0, and (iii) the biomass where the reproductive rate changes from negative to positive, SRR.

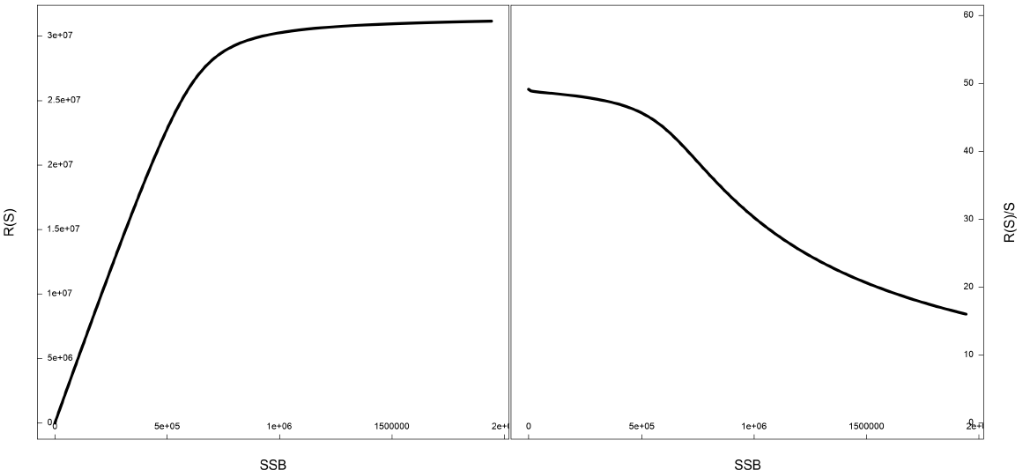
To evaluate rebuilding potential, stocks were projected 200 years without fishing in a simulation study and results were aggregated to fisheries guilds in a meta analysis. Across stocks, SMP was at 30% of the compensatory BMSY, S0 was at 20% of BMSY, and SRR was found at very low biomass. All three thresholds were higher for pelagic than for benthic and demersal stocks.

To compare rebuilding time, the biomass starting point leading to a median rebuilding time of two generation lengths was extracted from the simulations. Across stocks, this point was below 1% of BMSY for compensatory fits and at approximately 10% of BMSY for depensatory fits. For pelagic stocks, the increase was from 20% to 25% of BMSY. In the simulations, compensatory models would almost always rebuild in the absence fishing. However, for depensatory models, there was a 5% probability of stochastic collapse in the absence of fishing at 42% of BMSY for pelagic stocks, 26% for demeral stocks, and 1.2% for benthic stocks.

The simulations indicate that recruitment assumptions should be evaluated with additional care when biomass is below 30% of the compensatory BMSY, or 45% for pelagic stocks, including the possibility of depensation. In particular, ignoring depensation in recruitment, if present, will result in overoptimistic rebuilding projections and risk assessments from low biomass.

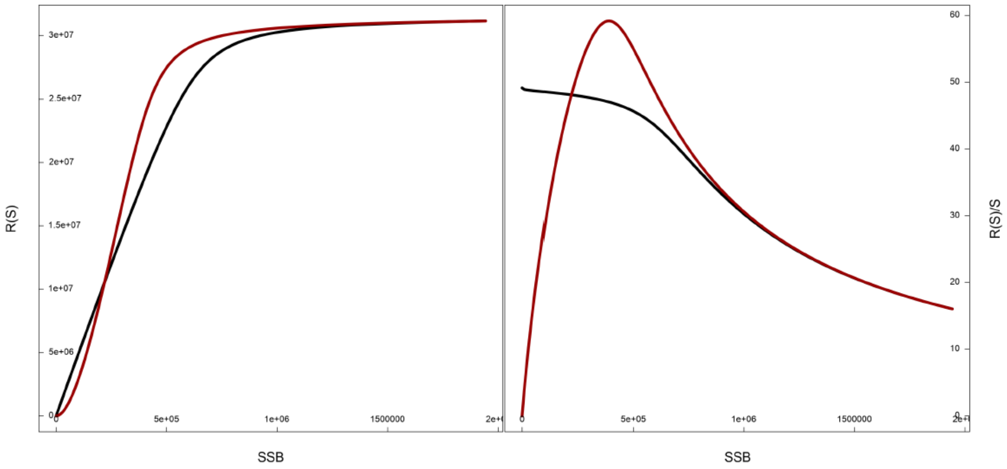
Purpose

Most procedures in ICES assumes compensatory recruitment (e.g., Hockey stick)

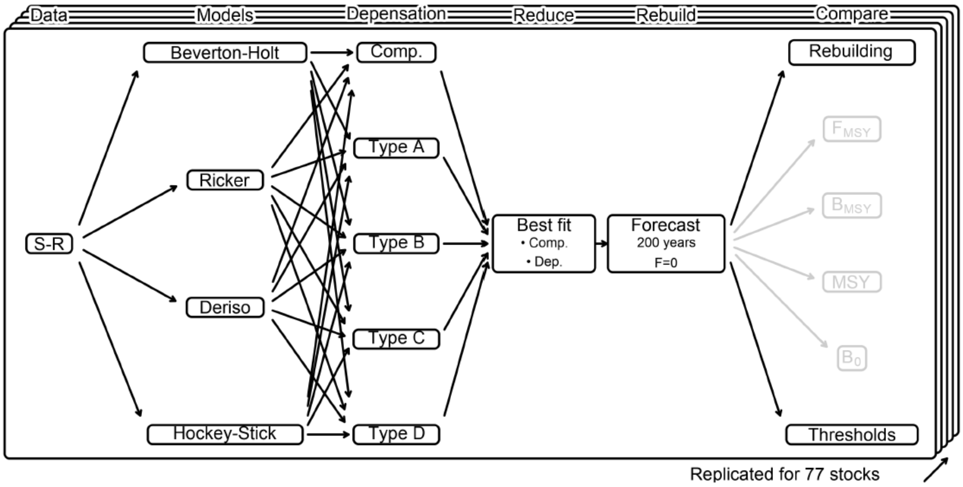


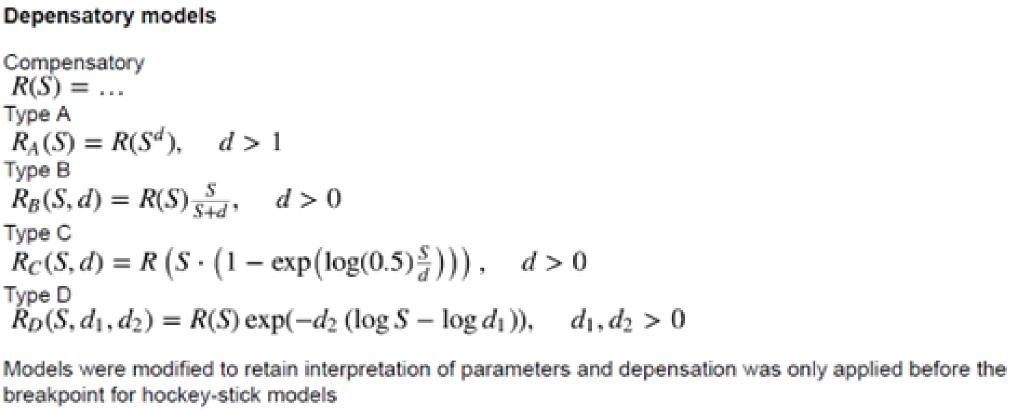
Purpose

How different is rebuilding potential if recruitment is actually depensatory?



Method




Depensatory models

Compensatory

$R(S) = \ldots$

Type A

$R_A(S) = R(S^d), \quad d > 1$

Type B

$R_B(S,d) = R(S)\frac{S}{S+d}, \quad d > 0$

Type C

$R_C(S,d) = R\left(S \cdot \left(1 - \exp\left(\log(0.5)\frac{S}{d}\right)\right)\right), \quad d > 0$

Type D

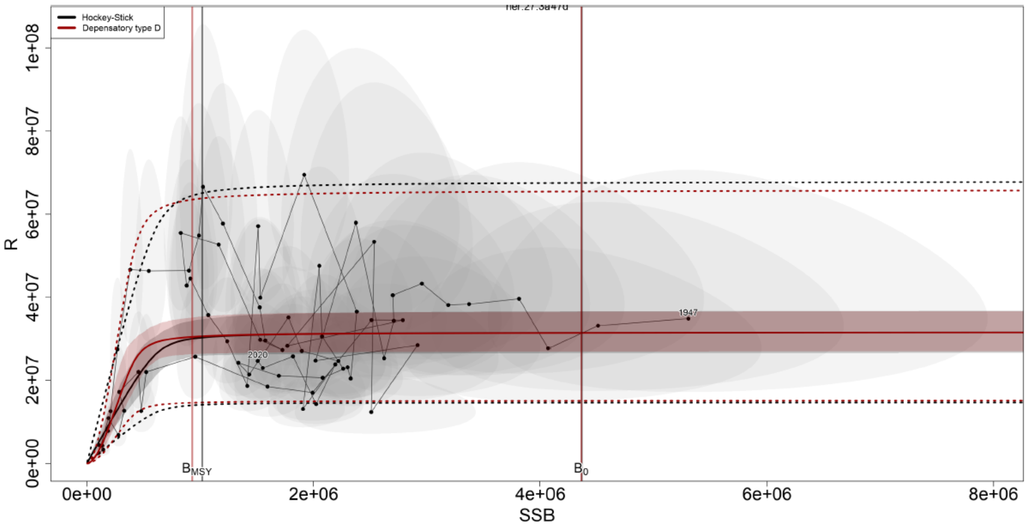
$R_D(S,d_1,d_2) = R(S)\exp(-d_2(\log S - \log d_1)), \quad d_1, d_2 > 0$

Models were modified to retain interpretation of parameters and depensation was only applied before the breakpoint for hockey-stick models

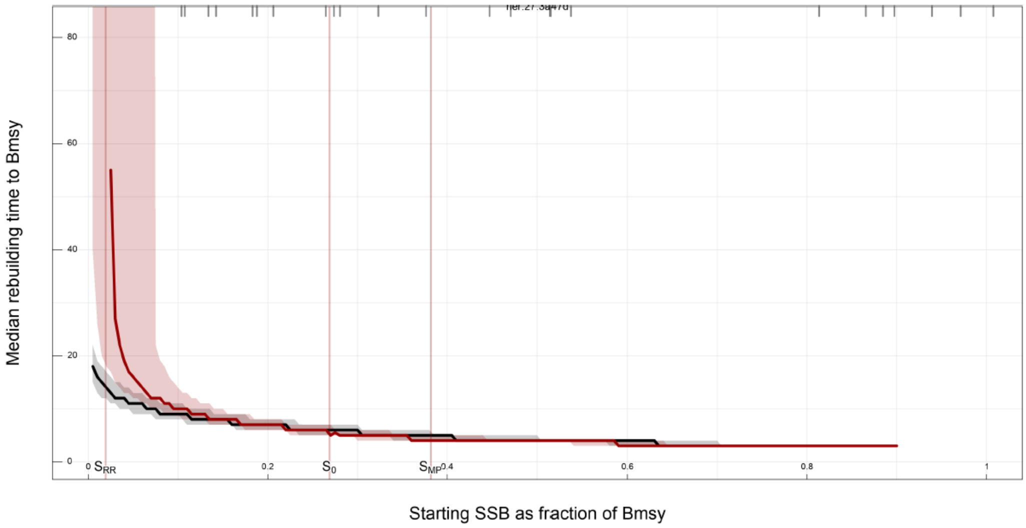
Depensatory thresholds:
SMP Point of maximum productivity.
S0 Point where recruitment function changes from convex to concave.
SRR Point where reproductive rate changes from negative to positive.

Note
Simulation study based on 77 stocks.
Not about individual stocks.
Stocks are used to get realistic life histories.
Fitted curves are not necessarily appropriate for assessment and advice.
S-R pairs are influenced by assessment model.

