



Anthropogenic and ecology research indicators of top commercial fish species in the Baltic Sea: Review

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Abstract. In many parts of the world, morality caused as a result of fishing actives is the only influencer affecting the status of top commercial stocks. This however is not the case in the Baltic Sea, which has a multitude of other processes that influence fish stock dynamics. This paper compartmentalises 250 publications that consider the cumulative effects and trade-offs some of the biggest anthropogenic and ecology stressors (temperature change, hypoxia, eutrophication, nutrient pollution

- 10 acidification, low salinity and food-web dynamics) have on the ecology of top commercial fish species in the Baltic Sea (cod, sprat, whiting, herring, flounder and plaice). The results illustrate the extent of academic research that can be applied to commercial fisheries knowledge in the Baltic Sea and identifies which pressures have the greatest negative impacts for which species. In addition, the findings demonstrate how well individual fish stocks have adapted to the changing environmental conditions of the Baltic Sea. In doing so, the review illustrates the next challenges and underlines what fish will likely dominate
- 15 in the future and which will struggle. With increased natural hazards, top commercial fish species have reacted differently, depending on the region and adaptive capabilities. In most cases, species in the *Clupeidae* family have adapted the best to their new surroundings, flatfish resilience is varied, whilst fish in the *Gadidae* family are finding the Baltic Sea too hostile.

1 Introduction

The Baltic Sea is the largest body of brackish water in the world, with a surface area of 420,000 km2, that is surrounded by 85 million inhabitants from 9 European states. Consequently, this semi-enclosed and moderately shallow sea with a mean depth of 54 m is one of the most exploited marine habitats in the world. These extensive human activities coupled with the increasing symptoms of climate change have imposed intense pressures on the health of the Baltic's ecosystem and its capacity to produce goods and services at a sustainable level (Voss et al. 2019, Meier et al. 2011). The resulting outcome negatively affects the economic contribution marine related activities can have in the Baltic Sea region. This is most felt in the fisheries sector which has undergone a drastic change in the last 40 years (Kijewska et al. 2016, Cederqvist et al. 2020, HELCOM 2018a). This created the populous notion that there are no fish in the Baltic Sea. A claim that is far from the truth. Despite its decline, in 2015, the number of active fishing vessels in the Baltic Sea was estimated at 6192 (State of the Baltic Sea HELCOM 2018). Their landing value totalled EUR 217 million, with a gross profit for those regions estimated at EUR 116 million (State of the Baltic Sea HELCOM 2018). In terms of employment, the 2015 figures estimate that the commercial



- 30 fishing industry employed 4704 people in full time employment and another 4336 in part time employment (State of the Baltic Sea HELCOM 2018). Traditionally, Cod Gadus morhua, herring *Clupea harengus* and sprat *Sprattus sprattus* stocks have had the highest commercial value in the Baltic Sea (HELCOM 2018b, 2018c, ICES 2019, 2022a, 2022b, 2022c, 2022d, 2022f, 2022g, 2022h).
- In addition, flatfish species including flounder *Platichthys flesus* and plaice *Pleuronectes platessa* are important for small-scale fisheries (HELCOM 2018b, ICES 2019, 2022a, 2022b, 2022c, 2022d, 2022f, 2022g, 2022h). These are monitored and managed by the EU Common Fisheries Policy (CFP) through the implementation of total allowable catch (TAC) allowances and divided into the following stocks by sub-division (s.d.): *Eastern cod–s.d. 25-32*, *Western cod–s.d. 22-24*, *Bothnian herring–s.d. 30-31*, *Western herring–s.d. 22-24*, *Central herring–s.d. 25-27*, 28.2, 29, 32, *Riga herring–s.d. 28.1*, *Sprat–s.d. 22-32* and *Plaice–s.d. 22-32* (European Commission 2022). Flounder and whiting stocks have no TAC quotas at
- 40 the time of writing (European Commission 2022). Their dominance as top commercial species is paramount to such an extent that 90% of the total fish catch in the Baltic Sea is made up of these stocks (State of the Baltic Sea HELCOM 2018). The International Council for the Exploration of the Sea (ICES) is responsible for gathering statistics for Baltic fish stocks in relation to their spawning stock biomass (SSB), fishing morality and more, based on their findings they assess the state of fish resources and inform the CFP (ICES 2019, 2022a, 2022b, 2022c, 2022d, 2022f, 2022g, 2022h). Besides targeted extraction
- 45 through fisheries, other pressures affect the status of these stocks. This paper reviews academic papers that shed a light on these additional anthropogenic stressors and ecology impacts. As changes in these parameters affect the status of stocks and their ability to provide sustainable goods and services.

2 Methods

2.1 Definitions

- 50 In order to enhance transparency and promote better comprehension of the review, it is essential to establish clear definitions for key terms. By "anthropogenic stressors" the paper refers to how pollutants, CO2 emissions and other greenhouse gases have resulted in a large-scale shift in climatic, oceanographic and biogeochemical parameters in the Baltic Sea region (Viitasalo and Bonsdorff 2022). In turn, top commercial fish stocks have increasingly become exposed to those natural hazards. With this in mind, anthropogenic studies have been divided into the following categories: (1) temperature rise, (2) hypoxia,
- (3) eutrophication, (4), nutrient pollution, (5) ocean acidification and (6) reduced salinity. By "ecological impacts" this paper refers to how stocks are not isolated from one other but exist as part of the wider food-web dynamics in the Baltic Sea. The health of these stocks is influenced by their ability to adapt through their reproduction capacity, habitat, food availability, wildlife competition, parasite resilience and natural predation. With this in mind, ecology studies have been divided into the following categories: (1) *Gadidae* family, (2) *Clupeidae* family, (3) Flatfish family and (4) food-web dynamics (Figure 1).









2.2 Sample collection

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Papers qualified for review where sourced using: Google Scholar, Scopus, Science Direct, Sage, Directory of Open Access Journals and Google. The search focused on the timeframe between 2010–2023 and was performed using several search terms in various combinations. These included (always) "Baltic Sea" and a fish species "cod, sprat, whiting, herring, flounder and plaice". This was followed by one of the following terms: climate change, temperature rise, hypoxia, eutrophication, salinity, ocean acidification, nutrient pollution, food-web dynamics, parasites, competition, status, health, predators, zooplankton, Cyanobacteria, phytoplankton, invasive species, diet composition, larvae, benthic habitat, nursery 70 habitat, stock, resilience, recovery, survival, changes, biodiversity, biomass and environment and ecosystem. Further articles were found using the snowball sampling approach, this process was achieved by reading the reference section of each relevant paper, in doing so one paper generated other viable articles (Naderifar et al. 2017). The process continued until no new papers started showing up indicating high quality coverage. Whilst the literature was being compiled, publications were systematically

75 analysed using strategic and critical reading methods (Matarese 2012). At length, through the data collection phase that lasted 12 months from March 2022 to March 2023 more than 12,150 articles were identified in the first step of the search. Ultimately 250 publications fit the inclusion within the 10 key topic areas (Figure 2).





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Figure 2. Article selection proses for the systematic literate review.

Articles included in the review had to meet a criteria of documenting information that could be attributed to "*top*" commercial fish species in the Baltic Sea. Other fish species with varying commercial value such as salmon *Salmo salar*, sea trout *Salmo trutta*, European perch *Perca fluviatilis and more* were excluded from the study to focus on species that shaped commercial fisheries in the Baltic Sea in the last 40 years (ICES 2019, 2022a, 2022b, 2022c, 2022d, 2022f, 2022g, 2022h). To keep the data manageable, the study filtered out articles published before 2010. Because of this, this paper is not a full systematic review of all research done on anthropogenic and ecology research indicators, but a collective summary of the key findings gathered from academic papers. In addition, the paper considered texts written only in English to focus on academia that can be accessed globally.

90 2.3 Analysis

Within each key topic, articles have been analysed against the following categories:

- Number of papers-This review method numerically illustrated the amount of research that has been conducted in the Baltic Sea region. In the case when articles addressed more than one research area, they were added into the statistics of multiple topics in accordance their relevancy.
- 2. *Country of publication*-This category referred to the nationality and university from which the authors of the journal article came from. In many cases an article had multiple authors from different countries, in those instances each country was marked as having a journal contributing to the research.
 - 3. *Baltic Sea s.d.*-ICES, a regional fishery advisory, divides the Baltic Sea region into 11 s.d. each one unique for its environment, bordering country and fish stocks (Figure 3) In the event that the study did not specify a s.d., this review categorized the paper as having findings relevant to the entire Baltic Sea region.
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- 4. *Key findings* Once the final papers were selected, significant time was spent reading articles to ensure that the most important findings from each topic were summarised in the discussion.







Figure 3. Statistical s.d. of the Baltic Sea (ICES 2019, 2022a, 2022b, 2022c, 2022d, 2022f, 2022g, 2022h).

