



TOP-DOWN AND BOTTOM-UP IMPACTS OF THE GREAT CORMORANT (*PHALACROCORAX CARBO SINENSIS*) ON COASTAL BENTHIC COMMUNITIES IN THE BALTIC SEA

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Cover image: Äggskär cormorant colony in the Archipelago Sea, northern Baltic Sea. Photo by Karine Gagnon.

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ABSTRACT

Community regulation depends on the interactions between top-down and bottom-up processes. In this thesis, I took advantage of the recent population growth of the Great Cormorant (*Phalacrocorax carbo sinensis*) in the Baltic Sea to explore how these processes interact with each other to affect multiple trophic levels in coastal benthic communities. Bottom-up nutrient enrichment from cormorant guano could simulate eutrophication effects while cormorant predation pressure on fish could cause trophic cascades. First, I determined whether nutrient enrichment occurred through stable isotope analysis. Then I studied how top-down and bottom-up processes affect algal, invertebrate and fish communities through both sampling of natural communities and manipulation of predation and herbivory pressure. Finally, I quantified the contribution of cormorant effects on producer communities relative to abiotic factors over a larger spatial scale.

Cormorant colonies had similar effects to eutrophication on macrophyte communities in the immediate vicinity of colonies (<100 m), due to bottom-up processes, with a decrease in the perennial species *Fucus vesiculosus* and increases in filamentous algal growth. There was also evidence of top-down control as herbivory on some algal species increased around colonies, and top-down control was further suggested with some fish species being less abundant around cormorant colonies. There were differences in invertebrate communities between colony and control sites, though the direction and magnitude of these differences depended on the species and habitat studied. These community shifts could be due to nutrient enrichment affecting the macrophytes community, thus modifying habitat availability, structure and shelter, and food availability; but top-down predation by fish on invertebrates affecting both abundance and habitat use is also a potential factor. Overall, bottom-up processes were easier to detect, likely due to their strong localised effect on communities in the vicinity of colonies, while cascading top-down processes probably occur over a larger area as cormorants can fly long distances to feed.

Over a larger scale (up to 5 km), cormorant impacts significantly affected macrophytes communities in conjunction with abiotic factors, but their strength depended on the depth and substrate type of communities. In shallow areas, temporal variability was high, probably due to quickly changing environmental conditions, and wave exposure was a very strong structuring force, while cormorant effects were less important. In deeper rocky substrates, the importance of cormorant colonies increased as communities became more temporally stable, but other factors such as the geographic area, nutrient concentration and turbidity were still the most important factors. In soft substrates, the importance of environmental factors varied with depth in a similar way to hard substrates, and cormorant effects were also a significant factor except in deeper waters. The patterns of cormorant impacts, with lower abundance of *Fucus vesiculosus* (the main habitat-forming species in hard substrates) and *Zostera marina* (which fulfils a similar role in soft substrates) in areas within 5 km of cormorant colonies, were similar to the results of the smaller-scale sampling and experiments. Similarly, there was a trend towards higher filamentous algal abundance as cormorant influence increased in both the small-scale experiments and the large-scale study.

Cormorant colonies do indeed impact benthic communities through both top-down and bottom-up processes, though they must be considered concurrently with abiotic environmental factors which structure communities. In addition, the relative importance of these processes depends on the scale considered: bottom-up nutrient enrichment affects communities in the vicinity of the colonies, while top-down trophic cascades occur over a larger scale.

TIIVISTELMÄ

Eliöyhteisöjen toimintaa säätelevät ravintoverkon ylemmiltä tasoilta alaspäin suuntautuvat prosessit kuten saalistus sekä alhaalta ylöspäin vaikuttavat tekijät kuten ympäristön ravinteisuus. Väitöskirjassani hyödynsin merimetson, *Phalacrocorax carbo sinensis*, nopeaa runsastumista Itämerellä tutkiakseen edellä mainittujen prosessien toimintaa ja niiden yhteisvaikutuksia vedenalaisissa eliöyhteisöissä. Merimetsoyhdykskunta voi vaikuttaa eliöyhteisöihin rehevöittämällä vesistöä paikallisesti ulosteiden ravinnevaluman vuoksi. Lisäksi merimetsojen kaloihin kohdistama saalistuspaine voi muuttaa ravintoverkon eri trofiasojojen lajikoostumusta ja runsautta. Väitöskirjassani tutkin merimetson vaikutusta vedenalaiseen luontoon selvittämällä ensin isotooppianalyysiin avulla, lisäävätkö merimetot ravinteiden määrästä pesimäyhdykskuntien läheisyydessä. Kokeellisessa tutkimuksessa estin kalojen ja kasvinsyöjen pääsyä perustuottajatasolle tutkiakseen miten merimetsoyhdykskunta vaikuttaa, joko kaloihin kohdistuvan saalistukseen tai lisääntyneen ravinteisuuden kautta, levien, selkärangattomien ja kalojen lajiston ja runsauteen. Lopuksi tutkin merimetsojen vaikutuksia perustuottajayhteisöihin laajassa maantieteellisessä mittakaavassa ja suhteutin niitä muihin tunnettuihin tuottajayhteisöihin vaikuttaviin abioottisiin ympäristötekijöihin.

Merimetsoyhdykskuntien läheisyydellä (<100 m) oli samanlainen vaikutus vesikasvi- ja leväyhteisöihin kuin rehevöitymisellä: monivuotinen rakkolevä, *Fucus vesiculosus*, vähentyi ja rihmamaisten levien kasvu lisääntyi. Havaitsin myös, että merimetson vaikuttavan kalastoon ja tämän heijastuvan myös ravintoverkon alemmille tasolle. Tämä ilmeni merimetsoyhdykskuntien läheisyydessä tiettyjen kalalajien vähäisempänä määrään sekä rihmamaisiin levii kohdistuvana voimakkaampana kasvinsyöntinä. Selkärangattomien yhteisöt olivat nekin erilaisia yhdyskuntien läheisyydessä verrattuna kontrollialueisiin, joskin näiden erojen suunta ja suuruus riippuivat tarkasteltavasta lajista ja elinympäristöstä. Havaitsemani erot eliöyhteisöissä voivat olla seurausta yhdyskuntien tuottamasta ravinnekuormituksesta: ravinteet vaikuttavat paikalliseen perustuottajayhteisöön, joka puolestaan vaikuttaa sekä selkärangattomille sopivien elinympäristöjen määrään että suojaapenkojen ja ravinnon saatavuuteen. Lisäksi tulokseni viittaavat siihen, että kalojen kasvinsyöjiin kohdistuva saalistus vaikuttaa kasvinsyöjen runsauteen ja elinympäristön käyttöön. Tuloksistani käy ilmi, että merimetson aiheuttaman ravinnekuormituksen vaikutukset ovat helpommin havaittavissa paikallisesti yhdyskuntien välittömässä läheisyydessä, kun taas ravintoverkossa ylhäältä alas päin suuntautuvat eli kalaston kautta tapahtuvat vaikutukset kohdistuvat laajemmille alueille merimetsojen lentäessä usein pitkiäkin matkoja ravintoa hakissaan.

Laajemmassa mittakaavassa (5 km asti) merimetsoyhdykskunnat vaikuttivat merenpohjan kasvi- ja leväyhteisöihin yhdessä abioottisten ympäristötekijöiden kanssa, mutta merimetsoyhdykskuntien vaikutusten voimakkuus riipui veden syvyydestä sekä pohjatyypistä. Matalilla alueilla perustuottajayhteisöjen ajallinen vaihtelu oli suurta, todennäköisesti nopeasti muuttuvien ympäristötekijöiden vuoksi. Erityisesti suojaisuus aaltojen vaikutuksilta oli merimetsojen vaikutusta tärkeämpi yhteisöjä muokkaava tekijä. Syvemmässä vedessä kovilla pohjatyyppiillä yhteisöt olivat ajallisesti vakaampia ja merimetsojen vaiketus niihin oli suurempi, vaikkakin muut tekijät kuten maantieteellinen alue, veden paikallinen ravinnepitoisuus ja veden sameus olivat edelleen tärkeimmät yhteisöihin vaikuttavat tekijät. Pehmeillä pohjatyyppiillä ympäristötekijöiden vaikutukset vaihtelivat syvyyden mukaan samalla tavoin kuin kovilla pohjilla ja merimetsoyhdykskunnilla oli vaikutuksia yhteisöihin muualla paitsi syvässä vedessä. Merimetsojen vaikutuksesta kovien ja pehmeiden pohjen perustajalajit, rakkolevä *Fucus vesiculosus* ja meriajokas *Zostera marina* vähenivät, ja tämä tapahtui johdonmukaisesti sekä eri mittakaavojen näytteenottoissa että kokeellisissa tutkimuksissa. Rihmamaisilla levillä oli myös taipumus runsastua merimetsojen vaikutuksen myötä sekä pienen mittakaavan kokeissa että laajemman mittakaavan näytteissä.

