Journal of Experimental Marine Biology and Ecology 476 (2016) 31–40

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Nutrient enrichment overwhelms top-down control in algal communities around cormorant colonies

Karine Gagnon *, Joakim Sjöroos, Juho Yli-Rosti, Marjo Stark, Eva Rothäusler, Veijo Jormalainen

Section of Ecology, Department of Biology, University of Turku, FI-20014, Turun Yliopisto, Finland

ARTICLE INFO

Article history:
Received 30 April 2015
Received in revised form 31 August 2015
Accepted 14 December 2015
Available online 20 December 2015

Keywords:
Bottom-up
Nutrient enrichment
Top-down
Trophic cascade
Cormorants
Fucus vesiculosus

ABSTRACT

Expanding populations of the piscivorous seabird Great Cormorant (*Phalacrocorax carbo sinensis*) in the Baltic Sea can have both bottom-up and top-down effects on lower trophic levels: nutrient runoff (bottom-up) from colonies increases algal growth, while predation on fish (top-down) can lead to decreased fish populations around colonies, potentially causing a trophic cascade and higher grazing pressure on algae due to higher herbivore abundances. In this study, we determined how these top-down and bottom-up processes interact to affect algal communities by using exclusion cages to manipulate the access of fish and herbivores to algae around both colony and control islands, and measuring algal recruitment and herbivory in these cages. The results showed that algal communities do indeed differ significantly between control and colony sites: *Fucus vesiculosus*, an important foundation species, had lower recruitment around colony sites. We found evidence of increased herbivory on *Fucus* around colony sites in one year, which may contribute to lower survival and reproduction, but the effect was not consistent. Instead, we suggest that lower recruitment is likely mainly due to nutrient enrichment which leads to increased competition from ephemeral algae, and thus decreased recruitment and abundance of *Fucus* around colonies. This was also indicated by higher recruitment of several ephemeral algal species around colonies in herbivore exclusion cages, indicating they do indeed benefit from nutrient runoff from colonies. Increased grazing around colonies was able to counteract this to some extent, but not completely. Overall, cormorants can indeed affect lower trophic levels, especially through local bottom-up processes, leading to shifts in community structure and potentially decreased biodiversity due to impairing conditions for the foundation species *F. vesiculosus*.

1. Introduction

Community regulation in coastal ecosystems involves both top-down and bottom-up processes (Burkepile and Hay 2006); earlier research has shown that top-down effects are especially strong in temperate littoral systems, such that predators can control prey populations, and herbivores can control algal dynamics (Heck and Valentine 2007; Poore et al. 2012). However, bottom-up effects, especially nutrient availability, can become the dominant process and overwhelm top-down control in the presence of high nutrient input (Lotze et al. 2001), thus leading to shifts in community structure. Determining how these processes interact is thus of primary importance in understanding how communities are structured, and how they might react to environmental changes.

Seabird colonies are an important biotic factor affecting coastal environments and, as a source of both locally concentrated nutrient input and intense fish predation, can potentially alter benthic communities through both bottom-up nutrient enrichment and top-down trophic cascades. The impact of seabird colonies on benthic communities is an increasing concern in the Baltic Sea, where the Great Cormorant (*Phalacrocorax carbo sinensis*) population has increased exponentially since the mid-1990s (Van Eerden and Gregersen 1995; Lehikoinen 2006; Beike 2014), to more than 20,000 breeding pairs along the Finnish coast in 2014 (monitoring data from the Finnish Environmental Institute SYKE). Benthic communities around colonies are indeed highly enriched in nitrogen from cormorant guano (Kolb et al. 2010; Gagnon et al. 2013), which can lead to increased algal productivity (Bosman and Hockey 1986) and decreased biodiversity of benthic fauna (Signa et al. 2015). Cormorants are also important fish predators, with each breeding pair consuming 1 kg of fish per day during the breeding season (Glahn and Brugger 1995; Ridgway 2010). These high consumption rates have led to conflicts with fisheries (Marzano et al. 2013), and therefore most research has focused on the impacts of cormorants on fish communities, with little attention on how this could lead to a trophic cascade affecting lower trophic levels. Fish removed by cormorants during the breeding season tend to be small and medium-sized species, especially perch (*Perca fluviatilis*), ruffe (*Gymnocephalus cernua*), roach (*Rutilus rutilus*), Baltic herring (*Clupea harengus membras*), and three-spine stickleback (*Gasterosteus aculeatus*), with some spatial and

