



Climate change or mismanagement?

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Abstract Climate change and deoxygenation are affecting fish stocks on a global scale, but disentangling the impacts of these stressors from the effects of overfishing is a challenge. This study was conducted to distinguish between climate change and mismanagement as possible causes for the drastic decline in spawning stock size and reproductive success in cod (*Gadus morhua*) and herring (*Clupea harengus*) in the Western Baltic Sea, when compared with the good or satisfactory status and reproductive success of the other commercial species in the area. Available data on water temperature, wind speed, and plankton bloom during the spawning season did not reveal conclusive correlations between years with good and bad reproductive success of cod or herring. Notably, the other commercial species in the area have very similar life history traits suggesting similar resilience against stress caused by climate change or fishing. The study concludes that severe, sustained overfishing plus inappropriate size selectivity of the main fishing gears have caused the decline in spawning stock biomass of cod and herring to levels that are known to

have a high probability of impaired reproductive success. It is pointed out that allowed catches were regulated by management and adhered to by the fishers, meaning that unregulated fishing did not occur. Thus, mismanagement (quotas that were too high and gears that selected too small sizes) and not climate change appears to be the primary cause of the bad status of cod and herring in the Western Baltic Sea.

Keywords Climate change · Mismanagement · Gear selectivity · Overfishing · Western Baltic Sea · Cod · Herring

Introduction

Climate change and deoxygenation are affecting the oceans in ways that transform the environment that commercial fish depend on for survival, growth, and reproduction (Brander 2010; Cheung et al. 2013; Poloczanska et al. 2016). Climate change has been suggested as a potential cause for declines and collapses of commercial fisheries (Möllmann et al. 2003; Rijnsdorp et al. 2009; Akimova et al. 2016), but such declines and collapses have also occurred before climate change had a major impact on the marine environment (Jackson et al. 2001; Hobday et al. 2011), basically as the result of fishing pressure exceeding maximum sustainable levels. Rather than being the primary cause of fish stock declines, climate change has been suggested as a factor aggravating the

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effects of overfishing (Pörtner and Peck 2010; Bodini et al. 2018; Free et al. 2019; Möllmann et al. 2021). Some studies (Hare et al. 2016; Spencer et al., 2019) argue that climate vulnerability assessments need to be conducted as part of a future fisheries management framework. However, disentangling impacts of climate change from impacts of inappropriate management is not straightforward as, for example, recruitment failure may be caused by unsuitable environmental conditions as well as too small spawning stock size.

The purpose of this study is to distinguish between climate change and mismanagement (e.g., too high catches or gears with inappropriate selectivity) as possible causes for recent collapses of two previously large and productive stocks in the Western Baltic Sea. Such distinction is important because if climate change is the main cause of decline, then there may be little that managers can do other than adjusting fishing to reduced productivity. If, however, mismanagement is the main cause of the decline, then ending mismanagement may lead to restoration of good stock status and profitable fishing despite impacts of climate change (Gaines et al. 2018).

The Baltic Sea has already experienced substantial changes in its hydrography as a result of recent warming, with an estimated increase in sea-surface temperature (SST) of up to 1 °C per decade for the period 1990–2008. Projections of future climate change suggest that this trend will continue in the future, with an estimated 2 °C increase in summer SST in the southern parts of the Baltic Sea. Such warming and the continuing influx of nutrients from agriculture are expected to lead to increasing areas of hypoxia and anoxia (Hansson et al. 2019; BACC (Baltic Earth Assessment of Climate Change) II Author Team, 2015). There can be no doubt that these changes will affect ecosystems and species by triggering complex nonlinear dynamics (Reusch et al. 2018; Ito et al. 2019), but the resilience of commercial species will, in addition, be affected by their history of exploitation and their current stock status (Free et al. 2019).

In order to disentangle the impacts of climate change and fisheries, this study examines the status of commercial species in the Western Baltic Sea. It compares their life history traits and related intrinsic resilience, their response to recent changes in environmental conditions, their relative stock sizes, and their history of exploitation. Finally, the study explores

options for rebuilding and sustainable future use of cod (*Gadus morhua*) and herring (*Clupea harengus*).

A novelty of the study lies in its use of data such as length, weight, gonad weight, and stomach content collected by commercial fishers in Kiel Bight in the Western Baltic Sea (Froese et al. 2020).

Materials and methods

Water temperature, wind speed, and chlorophyll a concentration

The GEOMAR Helmholtz Centre for Ocean Research in Kiel, Germany, situated near the southern tip of Kiel Bight, maintains records taken in 8-min intervals of water temperature, wind speed, and a number of other daily weather measurements. These measurements are taken on the roof of the institute and at the Kiel lighthouse, which is situated near the center of Kiel Bight at 54° 29.9' N 10° 16.4' E. Water temperature is determined at 5-m depth at the pier in front of the institute and at 1-m depth at the lighthouse. For the purpose of this study, daily median measurements at the institute and the lighthouse were used.

A time series of chlorophyll a concentration (µg/l) was extracted from the Oceanographic Database of the International Council for the Exploration of the Sea (ICES) (<https://ocean.ices.dk/HydChem/HydChem.aspx>). It includes all stations in the Western Baltic Sea delimited by longitude = [9°, 11°] E and latitude = [54°, 55°] N, from sea surface to a maximum depth of 44 m.

Selected years

The years 1997, 2003, 2016, 2019, and 2020 were selected for closer examination with regard to environmental conditions. These years showed better or worse reproductive success than the average of years when spawning stock biomass (SSB) was within safe biological limits, referring to a stock size below which recruitment is likely to be impaired (CFP 2013). To avoid confusion with number of recruits being reported for ages zero or one, reproductive success was reported for the year in which the spawning took place (WGBFAS 2021; HAWG 2021; Fig. 4). In particular, the selected years represent good reproductive success for cod in 1997 and 2003, for herring

in 1997 and 2003, and for plaice (*Pleuronectes platessa*) in 2016 and 2019. Below average reproductive success was reported for cod in 2019 and 2020; for herring in 2016, 2019, and 2020; and for plaice in 2003.

Occurrence of Lasker-events

Lasker (1975, 1978) proposed that a period of calm winds is essential for forming food-rich plankton patches that are crucial for the survival of first-feeding fish larvae. Pauly (1989) suggested to name such periods “Lasker-events,” and for the purpose of this study we used continuous 4-day periods with median wind speeds not exceeding 6 m/s as representative of such events. For the selected years, the occurrence of Lasker-events was counted from March to May. The period was chosen because the planktonic larvae of all considered species require high densities of zooplankton as food during these months, and too strong winds are considered detrimental for optimal feeding conditions (Lasker 1975, 1978; Cushing and Horwood 1994).

Examined species and life history traits

The species considered in this study represent all commercially relevant species that reproduce in the Western Baltic Sea (Petereit et al. 2014) (Table 1). Other commercial species are lemon sole (*Microstomus kitt*) and sprat (*Sprattus sprattus*), but they are of only minor commercial importance and do not reproduce in the area. The bulk of sprat distribution occurs in the northeastern Baltic Sea such as the Gulf of Finland (ICES 2020) while lemon sole can be found

mainly in the Kattegat (ICES 2021a). Data on life history traits (maximum length, length at which 50% of the females have reached maturity) were derived from records in DATRAS (2021), which were restricted to the Western Baltic Sea and years after 2000, and from commercial catches in Kiel Bight (Froese et al. 2020; this study). Fecundity ranges were derived from references compiled in FishBase (Froese and Pauly 2021). Information on fishing pressure, stock size, age composition in the commercial catch, and recruitment was derived from the stock assessments carried out by working groups of the International Council for the Exploration of the Seas (ICES) (ICES 2021b; HAWG 2021; WGBFAS 2021). Timing of spawning was derived from the gonadosomatic index of females caught by commercial fishers in Kiel Bight as part of this study. The gonadosomatic index was calculated as the weight of the ovaries divided by live body weight.