Väitöskirjatutkimukseni osoittaa että merimetsoyhdykskunnat vaikuttavat merenpohjan eliöyhteisöihin ravintoverkossa sekä ylhäältä alas että alhaalta ylöspäin säätelevien prosessien kautta, joskin näitä prosesseja tulee tarkastella yhdessä muiden yhteisöjä muokkaavien ympäristötekijöiden kanssa. Prosessien suhteellinen merkitys riippuu myös tarkasteltavasta mittakaavasta: ravinteiden valunta kolonioista vaikuttaa paikallisesti, kun taas ravintoverkon ylemmiltä tasoilta kohti alempia tasuja suuntautuvat vaikutukset tapahtuvat laajemmassa mittakaavassa.

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications and manuscript, hereafter referred to in the text by their Roman numerals:

- I** Gagnon K, Rothäusler E, Syrjänen A, Yli-Renko M, Jormalainen V. 2013. Seabird guano fertilizes Baltic Sea littoral food webs. – *PLoS One* 8(4): e61284. doi:10.1371/journal.pone.0061284
- II** Gagnon K, Yli-Rosti J, Jormalainen V. 2015. Cormorant-induced shifts in littoral communities. – *Marine Ecology Progress Series* 541: 15-30. doi:10.3354/meps11548
- III** Gagnon K, Sjöroos J, Yli-Rosti J, Stark M, Rothäusler E, Jormalainen V. 2016. Nutrient enrichment overwhelms top-down control in algal communities around cormorant colonies. – *Journal of Experimental Marine Biology and Ecology* 476: 31-40. doi:10.1016/j.jembe.2015.12.007
- IV** Gagnon K, Virtanen E, Rusanen P, Nurmi M, Viitasalo M, Jormalainen V. Detecting and quantifying cormorant impacts on Baltic Sea macrophyte communities. *Manuscript*.

AUTHOR CONTRIBUTIONS TO THE ORIGINAL MANUSCRIPTS

	I	II	III	IV
Original idea and planning	VJ	VJ, KG, JYR	VJ, KG, MS, ER	VJ, KG, MV, MN, PR
Field and lab work	VJ, AA, MYR	KG, JYR, VJ	KG, JS, JYR, VJ, ER, MS	
Statistical analysis	KG, ER, VJ	KG, JYR, VJ	KG, VJ	KG, VJ
Data compilation and modelling				EV, MV, MN, PR
Writing and commenting	KG, ER, VJ, MYR, AA	KG, JYR, VJ	KG, VJ, ER, JS, JYR, MS	KG, VJ, MV, EV, PR, MN

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1. INTRODUCTION

1.1. Community regulation and trophic networks

A primary focus of ecological studies is the interactions between species within a given space and time - i.e. a community. In a time when anthropogenic impacts threaten to cause major changes in ecosystems globally, understanding the factors regulating these interactions allows us to predict how biodiversity and ecosystem functioning could potentially be impacted by these environmental changes.

Ecosystems and communities can be represented as trophic networks by grouping species into trophic levels, with producers (plants and algae) on the bottom, then primary consumers (herbivores), and one or more levels of higher consumers (predators). While this is a simplification of the many complex interactions that make up a community or ecosystem, it allows us to more easily examine how energy and biomass flow between trophic levels and what processes determine and regulate the structure of the community, also providing the framework for predicting and managing the impacts of environmental changes. Historically, trophic networks had been considered to be regulated by bottom-up processes, i.e. the nutrients and resources available determined the abundance of producers, which then controlled the abundance of higher trophic levels. However, the “green world hypothesis” proposed by Hairston et al. (1960) instead suggested that through top-down processes such as predation, higher trophic levels could actually be driving the structure of many trophic networks, either on their own or in conjunction with bottom-up processes such as nutrient and resource availability (Paine 1980, Hunter and Price 1992, Terbough and Estes 2013).

1.2. Top-down processes and trophic cascades

The essential role predators and top-down processes play in structuring communities has since been confirmed in a variety of terrestrial, aquatic, and marine systems (e.g. Estes and Palmisano 1974, Pace et al. 1999, Polis et al. 2000, Carpenter et al. 2001, Schmitz et al. 2000, Beschta and Ripple 2009, Rudman et al. 2016). At the same time, a major aspect of anthropogenic environmental change has been the loss of top predators from many ecosystems around the world by way of overexploitation, habitat loss, pollution, and climate change (Myers and Worm 2003, Daskalov et al. 2007, Estes et al. 2011, Ripple et al. 2014). The subsequent ecosystem shifts have also revealed the importance of higher trophic levels in maintaining community stability and biodiversity. For example, top-down control by predators may allow for higher biodiversity in lower trophic levels by preventing any single species from becoming overly dominant. Therefore, in ecosystems where the top trophic levels are intact, higher functional diversity and overlapping niche use also promote resilience to disturbances (either natural or anthropogenic): the system is more likely to be able to cope with the loss of a single species with little or no loss of ecosystem function than a system with relatively low biodiversity (Walker 1992, Naeem 1996, Llope et al. 2011).

Accordingly, the loss of top predators can lead to trophic cascades affecting lower trophic levels, the shape of which depends on the number of trophic levels (which in itself varies with the ecosystem considered; for example marine trophic networks tend to have more levels than terrestrial networks). In a three-level system, herbivores tend to proliferate as they are released from predation pressure, while in a four-level system, mesopredators (intermediate predators) are instead released from predation and thus increase in abundance (e.g. Kurle and Cardinale 2011, Eriksson et al. 2012). In the latter case, herbivore abundance then declines and producers can take advantage of decreased herbivory, potentially causing producer communities to shift towards fast-growing opportunistic species and also leading to changes in structural complexity and associated biodiversity. However, the effects and the strength of trophic cascades are difficult to predict in natural systems, as they are highly context-dependent, and can vary greatly depending on the surrounding environmental factors, the individual species involved, and the productivity of the system (Oksanen et al. 1981, Polis and Strong 1996, Shurin et al. 2002, Hopcraft et al. 2010, Kurle and Cardinale 2011).

1.3. Bottom-up processes and nutrient enrichment

The bottom-up processes present in a system affect the strength of top-down trophic cascades – that is, nutrient and resource availability for lower trophic levels determine if and how predation can structure the trophic network (Oksanen et al. 1981, Polis et al. 2000, Jeppesen et al. 2003). This is of particular importance when considering that the anthropogenic input of terrestrial nutrients (i.e. eutrophication) has been a major driver of community shifts in coastal marine and aquatic systems around the world (Beeton 1965, Schiewer 1997, Smith et al. 1999, Kemp et al. 2005, Smith et al. 2006). Eutrophication is one of the main threats to coastal ecosystems, with ecological consequences including increased turbidity, increased sedimentation and benthic hypoxia (Goldman 1988, Cederwall and Elmgren 1990, Norkko and Bonsdorff 1996, Karlson et al. 2002, Thibodeau et al. 2006, Conley et al. 2009, Korpinen et al. 2015), while the increased productivity of algal and plant communities due to nutrient enrichment can lead to shifts in vegetation, generally favourising fast-growing species (Vogt and Schramm 1991, Valiela et al. 1997, Hauxwell et al. 2001, Boström et al. 2002, Krause-Jensen et al. 2008, Torn and Martin 2012). Changes in algal species composition and habitat structure can then affect higher trophic levels, often leading to decreased associated biodiversity (Råberg and Kautsky 2007, Korpinen et al. 2010, Kotta and Möller 2014), while environmental changes brought on by eutrophication can also affect the survival and behaviour of invertebrates and fish (Sandström and Karås 2002, Kraufvelin et al. 2006, Tuomainen and Candolin 2013, Snickars et al. 2015).

1.4. Top-down and bottom-up control in coastal ecosystems

Top-down and bottom-up processes do not structure ecosystems in isolation, but instead they interact with each other and with other abiotic environmental factors. In coastal ecosystems, top-down control has been shown to be essential in counteracting the effects of eutrophication, particularly algal blooms (Pace et al. 1999, Shurin et al. 2002), thus mitigating the negative ecological consequences of these blooms. Grazing by invertebrate herbivores can control filamentous algal blooms (Lotze et al. 1999, 2001, Lotze and Worm 2000, Sieben et al. 2011a, Teichberg et al. 2012, Östman et al. 2016) and thus, the loss of herbivores resulting from trophic cascades can lead to more severe algal blooms (Worm and Lotze 2006, Korpinen et al. 2007a, b). However, this top-down control of algal blooms depends on the synchronous timing of herbivory and algal growth (Svensson et al. 2012), and also has its limits as at very high nutrient levels herbivory cannot entirely counteract the increased growth of filamentous algae caused to nutrient enrichment (Hauxwell et al. 1998).

These interactions between top-down and bottom-up processes in eutrophicated areas thus involve higher trophic levels. The loss of top predatory fish, release of mesopredators and subsequent trophic cascade are often the cause of decreased herbivory levels, thus amplifying the effects of eutrophication when these processes occur concurrently (**Figure 1**). Indeed, the increase in mesopredators in the western Baltic Sea following the decline of predatory fish has been linked to increasing severity of algal blooms (Eriksson et al. 2009, Sieben et al. 2011b), while experimental removal or exclusion of mesopredators allows herbivore populations to recover thus attenuating blooms to a certain extent (Korpinen et al. 2007b, Eriksson et al. 2012, Östman et al. 2016). Therefore, environmental changes which cause a decrease in mesopredator abundance and/or increase in mesograzers abundance could have a positive impact on the ecosystem, by promoting herbivory on filamentous algae (Hughes et al. 2013).