105 **3 Results**

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Each article that fit the inclusion within the key topic areas was divided up accordingly and made into Table 1 (Rościszewski-Dodgson and Cirella 2023). From there key trends emerged. Within anthropogenic stressors, studies on eutrophication made up the highest number of articles with 47 respectively. This was followed by ocean acidification (33), temperature rise (31) and hypoxia (28). On the flip side, articles focused on the adverse consequences of a lack of inflow events and low salinity were the hardest to find, with 19 identified in this paper. Within the topics of ecology, fish species in the *Gadidae* family had the highest academic interest with 41 papers referenced in this study. Whilst articles discussing fish species in the flatfish family generated the lowest search results with 19 respectively. Food-web dynamics have a sizable sample of 44 papers included in the section due to the topic covering a wide range of issues. Thirty-two countries where accredited to a

publication related to the 10 topics areas, with all nations bordering the Baltic Sea making an appearance. Countries with the



- 115 greatest number of entries were Sweden (147), Germany (116), Finland (73), Denmark (67) and Poland (46) respectively. These countries achieved the highest overall research output and dominated the discussion. With relation to the ICES s.d., most research focused on the central region known as the Baltic Proper. With s.d. 25 being the most studied area with over 225 mentions. Other s.d. in the Baltic proper also had a high count with s.d. 26-28 mentioned 207, 204 and 206 times respectively. Sub-divisions 30-31 also known as The Gulf of Bothnia had the lowest academic interest with 150 and 139 120 mentions respectively. Despite this, the difference between the most and least researched s.d. did not exceed 38% indicating a
- balanced study effort.

Research area	Key topic	No. of papers	Reference	Country of publication	ICES Baltic Sea s.d.
Anthropogenic	Temperature rise	31	Arheimer et al. (2012), Barbosa and Donner (2016), Cederqvist et al. (2020), El-Shehawy et al. (2012), Friedland et al. (2012), Hägg et al. (2014), Hense et al. (2013), Hiddink et al (2012), Hinrichsen et al. (2011), Hordoir et al. (2012), Lehmann et al. (2011), Lindegren et al. (2010), Margonski et al. (2010), Meier et al (2012a), Meier et al (2012b), Meier et al. (2011a), Meier et al. (2011c), Meier et al. (2021), Meier et al. (2011d), Meier et al. (2019), Neumann (2010), Niiranen, et al. (2013), Philippart et al. (2011), Reusch et al. (2018), Rutgersson et al. (2014), Scharsack et al. (2021), Thøgersen et al. (2015), Viitasaloand Bonsdorff (2022), Voss et al. (2011), Voss et al. (2012), Voss et al. (2019)	Canada [1], Denmark [7], Estonia [2], Finland [4], Germany [18], Latvia [1], New Zealand [1], Norway [1], Poland [4], Portugal [1], Russia [2], Sweden [19]	21[23], 22[24], 23[26], 24[24], 25[26], 26[25], 27[25], 28[25], 29[25], 30[22], 31[22], 32[22]
	Нурохіа	28	Almroth-Rosell et al. (2011), Almroth-Rosell et al. (2021), Bange et al. (2010), Bendtsen and Hansen (2013), Breitburg et al. (2018), Carstensen et al. (2014a), Carstensen et al. (2014b), Casini et al. (2016), Conley et al. (2011), Díaz and Rosenberg (2011), Dietze and Löptien (2016), Gilbert et al. (2010), Gustafsson (2012), Hansson and Gustafsson (2011), Lehman et al. (2014), Meier et al. (2011b), Meier et al. (2017), Meier et al. (2018), Neumann et al. (2017), Norkko et al. (2012), Rabalais et al. (2010), Reed et al. (2011), Savchuk (2013), Stigebrandt et al. (2013), Vaquer-Sunyer and Duarte (2010), Vaquer-Sunyer and Duarte (2011), Villnäs et al. (2012), Zilí and Conley (2010)	Belgum [1], Canada [3], China [3], Denmark [3], Estonia [3], Finland [4], France [1], Germany [9], Kuwait [1], Latvia [3], Lithuania [1], Netherlands [1], New Zealand [1], Peru [1], Philippines [1], Poland [2], Russia [1], South Africa [1], Spain [1], Sweden [19], United States [3]	21[18], 22[19], 23[18], 24[19], 25[24], 26[23], 27[23], 28[23], 29[23], 30[13], 31[13], 32[19]

Table 1. Key topics and indicators of anthropogenic and ecology research areas related to top commercial fish species of the Baltic Sea.





Eutrophication	47	Andersen, et al. (2017), Andersson et al. (2015), Bergström et al. (2019), Brutemark et al. (2015), Cederqvist et al. (2020), Eilola et al. (2011), Dzierzbicka-Głowacka et al. (2011), El-Shehawy et al. (2012), Engström-Öst et al. (2011), Ferreira et al. (2011), Fleming-Lehtinen (2015), Gustafsson et al. (2012), Gustafsson et al. (2017), Hense et al. (2013), Hogfors et al. (2014), Kahru and Elmgren (2014), Kahru et al. (2020), Kaiser et al. (2020), Karlson et al. (2015), Klais et al. (2011), Legrand et al. (2015), Mazur-Marzec et al. (2013), Meier et al (2012a), Meier et al. (2019), Mort et al. (2010), Munkes et al. (2021), Murray et al. (2019), Neumann et al. (2012), Olenina et al. (2010), Olofsson et al. (2016), Ploug et al. (2010), Raateoja, et al. (2011), Rakko and Seppälä (2014), Reusch et al. (2018), Riemann et al. (2016), Śliwińska-Wilczewska et al. (2019), Stigebrandt et al. (2011), Varjopuro et al. (2014), Viitasaloand Bonsdorff (2022), Viktorsson et al. (2012), Voss et al. (2011), Walve and Larsson (2010), Wasmund et al. (2011), Wasmund (2017), Zillé and Conley (2010)	Belgum [2], Denmark [9], Estonia [3], Finland [17], France [1], Germany [14], Greece [1], India [1], Italy [1], Netherlands [2], Norway [3], Poland [6], Portugal [4], Russia [2], Samoa [1], Spain [1], Sweden [25], United Kingdom [3], United States [5]	21[21], 22[22], 23[22], 24[31], 25[33], 26[25], 27[36], 28[33], 29[27], 30[27], 31[22], 32[30]
Nutrient pollution	29	Andersson et al. (2015), Arheimer et al. (2012), Bring et al. (2015), Carstensen et al. (2011), Cederqvist et al. (2020), Dąbrowska et al. (2017), Gustafsson et al. (2014), Gustafsson et al. (2017), Hägg et al. (2010), Hägg et al. (2014), Hong et al. (2012), Hongisto et al. (2011), Korpinen et al. (2012), Kuss et al. (2020), Meier et al (2012a), Mort et al. (2010), Olofsson et al. (2016), Pihlainen et al. (2020), Ploug et al. (2010), Raateoja, et al. (2011), Räike et al. (2020), Reusch et al. (2018), Riemann et al. (2016), Savchuk (2018), Stigebrandt et al. (2014), Viktorsson et al. (2012), Wikner and Andersson (2012), Wulff et al. (2014), Yli-Hemminki (2016)	Australia [1], Denmark [6], Estonia [2], Finland [9], Germany [5], India [1], Latvia [1], Lithuania [1], Netherlands [1], Norway [2], Poland [2],Russia [1], Spain [3], Sweden [16], United States [1]	21[20], 22[19], 23[19], 24[22], 25[24], 26[20], 27[24], 28[23], 29[20], 30[19], 31[18], 32[20]
Low salinity	19	Berg et al. (2015), Brutemark et al. (2015), Engström-Öst et al. (2011), Fu, et al. (2010), Hansson and Gustafsson (2011), Kijewska et al. (2016), Kniebusch et al. (2019), Lehmann et al. (2022), Maar et al. (2011), Nissling and Dahlman (2010), Nowicki et al. (2016), Mohrholz et al. (2015), Rakko and Seppälä (2014), Reusch et al. (2018), Sanders et al. (2018), Śliwińska-Wilczewska et al. (2019), Takolander et al. (2017), Vuorinen et al. (2015), Westerbom et al. (2019)	Denmark [3], Estonia [3], Finland [8], Germany [7], Lithuania [2], Norway [1], Poland [4], Russia [1], Sweden [9], United Kingdom [1]	21[10], 22[10], 23[9], 24[10], 25[11], 26[12], 27[9], 28[10], 29[10], 30[9], 31[8], 32[10]