Life history reference points

The largest length (L_{max}) found for the Western Baltic Sea either in DATRAS (2021) or in the data from commercial fishers used in this study was taken as reference point for maximum size and as a proxy for the asymptotic length parameter (L_{inf}) in formal growth analyses (Froese and Binohlan 2000). Growth in body weight has an inflection point at 30% of asymptotic body weight (W_{inf}), which corresponds to $2/3 L_{inf}$ if the exponent of the length–weight relationship is close to 3. L_{opt} is the length at which cohort biomass reaches a maximum (Holt 1958), and it corresponds to $2/3 L_{inf}$ if the ratio between the average adult rate of natural mortality (M) and the somatic growth rate

weight, t_{max} is the maximum reported age, and t_m is the age at which more than 50% of the females reach first maturity

Table 1 Overview of life history traits of the commercial fishes in the Western Baltic Sea, where L_{max} is the maximum observed length, W_{max} is the corresponding maximum body

Species	Common name	L_{max} cm	W_{max} kg	t_{max} y	t_m y	Fecundity Millions	Eggs	Larvae	Main food
<i>Gadus morhua</i>	Cod	106	10.6	14	2–3	0.5–5	Pelagic	Pelagic	Benthic invertebrates; fish
<i>Scophthalmus maximus</i>	Turbot	58	4.2	22	3–4	5–15	Pelagic	Pelagic	Benthic invertebrates; fish
<i>Scophthalmus rhombus</i>	Brill	60	3.2	11	3–4	0.3–1.5	Pelagic	Pelagic	Benthic invertebrates; fish
<i>Pleuronectes platessa</i>	Plaice	57	1.5	25	2–4	0.05–0.5	Pelagic	Pelagic	Benthic invertebrates
<i>Platichthys flesus</i>	Flounder	52	1.4	26	2–4	0.4–2	Pelagic	Pelagic	Benthic invertebrates
<i>Limanda limanda</i>	Dab	47	1.1	12	2–3	0.05–0.15	Pelagic	Pelagic	Benthic invertebrates
<i>Clupea harengus</i>	Herring	36	0.26	17	3	0.013–0.065	Demersal	Pelagic	Zooplankton; benthic invertebrates

(K) is close to $M/K = 1.5$, as has been found in many commercial species (Froese et al. 2016). For the purpose of this study, it was assumed that $2/3 L_{\max}$ is a reasonable proxy for L_{opt} . Taking the allowed catch when cohort biomass is highest has the least negative impact on the fished stock and results in a mean age and size similar to the natural one without fishing. Since it is not possible to catch fish only at L_{opt} , a similar size and age structure can also be obtained if fishing with sustainable rates starts at a smaller length $L_{\text{c-opt}} = 0.56 L_{\text{inf}}$ and includes all subsequent length and age classes (Froese et al. 2016).

Data collected by fishers

GEOMAR has a collaboration with several commercial fishers operating in the southern Kiel Bight, south of a line from Damp to Fehmarn. The fishers operated with gill nets of 55- to 110-mm mesh size (knot to knot) which were set to up to 24 h in different locations, from shallow (e.g., 4 m) to deeper areas (about 15 m). In addition, in 2021, one fisher with a 14-m boat operated a small trawl with 120-mm stretched mesh size and a typical net opening of 10–11-m width and 2-m height. The collected data were locality, depth, gear used, and date and time of deployment, and for every species, length, wet weight, stomach weight, indication of main stomach

content, gonad weight, and indication of spawning activity based on visual examination of gonads (Froese et al. 2020).

Results

Environmental data

Median daily water temperatures in January to May in Kiel Bight for the selected years show a remarkable dichotomy of interannual variability, with very different trajectories and differences in temperature of up to 5 °C in January to March, and very similar trajectories with only up to 2 °C interannual differences in April and May (Fig. 1). The hottest year on record was 2020, whereas 2021 was one of the coolest years after mid of February.

The high monthly and annual variability in temperature in January to March makes it difficult to use temperature as a reliable environmental trigger for gonad development and spawning. For example, if an increase from lower temperatures to 4 °C was such a trigger, then that occurred in early February in 2016, in early March in 1997, in late March in 2003, 2019, and 2021, and never in 2020. Reproductive success of cod, herring, and plaice in the selected years does not consistently favor or disfavor any one year.

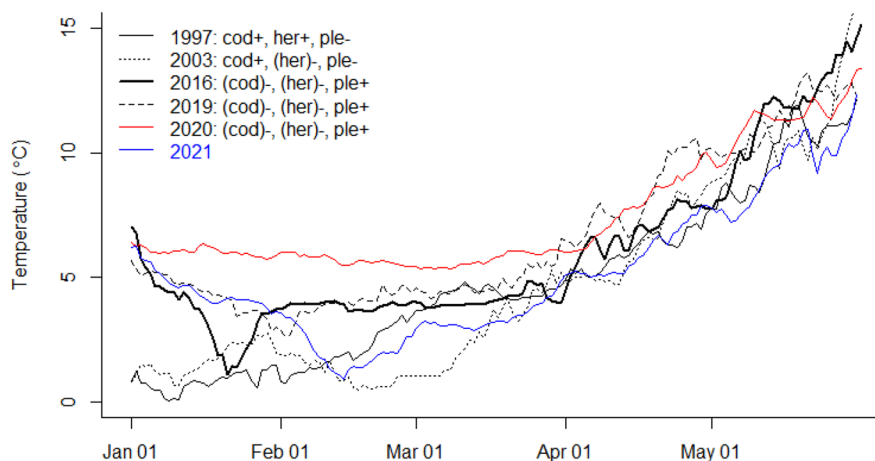


Fig. 1 Comparison of daily median water temperatures in Kiel Bight for the years indicated in the legend. Reproductive success in these years for cod, herring (her), and plaice (ple) is indicated as above+ or below– the average of years when biomass was within safe biological limits. If the stock size was

outside of safe biological limits in a given year, then the species name in the legend is enclosed in parentheses. Note that the depicted data for plaice refer to the stock in ICES subdivisions 21–23 [TmpWnd2.R]

However, reproductive success was below average when spawning stock biomass was outside of safe biological limits ($SSB < B_{pa}$) (CFP 2013) (Fig. 1).

The monthly distribution of median daily wind speed in March to May looked very similar across the selected years (Fig. 2), with the exception of 2019, when median wind speed was highest. The number of Lasker-events ranged from 3 in 2019 to 9 in 2003 and 2016. There was no apparent correlation between reproductive success of cod, herring, or plaice and the number of Lasker-events. In the year (2019) with the highest median wind speed

and the lowest number of Lasker-events, plaice had extraordinarily good recruitment (Fig. 4), whereas the bad recruitment of cod and herring may have been caused by their spawning stock biomass being outside of safe biological limits.

Monthly density of phytoplankton as represented by measurements of chlorophyll a (Chl) was similar across the selected years with available data (Fig. 3), with a peak in March and similar densities in May. , when densities in April and May were lowest compared with the other years. Yet, 2019

Fig. 2 Boxplot of wind speeds in selected years in March to May in Kiel Bight, with indication of number of calm periods (Lasker-events, bold numbers). Below the Lasker-event numbers, reproductive success of cod, herring, and plaice in the given year is indicated as above + or below - average. If stock size in the given year was outside of safe biological limits, the indicator is enclosed in parentheses. Note that the depicted data for plaice refer to the stock in ICES subdivisions 21–23 [TmpWnd.R]

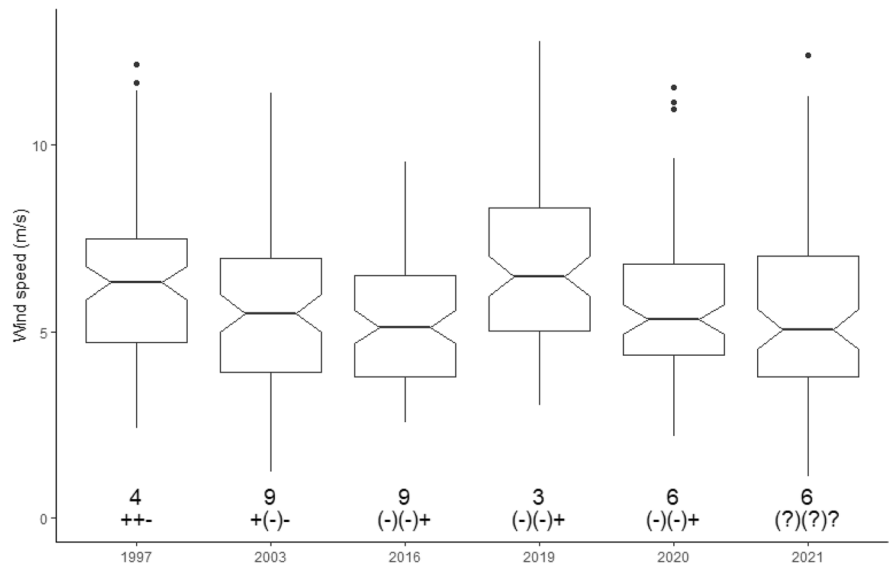


Fig. 3 Seasonal timing and density of phytoplankton blooms in the Western Baltic Sea. Phytoplankton dynamics are indicated by chlorophyll a (Chl) concentration