While the impacts of eutrophication (nitrogen loading and increased turbidity) have become increasingly important in structuring algal and plant (macrophyte) communities in coastal areas, these communities are also known to be driven by abiotic environmental factors – depth, exposure, salinity, and substrate type are especially important (Kautsky and van der Maarel 1990, Rinne et al. 2011, Kotta and Möller 2014). Abiotic factors also play a strong role in regulating the interactions between top-down and bottom-up processes (Menge 1992, 2000, Jorgensen et al. 2007, Korpinen et al. 2007a, b, Whalen et al. 2013), as do additional anthropogenic stressors such as climate change (Jochum et al. 2012), so that these should be considered concurrently to properly determine the relative importance of different types of processes and how they occur over different spatial scales. As associated epifaunal and fish communities are dependent on both abiotic environmental factors and the type of macrophyte habitat available (Pihl 1986, Pihl et al. 1994, 1995, Korpinen et al. 2007c, Christie et al. 2009, Kotta 2013), shifts in the producer community (especially the loss of perennial species) may have consequences for all associated species at multiple trophic levels.

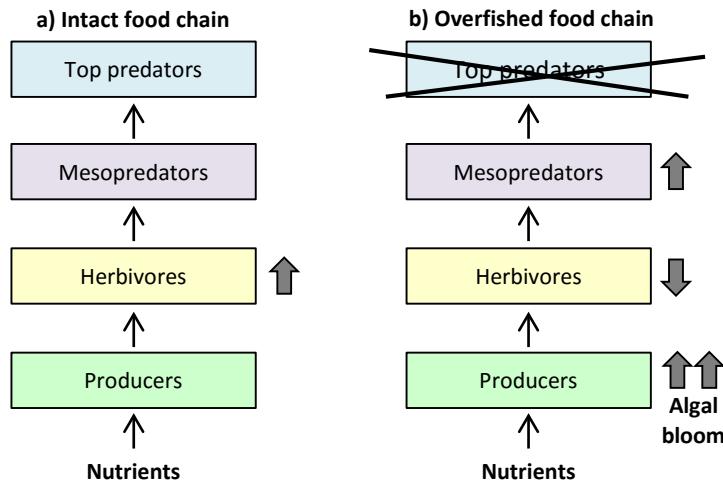


Figure 1. Effects of nutrient enrichment on marine trophic networks in the presence and absence of top predators. In (a), top predators are present, and the addition of nutrients causes an increase in herbivore density and/or abundance (grey arrow) as herbivores consume the excess algal production which occurs due to higher nutrient availability. In contrast, in a system where the top trophic level is absent or reduced (b), mesopredators are released from predation and thus highly abundant. Thus, if nutrient enrichment happens to the same extent, algal blooms are more likely to occur as herbivory is suppressed by overabundant mesopredators. Algal blooms may also then further reduce the recruitment of top predatory fish, by decreasing water and habitat quality (Lehtonen et al. 2009), thus propagating further blooms.

1.5. Seabird colonies and impacts on benthic communities

Seabird colonies have been shown to be important local sources of nutrients for both marine and terrestrial communities (e.g. Smith and Johnson 1995, Wainright et al. 1998) due to their nutrient-rich guano. In marine systems, the high nitrogen and phosphorus content of guano has been shown to have both direct and indirect effects on intertidal and subtidal algae, generally promoting the growth and abundance of fast-growing species (Zelickman and Golovkin 1972, Bosman and Hockey 1986, Bosman et al. 1986, Woottton 1991). These effects are carried through to higher trophic levels (Zmudczyńska-Skarbek et al. 2015), which can, for example, result in increased biomass of herbivores feeding on these enriched algae (Kolb et al. 2010).

In addition to these bottom-up effects, seabirds also play an important role in marine systems as predators, as piscivorous birds can exert top-down predation pressure (e.g. Draulans et al. 1988), but these effects tend to be more difficult to evaluate due to the mobility and stochasticity of fish populations. Most research on the role of seabirds in trophic networks has either focused exclusively on nutrient effects (e.g. Marion et al. 1994, Nakamura et al. 2010, Gwiazda et al. 2010, Zwolicki et al.

2013, Klimaszyk et al. 2014, 2015) or evaluated seabird impacts on fish stocks in the context of conflict with fisheries (e.g. Hobson 2009, Doucette et al. 2011, Marzano et al. 2013), leaving a knowledge gap about how these bottom-up and top-down processes might interact to affect coastal benthic communities.

1.6. Aims of the thesis

The primary aim of this thesis was to determine if a piscivorous seabird, the Great Cormorant (*Phalacrocorax carbo sinensis*) had any detectable effects on benthic ecosystems in the Baltic Sea, and if so, whether these impacts were caused by bottom-up or top-down processes, or both. To accomplish this, I first checked whether bottom-up nitrogen enrichment was present around cormorant colonies using stable isotope analyses (I). Then, I identified cormorant impacts on different trophic levels (fish, invertebrates, algae), and how bottom-up and top-down processes interacted to affect these communities (II, III). This was done first by using a paired design with cormorant and control colonies and comparing nutrient enrichment, benthic communities, and algal growth and biomass accumulations (I, II), then by manipulating the access of fish predators and herbivores around colony and control islands to directly compare the role of top-down and bottom-up processes (III). Finally, in the last part of the thesis, I wanted to place cormorant impacts in a larger spatial context, by using a large dataset covering the coast of Finland and examining the importance of cormorant influence relative to other environmental factors, thus determining whether impacts could be detected over a larger scale (within 5 km), not just in the immediate vicinity of the colonies (IV).

2. MATERIALS AND METHODS

2.1. Study area and ecosystem

2.1.1. Baltic Sea coastal communities and key species

The Baltic Sea is a large atidal brackish water body characterized by strong geographic gradients in salinity (due to high freshwater river runoff and limited exchange between the Baltic and North Seas), temperature and ice cover (along a north-south gradient), and wave exposure (due to the presence of extensive archipelago areas). These studies took place along the Finnish coast of the Baltic Sea including the Archipelago Sea, the Sea of Bothnia, and the Gulf of Finland. In general, salinity in the study areas ranged from 3-7 psu, with maximum summer water temperatures of 18-22 °C. In the winter, the study areas are usually partially or completely ice-covered for several months, and waters temperatures are close to or just above 0 °C.

Due to the low salinity and strong environmental gradients, biodiversity in the Baltic Sea is relatively low (HELCOM 2009, 2012) and includes a mix of marine, brackish-water and freshwater species. Top predatory fish include marine species such as Atlantic cod *Gadus morhua*, anadromous species such as Atlantic salmon *Salmo salar*, and freshwater species such as brown trout *Salmo trutta*, pike *Esox lucius*, and pike-perch *Sander lucioperca*. Many of these species have decreased in abundance in the past 10-20 years due to overfishing, especially in the central and western Baltic Sea (Ljunggren et al. 2010, Eriksson et al. 2011), a trend which may have important repercussions on lower trophic levels (see below). Common mesopredatory or zooplanktivorous fish include whitefish *Coregonus lavaretus*, Baltic herring *Clupea harengus membras*, smelt *Osmerus eperlanus*, sprat *Sprattus sprattus*, European perch *Perca fluviatilis*, Eurasian ruffe *Gymnocephalus cernua*, several cyprinid species (roach *Rutilus rutilus*, bleak *Alburnus alburnus* and bream *Abramis brama*, amongst others), and sticklebacks (three-spined *Gasterosteus aculeatus* and nine-spined *Pungitius pungitius*). Benthic fish such as gobies (*Pomatoschitus* spp., *Gobius niger*), eelpout *Zoarces viviparus*, flounder *Platichthys flesus*, and turbot *Scophthalmus maximus*, are also commonly seen.

The invertebrate fauna in the littoral zone is dominated by amphipods (mostly *Gammarus* spp.), isopods (*Idotea* spp. and *Jaera* spp.), gastropods (*Theodoxus fluviatilis*, *Hydrobia ulvae*), and bivalves (*Mytilus trossulus*, *Cerastoderma glaucum*). Among these, the isopod *Idotea balthica* plays a major role as adult isopods are the main herbivores of the perennial habitat-forming macroalgal species *Fucus vesiculosus* and *Fucus radicans* (Salemaa 1987, Haavisto and Jormalainen 2014), while amphipods, gastropods, and other isopods are important mesograzers of periphyton and filamentous algae (Malm et al. 1999, Goecker and Kåll 2003). In addition to *Fucus*, common algal species in shallow (<5 m depth) rocky areas include *Cladophora* spp., *Ulva* spp., *Ulothrix* spp., *Chorda filum*, *Ectocarpus siliculosus*, *Pilayella littoralis*, *Ceramium tenuicorne*, and *Polysiphonia* spp. (**Figure 2**). In soft-bottom habitats, eelgrass *Zostera marina* forms extensive meadows, especially in sandy areas where it plays a similar role to *Fucus* spp., providing perennial habitat for invertebrate and fish species (Boström et

al. 2006). Aquatic vascular plants such as *Ceratophyllum* spp., *Myriophyllum* spp., *Potamageton* spp., *Ruppia* spp., and *Zannichellia* spp., are also common in soft-bottom habitats, often growing interspersed with *Zostera*, and filamentous algae can also accumulate in these soft-bottom areas (**Figure 2**).