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	Ocean acidification	33	Beldowski et al. (2010), Brutemark et al. (2011), Carstensen et al. (2011), Dzierzbicka-Glowacka et al. (2011b), Fitzer et al. (2012), Frommel et al. (2012), Frommelet al. (2014), Graiff et al. (2015), Graiff et al. (2017), Gülzow et al. (2013), Gustafsson et al. (2014), Hammer et al. (2014), Hammer et al. (2017), Kuliński and Pempkowiak (2011), Kuliński et al. (2014), Maneja et al. (2013), Melzner et al. (2011), Müller et al. (2016), Omstedt et al. (2012), Omstedt et al. (2014), Reindl and Bolałek (2014), Reusch et al. (2018), Sanders et al. (2018), Scharsack et al. (2021),Skoog et al. (2011), Stiasny et al. (2016),Szczepańska et al. (2012), Takolander et al. (2019), Thomsen et al. (2017), Voss et al. (2019), Wahl et al. (2018), Wahl et al. (2020), Yli-Hemminki (2016)	Australia [1], Bermuda [1], Denmark [2], Estonia [2], Finland [6], Germany [22], Israel [1], Latvia [3], Lithuania [1], Norway [3], Poland [10], Portugal [1], Saudi Arabia [1], Spain [1], Sweden [6], United Kingdom [2]	21[25], 22[27], 23[27], 24[26], 25[26], 26[27], 27[24], 28[22], 29[13], 30[23], 31[23], 32[23]
Ecology	<i>Gadidae</i> family	41	Berg et al. (2015), Casini et al. (2012), Casini et al. (2016), Casini et al. (2021), Frommel et al. (2012), Gårdmark et al. (2013), Gårdmark et al. (2015), Haase et al. (2020), Heikinheimo (2011), Hinrichsen et al. (2012), Horbowy et al. (2016), Hüssy et al. (2010a), Hüssy et al. (2010b), Hüssy et al. (2011), Hüssy et al. (2012),Kijewska et al. (2016), Kristensen et al. (2014), Lindegren et al. (2010), MacKenzie et al. (2011), Mackenzie and Gislason (2011), Maneja et al. (2013), Margonski et al. (2020), Nielsen et al. (2013), Nielsen et al. (2014), Orio et al. (2017), Orio et al. (2019), Orio et al. (2020), Pachur et al. (2013), Petereit et al. (2014), Podolska et al. (2016), Ross et al. (2016), Ross and Hüssy (2013), Ryberg et al. (2021), Schaber et al. (2012), Stiasny et al. (2013), Tomczak et al. (2012), Voss et al. (2012)	Denmark [19], Estonia [1], Finland [3], Germany [14], Italy [2], Latvia [8], Netherlands [2], Norway [5], Poland [7], Spain [1], Sweden [15], United Kingdom [2], United States [2]	21[11], 22[19], 23[15], 24[22], 25[27], 26[23], 27[20], 28[20], 29[18], 30[10], 31[10], 32[10]
	<i>Clupeidae</i> family	30	Atmore et al. (2022), Casini et al. (2010), Casini et al. (2011), Dippner et al. (2019), Dodson et al. (2019), Dziaduch (2011), Eero (2012), Frommel et al. (2014), Heikinheimo (2011), Kleinertz et al. (2011), Kulke et al. (2018), Livdane et al. (2016), MacKenzie and Ojaveer (2018), MacKenzie et al. (2012), Margonski et al. (2010), Miethe et al. (2014), Ojaveer and Kalejs (2010), Ojaveer et al. (2011), Ojaveer et al. (2018), Polte et al. (2021), Raid et al. (2010), Rajasilta et al. (2019), Skrzypczak and Rolbieck (2015), Soerensen et al. (2022), Thøgersen et al. (2012), Unger et al. (2014), Voss et al. (2011), Voss et al. (2012)	Canada [1], Denmark [5], Estonia [7], Finland [4], France [1], Germany [10], Italy [1], Latvia [7] Norway [1], Poland [1], Russia [1], Sweden [8], United Kingdom [2], United States [1]	21[10], 22[11], 23[10], 24[17], 25[18], 26[20], 27[16], 28[19], 29[17], 30[10], 31[9], 32[12]
	Flatfish family	19	Cardinale et al. (2010), Borg et al. (2014), Dąbrowska et al. (2017), Florin and Lavados (2010), Haase et al. (2020), Järv et al., (2011), Jokien et al. (2019), Jokinen et al. (2019), Kuciński et al. (2023),	Belgium [1], Denmark [3], Estonia [2], Finland [5], Germany [4], Italy [1], Latvia [5], Lithuania [1],	21[6], 22[6], 23[4], 24[7],



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		Momigliano et al. (2018a), Momigliano et al. (2018b), Nissling and Dahlman (2010), Orio et al. (2017a), Orio et al. (2017b), Orio et al. (2019), Orio et al. (2020), Petereit et al. (2014), Polak-Juszczak (2017), Ustups et al. (2013), Ulrich et al. (2013)	Netherlands [2], Poland [4], Sweden [11], USA [1]	25[11], 26[12], 27[8], 28[9], 29[10], 30[2], 31[1], 32[6]
Food-web dynamics	44	Adam et al. (2016), Almqvist et al. (2010), Brulińska et al. (2016), Casini et al. (2010), Casini et al. (2012), Darr et al. (2014), Edrén et al. (2010), Engstedt et al. (2010), Gorokhova et al. (2016), Hogfors et al. (2014), Horbowy et al. (2016), Jakubavičiūtė et al. (2017), Janßen et al. (2013), Järv et al., (2011), Jaspers et al. (2011), Kleinertz et al. (2011), Koivisto and Westerbom (2010), Koivisto and Westerbom. (2012), Kuciński et al. (2023) Labuce et al. (2021), Larsson et al. (2015), Lefébure et al. (2014) Löfstrand et al. (2010), Lundström et al. (2010), MacKenzie et al. (2011), Mohamed et al. (2020), Nilsson et al. (2014), Ojaveer et al (2018), Olin et al. (2022), Olsson (2019), Otto (2014), Podolska et al. (2016), Roos et al. (2021), Ryberg et al. (2021), Schaber et al. (2011), Skrzypczak and Rolbiecki (2015), Stoltenberg et al. (2021), Unger et al. (2014), van Eerden et al. (2022), Vehmaa et al. (2013), Veneranta et al. (2020), Viitasaloand Bonsdorff (2022), Westerbom et al. (2019), Zaiko et al. (2010)	Denmark [10], Estonia [3], Finland [10], Germany [13], Latvia [6], Lithuania [4], Netherlands [1], Norway [1], Poland [6], Spain [1], Sweden [19], Switzerland [1], United Kingdom [1]	21[8], 22[10], 23[9], 24[13], 25[25], 26[20], 28[21], 29[19], 30[15], 31[13], 32[15]

4 Discussion

125 The study examined a range of academic papers, which collectively shed light on the ecological effects of key anthropogenic stressors on commercially important fish species. The findings underscore the ongoing rise in natural hazards and highlight the diverse responses exhibited by individual fish stocks, which are influenced by factors such as geographical location and their adaptive capacities. When comparing the stocks against one another there are clear winners and losers (Figure 4).









4.1 Anthropogenic studies

4.1.1 Temperature rise

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Studies that identified how long-term shifts in temperatures and weather patterns affect the Baltic Sea ecosystem were selected. The consensus among the 31 identified papers, is that the Baltic Sea and its ecosystem have already shown clear evidence of change in response to climate change. For example, a paper by Voss et al. (2019) through the ecological-economic modelling in cod fish catch, underscored how human induced ocean warming of +1.7 °C drastically decreases cod fishing opportunities in the region, whilst a +2 °C would completely diminish cod's changes of recovery due to cod larvae preferring

140 colder temperatures (Voss et al. 2019). This was further reinforced by studies conducted by Lindegren et al. (2010) Margonski et al. (2010) and Voss et al. (2012) who show in their results how temperature change negatively influenced cod and herring stock-recruitment abilities. Similarly, Thøgersen et al. (2015) did a forecast of the management difficulties and economic impacts climate change will have on Baltic Sea fisheries through the use of management scenarios based on the age structured Fishrent Age models. A study by Hinrichsen, et al. (2011) underlined how reducing fish catch mortality is not enough, by



- 145 placing an emphasis on how climate-driven long-term temperature trends in oxygen concentrations will be the greatest contributor for the Western and Eastern cod population downfall. Another study by Hiddink et al. (2012) revealed how the effect of temperature rise on marine fish biodiversity will be most felt in areas with low population connectivity, which the Baltic Sea has.
- Neumann (2010) calculated that the most serious impact of temperature change will be alterations in the physical parameters of species, who will have to alter habitat conditions and distribution patterns. Furthermore, Neumann (2010) emphasised how the activated warming will be favourable for cyanobacteria growth, creating longer lasting and wider blooms. Studies conducted a decade later by Meier et al. (2021) and Cederqvist et al. (2020) reinforce those earlier findings. In addition, other notable studies that discussed the impact of climate change on the Baltic Sea ecosystem are, Brander's climate cycle forecast study, Meier et al.'s (2011a) and (2011c) simulation studies, Andersson et al.'s (2015) future ecosystem management
- 155 study, Hordoir et al.'s (2012) thermal stratification experiment in the Baltic Sea, as well as, Meier et al.'s (2012) and Hägg et al.'s (2014) future nutrient load scenario studies. Other notable reads on the topic of temperature increases are Barbosa and Donner (2016), Philippart et al. (2011), Lechmann et al. (2011), Friedland et al. (2012), Niiranen, et al. (2013), Rutgersson et al. (2014) and Viitasaloand Bonsdorff (2022). Climate change is a wide concept that has influenced other anthropogenic hazards including, deoxygenation, eutrophication and reduced saltwater inflows that will also be considered in the following subsections.