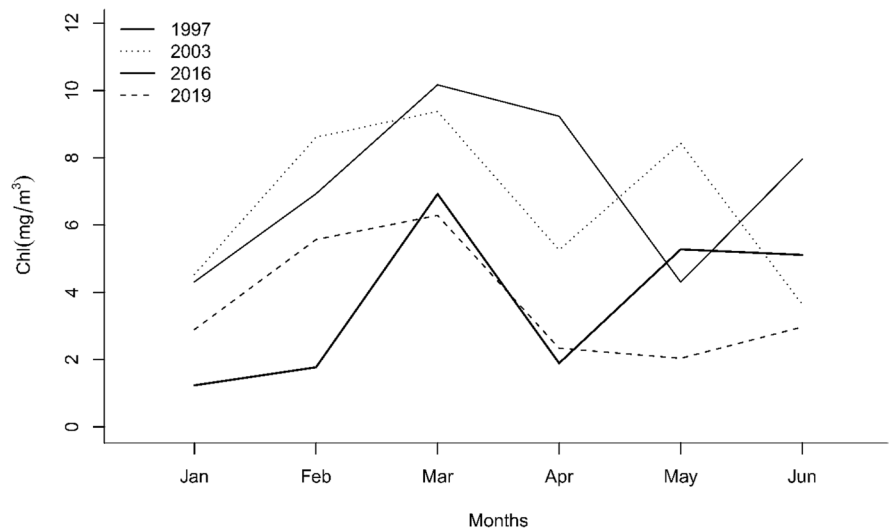
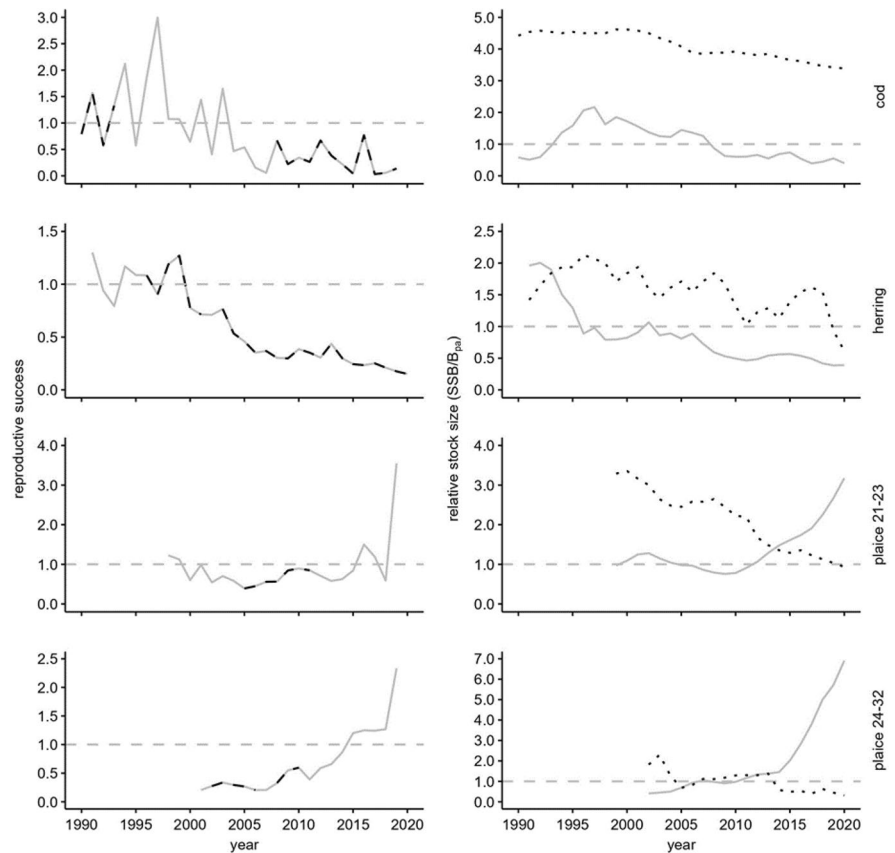


Fig. 4 Time series of relative reproductive success, fishing pressure, and spawning stock sizes for Western Baltic cod, herring, and plaice. Reproductive success is expressed relative to the average of years when the stock was within safe biological limits. Reproductive success in years outside of safe biological limits is indicated as dashed lines. Fishing pressure is expressed as annual fishing mortality relative to the maximum sustainable level (F/F_{msy}) and shown as dotted lines. Spawning stock size is shown relative to the one marking the border of safe biological limits



was the year with extraordinary good reproductive success of plaice (Fig. 4).

Life history traits

The commercially important fish species in the Western Baltic Sea consist of 5 flatfish species in addition to cod and herring. With the partial exception of herring, their life history traits are remarkably similar with regard to habitat (demersal), maximum body size (1–10 kg), food (mostly benthic invertebrates, some fish), longevity (11–26 years), age at maturity (2–4 years), spawning season (spring), and high fecundity with pelagic eggs and larvae. Herring differs by being the smallest species (0.26 kg), feeding mostly on zooplankton, with demersal deposition of eggs (Table 1).

Exploitation and recent stock status

With the possible exceptions of dab (*Limanda limanda*) and flounder (*Platichthys flesus*), all commercial fish in

the Western Baltic Sea have been overexploited at some point during the past 30 years (1990–2020) (Table 2, Fig. 4) (HAWG 2021; WGBFAS 2021). However, while the overexploitation of flatfish was less severe and ended in recent years (WGBFAS 2021) (Fig. 4), continuous overexploitation of cod and herring was 2–5 times the maximum sustainable level since the 1990s (Fig. 4).

Recent (2020) stock status was above or around the level that can produce maximum sustainable yields (MSY) (CFP 2013) for all commercial fish except cod and herring, which were suffering from depleted stock sizes and very low reproductive success (Table 2, Fig. 4) (HAWG 2021; WGBFAS 2021). Herring has supported the highest catches in the area with nearly 200,000 tonnes in 1992, followed by cod with 49,000 tonnes in 1996. In comparison, the sum of the highest catches of flatfish is only about 15,000 tonnes. But catches of herring in 2020 were only 22,000 tonnes and for cod 4,363 tonnes, i.e., about only 10% of previous maximum catches, indicating the depleted status of these stocks.

Table 2 Recent (2020) stock status, fishing pressure, commercial interest, and related comments for the commercial fishes in the Western Baltic Sea. The maximum catch is meant to give an impression of relative stock size and importance to the fishery

Name	Stock status	Fishing pressure	Commercial interest	Comments
Cod	Truncated age/size structure; very low biomass; repeated recruitment failures	Severe overfishing in the past; ongoing overfishing. Max catch 49,000 tonnes in 1996	Used to be the commercially most important species in the fishery	Only the 2016 year class supports the remaining fishery and reproduction; gear selectivity is too small for this large species
Turbot	Below MSY level	Above MSY level. Max catch 1,200 tonnes in 1996	High market value but low abundance	No MSY level assessment; gear selectivity is too small for this large species
Brill	Probably around MSY level	Probably around MSY level. Max catch 160 tonnes in 1995	Good market value but low abundance	No MSY level assessment; stock size indicator about stable since 2004; gear selectivity is too small for this large species
Plaice	Recently above MSY level	Severe overfishing in the past; recently near MSY level. Max catch 8,000 tonnes in 2002	Currently the most important species in the fishery	Recovery despite ongoing overfishing not well understood
Flounder	Apparently around MSY level	Apparently around MSY level. Max catch about 3,000 tonnes in 2001 in the area	Limited market in Germany	No MSY level assessment; recent decline in catch and stock size suggests MSY level has been reached
Dab	Apparently above MSY level	Apparently below MSY level; no targeted fishing but common bycatch. Max catch 3,100 tonnes in 1994	No market in Germany, exported to the Netherlands	No MSY level assessment; stock size indicator and size structure suggest healthy stock size; gear selectivity optimal for this small species
Herring	Very low biomass; very low recruitment	Severe overfishing. Max catch 194,000 tonnes in 1992	Used to be the staple species	Scientific advice is for zero catch since 2019 but fishing continues

The age structure of cod in 2020 was strongly truncated, with the stock consisting nearly exclusively of one year class of 4-year-old cod, instead of the seven year classes being present in 1985–2020 (WGBFAS 2021) (Fig. 5). Exploitation of this remaining year class continued with a fishing pressure of $F=0.8$ compared to the maximum sustainable level of $F_{msy}=0.26$ applicable to a stock within safe biological limits (ICES 2021b).

The age composition of herring in commercial catches in 2020 in the Western Baltic Sea (HAWG 2021) shows a severe lack of individuals in all age classes when compared with the mean of 2000–2005, indicating a severely reduced stock size and a lack of recruitment in recent years (Fig. 6).

Selectivity

Table 3 reports reference points for healthy size structure (L_{opt} , W_{opt}), for optimum selectivity of gears ($L_{c_{opt}}$, $W_{c_{opt}}$), and for maturation (L_{m90} and L_{m50}) for the commercial fish species in the Western Baltic Sea. For comparison with L_{opt} and W_{opt} , Table 3 presents the mean length and weight of the catch of common gears, and for comparison with $L_{c_{opt}}$ the selectivity (L_c) of some of these gears. Mean length, mean weight, and mean length at first capture were derived from data

provided by commercial fishers in Kiel Bight (Froese et al. 2020 and this study). No comparison with the reference points was possible for herring because they were not caught by the analyzed gears.

Mean weight in trawl catches of about 4 kg was above W_{opt} for cod; however, this is due to the absence of smaller cod (Fig. 5), which would have been otherwise retained by the gear designed to catch cod from 35 cm and about 0.5 kg onward, and their presence would have reduced the mean. Despite the distorted size distribution, L_{mean} and L_c were below L_{opt} and $L_{c_{opt}}$ in the 55- and 75-mm gill nets, indicating that selectivity of all gears was too small for cod.

