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Published in:
ICES Journal of Marine Science

DOI:
10.1093/icesjms/fsac073

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Document Version
Publisher's PDF, also known as Version of record

Publication date:
2022

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):
Olin, A. B., Olsson, J., Eklöf, J. S., Eriksson, B. K., Kaljuste, O., Briekmane, L., & Bergström, U. (2022). Increases of opportunistic species in response to ecosystem change: The case of the Baltic Sea three-spined stickleback. *ICES Journal of Marine Science*, *79*(5), 1419-1434. https://doi.org/10.1093/icesjms/fsac073

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ICES Journal of Marine Science, 2022, **79**, 1419–1434
DOI: 10.1093/icesjms/fsac073
Advance access publication date: 5 May 2022
Review Article

Increases of opportunistic species in response to ecosystem change: the case of the Baltic Sea three-spined stickleback

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Under rapid environmental change, opportunistic species may exhibit dramatic increases in response to the altered conditions, and can in turn have large impacts on the ecosystem. One such species is the three-spined stickleback (*Gasterosteus aculeatus*), which has shown substantial increases in several aquatic systems in recent decades. Here, we review the population development of the stickleback in the Baltic Sea, a large brackish water ecosystem subject to rapid environmental change. Current evidence points to predatory release being the central driver of the population increases observed in some areas, while both eutrophication and climate change have likely contributed to creating more favourable conditions for the stickleback. The increasing stickleback densities have had profound effects on coastal ecosystem function by impairing the recruitment of piscivorous fish and enhancing the effects of eutrophication through promoting the production of filamentous algae. The increase poses a challenge for both environmental management and fisheries, where a substantial interest from the pelagic fisheries fleet in exploiting the species calls for urgent attention. While significant knowledge gaps remain, we suggest that the case of the Baltic Sea stickleback increase provides generalisable lessons of value for understanding and managing other coastal ecosystems under rapid change.

Keywords: cross-system coupling, mesopredatory fish, mesopredator release, predator-prey reversal, top-down cascade.

Introduction

In the current era of rapid anthropogenic environmental change, some species struggle while others benefit from the altered conditions. Such “winners” tend to be small, highly fecund and widespread generalists (McKinney and Lockwood, 1999; Clavel *et al.*, 2011; Iacarella *et al.*, 2018). These traits allow for rapid responses to changes such as temperature-driven increases in productivity, or reduced predation pressure as a result of overfishing of predatory fish. For example, in the early 1990s, Limfjorden in northern Denmark shifted from being dominated by long-lived, large demersal fish species with a narrow environmental tolerance to being dominated by smaller, opportunistic species, and this shift was linked to high anthropogenic nutrient input and a strong fishing pressure (Tomczak *et al.*, 2013). Similarly, along the Canadian coastline, Iacarella *et al.* (2018) found that seagrass meadows subject to high levels of human disturbance, for example in the form of heavy boat traffic, were associated with high abundances of generalist, opportunistic fish species.

The increase of opportunistic species may in turn itself have large impacts on the ecosystem, exacerbating impacts of ongoing environmental change (Pratchett and Cumming, 2019). Via positive feedback mechanisms, the system may even become locked in a new regime dominated by the opportunistic species. For example, declines in perennial canopy-forming macroalgae, which have been observed around the globe and are driven by multiple stressors such as eutrophication and overfishing, often co-occur with a shift towards assemblages dominated by small, opportunistic turf-forming algal species (Strain *et al.*, 2014). This shift may be associated with drops in productivity, reduced complexity of the food web and a homogenisation of community composition over large spatial scales (Álvarez-Losada *et al.*, 2020). Further, through increased sediment retention, the recovery of canopy-forming macroalgae is prevented. Opportunistic species exhibiting rapid increases can thus have large and sometimes nonlinear impacts on the local ecosystem, representing a major challenge to the management of marine ecosystems (Pratchett and Cumming, 2019).

One example of an opportunistic species is the three-spined stickleback (*Gasterosteus aculeatus*, hereafter: “stickleback”), a small, mesopredatory fish occupying marine, brackish and freshwater habitats across the northern hemisphere. Its adaptability, short life cycle, wide environmental tolerance, and ability to complete multiple spawning cycles per year in response to favourable conditions allow it to rapidly colonise new environments, as well as to exhibit dramatic increases in previously occupied habitats in response to altered conditions (Barber and Nettleship, 2010). In recent decades, stickleback population increases have been observed in several aquatic systems, including the White Sea (Lajus *et al.*, 2021), Lake Constance (Germany) (Roch *et al.*, 2018; Rösch *et al.*, 2018)

Received: December 23, 2021. **Revised:** March 14, 2022. **Accepted:** April 6, 2022

and the above-mentioned Limfjorden (Tomczak *et al.*, 2013). These increases have in several cases been linked to anthropogenic environmental change, such as increasing water temperatures (Lajus *et al.*, 2021).

Importantly, the stickleback not only responds rapidly to novel conditions, but may itself have substantial impacts on the ecosystem. For example, in Lake Constance, the stickleback increase is thought to explain a sharp decline of whitefish (*Coregonus* spp.), as the stickleback compete with whitefish for food and predate on their offspring (Roch *et al.*, 2018; Rösch *et al.*, 2018). As sticklebacks may via these mechanisms suppress the recruitment of their own predators, they can act to reinforce a state with low densities of predators (Eklöf *et al.*, 2020), resulting in subsequent top-down trophic cascades (e.g. Eriksson *et al.*, 2009; Östman *et al.*, 2016). As such, the observed stickleback increases exemplify some fundamental ecological mechanisms which are likely to play a particularly important role under changing environmental conditions, such as increases of opportunistic species, top-down cascades and predator-prey role reversal. Studying the drivers of these increases and their ecological consequences may thus provide generalisable lessons for the management of other ecosystems in a state of rapid environmental change.

This review focuses on the causes and consequences of the rapid increases in stickleback abundances observed since the early 2000s in parts of the Baltic Sea, one of the largest brackish water bodies in the world (Ljunggren *et al.*, 2010; Bergström *et al.*, 2015; Olsson *et al.*, 2019). The increases have taken place against the backdrop of a rapidly changing ecosystem under high anthropogenic pressure (Reusch *et al.*, 2018) and have given rise to large, often detrimental, impacts on the structure and functioning of the coastal ecosystem (e.g. Eriksson *et al.*, 2009; Byström *et al.*, 2015; Nilsson *et al.*, 2019). Here, we synthesise existing knowledge on Baltic Sea stickleback ecology and present time series documenting the stickleback population development and distribution in the Baltic Sea. Further, we review the literature on possible drivers of observed population trends with the aim of formulating hypotheses that can be tested quantitatively in future studies. Following this, we describe the effects of high stickleback densities on the ecosystem, consider implications for management, and discuss the current interest by Baltic Sea pelagic fisheries fleets in exploiting the species (Bergström *et al.*, 2015; BSAC, 2021). Finally, we formulate some generalisable lessons from the case of the Baltic Sea stickleback increase.

Approach

To identify published material on Baltic Sea stickleback ecology, including drivers of demographic rates, impacts on the surrounding ecosystem and links to management, we performed a literature search based on the search terms "Baltic Sea" and "stickleback" using both Google Scholar and Google. Further material was identified by, for relevant publications, searching through references and articles citing the publication, as well as by personal contact with researchers on the topic. When identified material was considered redundant as a result of several other studies presenting similar findings, or when it focused on questions with only tangential connections to key topics of this review (e.g. detailed studies of the parasitic community associated with Baltic Sea stickleback), it was excluded from the review. Material used to put the findings of the review into a wider context were identified from the reference lists of relevant Baltic Sea stickleback publications, from appropriate literature searches (e.g. "opportunistic fish," "mesopredator release," or "EU Marine Strategy Framework Directive"), and from our own previous knowledge. Literature searches were conducted between September 2020 and December 2021.

While the main aim of this review is to synthesise published information, we also present some updated time series on stickleback abundances. The available time series were identified from previous publications (Bergström *et al.*, 2015; Olsson *et al.*, 2015; Olsson *et al.*, 2019; Candolin and Voigt, 2020; Eklöf *et al.*, 2020) and obtained by approaching the data owners. To examine trends in the data, we fitted Generalised Additive Models (GAMs) to the time series of average values using the package *mgcv* (Wood, 2017) in R 4.1.0 (R Core Team, 2021). Since all values were continuous and non-negative, we fitted the models with a log link function and a gamma response distribution as follows:

$$\log\left\{\mathbb{E}\left(\text{stickleback}_i\right)\right\} = \beta_0 + f\left(\text{year}_i\right), \quad \text{stickleback}_i \sim \text{gamma} \qquad (1)$$

where f indicates a smoothing function, which in our case was always a thin plate spline. Optimal smoothing parameters were selected using restricted maximum likelihood. We evaluated the adequacy of the smooths using the function *gam.check*. Three metrics were produced to assess the support for trends in the data: (1) *p*-values (only approximate; see Wood, 2017), (2) the Akaike Information Criterion corrected for small sample sizes (AIC_C, Hurvich and Tsai, 1989), where $\Delta\text{AIC}_\text{C} = \text{AIC}_\text{C}$ model *with* year effect − AIC_C model *without* year effect, with $\Delta\text{AIC}_\text{C} < -4$ indicating strong support for a year effect (Burnham and Anderson, 2002), and (3) a variable selection approach that adds a penalty to functions in the null space, penalising the smooth term out of the model when the explanatory power is low (Marra and Wood, 2011).