4.1.2 Hypoxia

Within a sub-group of anthropogenic studies, deoxygenation of the Baltic Sea and the creation of hypoxia or dead zones is intensely researched, with 28 articles highlighted in this paper. Their findings underscore the expansion of dead zones. For example, Conley et al. (2011) identified 115 sites that have experienced hypoxia during the period between 1955–2009,

- 165 underscoring how the Baltic Sea contains over 20% of all known hypoxic sites worldwide. Other studies conducted by Gustafsson (2012), Savchuk (2013) and Hansson and Gustafsson (2011) modelled long-term development, volume and dynamics of hypoxic areas in various Baltic sub-regions. With all three papers highlighting how things are worsening. This notion is reinforced in studies conducted by Meier et al. in (2011, 2017), with the team of researchers creating a model that looked at how accelerated mean sea level rise will exacerbate the spread of dead zones. Similarly, Bendtsen and Hansen (2013)
- 170 conducted a study in the Baltic Sea-North Sea transition zone. Using an ocean model, they showed that the simulated effects from a 3 °C temperature rise on the sea floor will reduce oxygen concentration export production by a further 30% (Bendtsen and Hansen 2013). Other studies that indicated an extensive expansion of hypoxic areas are: Zilí and Conley (2010), Bange et al. (2010), Gilbert et al. (2010), Rabalais et al. (2010), Vaquer-Sunyer and Duarte (2011), Reed et al. (2011), Lehman et al. (2014), Breitburg et al. (2018) and Hansson and Gustafsson (2011). Whilst Almroth-Rosell et al. (2021) in their study
- 175 concluded that a worst-case scenario for the extent of hypoxic areas in the Baltic Sea has been reached.

With this heightened awareness that hypoxic areas are here to stay, academics have begun to study the effects increasing range and periods of hypoxia have on the local ecosystem of the Baltic Sea. For example, Díaz and Rosenberg



(2011) published an article on the potential environmental and economic consequences of deoxygenation, they discuss how a decrease in dissolved oxygen causes marine animals to become susceptible to diseases. Moreover, it reduces mobility, 180 survivability, growth and reproductive success. Such impacts are also discussed by Cartesnen et al. (2014), Vaquer-Sunyer et al. (2010) and Villnäs et al (2012) who in their papers emphasise how an increasing bottom-water hypoxia are the main stressors impacting benthic communities including: cod, whiting flounder and plaice, in the Baltic Proper and the Gulf of Finland. They cite how deoxygenised benthic region create barren wastelands on the sea floor devoid of life (Cartesnen et al. 2014, Vaguer-Sunver and Duarte 2010, Villnäs et al. 2012). Casini et al. (2016) showed the adverse consequences of hypoxia 185 on cod populations. Their paper discusses how hypoxia affects the species size, physiology, behaviour and trophic interactions, with statistical evidence demonstrating how there is a hypoxia-induced habitat compression on cod who are forced to crowd and compete for fewer resources. This was further reinforced in their 2021 study, which showed correlations between oxygen stratification, depth and distribution of Eastern Baltic Sea cod populations (Casini et al. 2021). On a positive note, a study by Norkko et al. (2012), demonstrates how increased abundances of the invasive species polychaetes *Marenzelleria spp* in the Baltic Sea, have helped mitigate some spread of hypoxia. Whilst studies conducted by Neumann et al. (2017), Dietze and 190 Löptien (2016) and Stigebrandt and Kalén (2013) highlight how major Baltic inflows have the potential to oxygenate the central Baltic Sea by importing heavy salty oxygen rich water across the Danish Straits. This oxygenized salt water would then

However, the last major saltwater inflow event occurred in 2015.

195 4.1.3 Eutrophication

Harmful cyanobacteria blooms as a result of eutrophication are considered one the biggest threats to the Baltic Sea's ecosystem, with a wide scope of literature dedicated to studying its causes, impacts and future trends (Zillé and Conley 2010). In the context of this paper, 46 studies have been selected. The most visible sign of eutrophication is increased algal growth which reduces water clarity and blocks sunlight from penetrating as deeply as before. A study by Bergström et al. (2019) on
the relative impacts of eutrophication identified how differences in water clarity affect fish directly, influencing the relative reproductive output and feeding efficiency. Each species has also highly individualised responses to cyanobacteria blooms, for example carnivorous fish are more negatively affected than their herbivore counterparts who gain a greater food source as a result of algae blooms (Bergström et al. 2019). This has adverse consequences for cod, whiting, plaice and flounder who predate on other fish. Moreover, benthic habits where *Gadidae* and flatfish species reside are expected to be under the biggest pressure, with cyanobacteria blooms contributing to the spread of hypoxia on the sea floor (Legrand et al. 2015, Dzierzbicka-Głowacka et al. 2011a). However, species in the *Clupeidae* family are also negatively affected as suggested by Suikkanen, et al. (2013) who demonstrates that plankton communities in the Baltic Sea have shifted the food web structure of smaller sized organisms, leading to decreased energy available for zooplankton and in turn herring, which rely on zooplankton as a food

settle on the sea floor in oxygen deprived areas potentially giving them a new lease of life (Stigebrandt and Kalén 2013).

source. Moreover, studies undertaken by Walve and Larsson (2010), Ferreira et al. (2011), Meier et al. (2012), Karlson et al.





- (2015), Kahru et al. (2020) and Viitasaloand Bonsdorff (2022) underscore how these blooms impact fisheries species because 210 when cyanobacteria decompose, it releases nitrogen and uses up oxygen in the water, creating an uninhabitable environment. Papers on the trends in phytoplankton composition and growth in the Baltic Sea published by Wasmund et al. (2011), Olenina et al. (2010), Ploug et al. (2010 Klais et al. (2011), Kahru and Elmgren (2014), Varjopuro et al., (2014), Mazur-Marzec et al. (2013), Meier et al. (2018), Kaiser et al. (2020) and Munkes et al. (2021) reinforce how large-scale shifts in climatic parameters will increase the occurrence of such events. Using a cyanobacteria life cycle model CLC, a study by Hense et al. 215
- (2013) revealed how compared to other phytoplankton groups, cyanobacteria generally prefer high water temperatures for growth, enabling them to benefit from climate change. The findings of this study are further reinforced by Neumann et al. (2012) who demonstrates how in the future, cyanobacteria blooms could make up 50 % of the total nitrogen load in the Baltic Sea. Meier et al. (2019 and 2018), Murray et al. (2019) and Voss et al. (2011) in their nutrient load scenarios, predicted record-
- 220 breaking cyanobacteria blooms events in the region. Other articles with similar conclusions were published by Śliwińska-Wilczewska et al. (2019) and El-Shehawy et al. (2012). Whist, long-term temporal and spatial trend studies by Andersen et al. (2018), Fleming-Lehtinen (2015) and Gustafsson et al. (2012) revealed that the Baltic Sea eutrophication problem is expanding.

4.1.4 Nutrient pollution

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In order to grasp why cyanobacteria blooms, occur in the Baltic Sea, nutrient pollution needs to be considered. For decades the Baltic Sea has been polluted by excessive richness of nutrients, namely nitrogen and phosphorus that enter the water though agricultural river run-off. This issue is exacerbated by the fact that the Baltic Sea has more than 250 rivers and streams emptying their waters into it. Scientists have closely monitored the extent of nutrient pollution in the Baltic Sea, with 29 papers highlighted in this review. Increased nutrient pollution negatively affects the health of commercially valuable fish 230 species who often spawn in various coastal lagoons and estuaries (Dodson et al. 2018, Kuss et al 2020). This is reinforced by Raateoja et al. (2011), Mort et al. (2010), Viktorsson et al. (2012), Stigebrandt et al. (2014), Ploug et al. (2010), Andersson et al. (2015), Olofsson et al. (2016), Yli-Hemminki (2016) and Gustafsson et al. (2017). These papers highlight how excess nutrient inputs of nitrogen and phosphorus in the Baltic Sea help promote cyanobacteria growth much earlier than is expected, creating longer and more damaging blooming cycles throughout the year. Phihlainen et al. (2020) projected how if things stay

- 235 the same, by 2100 the overall nutrient loading in the Baltic Sea will increase from 52% to 115% from its current levels. Highlighting how agricultural related nitrogen and phosphorus emissions represent more than two thirds of the current loading to the Baltic Sea. In addition, Räike et al. (2020) notes how nutrient export from Finnish rivers into the Baltic Sea have not decreased despite water protection measures. This sentiment is not shared by all academics, for example Kuss et al. (2020) underscores how anthropogenic nitrogen input to the Western part of the Baltic Sea had a gradual 30% decrease since 1995,
- 240 whereas the phosphorus input, experienced a sharp decline of 25% between 1995 to 2000, remaining the same ever since. Hägg et al. (2010, 2014) considered the 'worst 'and 'best 'case scenarios of nutrient pollution from an environmental perspective, noting how in the future, it is still possible to obtain increases and decreases in nitrogen and phosphorus loads. In





doing so, they undercore how with improved agriculture waste disposal management, can bring about improved conditions for the Baltic Sea despite the warmer weather. Furthermore, Gustaffson et al. (2012) noted how simultaneously reducing nitrogen and phosphorus loads would have a larger positive effect on the oxygen conditions of the sea floor, combating hypoxic areas and allowing marine life to reintroduce itself back into those benthic regions. This is reinforced by Riemann et al. (2016) who showed how partial post-nutrient pollution recovery is attainable, by investigating 45 Danish coastal ecosystems and revealing clear signs of recovery for benthic macrofauna, macroalgee and eelgrass. However, articles by Carstensenet al. (2011), Arheimer et al. (2012), Bring et al. (2015) and Meier et al. (2012a) underscore that climate change will only exacerbate the eutrophic dangers associated with riverine nutrient pollution and limit the recovery success for many commercially valuable fish species most notably cod and flatfish species. Other relevant studies conducted on the topic of nutrient pollutants and riverine discharge are Hong et al. (2012), Hongisto et al. (2011), Korpinen et al. (2012), Wikner and Andersson (2012), Wulff et al. (2014) and Savchuk (2018). Direct studies linking the effects of nutrient pollution on top commercial fish species have not been conducted, instead they focus on eutrophication (see section 4.1.3), the by-product of increased nitrogen and

255 phosphorus run-off.