---

* Corresponding author.
E-mail address: karine.gagnon@utu.fi (K. Gagnon).

http://dx.doi.org/10.1016/j.jembe.2015.12.007
0022-0981/© 2015 Elsevier B.V. All rights reserved.

temporal variation in the diet composition (Engström 2001; Lehikoinen 2005; Žydelis and Kontautas 2008; Pūtys and Zarankaitė 2010; Boström et al. 2012; Salmi et al. 2015). Several of these species are important consumers of mesograzers, especially three-spine sticklebacks (which consume amphipods Sieben et al., 2011a, 2011b) and perch <20 cm (the size classes preferred by cormorants (Lehikoinen 2005; Salmi et al. 2015) which consume amphipods and isopods; Lappalainen et al. 2001; Mustamäki et al. 2014), thus their decrease around cormorant colonies may lead to higher abundances of invertebrate grazers and thus to a trophic cascade affecting algae.

Predictions about cormorant impacts on benthic communities are rendered even more difficult as recent research has shown that trophic cascades (i.e. top-down effects) can modulate the outcome of eutrophication in coastal ecosystems (Pace et al. 1999; Carpenter et al. 2001; Worm et al. 2002; Deegan et al. 2007; Gruner et al. 2008; Eriksson et al. 2012). High trophic level predators may inhibit algal blooms by controlling mesopredators, thereby releasing predation pressure on herbivores that, in turn, can control algae; accordingly, declines in top predators can exacerbate algal blooms (Eriksson et al. 2009; Sieben et al. 2011a). Although this top-down control of algae by herbivores is generally effective in rocky littoral ecosystems, it breaks down at high nutrient levels (Pace et al. 1999; Lotze et al. 2001; Lotze and Worm 2002; Worm et al. 2002; Worm and Lotze 2006; Korpinen et al. 2007a, 2007b; Sieben et al. 2011b; Eriksson et al. 2012). In addition, species within a trophic level usually do not respond equally to changes in nutrient availability and/or predation risk, due to differences in competitive ability or predation susceptibility, which will lead to shifts in invertebrate or algal community structure (Steen 2004; Korpinen et al. 2007b; Korpinen and Jormalainen 2008; Eriksson et al. 2009).

In this study, we investigated how trophic cascades and nutrient enrichment interact to modify algal communities around cormorant colonies. To this end, we conducted multi-year field experiments in which we manipulated the access of herbivores and fish to algae using exclusion cages, and measured a) the resulting recruitment of common algal species, and b) grazing pressure on the perennial brown alga *Fucus vesiculosus* (hereafter *Fucus*). We placed cages in the littoral of both colony and control islands which also allowed us to evaluate the effects of colony presence, i.e. top-down cascades from the cormorants and/or the nutrient run-off from guano on algae.

In control sites, we expected that herbivores could limit algal recruitment and that fish would have a cascading effect on producers, and therefore we predicted that algal recruitment would be highest in the herbivore exclusion cages, lowest in the fish exclusion cages, and intermediate in open cages, while trends for grazing should follow the opposite pattern. We then envisioned three scenarios of how algal settlement and grazing pressure could vary due to effects of colonies (Fig. 1). (**1**) Algae around cormorant colonies are only affected by nutrient enrichment; in this case we expected that there would be higher algal recruitment than in control sites, but that the pattern of the cage treatments would be the same as in the control sites. We further predicted that in this scenario, grazing might increase slightly in the fish exclusion and open cages, due to nitrogen enrichment making algae more palatable to herbivores (e.g. Hemmi and Jormalainen 2002; Kraufvelin et al. 2006). (**2**) Algae are only affected by a trophic cascade arising from cormorants, thus algal recruitment in the herbivore exclusion cages should be similar to that in control sites, but that grazing pressure should be higher than in the control sites, with little difference between fish exclusion and open cages, due to cormorants removing fish predators. (**3**) Finally, if both nutrient enrichment and cormorant cascades are present and have additive effects, we expected to see higher algal recruitment in colonies than controls in herbivore exclusion cages, but similar levels of recruitment in fish exclusion cages and open cages (due to increased herbivory and nutrient enrichment essentially counteracting each other). However, increased nutrient enrichment and higher grazer abundance should combine to lead to very high grazing pressure in both fish exclusion and open cages.