Stickleback in the Baltic Sea

The Baltic Sea is a large, shallow, semi-enclosed and relatively young brackish water body in northern Europe, with low rates of water exchange with the adjacent North Sea (see Figure 1a, annotated with locations referred to in the text). It is one of the most rapidly warming seas in the world, and has also been subject to decades of eutrophication, pollution and overfishing (Reusch *et al.*, 2018; HELCOM, 2018a; Kniebusch *et al.*, 2019). It displays a strong gradient in both temperature and salinity, from cold temperatures and close-to-freshwater salinities in the north-east to warmer temperatures and close-to-marine salinities adjacent to its connection with the North Sea in the south-west, which is also mirrored by a gradient in species composition (Elmgren and Hill, 1997; Ojaveer *et al.*, 2010). In general, species diversity is low, but productivity relatively high (Elmgren and Hill, 1997; Reusch *et al.*, 2018). The offshore fish community is made up primarily of Atlantic herring (*Clupea harengus*, hereafter: "herring"), European sprat (*Sprattus sprattus*, hereafter: "sprat"), and Atlantic cod (*Gadus morhua*, hereafter: "cod") (Ojaveer *et al.*, 2010). Coastal areas are dominated by freshwater species such as European perch (*Perca fluviatilis*, hereafter: "perch"), common roach (*Rutilus rutilus*), as well as other cyprinid species (Ojaveer *et al.*, 2010). In recent decades, populations of

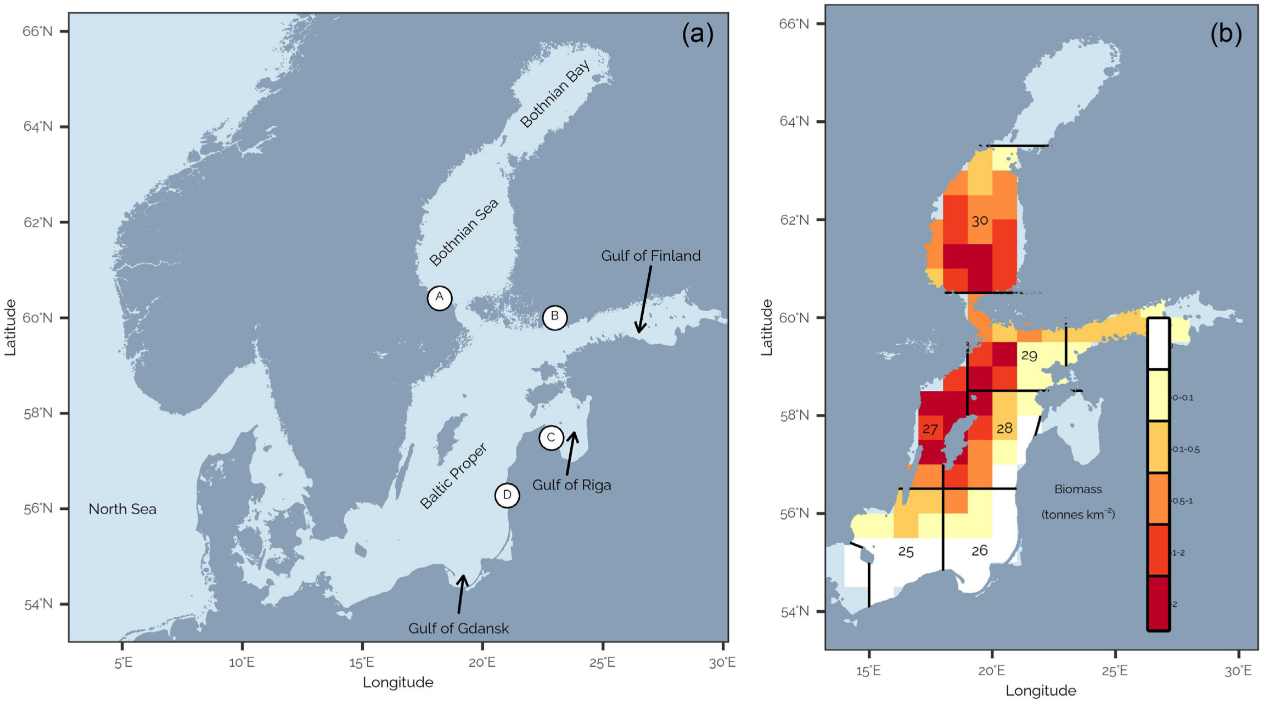

Figure 1. (a) The Baltic Sea annotated with geographical areas mentioned in the text. Letters indicate the locations of (A) Forsmark (Figure 2g–h), (B) Tvärminne (Figure 2i), (C) Kolka (Figure 2k) and (D) Pape (Figure 2j) sampling sites. (b) Stickleback biomass (tonnes km^{-2}) per ICES rectangle based on the ICES Baltic International Acoustic Survey in September–October. Colours indicate median values over the years 2015–2019 (light blue indicates rectangles with no or less than three years of sampling). Numbers and black lines indicate ICES subdivisions. See Olsson *et al.* (2019) for details. Coastline shapefile was obtained from the European Environment Agency (2017), ICES subdivisions from ICES (2016).

fish-eating top predators have increased substantially, in particular grey seals (*Halichoerus grypus*) and great cormorants (*Phalacrocorax carbo*) (Reusch *et al.*, 2018).

Baltic Sea stickleback ecology

Three members of the stickleback family (Gasterosteidae) are present in the Baltic Sea: the three-spined stickleback, the nine-spined stickleback (*Pungitius pungitius*) and the fifteen-spined stickleback (*Spinachia spinachia*). While three-spined and nine-spined stickleback largely occupy the same habitats and are ecologically similar, the three-spined stickleback is much more abundant in the Baltic Sea (e.g. Peltonen *et al.*, 2004; DeFaveri *et al.*, 2012; Adill *et al.*, 2021; Erlandsson *et al.*, 2021). Fifteen-spined stickleback on the other hand displays different and more narrow habitat preferences (Wootton, 1984) and occurs much more rarely in the Baltic Sea than the other two species (e.g. Erlandsson *et al.*, 2021). In addition to being more common and widespread, the three-spined stickleback is the subject of the absolute majority of recent literature on the ecology of stickleback in the Baltic Sea. For these reasons, this review focuses solely on this species, and consequently, we hereafter refer to the three-spined stickleback simply as "stickleback."

Most Baltic Sea sticklebacks spend the majority of their lives out in the open sea, but at around two years of age, they migrate towards the coast in spring (April–May) to spawn (Bergström *et al.*, 2015). Spawning mainly takes place in shallow bays close to the open sea (Gagnon *et al.*, 2017; Eklöf *et al.*, 2020), but studies of otolith microchemistry suggest that some spawning also takes place in freshwater bodies close to the coast (Eesti Mereinstituut, 2017). During the spawning period, which extends roughly from May to July, and into August further north (Bergström *et al.*, 2015), the males build nests for the eggs and defend their territories against predators and other males (Borg, 1985). Individuals may complete several rounds of spawning and the spawners often die afterwards (Borg, 1985; Candolin *et al.*, 2008). In early autumn (September–October), most juveniles and surviving spawners migrate from the coastal spawning grounds out to feeding areas in the open sea (Bergström *et al.*, 2015). However, some individuals remain close to the coast throughout the year (Bergström *et al.*, 2015; Eesti Mereinstituut, 2017).

While at the coast, the sticklebacks feed on a highly diverse diet consisting predominantly of copepods, cladocerans, chironomid larvae, amphipods, isopods, mysids, ostracods as well as eggs and larvae of fish (Thorman and Wiederholm, 1986; Nilsson, 2006; Reiss *et al.*, 2014; Candolin *et al.*, 2016; Pawelec *et al.*, 2016; Jakubavičiūte *et al.*, 2017a; Gagnon *et al.*, 2019; Nilsson *et al.*, 2019; Skarp, 2019). In the open sea, the stickleback diet is made up mainly of planktonic copepods and cladocerans (Peltonen *et al.*, 2004; Ojaveer *et al.*, 2017; Jakubavičiūte *et al.*, 2017b).

The stickleback is in turn prey for a number of species, both at the coast and in the open sea. In shared spawning grounds, stickleback can make up a substantial part of the summer diet of piscivorous fish such as perch and northern pike (*Esox lucius*, hereafter: "pike") (Reiss *et al.*, 2014; Donadi *et al.*, 2017; Jacobson *et al.*, 2019). Further, cod has been found to occasionally consume considerable amounts of stickleback in coastal areas of the southern Baltic Proper (Almqvist *et al.*, 2010). In the open sea, the stickleback may also be preyed upon by Atlantic salmon (*Salmo salar*)

(Hansson *et al.*, 2001; Vuorinen *et al.*, 2014) and large herring (Parmanne *et al.*, 2004). In addition, sticklebacks are eaten by several bird species, such as great cormorants, mergansers (*Mergus* spp.) and terns (*Sterna* spp.) (Lemmetyinen, 1973; Hansson *et al.*, 2018). Finally, ringed seals (*Pusa hispida*) in the Bothnian Bay have also been found to consume considerable amounts of stickleback (Suuronen and Lehtonen, 2012; Lundström *et al.*, 2014).

