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TITLE   Cormorants have negligible seascape-scale impacts on benthic vegetation communities

YEAR   2020

VERSION   Final draft

Colonial piscivorous seabirds have negligible seascape-scale impacts on benthic vegetation communities

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Abstract

Cormorant populations in the Baltic Sea have rapidly expanded since the 1990s, raising concerns about their ecosystem impacts. Nutrient runoff from colonies, as well as cormorant predation on fish, can affect surrounding producer communities. Past studies have found cormorant impacts on producers in the immediate vicinity of colonies, but the importance of cormorants over a larger spatial scale is unknown, especially compared to other environmental variables. We used an extensive underwater vegetation inventory dataset (~18 000 data points along the Finnish coast) to determine the effects of cormorant colonies on macroalgae and plants. We compared community structure and species abundance/occurrence in near-colony (<5 km from a colony) and control (>10 km from a colony) points, and determined the importance of cormorant influence (using an index incorporating colony size and distance from the colony) in near-colony sites. We found no significant differences in community structure between near-colony and control points in most habitats, and adding cormorant index only infinitesimally improved statistical models after incorporating other environmental factors. However, the abundance of several species did differ, in particular the foundation species bladderwrack (*Fucus vesiculosus*) and eelgrass (*Zostera marina*) were either less likely to occur in near-colony points or negatively correlated with cormorant index, possibly due to the effects of nutrient enrichment from colonies. Our findings confirm that cormorants can have effects on some producer species, but highlight that these effects are negligible when taking into account the scale and magnitude of other bottom up and top-down processes occurring in the Baltic Sea.

Keywords: cormorants, nutrient enrichment, macroalgae, macrophytes, Baltic Sea

1. Introduction

Benthic vegetation communities (macroalgae and vascular plants) are affected by a number of environmental factors, acting in concert and often interactively. Abiotic factors such as light, temperature, salinity, turbidity, depth, substrate type, nutrient richness, and wave exposure are of primary importance in determining species composition (Malm & Isæus 2004, Eriksson & Bergström 2005, Konar et al. 2010, Rinne et al. 2011). At the same time, biotic interactions such as herbivory, competition for space, light and nutrients affect relative species abundance within the community (e.g. Korpinen et al. 2007a). The relative importance of bottom-up and top-down processes varies across ecosystems and depends on abiotic environmental factors as well as the level of resource limitation, grazing intensity, biodiversity, and the strength of the trophic links above herbivores (Menge 2000, Oksanen & Oksanen 2000, Hillebrand et al. 2017, Gruner et al. 2008). In addition, the strength of bottom-up and top-down processes varies temporally, both seasonally (due to the phenology of both producers and grazers; Svensson et al. 2012, Haavisto & Jormalainen 2014) and over multiple years (due to variation in environmental factors such as light conditions, hydrodynamics, and food availability; Åberg & Pavia 1997, Underwood & Chapman 1998). Finally, the relative strength of these processes also varies spatially, over multiple scales, due to differences in e.g. microhabitat, substrate availability, hydrodynamics, temperature, ice cover, and/or salinity (Korpinen et al. 2007a, Korpinen & Jormalainen 2008).

The structure and composition of benthic producer communities is particularly sensitive to nutrient availability because coastal primary production is often nutrient-limited by nitrogen and phosphorus (Elser et al. 2007). For example, nutrient enrichment in the Baltic Sea has lead to fast-growing algae outcompeting perennial macroalgae and seagrass, restricting the growth of perennial species by reducing light availability (Cummins et al. 2004, Råberg 2005, Gustafsson & Boström 2014) and inhibiting recruitment (Berger et al. 2003). Phytoplankton blooms that limit light penetration can also form in response to high nutrient loads, reducing

the lower depth limit of algae and seagrass (Kautsky et al. 1986, Eriksson et al. 1998, Torn et al. 2006, Kruk-Dowgiałło & Szaniawska 2008, Rohde et al. 2008, Alexandridis et al. 2012). Nutrient enrichment can emerge from large-scale diffuse sources (agricultural runoff, atmospheric deposition) and local point sources (wastewater outlets, aquaculture, and, in some areas, from seabird colonies).