4.1.5 Low salinity

Salinity levels and their impacts on marine life are highly researched in the Baltic Sea with 19 articles highlighted in this study. The Baltic Sea has the lowest salinity of any sea in the world, with an average salinity level of 10 ppt (parts per thousand), that changes sightly within each ICES s.d. Several key topics have been investigated on salinity, including studies by Kniebusch et al. (2019) and Mohrholz et al. (2015) on the changing salinity gradients in the Baltic Sea. They highlight how unfavourable weather patterns for saltwater inflows from the North Sea, coupled against the hundreds of rivers that are flow into the Baltic Sea, have resulted in significantly more freshwater being added to the Baltic Sea each year (Kniebusch et al. 2019). This occurs to such an extent that if significant inflows events do not happen in this century the Baltic Sea could potentially become a lake (Mohrholz et al. 2015, Reusch et al. 2018) A study by Lehmann et al. (2022) underscored how any given ecosystem is adapted to the current salinity level and sudden change in the salinity balance would lead to ecological stress. Consequently, marine-tolerant species will be disadvantaged, and their distributions will reduce, with freshwater species successfully colonizing the area (Lehmann et al. 2022). Miethe et al. (2014) suggests that the distribution pattern of herring was related to the environmental conditions of saltwater inflow events into the Baltic Sea. Despite the fact that herring can tolerate a wide variety of salinities and temperatures, central herring stocks were observed to avoid water layers with the lowest

- 270 oxygen saturation and salinity levels. Whilst Vuorinen et al. (2015) underlines how reduced saline shifts the distribution for marine benthic foundation species including cod, plaice and flounder. This change would extend over hundreds of kilometres and have extensive cascading effects for fish ecology and fisheries (Vuorinen et al. 2015, Nissling and Dahlman 2010). Kijewska et al. (2016) studied the stress response to different salinities in the Eastern and Western Baltic cod populations. Their results showed how cod that spent a lifetime in higher salinities conditions in the Kile Bight (18%) would not migrate to
- 275 less saline regions Gdansk Bay (8%). In doing so, salinity is shown to create a barrier maintaining the physical and genetic



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separations between the different cod stocks. This is reinforced by Berg et al. (2015) who in their study showed how cod colonised the central Baltic Sea when the surface salinity was 12-14%. Since then, surface salinity has gradually decreased to around 7%. Hence, low saline waters are a major force influencing the spawning success of cod in the Baltic Sea (Berg et al. 2015). Additionally, reduced salinity promotes harmful bacterial blooms, as low salinity creates a favourable environment for *Dolichospermum* spp (Brutemark et al. 2015). Similar experiments were conducted by Engström-Öst et al. (2011) and Rakko and Seppälä (2014), with their results displaying the positive effect reduced salinity has on the growth rates of various cyanobacteria species. Consequently, low salinity in the Baltic Sea contributes to eutrophication and hypoxia.

4.1.6 Ocean acidification

- The marine CO₂ system is currently the focus of many investigations in marine research aimed at understanding ocean acidification and the processes linked to the consumption or production of CO₂ in the Baltic Sea. This region is considered to be especially vulnerable to ocean acidification because it has is considerably lower alkalinity levels when compared to the ocean (Omstedt et al. 2014). Multiple studies focus on the distribution and spread of CO₂ with 33 highlighted in this study. For example, Beldowski et al.'s (2010) measurement programme resulted in a comprehensive mapping of the distribution pattern of the total CO₂ and alkalinity in the region. They calculated that an annual increase of CO₂ by 1.2–1.5 ppm will
- 290 decrease pH by 0.002 units per year (Beldowski et al. 2010). Other studies that measured the unfavourable prognostics of organic carbon as well as nitrogen and phosphorus cycling the Baltic Sea induce; Dzierzbicka-Glowacka et al. (2011b), Gustafsson et al. (2014), Müller et al. (2016), Omstedt et al. (2012) and Brutemark et al. (2011). These papers discussed how the accumulation of CO₂ is controlled by the input of organic matter through rivers, the frequency of saltwater renewal and the warming of atmospheric conditions. Consequently, Kulinski and Pempkowiak (2011) noted how the Baltic Sea has at least 3–
- 5 times higher organic carbon concentrations than the North Sea. Whilst. Melzner et al. (2013) underscored how ocean acidification amplifies hypoxia throughout coastal habitats. Higher concentrations of Methane also exacerbate the warming of the Baltic Sea and make the seawater more acidic (Gülzow et al. 2013, Schamade et al. 2010, Reindl and Bolałek 2014). This can have serious consequences for marine life because some species cannot tolerate the more acidic environment. Melzner et al. (2010) emphasised how calcifying organisms such as blue muscles *Mytilus edulis* will be particularly vulnerable to pH
- 300 alterations, by falling in abundance and size. This sentiment was also shared by Whal et al. (2018), Thomsen. et al. (2017) and Sanders et al. (2018). Whilst in the context of rocky seaweeds, Graiff et al. (2017) noted how ocean acidification and warming could negatively impact the reproduction of keystone species such as *Fucus vesiculosus*. Other important macroalgae studies related to ocean acidification have been published by Graiff et al. (2015), Takolander et al. (2017) and Wahl et al. (2020). Although these studies don not address top commercial fish stocks directly, the destruction of blue mussels and seaweed beds
- 305 could cascade up the food chain and negatively affect cod, plaice and flounder who rely on these species as a food source or nursery habitat. There is also evidence to show that ocean acidification negatively affects cod and herring larvae survival see section *4.2.1* and *4.2.2* (Stiasny et al. 2016, Frommel et al. 2012, 2014).



4.2 Ecology studies

4.2.1 Gadidae family: Cod and whiting

- 310 The most numerously researched group of commercially valuable fish species in the Baltic Sea are in the *Gadidae* family. Among them, whiting *Merlangius merlangus* and the Atlantic cod *Gadus morhua* a species that was once synonymous with Baltic Sea's fishing power. Cod are divided into Eastern and Western stocks (ICES 2019). However, since their population decline in the last four decades and the subsequent closure of targeted cod fisheries in 2019, scientists have been intensely studying the species in order to understand why this happened, with 37 papers highlighted in this study. A number of articles
- 315 looked at the early life stage survival of cod against the threats discussed in anthropogenic study section. Stiasny et al. (2016) conducted mortality estimates on Western cod larvae populations and incorporated their recruit models under ocean acidification. Their results demonstrated how larvae recruitment was reduced to an average of 8% against the current recruitment levels (Stiasny et al. 2016). Frommel et al. (2012) reinforced how exposure to increased CO₂ can lead to lethal tissue damage in many internal organs of cod larvae, consequently ocean acidification acts as an additional source of fish
- 320 mortality at an early life stage. Hussy (2011) further emphasised how salinity and oxygen are the key drivers influencing the water depth at which cod eggs are buoyant and capable of hatching. Noting how cod larvae have limited survival success in regions with oxygen-poor depths Hussy (2011). Whilst Petereit et al. (2014) noted how cod larvae have the highest changes of survival in April and May but no cohorts that drifted into the central Baltic Sea survived due to the lower saline and oxygen levels. Studies on cod larvae with similar conclusions were conducted by: Margonski et al. (2010), Voss et al. (2012), Manjena
- 325 et al. (2013), Hinrichsen et al. (2012), Ljunggren et al. (2010) and Ojaveer et al. (2011) respectively. Lastly, according to Mion et al. (2018) the disappearance of larger female individuals has also reduced cod spawning capacity because larger and older individuals produce a higher number of eggs (Mion et al. 2018). Consequently, the remaining smaller females in the Baltic are producing fewer eggs, further limiting their ability to repopulate.

Population distribution, feeding and growth of commercially valuable fish stocks was also highly researched by

- 330 academics. Neuenfeldt et al. (2020) demonstrated why cod reduced in size over the last two decades. Their study showed how food reduction led to high densities of smaller cod competing for scarce resources, stunting their growth. Pachur et al. (2013) emphasised this, when they studied the food composition of Eastern cod catches within the Polish Exclusive Economic Zone. Their results showed that cod diet has undergone changes since the 1980s, noting how sprat became the main diet component rather than herring that where traditionally their most numerous sources of food (Pachur et al. 2013). A study by Gårdmark et
- 335 al. (2015) also underscored how cod's diet has changed, noting that this has further impacts on spatio-temporal dynamics of other structured populations. Casini et al. (2016) studied the body conditions of cod, their analysis revealed how changes in cod conditions are related to feeding opportunities, induced by density-dependence and food limitations, citing how their reductions in size had large implications for fisheries. Furthermore, Casini et al. (2012, 2016) showed how hypoxic areas further deteriorate cod's health through mechanisms related to physiology, behaviour and trophic interactions. In a study
- 340 conducted by Schaber et al. (2012) on the distribution patterns of cod in the Bornholm Basin they noted how both salinity and