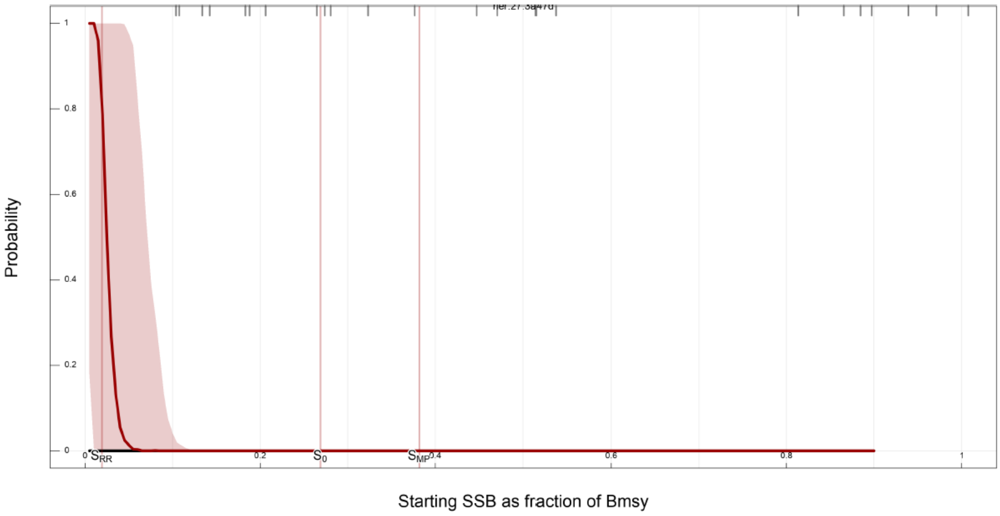
Example: North Sea Herring



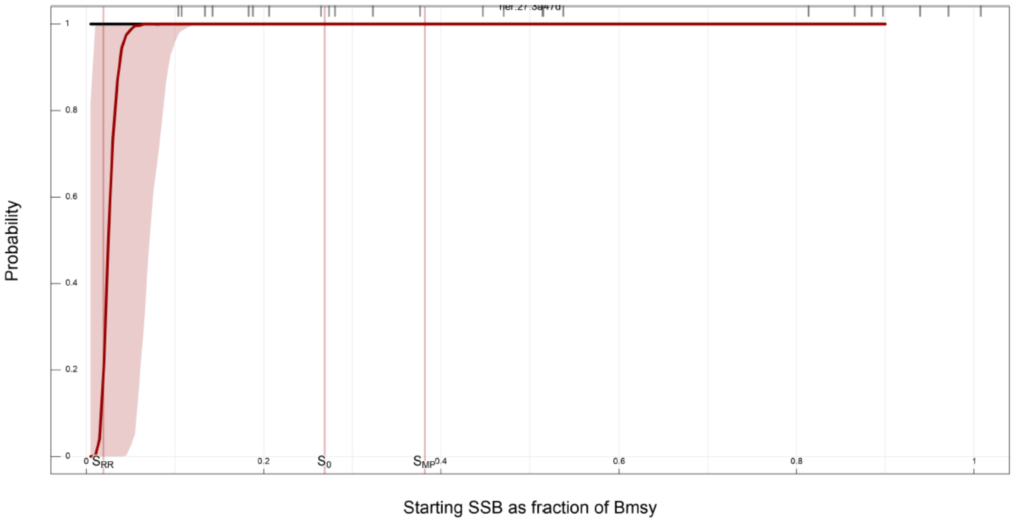
Median rebuilding time to (compensatory) B$_{MSY}$



Probability of collapse (SSB < 1)

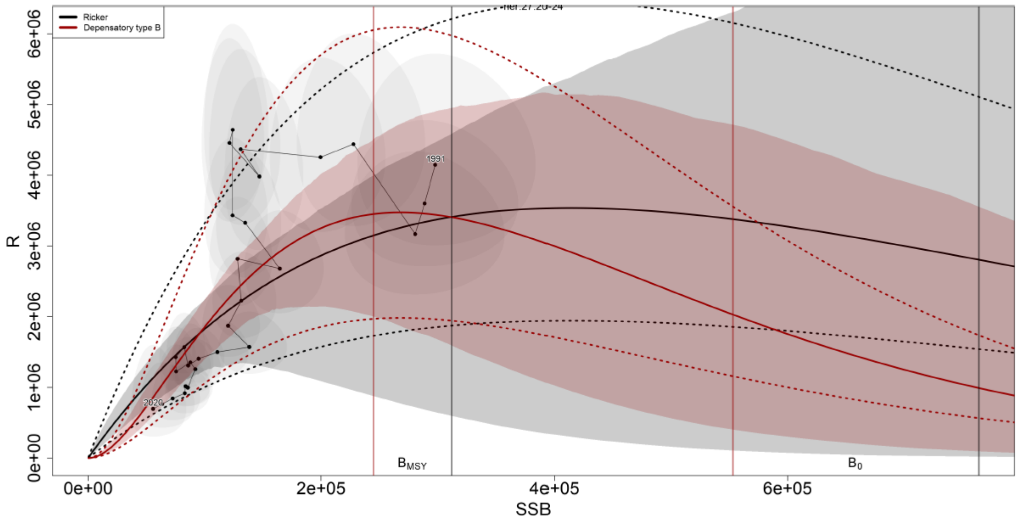


Probability of rebuilding in 200 years

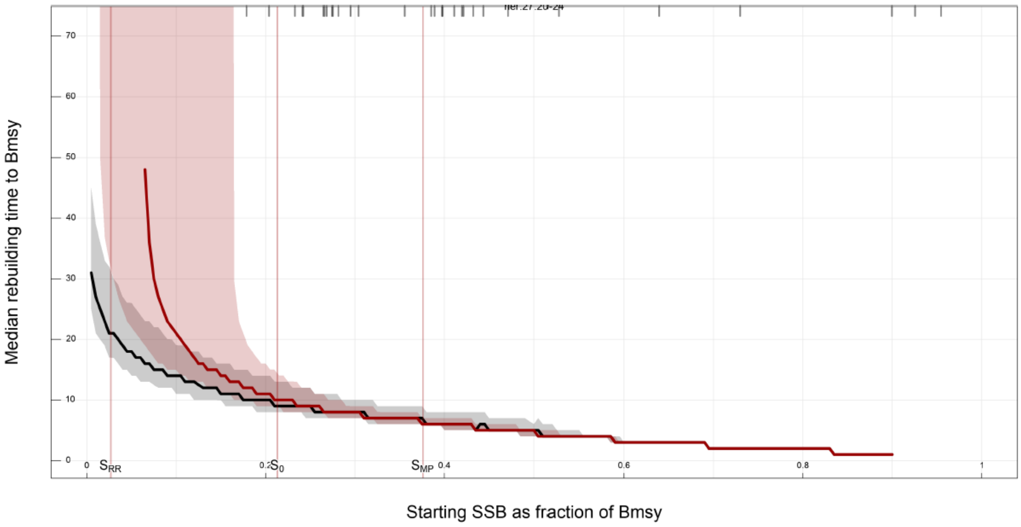


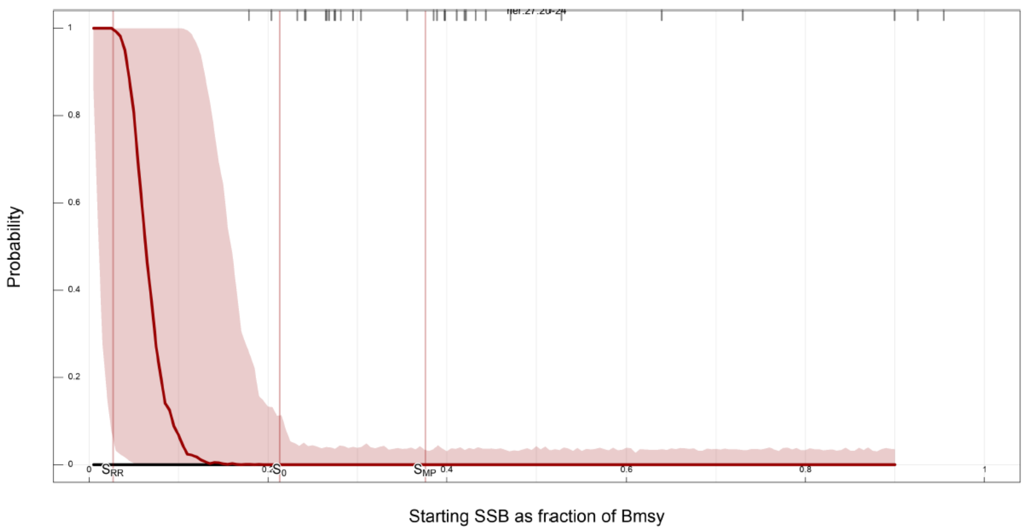
Black compensatory Red depensatory

Western Baltic Spring Spawning Herring



Median rebuilding time to (compensatory) B_{MSY}




Probability of collapse (SSB < 1)

Black compensatory Red depensatory

5.1.3 SUMMARY

- Assessment and advice often use compensatory recruitment models.
- Models assume that productivity increases as stock size decreases.
- If not, (perceived) rebuilding time and probability of stochastic collapse may increase a lot.
- Pelagic fish are the most affected.
- On average, maximum productivity is at 30% of the compensatory B[MSY]
- S[0] threshold is at 20% of the compensatory B[MSY]
- 5% risk of collapse at 25% B[MSY], ~45% for pelagic, ~12% for demersal, ~0% for benthic
- Any risk of collapse at almost 90% of B[MSY]

5.2 Rebuilding WBSS in a Multifleet multi-stock context

5.2.1 Multifleet multi-stock assessment models

Given the current management in place, rebuilding of WBSS herring is highly dependent on the status of NSASH. It is therefore necessary to consider both stocks in the rebuilding plan evaluation for WBSS herring. The current multifleet assessment for NSASH includes three fleets (A, B&D, C, ICES (2022)). Indeed, for convenience the B-fleet and the D-fleet (the two bycatch fleets) were combined into one. To allow a combined forecast for both stocks, a new multifleet assessment was developed for NSASH where the B- and D-fleets are uncombined so that both stocks share the same fleets in the assessment. The new model is available on stockassessment.org with the name “NSAS_herring_2022”. The model was tuned so it corresponds to the best version of the model and presents very similar outputs as the 2022 advice model (Figure 5.2.1).