Guano runoff from seabird colonies can be important local sources of nitrogen and phosphorus (Smith & Johnson 1995, Wainright et al. 1998, Signa et al. 2015), often resulting in increased algal production (Bosman & Hockey 1986, Bosman et al. 1986). However, the magnitude of impacts from seabird guano can be variable and depend on physical factors that affect runoff, such as the slope of the shore, wave exposure, and precipitation (Wootton 1991, Zmudczyńska-Skarbek et al. 2015), as well as the species involved and the size of the colony (Kolb et al. 2010, Gagnon et al. 2013, 2016). Piscivorous seabirds can also affect primary producer communities through top-down processes similarly to the trophic cascades arising from top predatory fish (Engkvist et al. 2004, Korpinen & Jormalainen 2008), which can modify the intensity of invertebrate grazing (Eriksson et al. 2009, Baden et al. 2010). Herbivores typically exert strong top-down control on the abundance of littoral primary producers (Poore et al. 2012), and thus changes in herbivore abundance also affect producer community composition by modifying the outcomes of interspecific competition (Hillebrand et al. 2007), and controlling the amount of filamentous algae (Korpinen et al. 2007). For example, depletion of predatory fish stocks in the western Baltic Sea has led to overabundant mesopredators and, consequently, to reduced herbivore populations, causing filamentous algal blooms (Sieben et al. 2011).

The great cormorant *Phalacrocorax carbo sinensis* recolonized the Baltic Sea in the 1990s (Van Eerden & Gregersen 1995, Lehikoinen 2006, Beike 2014) and the Baltic population reached 165 000 breeding pairs in 2014 (Bregnballe et al. 2014), after which it seems to have stabilised (Reusch et al. 2018). The rapid population increase has led to human-cormorant

conflicts (Marzano et al. 2013), mostly focused on the perceived threat of cormorant predation to fisheries (e.g. Östman et al. 2013, Heikinheimo et al. 2016, Hansson et al. 2018), and have led to loud demands for management action such as colony eviction and culling (Rauschmayer & Weiss 2013). However, cormorant effects on both marine and terrestrial ecosystems are far more complex than just affecting fish populations (Klimazsyk & Rzymski 2016), and a comprehensive understanding of cormorant effects beyond fish and across the seascape scale (i.e. across an entire sea area) is needed. At lower trophic levels, it is known that the accumulation of nutrient-rich guano on cormorant colony islands can fertilize the surrounding food webs (Kolb et al. 2010, Gagnon et al. 2013). Cormorants can thus promote higher ephemeral algal growth and abundance in rocky habitats in the immediate vicinity of colony islands, while habitat-forming bladderwrack *Fucus vesiculosus* tends to be less abundant, especially around older, denser colonies (Kolb et al. 2010, Gagnon et al. 2015, 2016). In the northern Baltic Sea, cormorants mostly prey on small and medium-sized fish (mesopredators) during the breeding season and can reduce their abundance (Lehikoinen 2005, Boström et al. 2012, Östman et al. 2012, Salmi et al. 2015), potentially affecting invertebrate abundance and modifying grazing pressure on algae through trophic cascades. This can somewhat counteract the nutrient enrichment effects of cormorants, by increasing invertebrate herbivore abundance and thus grazing pressure on filamentous algae (Gagnon et al. 2016). Cormorant-induced trophic cascades likely occur on a larger spatial scale than bottom-up effects (Gagnon et al. 2015, 2016), as mean cormorant foraging range is thought to be 5-10 km during the breeding season with trips extending up to 40 km (Platteuw & Van Eerden 1995, Thaxter et al. 2012, Hentati-Sundberg et al. 2018).

Previous studies of cormorant effects on herbivores and primary producers (Kolb et al. 2010, Gagnon et al. 2015, 2016) have only focused on the immediate vicinity of the colonies (within 100 m of colony islands), but nothing is known the occurrence and magnitude of these effects on a larger seascape scale, and their relative importance compared to other large-scale

environmental factors affecting producer communities. In the Baltic Sea, community structure over a seascape scale is driven primarily by large-scale gradients and temporal variations in environmental conditions and drivers such as nutrient concentration, turbidity, salinity, and wave exposure (Hänninen et al. 2007, Rinne et al. 2011). Thus, a proper analysis of cormorant impacts on benthic communities over the entire seascape should consider and quantify natural variation in environmental conditions, as well as the impacts of large-scale anthropogenic nutrient enrichment and top-down processes driven by fisheries and natural predation. Such a study will provide much-needed perspective to the fierce debate about the importance of cormorants as predators and competitors to fisheries, as the current scientific literature gives somewhat conflict results. For example Vetemaa et al. (2010) and Östman et al. (2013) found significant effects on local fish populations, while Lehikoinen et al. (2011) and Östman et al. (2012) found only minor effects, albeit depending on species.