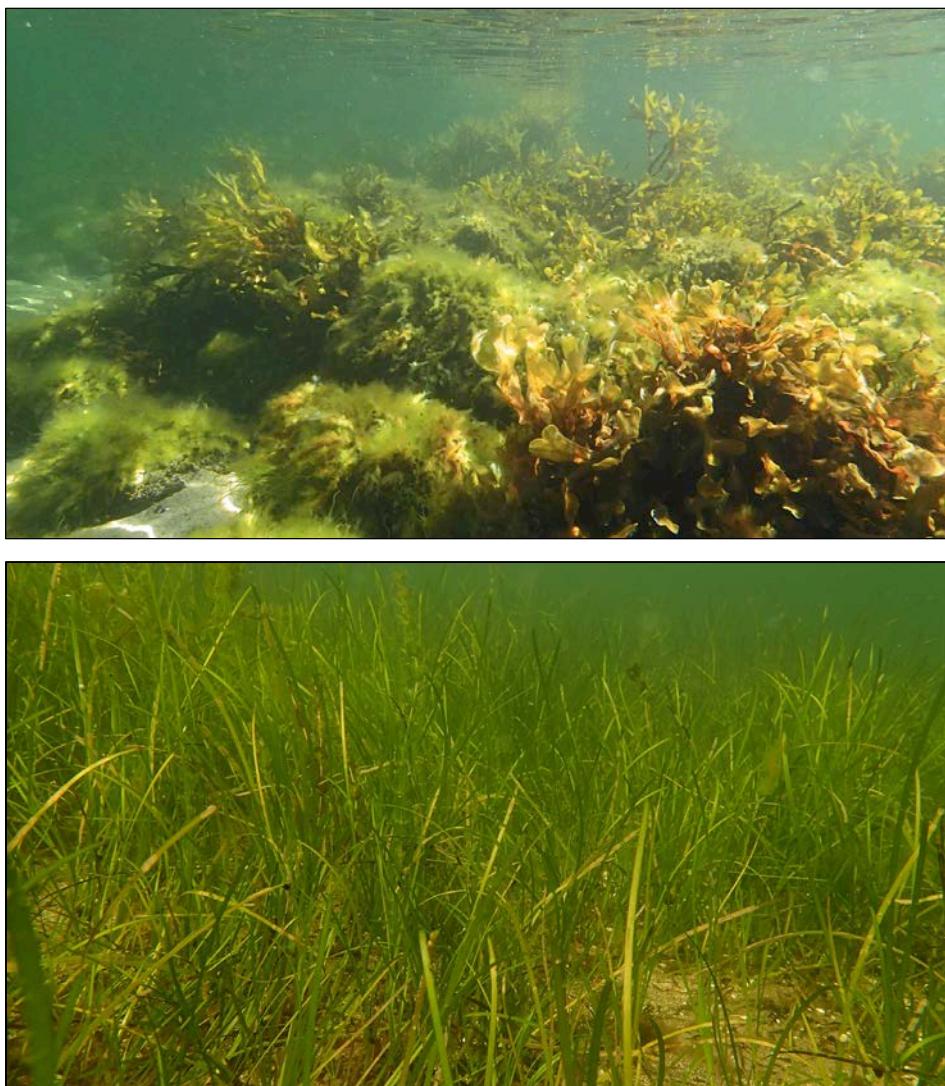


Figure 2. Typical macrophyte communities in shallow (2-3 m depth) hard-substrate (top) and soft-substrate (bottom) habitats in the Archipelago Sea, northern Baltic Sea. In the top photo, the algal community is dominated by bladderwrack *Fucus vesiculosus* and filamentous algae. In the bottom photo, eelgrass *Zostera marina* grows in a dense meadow, along with *Potamageton perfoliatus*. (Photos: K. Gagnon)

2.1.2 Environmental changes in the Baltic Sea

Human-induced environmental changes have had major effects on the Baltic Sea ecosystem since the second half of the 20th century, leading to most areas of the Baltic Sea being classified as in ‘moderate’, ‘poor’, or ‘bad’ ecosystem health according to HOLAS (‘tool for the Holistic Assessment of Ecosystem Health Status’; HELCOM 2010, Andersen et al. 2011, 2016).

As in many other coastal areas, eutrophication caused by nutrient-rich runoff (in particular nitrogen and phosphorus), is a major problem in most of the Baltic Sea (Cederwall and Elmgren 1990, Bonsdorff et al. 1997a, HELCOM 2010, Gustafsson et al. 2012). While nutrient inputs into the sea have slightly decreased since the 1980s, low connectivity between the Baltic Sea and North Sea has ensured that nutrient levels remain high to this day (HELCOM 2010). Among the major impacts of eutrophication have been an increase in phytoplankton and filamentous algal blooms (Bonsdorff et al. 1997b, Schramm 1999, Vahtera et al. 2007), hypoxia of bottom sediments (Vahtera et al. 2007, Conley et al. 2011), increased turbidity (Bonsdorff et al. 1997b) and increased sedimentation (Bonsdorff et al. 1997a).

These environmental changes have had important repercussions for some key species. Of particular importance, the abundance of *Fucus* spp. has decreased significantly (Kangas et al. 1982, Vogt and Schramm 1991, Snickars et al. 2014), likely because of decreased recruitment and growth due to high sedimentation and filamentous algal load, and to decreased Secchi depth (Worm et al. 2001, Berger et al. 2003, Korpinen and Jormalainen 2008). In addition, while *Fucus* has historically been found growing down to 10 m depth in some areas, it is now limited to <5 m (Schramm et al. 1996, Torn et al. 2006), which may have important repercussions due to its role in providing food and shelter for a large number of associated species (Kautsky et al. 1992, Råberg and Kautsky 2007). Similarly, eutrophication has also had negative impacts on eelgrass *Zostera marina* in sandy soft-bottom habitats (Kruk-Dowgialło and Szaniawska 2008), where shading and increased turbidity caused by sedimentation and filamentous algae can reduce eelgrass growth and promote mortality (Gustafsson and Boström 2014). Eutrophication has also caused a shift in the fish community, towards communities dominated by cyprinids and sticklebacks (Bonsdorff et al. 1997b, Lappalainen et al. 2001, Sandström and Karås 2002, Ådjers et al. 2006, Olsson et al. 2012), which can outcompete other species in eutrophicated waters.

As mentioned above, eutrophication may be exacerbated by overfishing, as many stocks of predatory fish have decreased (such as cod, pike, and pike-perch; Nilsson et al. 2004a, b, Lehtonen et al. 2009, Ljunggren et al. 2010, Mustamäki et al. 2014, Bergström et al. 2016), and caused shifts in fish communities (Österblom et al. 2007). Subsequently, populations of smaller mesopredatory fish such as sticklebacks have quickly increased (Ljunggren et al. 2010, Sieben et al. 2011a, Bergström et al. 2015, Byström et al. 2015). Released from predation pressure, these fish can consume large quantities of important grazers (such as isopods and amphipods), thus reducing top-down control on

filamentous algae and enabling algal blooms (Eriksson et al. 2009, Sieben et al. 2011a Östman et al. 2016).

Finally, in addition to these regional threats, the Baltic Sea is not immune to general global environmental changes such as the spread of invasive species and climate change. Invasive species have arrived in the Baltic Sea through anthropogenic means (ballast water and aquaculture), and several have quickly colonised and become more abundant and widespread, potentially causing disturbances to the communities through predation, competition or habitat modification. Biological invasions over the past 20 years along the coastal areas of the northern Baltic Sea include, among others, the mud crab *Rhithropanopeus harrisii* (Fowler et al. 2013), the glass shrimp *Palaemon elegans* (Katajisto et al. 2013), and the round goby *Neogobius melanostomus* (Almqvist et al. 2010). These species all have broad diets and thus the ability to impact invertebrate and small fish communities through predation, especially as native species may lack any defense mechanisms. As for climate change, predictions for the northern Baltic Sea indicate a 3-4 °C rise in sea temperature, along with a concurrent decrease in salinity (Neumann 2010, Störmer et al. 2011, Andersson et al. 2015, HELCOM 2013). This will certainly lead to increased stress and mortality of cold-adapted and marine species, while some freshwater species may spread and become more abundant. In addition, environmental changes caused by climate change may lead to an accelerated rate of invasions (especially those native to warmer climates) and to higher impacts by invasive species (Gritti et al. 2005, Hellmann et al. 2008). In fact, none of the above environmental changes listed above can be considered independently (Jochum et al. 2012), and one of the themes of this thesis has been to determine how cormorant colonies interact with other environmental factors to affect benthic communities and trophic networks.