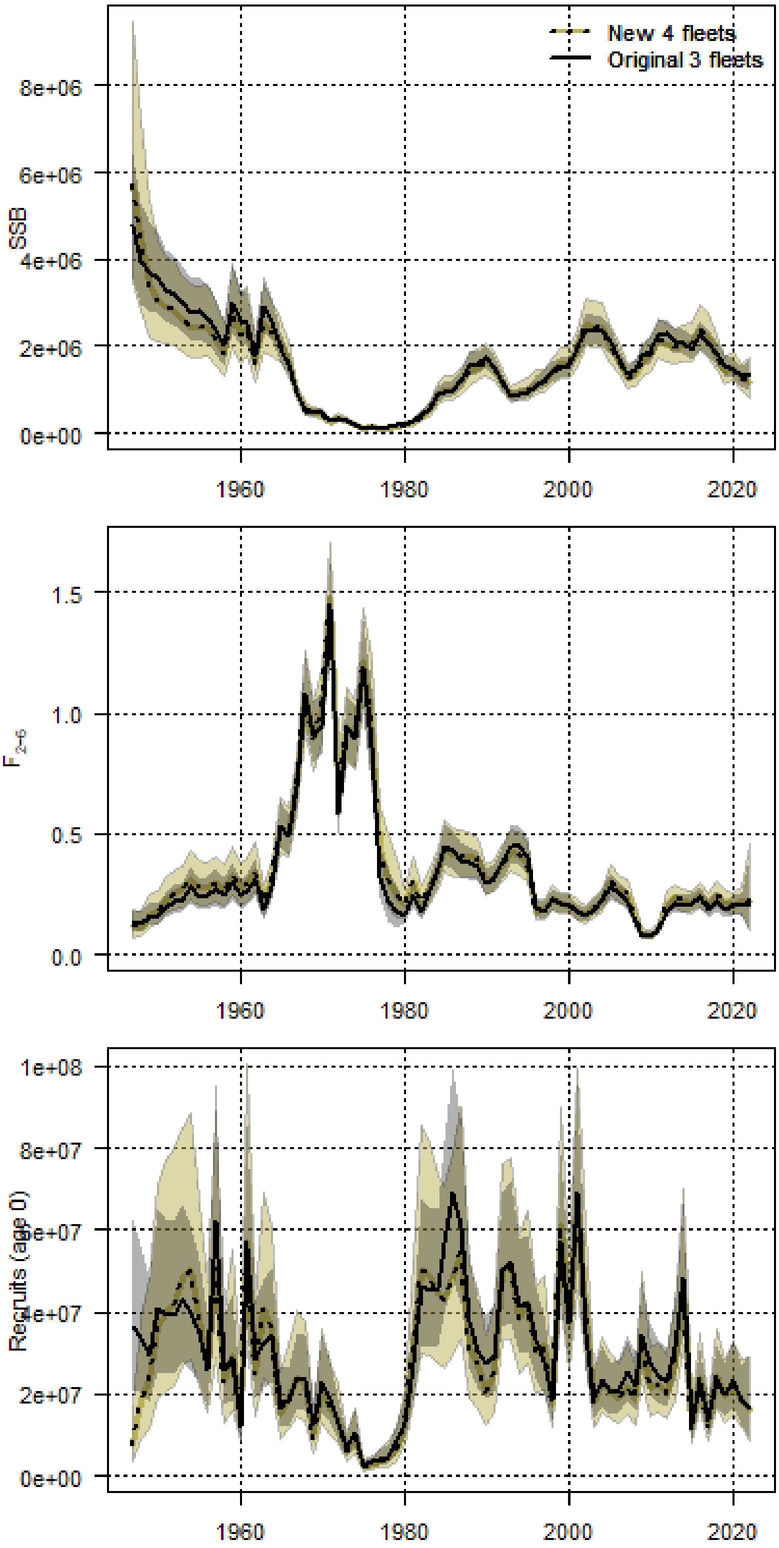


Figure 5.2.1: Comparison of original 2022 NSASH assessment outputs with the new assessment with four fleets.

Given this new NSASH model configuration and the one from the 2022 multifleet WBSS herring model (ICES 2022), we used the multiStockassessment R-package to fit a multifleet model for both WBSS herring and NSAS herring. We also fitted the model assuming a stock recruitment relationship (SRR) instead of a random walk in recruitment, as it can be important to consider the link between SSB and recruitment in long-term projections. We fixed the SRR to correspond as closely as possible to the ones use for the last estimation of reference points so that our forecast is consistent with the reference points (Figure 5.2.2). Assuming a SRR did not affect the outputs of the model drastically and the model is therefore assumed valid for this study (Figure 5.2.3).

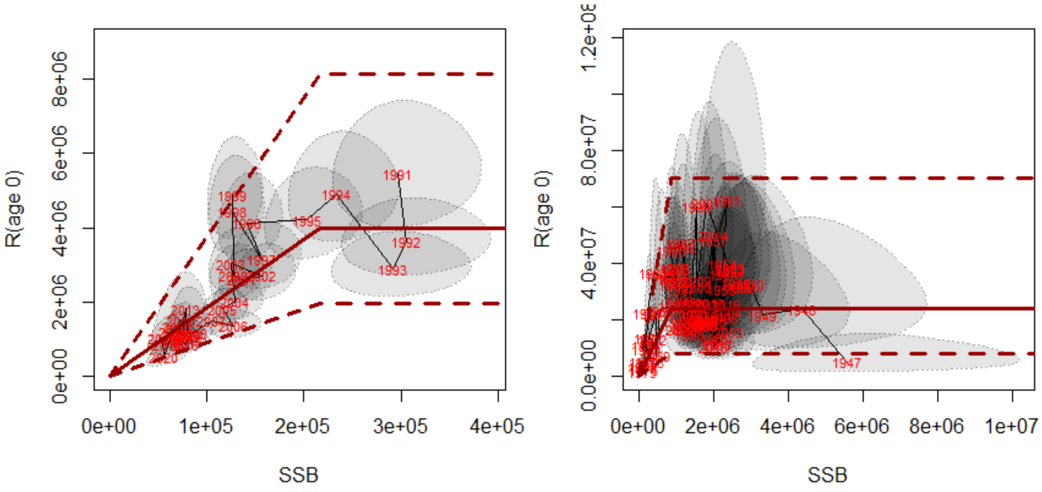


Figure 5.2.2: Stock-recruitment relationship assumed for one of the assessment models. The ellipses show the uncertainty in the recruitment and SSB estimates and the dashed lines show the predictive uncertainty.

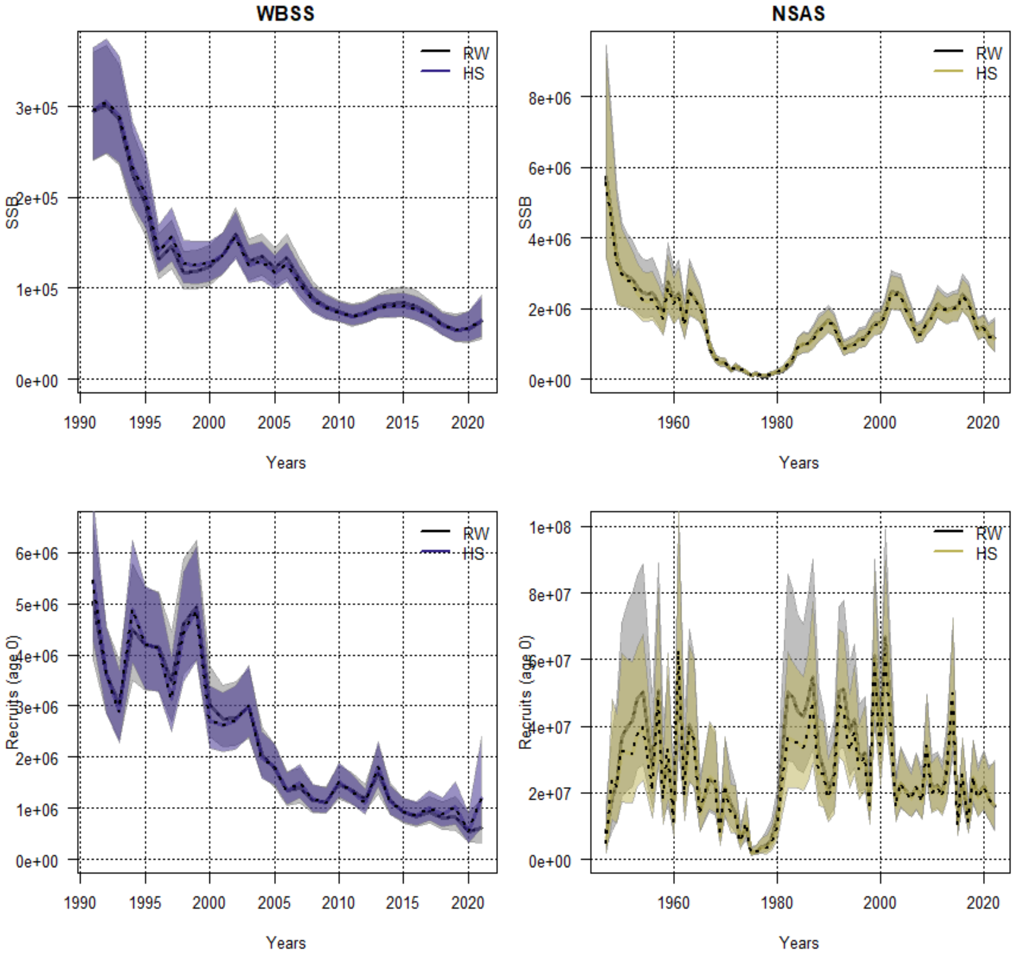


Figure 5.2.3: Multifleet multi-stock SSB estimates per recruitment assumptions, i.e., RW=Random walk recruitment, and HS=Hockey-stick recruitment.

5.3 Rebuilding WBSS by ecosystem services management

5.3.1 Introduction

The Western Baltic Spring Spawning (WBSS) herring stock is in a deplorable state. Statistical analyses indicate that the stock may be in a depensatory population dynamic state where lower spawning biomass yields relatively lower per capita recruitment and slower rebuilding capacity. The purpose of this section is to identify the causes that have led to this state and provide a plan to improve the state by suggesting remedies that will make the Western Baltic Herring stock thrive again.

What is wrong?

ICES has been monitoring the state of the WBSS herring stock for more than 30 years (ICES, 2023). In figure 5.3.1 it can be seen that the spawning biomass has been below safe limits for the past 15 years.

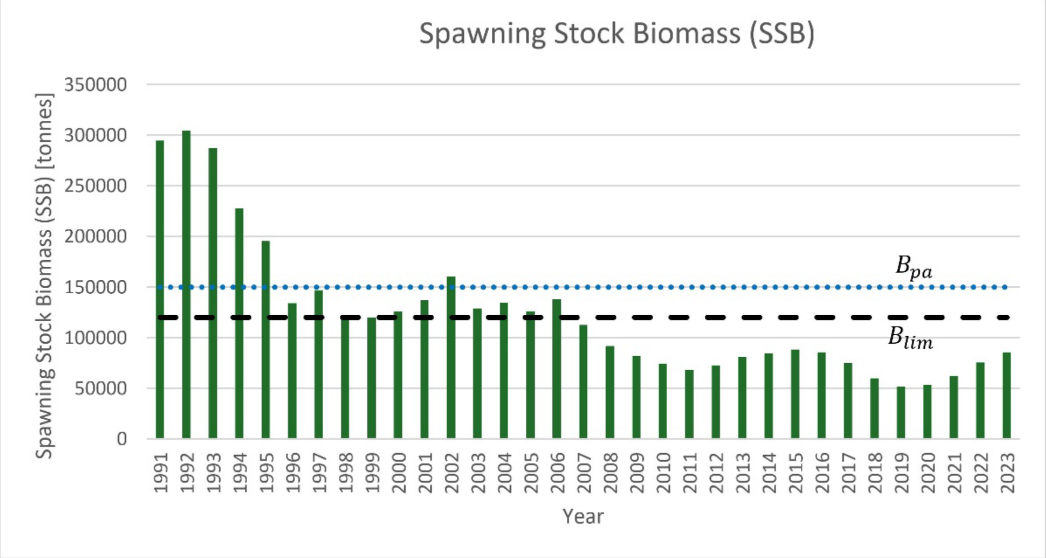


Figure 5.3.1 Spawning stock biomass of the WBSS herring (ICES, 2023).