Our aim in this study was two-fold. Firstly, we wanted to understand the ecological impacts of cormorant colonies, along with other environmental drivers, on producer community structure in the northern Baltic Sea. Secondly, we wanted to quantify cormorant effects in a way that could be used to aid in decision-making of cormorant management plans. To do this, we used an extensive dataset of macroalgae and vascular plants abundance and occurrence in Finnish waters (cf. Virtanen et al. 2018, Lappalainen et al. 2019). We first compared underwater vegetation community structure in near-colony and control data points. Then, we quantified whether adding an index indicating the magnitude of cormorant influence (based on an index incorporating colony size and distance from the colony) improved the fit of statistical models of producer community structure which already accounted for spatial and temporal variation, and abiotic environmental variables (depth, exposure, salinity, temperature, turbidity, and nutrients). Finally, we compared the abundances of several macrophyte taxa in near-colony and control points, paying particular attention to the foundation species *Fucus* spp. and *Zostera marina.* We hypothesized that if communities

differed significantly between near-colony and control points, and cormorant index significantly contributed to community structure, after taking into account other environmental factors, we could take this as evidence that cormorants affect primary producers beyond the immediate vicinity of the colony. While we did not explicitly consider whether these impacts might occur through top-down or bottom-up processes, we assumed that since nutrient run-off dilutes exponentially with increasing distance from colonies, larger-scale impacts are likely to be caused by cascading top-down processes.

2. Methods

2.1. Study system

The study included underwater inventory data points along the entire Finnish coast (Fig. 1; Fig. S1; Table S1), covering a wide range of environmental variables including salinity, nutrient availability, wind and wave exposure, temperature, and ice cover. Great cormorants have been breeding in Finnish waters since 1996, and after several years of high population growth the population has stabilised at approximately 26 000 breeding pairs (Fig. S2). In this area, they nest exclusively on small coastal islands (<6 ha) in colonies of up to 4 000 breeding pairs, with 47 colonies on 82 islands (some colonies consist of multiple islands located within ~1 km distance) recorded in 2019, though this number varies annually as they occasionally change nesting sites (Finnish Environment Institute 2019). Cormorants mostly overwinter in central Europe, then migrate to and occupy Baltic Sea breeding colonies from April-September. Chicks usually hatch in late May and fledge in late July-early August, thus cormorant influence increases over the summer, due to increasing guano accumulation on and around the islands (Gagnon et al. 2013) and higher predation pressure on fish as demand for food increases with chick growth.

2.2. Vegetation and environmental data

The producer community dataset used in this study was collected during the Finnish Inventory Programme for the Underwater Marine Environment (VELMU), an ongoing effort to sample and describe benthic marine communities and characterize biodiversity patterns in Finnish marine waters (Virtanen et al. 2018; www.ymparisto.fi/en-US/VELMU; http://paikkatieto.ymparisto.fi/velmu/). We used underwater vegetation inventory data points from diving and video observations from 2005-2015, including data points collected during the growing season (June to September) that were shallower than 15 m depth (vegetation growth is limited below that depth due to light limitation). All data points included this study have only been sampled once.

The diving data included both individual data points, as well as points taken along a transect extending perpendicular from the shore; in both cases a diver used a 4 m × 1 m quadrat and estimated the percent coverage of all plants and macroalgae present. The video data points included random single data points as well as data points arranged on a pre-determined grid; using either a drop camera or a remotely-operated submersible (ROV), which filmed the seabed for 60 seconds. Percent coverage of plant and macroalgae species was then estimated from the video. Closely related and/or morphologically similar species were grouped due to uncertainty in identification (Table S2).

We conducted two types of analyses in which we first compared producer communities between data points within and outside cormorant influence, and then, within the former group, estimated the influence of colony size and distance on producer communities. We first divided the data points into two categories: those located within a 5 km radius of a colony island (hereafter referred to as "near-colony" points; Fig. S3) and those located within a 5 km radius of a control site ("control" points). These control islands were randomly-chosen sites located 15 to 25 km from the nearest colony island (except for one control site in the eastern Gulf of Finland which was ~12 km from the nearest colony), so the majority of control points

were located 10-30 km from colony islands. We choose the 5 km threshold because it allowed

a reasonable amount of data points for each colony and control site while keeping the dataset

to a manageable size, and because there is some indication that cormorant foraging range

could be of that magnitude (see discussion). The near-colony data points included points

taken near active colonies with >10 breeding pairs, and we did not include any newly-formed

colonies in their first active year, as we considered it might take some time for cormorant

effects to be manifested in the environment. Based on the above criteria, we analysed a total

of 17 780 data points: 8 298 were near-colony points (from 37 different colonies; Table S1)

and 9 482 were control points (from 32 control sites).