2.1.3. Cormorants in the Baltic Sea

The Great Cormorant (*Phalacrocorax carbo sinensis*) was originally present in the Baltic Sea until the 1800s, before being essentially driven extinct in northern Europe due to hunting pressure (Beike 2014). After the enactment of protection measures and the ban on DDT, cormorants began returning to northern Europe in the middle and late 20th century and populations subsequently increased rapidly (Van Eerden and Gregersen 1995, Beike 2014). In Finland, the first breeding pair was recorded in 1996 in the Gulf of Finland (Rusanen et al. 2003, Lehikoinen 2006). Since then, the population has grown to nearly 24 000 breeding pairs in 2015 (**Figure 3**; unpublished data from Finnish Environmental Institute SYKE), while the total population in the Baltic Sea is estimated at approximately 165 000 breeding pairs, spread across 520 colonies (Bregnalle et al. 2014).

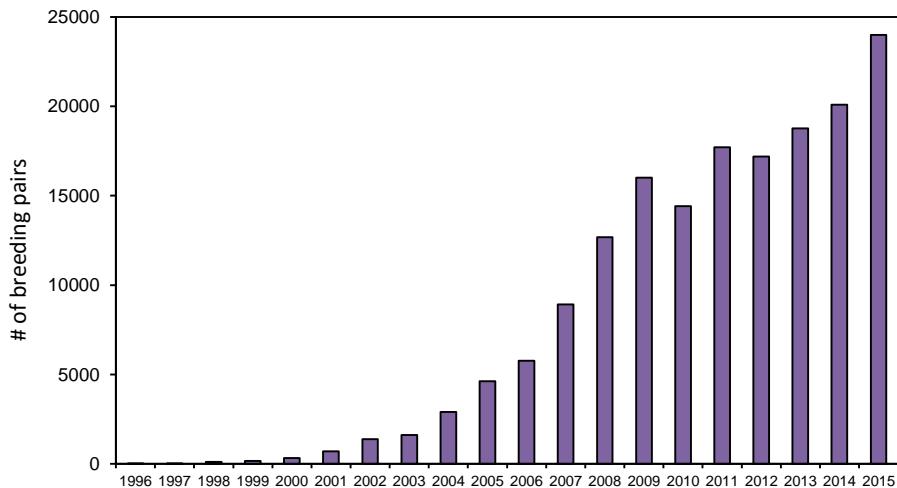


Figure 3. Cormorant population (number of breeding pairs) in Finland 1996-2015.

In Finland, cormorants breed exclusively on islands in the Baltic Sea, using these colonies from April-August (and migrating southwards over the winter). There are approximately 40 colonies in Finland (some consisting of more than one island) located along the Finnish coast, though the exact number fluctuates on a yearly basis with islands being abandoned and colonised. The increasing population has led to public controversy and discussion on management in Finland (and around the world), with the smell of guano emanating from the colonies and competition with fisheries often mentioned as concerns (Marzano et al. 2013). Several studies have shown a potential for competition between commercial fisheries and cormorant colonies on a local scale (e.g. Vetemaa et al. 2010, Östman et al. 2013, Salmi et al. 2015), and there is evidence that nitrogen runoff from colonies enriches algae (Kolb et al. 2010). However there is a lack of knowledge about cormorant impacts on the trophic network as a whole, and the scale and importance of these impacts.

Cormorant diets have been analysed around the Baltic Sea and seem to vary over both time and space, with prey composition varying with changes in fish communities (Lehikoinen et al. 2011, Boström et al. 2012). It is known that a breeding pair will consume up to 1 kg fish day⁻¹ during the breeding season (Grémillet et al. 1995, Ridgway 2010), so that the total fish consumption by cormorants along the Finnish coast is approximately 3 million kg (in 2015). By contrast, the total commercial fish catch is 138 million kg (2013 data; Finnish Game and Fisheries Research Institute 2014), mostly composed of herring and sprat (88 % and 8 % respectively). Cormorants are generalist predators, and small and medium-sized species such as sticklebacks, herring, eelpout, ruffe, roach, and perch are the most common prey species, and the proportion of sticklebacks in their diet has increased in areas where sticklebacks have become abundant (Zarankaitė 2010, Vetemaa et al. 2010, Boström et al. 2012, Östman et al. 2013, Salmi et al. 2015). The size of prey fish (and therefore the species consumed) also varies over the breeding season, with smaller prey targeted after the eggs

have hatched in early summer and increasing in size as the chicks grow (Lehikoinen 2005), but cormorants generally seem to consume smaller-sized fish than fisheries do (Pūtys and Zarankaitė 2010, Troynikov et al. 2013, Salmi et al. 2015).

2.1.4. Study sites

It is unknown how or why cormorants choose their breeding colonies; colony islands along the Finnish coast range in size from 0.18 to 5.4 hectares and include both large islands with trees (though the trees are eventually killed due to high nutrient concentrations from cormorant guano; Ellis et al. 2006) and smaller low-lying rocky islands (**Figure 4**).



Figure 4. Cormorant colonies in the Archipelago Sea, northern Baltic Sea. Colony islands can range from small rocky islets (left) to large forested islands (right). The photo on the left was taken in July when chicks were close to fledging and large amounts of guano have been deposited on the island, while the photo on the right was taken in early June when chicks had recently hatched and guano had not yet accumulated to the same extent. (Photos: K. Gagnon)

In chapters I and II, a paired block design was used, with nine (I) and eight (II) colonies, respectively, and their corresponding control islands, along a 200-km stretch of the Finnish west coast (**Figure 5**). The control site was a nearby (5–10 km) island without cormorants, allowing us to compare each colony to its control island while controlling for factors such as salinity, temperature and exposure. Study III focused on the Archipelago Sea area, with seven colonies and seven control islands within a 30 km radius. The aim of study IV was to examine cormorant effects over a larger scale, using a dataset of over 4000 points and 15 cormorant colonies along the entire southwestern and southern Finnish coast (**Figure 5**).

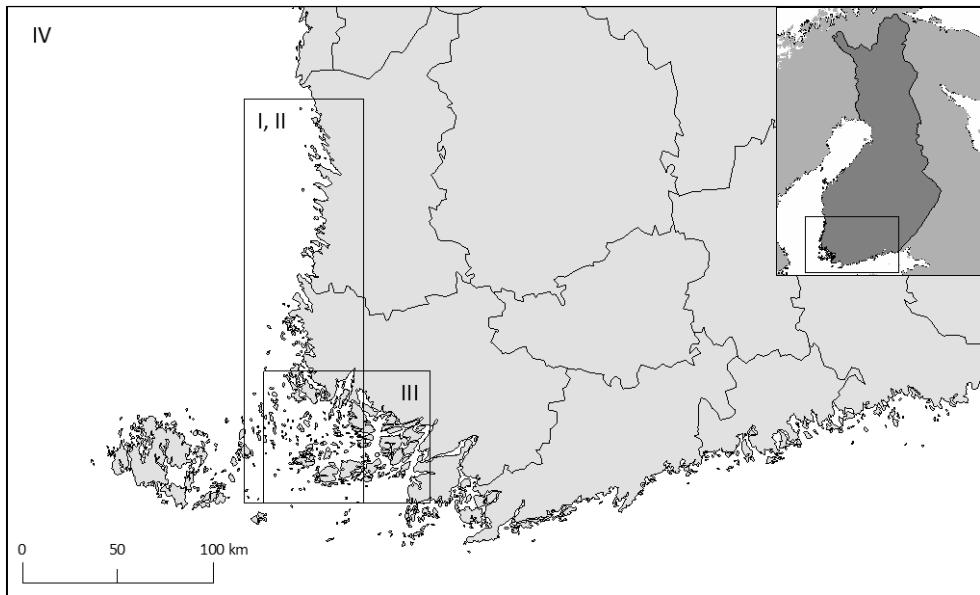


Figure 5. Extent of study areas used in each chapter of the thesis (indicated by Roman numerals in the corners) and location within Finland (inset).

2.2. Sampling and experiments

2.2.1. Stable isotope sampling and analysis (I)

To determine whether cormorants could affect benthic species, I first determined if nutrient enrichment could be detected in the immediate vicinity of colony islands (i.e. within 100 m). Guano from seabirds has a distinctively high $\delta^{15}\text{N}$ ratio due to their diet of fish, and this $\delta^{15}\text{N}$ signature should be detectable in lower trophic levels around colonies if enrichment indeed occurs. To this end, I analysed the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of organisms in shallow (<3 m depth) rocky habitats around colony islands, including herbivores (the isopod *Idotea balthica* and the gastropod *Theodoxus fluviatilis*), algae (the foundation species *Fucus vesiculosus*, and two ephemeral green algae: *Cladophora glomerata* and *Ulva* spp.), periphyton scraped off the surface of *Fucus* thalli, and guano collected directly from the colony island. To determine the extent of nitrogen enrichment, I compared these values to samples collected from control islands (and added particulate organic matter collected from the water column around control islands to compare to guano collected from the colony islands). I also checked whether enrichment varied with exposure of the island, and with cormorant abundance and density, as these are variables that could affect the quantity of guano reaching the shallow littoral zone. I then used the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios from colony and control sites in diet mixing models to determine if there were differences in herbivore diet between colony and control sites.

Enrichment likely increase over the breeding season as guano accumulates and runoff into the sea increases, so *Fucus* samples were collected from three different parts of the thallus: the base, the

middle, and the tip of the apices, and the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios were analysed separately from each part. As the growth rate of *Fucus* was previously known (Hemmi et al. 2005), these samples represented how enrichment varied over the breeding season: the base was formed in May before cormorant eggs had hatched, the middle part grew in July when nestlings were quite large but still in the nest, and the tip formed in August after the chicks had fledged.