Population structure and development

Genetic data suggest that the stickleback colonised the Baltic Sea around 10 000 years ago, after the last glaciation, when a connection between the North Sea and the Baltic basin opened up (Mäkinen *et al.*, 2006). The population does not exhibit any pronounced spatial structure, with genetic data showing a weak pattern of isolation by distance (DeFaveri *et al.*, 2013; Guo *et al.*, 2015; but see Lind and Grahn, 2011). However, evidence from otolith microchemistry studies suggests that at least those Baltic Sea sticklebacks hatched in freshwater tend to return to their place of birth to spawn (Eesti Mereinstituut, 2017). There is also some evidence of local adaption to variation in salinity, temperature and potentially also predation pressure and pollution levels (Lind and Grahn, 2011; DeFaveri *et al.*, 2013; Guo *et al.*, 2015; Jakubavičiūte *et al.*, 2018; Eriksson *et al.*, 2021; Yanos *et al.*, 2021). Further, the Baltic Sea stickleback shows spatial variation in size and condition, with fish in the Bothnian Sea generally being larger than those in the Baltic Proper (Bergström *et al.*, 2015; Jakubavičiūte *et al.*, 2018; Olsson *et al.*, 2019).

Acoustic surveys in the open sea in early autumn show that peak stickleback abundances in recent years have been found in the north-western Baltic Proper as well as in the central Bothnian Sea (Figure 1b; Olsson *et al.*, 2019). The surveys point to lower abundances in the offshore areas of southern and eastern parts of the Baltic Proper. It should be noted that some areas are not covered by the acoustic surveys, and are data deficient in general. This is true in particular for the Bothnian Bay. A one-off acoustic survey from 1991 found that stickleback densities in the Bothnian Bay were around 5 times higher than those in the Bothnian Sea (Jurvelius *et al.*, 1996), and more recent data on juveniles from the Swedish coast also point to an increase in abundances with increasing latitudes (Eklöf *et al.*, 2020; most data from 2000 onwards).

Offshore data suggest that stickleback numbers have increased rapidly in the Bothnian Sea and the central Baltic Sea since the early 2000s (Figure 2b–c; Ljunggren *et al.*, 2010; Bergström *et al.*, 2015; Olsson *et al.*, 2019). There are also signs of a more recent increase in the south-western Baltic Proper (ICES subdivision 25) (Figure 2a; Olsson *et al.*, 2019). As a result of the observed increases, stickleback now makes up a substantial proportion of the pelagic fish in large parts of the Baltic Sea—an estimated 10% of the pelagic fish biomass in the Baltic Proper was made up of stickleback in the period 2011–2014 (Olsson *et al.*, 2019). Coastal data from these areas provide a more mixed picture with some datasets showing strong evidence for an increase (Figure 2g and h), others showing weak evidence for an increase (Figure 2d, i) and others not clearly showing any particular trend (Figure 2e and f).

In the southernmost parts of the Baltic Proper, off the coasts of Poland, Lithuania, Latvia, and Estonia, the acoustic data point to low stickleback densities. In line with this, data collected with beach seines on the west coast of Latvia during the summer spawning season 1998–2020 do not show any evidence of an increase (Figure 2j), and corresponding data from the western Gulf of Riga (1986–2020) even point to a decline in stickleback densities (Figure 2k; Olsson *et al.*, 2015). In addition, from completely dominating the coastal fish community in the 1990s, declines have also been observed in the Gulf of Gdansk (Morozińska-Gogol, 2015). As such, the direction and shape of trends in the Baltic Sea stickleback population vary markedly over space.

Review of potential drivers of Baltic Sea stickleback demography

In this section, we review the existing literature on potential drivers of Baltic Sea stickleback demography in general, and of observed spatio-temporal stickleback trends in particular. As described below and illustrated in Figure 3, the number of potential drivers is large and their combined effect on stickleback populations likely complex, with drivers potentially covarying and interacting, spanning multiple habitats and life stages, and the available data of mixed spatio-temporal extent and resolution. Teasing apart single and interactive effects likely requires applying complex statistical approaches (see e.g. Grace *et al.*, 2016) at multiple spatial and temporal scales, which is beyond the scope of this literature review. Instead, we focus on reviewing published proposed mechanisms, and also briefly describe trends in the potential drivers in the context of population trends in stickleback, with the hope that the synthesis can act as a guide for future studies.

Predation pressure

Small, intermediate predators, such as the stickleback, may show rapid increases as the density of their predators declines; a mechanism commonly referred to as "mesopredator release" (Prugh *et al.*, 2009). In the Baltic Sea, it has been observed that large spring abundances of perch and pike in the shared spawning bays have a marked negative effect on stickleback abundances, which also has direct consequences for stickleback recruitment due to a strong spawning stock-recruitment relationship (Eklöf *et al.*, 2020). In line with this, experimental exclusion of large predatory fish using cages can increase stickleback abundances (Eriksson *et al.*, 2009), and rapid stickleback increases have in several instances been preceded by drops in local populations of piscivorous fish (Nilsson *et al.*, 2019; Eklöf *et al.*, 2020). Along the Baltic Sea coast, populations of these piscivorous fish show variable trends. Abundances of perch, a key predator of Baltic Sea stickleback (Jacobson *et al.*, 2019), have decreased in several locations around the Baltic Sea, in particular in the central Baltic Proper (Olsson, 2019; Figure 4a), where the stickleback has increased. However, in some areas where the stickleback has increased, such as in large parts of the Bothnian Sea and the northern Baltic Proper, perch densities have also increased (Olsson, 2019; Figure 4a). Data on pike are scarcer but also point to declines in the central Baltic Sea (Olsson, 2019; Figure 4a). Where declines in local perch and pike populations are occurring, they are likely the result of multiple factors, including (i) degradation of spawning habitats through wetland drainage, coastal exploitation and eutrophication (Sandström and Karås, 2002; Hansen *et al.*, 2019; Hansen *et al.*, 2020), (ii) locally strong fishing pressure (Bergström *et al.*, 2016), as well as (iii) increased predation pressure from great