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oxygen concentration were identified as key parameters affecting cod distribution. Consequently, increased hypoxia and eutrophication in the Baltic Sea forced cod out of their previously favoured habitats (Schaber et al. 2012). Whilst a study, by Nielsen et al. (2013), noted how their abundance has changed considerably as a result of variations in the environment, indicating that unlike their North Sea counterparts, juvenile cod in the Baltic Sea do not aggregate in dense schooling patterns. Other notable cod related studies that looked at the age structure and spatio-temporal dynamics, similarly suggest that there is less large adult cod (Hüssy et al. 2010a, 2010b, 2012, Nielsen et al. 2015, Kristensen et al. 2014, Mackenzie and Gislason

- 2011, Orio et al. 2017, 2019). As cod biomass declined in the last 30 years, sprat and herring where able to take over as the key species in the Baltic Sea. With Tomczak et al. (2012, 2013) suggesting that cod's decline resulted in trophic effects that cascaded down to *Clupeidae* fish who lost their main predator.
- Whiting *Merlangius merlangus* is also commercially fished species in the *Gadidae* Family predominately fished in the western Baltic Sea, its economic value is much smaller when compared to cod. In accordance with its less significant status, there is fewer research published on whiting, with two papers highlighted in this study from the same leading author. They conducted a study on the diet of whiting in the Western Baltic Sea noting how clupeids made up 90% of the diet of adults, whilst gobies, brown shrimps and polychaetes were the main prey for juvenile whiting (Ross et al. 2013, 2016). In doing so, they acknowledged how whiting are a top predator in the Western Baltic Sea and it is important to investigate their ecology
- and population dynamics. So far extensive population assessments of whiting have only been conducted in the North Sea and not much is known about the impact anthropogenic stressors have on their population.

4.2.2 Clupeidae family: Herring and sprat

- Herring and sprat from the *Clupeidae* family are major marine fish species of the highest commercial value in the 360 Baltic Sea. With ICES initiating the management of herring stocks in the Baltic Sea since the 1970s. Herring is assessed in four stocks; Bothnian, Western, Central and Riga herring. Their status varies, for example the spawning stocks biomass (SSB) for Bothnian and Central herring stabilised in the last 6 years. Whilst Riga herring continue to grow in number. In contrast, Western herring are on the brink of collapse having experienced substantial SSB declines in the last decade (ICES 2022b, 2022c, 2022d, 2022e). With this in mind, intense research is carried out to closely monitor herring. For example, Raid et al.
- 365 (2010) looked at the recruitment dynamics herring populations in the Gulf of Riga. Their study highlighted how herring are in a better state than cod, because they demonstrate remarkable geographical variability, with all 12 local populations having adapted to the highly variable environmental conditions in the region. This has enabled Riga herring socks to remain consistent throughout the decades, experiencing gradual periods of decline, growth and vice versa. This was reinforced by Atmore et al. (2022) who showed how different stocks had varied spawning success, with autumn spawners often making up 90% of Riga
- 370 herring landings. However, MacKenzie and Ojaveer (2018) underscored how despite having large numbers of offspring that grow and reproduce quickly, herring can still undergo drastic population declines over time. Dodson et al. (2018) studied the environmental determinants of western larval stocks. With their results indicating that the abundance of yolk-sac larvae was significantly higher during the optimal temperatures of 9°C to 13°C, with herring hatching healthy and in great numbers. In



contrast, as the temperatures rose, many herring larvae began to deform (Dodson et al. 2018). Polte et al. (2021) similarly 375 pointed out how Western Baltic herring have reduced reproductive success capabilities during warmer winters. Their results revealed that the late seasonal cold periods have led to a reduced abundance of juveniles. With each winter day delay resulting in a 3% reduction in the annual herring reproduction index (Polte et al. 2021). Frommel et al. (2014) also showed how exposure to increased CO_2 can cause lethal tissue damage and increased mortality in herring larvae.

- Herring populations in the Bothnian and central Baltic Sea are ten times higher in the North and West. However, this 380 does not mean that the population is healthy. In a study conducted by Dziaduch (2011), on the diet composition of central herring, he highlights how out of the 1615 analysed herring, no stomach was full of food, on the contrary in the Southern Middle Ban region, 90% of all herring had empty stomachs. This reduction in food consumption was likely initiated by a change in the species composition of their prey (zooplankton) and by increased food competition between other herring and sprat (Dziaduch, 2011). This was further reinforced by Livdane et al. (2015) who noted how zooplankton availability is a major
- 385 factor affecting their well-being. Furthermore, Casini et al. (2010), showed how herring growth is triggered by the abundance of sprat, consequently herring growth is considerably lower when there is a high sprat density. Dipper et al. (2019) observed a decreasing trend of 3-year-old central Baltic herring in terms of their mean weight from 50-70g in the 1970s to 25–30g today. Attributing increasing precipitation, reduction in the marine habitats and a change in the prey community as the main stressors. With the overall consensus among academic literature indicating that although still sizeable in number, herring stocks can be
- 390 vulnerable to the combined challenges of overfishing, eutrophication, climate change, reduced salinity and competition from expanding sprat populations (Atmore et al. 2022). Other notable studies on the population dynamics of herring have published by Soerensen et al. (2022), Meithe et al. (2014) and Rajasilta, et al. (2019) respectively.

Sprat Sprattus sprattus is the smallest fish species in the Clupeidae family and there is slightly less research published on sprat when compared to herring. Sprat in the Baltic Sea are monitored as a single stock that encompasses s.d. 22-32 (ICES 395 2022h). They are currently the single biggest stock in the Baltic Sea with the largest TAC quotas. Voss et al. (2011) noted how sprat have displayed positive population fluctuations thanks to increasing temperatures improving recruitment success during their early life stage. For instance, higher temperatures result in lower egg mortality because larvae develop faster and in

greater numbers resulting in lower predation and accelerated growth (Voss et al. 2011). MacKenzie et al. (2012) attributed

how rising temperatures have the greatest positive influence on sprat. Utilising a climate-ocean-fish population model, they 400 estimated that with sea temperature rise of 2-5°C and presently defined levels of sustainable exploitation, median sprat spawning biomass could increase to 1.5 million tonnes in the upcoming century (MacKenzie et al. 2012). In doing so, research on sprat suggests that they are among the few commercial fish species that could benefit from the effects of ocean warming.

Sprat experience different levels of success depending on the region. With 75% of the total sprat stock caught in the Northern Baltic and the Gulf of Finland (Casini et al. 2011). A study by Kulke et al. 2018 on the feeding dynamics of vertically 405 migrating sprat, revealed significantly higher mean stomach contents for the Bornholm Basin when compared to the Aroka and Gotland Basin. With the preferred feeding depth of 26 m where light intensity is higher and plankton is visible (Kulke et al. 2018). Whilst Ojaveer et al. (2010) highlighted how the environment for sprat is the most stable in the South Western region



and attributed the freshwater discharge variations as the main factor affecting the periodical changes in the abundance of Baltic sprat. Noting, how during periods of high river runoff sprat habitat expands and their stocks increase (Ojaveer et al. 2010).
Furthermore, low salinity hinders effective reproduction of cod (their top predator). Consequently, as the abundance of cod decreases, sprat populations increase in number. Voss et al. (2012) also noted how sprat's larvae survival time increased by an additional 4 days (~ 45%), indicating a reproduction advantage for sprat under forecasted future temperature increases. Eero (2012) noted how sprat have positively reacted to the changing environment, reduction of cod populations and are outperforming herring in many categories. For example, Ojaveer et al. (2018) compared the stomach contents of herring and sprat, they highlighted how when it comes to feeding on zooplankton, the share of empty stomachs was lower for sprat, indicating how sprat seems to be more successful than herring at finding and consuming prey. Other research that studied the relationships between cod, herring and sprat in the changing environment of the Baltic Sea with similar conclusions include: Margonski et al. (2010), Casini et al. (2011), Heikinheimo (2011) and Tomczak et al. (2012).

4.2.3 Flatfish family: Flounder and plaice

- 420 Since the decline of cod, flatfish have become one of the most economically important species for small-scale fisheries in the Central Baltic Sea. Of all the flatfish species, flounder *Platichthys flesus* are the focus of most academic flatfish studies. The European plaice is the only flatfish with imposed TAC limits, those quotas have annually increased due to high recruitment. ICES (2022f, 2022g) monitors plaice fisheries as two separate stocks, one in s.d. 21-23, (Kattegat, Belt Seas, and the Sound regions) and the other in s.d. 24–32 (Baltic Sea, excluding the Sound and Belt Seas). Whilst the CFP monitors plaice
- 425 as a single unit (European Commission, 2022). Flounder have no catch restrictions imposed on them due to their perceived healthy status. Conversely, with their increasing significance, a small contingent of academic research has been dedicated to them with 19 highlighted in this study.

Haase et al. (2020) noted how flounder populations increased in the past two decades and hypothesised that flounder have deprived cod of benthic food resources through competition. Orio et al. (2017a) illustrated how flounder and cod have progressively been migrating to shallower depths as a result of expanded hypoxia in deep waters, forcing them to compete with one another. As a result, a general decline in size and weight was evident for both, with Orio et al. (2017a) indicating that demersal fishes in the Baltic Sea are progressively dominated by smaller individuals. Moreover, pelagic spawning flounder had a negative reaction to rising temperature. Consequently, despite a positive relation with the current salinity levels, spawning areas of flounder in the Bornholm Basin have reduced (Orio et al. 2017b). This was further reinforced in Orios et

435 al.'s (2019 and 2020) papers which showed further spatial contraction of cod and flounder populations in the last 40 years as a result of significant anthropogenic and hydrological changes. Furthermore, Momigliano et al. (2018a) attributed poor genetic diversity as one of the leading causes threatening the adaptability of flounder. Using, DNA samples, they showed how reduced genetic diversity in the Åland Sea and the Gulf of Finland made flounder less capable and more vulnerable to changing environmental conditions (Momigliano et al. 2018a). This issue was also highlighted by Jokinen et al. (2019) who revealed on



440 the basis of genetic analyses that in 1983 the fishery unknowingly targeted primarily one gene pool of flounder, wiping out genetic diversity sustenance of those flounder stocks (Jokinen et al. 2019).