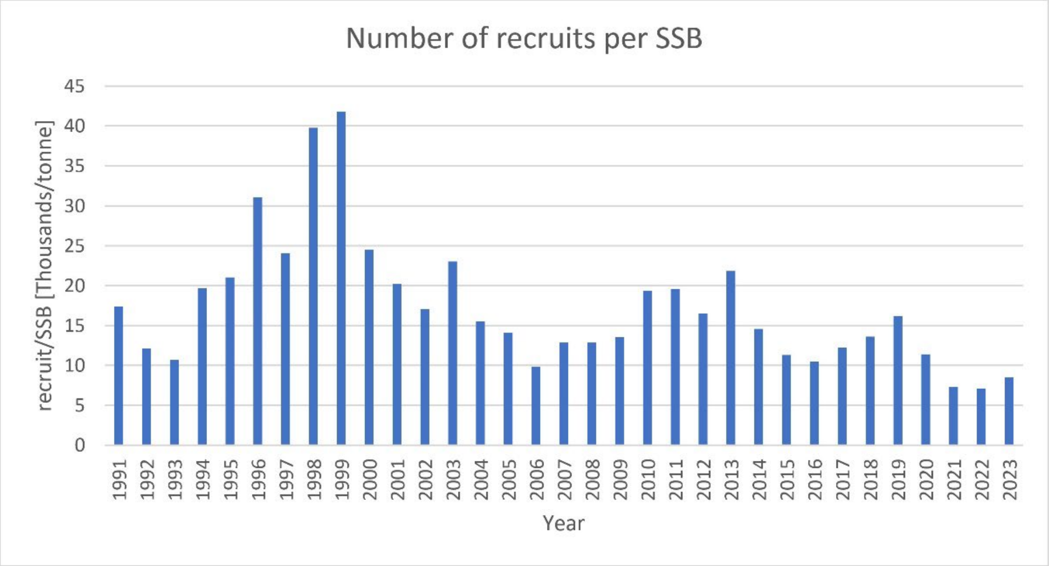


Figure 5.3.2 Recruitment success of the WBSS Herring (ICES, 2023).

The reproductive success is currently at an all-time low, as can be seen from figure 5.3.2 that shows the number of recruits per spawning stock biomass.

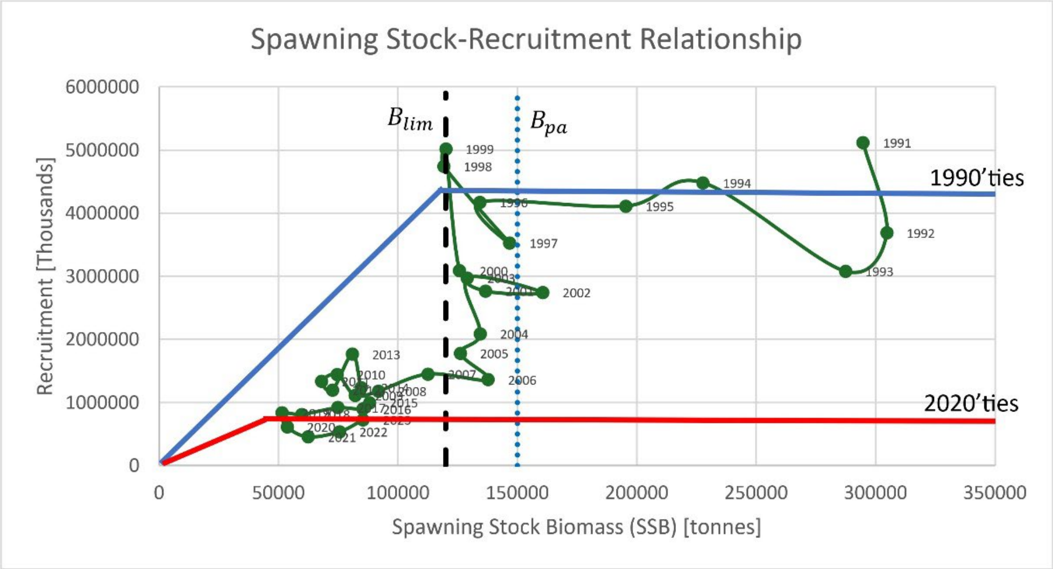


Figure 5.3.3 Spawning Stock-Recruitment relationship of the WBSS herring (ICES, 2023).

The spawning stock-recruitment relationship in figure 5.3.3, shows a major change from 1999 to 2006. Currently, the reproductive success of the WBSS herring stock is so low, that rebuilding the stock solely by reducing fishing pressure will have limited success. The WBSS herring is an integral part of the Western Baltic Ecosystem. The current state of the ecosystem is undesirable from many points of view. In a desirable state, a stable, self-organizing, dynamic equilibrium is maintained between interacting species. Until this state is reached, the herring stock must be supported by external means.

Does it matter?

In the past, the herring in Danish waters was of major economic importance. The Danish society we know today is built on herring. Many of our cities arose or grew large in the Middle Ages due to the trade in salted herring. Copenhagen is in many ways the result of the large herring fisheries in the Øresund. To the individuals who until recently had a livelihood from fishing and processing herring, the WBSS herring stock was very important. On the societal level, the WBSS herring stock is a public good, which is shared among nations bordering its habitat. It provides seafood, cultural and supporting ecosystem services as it serves as food for other valued species like marine mammals, cod, and seabirds. Further, the herring carries valuable nutrients to the Baltic food web from its saline feeding areas during its foraging migration to the North Sea (van Deurs et al., 2016).

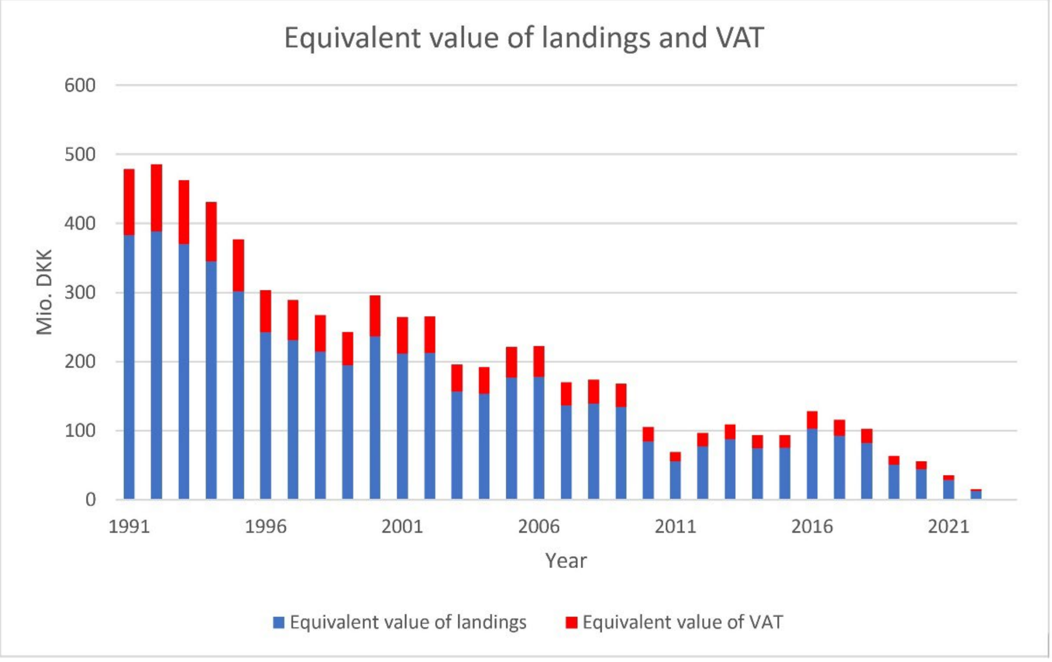


Figure 5.3.4. A rough estimate of the economic value of WBSS herring fisheries.

A rough, conservative estimate of the economic importance of the WBSS herring can be obtained by multiplying the historical catches (ICES,2023) by a nominal value of 2.0 DKK/kg. Further, it can be assumed that the societal value in terms of taxes is at least 25%, corresponding to VAT, of the revenue. The result is presented in figure 5.3.4. Rebuilding the WBBS herring stock to the level of 1990 could be of some economic importance, both to the owners of fishing quotas and to the coastal states. Rebuilding the WBSS herring stock will not bring back the traditional fishing communities and the activities of the past, but other valuable uses of the herring will be possible.

The economic value of other marine ecosystem services that do not depend on life in the sea, such as e.g., energy, transportation, coastal protection, mineral resources, and water discharge, on the other hand, is larger than the economic value of living resources. The question is therefore whether our democratic society is willing to prioritize an investment in rebuilding the WBSS herring stock.

Why are things so wrong?

Could the collapse of the WBSS herring stock have been avoided by proper fisheries management? Yes, but as can be seen from figure 5.3.1, the spawning stock has been below current safe limits since 1996. A change in the management regime occurred in 2018 when the value of B_{lim} was raised from 90,000 t to its current value of 120,000 t. Besides a previous high fishing pressure, another cause of the problem is reduced reproductive success caused by disturbances from other factors in the ecosystem than fishing. This problem could, most likely, have been avoided by proper ecological management of factors that have an impact on the early life stages of the herring. This is currently outside the responsibility of the EU Common Fisheries Policy (CFP). With the increasing human activity in the marine environment, the marine ecosystem will be subject to many new disturbances, which all must be managed by the system of single species fisheries management. If the natural mortality of a species for some reason increases, the fishing mortality must decrease accordingly, and the allowable catch reduced. A more holistic approach to marine management should thus be considered.

What should be done?

Some of the suggestions in the following, such as introducing ecosystem services management and making changes to the principles of the EU common fisheries policy might, at first, seem unrealistic and unobtainable, but given enough time, it will be possible. These suggestions can be considered as the seeds of change.

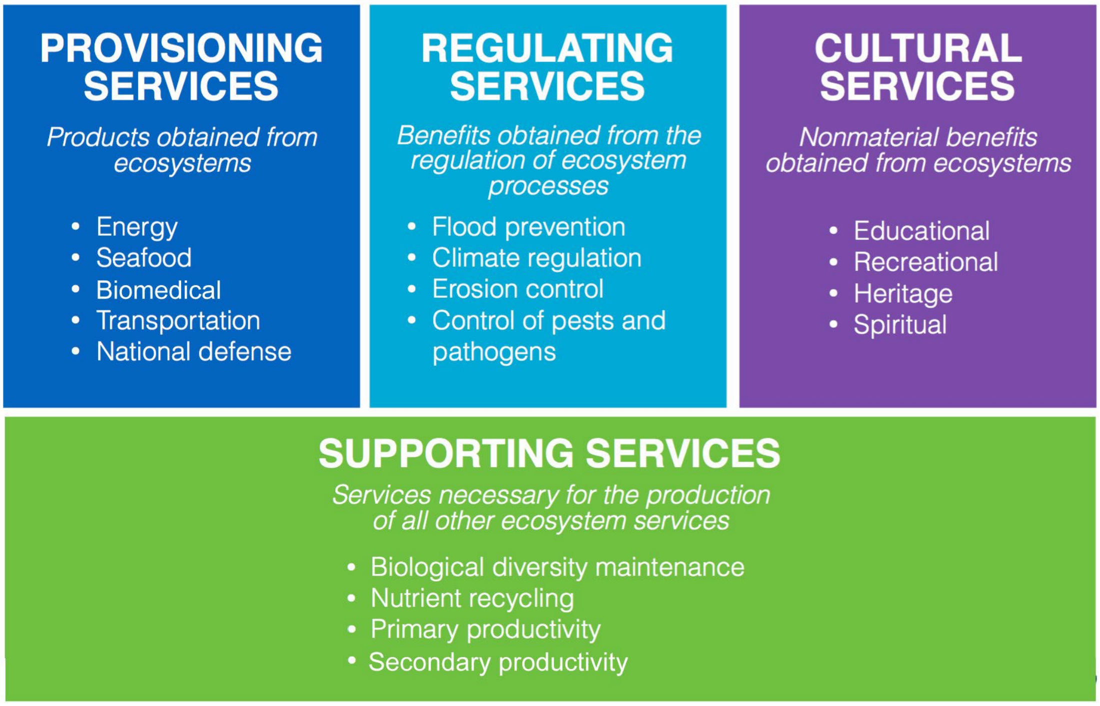


Figure 5.3.5. Examples of ecosystem services.

Ecosystem services are the benefits that people get from using the ecosystem. Examples of ecosystem services are illustrated in figure 5.3.5. There are four types of benefits: provisioning services, regulating services, cultural services, and supporting services. It is recommended that ecosystem services management should be the future framework for an integrated approach to marine management.