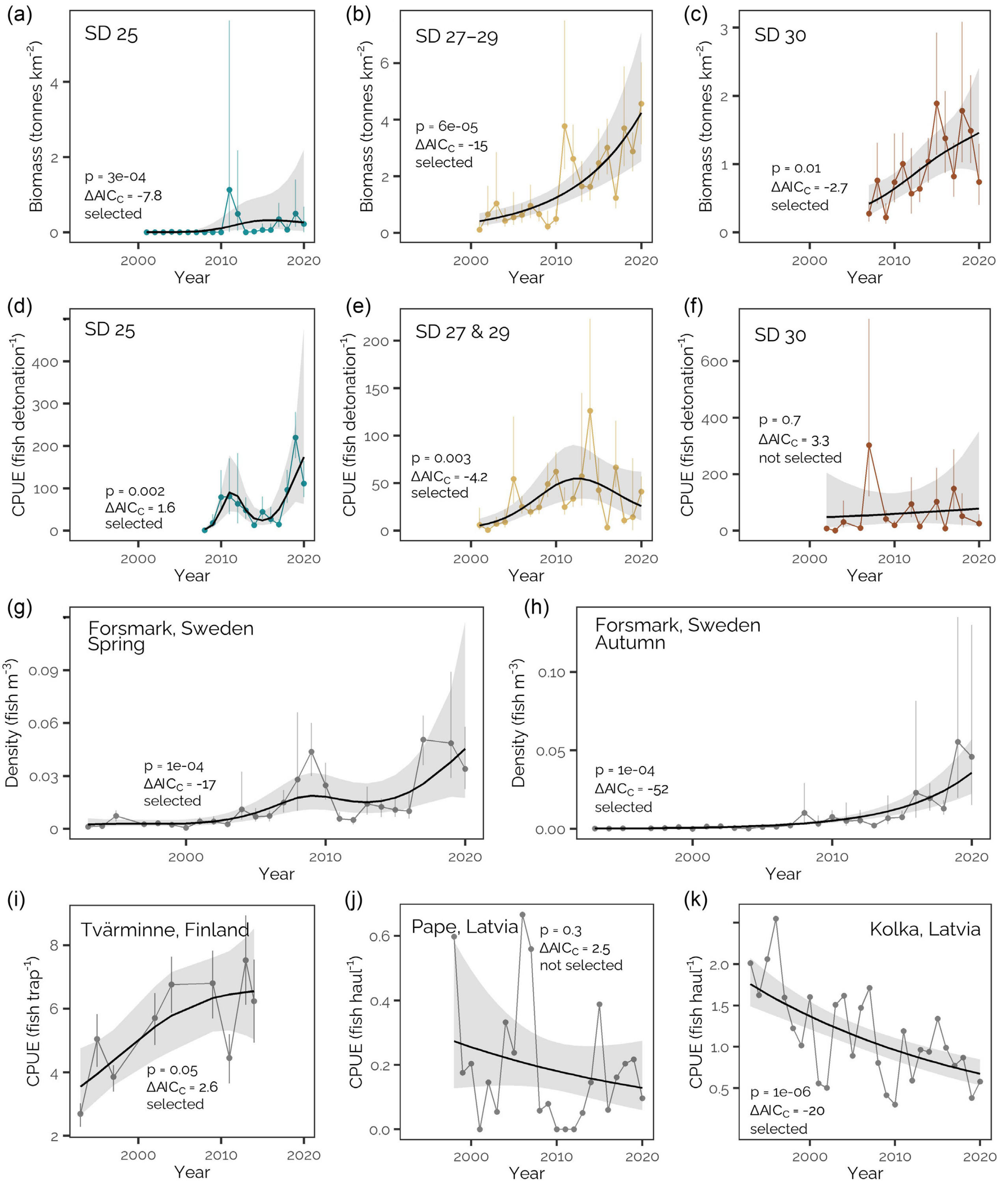

Figure 2. (a–c) Average stickleback biomass per km^2 in the south-western Baltic Sea (a; ICES SD 25), the central Baltic Sea (b; ICES SD 27–29) and the Bothnian Sea (c; ICES SD 30), based on data from the ICES Baltic International Acoustic Survey in September–October (see Olsson *et al.*, 2019 for details). (d–f) Average abundances of stickleback juveniles caught during the spawning season using underwater detonations along the Swedish coast of the south-western Baltic Sea (d; ICES SD 25), the central Baltic Sea (e; ICES SD 27 and 29) and the Bothnian Sea (f; ICES SD 30) (see Eklöf *et al.*, 2020 for details). Note that included bays vary between years. (g–h) Average number of sticklebacks caught per m^3 in the cooling water intake of the Forsmark nuclear power plant on the Swedish coast of the southern Bothnian Sea in spring (g; weeks 17–24) and autumn (h; weeks 37–48) (see Adill *et al.*, 2021 for details). (i) Average number of sticklebacks caught per trap during the spawning season (early May to mid-July) in three bays close to the Tvärminne Zoological Station in southern Finland (see Candolin and Voigt, 2020 for details). (j–k) Number of sticklebacks caught per beach seine haul during summer at two Latvian sampling sites, Pape on the west coast (j), and Kolka in the Gulf of Riga (k) (see Olsson *et al.*, 2015 for details). Error bars represent 95% confidence intervals where uncertainty estimates were available, thick black lines and shaded areas show GAM predictions with associated 95% confidence intervals. *P*-values, ΔAIC$_C$-values and results from the added penalty variable selection (selected/not selected) for each GAM are also included.

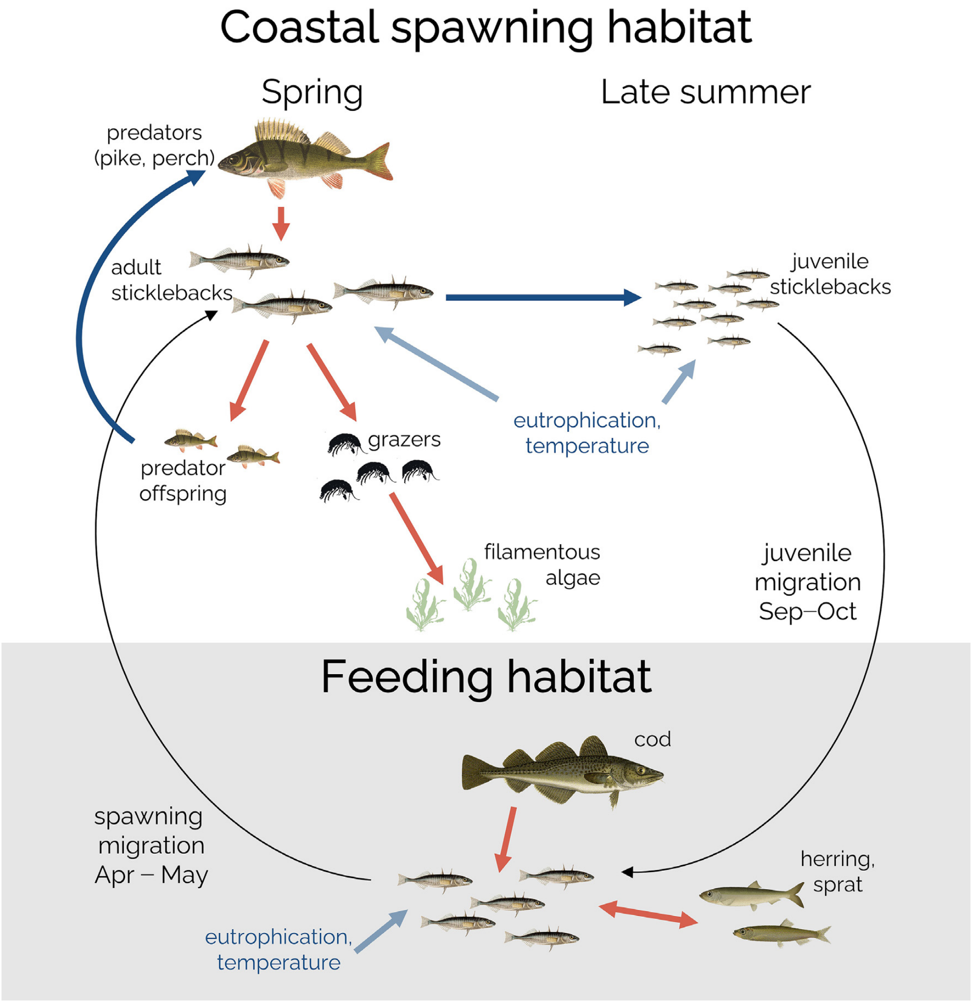

Figure 3. Illustration of key processes and interactions directly involving the Baltic Sea stickleback, as described in this review. Thick orange and blue arrows indicate negative and positive effects, respectively, with the faded blue lines illustrating that effects of temperature and eutrophication may be indirect and nonlinear. Thin black lines indicate migration. Mesograzer and algae illustrations from the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

cormorant and grey seal in some areas (Veneranta *et al.*, 2020; Ovegård *et al.*, 2021; Svensson, 2021). In addition, increasing stickleback densities are likely to reinforce ongoing declines themselves through increased predation rates on the eggs and larvae of perch and pike (Nilsson *et al.*, 2004; Nilsson, 2006; Byström *et al.*, 2015; Nilsson *et al.*, 2019; see further below).

Along the coast, Baltic Sea stickleback is also predated upon by birds and ringed seals (Lemmetyinen, 1973; Suuronen and Lehtonen, 2012; Lundström *et al.*, 2014; Hansson *et al.*, 2018). However, the extent to which these predators affect stickleback population dynamics has not been studied.

Predator populations are also changing in the sticklebacks' open sea feeding habitat. Baltic Sea cod declined rapidly during the 1980s (see Figure 4b), likely as a result of overfishing and unfavourable environmental conditions (Möllmann *et al.*, 2008). Alongside this, their range contracted so that the core area is now situated in the southernmost Baltic Sea (Orio *et al.*, 2019), where stickleback abundances have generally remained low (Figure 1b). In the Baltic Proper and the Bothnian Sea, predation mortality may have been reduced further between the 1980s/1990s and the 2000s through declines in the abundance of herring (Figure 4d–e), as large individuals have been found to feed on stickleback (Parmanne *et al.*, 2004; U. Bergström, unpubl. data). In the Gulf of Riga, where stickleback densities seem to be decreasing (Figure 2k), herring densities have instead increased since the 1980s (Figure 4f). As such, spatio-temporal patterns in predator populations appear to match the spatially variable trends in the Baltic Sea stickleback population; stickleback has increased mainly in areas where predators have declined. Moreover, some historical accounts also point to the importance of the open sea fish community in driving stickleback dynamics: large stickleback abundances in the southern Baltic Sea in the early 20th century (Charlesen, 2000) coincided with smaller population sizes of both herring and cod (see MacKenzie *et al.*, 2002).