An earlier study by Jokinen et al. (2016) on flounder in the Northern Baltic Sea, emphasised how shallow habitats for juvenile flatfish are most vulnerable to coastal eutrophication (Jokinen et al. 2016). This was shown by exploring quantitative relationships between juvenile flatfish abundance and vegetation density. The results revealed a negative correlation, whereby

- the occurrence of flatfish was sparser when there is greater vegetation cover in an area (Jokinen et al. 2016). Furthermore, using historical and current data on juvenile flounder in nursery areas along the Finnish coast, Jokinen et al. (2016) demonstrated 40 times decline in juvenile flounder densities since the 1980s. A study by Nissling and Dahlman (2010) noted how salinity governs the reproductive success of flounder. They assessed flounder in five locations along the salinity gradient in s.d. 25, 27, 28 and 29, with their results indicating how reduced salinity negatively affected flounder's ability to reproduce
- 450 in those areas (Nissling and Dahlman 2010). Similarly, a study by Ustups et al. (2013), reinforced that flounders recruitment success is based on their ability to produce eggs that can float in less dense (low saline) waters. Their study demonstrates how spawning stock biomass and reproductive volume are the most significant factors in determining flounder larvae abundance in the region (Ustups et al. 2013). Moreover, Borg et al. (2014) highlighted how flatfish exhibit significant year to year variation in recruitment and distribution. With females and males have alternative diet and habitat preferences. Whilst Momigliano et
- 455 al. (2018b) and Lavados (2010) noted how flounder in the Baltic Sea display contrasting reproductive behaviours and diet preferences consequently their resilience varies in each location.

Despite their sizable TAC allowance and regional significance, studies that strictly focus on plaice *Pleuronectes platessa* in the Baltic Sea are limited with 2 highlighted in this study. The most detailed study on plaice was conducted by Ulritch et al. (2013) on the variability and connectivity of plaice populations from the Eastern North Sea and Western Baltic

- 460 Sea. Their results suggest that plaice in Skagerrak, Kattegat, the Belts and Sound Baltic Sea regions have a local population but are also closely linked with plaice in the North Sea (Ulritch et al. 2013). Spawning in the Kattegat usually occurs between February and March between 30 and 40 m depth in temperatures of 4 °C (Ulritch et al. 2013). However, a significant portion of the eggs and larvae settling in shallow waters of Skagerrak are considered to come from the North Sea. This drift is reinforced during winter which has stronger winds, allowing larvae to drift further into the Kattegat. Free-floating eggs are
- 465 even found in the deeper basins of the South Baltic Sea, with spermatozoa and eggs well adapted to the low salinity conditions that enable plaice to prevail in those areas (Ulritch et al. 2013). Furthermore, the analyses revealed how plaice stocks have strong genetic diversity indicating a healthy population (Ulritch et al. 2013). However, Ulritch et al. (2013) noted how the Danish tagging data revealed limited movements for adults and juveniles, most notably in the Belt, Western Baltic, Kattegat and North Sea, where up to 90% of the fish were recaptured in the same area as they were released. Regional migration
- 470 dynamics were only present in 5–10% of the tagged individuals, as such it is easy to conclude that plaice have non-migratory behaviours, making them more susceptible to the environmental damage and habits loss caused by anthropogenic stressors. Cardinale et al. (2010) studied population size and distribution of plaice in the Kattegat–Skagerrak. They showed how the current adult biomass has reduced by approximately 60% when compared to the 1960s. Moreover, the average maximum



individual length for adult plaice has fallen by 10 cm over this time period. With reduced trends in mean length linked to
increased fishing mortality in the last 20 years Cardinale et al. (2010). Despite this, recruitment was the highest on record recently, with Cardinale et al. (2010) suggesting that the alleged link between coastal environmental degradation and juvenile survival is low.

4.3 Food-web dynamics

4.3.1 Prey-predator relationships

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This century, fishing and anthropogenic changes have led to a food–web reorganization for most species (Tomczak et al. 2012, 2013). The Baltic Sea has a low biodiversity, this means that there are only a few animal groups driving the systems food-web dynamics. Interactions between commercial fish species have been previously discussed. Instead, the 44 highlighted in this section, showcase the impact other marine predators and prey have had on the status of commercial fish. One example are bivalves such as clams, oysters and mussels, who are among the most important taxonomic groups in benthic habitats

(Zaiko et al. 2010). Studies conducted by Löfstrand et al. (2010), Darr et al. (2014) and Koivisto, and Westerbom (2010, 2012) on the habitat structure and biodiversity of blue mussels. impacts wider population structures, namely flatfish who depend on mussels as a primary food source. Moreover, blue mussels are filter feeders that consume nutrients in the water, consequently Koivisto (2010 and 2012) underscore their immense value in mitigating eutrophication. Westerbom et al. (2019) notes how adult abundance of blue mussels was related salinity, winter severity, wave exposure and depth. In the Gulf of Finland, a population peak was recorded in 1998, since then the biomasses of blue mussels dropped by 80%, indicating a potentially

alarming future for benthic stocks as the Baltic Sea continues to become less saline (Westerborn et al. 2019).

Zooplankton and copepods community structures and dynamics studies are also key when determining the health of herring and sprat, who predominately feed on these tiny organisms to survive (Otto 2014, Vehmaa et al. 2013, Gorokhova et al. 2016, Labuce et al. 2021). Otto (2014) investigated the long-term dynamics of three dominant zooplankton species in the

- 495 central Baltic Sea *Acartia spp., Temora longicornis*, and *Pseudocalanus acuspes*. With the study suggesting that when climate changes, zooplankton species can change in shape, size and behaviour (Otto 2014). Some zooplankton species benefiting from increasing temperatures by growing in abundance, whilst other species fall in number, migrate or undergo local extinctions. In doing so, Otto (2014) showed how *Acartia spp.* and *T. longicornis* had a positive response to increasing spring temperatures by having highest egg production rates in temperatures of up to 18°C. Hogfors et al. (2014) also demonstrated how bloom-
- 500 forming cyanobacteria promote higher copepod reproduction, providing a greater food-source for adult herring and sprat. Whilst Ojaveer et al. (2018) did a taxonomic analysis of stomach content of herring and sprat and showed a positive correlation between the predators and prey. With the stomach fullness of *Clupeidae* fish increasing in areas with a greater number of zooplankton.

On the opposite end, is vital to consider the dietary dynamics of species who predate on commercially valuable fish. 505 For example, a study by Lundström et al. (2010) on the diet composition of grey seals *Halichoerus grypus* in the Baltic Sea,



noted how herring are the most commonly sourced prey in all regions and age groups, followed by sprat in the South, and whitefish in the North, with juveniles eating considerably more small non-commercial species than older seals. However, MacKenzie et al. (2011), emphasised that seal predation had a much lower impact on cod recovery, compared to the effects of anthropogenic stressors and fisheries. Whilst Roos et al. (2012) underscored how even though the number of grey seals is
slowly recovering, they do not impact stock dynamics. A similar sentiment was shared by Edrén et al. (2010) who modelled spatial patterns of harbour porpoises *Phocoena phocoena*, despite predating on herring, cod and sprat, their population is so small that their interactions do not negatively affect fisheries. Other predators such as the Northern pike *Esox luciu*, predate on smaller fish, but not much is known about their interactions with sprat and herring (Engstedt et al. 2010, Nilsson et al., 2014 and Larsson et al. 2015).

