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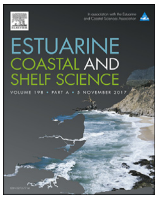

Shifts in coastal fish communities: Is eutrophication always beneficial for sticklebacks?

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ABSTRACT

Following declines of predatory fish, mesopredators such as sticklebacks have been linked to shifts in coastal trophic networks through both top-down (preying on mesograzers and facilitating algal blooms) and bottom-up (benefitting from eutrophicated conditions) processes. Here, we tested whether the association between eutrophication effects (filamentous algae and turbidity) and sticklebacks held true in the Finnish Archipelago Sea where predatory fish populations have remained stable. If so, sticklebacks should be more abundant in the middle archipelago, where eutrophic conditions have led to increased turbidity, higher filamentous algal loads, and decreased cover of submerged aquatic vegetation (SAV), than in the outer archipelago, where environmental conditions are better. We measured the spatial and seasonal variation of sticklebacks (three-spined *Gasterosteus aculeatus* and nine-spined *Pungitius pungitius*) in middle and outer archipelago sites, as well as environmental variables potentially affecting their abundance.

Adults and juveniles of both species were more abundant in the outer than middle archipelago. The outer archipelago was characterized by greater Secchi depth throughout the summer and higher SAV cover in late summer. Secchi depth was positively correlated with stickleback abundance of both species, while SAV cover was also positively correlated in late summer. Filamentous algal cover was high in both the middle and outer archipelago, but not consistently associated with stickleback abundance throughout the summer. While sticklebacks have been thought to both contribute to, and benefit from, eutrophication, our results instead suggest that the resulting environmental changes may have adverse effects on sticklebacks, especially if predators are present. This may lead them to shift their breeding grounds and spatial distribution to less eutrophicated areas where lower turbidity and the resulting increased availability of SAV provide refuge from predators for juveniles, and higher quality breeding and feeding grounds for adults.

1. Introduction

Marine ecosystems face multiple anthropogenic impacts, leading to shifts in community structure and ecosystem functioning (Lotze, 2006; Worm at el., 2006). In coastal areas, eutrophication caused by nutrient runoff has led to phytoplankton and filamentous algal blooms, increasing epiphytic loads on perennial vegetation, and increased turbidity (Short et al., 1995; Smith et al., 2006). At the same time, the overexploitation and collapse of predatory fish populations has lead to trophic cascades (Jackson et al., 2001; Myers and Worm, 2003) in diverse marine ecosystems such as kelp forests (Estes et al., 1998), rocky shores (Menge, 2000), and seagrass meadows (Baden et al., 2010).

In the Baltic Sea, nutrient runoff had led to decreases in water quality and Secchi depth since the mid-twentieth century (Bonsdorff et al., 1997; HELCOM, 2010). The resulting water turbidity and overgrowth of filamentous algae limits the growth and recruitment of habitat-forming macrophytes (such as bladderwrack *Fucus vesiculosus* and eelgrass *Zostera marina*), leading to reduced abundance and decreased depth limits of these species (Torn et al., 2006; Boström et al., 2014). As many invertebrate and fish species utilise these perennial macrophytes for food and habitat, their decline may have hastened biodiversity loss in the Baltic Sea (HELCOM, 2010). At the same time, decreasing predatory fish stocks in the western Baltic Sea (Ljunggren et al., 2010; Bergström et al., 2016a), have caused major ecological transitions

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or regime shifts (Österblom et al., 2007). In coastal areas, three-spined sticklebacks (*Gasterosteus aculeatus*) have become more abundant following pike (*Esox lucius*) and perch (*Perca fluviatilis*) population declines (Nilsson et al., 2004; Ljunggren et al., 2010), the latter being a main predator of sticklebacks (Lappalainen et al., 2001).