Food competition

Several studies show that greater food availability has a positive impact on both reproduction and growth rates in

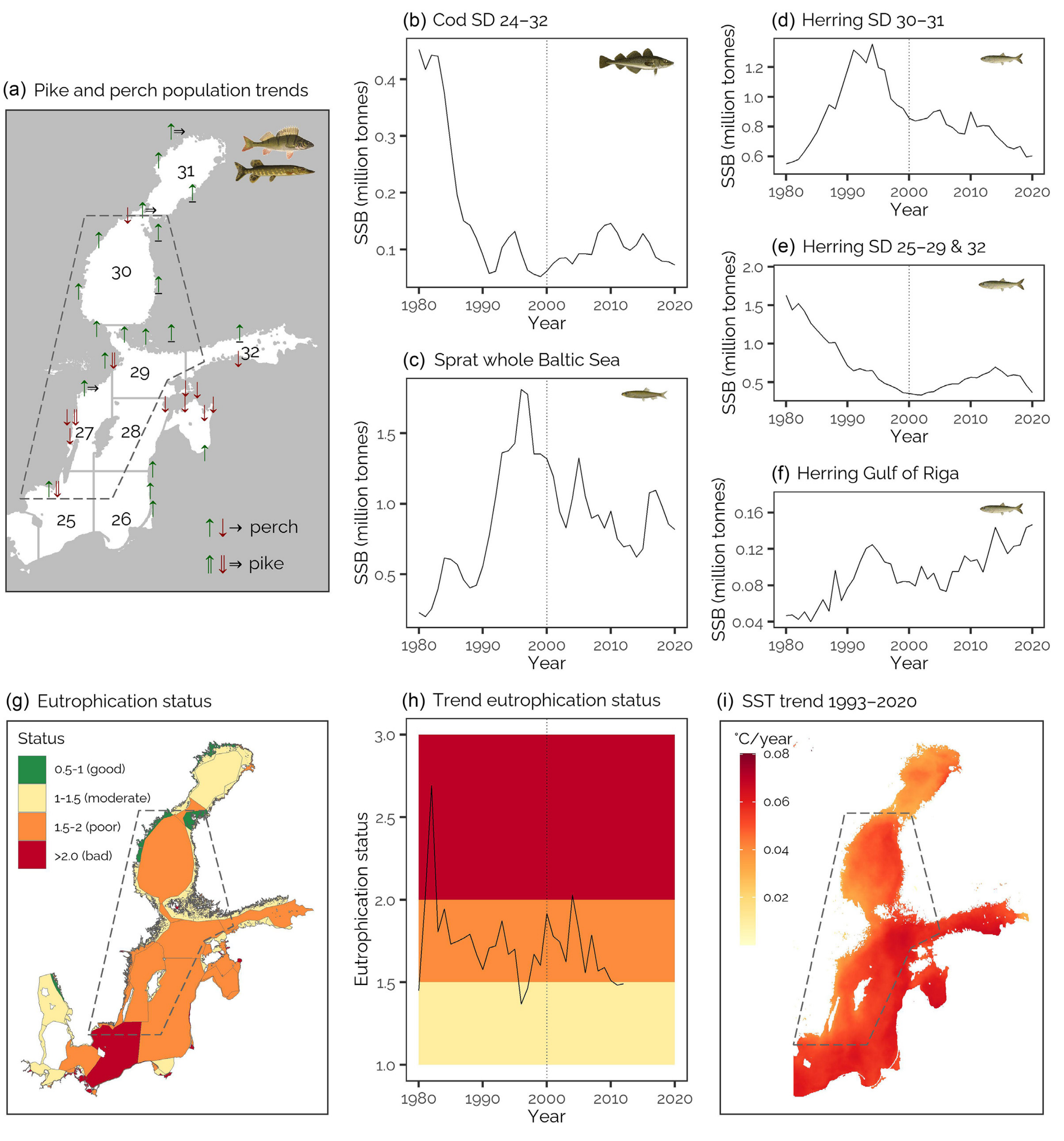

Figure 4. Trends and spatial patterns in potential drivers of Baltic Sea stickleback demography. (a) Trends in coastal piscivores (increase/decrease/no trend since ca. mid-2000s; data extracted from Olsson, 2019), underlined arrows indicate that data refer to larger areas (generally ICES sub-division). Coastline shapefile was obtained from the European Environment Agency (2017), ICES subdivisions from ICES (2016). (b–f) Time series of spawning stock biomass of cod, sprat and herring at the spatial scales at which each stock is assessed (data from ICES Stock Assessment Database, 2021; note that (e) excludes the Gulf of Riga, which is assessed independently). (g) Eutrophication status of HELCOM assessment units in 2011–2016 based on an integrated assessment of nutrient levels and direct as well as indirect effects of eutrophication, in relation to targets (data from HELCOM, 2018c). (h) Time series of estimated eutrophication status integrated over the whole of the Baltic Sea (data extracted from Figure 7 in Andersen *et al.*, 2017). (i) Trend in sea surface temperature anomalies 1993–2020 based on satellite data (data from EU Copernicus Marine Service, 2021). Dotted polygons in maps provide a rough indication of where available data suggest increasing densities of stickleback in the last two decades (Figure 2; note that the Bothnian Bay and the Gulf of Finland do not have enough data to assess the presence of any trends). Vertical dotted lines in time series plots indicate the time when stickleback densities started increasing (Figure 2; Bergström *et al.*, 2015; not included in (f) as no increases seen in the Gulf of Riga).

stickleback (e.g. Wootton, 1973; Allen and Wootton, 1982). In addition to changes driven by temperature and nutrient availability (discussed below), the presence of competitors can also have a large impact on food availability. For example, an experiment in a lake in northern Canada found that the exclusion of cut-throat trout (*Oncorhynchus clarkii*) and prickly sculpin (*Cottus asper*) from shared habitat allowed sticklebacks to increase their ingestion rates markedly due to lowered food competition (Bolnick *et al.*, 2010).

In the Baltic Sea, stickleback can show large diet overlap with sprat and herring during parts of the year (Peltonen *et al.*, 2004; Ojaveer *et al.*, 2017; Jakubavičiūtė *et al.*, 2017b; but see Lankov *et al.*, 2010). It is thus possible that the stickleback has benefitted from reduced food competition as a result of population declines in these two dominant planktivores. The spawning stock biomass of herring showed a gradual decline in the Baltic Proper and the Gulf of Finland (ICES subdivisions 25–29 and 32) between the 1980s and the early 2000s, followed by a weak increase, after which the trend turned downwards again in recent years (Figure 4e). Declines have also occurred in the Bothnian Sea and the Bothnian Bay since the beginning of the 1990s (ICES subdivisions 30–31; Figure 4d). However, again, in the Gulf of Riga, herring biomass has increased since the 1980s (Figure 4f). Sprat, which is assessed as a single unit in the Baltic Sea (ICES subdivisions 22–32), has declined since the late 1990s, levelling off in recent years (Figure 4c). As such, the densities of competing planktivores have generally decreased in areas where stickleback densities have increased, either prior to or parallel with the stickleback increase, indicating that a release from competition for zooplankton could have contributed to the increase in stickleback in large parts of the Baltic Sea.

Eutrophication

The high degree of eutrophication in the Baltic Sea (Reusch *et al.*, 2018) is likely to have improved conditions for stickleback in several ways (Candolin, 2019). Moderate nutrient addition promotes vegetation growth, which may favour sticklebacks, as both adults and juveniles are found in greater numbers in areas with high vegetation cover (Eklöf *et al.*, 2020). Further, eutrophication-driven increases in turbidity will likely result in lower predation risk from visual predators (Candolin, 2019), as well as fewer aggressive interactions between stickleback males during spawning, which allows for a higher density of nests and the completion of more spawning rounds, due to less energy wasted on nest defence (Candolin *et al.*, 2008; Candolin *et al.*, 2014). In addition, eutrophication-driven improvements in food availability have been linked to greater fecundity as well as greater juvenile survival and growth rates (Candolin *et al.*, 2014; Candolin, 2019; Saarinen and Candolin, 2020). However, the negative impact of decadal eutrophication on habitat-forming macrophytes, such as bladderwrack (*Fucus vesiculosus*) (Bergström *et al.*, 2013), may indirectly increase stickleback mortality rates, as they normally provide sticklebacks with refuge from predators (Gagnon *et al.*, 2017; Donadi *et al.*, 2020). In addition, the increased turbidity may have resulted in a reduced ability to detect both predators and prey (Candolin, 2019).

While eutrophication may thus have both positive and negative impacts on sticklebacks, it seems as if, in general, the stickleback benefits from moderate levels of eutrophication, but is negatively impacted at more extreme levels (see Candolin, 2019 for a review). This lines up quite well with spatial patterns of eutrophication status in the Baltic Sea, where eutrophication levels are generally high in the area where stickleback has increased, but where the status is particularly poor in areas where abundances have remained low or even decreased, such as in parts of the Gulf of Riga and in the southernmost Baltic Proper (Figure 4g). However, while high levels of eutrophication may have provided good growth and reproduction conditions, it seems unlikely that a change in eutrophication levels has triggered the observed increase, as there has been no clear trend in eutrophication status prior to or during the stickleback increase (Figure 4h).

Temperature

Temperature affects stickleback directly through multiple pathways. If sufficient food is available, ingestion rates increase with temperature (Kotterba *et al.*, 2014; Lefébure *et al.*, 2014), which in turn results in greater growth rates (Allen and Wootton, 1982; Lefébure *et al.*, 2011). Further, warmer temperatures also boost reproductive rates by allowing the stickleback to complete more breeding cycles as a result of an earlier start and/or shorter cycles (Hovel *et al.*, 2017; Rottenbiller, 2020). At the same time, other aspects of stickleback reproduction, such as larval growth and survival rates, as well as male body condition and behaviour, appear to be negatively affected by increasing temperatures (Hopkins *et al.*, 2011; Rottenbiller, 2020). As such, the net direct effect of temperature increases of the scale seen in the Baltic Sea is unclear.