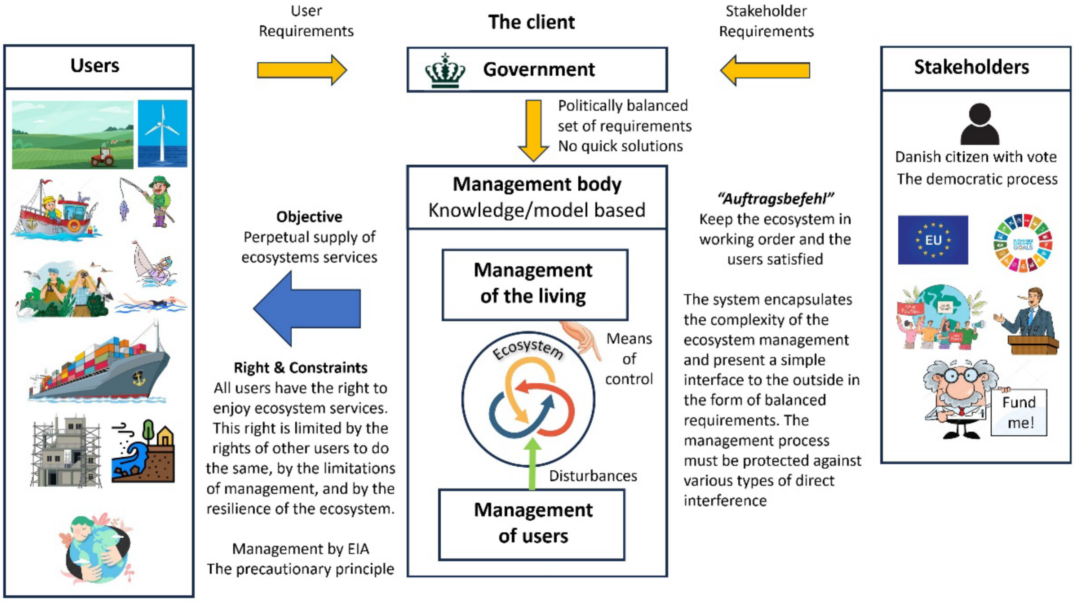


Figure 5.3.6. An example of an Ecosystem Services Management System.

An Ecosystem Services Management System is necessary for marine management in the future. The first step in the engineering design of a system (Dym et al., 2013) is to identify the client, who operates and pays for the system, the users, and other stakeholders. In figure 5.3.6, the government is identified as the client, individuals, and enterprises with a direct interest in ecosystem services are identified as users and international organizations and participants in the democratic process without direct interest in ecosystem services are identified as other stakeholders. The users can be divided into those whose activities generate taxable revenue and those who do not. The stakeholders can be divided into those who have a vote and those who influence those who have a vote, in some cases to serve their own interest.

The task of the Ecosystem Services Management body can be stated briefly as "Keep the ecosystem in working order and the users satisfied." To achieve this, the management body must be able to manage users as well as the ecosystem. Activities of the users and natural processes, such as invasion of a new species, cause ecosystem disturbances. If these disturbances are infrequent and insignificant, the resilience of the ecosystem can handle these disturbances through minor dynamic changes to the ecosystem state. But if the disturbances are significant or frequent, managerial action must be taken, either to manage the activities of the users or to manage the ecosystem, to maintain the ecosystem in a desired state. The management must be based on a solid scientific basis of up-to-date knowledge. This requires monitoring of the ecosystem and complex mathematical models of the ecosystem for decision support. The ability to manage the ecosystem is limited by cost and available means for effective control actions. An hypothetical example using biomanipulation: a means for controlling the unwanted, invasive round goby is to release turbots from hatcheries into the sea. This might change the state of the ecosystem in the local coastal areas in favor of the user group of anglers and create a supporting service in terms of niches for other species, as the disturbance of the round goby to the ecosystem will diminish. Innovation of new means of ecosystem control is needed. One such example is Single Species Life Cycle Management for rebuilding fish stocks, which will be presented later in this section. The disturbances to the ecosystem can be expected to be more significant and more frequent in the future. This will increase the cost of managing the ecosystem or, as an unfortunate alternative, control of the ecosystem will be lost, as is the case in the Western Baltic ecosystem.

The objective of ecosystem services management is to provide services for users, resolve conflicting interests among users by prioritizing their requirements and keep the ecosystem in good working order. A constraint imposed by the client is that the cost of management should be low.

The requests from users of ecosystem services and stakeholders are conflicting and often unrealistic. The corresponding requirements must therefore be balanced politically. If, e.g., it is decided to use the available secondary production to increase the production of valuable herring and thus decrease the production of the not so valuable sprat, the conflict between owners of Herring fishing rights and the owners of Sprat fishing rights, must be resolved reasonably. The government instructions to the management body should preferably be given as balanced requirements, not solutions. A requirement can be fulfilled in many ways. And there is a simple, wrong solution to any problem.

An example of strategic political prioritization is the Danish Marine Spatial Plan. Within designated geographical areas, some users and their requirements will have higher priority than requirements from other users of ecosystem services. The Danish Marine Spatial Plan is a big step forward towards conflict resolution.

In the future, geographical areas, where the activities of specific users, such as fishermen are given priority, can be added. Spawning and nursery areas for fish populations may be assigned protection status in the same way as breeding grounds for seabirds. Protected areas for fish may thus become part of the planning basis in the future. An example of conflict resolution between windmill park operators and fishermen could be that it was required that the windmill park be designed to provide ecosystem support services and allow fishing along trawling corridors within the windmill park. There can be many other solutions. Clever, innovative solutions to user conflicts are preferable to bad solutions achieved by the ruthless application of political or economic power.

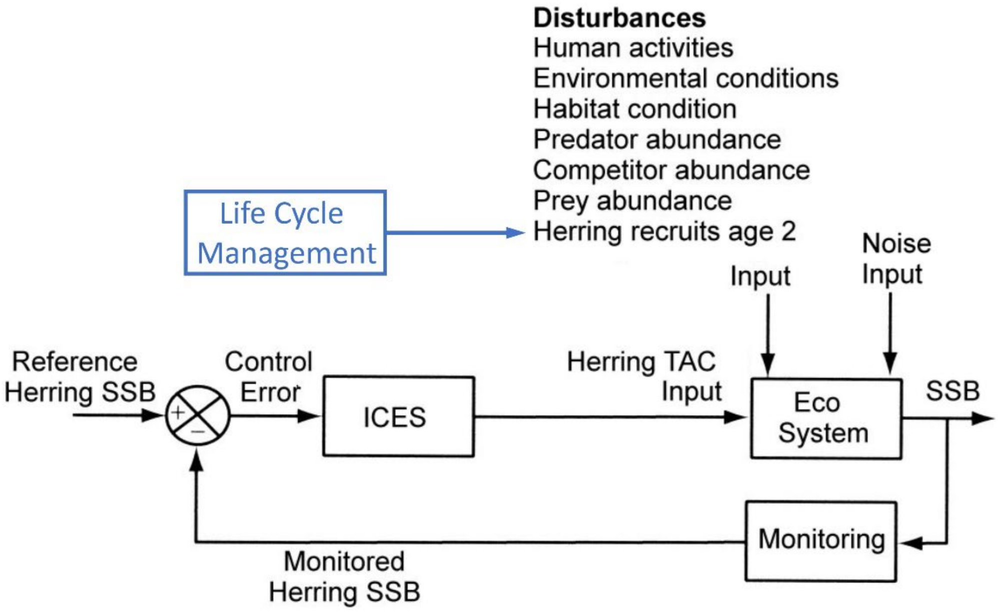


Figure 5.3.7. Illustration of the basic principles of Single Species Herring Management.

The basic principle underlying Single Species Herring Management is feedback control (Hellerstein et al., 2004) as is illustrated in figure 5.3.7. A desired reference value of the herring spawning stock biomass (SSB) is selected based on sustainable stock exploitation. Under normal circumstances this reference value is derived from the CFP requirement that the stock must be exploited at Maximum Sustainable Yield (MSY). This reference value is compared to the actual SSB in the ecosystem measured by monitoring. If the actual SSB is higher than the reference SSB the difference can be allocated by predictive management by ICES to a Total Allowable Catch (TAC) for fishery the following year. If the difference of the SSB reference value and the actual monitored SSB is negative, there is a problem, as fishery cannot add fish to the ecosystem. When the fishery is performed, it will disturb the ecosystem, but hopefully not more than it can be absorbed by its resilience. Many other disturbances are present, as illustrated in the figure. These disturbances are considered in ICES management using advanced mathematical models, where e.g., natural mortality (M) is input as estimated predation pressure plus other types of mortality from known and unknown sources. If a management regime of the early life stages of herring is introduced, it will result in a positive disturbance in the existing control system as herring recruits of age 2 enter the spawning biomass pool. In this way, a new Single Species Life Cycle Management method is easily integrated into the existing management system.

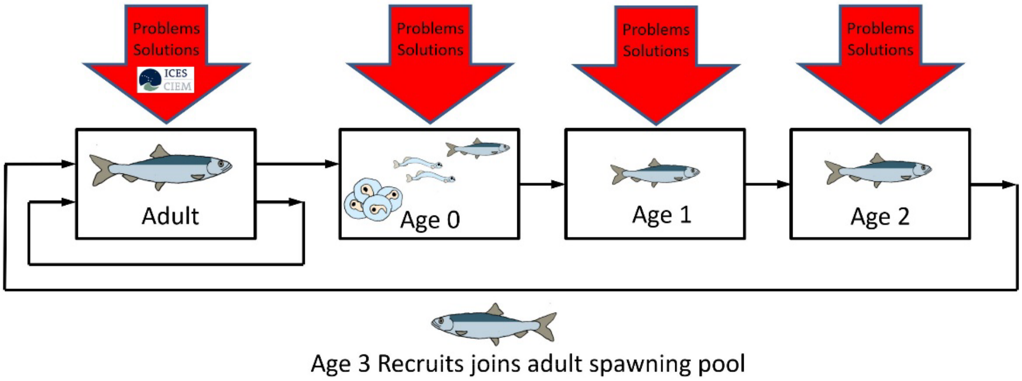


Figure 5.3.8. Optimizing the herring production by Single Species Life Cycle Management

The principle of Lifecycle Management is illustrated in figure 5.3.8. The traditional management by ICES is applied solely to the adult life stage using fishing as the means of control (e.g., focusing on reference fishing mortalities of a selected range of ages, for WBSS: F_{3-6}). Management of early life stages will require novel means of control. The yield of spawning, defined as the number of age 3 recruits entering the spawning pool divided by the SSB at the time of spawning, can be used as an objective function for maximizing herring productivity. Assuming a fixed amount of funds is available for rebuilding the herring stock, the question is at which life stage, the management will provide the highest benefit. If there are problems with excessive mortality in any of the life stages, the problems must be identified, and solutions must be found. This is the principle of Single Species Life Cycle management.