Selectivity of the 55-mm gill net was too small for turbot, plaice, and flounder, but adequate for dab. Selectivity of the 75-mm gill net was too small for turbot but adequate for the other flatfish.

Mean weight in the trawl catch was below W_{opt} for plaice, flounder, and dab, and presumably also for the larger turbot and brill for which insufficient data were available, indicating that the selectivity of the trawl was too small for these species.

Aggregated length frequencies for plaice, flounder, and dab in commercial gill net catches in 2020 and 2021 in Kiel Bight show frequency peaks near or above L_{opt} (Fig. 7), indicating that these stocks were in reasonably good condition and not subject

Fig. 5 Age composition of commercial catches of Western Baltic cod in millions by age class in 2020 (dark gray) compared with mean catches in 1985–2000 (light gray) [WBS_2020.xlsx]

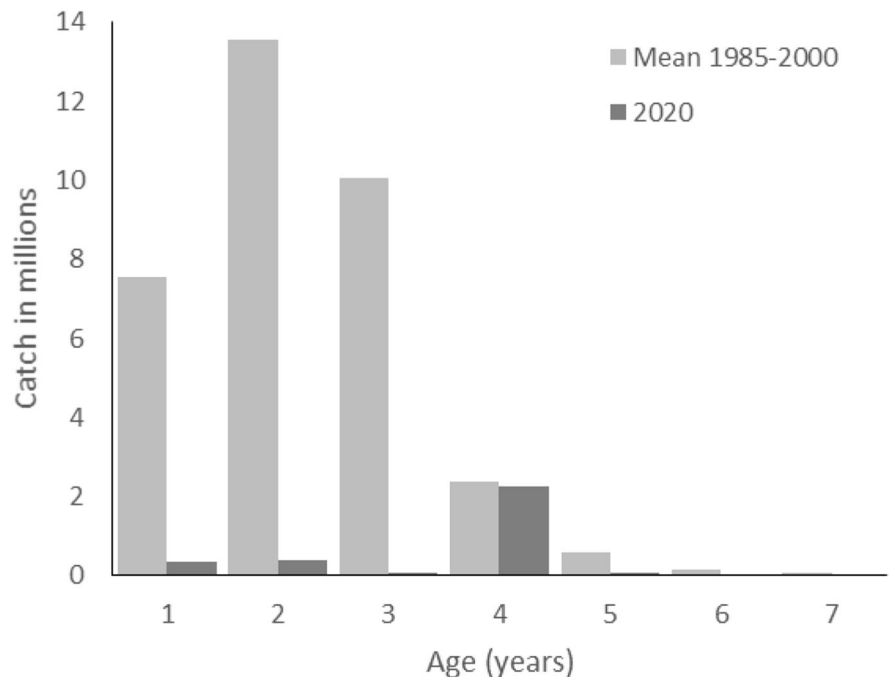


Fig. 6 Age composition of commercial catches of herring in the Western Baltic Sea, in millions at age. The light gray bars are the mean of 2000–2005 whereas the dark bars indicate the abundance in 2020 [WBS_2020.xlsx]

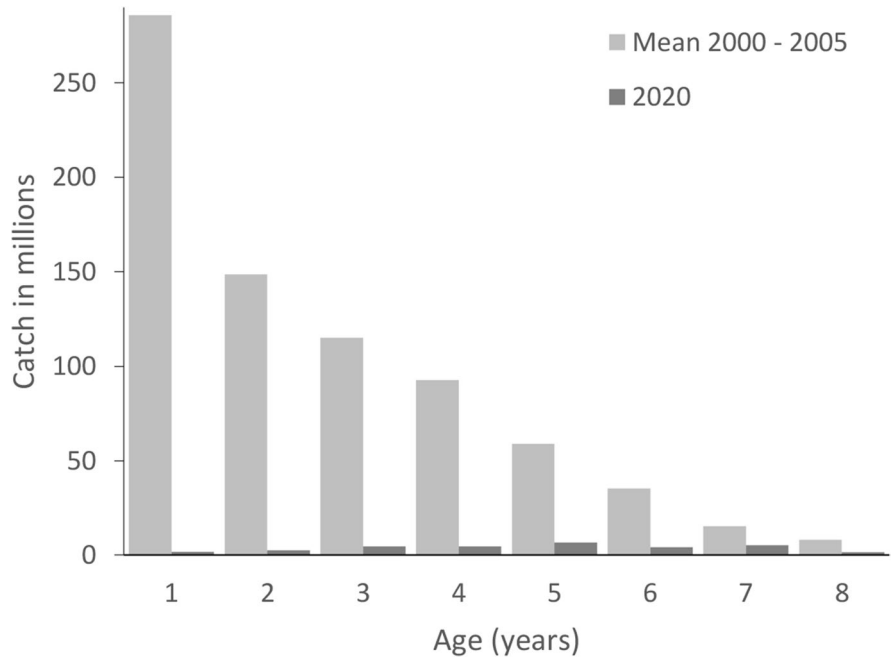


Table 3 Reference values for length (L_{opt}) and weight (W_{opt}) for which increase in body weight is highest, length ($L_{c_{opt}}$) and weight ($W_{c_{opt}}$) when fishing should start, length at which 90% and 50% of the females reach maturity (L_{m90} , L_{m50}). This is compared with selectivity of gill nets with 55-mm and

75-mm mesh size (knot to knot) and a bottom trawl with 120-mm stretched mesh size, as observed in this study. Bold values indicate suitability of the gear for the respective species. Lengths are given in centimeters and weights (W_{opt} , $W_{c_{opt}}$) in grams

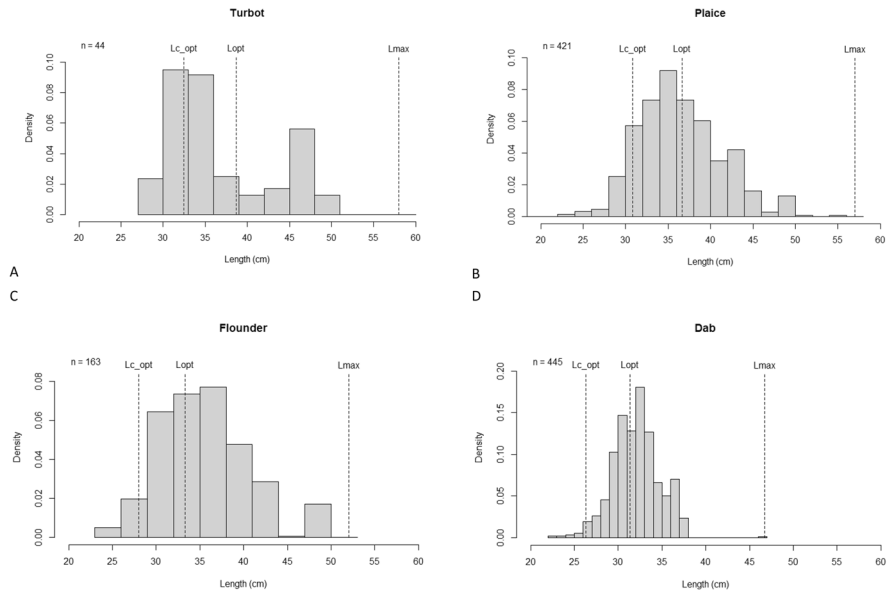
Name	L_{opt}	W_{opt}	$L_{c_{opt}}$	$W_{c_{opt}}$	L_{m90}	L_{m50}	55-mm net		75-mm net		Trawl W_{mean}
							L_{mean}	L_c	L_{mean}	L_c	
Cod	71	3202	59	1984	36	27	46	40	58	40	4011
Turbot	38	1275	32	761	38	26	33	31	36	30	NA
Brill	40	927	33	544	40	28	NA	NA	43	36	NA
Plaice	38	532	32	342	31	20	32	28	37	33	263
Flounder	35	471	29	283	33	21	32	28	36	31	285
Dab	31	339	26	184	23	17	29	27	33	30	197
Herring	22	77	18	46	16	14	NA	NA	NA	NA	NA

to overfishing (Froese et al. 2016, 2018). The situation was different for the larger-sized turbot, for which the frequency peak occurred before $L_{c_{opt}}$ and several of the larger length classes were under-represented, indicating less satisfactory stock size and at least temporary overexploitation.

Timing of spawning

Gonadosomatic index values of female fish caught by commercial fishers in Kiel Bight from January to May were available in 2020 and 2021 for cod and in 2021 for plaice and dab. Gonadosomatic index values

Fig. 7 Length frequencies for turbot, plaice, flounder, and dab in commercial catches in 2020 and 2021 in Kiel Bight, with gill nets ranging from 55- to 110-mm mesh size (knot to knot) [Kfish_27.R]



above 0.07 were used as indication of active spawning (Froese et al. 2020).