In addition, increasing temperatures may also affect stickleback populations indirectly, for example by driving changes in the prey base. In general, there is little evidence for any parallel increases in total zooplankton biomass in the areas where stickleback densities have increased, with data even pointing to a decline in the western Baltic Proper (Sukkainen *et al.*, 2013; Kuosa *et al.*, 2017; HELCOM, 2018b). However, temperature-driven changes in zooplankton community composition may have improved stickleback feeding conditions in some areas. For example, abundances of *Bosmina* spp., a key prey item for stickleback (Peltonen *et al.*, 2004; Lankov *et al.*, 2010; Ojaveer *et al.*, 2017; Jakubavičiūte *et al.*, 2017b), have increased in the Bothnian Sea since the 1980s, a trend which has been linked to increasing temperatures and decreasing salinity (Lindegren *et al.*, 2011; Kuosa *et al.*, 2017). Similarly, in the offshore northern Baltic Proper, an increase in rotifer abundances since the late 1990s has also been linked to warming temperatures and lower salinity (Suikkanen *et al.*, 2013). A small dataset collected in the Baltic Proper in spring suggest that this may have led to increased offshore feeding opportunities for sticklebacks, as they seem to utilise this food source to a higher degree than sprat and herring (Novotny, 2021). However, more extensive sampling of both fish and potential prey across seasons and locations is needed to test this hypothesis. Further, it has been suggested that in addition to increased food availability offshore, increasing temperatures have created favourable feeding conditions at the spawning sites (Candolin and Voigt, 2020). As such, it is possible that temperature-driven changes in food availability and composition could have contributed to the stickleback increases seen in the central Baltic Sea and the Bothnian Sea.

In addition to impacts on food availability, temperature changes could also impact stickleback indirectly via other interacting species, such as predators and competitors. For example, studies in the artificially heated Biotest basin outside the Forsmark nuclear power plant in the southern Bothnian Sea show that perch growth and recruitment benefit greatly from the higher temperatures (Svensson *et al.*, 2017). In parallel, densities of stickleback and other mesopredatory fish have declined to very low levels, which could potentially result from direct predation effects, or an unwillingness to enter enclosed areas with high predator densities.

Since the early 1980s, Baltic Sea sea surface temperatures have warmed with around 0.5°C per decade (Kniebusch *et al.*, 2019). While the net effect of observed temperature changes on local stickleback populations has never been studied, it seems unlikely that increasing temperatures is the main driver of the spatially variable trends in stickleback abundances, as there is no suggestion that areas where stickleback densities have increased are warming particularly rapidly (Figure 4i). However, as the ecosystem is responding to absolute temperatures rather than relative trends, with responses likely varying over the north-south temperature gradient in the Baltic Sea, it is difficult to make any judgements regarding the role of temperature in the stickleback population development based on observed temperature trends. It is possible that the southernmost populations may surpass temperature optima for some demographic rates, while more northerly populations benefit from the increasing temperatures.

Summary of potential drivers of Baltic Sea stickleback population development

Taken together, the available literature suggests that predator pressure could play an important role in driving the demography of Baltic Sea stickleback, and that changes in the predator populations may have contributed to the increases seen in the central Baltic Sea and the Bothnian Sea and the fairly low abundances in the southern Baltic Sea and at the eastern Baltic coast. Several predator species may have played a role here, but their relative contributions can at present not be teased apart. It is also possible that temperature- and salinity-driven changes in zooplankton composition and reduced competition for food in the open sea have contributed to the observed increases. Further, warmer temperatures and eutrophication have likely created favourable conditions for the stickleback to respond to these changes.

What is behind the stickleback declines reported in the Gulf of Gdansk (Morozińska-Gogol, 2015) and the Gulf of Riga (Figure 2k) is not clear. Morozińska-Gogol (2015) suggested that the decline in the Gulf of Gdansk could be the result of increased predation rates from introduced rainbow trout (*Oncorhynchus mykiss*) and great cormorant (to which the sticklebacks may have become more vulnerable as a result of heavy parasite loads), as well as competition from the invasive round goby (*Neogobius melanostomus*). Interestingly, this suggests that the increase of great cormorant observed in the Baltic Sea could potentially have contributed to declines of stickleback in some areas (where preferred larger prey may be scarce), while instead creating more favourable conditions for sticklebacks in other areas by predating on stickleback predators, such as perch (see Veneranta *et al.*, 2020; Ovegård *et al.*, 2021). Morozińska-Gogol's study also points towards a need for further studies on the role of parasites in regulating the Baltic Sea stickleback population, especially as this is something that historically was thought to be an important driver (Svedäng and Rolff, 2021) and has been shown to have dramatic effects in other systems (e.g. Threlfall, 1968).

Ecosystem effects of high stickleback densities

Increased biomass of filamentous algae

Experimental studies from the Swedish Baltic Sea coast show that low predator densities and associated high stickleback abundances lead to reduced numbers and changed composition of the sticklebacks' invertebrate prey, which in turn result in increased biomass of filamentous algae due to a decrease in invertebrate grazing pressure (Eriksson *et al.*, 2009; Sieben *et al.*, 2011a; b; Reiss *et al.*, 2014; Figure 3). This trophic cascade has also been observed in mesocosm experiments (Candolin *et al.*, 2016) and explains why filamentous algae biomass has been found to correlate negatively with abundances of coastal piscivorous fish and positively with stickleback abundances across space (Eriksson *et al.*, 2009; Donadi *et al.*, 2017; but see Candolin *et al.*, 2016). The high stickleback densities observed along large portions of the Baltic Sea coast today thus contribute to algal blooms, thereby exacerbating the habitat degradation caused by eutrophication (Eriksson *et al.*, 2009; Donadi *et al.*, 2017). Interestingly, the stickleback trophic cascade also seems to interact with eutrophication effects, where the positive effect of higher stickleback abundances on filamentous algae recruitment increases when nutrient loads are higher (Sieben *et al.*, 2011a; Östman *et al.*, 2016).

Adverse impacts on fish recruitment

Another well-documented effect of the stickleback increase along the Swedish Baltic Sea coast is greater predation pressure on the eggs and larvae of perch and pike (Nilsson *et al.*, 2004; Nilsson, 2006; Byström *et al.*, 2015; Nilsson *et al.*, 2019). Locally, the effect can be dramatic, with one study finding that stickleback predation resulted in an up to 96% reduction in the survival rate of pike larvae (Nilsson *et al.*, 2019). The relationship is highly size-dependent, with larvae being sensitive to predation only up to a body size of 25–35 mm (Byström *et al.*, 2015; Nilsson *et al.*, 2019). This means that relative phenology is of crucial importance to predator recruitment, with a larger negative effect observed in spawning areas where the sticklebacks arrive early.

As the negative effect of stickleback predation on pike and perch recruitment might eventually result in smaller adult predator population sizes, and thus lower predation rates on stickleback, this creates a self-reinforcing feedback loop (Figure 3). This feedback mechanism may be further strengthened by stickleback competing for food with predator juveniles (Ljunggren *et al.*, 2010; Jakubavičiūte *et al.*, 2017a; but see Byström *et al.*, 2015; Skarp, 2019), and by stickleback reducing the quality of the predators' nursery habitat through promoting the production of filamentous algae (see Donadi *et al.*, 2017). At the same time, positive feedback mechanisms also act in the opposite direction in areas where perch and pike dominate. The strong negative effect of adult predator densities on stickleback abundances (Eklöf *et al.*, 2020) reduces the negative impact of stickleback on the predators' offspring, which in turn should increase predation pressure on stickleback in future years.

The observed feedback mechanisms tend to result in shared spawning bays at the end of summer being dominated either by perch and/or pike juveniles, or by stickleback juveniles (Nilsson *et al.*, 2004; Bergström *et al.*, 2015; Eklöf *et al.*, 2020). The occurrence of bays dominated by stickleback juveniles rather than predator juveniles has increased over