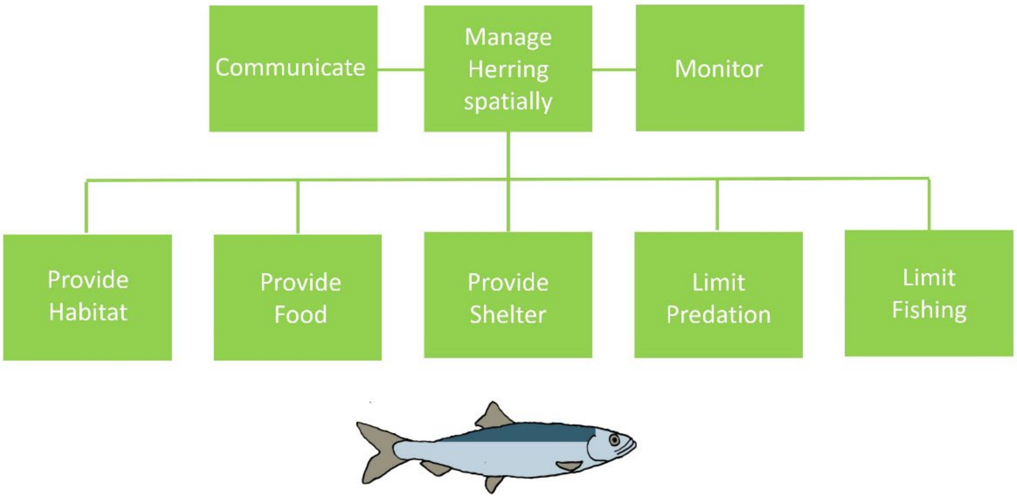


Figure 5.3.9. The principal functions of a Herring Life Cycle Management System

The principal functions of a herring management system are illustrated in figure 5.3.9. The bottom row of functions groups is the control functions. Each function can be fulfilled by different means that will assure improved survivability of the herring.

Some possible means, not necessarily practically viable, can be:

- Provide habitat: Increase spawning substrate (macro algae and eelgrass).
- Provide food: Reduce eutrophication levels to improve quality of pelagic primary and secondary production in relation to herring larvae and juvenile requirements. Reduce the number of competitors by pruning e.g. reduce stickleback biomass by selective fishing.
- Provide shelter: Fence out or collect fertilized eggs in the wild, rear ashore and release to the wild as juveniles.
- Limit predation: Scare away predators with terrifying sounds and flashing green laser lights at nighttime.
- Limit fishing: This means is available in the adult life stage, but also bycatching in the juvenile stage can occur.

The imagination is the only limit to innovation of means as the number of possible means to fulfill each of the functions is unbounded. The best means will be those that increase the herring production at the lowest cost. Monitoring and communication are other principal functions that can be optimized by proper design.

The fundamental question is, who will be motivated to invest in rebuilding the herring stock? The owners of the fishing quotas will have a strong incentive. Unfortunately, the fishing quotas are assigned to fishing areas and not to fish stocks, but if the overlap between fishing area and fish stock is sufficiently high, the incentive will be present. Also, the State has a high interest in rebuilding the fish stocks as future catches will generate taxable revenue.

To what size should the fish stocks be rebuilt? Application of the current CFP principle of MSY will have a tendency to prevent the fish stocks from becoming great again as the surplus above bare survivability will be caught. Another management principle is stable Maximum Economic Yield. If the group of quota owners (users) can agree on maintaining a stock considerably greater than what the MSY principle dictates, they will gain the advantages of lower fishing effort to get a catch and stability in the yearly catches, which is something the costumers, the fish processing industry desires. Further, the supporting services of the ecosystem will be greatly improved. Can the quota owners agree? Today, the fishing quotas are concentrated on fewer hands than in the past, in large businesses that have the competitive advantage of scale. It is not unlikely that the major players can agree on not fishing their quotas for some years, but instead investing in a larger stock. Not fishing will not generate revenue, but instead, the value of the quotas will increase.

What is the value of a rebuilt stock, and how much can be invested in the rebuilding? As an example, consider rebuilding the WBSS stock to a biomass of 300.000 ton. Harvesting just 10% per year is 30.000 tons, with 2 DKK/kg this is equivalent to a revenue of 60 Mio. DKK/year. If the cost of fishing amounts to 90% of the revenue, the profit from the operation will be 6 Mio. DKK/year. This is the equivalent of a goose that lays golden eggs. How much is such a goose worth? By assuming an interest rate of 3%, a simple calculation can provide the answer:

$$\text{Yearly income} = \text{Interest rate} * \text{Value}$$

$$\Downarrow$$

$$\text{Value} = \frac{\text{Yearly income}}{\text{Interest rate}} = \frac{\text{6 Mio. DKK}}{0.03} = \text{200 Mio. DKK}$$

The maximum the quota owners should be prepared to invest in rebuilding the stock is thus 200 Mio DKK based on the above conservative assumptions. In practice, the yearly harvest can be larger than 10%. The State will receive at least 25% VAT of the total revenue of 60 Mio. DKK which is 15 Mio. DKK and the corresponding maximum investment is 500 Mio DKK. The total value is thus 700 Mio DKK. The above calculation can be made using more realistic, less conservative assumptions. In addition, the probability of failure to rebuild the stock must be considered. But overall, investing in the rebuilding of the WBSS herring stock is a very good investment.

5.3.2 Single Species Life Cycle Management of the WBSS herring Stock

The life of a Herring can be divided into stages, where the processes governing each life stage are nearly constant to reduce the complexity of analysis in each life stage. The effect of the processes can be described by a relationship governing the transition from one life stage to the next. An example is the Stock-Recruitment relationship in figure 5.3.3. Another example is the Paulik diagram in figure 5.3.9 where the life of a herring is divided into 4 stages. The diagram makes it easy to identify the life stages that limit the growth of a population. In the example in figure 5.3.9, the population growth is limited by density-dependent processes in the juvenile life stage. For the sake of simplicity, it has here been chosen to divide the herring life into 4 stages although the processes within these 4 stages hardly can be considered constant.

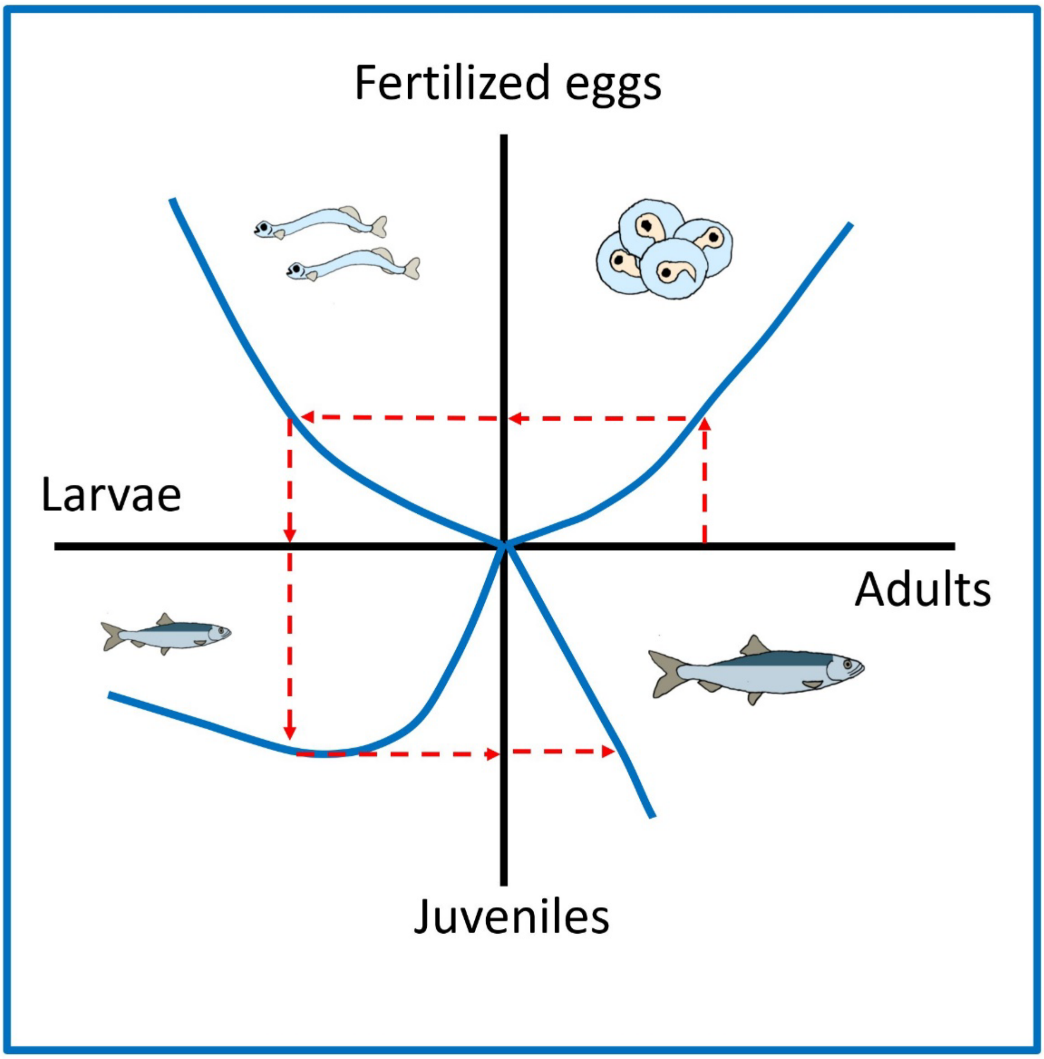


Figure 5.3.9 Paulik Diagram – Divided into 4 life stages.

In the following, each of the of the life stages is analyzed by asking the four questions: *What is Wrong? Does it matter? Why Are Things So Wrong? and What Should Be Done?* Management means doing something to correct a situation. The division into life stages and the four questions constitute the core of the Single Species Life Cycle Management Method

Life stage: Spawning

After overwintering the adults assemble at the spawning sites and commence spawning in the littorals. Two problems have been identified in this life stage: the location of the spawning grounds and the offspring mortality at the spawning grounds.

Location of Danish spawning grounds

What is Wrong? We generally do not know their locations, the extent of their utilization by spawning herring, or the quality of the spawning habitats. Maps of spawning sites from various sources of information have been produced during the years, often originals have been hand-drawn maps with information from local fishers (Fig. 5.3.10).

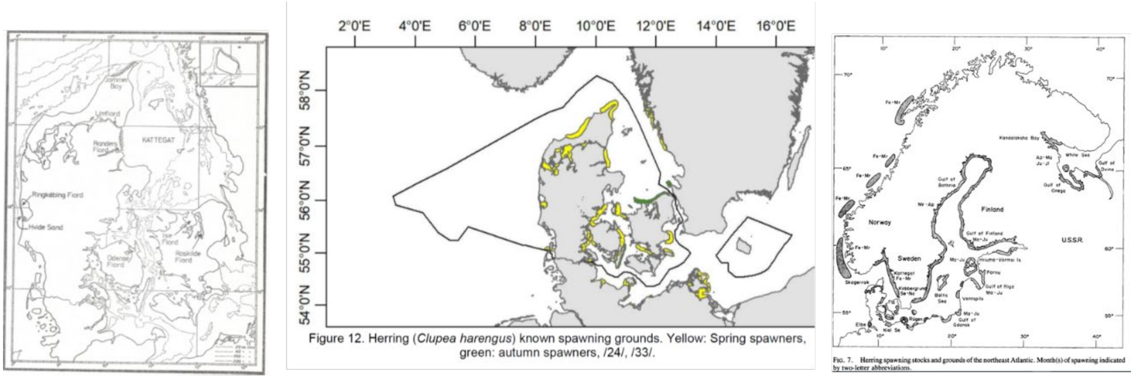


Figure 12. Herring (*Clupea harengus*) known spawning grounds. Yellow: Spring spawners, green: autumn spawners, /24/, /33/.

FIG. 7. Herring spawning stocks and grounds of the northeast Atlantic. Month(s) of spawning indicated by two-letter abbreviations.

Figure 5.3.10. Examples of published herring spawning areas from: Left: (Ackefors, 1977). Mid: (Worsøe et al., 2003) Right: (Haegele and Schweigert,1985).

Does It Matter? Yes, we need to know more precisely in order to manage. In Canada herring spawning stocks are monitored by sampling of seaweed to measure coverage of egg matts and their thickness in form of number of layers (Hay et al. 2019). In this way monitoring of deposited egg coverage and spawning female fecundity will yield a measure of spawning stock biomass, and its distribution among local spawning aggregations over the spawning season. To get a precise measure, the gonadosomatic index must be monitored in relation to the age and size structure of the stock. With possibilities of genetic differentiation between fish from different regional sub-populations a higher resolution of the population dynamics may be obtained.