2.2.2. Benthic communities around colony islands (II)

In the second part of the thesis, I examined natural communities around colony and control sites to determine if there were any differences in community composition, biodiversity, or abundance of individual species, and whether these might arise through top-down or bottom-up processes. I focused on three groups of organisms corresponding to three trophic levels: fish (predators), invertebrates (herbivores), and macrophytes (producers; including both plants and algae). To get a more accurate picture of the community, communities were sampled in several different ways: fish were caught in multi-series gill nets and also counted during night diving transects, invertebrates were collected from bottom traps and also from *Fucus* thalli, algal/plant communities were measured during mapping transects at different depths, while growth of *Fucus* fragments and filamentous algal biomass (on settlement tiles) were measured separately. As with the previous study, all sampling and experiments took place within 100 m of the colony and control islands, and the fish, invertebrate and macrophyte communities were sampled from predominantly rocky habitats around these islands. The fish and invertebrate samples were collected (or counted while diving) at 2-3 m depth, while macrophyte communities were sampled at four depth zones from 0-4 m depth.

After collecting and identifying all samples (to genus or species level), I compared fish, invertebrate and algal communities in colony and control sites, by using multivariate analyses for comparing communities and general linear mixed models to compare the abundance of some of the more common species, biodiversity indices of the different communities, as well as algal growth and biomass. In all cases, the paired block design allowed me to control for geographic differences in environmental factors by including the pair as a random factor in the analyses. The individual species studied included: Baltic herring, perch, roach, ruffe, and three-spined sticklebacks; isopods *Idotea* spp., amphipods, *Gammarus* spp., gastropods *Theodoxus fluviatilis* and *Hydrobia ulvae*, and blue mussels *Mytilus trossulus*; bladderwrack *Fucus vesiculosus*; and ephemeral algae *Ceramium tenuicorne*, *Cladophora glomerata*, *Ectocarpus siliculosus*, *Pilayella littoralis*, and *Ulva* spp.. These particular species were chosen for detailed analysis because they are common and abundant (i.e. present in most samples) and play important roles in the ecosystem.

2.2.3. Experimental manipulation of top-down and bottom-up processes (III)

After considering natural populations in the first two chapters, in the third part of the thesis I manipulated the access of predators (fish) and herbivores (isopods, amphipods, and gastropods) to algae using a series of exclusion cages with different-sized meshes (**Figure 6**) in which I placed settlement tiles and *Fucus* fragments. The cages were placed around colony and control sites in the Archipelago Sea for four months. The cages were cleaned every week, and recruitment counted every month, at which point the cages were also checked to ensure no fish or herbivores had entered them. Similar cages and meshes had previously been in field experiments, and proven successful in excluding fish and herbivores (e.g. Haavisto and Jormalainen 2014), and they were also highly effective in this experiment. The herbivore exclusion cages were constructed with a 1 mm × 1 mm mesh, thus excluding all organisms larger than 1 mm (i.e. gastropod, amphipod and isopod grazers), allowing algae to settle and grow without being grazed. The fish exclusion cages were constructed with a 10 mm × 10 mm mesh on the sides and bottom (1 mm × 1 mm mesh on the top), excluding fish with a girth larger than 10 mm but allowing herbivores access to the settlement tiles and the *Fucus* fragments, so that in theory herbivores should graze heavily as they are freed from predation pressure. Finally, control cages were open on the sides but had a 1 mm × 1 mm mesh on the top, but were open on the sides to control for any shading effects on algal growth. By comparing algal recruitment and herbivory in different cages in colony and control sites, I could then qualitatively determine whether top-down or bottom-up effects were occurring, which processes were most important, and which species were most affected.

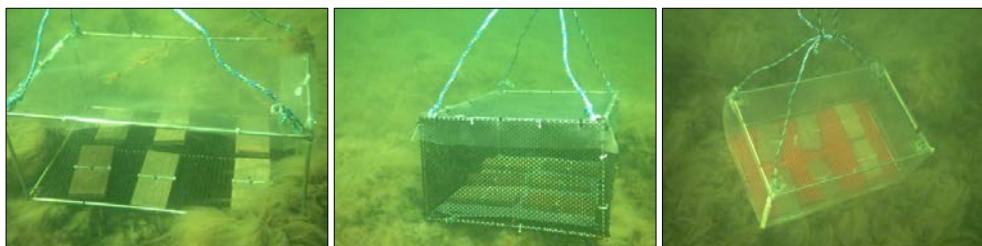


Figure 6. From left to right: open control, fish exclusion, and herbivore exclusion cages used in chapter III. The settling tiles used for measuring algal recruitment can be seen in the cages. (Photos: K. Gagnon)

2.2.4. The scale and relative importance of cormorant impacts (IV)

Finally, some questions that arose in the course of this research project were related to the scale of cormorant impacts and how important they were relative to other environmental factors in the Baltic Sea. In the preceding chapters, I sampled rocky communities and performed experiments to determine cormorant effects within 100 m of cormorant colonies, without considering if any of the effects I found could also occur further from the colonies or how they compared to the impacts of

other abiotic factors. To explore this, I used a large dataset (~4100 points) of producer communities from video surveys completed during the Finnish Inventory Programme for the Underwater Marine Environment (VELMU) from 2004-2013. For each data point, I calculated a cormorant index based on the distance from the colony and abundance of cormorants in the colony. I then compiled the percent cover of algal and plant taxa at each data point as well as the substrate type (hard or soft), and the depth (which was divided into three depth zones: 0-2.5 m, 2.5-5 m, and 5-10 m). In addition, for each data point I obtained modeled values of exposure, salinity, turbidity (Secchi depth), and nutrient concentration (nitrogen and phosphorus, though these were highly correlated with each other and so I only used the former; exposure data from Suominen et al. 2007, other environmental data from Virtanen, in prep.), all of which have been previously shown to play important roles in structuring producer communities (e.g. Rinne et al. 2011).

I first compared producer communities within 5 km of the colonies ("colony" points) to those 10-15 km from colonies ("control" points), using permutational manova (PERMANOVA). Then, I used distance-based linear modelling (DistLM) on the same dataset to determine (a) if cormorant index contributed significantly to the best-fitting model, and (b) how much it contributed to the model relative to the other abiotic factors, as well as the year-to-year temporal variation and the spatial variation over different geographic areas. I then repeated this analysis for producer communities in hard- and soft-substrate habitats and different depths (shallow: 0-2.5 m, intermediate: 2.5-5 m, and deep 5-10 m), to determine how cormorant impact depended on the habitat and type of community (algal-dominated communities in hard substrates and angiosperm communities in soft substrates). Finally, I used similar methods to compare the abundance of *Fucus*, *Zostera*, and several species of filamentous algae between colony and control points, then also determined the significance and relative importance of cormorant index in determining the abundance of these species.

3. RESULTS AND DISCUSSION

3.1. Bottom-up effects of cormorant colonies

In the first study (**I**) I found that nutrient enrichment was indeed occurring in lower trophic levels around cormorant colonies, as indicated by the higher $\delta^{15}\text{N}$ ratio found in algae and herbivores near colonies than control islands (**Figure 7**). Enrichment also increased over summer as guano accumulated, and also increased with cormorant density, so that benthic communities around smaller islands with higher cormorant populations were more affected by nutrient runoff, supporting previous results from the western Baltic Sea (Kolb et al. 2010a). While I mostly considered nitrogen in these studies, the enrichment effect may actually be due to both nitrogen and phosphorus present in cormorant guano.

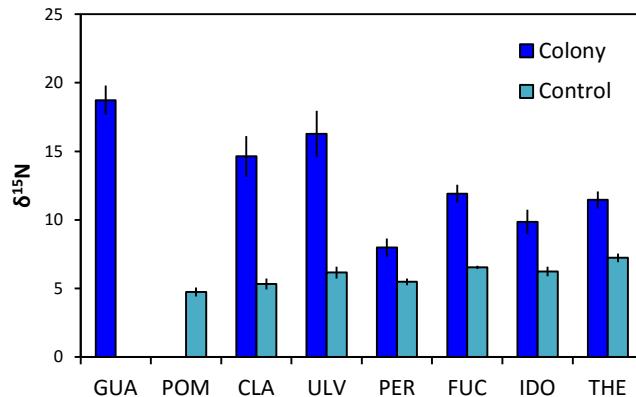


Figure 7. Nitrogen enrichment (mean \pm SE of $\delta^{15}\text{N}$) of algal and invertebrate herbivore species around colony and control islands (n = 9 colonies and 8 controls). GUA = cormorant guano collected from colony islands, POM = particulate organic matter from water column near control islands, CLA = *Cladophora glomerata*, ULV = *Ulva* spp., PER = periphyton scraped from the surface of *Fucus vesiculosus*, FUC = *Fucus vesiculosus*, IDO = *Idotea balthica*, THE = *Theodoxus fluviatilis*.