Cod spawning commenced in December (data before mid-February 2020 are missing), peaked in early March, and ended in early April in both 2020 and 2021. Spawning of plaice commenced in December 2019 and ended at the end of February 2020. Spawning of dab started in January 2020 and ended in early May (Fig. 8).

Discussion

The purpose of this study was to distinguish between climate change and mismanagement as the possible cause for the bad status of herring and cod in the Western Baltic Sea. The first approach to answer this question was to look at patterns of water temperature, wind speed, and chlorophyll a density in selected years when reproductive success of cod or herring was above or below average. The second approach was to compare life history traits and management of herring and cod with those of the other commercial fishes in the area.

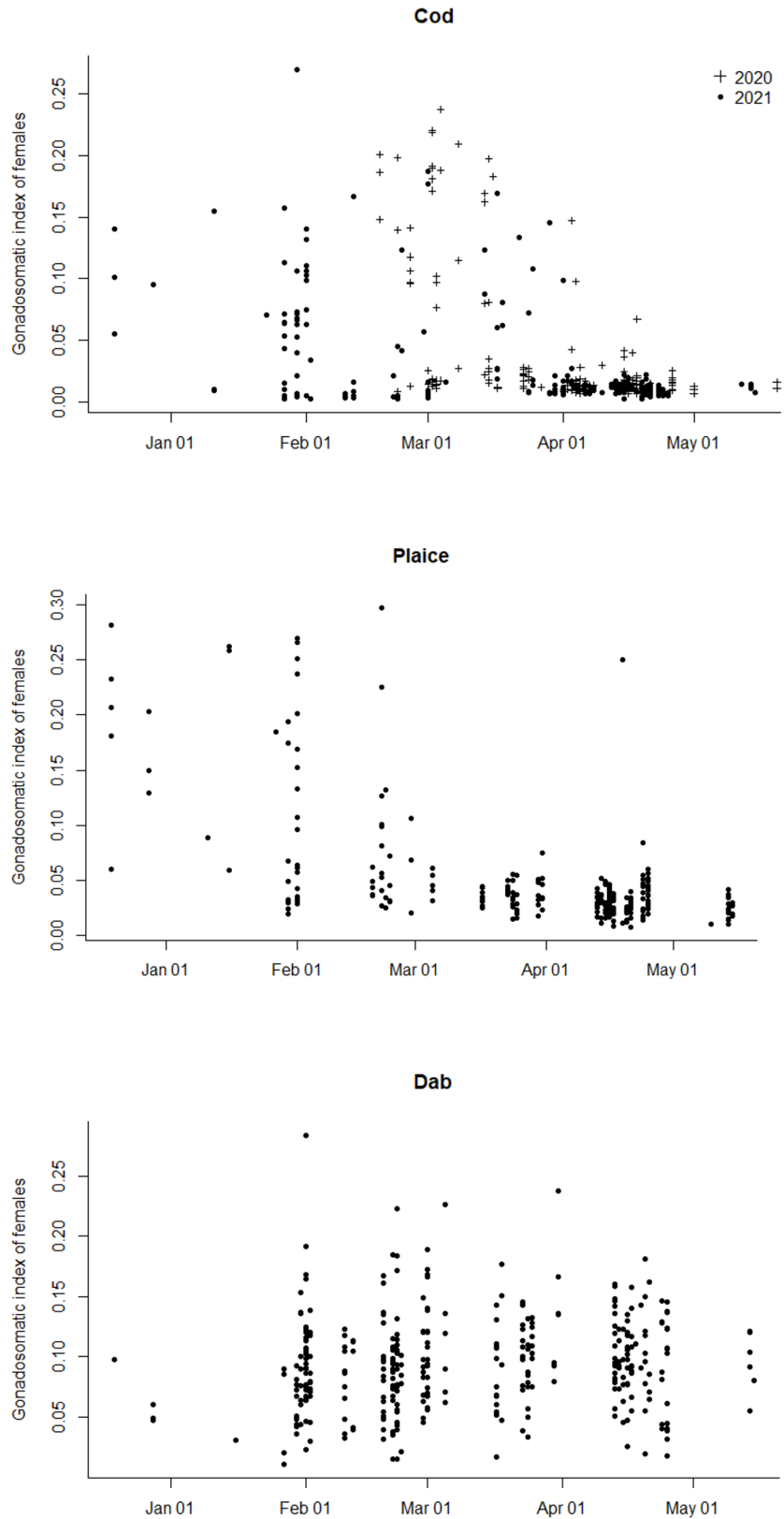
Climate change and resilience

Influence of climate change on interannual variability of water temperature may be visible in the study

area (Kiel Bight) in January and February, when temperatures in 1–5-m depth in recent years were 3–5 °C higher than in, e.g., 1997 or 2003, but not in March to May, when temperatures were very similar (Fig. 1). Seasonal timing and density of phytoplankton blooms show no major differences between years with good and bad reproductive success of cod and herring (Fig. 3). The year 2019 had intermediate water temperatures but strong wind, few Lasker-event, low chlorophyll a concentration in April and May, and below-average reproductive success of cod and herring; however, it supported extraordinary good reproductive success of plaice throughout the area (Fig. 4).

All commercial species in the Western Baltic Sea feed on benthic invertebrates (polychaete worms, crabs, shrimps, bivalves, and small benthic fish) except for herring, which feeds on zooplankton and some benthic invertebrates. Large cod, turbot, and brill also feed on larger fish (Table 1). All species are highly fecund with pelagic eggs (except herring, which has demersal eggs) and planktonic larvae (Table 1), and spawn in the area between January and May (Fig. 8). They mature between 2 and 4 years of age, suggesting similar generation times and thus similar intrinsic rates of population increase (Pianka 2000). Based on a combination of life history traits, all species are classified in FishBase as having medium resilience and potential to recover from low population sizes (Froese and Pauly 2021), and one

Fig. 8 Gonadosomatic index of females in Kiel Bight in 2020 for cod, plaice, and dab. Index values above 0.07 are interpreted as active spawning. Data for cod in 2020 are incomplete as sampling started only in mid-February [Kfish_27.R]



would expect them to have similar responses to environmental changes in the Western Baltic Sea.

Available length-frequency data for turbot, plaice, flounder, and dab in commercial catches in Kiel Bight (Fig. 7) show no gaps that would suggest recent years with bad reproductive success. In contrast, the age composition of cod in commercial catches in the Western Baltic Sea in 2020 (WGBFAS 2021, Fig. 5) shows practically only one remaining year class (of 2016), and a comparison with mean age composition in 1985–2000 indicates that millions of cod are missing in the other age classes, suggesting numerous recruitment failures. This is confirmed by observed recruitment data, shown as reproductive success of the respective years in Fig. 4, with very low reproductive success in 2007, 2015, and 2017, and according to preliminary data also in 2018, 2019, and 2020 (WGBFAS 2021). The period of low reproductive success coincides with the periods from 1998 (ICES 2018) or 2008 (WGBFAS 2021) onward, when spawning stock biomass was considered too low to ensure successful reproduction.

The age composition of herring in commercial catches in the Western Baltic Sea (Fig. 6) shows the presence of all age classes, suggesting no complete failure of reproduction in recent years. However, abundances especially at ages 1 to 4 are only 0.6–5% of the mean of 2000–2005 and lower than in subsequent year classes, highlighting hundreds of millions of missing herring and suggesting declining reproductive success in recent years. This is confirmed by observed recruitment data, shown as reproductive success in the respective years in Fig. 4, with declining reproductive success since 2004 and lowest success on record in 2020. The period of low reproductive success coincides with the period from 2003 onward, when spawning stock biomass is considered too low to ensure successful reproduction (HAWG 2021) (Fig. 4).

It has been suggested (Froese et al. 2020) that the unusually warm water temperature in January–March 2020 (Fig. 1) has led cod to spawn too early such that its zooplankton-feeding larvae missed the zooplankton bloom expected to occur in late March, April, and May. However, subsequent gonadosomatic index data for female cod in Kiel Bight in 2020 (Fig. 8) confirm spawning activity until end of March, similar to the regular spawning activity of plaice and dab (Fig. 8). Instead, it seems more likely that cod spawning stock

biomass was too small (as confirmed by Figs. 4 and 5) to supply all of its spawning area with sufficient numbers of eggs during the whole duration of spawning season.

Given that the other commercial stocks in the Western Baltic showing no signs of suffering from climate change are all flatfish, one could suspect that flatfish are somehow more resilient to climate change than herring and cod. However, previous studies suggest that flatfish in the Baltic Sea have similar or even less resilience to climate change (MacKenzie et al. 2007; HELCOM 2021).

In summary, available time series of water temperature, wind speed, and chlorophyll a concentration show no conclusive connection with the reproductive failures of cod or the continuously declining reproductive success in herring (Fig. 4). Instead, the available data suggest that the environmental conditions supported regular and even better-than-average reproductive success of the other spring-spawning commercial fish in the area.

Management

The second approach to disentangle impacts of climate change or mismanagement as causes for the bad status of cod and herring in the Western Baltic Sea was to compare exploitation and stock status of herring and cod with those of the other commercial fishes in the area, with the sub-population of cod in the Öresund, and with three herring stocks in the Central and Northeastern Baltic Sea.