Why Are Things So Wrong? Nobody has recently been interested in other subpopulations than the large Rügen component spawning in the Greifswald bay. This population on the other hand has been subject to a large number of studies through more than a century related to spawning migrations and behavior, egg deposition and survival, larval hatching, growth, and survival as well as investigations of the local fishery. Focusing on the reproduction of a single spawning aggregation as a proxy for an entire herring stock is a vulnerable strategy if population dynamics of different sub-stocks diverge over time.

What Should Be Done? Determine potential sites with maps and locate by survey. Spawning sites may be defined by parameters like benthic substrate, depth, wave exposure, macrophytes, temperature, salinity, oxygen, and potential biotic interactions. A map database has been developed by HELCOM that provides an overview of candidate spawning location in the Baltic area (Figure 5.3.11).

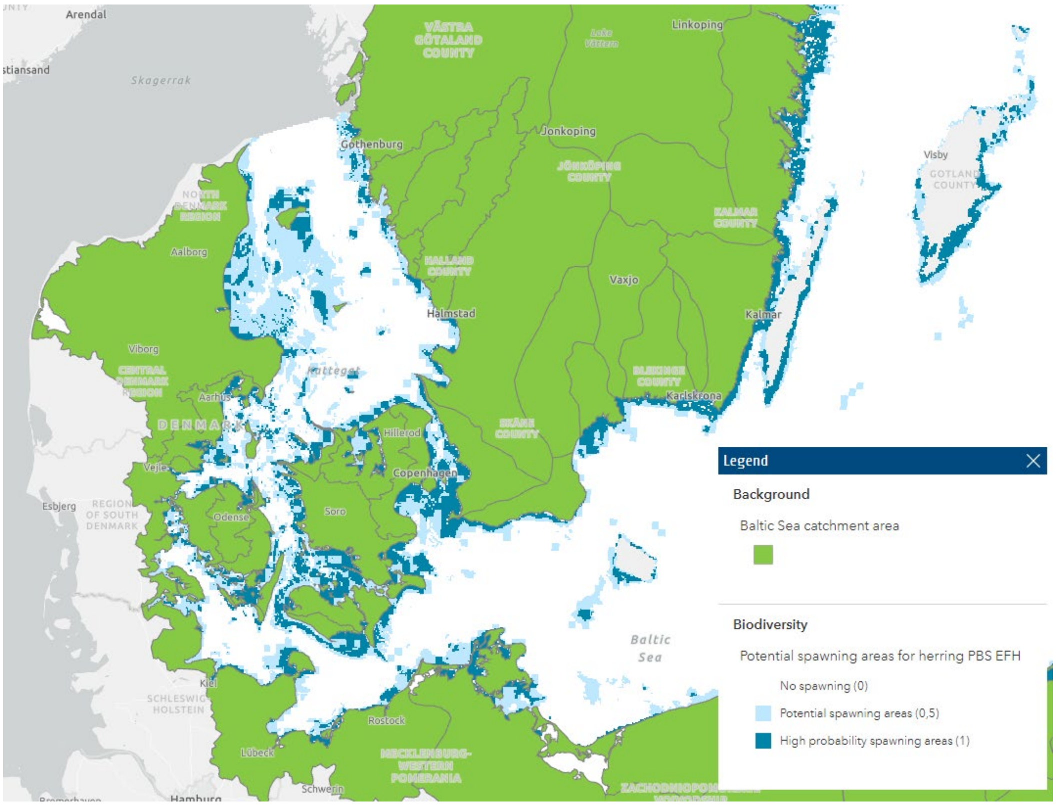


Figure 5.3.11. HELCOM Map and data service. Land: Baltic catchment areas, Sea potential spawning areas for herring.

At active spawning locations the three main life stages can be surveyed:

Acoustic surveys of adult spawning herring. Both estimates of spawning biomass at the location as well as indications of spawning behavior may be achieved. Spawning schools should be sampled by fishing to collect biological information such as size, age, maturity and genetics. Restrictions are imposed by vessel size in relation to depth. Deployment of sailing or flying drones may be an option when research vessels are not suitable.

Surveys of deposited eggs. Qualitative underwater observations may be supplemented by stratified random sampling of substrates with adhering egg matts.

Larval surveys may be carried out in the vicinity of spawning locations. Abundance of newly hatched larvae is a proxy of the spawning biomass until nonlinear physical distribution and mortality makes this index uncertain.
The importance of each site in terms of spawning contribution should be assessed. For acoustic surveys to coincide with active spawning a large effort is needed in time and space, whereas egg deposition may be sampled using a statistical design at candidate stations at intervals over the season to cover the entire potential spawning. Larval sampling includes a number of assumptions, where hydrographical and biological modelling may help back-calculating spawning sites and intensity.

In this project spawning site surveys have been carried out using both sampling of spawning herring and deposited eggs. (see section 2 of this report).

Mortality at Danish spawning grounds

What is Wrong? We assume two working hypotheses: Lack of adults homing to the spawning site and high egg mortality at the site. Migrating herring schools homing for reproduction may not find a suitable spawning ground, due to physical alterations or lack of cues leading the migration in the right direction. Egg mortality at spawning sites may be caused by physical/chemical pressures. Temperatures outside the biological limits for herring reproduction may cause death or retardation of embryo development (see this report section 3). Oxygen limitations in the egg matts is an important cause of embryonic mortality, this may be caused by suffocation by filamentous algae (Nordheim et al. 2020), or where superimposition of several layers of eggs lead to increased mortality of all layers with the highest effect on the deepest layer near the substrate surface (Finke et al. 2022). Mechanical damage by storm induced wave actions also have detrimental effects on survival. Likewise biological interactions from predators like crabs, sticklebacks, gobies, or attacks from parasites, fungus, bacteria or virus impose increased mortality.

Does It Matter? Yes, it is important for recruitment. Assuming that a local spawning unit utilizes a chosen spawning ground, then density independent egg mortality will have an increasingly large effect when population size decreases below levels where very strong compensatory mechanisms are in place. An example could be the transition from relatively low to constant larval production per capita spawner, when dense spawning aggregations that produce multiple superimposed egg layers with high mortality are substituted by sparce populations that produce single egg layers where suffocation does not affect survival.

Why Are Things So Wrong? Nobody has been interested in the detailed mechanisms so far, but a recent large effort by the project-collaborating Thünen Institute investigating conditions spawning in the Greifswald bay has paved the way for more mechanistic studies. Also, the present project demonstrates methodological development for experimental studies of mechanisms influencing offspring survival (see section 3.2). The knowledge of genetic and ecological diversity at relatively low spatial scale is an emerging insight that will have huge impact on how we view state of a stock complex like the western Baltic spring spawning herring. The fitness of local spawning components is probably a combination of genetic adaptation and learned behavior. Further, beyond genetic variation ecological grouping driven by learned behavior may also be identified using natural biomarkers like fingerprints of otolith microchemistry.

What Should Be Done? The causes of mortality should be determined and means for protection should be devised. It should be investigated if density dependent mortality is acting on local spawning aggregations by sampling of egg layer thickness and egg matt coverage within suitable habitats in the spawning area. If coverage is low introducing means to extend available spawning substrate may not be a solution. If egg matt density is low other sources of mortality should be investigated.

Life stage: Larvae

The main challenge in the larvae life stage is growth and survival:

What is Wrong? We assume (working hypothesis) mismatch, where lack of suitable food (synchronization) leads to starvation and/or impeded growth, and thus increased vulnerability to predation for a longer period. For herring, cohort specific competition is often assumed to play a major role in density dependent population regulation. The early Multiplicative Larval Abundance Index from the North Sea (MLAI) is therefore only indicative of the spawning stock size. However, when initial mortality and increasing dispersal stabilize the abundance of the larval population, an index related to recruitment may be achieved, where variability in the production of larvae largely accounts for the major fluctuations in stock abundance of NSAS herring (Nash et al. 2009). However, the relationship between dispersal and retention may play a role for successful growth and survival through the larval period, where retention appears important for WBSS (Bauer et al. 2013).

Does It Matter? Yes, late herring larvae are important for recruitment.

Why Are Things So Wrong? With reduced spawning population size and a stunted age distribution a narrow peak of larval abundance is more likely to mismatch with a peak in suitable zooplankton production amplified by higher winter temperatures.

What Should Be Done? Determine causes of mortality and reduced growth. Devise means to protect larval survival and manipulate ecosystem mechanisms that influence zooplankton composition to species with production peaks matching larval peaks.

Life stage: Juvenile
Two potential problems have been identified in this life stage: the location of the nursery areas and the mortality in these areas:

Location of Danish nursery areas
What is Wrong? We do not know their locations or their present suitability. After larval metamorphosis herring juveniles migrate towards coastal shallow water areas for their initial growth.

Does It Matter? Yes, we need to know in order to monitor growth and survival and judge about potential management.

Why Are Things So Wrong? Nobody has been interested in the extra effort so far. Juvenile herring occupy coastal areas that are not easily surveyed.

What Should Be Done? Determine potential sites with maps and locate by survey. At the very smallest stages juveniles may be sampled by beach seines during the summer period, however at a certain point they disappear from the beach zone into slightly deeper waters where most research vessels are unable to catch them or detect them by acoustic methods. Thus, the acoustic estimates of 0-group herring in the summer (HERAS) and the autumn (GERAS) are noisy and unreliably low as population indices. Other sources of information could be explored, shrimp trap nets apparently are able to catch young of the year herring in the near coastal zone. The importance of each site in terms of nursery contribution should be assessed.

In the present project a collaboration with the Thünen Institute on beach seine sampling of juveniles showed that timing is essential for a successful survey.

Mortality in Danish nursery areas

What is Wrong? We assume (working hypothesis) high mortality. Rapid growth through a vulnerable phase with a wide predator field is crucial for survival until recruitment into larger schooling herring. Access to high quality pelagic zooplankton food items like copepods is important for herring from the early juvenile to the adult stage. Competition with juveniles from demersal and benthic fish species initially plays a role. Whereas both juveniles and adults from other pelagic species like sprat and sandeels compete for a longer period. Also, jellyfish has been identified as a major source of competition with herring (see section 1.2 on the Limfjord case study).

Does It Matter? Yes, the juvenile stage is important for recruitment adding proportionally into spawning biomass.

Why Are Things So Wrong? So far nobody has been able to explain the mechanism behind the general decline of the coastal fish communities dominated by juvenile stages.

What Should Be Done? Determine causes of mortality. Devise means to protect.