Similarly, several species of filamentous algae increased in abundance around cormorant colonies, as did the accumulation of biomass of filamentous algae in general, and these were positively correlated with cormorant abundance, density, and/or the age of the colonies (**II**). As this occurred in cages where herbivores and fish were excluded, it appears that bottom-up nitrogen enrichment is the most important factor causing shifts in algal communities around cormorant colonies (**III**). The most important ecological consequence is likely the decrease in *Fucus* and *Zostera* abundance and presence (**II, IV**) and *Fucus* recruitment (**Figure 8**) that accompanies filamentous algal blooms (**III**). Filamentous algae have long been known to be detrimental to perennial macrophytes, as they can

inhibit growth through shading and direct competition for space (Worm et al. 2001, Steen 2004, Korpinen and Jormalainen 2008, Gustafsson and Boström 2014), while increased sedimentation (Chapman and Fletcher 2002, Berger et al. 2003) and the release of toxic compounds (Råberg et al. 2005) can also adversely affect *Fucus* recruitment (Bergström et al. 2003).

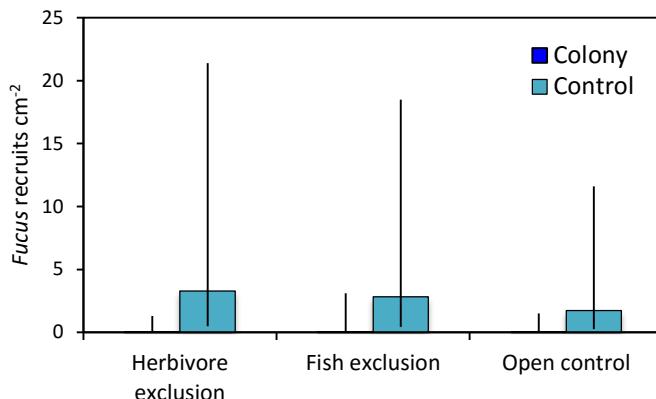


Figure 8. *Fucus vesiculosus* recruitment (mean and 95 % confidence intervals) in three cage treatments around colony and control islands ($n = 2$ cages of each treatment at 6 colonies and 6 control sites).

In this sense, the changes in the algal community observed around cormorant colonies mirror changes that have occurred in many parts of the Baltic Sea as eutrophication has become a major problem – with negative impacts on *Fucus* and *Zostera*, and frequent filamentous algal blooms (Schramm 1999, Worm et al. 2001, Boström et al. 2014, Gustafsson and Boström 2014, Snickars et al. 2014). Indeed, the bottom-up impact of cormorants in the Baltic Sea is probably lower than it would be in a pristine sea, as nutrient loads are already very high (HELCOM 2010): while the stable isotope analysis revealed enrichment from guano-derived nitrogen, the total nitrogen content of algae and herbivores was quite similar in colony and control sites (I). Communities around cormorant colonies, especially those in highly eutrophicated areas, are thus subject to even higher stress from nutrient enrichment than other coastal communities in the area.

The negative impacts of nutrient enrichment on *Fucus* and *Zostera*, whether around colonies or in the Baltic Sea in general, threatens to affect associated invertebrate and fish communities. These effects have been more difficult to detect than those on algae, and may also be due to simultaneous top-down effects (II). But, as *Fucus* and *Zostera* are the major habitat-forming species in the northern Baltic Sea, changes to their distribution and abundance are likely to have multiple and long-lasting effects. In the statistical analysis I controlled for *Fucus* biomass when analyzing invertebrate abundances but *Fucus* thalli were smaller around colonies (II). Thus, they may support lower overall numbers of associated invertebrates (Schagerström et al. 2014) thus limiting top-down control of

filamentous algae around colonies if gastropod and amphipod abundances are affected. On the other hand, if the isopod *Idotea balthica* also declines, this could actually benefit *Fucus*, as this species is the main grazer of *Fucus* and capable of completely defoliating *Fucus* stands (removing up to 70 % of the biomass; Engkvist et al. 2000, Jormalainen and Ramsay 2009, Haavisto and Jormalainen 2014). Therefore the identity of the invertebrate species affected is also an important component in determining how algal communities are affected. However, there was very little grazing by isopods in either colony or control sites during the 2013 and 2014 experiments, potentially due to the concurrent invasion of the mud crab *Rhithropanopeus harrisii* which may instigate a trophic cascade itself by feeding on mesograzers (Forsström et al. 2015, Jormalainen et al. 2016). Despite this, *Fucus* still fared badly around colonies, so that herbivory by isopods does not seem to be the sole determining factor in its abundance.

In general though, the decline in *Fucus* caused by nutrient enrichment leads to changes in invertebrate community structure. In the short term, invertebrates may actually benefit from feeding on nutrient-enriched algae (Kolb et al. 2010, Korpinen et al. 2010). For example, *Idotea balthica* has higher growth rate and reproductive output when feeding on nutrient-enriched algae (Hemmi and Jormalainen 2002). However, this advantage decreases over time as *Fucus* populations decrease and filamentous algae take over. Filamentous algae can assume some of the structural habitat role and food source role of *Fucus* during the summer months (Kraufvelin and Salovius 2004), but detach and degrade in autumn, unlike *Fucus* which can provide year-round structured habitat. As such, invertebrate biomass and abundance tends to be lower in areas without *Fucus* than in areas where *Fucus* is present (Wikström and Kaustky 2007). Similarly, declines in eelgrass *Zostera marina* are also associated with shifts in the associated epifaunal community (Reed and Hovel 2006). Over larger areas, abiotic factors tend to drive most of the variation in algal and plant communities, but even at this scale, the cormorant colonies had a negative impact on both *Fucus* and *Zostera* (IV). Given the importance of these species in providing perennial structured habitat, such an effect may have disproportionate impacts on the associated biodiversity.

While the Baltic Sea is a prime example of a eutrophicated sea, it is certainly not unique in that regard, as shifts in community structure due to eutrophication have been noted in marine and freshwater systems around the world (reviewed in Smith et al. 2006). For example, filamentous algae overgrowing perennial macrophytes (both macroalgae and seagrasses) due to eutrophication has been documented in other areas of the Baltic (Vogt and Schramm 1991), the North Sea (Eriksson et al. 2002), the Adriatic Sea (Munda 1993), and the NW Atlantic (Worm and Lotze 2006). Indeed, I found that nutrient concentration was an important driver of algal and plant communities (IV), and cormorant colonies are essentially concentrating nutrients around colonies in an environment where terrestrial nutrients are already highly abundant, which may mask some of the effects they would have in a less eutrophicated environment.

3.2. Top-down trophic cascades from cormorants

As invertebrate grazing is capable of controlling the increased growth of filamentous algae in the presence of nutrient enrichment (e.g. Hillebrand et al. 2000, Worm and Lotze 2006, Korpinen et al. 2007a, b, Östman et al. 2016), I had expected that the top-down effects of cormorants could mediate some of the nutrient enrichment impacts by indirectly increasing herbivore abundances.

However, the top-down effects from cormorants were much more difficult to detect (**II, III**), and appeared to be limited to a small number of fish species (perch and ruffe, **II**). This may be due to the transient nature of fish populations and limited sampling of fish (**II**). Repeated sampling over the summer around the colony and control sites would give more reliable information on fish community shifts, but in general, it is likely that top-down effects on fish are much more diffuse than bottom-up effects on algae (**II**). Cormorants do not necessarily fish near their colony islands: in some areas they are known to travel up to 40 km if food is scarce, though their (e.g. Boldrighini et al. 1997), although their mean foraging distance seems to be ~5 km (Thaxter et al. 2012). If this is also the case in the Baltic Sea, there is an important difference in scale between the top-down and bottom-up impacts of cormorants.

Despite this, I did detect some limited top-down control around colonies, in terms of increased grazing on some ephemeral algal species (particularly *Ectocarpus siliculosus* and *Ulva* spp.) (**III**) and shifts in the abundance or habitat use of some invertebrate species (**II**), the latter being potentially caused by mobile invertebrates spending less time in sheltered habitats with decreased fish predation around colonies. In general though, any increase in top-down control does not seem able to fully control the increased filamentous algal growth caused by bottom-up nitrogen enrichment (**III**). Again, this may be due to the more diffuse nature of top-down effects from cormorants fishing over a large area rather than close to the colony, while nutrient enrichment occurs continuously over the same restricted area.

In addition, the trophic cascade likely does not affect all mesograzers equally. The community may be able to compensate for the decreased abundance of some mesograzers, if other mesograzers are released from competition. In such a case, the overall grazing rate may remain similar or even increase depending on the consumption levels of the newly dominant species, although the compensatory effect likely increases with biodiversity (in highly diverse systems there are many species available to fill the niches left behind, e.g. Duffy et al. 2007, Douglass et al. 2008, Kurle and Cardinale 2011) and so may be less important in the Baltic Sea.

Finally, the importance of cormorant predation on fish abundance may pale in comparison to the pressure exerted by commercial fishing, as cormorants remove approximately 2 % of the fish as commercial fisheries do. Cormorants slightly reduced the abundance of perch and ruffe, but not sticklebacks (**II**) which have been noted for promoting algal blooms in the western Baltic Sea (Eriksson et al. 2009, Sieben et al. 2011a, Östman et al. 2016), despite sticklebacks being an increasingly common prey item for cormorants (Boström et al. 2012). However, predation on

sticklebacks by cormorants likely does not mitigate the increase in stickleback abundance following loss of piscivorous fish which previously controlled stickleback abundance (which have decreased in numbers following extensive fishing efforts and declining water quality; Nilsson et al. 2004a, Lehtonen et al. 2009, Ljunggren et al. 2010, Eriksson et al. 2011, Mustamäki et al. 2014).