Since 1997, fishing pressure on cod was 3–5 times the maximum value that the stock can support. Consequently, spawning stock biomass shrunk by 64% from 1997 to 2018 (WGBFAS 2021) (Fig. 4). Despite the obvious biomass decline and the stock being outside of safe biological limits (CFP 2013), severe overfishing never stopped, with F still 3 times the MSY level in 2020 (ICES 2021b). Similarly, herring was subject to severe overfishing ($F/F_{msy} > 1.5$) from 1997 to 2009 and 2016 to 2018, despite spawning stock biomass being outside of safe biological limits and declining by 60% from 1997 to 2020 (HAWG 2021) (Fig. 4). Since 2019, the International Council for the Exploration of the Sea (ICES) recommended closure of the herring fishery, but management allowed fishing to continue.

Similar to cod and herring, plaice was subject to very high levels of fishing pressure from 1999 to 2016, but other than in cod and herring, spawning stock biomass kept fluctuating around the border of safe biological limits (CFP 2013) and started increasing in 2013, despite ongoing overfishing of $F/F_{\text{msy}} = 1.5$. The continued increase in biomass then led to a decline in fishing pressure, below F_{msy} in 2020, ending overfishing of plaice for the first time in the time series. It is important to note that this recovery is not due to management reducing catches to allow the stock to recover, because total catches (landings + discards) increased from 3,594 tonnes in 2013 to 4,470 tonnes in 2020 (+24%). The reasons for the recovery of the plaice stock despite ongoing overfishing and increasing catches are not well understood and beyond the scope of this study. It may be a mixture of improved reproductive success since 2009 (Fig. 4), reduced natural mortality of juveniles due to absence of large cod before 2020 (Fig. 5), reduced competition for benthic food due to repeated reproductive failures and thus absence of juvenile cod (Fig. 5), more appropriate selectivity of the main gears (Table 3), and overfishing being less severe than in cod and herring due to limited demand. But clearly, better than average plaice reproduction and increase in stock size (Fig. 4) happened despite full exploitation and impact of climate change on the Western Baltic environment. Similarly, the available length frequencies (Fig. 7) and stock size indicators (WGBFAS 2021) of the other commercial fish in the area (Table 3) do not show signs of reproductive failure, depleted stock size, or severe overexploitation.

The importance of capturing fish at the right size is not to be underestimated: it has been formally shown that it is theoretically impossible to collapse a stock if all individuals are allowed to reproduce before capture (Myers and Mertz 1998). With regard to the appropriateness of management of technical measures such as the size selectivity of the allowed gears, the peak in length frequencies of plaice, flounder, and dab was slightly above L_{opt} , suggesting that gear selectivity was appropriate for these species (Table 3, Fig. 7). In turbot, the peak in frequencies was below L_{opt} and $L_{\text{c_opt}}$, suggesting that gear selectivity was inappropriate (too small, too early) for this large species. This may be one of the reasons for the less satisfactory stock status of turbot (WGBFAS 2021). Available data were

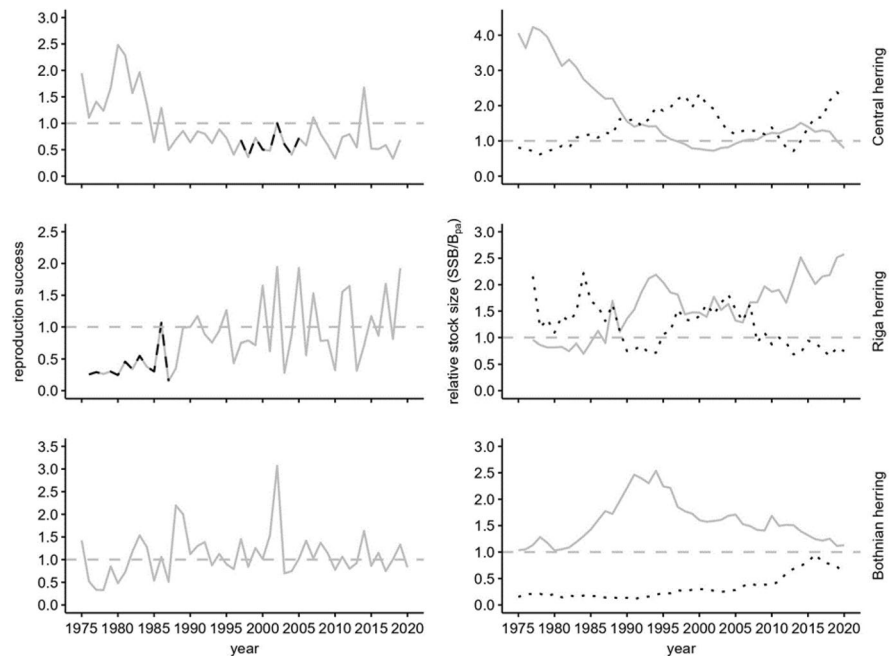
insufficient for brill, but given its similarity in size and body shape to turbot, the turbot assessment probably also applies to brill.

No length-composition data were available for herring, but the very high abundance of immature 1- and 2-year-old herring in commercial catches shown in Fig. 6 suggests that gear selectivity was inappropriate. For cod in the Western Baltic Sea, current commercial gear selectivity was difficult to establish because of the strongly truncated age structure, but the minimum marketing size is 35 cm (WGBFAS 2021) whereas optimum length at first capture is $L_{\text{c_opt}} = 59$ cm (Table 3). Age composition in the commercial catch of 1985–2000 shows a high abundance of immature cod of 1–2 years of age. Together with far too high fishing pressure, this inappropriate early onset and thus extended duration and impact of fishing mortality is one of the reasons for the bad status of the cod stock.

In summary, inappropriate selectivity of the main commercial gears has contributed to the truncated age structure of cod (Fig. 5) and the distorted age structure of herring, whereas the more appropriate gear selectivity for dab, plaice, and flounder has contributed to their good size structure, stock status, and apparent resilience against climate change.

It has been shown that the sub-population of cod in the Öresund, which are part of the Western Baltic cod stock (ICES 2021b), did not show a truncated age structure in 2010 (Svedäng and Hornborg 2017, their Fig. 3), presumably because trawling is banned in that area since 1932, common gill nets have slightly larger mesh sizes (65 mm instead of 55 mm knot-to-knot), and the shipping traffic lanes act as de facto no-take zones. However, fishing pressure was always high and practically unlimited in the area, thus attracting fishers from neighboring areas when their catches were low (Lindegren et al. 2013). For example, in the period 2017–2020, the mean proportion of Öresund landings of the overall cod landings increased by 71% compared to 2000–2016 (ICES 2021b, their Table 9). In 2020, 89% of the Öresund landings consisted only of 4-year-old individuals, thus showing the same truncated age structure as the rest of the Western Baltic Sea (WGBFAS 2021, Table 2.32 at page 146) and suggesting that slightly larger mesh sizes, trawling ban, and no-take zones are not sufficient to counteract fishing pressure up to 5 times the maximum sustainable level (Lindegren et al. 2013, their Fig. 2b).

Fig. 9 Time series of relative reproductive success, fishing pressure, and spawning stock sizes for adjacent herring stocks in the Central Baltic, the Gulf of Riga, and the Gulf of Bothnia. Reproductive success is expressed relative to the average of years when the stock was within safe biological limits. Reproductive success in years outside of safe biological limits is indicated as dashed lines. Fishing pressure is expressed as annual fishing mortality relative to the maximum sustainable level (F/F_{msy}) and shown as dotted lines. Spawning stock size is shown relative to the one marking the border of safe biological limits



There are three neighboring herring stocks to the Western Baltic Sea, with different stock status and reproductive success (Fig. 9). Gulf of Riga and Gulf of Bothnia herring show regular reproductive success fluctuating around the long-term mean with stock sizes within safe biological limits, apparently being resilient to effects of climate change so far. In contrast, reproductive success of Central Baltic herring has been mostly below average, with spawning stock biomass fluctuating around the border of safe biological limits since 1995, caused by exploitation mostly above the MSY level since 1990. This comparison of herring stocks within the same large marine ecosystem suggests that reproductive success was not a function of climate change but rather a function of spawning stock biomass being inside or outside of safe biological limits (Figs. 4 and 9).

Conclusion

The available data indicate that the commercial fish in the Western Baltic Sea have similar resilience against pressures such as fisheries or climate change. But while plaice, turbot, flounder, dab, and brill (as well as herring in the Gulf of Riga and the Gulf of Bothnia) show good or satisfactory relative population size

and regular reproductive success (Figs. 4, 7, and 9), herring and cod (as well as herring in the Central Baltic) suffer from overexploitation, which has led to low population size outside of safe biological limits. Too small spawning stock size reduced the probability to spawn at the right place and time, which is a moving, unpredictable target (Sinclair 1988). The small spawning stock sizes were not caused by climate change but were the predicted and unavoidable result of fishing pressure far above maximum sustainable levels, exacerbated by inappropriate gear selectivity. Excessive fishing pressure continued even when the stocks were already far outside of safe biological limits with high probabilities of recruitment failure.

