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Stickleback increase in the Baltic Sea – A thorny issue for coastal predatory fish

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ABSTRACT

In the Baltic Sea, the mesopredator three-spined stickleback (*Gasterosteus aculeatus*) spends a large part of its life cycle in the open sea, but reproduces in shallow coastal habitats. In coastal waters, it may occur in high abundances, is a potent predator on eggs and larvae of fish, and has been shown to induce trophic cascades with resulting eutrophication symptoms through regulation of invertebrate grazers. Despite its potential significance for the coastal food web, little is known about its life history and population ecology. This paper provides a description of life history traits, migration patterns and spatiotemporal development of the species in the Baltic Sea during the past decades, and tests the hypothesis that stickleback may have a negative impact on populations of coastal predatory fish. Offshore and coastal data during the last 30 years show that stickleback has increased fourfold in the Bothnian Sea, 45-fold in the Central Baltic Sea and sevenfold in the Southern Baltic Sea. The abundances are similar in the two northern basins, and two orders of magnitude lower in the Southern Baltic Sea. The coastward spawning migration of sticklebacks from offshore areas peaks in early May, with most spawners being two years of age at a mean length of 65 mm. The early juvenile stage is spent at the coast, whereafter sticklebacks perform a seaward feeding migration in early autumn at a size of around 35 mm. A negative spatial relation between the abundance of stickleback and early life stages of perch and pike at coastal spawning areas was observed in spatial survey data, indicating strong interactions between the species. A negative temporal relationship was observed also between adult perch and stickleback in coastal fish monitoring programmes supporting the hypothesis that stickleback may have negative population level effects on coastal fish predators. The recent increase in stickleback populations in different basins of the Baltic Sea in combination with negative spatiotemporal patterns and previously observed interactions between stickleback and coastal predatory fish suggests that this species may have gained a key role in the coastal food webs of the Baltic Sea. Through its migrations, stickleback may also constitute an important vector linking coastal and open sea ecosystem dynamics.

1. Introduction

Many fish species undertake extensive migrations from feeding grounds towards specific spawning and nursery habitats, sometimes across ecosystem boundaries (Gross et al., 1988; Gillanders et al., 2003). Apart from the well-known effects of mass migration of anadromous species into freshwaters (Willson and Halupka, 1995; Bilby et al., 1996), migrations between offshore and coastal areas of abundant planktivore (Deegan, 1993; Varpe et al., 2005) and large piscivore fish species (Casini et al., 2012) may have profound effects on energy fluxes and trophic interactions. In particular, changes in major offshore fish stocks may initiate cascading effects in coastal food webs, where outbursts of small-bodied mesopredatory fish have induced fundamental changes in nearshore habitats, such as an excessive growth of filamentous algae and a subsequent loss of seagrasses and large brown algae (Ritchie and Johnson, 2009; Eriksson et al., 2011; Baden et al., 2012). These

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mesopredator increases in marine ecosystems often involve complex interactions with large piscivore fishes, where the piscivore feeds on the mesopredatory fish and adult mesopredators feed on or compete with early life stages of the piscivore. These processes have been referred to as intraguild predation (Polis et al., 1989), cultivation-depensation (Walters and Kitchell, 2001), predator-prey reversal (Barkai, 1988) or trophic triangle (Collie et al., 2013), and constitute a destabilizing force in food webs, making them prone to shifts between alternative stable states. Thus, in order to understand marine food web dynamics, it is vital to encompass the spatial dimension of species interactions, including the effects of cross-ecosystem migrations (Loreau et al., 2003).

In the Baltic Sea, the offshore pelagic fish community is typically dominated by herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). The dynamics of these populations are relatively well-studied, and have been shown to be governed by a combination of environmental forcing, intra- and interspecific competition and top-down control (Casini et al., 2008, 2011). A less-studied component of the Baltic offshore pelagic fish community is the three-spined stickleback (*Gasterosteus aculeatus*, hereafter referred to as stickleback). This species is a widespread and highly adaptive small mesopredatory fish abundant in northern temperate coastal seas and estuaries, as well as in many lakes and streams (Banister, 1986). Stickleback has received considerable attention in behavioural and evolutionary ecology in freshwater systems, demonstrating how environmental variation may lead to rapid divergence (Hendry et al., 2013), which in turn may affect species interactions (Ingram et al., 2012) and ecosystem functioning (Harmon et al., 2009; Des Roches et al., 2013). Less is known about its function in coastal and marine food webs.