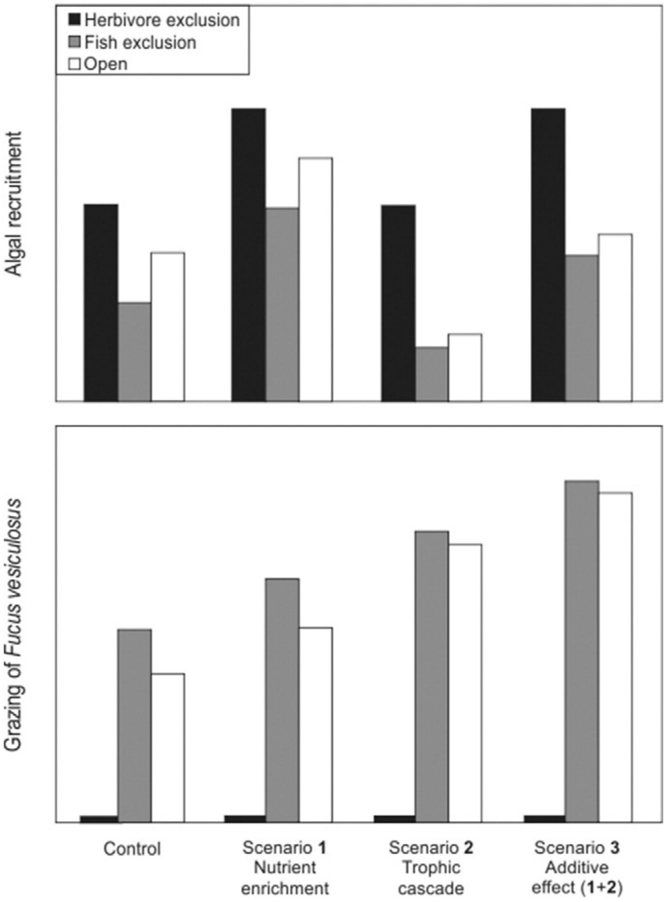

Fig. 1. Predicted algal recruitment and grazing pressure on *Fucus vesiculosus* in cages around control sites, and under three scenarios around colony sites: (1) nitrogen enrichment is the main factor, (2) a trophic cascade arising from cormorant predation is the main factor, causing an increase in herbivore abundance, and (3) both effects are additive. In these scenarios, we considered that nitrogen enrichment would lead to a 50% increase in recruitment, and a 25% increase in grazing (due to higher palatability), while a trophic cascade would cause a 50% increase in grazing. Dark bars are herbivore exclusion cages, grey bars are fish exclusion cages, and white bars are open cages.

The above scenarios are simplifications of the joint effects of bottom-up and top-down regulation on a complex algal community. The actual algal recruitment and grazing pressure in cages may differ due to interactive effects of cascades and nutrients, varying responses of species to nutrient availability and/or herbivory (i.e. some ephemeral species could respond very quickly to nutrient enrichment and thus grazing could have little impact on them), or long-term changes in algal communities in colony sites, which may affect the amount of recruitment (due to different propagule pressure from control sites). For example, we expected that *Fucus* might respond negatively to nutrient enrichment around cormorant colonies (i.e. an opposite of what is predicted above), as it can be outcompeted by faster-growing species in high-nutrient environments.

2. Methods

2.1. Study area and sites

This study was carried out in the Archipelago Sea, along the southwestern Finnish coast (Table 1, Fig. 2). A pilot study was carried out in 2012 with two sites: one cormorant colony and one control island (sites A and B). In 2013, we conducted the experiment (with slight modifications to the cages, see Section 2.2) at the same two sites, and added six more sites. In 2014, we again used the same two original sites, and added six new sites that differed from the ones used in