Considerations for future management

With the collapse of the high catches previously supported by large stocks of cod and herring, it will be tempting for managers to allow higher catches on the remaining species to fill the gap. However, fishing pressure on these species is already at or near the maximum sustainable level (Table 2, Fig. 7) and any increase will quickly lead to a decline in stock size and catch. In any case, these stocks are too small to replace the potential catches from healthy cod and

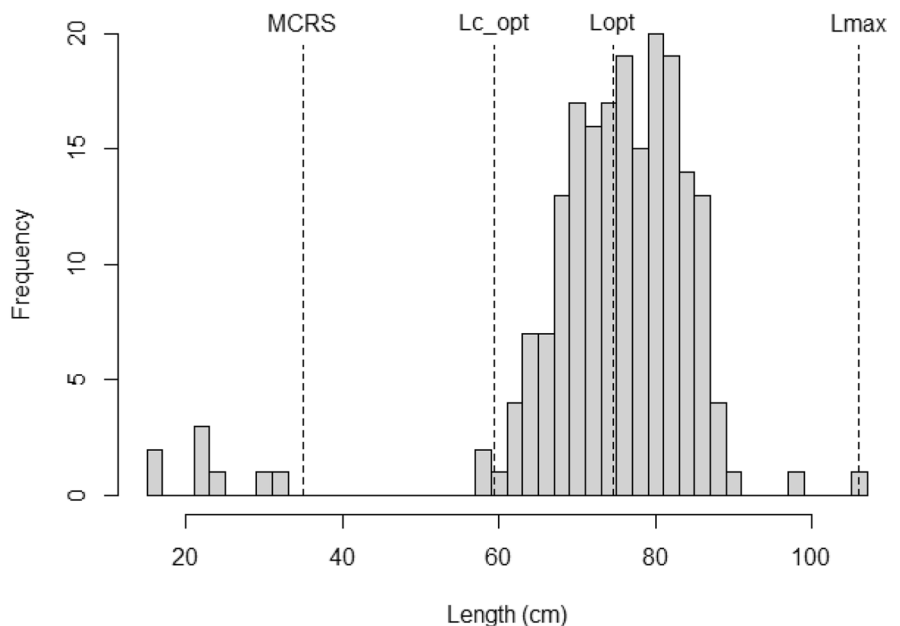
herring stocks (see maximum catches in Table 2). Instead, the job at hand is to preserve high catches (e.g., 90% of the MSY level) of the remaining flatfish stocks while getting serious about rebuilding the cod and herring stocks. For herring, the solution is straightforward and has been recommended by ICES since 2019: stop all catch and bycatch, commercial and recreational, in all of its area, until the stock has sufficiently recovered. This is straightforward because the gears used to catch herring are not used for any of the other species and there is no bycatch of herring in the main gears used for the other species. The age structure of herring is still complete and reproductive success better than the recent average was observed last in 2013, suggesting that herring reproduction is still functioning and is likely to improve once fishing stops and spawning stock biomass is allowed to increase. For example, the estimated spawning stock biomass in April 2020 was 58,434 tonnes while catches in 2020 were 22,130 tonnes (HAWG 2021), preventing a recovery of the stock. This remaining fishing must end.

The situation is more complicated for cod, with a severely truncated age structure (Fig. 5) and thus severely reduced genetic diversity and experience of spawners. However, successful reproduction occurred as recently as 2016, and the resulting year class was in excellent condition (Froese et al. 2020) and has been

growing fast, reaching on average 4 kg for 5-year-old cod in commercial trawl catches in Kiel Bight in April 2021 (Table 3, Fig. 10). But Fig. 10 also shows the problems of the only remaining year class being targeted by the allowed catches, and the inappropriate setting of the minimum conservation reference size (MCRS = 35 cm) and the corresponding selectivity of the gear, which would catch cod far smaller than the optimum size ($L_{opt} = 75$ cm) or the optimum size at first capture ($L_{c_opt} = 59$ cm). Also, cod are vulnerable to all the gears used to capture the other commercial species.

The required measures to conserve and rebuild the cod stock then are as follows: selectivity of the common gears has to be changed towards L_{c_opt} for cod. This will also benefit the size and age structure of the larger flatfish (turbot, brill, plaice, and flounder) and decrease the catch of unwanted small dab (Table 3, Fig. 7) and small or juvenile flatfish in general. For example, the selectivity of the allowed gill nets summarized in Table 3 shows that the 55-mm (knot to knot) gill nets are suboptimal for cod and all flatfish but dab. The 75-mm gill nets are optimal for brill, plaice, flounder, and dab while still suboptimal for turbot and cod, but a step in the right direction. Mean body weight in the catch compared with W_{opt} suggests that selectivity of the 120 mm (stretched mesh) trawls is inappropriate for cod and

Fig. 10 Length frequency distribution of cod in commercial trawl catches with 120 mm stretched mesh size in Kiel Bight in April 2021. MCRS is the official minimum conservation reference size and probably close to the length L_c at which 50% of the individuals are retained by the gear. L_{c_opt} is the length at first capture that would result in a mean length of L_{opt} in the catch and L_{max} is the maximum length observed in the area



for flatfish (Table 3). Also, existing gears need to be modified such that they continue to catch flatfish but reduce bycatch of cod. This can be achieved by strongly reducing the reach/height of the gears above the seafloor and by restrictions to trawling. Such measures need to remain in place until new year classes have rebuilt the spawning stock to a level that is large enough to ensure successful reproduction. Subsequent exploitation should not exceed 90% of the maximum sustainable level.

Fishers are not the culprits of the bad status of cod and herring in the Western Baltic Sea, as their catches corresponded, with small deviations in both directions, to the amounts set by management (HAWG 2021; WGBFAS 2021). Fishers need compensation for their losses caused by mismanagement and incentives to actively avoid the capture of cod while fishing for flatfish, e.g., by avoiding times and places where cod is likely to be present, and by modifying their gears such that cod are less likely to be caught or retained.

The available data suggest that rebuilding of herring and cod with highly profitable future fisheries with catches close to the maximum sustainable level is still possible in the Western Baltic Sea, if the prescriptions of the Common Fisheries Policy of the EU (CFP 2013) are finally implemented as intended. Only such rebuilt stocks will be able to cope with the challenges posed by climate change. Returning to the original question posed by this study, the available data indicate that mismanagement and not climate change was responsible for the bad status of cod and herring.

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Declarations

Data and code availability All the data used here are presented in the text and figures; data and code are in addition available from <https://oceanrep.geomar.de/53154/>.

The research reported herein did not involve human subjects and/or live animals or cell lines.

Consent The work described has not been published before and is not under consideration for publication anywhere else. Its publication has been approved by all co-authors. RF collected and analyzed the environmental and fisheries data; MS provided the plankton data and assessment; EP provided context for the environmental data; all authors reviewed and approved the final draft.

Conflict of interest The authors declare no competing interests.

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References

- Akimova A, Núñez-Riboni I, Kempf A, Taylor MH (2016) Spatially-resolved influence of temperature and salinity on stock and recruitment variability of commercially important fishes in the North Sea. *PLoS ONE* 11:e0161917. <https://doi.org/10.1371/journal.pone.0161917>
- BACC (Baltic Earth Assessment of Climate Change) II Author Team (2015) Second assessment of climate change for the Baltic Sea Basin. *Regional Climate Studies*. Accessed on 30 June 2021. <https://doi.org/10.1007/978-3-319-16006-1>
- Bodini A, Rocchi M, Scotti M (2018) Insights into the ecology of the Black Sea through the qualitative loop analysis of the community structure. *Limnol Oceanogr* 63:968–984. <https://doi.org/10.1002/lno.10713>
- Brander K (2010) Impacts of climate change on fisheries. *J Mar Syst* 79:389–402. <https://doi.org/10.1016/j.jmarsys.2008.12.015>