- 515 More recent invasive species seemed to have had greater negative impacts on commercially valuable stocks, for example Järv et al. (2011) illustrates how the recent introduction of round gobies *Neogobius melanostomusin* in Mugga Bay may negatively affect flounder. They highlight significant overlap in terms of the diet composition between these species, with gobies shown to have a larger diet variability and fuller stomach contents, suggesting that they may be outperforming flounder in the area (Järv et al. 2011). In addition, three-spined stickleback populations have recently increased in many coastal areas
- 520 of the Baltic Sea. With Olin et al. (2022) pointing how reduced predation and eutrophication have created more favourable conditions for sticklebacks. Their presence has the potential to alter the food-web dynamics as they outcompete other fish, and can also feed on their larvae (Jakubavičiūtė et al. 2017, Lefébure et al. 2014). Another predator that should not be overlooked is the Great cormorant *Phalacrocorax carbo* whose numbers in the Eastern and Northern Baltic Sea are expanding (van Eerden et al. 2022, Veneranta et al. 2020). Thus far studies of cormorants focused primarily on their consumption of perch *Perca*
- 525 *fluviatilis*, with Veneranta et al. (2020) highlighting how the high density of cormorants can reduce perch catches locally. van Eerden et al. (2022) notes how in the Finish Gulf significant interaction between Cormorants and fisheries is unlikely, although local measurable effects of Cormorant consumption on the commercial yield of perch may exist. Although there are no studies investigating the impact of these invasive species on top commercial fish stocks. Monitoring cormorant, stickleback and round goby distribution, population and feeding habits can be used to assess food-web interactions in the Baltic Sea.
- 530 Perhaps the single biggest group of invasive species that serve as a competitors and predators for many commercially valuable species are jellyfish, including the moon jellyfish *Aurelia aurita* and lion's mane jellyfish *Cyanea capillata*. Their growing number should be taken into consideration, as both species can consume cod larvae and compete with sprat and herring for the same zooplankton resources (Janßen et al. 2013). Stoltenberg et al. (2021) noted how large outbreaks of moon jellyfish overlap in time with late spawning cod in the Borholm basin, citing older papers they conclude that both *Aurelia*
 - *aurita* and *Cyanea capillata* heavily prey on eggs of Eastern cod (Stoltenberg et al. 2021). Furthermore, they highlight how cod eggs were found in 49.3% in guts of lion's mane jellyfish and in 5.5% in the guts of moon jellyfish (Stoltenberg et al. 2021). On the flip side, Stoltenberg et al. (2021) mentioned how adult whiting and herring have been documented predating on moon jellyfish, although no studies in the Baltic Sea have recoded such behaviour. In the Western Baltic, the invasive warty comb jelly *Mnemiopsis leidyi* was recorded for the first time in autumn 2006 (Schaber et al. 2011). The lowering salinity





540 gradient prevents the species having a self-sustaining population in the rest of the Baltic Sea (Jaspers et al. 2011). Despite this, the comb jelly has travelled with the currents and it is often found predating in important spawning grounds of top fish stocks (Schaber et al. 2011). Brulińska et al. (2016) highlighted how increased jellyfish outbreaks are caused by climate change, eutrophication and nutrient pollution and will likely continue to become more frequent in the Baltic Sea. Therefore, understating the population dynamics and feeding preferences of these predators has the potential to inform wider fisheries 545 management strategies.

4.3.2 Parasitises of Fish

Parasitic presence in the alimentary tract of fish is a universal problem, with the ability to cause organ, physiological, behavioural and reproductive damage in many species. In total, 9 papers tackling the issues of parasitic infections in top commercial fish species have been highlighted in this review. Ryberg et al. (2021) conducted a study on 642 livers in the
Eastern Baltic Sea. Their results showed how the probability of cod being in a critical condition increased when the parasitic nematode *Contracaecum osculatum* was detected. Whereas studies by Horbowy et al. (2016) and Podolska et al. (2016) showed how in the case of the Eastern cod stock, the body condition of infected individuals was 20% lower than of fish free of *Contracaecum* parasites. This is further reinforced by Mohamed et al. (2020) who illustrate that Parasitic presence slows the downregulation of growth in cod. Moreover, the prevalence and intensity of infection was highest in adult cod with the length between 70–80 cm. For herring, Unger et al. (2014) conducted a study on Central, Western and the Gulf of Finland herring stocks. Their findings showed how the distribution and abundance of the parasite species differed according to region, with a decreasing presence towards the East of the Baltic Sea. In the case of sprat, Skrzypczak and Rolbiecki (2015) examined the

- presence of parasites in s.d. 25-26. The overall prevalence of parasites was low with 3.2% of sampled sprat found with either *Lecithaster gibbosus, Hysterothylacium aduncum* and *Contracaecum* spp. This is reinforced by Kleinertz et al. (2011)
- 560 who highlight how the Baltic Sea contains sprat with a lower number of parasite infections when compared to the North Sea. For flounder, Kuciński et al (2023) explains that a notable decline in the fitness and catch volume of flatfish species has been observed. They sampled Slupsk Bank, in order to determine possible factors behind the changes. Their results revealed a prevalent *Glugea stephani* presence with a mean infection intensity of 9.15 and the presence of the microsporidiosis parasite in 42 % of the investigated flounder, much higher than expected. Although this sample of papers show the presence of parasitic
- 565 fauna on commercial fish species, the extent of their impacts is still not well explored in the Baltic Sea.

5 Data availability

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The data that support the findings of this study are openly available in the repository "figshare" at https://doi.org/10.6084/m9.figshare.22885913. Rościszewski-Dodgson and Cirella (2023) have conducted a comprehensive compilation of topological datasets, focusing on the categorization and geographical distribution of anthropogenic and ecological indicators of fish species in the Baltic Sea.



6 Conclusions

Overall, academic papers reviewed in this study provide insights on how key anthropogenic stressors impact the ecology of top commercial fish species. They key outcomes are that natural hazards will continue to increase in the future and that each stock has reacted differently, depending on the region and adaptive capabilities. Western and Eastern cod stocks are struggling the most. This is because they are most susceptible to impacts of temperature rises, reduced salinity and eutrophication which stunts their growth, limits their reproductive success and early life stage survival. Moreover, as a result of hypoxia cod are losing their benthic habits and are outperformed by other species, when competing for the same resources. Parasite infection and predation form invasive jellyfish species was also highest in cod. As such, with current predictions, cod stocks chances of recovery are extremely unlikely and targeted fisheries capture will remain closed for the unforeseeable future. Due to the fact that very few academic studies have conducted on whiting in the Baltic Sea region. It is impossible to make a solid opinion on the impact's natural hazards and food web dynamics have on their current population, leaving them data deficient. The only indicator of their status can be linked to their family connections with cod. With whiting living in similar benthic environments and predating on the same food. As such, it is not improbable to assume that whiting are similarly struggling to adapt to the large-scale shifts of the changing environment. However, more research needs to be conducted to

585 reaffirm this.

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Flounder's status is somewhat mixed, on one hand studies suggest that they are doing far better than cod, with flatfish growing in number in some regions. Whilst other literature underscores that the status of flounder has worsened as a result of reduced salinity and deoxygenation, which has reduced their size, habitat and recruitment success. Moreover, the presence round gobies and high parasitic infection rates have further deteriorated flounder's health in some locations. Consequently, the status of these species varies depending on the region. Plaice are likely to be in a similar situation to flounder, having benefited from a reduction in cod numbers, their populations in many parts of the Baltic Sea have increased, prompting TAC increase

this decade. Due to a lack of academic papers discussing plaice, there is not enough information on their behaviour in response to anthropogenic and ecological stresses. However, their physiology is similar to other flatfish, with plaice likely to face the same dangers as flounder in the Baltic Sea. As such, it is to be expected that the current status of their stocks is relatively
healthy but fragile.

The status of herring is highly depended on their individual stocks. For example, Riga herring are doing the best, followed by Bothnian and central herring which are stable but more susceptible to completion from sprat. In general, herring are shown to be highly adaptive and capable or reproducing quickly. Algal blooms in the Baltic Sea have also provided *Clupeidae* species with an additional food source as more phytoplankton is available. Moreover, eutrophication reduces

600 visibility, crating harder conditions for cod and flatfish to predate on herring. The former was once their main predator, by definition, as cod population fell, herring numbers grew. With this in mind, the spawning stocks biomass of those three stocks is healthy enough to withstand current food-web dynamics and anthropogenic pressures. Western herring are the exception, as their stock declined substantially in the last decade. Besides overfishing, Western herring have been shown to have reduced



reproductive capabilities as a result of ocean acidification, increasing temperatures and rescued sanity levels. Their example 605 should be closed monitored in order to prevent other herring stocks from collapsing. Out of all the stocks sprat are the definitive winners. Similarly, to herring, the changing environmental conditions of the Baltic Sea have benefited sprat by providing a greater food source and reducing predation. Moreover, in most regions sprat are more successful than herring in larvae survival, population distribution, feeding and low parasitic resilience. This has made sprat arguably the most adaptive and successful commercial fish species. However, sprat abundance depends on the region. With the majority of the stock moving towards the Northern Baltic Sea and the Gulf of Finland.

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Commercial fish stocks in the Baltic Sea benefit from being one of the most intensely researched fisheries regions in the world. This has allowed for a review of this type to conducted. However, there is still much to learn about the pressures mentioned here. More often than not, academia discussed anthropogenic stressors and food web-dynamics in wider context, forcing the authors to make connections. Moreover, there are clear disparities between the amount of academic interest placed

615 on various species, which information on cod widely available despite the fact that they are no longer a viable commercial species. Whilst flatfish and sprat studies are still small despite their growing significance in the fisheries sector. Furthermore, there are growing concerns that the threats posed by invasive species, hypoxia, climate change, eutrophication and low sanity will continue to increase and further alter the ecosystem of the Baltic Sea. This article provides a synopsis on the current environmental factors affecting the top fish stocks in the Baltic Sea, but it is paramount that researchers continue to conduct 620 further studies in this field.

Author contribution

MJR-D contributed to the conceptualization, data curation, formal analysis, investigation, methodology, resources, validation and writing—original draft, review and editing; GTC contributed to the formal analysis, investigation, project administration, supervision, visualization and writing-review and editing.

625 **Competing interests**

The authors declare that they have no conflict of interest.

Acknowledgements

The authors are grateful to the Faculty of Economics, University of Gdansk, for supporting this work. We are also thankful to several faculty members who have given us advice in piecing together the manuscript and conceptual development. 630 The authors received no financial support.



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