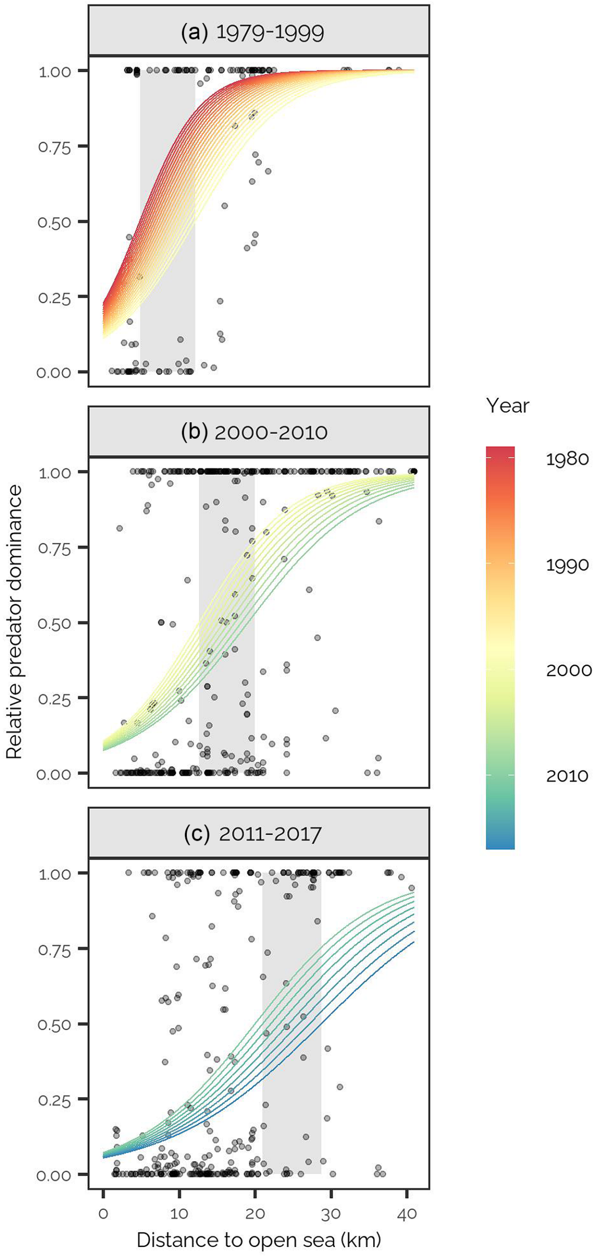

Figure 5. Illustration of the "stickleback wave" showing relative predator dominance (abundance of pike and perch juveniles divided by the sum of pike, perch and stickleback juveniles in spawning bays at the end of summer along the Swedish Baltic Sea coast) as a function of the distance to the open sea for (a) 1979–1999, (b) 2000–2009 and (c) 2010–2017 (data from Eklöf *et al.*, 2020). Semitranslucent markers show values for individual bay-years. Lines show predictions for individual years based on a generalised linear model with relative dominance as a function of year, distance from the open sea, wave exposure and latitude (see Eklöf *et al.*, 2020 for details; wave exposure and latitude are kept at average values). Grey shaded areas indicate the range of values within the given time period where local stickleback and predator dominance are equally likely.

time along long stretches of the Swedish Baltic Sea coast since the beginning of the 2000s and also seems to be spreading deeper and deeper into the archipelago like a "stickleback wave" (Figure 5; Eklöf *et al.*, 2020). In parallel, the extent of productive recruitment areas for coastal predatory fish has likely decreased significantly. Further research is needed to determine to what extent the increase in stickleback in previously predator-dominated bays is simply a response to a decline in predators driven by other factors, and to what extent the stickleback itself may have actively contributed to the predator declines.

Stickleback may also impact the recruitment of other fish species in the Baltic Sea. Sticklebacks along the German coastline have been found to consume substantial numbers of herring eggs, which likely results in local reductions in herring productivity (Kotterba *et al.*, 2014). It has also been suggested that sticklebacks have a negative impact on whitefish by competing for food and predating on whitefish offspring (Florin *et al.*, 2019), as observed in Lake Constance (Roch *et al.*, 2018; Rösch *et al.*, 2018). Finally, a strong negative relationship has been identified between juvenile abundances of stickleback and common roach along the Swedish Baltic Sea coast (U. Bergström, unpubl. data), suggesting that the stickleback could have negative effects on the recruitment of coastal cyprinids. Further studies on the impact of stickleback on additional fish species in the Baltic Sea should therefore be prioritised.

Knowledge gaps

Several knowledge gaps remain regarding the impact of increased stickleback densities on the ecosystem. The first one is the role of stickleback as a vector of energy and nutrient transfer between different parts of the ecosystem. Through its annual migrations, the stickleback acts as a link between the coast and the open sea of the Baltic Sea (Eriksson *et al.*, 2011), resulting in a significant flux of energy and materia (Sieben *et al.*, 2011b). Specifically, the sticklebacks that migrate to the coast to spawn and then die in the middle of the summer could account for a non-negligible contribution of nutrients at a time when the coastal nutrient pool is often depleted. It has been estimated that while the main component of coastal nutrient flux is in the form of water exchange with the open sea (Bryhn *et al.*, 2017), the input from sticklebacks can in some water bodies along the Swedish coast be of the same magnitude, or higher, than the nutrient input from land (A. Bryhn, pers. comm.). This points towards a need for further research into the degree to which the stickleback increase may counteract efforts to improve the eutrophication status of coastal areas by reducing nutrient flows from land-based sources.

The second knowledge gap concerns the possibility that increasing densities of stickleback in the Bothnian Sea and the central Baltic Sea could lead to higher levels of food competition for herring and sprat (see Casini *et al.*, 2011a; Olsson *et al.*, 2019). However, stickleback biomass is still low in comparison with that of sprat and herring (Olsson *et al.*, 2019), and there is no clear temporal decline in sprat and herring body condition that matches the timing of the stickleback increase (see Casini *et al.*, 2011a). While this suggests that at least up to the late 2000s, the impact of the stickleback increase on sprat and herring foraging opportunities were minor, further analyses are needed to explore whether this is still the case, as offshore stickleback abundances have increased since (Figure 2a–c).

As most studies, and this review, have focused on the detrimental impacts of high densities of stickleback, the final knowledge gap concerns the possibility that some parts of the ecosystem may have instead benefitted from the higher stickleback abundances. The stickleback is an important prey item for several predators, including fish, birds and mammals, where, for example, the increasing abundances in the central Baltic Sea and the Bothnian Sea may have contributed to increasing numbers of some fish-eating bird species (see HELCOM, 2018a). Thus, the possibility of positive impacts of increasing local stickleback densities on the survival, growth and reproductive success of stickleback predators needs to be investigated further.

Implications for management

Given the stickleback's ability to impair the recruitment of several fish species and strengthen adverse impacts of eutrophication on coastal ecosystems, maintaining and establishing complete and consistent monitoring programmes is important. The Baltic International Acoustic Survey, while not specifically designed to target stickleback, is useful in this respect for monitoring stickleback in the open sea (see Olsson *et al*., 2019; Figures 1b and 2a–c). However, the survey should ideally expand to also cover the Bothnian Bay, at least occasionally. Further, while it provides useful information for assessing trends, there is space for methodology improvements to increase the accuracy of absolute densities (e.g. using hydroacoustic sensors that better allow for detection of fish close to the surface) (Olsson *et al*., 2019). With the exception of a large dataset of juvenile densities from the Swedish coast as well as some local surveys (Figure 2d–k), coastal data are generally scarce. A methodologically consistent coastal survey across the Baltic Sea would therefore be helpful for getting a better grasp of spatially variable densities, and how coastal densities relate to open sea densities.

The development of indicators capturing the temporal dynamics of stickleback both in offshore and coastal areas of the Baltic Sea based on existing data (Figure 2) would likely benefit the general assessment of the state of the Baltic Sea ecosystem, such as in, for example, the next HELCOM holistic assessment (HOLAS III), to be published in 2023. These stickleback abundance indicators could potentially also be included as part of the assessment work in relation to the EU Marine Strategy Framework Directive (EC, 2008). In particular, they may be relevant in relation to Descriptor 4 (food webs), which states that "all elements of the marine food webs, to the extent that they are known, occur at normal abundance and diversity and levels capable of ensuring the long-term abundance of the species and the retention of their full reproductive capacity" (EC, 2008). Here, an evaluation of indicators of stickleback abundance in relation to existing indicators for coastal predatory fish could be highly relevant for large stretches of the Baltic Sea coast.

To avoid self-reinforcing feedback mechanisms pushing coastal reproduction areas toward stickleback domination, with the accompanying effects on coastal ecosystem functions, measures aiming to strengthen populations of coastal piscivorous fish should be a priority. As stickleback predators are affected by several sources of human impact, including fishing (Bergström *et al*., 2016), habitat exploitation (Hansen *et al*., 2019), and high levels of eutrophication (Bergström *et al*., 2013), measures and management plans should integrate fisheries and environmental management in concert, from local to regional levels. Interactions with stickleback should be explicitly considered when designing future measures to improve the status of coastal piscivorous fish. For example, limiting dredging and canalisation of currently enclosed bays may protect piscivorous fish spawning habitat from migrating sticklebacks (Donadi *et al*., 2020).

Currently, local culling of grey seal and great cormorant is carried out in some Baltic Sea countries, primarily in order to reduce negative impacts on fisheries (HELCOM, 2018a). As predation on coastal predatory fish from grey seal and great cormorant can be substantial locally (Hansson *et al*., 2018; Veneranta *et al*., 2020; Ovegård *et al*., 2021; Svensson, 2021), the ability of these measures as a way to restore predatory fish populations and generate desired top-down effects on stickleback in an effective, sustainable and ethically defendable manner should be evaluated. This should ideally be done through small-scale pilot studies. In general, all efforts aimed at strengthening populations of coastal stickleback predators should be acompanied by close monitoring of stickleback as well as other parts of the ecosystem, to improve our understanding of the system and to avoid unintended consequences.