Healthy populations of top predators allow herbivores to proliferate by controlling the abundance of intermediate predators (Myers et al., 2007; Heithaus et al., 2012). This provides stability and resilience in the face of eutrophication because herbivore grazing can compensate for algal growth caused by increased nutrient input (Korpinen et al., 2007; Hughes et al., 2013). The decline of predatory fish stocks can lead to trophic cascades and mesopredator release, thus reducing herbivory and enhancing the

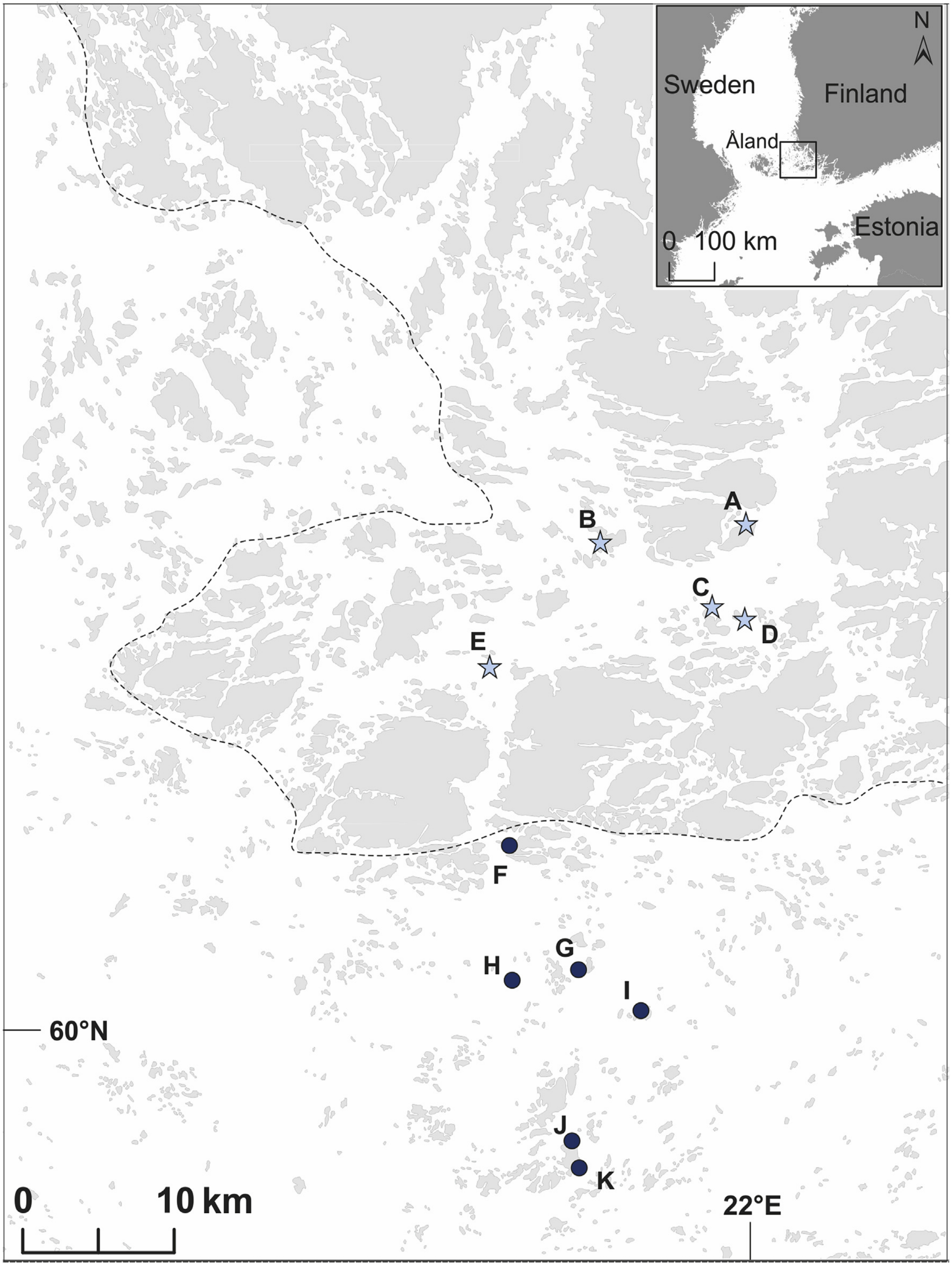

Fig. 1. Location of sampling sites in the Archipelago Sea. Sites A-E are located in the middle archipelago (stars), and sites F-K are located in the outer archipelago (circles). The dashed line indicates the border between the middle and outer archipelago zones, as described in Häyrén (1900).