3.3. Scale and relative importance of cormorant impacts

In the first three chapters I sought to minimise the influence of abiotic factors and isolate the impacts of nutrient enrichment and trophic cascades on the communities, by using a paired design (in which each colony island studied had a corresponding control island in the vicinity, chapters **I** and **II**), or by studying sites within a small geographic area (the Archipelago Sea, chapter **III**). In those cases, cormorant impacts, especially through bottom-up processes, were readily apparent in communities near colony islands. At a larger scale (**IV**), they were still detectable as there were significant differences in producer community structure between sites <5 km from a colony and sites 10-15 km away. Over this larger scale, abiotic environmental factors were important factors, but cormorant index (a measure of cormorant impact based on the distance from a colony and cormorant abundance at said colony) did contribute significantly to structuring macrophytes communities (**IV**; **Figure 9**).

In general, cormorant impacts were more important in hard-substrate than soft-substrate habitats. In the former, their importance increased with depth due to the strong temporal variation and influence of wave exposure in shallow (0-2.5 m) areas, as previous studies have suggested (Korpinen et al. 2007a, b, Kraufvelin et al. 2010). In intermediate and deeper waters (2.5-5 m and 5-10 m), communities were more stable over time, and both nutrient enrichment and cormorant index importance increased. A decrease in *Fucus* abundance and presence, and increase in filamentous algae was noted with higher cormorant index, likely due to a combination of the above factors. However, though it did contribute significantly, the actual additive effect of cormorant index was lower than that of most other abiotic factors (2.5-3.5 % of total cumulative explained variation).

In soft-bottom substrates, there were some similar patterns: yearly variation and exposure being more important in shallower areas and nutrient concentration affecting deeper communities. In the shallow and intermediate depth zones, there was a small but significant effect of cormorant index (1.5-2.5 % of total cumulative explained variation), potentially due to the decreased abundance and presence of *Zostera* and increased filamentous algae abundance. However, cormorant index was not a significant factor in determining communities in the deepest (5-10 m) soft-substrate communities considered.

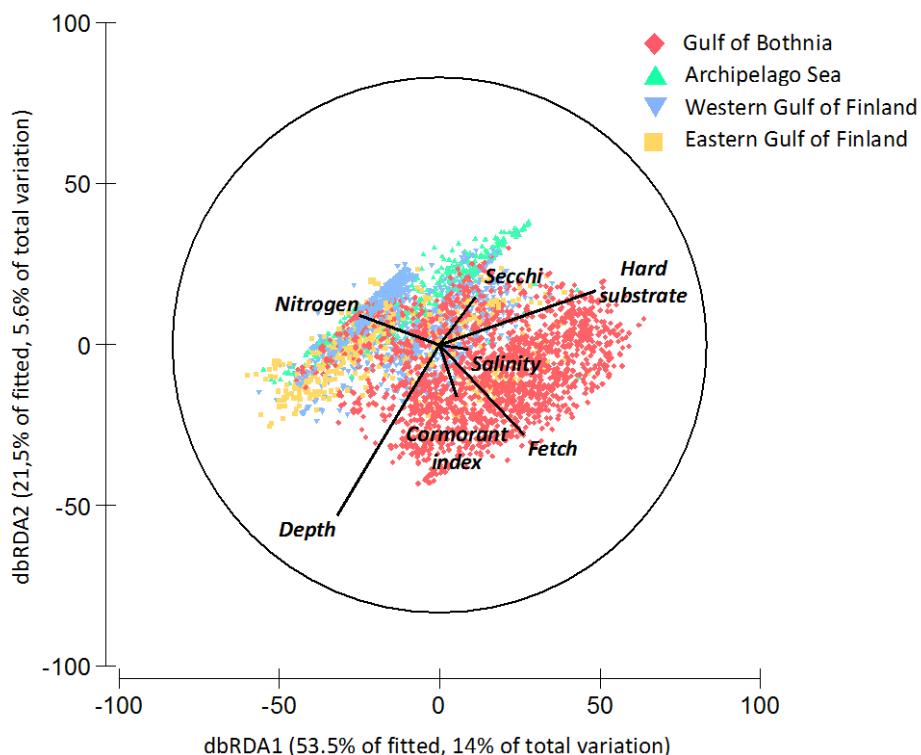


Figure 9. Distance-based redundancy analysis (dbRDA) plot of all pooled producer community data points (0–10 m depth) showing significant environmental factors. The length of each line signifies the multiple partial correlation of the indicated factor to RDA axes and can be interpreted as an indication of that factor's contribution to the explained variation in the DistLM analysis.

This is the first time cormorant impacts have been considered over such a large scale, and even when taking important structuring abiotic factors into account, cormorants can indeed affect macrophyte communities beyond the immediate vicinity of the colonies. In addition, the results of this large-scale analysis generally support the conclusions of experiments performed close to cormorant colonies, with cormorants having negative impacts on perennial habitat forming species while promoting filamentous algal blooms close to colonies, through both top-down and bottom-up effects.

4. CONCLUSIONS AND FUTURE DIRECTIONS

The results of this thesis give insights into how bottom-up and top-down processes might interact with each other and with the surrounding environment, showing the multiple ways in which a single species can affect other trophic levels. The bottom-up nutrient enrichment effects of cormorants are clearly an important structuring force for producer communities around cormorant colonies, driving a community shift similar to that caused by human-induced eutrophication in the Baltic Sea. The shift towards filamentous algae, away from perennial *Fucus vesiculosus* (or *Zostera marina* in soft substrates), extends to associated invertebrate and fish species which depend on these structured habitats (Pihl et al. 1995, 2006, Reed and Hovel 2006, Wikström and Kautsky 2007, Korpinen et al. 2010, Kersen et al. 2011) and could have both ecological and economic consequences (Rönnbäck et al. 2007).

Based on previous studies, I expect that the short-term effects of nutrient enrichment from colonies may be beneficial as species richness, growth and reproductive output increase due to feeding on nutrient-enriched algae (Hemmi and Jormalainen 2002, Korpinen et al. 2010). Similarly, some species prefer filamentous algal habitat (e.g. small gastropods such as *Hydrobia* spp.; Kraufvelin and Salovius 2004), and large macrophytes may also initially benefit from high nutrient availability (Boström et al. 2002). However, in the long term, many important mesograzers such as *Theodoxus fluviatilis*, *Idotea balthica*, or *Gammarus* spp. could decrease in abundance due to the lack of perennial habitat and food sources as *Fucus* becomes less common (Korpinen et al. 2010, Kraufvelin and Salovius 2004, Wikström and Kautsky 2007).

However, the results also show that concurrent factors should not be ignored – in this case I also studied the simultaneous top-down effects of cormorants arising from their high predation pressure on fish. These effects were less important than bottom-up effects for primary producers in the immediate vicinity of the colony, perhaps due to the differences in spatial scales of these impacts. Little is known about their feeding habits, and there is no data about their preferred feeding grounds in the Baltic Sea, which would help in properly assessing their top-down effects. However, they were important for some of the filamentous algal species, likely due to increased grazing from lower mesopredator abundance (Östman et al. 2016), and became more important over a larger spatial scale. Finally, abiotic factors are important structuring factors for macrophytes communities, and determine the relative strength and contribution of these top-down and bottom-up effects, so that these must be taken into account.

Looking forward, there is still a lack of knowledge about the larger ecological role of cormorants in the Baltic Sea. If cormorants exert effects on a radius of 5 km around each colony (as in chapter IV), the total area affected by cormorants over the whole Baltic Sea with 520 colonies could be as high as 41 000 km², or 10 % of the total area of the Baltic Sea (in reality, this area is likely smaller, due to overlapping effects of multiple colonies within a small area, or some of the affected areas occurring over land). However, guano deposition on colony islands also affects terrestrial trophic

networks as not all guano is washed into the sea (Kameda et al. 2006, Kolb et al. 2010b, 2015, Kolb and Hambäck 2015, Zmudczyńska-Skarbek et al. 2015), and so cormorants form an important link in transferring nutrients between marine and coastal terrestrial systems (Ellis et al. 2006, Klimaszyk and Rzymski 2016). In this way, while cormorants concentrate nutrients around colony islands, with some negative impacts as documented here, their overall impact on the nutrient balance of the Baltic Sea may be positive as they are effectively removing nutrients from the sea.

Similarly, cormorants form other trophic linkages in addition to preying on fish, as they are themselves preyed upon, especially by white-tailed sea eagles which are often seen around cormorant colonies, and they could play an important role in the recovery of the sea eagle population (while sea eagles may in turn contribute to stabilising the growth of cormorant populations). Cormorant colonies could also provide safer breeding grounds for other coastal birds such as gulls, eiders, guillemots and razorbills, so their impacts are not limited to the marine system. In any case, cormorants are an important and growing component of the coastal ecosystem, with impacts on multiple trophic levels through both top-down and bottom-up processes.

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