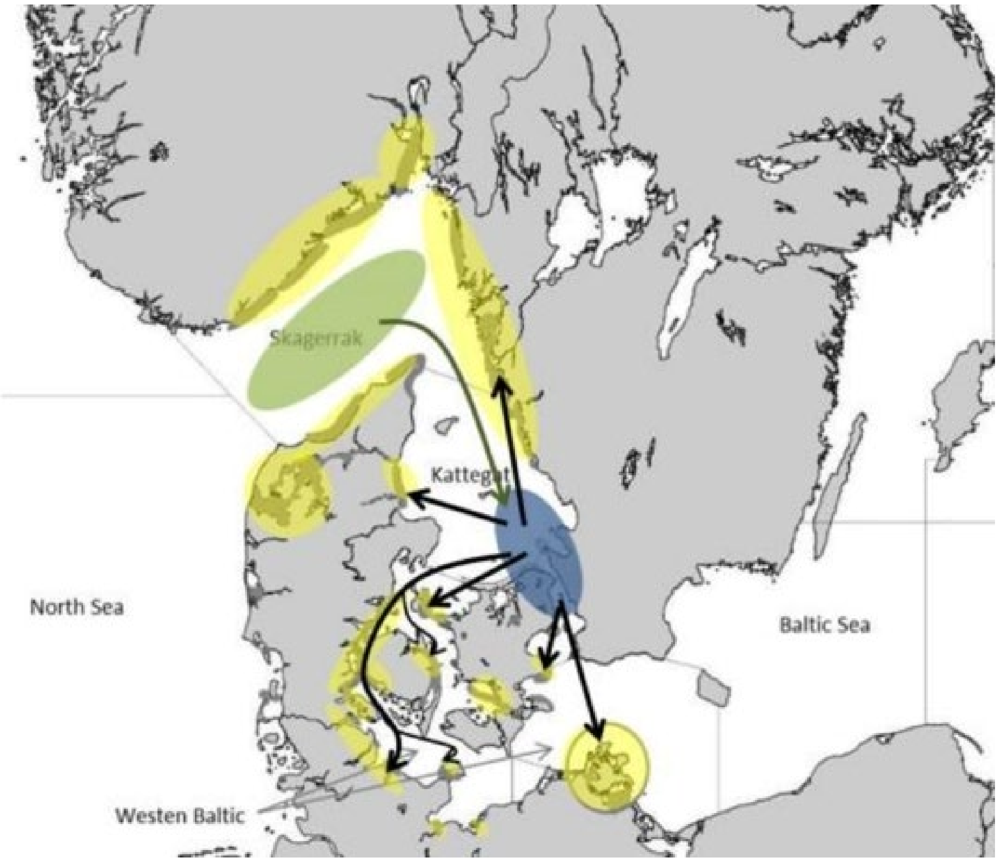


Figure 5.3.12. Assumed adult migration

Life stage: Adult
After spawning, the adults will migrate to the foraging areas in the North Sea and adjacent areas, and in autumn migrate to the overwintering sites such as the historically important Øresund area, as illustrated in figure 5.3.12. Two potential problems have been identified in the adult life stage:

Mortality in Foraging areas
What is Wrong? We assume (working hypothesis) relative high fishing mortality in the North Sea outside the management areas for WBSS. Due to limited information about predator fields along the migration routes, natural mortality is not estimated for WBSS by the multispecies model applied for the North Sea.

Does It Matter? Yes, is important for stock rebuilding.

Why Are Things So Wrong? Bycatch when mixing with other stocks is difficult to monitor and control.

What Should Be Done? Close all fishery or employ real time monitoring and regional fishery closure.

Location of Danish overwintering areas
What is Wrong? We do not know the location or the extent of the overwintering sites, except for the, at least historically important, Øresund.

Does It Matter? Yes, it is important for biomass estimation

Why Are Things So Wrong? This has not previously been of interest.

What Should Be Done? Locate overwintering sites using harbor porpoise winter habitats as a proxy and verify using acoustic surveys.

Mortality in overwintering areas
What is Wrong? We assume (working hypothesis) High predation mortality?

Does It Matter? Yes, is important for rebuilding of SSB.

Why Are Things So Wrong? We do not know the overwintering sites and the impact of predation.

What Should Be Done? Locate overwintering sites for further assessment of predation impact.

5.3.3 Life cycle effects on population dynamics

All four life stages are potentially critical and should be viewed in their interactive effects on overall population dynamics.

The Allee effect is a phenomenon in population ecology where the fitness of individuals in a population increases with population density up to a certain point. It suggests that at low population densities, individuals may struggle due to reduced opportunities for mating or cooperation, and increased predation, leading to decreased reproductive success and, consequently, a decline in population size.

For herring a number of studies have addressed compensation versus depensation in their population dynamics (see section 5.1).

In studies investigating Allee effects in marine fish populations, Keith and Hutchings (2012) e.g. investigated the population dynamics of different species at low abundance, revealing variability among exploited fish stocks. They found that while some species exhibit strong compensatory dynamics, others like herring show weaker compensation or evidence of Allee effects, impacting their recovery rates (Keith & Hutchings, 2012). Saha et al. (2013) developed a deterministic model focusing on herring populations, revealing significant evidence supporting a strong Allee effect. Their analysis highlighted the vulnerability of these populations to extinction due to external perturbations or uncontrolled harvesting, particularly when the population size falls below the Allee threshold (Saha et al., 2013). Expanding on this work, Sau et al. (2020) extended the stochastic Allee model for herring populations, incorporating the effects of harvesting. Their findings stressed the necessity of accurately modeling harvesting practices and proposed a threshold for handling times to minimize the risk of extinction during harvesting (Sau et al., 2020). Addressing the challenge of detecting Allee effects with traditional models, Sugeno and Munch (2013) introduced a Bayesian method, aiming to overcome limitations in identifying Allee effects. Analyzing herring datasets using this approach, they suggested that Allee effects might not be as rare in marine fishes as previously believed (Sugeno & Munch, 2013).

In a study contesting the notion of rare Allee effects in marine fishes, Perälä and Kuparinen (2017) examined Atlantic herring populations using Bayesian statistics. They highlighted methodological limitations in previous studies and demonstrated how evidence for Allee effects can vary based on observations made at low population abundances (Perälä & Kuparinen, 2017). The study indicated strong Allee effects for North Sea Autumn Spawning herring, Bothnian Sea herring and Gulf of Riga herring but also a potential for strong dispensary mechanisms acting on Western Baltic Spring Spawning herring, however estimated with higher uncertainty (Fig. 5.3.13). The studied time series encompassed the year range between 1991-2014 where the SSB decline during the recent decade was obviously not available. WE have added the most recent data points from 2015-2022 which does not appear to disrupt the impression of a potential Allee effect.

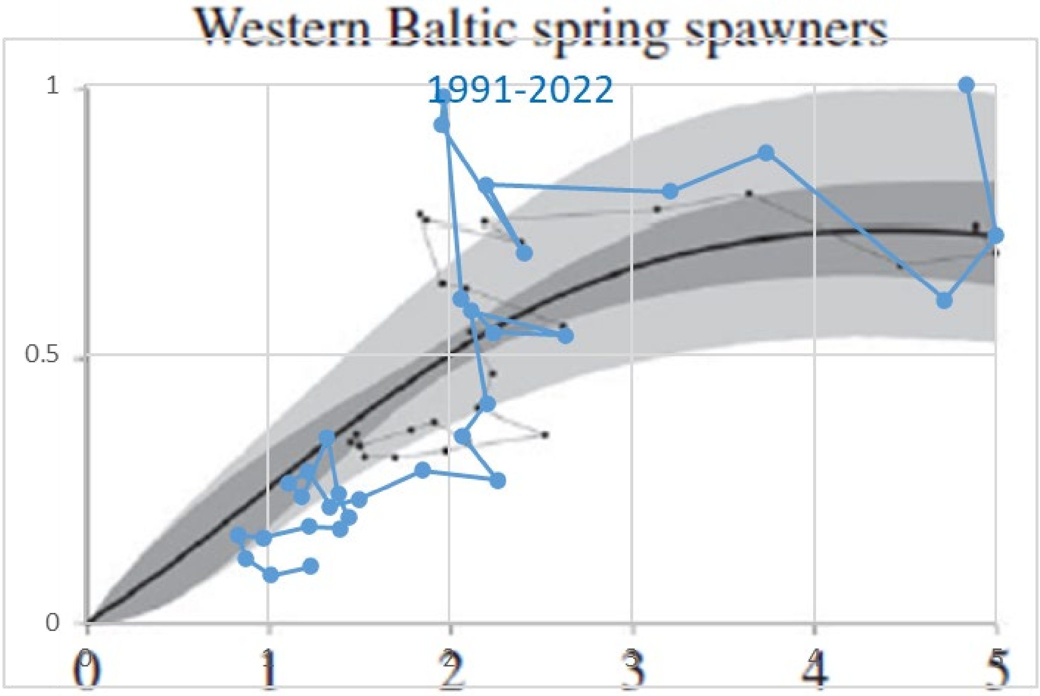


Figure 5.3.13. Illustration of Allee effects.

The statistical approach does not help the understanding of the underlying mechanisms. The strong correlation with the timeline could indicate an environmentally driven development where recruitment has been decoupled from the spawning biomass.

Thus, there appears to be shift in the views of population control from herring being seen as a species where depensation does not occur even at very low relative population sizes (Myers et al. 1995, Keith and Hutchings, 2012) to analyses with more data and model analysis power that indicate that even earlier examples of typical compensation regulated populations like NSAS may be viewed as having depensatory patterns (Perälä and Kuparinen, 2017).

Examples of mechanisms leading to Allee effects or depensation of recruitment at low population sizes in marine fish populations:
Limited Genetic Diversity: Low population sizes can lead to inbreeding and reduced genetic diversity, affecting the fitness and adaptability of the species.

Decreased Effective Fertilization: Many fish species rely on external fertilization. Low population densities reduce the likelihood of successful fertilization due to fewer encounters between eggs and sperm.

Interrupted Information Transfer: Some fish rely on social learning for survival, such as migration routes or predator avoidance. Low population sizes can disrupt the transmission of this crucial information, and hypothetically lead to “confusion” in relation to both spawning time and location as indicated in section 4.

Reduced Social Cues: Behavioral cues critical for successful reproduction might be missed at low population densities, leading to lower reproductive rates.
Reduced Cooperative Behaviors: Cooperation for feeding, defense, or navigation might become less effective or cease entirely at low population densities, impacting survival rates.

It is presently not possible to judge whether regime shifts of environmental forcing, Allee effects or both are responsible for the lack of recovery of the WBSS herring stock. Both effects appear as empirically emerging patterns but provide no explanation about the underlying mechanisms.

Recognizing the underlying mechanisms is crucial for managing and conserving marine fish populations. Conservation efforts often focus on maintaining or restoring population sizes to levels where Allee effects are minimized, ensuring the sustainability of these populations. However, disentangling interactions with manageable or non-manageable environmental forcing should be an important focus.

5.3.4 Conclusions and Recommendations

The western spring spawning herring stock has collapsed and is unlikely to recover in the current state of the ecosystem.

It is recommended to initiate a stock recovery program based on the principles of Single Species Life Cycle Management. Here a mapping of all compensatory and depensatory mechanisms in action is crucial. Single Species Life Cycle Management is easily integrated into existing fisheries management practices, and thus fully compatible with the management principles of the CFP.

The working hypothesis is that the recruitment of the past was the sum of contributions from many spawning sites, distributed along the Danish coastline. As the population decreased, the spawners at the smaller spawning sites became extinct due to Allee effects. The spawning sites remaining today may still have a population of spawners sufficient for sustainable reproduction. The population must be rebuilt based on the remaining spawning sites. As the population grows, it is expected that former spawning grounds will be repopulated. To monitor the repopulation process, DNA and otolith analysis are enabling technologies.

All four life stages are important. The critical importance of the life stages should be determined in an experimental pilot survey to focus the stock rebuilding efforts on areas with the greatest effect. It should be investigated if the indication of a relative decline of the WBSS_IDW contribution to the total population complex is real and which local components still exist and exhibit the best rebuilding potential.

The stock recovery speed depends on the achievable recruitment rate and the presence of possible density-dependent population ceilings.

A stock recovery program is an attractive investment opportunity both to quota owners and the State.

The payback time for the investment in rebuilding the stock is an important economic indicator. An estimate of the break-even point in time should be made and continuously revised during the stock rebuilding process. The future yearly operating cost for stock management should be related to the future gain from the rebuilt stock by cost benefit analysis.

It is recommended that the Ecosystem Services Management approach is promoted as the future framework for marine management. The CFP fisheries management is already in accordance with the principles of Ecosystem Services Management, so nothing needs to be changed. The CPF management can be inspiration for other types of marine management not complying with Ecosystem Services Management principles. The Danish Marine Spatial Plan is seen as an important and integrated part of such management. Geographical areas where fishing activities are given priority should be added to the plan. Spawning and nursery grounds for fish populations are vulnerable and deserve protection. Protected areas for fish and fisheries will become part of marine spatial planning in the future.

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