Stickleback in the Baltic Sea utilises the shallow coastal zone for reproduction, but is believed to spend a large part of its life in pelagic open sea areas (Borg, 1985; Ljunggren et al., 2010). The peak spawning time for stickleback occurs between May and July in the Baltic Sea, starting a bit earlier in the southern areas (Borg, 1985; Candolin et al., 2007, Byström P. pers. com.). Genetic structuring between coastal areas appears to be weak, although a strong pattern of isolation by distance and few genetic clusters in the Baltic Sea indicates that gene flow occurs mainly between adjacent areas (DeFaveri et al., 2012, 2013). Stickleback may constitute a considerable proportion of the total pelagic fish biomass in the open sea, up to 10–20%, (Jurvelius et al., 1996; Ljunggren et al., 2010), and in some coastal areas it may even dominate the fish community by biomass (Ljunggren et al., 2010; Sieben et al., 2011). This species is an important prey for large predatory fish, such as cod (*Gadus morhua*) (Almqvist et al., 2010) and salmon (*Salmo salar*) (Hansson et al., 2001) in the open sea, and perch (*Perca fluviatilis*) (Mustamäki et al., 2014; Jacobson, 2015) and pike (*Esox lucius*) (Lemmetyinen and Mankki, 1975; Jacobson, 2015) in the coastal zone. Simultaneously, there are indications that stickleback may induce negative effects on perch and pike recruitment in the Baltic Sea through predation and potentially competition (Nilsson et al., 2004; Ljunggren et al., 2010; Byström et al., 2015). In lakes and lagoons, stickleback may cause trophic cascade effects through their top-down regulation of phytoplankton biomass (Jakobsen et al., 2004; Norlin et al., 2005). Similarly, during spawning in shallow vegetated areas of the Baltic Sea, they may induce blooms of filamentous algae in the benthic system through predation on small grazers (Eriksson et al., 2009; Sieben et al., 2011), thus causing ecosystem changes similar to those brought about by eutrophication. Thus, these studies suggest that stickleback may disrupt coastal food web dynamics of the Baltic Sea. Despite the potential ecological importance of this species, the life history and the population dynamics of stickleback in relation to interacting species have remained largely unknown.

Stickleback is also of economic importance, and has been subject to commercial fishery in the Baltic Sea. In 1991–2010, mean annual reported catches in the Baltic Sea were 125 tons according to ICES official catch statistics. In 1973–1990 annual landings averaged 5900 tons, when stickleback was targeted for animal feed and fishmeal production by the former Soviet Union states in the eastern Baltic, (Ojaveer, 1999). Further back, up to the early 20th century, a stickleback fishery using beach seines was locally very important along the Baltic Sea coasts, indicating that the species has been abundant in Baltic Sea coastal areas for a long time (Jansson, 1995). During this period stickleback was boiled to separate the valuable oil which was used as lamp fuel or in varnish, while the residue was used as animal feed or fertilizer. Today, there is a rising interest from the large pelagic fishing fleet in the Baltic Sea to start exploiting stickleback for fishmeal and biogas production. So far, however, no fishing permits have been issued by the responsible authorities, partly because of the lack of knowledge about the potential ecological consequences such a fishery could have on the ecosystem.

In this study, we aim to describe the population dynamics of three-spined stickleback in different basins of the Baltic Sea, as well as its life history and migrations between the open sea and coastal reproduction areas. By analysing the spatiotemporal patterns in recruitment and population dynamics of stickleback in relation to the main coastal piscivores perch and pike, we test the hypothesis that stickleback may negatively affect these piscivore populations. We discuss the rising role of stickleback in the Baltic Sea ecosystem, which provides an example of how migratory mesopredatory fish may reshape coastal food webs and serve as vectors between offshore and coastal systems.

2. Methods

Data from several different fish surveys and monitoring programmes were compiled and used to describe population trends and life history characteristics of stickleback in open sea and coastal areas of the Baltic Sea, and to evaluate potentially negative effects of stickleback on coastal piscivorous fish species, such as perch and pike, indicated by spatial patterns in recruitment and temporal population trends in the piscivore populations.

2.1. Spatiotemporal dynamics

Abundance data on three-spined stickleback in offshore areas of the Baltic Sea between 1980 and 2011 was retrieved from the Swedish part of the ICES Baltic International Acoustic Survey (BIAS), in which hydroacoustics in combination with pelagic trawl hauls are used for estimating abundances of Baltic herring and sprat (ICES, 2008). The data covers open sea areas in a 900 km south-north gradient from the Southern Baltic Sea to the northern Bothnian Sea (Fig. 1). Data are presented for three basins: the Southern Baltic Sea (corresponding to ICES subdivision (SD) 25), the Central Baltic Sea (SD27-29) and the Bothnian Sea (SD30). The hydroacoustic survey is not specifically designed to assess stickleback abundances, as this species primarily occurs in surface waters while the acoustic method estimates fish densities efficiently from 10 m depth downwards. However, the control trawl hauls performed during the survey to estimate species compositions can be used to follow the changes in stickleback catch per unit effort (CPUE, kg h^{-1}) over time. The number of replicate trawl hauls per area and year varied between 10 and 90, except in 1980–83 when the number of hauls was as low as 4–7 in the Southern Baltic Sea and in the Bothnian Sea. These replicate hauls were used to calculate mean and standard error of CPUE per area and year. In the Bothnian Sea, no survey was performed in 1984–1990 and 1992–2006. To get a