As stickleback makes up an increasingly large proportion of pelagic biomass in parts of the open sea of the Baltic, interactions with sprat, herring and cod, key targets for commercial fisheries, become more and more important to consider. Currently, the stocks of these species are all regulated by quotas informed by advice from ICES. Recommendations are currently based on catches that aim for reaching maximum sustainable yield of each stock, which is the central objective of the EU Common Fisheries Policy (EU, 2013). However, managing fish stocks separately for maximum sustainable yield does not explicitly consider indirect effects on other species and ecosystem functions. For example, if herring quotas were set lower, this would likely result in increased competition with, and potentially predation on, stickleback and could thus influence the future development of the species in the Baltic Sea.

In addition, the increasing densities of stickleback may also influence growth and spawning conditions for sprat, herring and cod. In particular, stickleback densities may impact herring recruitment (Kotterba *et al*., 2014), sprat and herring food competition (Casini *et al*., 2011a; Olsson *et al*., 2019), and food availability for cod and large herring (see Parmanne *et al*., 2004; Almqvist *et al*., 2010). In order to determine the overall effect of these interactions on the demographics of sprat, herring and cod, and if/how much this may impact the ability of the stocks to withstand a given level of fishing pressure, these processes need to be better quantified. The consumption rates and the degree of overlap in the diets of stickleback, sprat and herring are relatively well studied but should be combined with biomass estimates to quantify the impact on sprat and herring food availability. However, targeted, systematic studies are needed to quantify impacts on herring recruitment as well as food availability for large herring and cod as previous studies are limited in time and space.

The use of multispecies models and inclusion of ecosystem considerations when providing advice on quota setting is still very limited. In the meantime, however, a better understanding and appreciation of interactions between stickleback and these key offshore species will provide at least a qualitative basis for evaluating stock development in the context of impacts from, and on, stickleback, as well as guide future quota setting.

Fishing for stickleback in the Baltic Sea

In response to the increasing stock size, the interest in fishing for stickleback has increased in recent years (Appelberg *et al.*, 2020; BSAC, 2021). Stickleback has historically been an important fishery species for coastal communities in the Baltic Sea. It was mainly fished using beach seines, and was used to produce lamp oil and varnish up until the early 20th century (Eesti Mereinstituut, 2017; Svedäng and Rolff, 2021). Residues were used as animal feed or fertiliser. Later, during the second half of the 20th century, Soviet states produced fish meal from Baltic Sea stickleback (Ojaveer, 1999). However, since the end of the 20th century, registered catches of stickleback in the Baltic Sea have been low and as it is prevented by minimum mesh size regulations of pelagic trawls, there is currently no targeted stickleback fishery (Bergström *et al.*, 2015). In recent years, however, the pelagic fishing fleet has shown a growing interest in exploiting this species (BSAC, 2021) and there are also a number of initiatives aiming to reduce local abundances through smaller-scale coastal fisheries (Appelberg *et al.*, 2020). Fished stickleback could be used for fishmeal, but other uses, such as producing food supplements or biofuel, are also possible.

Targeted removals may in theory be a way to break out of a state dominated by mesopredators, and could also generate positive knock-on effects (Nyström *et al.*, 2012). For example, persistent removal of planktivorous and benthivorous fish from eutrophic lakes often results in improved water quality, at least in the short term (Bernes *et al.*, 2015). However, it is often difficult to limit mesopredator populations via direct control (Prugh *et al.*, 2009), and particularly so in large open systems like the Baltic Sea. Even in Lake Constance (an enclosed and much smaller system), calculations show that reducing the stickleback population to minimise their negative impacts on the local whitefish population would require substantial efforts (Gugele *et al.*, 2020). Further, as pelagic fishing for stickleback requires the use of a fine mesh trawl in surface waters, the risk of bycatch of, for example, herring, sprat, Atlantic salmon and juvenile cod is substantial (Appelberg *et al.*, 2020). Fishing trials by the pelagic trawling fleet to optimise gear and technique for catching stickleback, as well as to estimate bycatch rates and composition, are currently in progress (BSAC, 2021). Additional prerequisites for a Baltic Sea stickleback fishery include the establishment of an analytical stock assessment as well as systems for landings control, onboard sampling to estimate bycatch rates, and evaluation of the ecosystem effects of the fishery (Appelberg *et al.*, 2020).

Given the large uncertainties that remain regarding interactions between stickleback and other components of the Baltic Sea ecosystem, we caution against initiating a large-scale targeted stickleback fishery until we have a better understanding of what the ecological impacts of such a fishery would be. Instead, we encourage further restricted fishing trials as these will allow us to evaluate the indirect effects of targeted removals and improve our understanding of the stickleback's role in the Baltic Sea ecosystem. Finally, it is important to recognise that the stickleback increase is a manifestation of underlying changes in the Baltic Sea ecosystem, and, if the goal is to restore the ecosystem and its functions, the sustainable long-term approach is to address the root causes of the increase, such as the depletion of populations of predatory fish, rather than focusing on relieving the impacts via an extensive fishery on stickleback.

Increases of opportunistic species in response to ecosystem change

While it is still unclear what has driven the stickleback increase observed in parts of the Baltic Sea, it seems likely that a decline in predation pressure has played a large role, and the increase can thus be considered a form of mesopredator release. With widespread declines in marine (top) predators, increases in mesopredator densities have been observed in many marine ecosystems (Daskalov, 2002; Myers *et al.*, 2007; Heithaus *et al.*, 2008; Prugh *et al.*, 2009; Eriksson *et al.*, 2011). For instance, collapses of the cod stocks in the north-western Atlantic (Frank *et al.*, 2005) and the Baltic Sea (Casini *et al.*, 2008) preceded rapid increases in the populations of their prey, such as, for example, snow crab (*Chionoecetes opilio*) in the Atlantic and sprat in the Baltic. Opportunistic, generalist mesopredators, such as the stickleback, may be particularly good at responding to reduced predation pressure, as well as other types of ecosystem change, as they can rapidly adapt to and exploit novel conditions. This is in line with the recent stickleback increases observed in other marine (Lajus *et al.*, 2021) and freshwater (Roch *et al.*, 2018; Rösch *et al.*, 2018) ecosystems, as well as the increases in the proportion of small, opportunistic species that have been observed in marine ecosystems in general (e.g. Tomczak *et al.*, 2013; Pecuchet *et al.*, 2017).

As with the observed stickleback-induced cascade resulting in increased filamentous algae biomass, other mesopredator increases have also been shown to have knock-on effects on lower trophic levels (Heithaus *et al.*, 2008; Prugh *et al.*, 2009). For instance, similar increases in filamentous algae in response to mesopredator increases has been seen in seagrass meadows in several locations in the North Atlantic (see Östman *et al.*, 2016 for a meta-analysis), as well as in the Pacific (Hughes *et al.*, 2013). As suggested here for Baltic Sea stickleback, efforts aiming to stem the shift towards aquatic ecosystems dominated by mesopredators, and subsequent cascading effects, may gain from measures focusing on maintaining and restoring strong populations of large predatory fish. Here, the stickleback case points to the importance of early action, as predator-prey reversal feedback mechanisms may otherwise lock the system in an alternative (semi-) stable state. This type of feedback mechanism that acts to reinforce either a prey- or a predator-dominated state is quite common (Walters and Kitchell, 2001). For example, predator-prey reversal has been invoked as a possible explanation for shifts towards high densities of clupeids observed both in the North Sea and the Baltic Sea, where crashes in the cod populations resulted in reduced predation pressure on clupeids, and growing clupeid populations in turn may have suppressed the recruitment of cod by feeding on their eggs, maintaining the system in a prey-dominated state (Fauchald, 2010; Casini *et al.*, 2011b). Finally, the Baltic Sea stickleback case also points towards the importance of allocating resources to the study of the ecological role of opportunistic mesopredator species, as the sudden increases they may exhibit under rapid environmental change can have large consequences for the ecosystems of which they are part. This type of knowledge is key for supporting a continued move towards an ecosystem-based management approach that considers not only commercially exploited species, but also interlinked species and processes (see Pikitch *et al.*, 2004)—a shift which is crucial for the sound management of marine ecosystems in the current era of rapid anthropogenic environmental change.

Data availability

The data and code used to produce Figures 1, 2, 4, and 5 are available at github.com/agnesolin/sticklebackREVIEW.

Funding

The work was supported by the Swedish Agency for Marine and Water Management (grant number 1049–20) and the Swedish research council Formas (grant number 2019–00310).

Author contributions

Conceptualization: U.B and A.B.O.; Data curation: O.K. and L.B.; Formal analysis: A.B.O.; Funding acquisition: U.B. and J.S.E.; Project administration: U.B. and J.S.E.; Visualization: A.B.O.; Writing—original draft: A.B.O.; Writing—review & editing: all authors

Acknowledgements

We want to thank all the member states of ICES, the Swedish Agency for Marine and Water Management, country administrative boards, Forsmarks Kraftgrupp AB, Ulrika Candolin and Didzis Ustups for collecting and providing access to the data presented in Figures 1, 2, and 5. We are also grateful to Hedda Kjelldahl, Anders Adill and Mårten Erlandsson for help with collating and processing the juvenile and Forsmark data in Figure 2. Finally, we wish to thank Henn Ojaveer, Howard Browman and two anonymous reviewers for insightful comments on earlier versions of the manuscript.

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Handling Editor: Henn Ojaveer