- CFP (2013) Common Fisheries Policy. Regulation (EU) No 1380/2013 of the European Parliament and of the Council of 11 December 2013 on the Common Fisheries Policy. Off J Eur Union 354:22–61
- Cheung WWL, Watson R, Pauly D (2013) Signature of ocean warming in global fisheries catch. *Nature* 497:365–369. <https://doi.org/10.1038/nature12156>
- Cushing DH, Horwood JW (1994) The growth and death of fish larvae. *J Plankton Res* 16:291–300. <https://doi.org/10.1093/plankt/16.3.291>
- DATRAS 2021. Accessed on 11 May 2021. https://datras.ices.dk/Data_products/Download/Download_Data_public.aspx
- Free CM, Thorson JT, Pinsky ML, Oken KL, Wiedenmann J, Jensen OP (2019) Impacts of historical warming on marine fisheries production. *Science* 363:979. <https://doi.org/10.1126/science.aau1758>
- Froese R, Binohlan C (2000) Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. *J Fish Biol* 56:758–773. <https://doi.org/10.1111/j.1095-8649.2000.tb00870.x>
- Froese R, Winker H, Gascuel D, Sumaila UR, Pauly D (2016) Minimizing the impact of fishing. *Fish Fish* 17:785–802. <https://doi.org/10.1111/faf.12146>
- Froese R, Winker H, Coro G, Demirel N, Tsikliras AC, Dimarchoyopoulou D, Scarcella G, Probst WN, Dureuil M, Pauly D (2018) A new approach for estimating stock status from length frequency data. *ICES J Mar Sci* 75:2004–2015. <https://doi.org/10.1093/icesjms/fsy078>
- Froese R, Pauly D (2021) FishBase. World Wide Web electronic publication, version (02/2021). Accessed on 20 Jun 2021. <https://www.fishbase.org>.
- Froese R, Flindt F, Meyer E, Meyer J, Egerland O (2020) Untersuchung zum Laichverhalten des Dorsches in der Kieler Bucht im Frühjahr 2020. Accessed on 24 June 2021. <https://www.fishbase.de/frfroese/LaichDorsch2020.pdf>
- Gaines SD, Costello C, Owashi B, Mangin T, Bone J, Molinos JG, Burden M et al (2018) Improved fisheries management could offset many negative effects of climate change. *Sci Adv* 4:eaa01378. <https://doi.org/10.1126/sciadv.aao1378>
- Hansson M, Viktorsson L, Andersson L (2019) Oxygen survey in the Baltic Sea 2019 - extent of anoxia and hypoxia, 1960–2019. SMHI Stockholm, Report Oceanography 67, 84 p. Accessed on 30 June 2021. https://www.smhi.se/polopoly_fs/1.158302!/Oxygen_timeseries_1960_2019_final.pdf
- Hare J, Morrison WE, Nelson MW, Stachura MM, Teeters EJ et al (2016) A vulnerability assessment of fish and invertebrates to climate change on the Northeast U.S. Continental Shelf. *PLOS ONE* 11:e0146756. <https://doi.org/10.1371/journal.pone.0146756>
- HAWG (2021) Herring in Division 3.a and subdivisions 22–24, spring spawners [Update Assessment]. Accessed on 20 June 2021. <https://www.ices.dk/sites/pub/Publication%20Reports/Forms/DispForm.aspx?ID=37880>
- HELCOM (2021) Climate change in the Baltic Sea. 2021 Fact Sheet. Baltic Sea Environment Proceedings n°180. HELCOM/Baltic Earth 2021.
- Hobday AJ, Smith ADM, Stobutzki IC, Bulman C, Daley R, Dambacher JM, Deng RA et al (2011) Ecological risk assessment for the effects of fishing. *Fish Res* 108:372–384. <https://doi.org/10.1016/j.fishres.2011.01.013>
- Holt SJ (1958) The evaluation of fisheries resources by the dynamic analysis of stocks, and notes on the time factors involved. ICNAF Special Publication 1:77–95
- ICES (2018) Cod (*Gadus morhua*) in subdivisions 22–24, western Baltic stock (western Baltic Sea). Accessed on 23 Jun 2021. <https://www.ices.dk/sites/pub/Publication%20Reports/Advice/2018/2018/cod.27.22-24.pdf>
- ICES (2019) Cod (*Gadus morhua*) in subdivisions 22–24, western Baltic stock (western Baltic Sea). Accessed on 23 Jun 2021. <https://www.ices.dk/sites/pub/Publication%20Reports/Advice/2019/2019/cod.27.22-24.pdf>
- ICES (2020) Sprat (*Sprattus sprattus*) in subdivisions 22–32 (Baltic Sea). Accessed on 3 December 2021. <https://www.ices.dk/sites/pub/Publication%20Reports/Advice/2020/2020/spr.27.22-32.pdf>
- ICES (2021a) Lemon sole (*Microstomus kitt*) in subarea 4 and divisions 3.a and 7.d (North Sea, Skagerrak and Kattegat, eastern English Channel). Accessed on 3 December 2021. <https://www.ices.dk/sites/pub/Publication%20Reports/Advice/2021/2021/lem.27.3a47d.pdf>
- ICES (2021b) Cod (*Gadus morhua*) in subdivisions 22–24, western Baltic stock (western Baltic Sea). Accessed on 10 September 2021. <https://www.ices.dk/sites/pub/Publication%20Reports/Advice/2021/2021/cod.27.22-24.pdf>
- Ito M, Scotti M, Franz M, Barboza FR, Buchholz B, Zimmer M, Guy-Haim T, Wahl M (2019) Effects of temperature on carbon circulation in macroalgal food webs are mediated by herbivores. *Mar Biol* 166:1–11
- Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH et al (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–637. <https://doi.org/10.1126/science.1059199>
- Lasker R (1975) Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. *United States Fishery Bulletin* 73:453–462
- Lasker R (1978) The relation between oceanographic conditions and anchovy food in the California Current: identification of factors contributing to recruitment failure. *Rapp P-V Reun Cons Int Explor Mer* 173:212–230
- Lindgren M, Waldo S, Nilsson PA, Svedäng H, Persson A (2013) Towards sustainable fisheries of the Öresund cod (*Gadus morhua*) through sub-stock-specific assessment and management recommendations. *ICES J Mar Sci* 70:1140–1150. <https://doi.org/10.1093/icesjms/fst042>
- Mackenzie BR, Giglason H, Möllmann C, Köster FW (2007) Impact of 21st century climate change on the Baltic Sea fish community and fisheries. *Glob Change Biol* 13:1348–1367. <https://doi.org/10.1111/j.1365-2486.2007.01369.x>
- Möllmann C, Kornilovs G, Fetter M, Köster FW, Hinrichsen HH (2003) The marine copepod, *Pseudocalanus elongatus*, as a mediator between climate variability and fisheries

- in the Central Baltic Sea. *Fish Oceanogr* 12:360–368. <https://doi.org/10.1046/j.1365-2419.2003.00257.x>
- Möllmann C, Cormon X, Funk S, Otto SA, Schmidt JO, Schwermer H, Sguotti C et al (2021) Tipping point realized in cod fishery. *Sci Rep* 11:14259. <https://doi.org/10.1038/s41598-021-93843-z>
- Myers RA, Mertz G (1998) The limits of exploitation: a precautionary approach. *Ecol Appl* 8:165–169. [https://doi.org/10.1890/1051-0761\(1998\)8\[S165:TLOEAP\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1998)8[S165:TLOEAP]2.0.CO;2)
- Pauly D (1989) An eponym for Reuben Lasker. *US Fish Bull* 87:383–384
- Petereit C, Hinrichsen H-H, Franke A, Köster FW (2014) Floating along buoyancy levels: dispersal and survival of western Baltic fish eggs. *Prog Oceanogr* 122:131–152. <https://doi.org/10.1016/j.pocean.2014.01.001>
- Pianka ER (2000) *Evolutionary ecology*, 6th edn. Benjamin / Cummings, San Francisco, p 512
- Poloczanska ES, Burrows MT, Brown CJ, García Molinos J, Halpern BS, Hoegh-Guldberg O, Kappel CV et al (2016) Responses of marine organisms to climate change across oceans. *Front Mar Sci* 3:62. <https://doi.org/10.3389/fmars.2016.00062>
- Pörtner HO, Peck MA (2010) Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *J Fish Biol* 77:745–1779. <https://doi.org/10.1111/j.1095-8649.2010.02783.x>
- R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Accessed on 10 September 2021. <http://www.R-project.org/>.
- Reusch TBH, Dierking J, Andersson HC, Bonsdorff E, Carstensen J, Casini M, Czajkowski M et al (2018) The Baltic Sea as a time machine for the future coastal ocean. *Sci Advances* 4:eaar8195. <https://doi.org/10.1126/sciadv.aar8195>
- Rijnsdorp AD, Peck MA, Engelhard GH, Möllmann C, Pinnegar JK (2009) Resolving the effect of climate change on fish populations. *ICES J Mar Sci* 66:1570–1583. <https://doi.org/10.1093/icesjms/fsp056>
- Sinclair M (1988) *Marine populations*. Washington Sea Grant Program, University of Washington, An essay on population regulation and speciation, p 252
- Spencer PD, Hollowed AB, Sigler MF, Hermann AJ, Nelson MW (2019) Trait-based climate vulnerability assessments in data-rich systems: an application to eastern Bering Sea fish and invertebrate stocks. *Glob Change Biol* 25:3954–3971. <https://doi.org/10.1111/gcb.14763>
- Svedäng H, Hornborg S (2017) Historic changes in length distributions of three Baltic cod (*Gadus morhua*) stocks: evidence of growth retardation. *Ecol Evol* 7:6089–6102. <https://doi.org/10.1002/ece3.3173>
- WGBFAS (2021) Baltic Fisheries Assessment Working Group (WGBFAS). *ICES Scientific Reports* 3:53. 717 pp. <https://doi.org/10.17895/ices.pub.8187>

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