For the near-colony points we then calculated an index of cormorant pressure, based on

the distance of the data point from the colony and the number of breeding pairs in the colony

during the sampling year of that particular data point (following Östman et al. 2012):

Cormorant index = # *of breeding pairs* $\times \left[\text{cosine} \left(distance \times \frac{\pi}{maxdist} \right) / 2 + \frac{1}{2} \right]$,

where *maxdist* is the maximum distance (5 km) of near-colony points. The index reaches a

minimum value of zero at 5 km from the colony, and a maximum value equal to the *# of*

breeding pairs when adjacent to the colony. For colonies consisting of several islands, the

distance was measured from the geographic centre of all islands. 222 data points were within

5 km of two different colonies, so we calculated the sum of the cormorant index of both

colonies as the overall cormorant index.

For each data point, we then extracted environmental data from the Hertta database of the

Finnish Environmental Administration (https://www.syke.fi/avointieto) for June-August in

2005-2015, consisting of mean seawater temperature, bottom salinity, depth-attenuated

wave exposure, nutrient concentration (nitrogen and phosphorus), and Secchi depth.

Temperature, salinity, nutrient concentrations were based on models developed specifically

for the VELMU project, based on data from 2003-2014 (Virtanen et al. 2018), and wave

exposure was calculated based on the method described by Bekkby et al. (2008). Secchi depth values were an end-product of an optical model, interpreted from full resolution images (300 m, 3rd re-processing) of a MERIS (Medium Resolution Imaging Spectrometer) satellite sensor from 2004-2011 (Lappalainen et al. 2019). Substrate type and percent cover were recorded in situ during sampling, from which we calculated the percent cover of hard and soft substrate (hard: bedrock, boulders, stones; soft: gravel, sand, silt, mud, clay). The environmental variables were similar in near-colony and control points, except Secchi depth, which was higher in control points (Fig. S4).

2.3. Multivariate statistical analyses (communities)

All multivariate analyses were run using the program PRIMER-E v7 with the PERMANOVA + add-on package (Clarke & Gorley 2015, Anderson et al. 2008). We assigned each data point to a geographic area ("Area": Bothnian Bay (BOTB), Kvarken (KVA, Bothnian Sea (BOTS), Archipelago Sea (ARC), western Gulf of Finland (WGF), eastern Gulf of Finland (EGF); Fig. 1). We also included "SiteID" as a variable, which was the nearest colony or control site (for data points within 5 km of two sites, we used the nearest of the two), to limit any effects of pseudoreplication. As the dataset covers a 10-year period, we included sampling year in the analysis to account for year-to-year variations in environmental conditions (e.g. precipitation, light, temperature, wind), and sampling month to account for phenological differences between species. Area, SiteID (nested in Area), Year, and Month were coded as categorical variables (Anderson et al. 2008), while the others were continuous. We excluded phosphorus concentration to prevent collinearity problems (Dormann et al. 2012) as it was highly correlated with nitrogen concentration (Pearson $R^2 = 0.82$), thus nitrogen can be considered as a proxy of total nutrient availability in the water column. The multivariate analyses thus included 11 environmental variables (Area, SiteID, Year, Month, Depth, Substrate, Exposure, Temperature, Salinity, Secchi depth, Nitrogen), and either Treatment

(near colony vs. control) or Cormorant index, all of which were normalized prior to analysis.

We first created a resemblance matrix for the whole dataset using zero-adjusted Bray-Curtis similarity (Anderson et al. 2008). Then, we used PERMANOVA (with 999 permutations) to determine whether there were significant differences in community structure between near-colony and control sites. We included Area, Year, Month, and Treatment as fixed factors, SiteID as a random factor, and the other continuous environmental variables as covariates. To quantify the importance of cormorant colonies on their surrounding communities, we used distance-based linear modelling (DistLM: "Best" model selection by AICc) on the near-colony points only, including all environmental variables and Cormorant index, to determine the best model. We then repeated the DistLM on the near-colony points using "Specified" model selection with the variables identified in the best model. We checked the output of the sequential tests to determine if adding Cormorant index improved the model fit (significantly lowered AICc) and how much Cormorant index contributed to the explained variation.

We then split the dataset into eight subsets representing different habitats: two substrates (hard and soft) and four depth zones (0-2.5 m, 2.5-5 m, 5-10 m, 10-15 m) and analysed each of these separately (Table S3). As the dominant vegetation types and relative importance of environmental factors vary by substrate and depth (e.g. Korpinen et al. 2007a, Rinne et al. 2011) this allowed us to quantify the importance of cormorant impacts on these different community types. We repeated both analyses above (PERMANOVA on all points, followed by DistLM on the near-colony points), on each data subset, using the same variables as above.

2.4. Univariate statistical analyses (species)

We performed univariate analyses on the following taxa: filamentous algae (hard and soft substrates; 0-10 m), *Cladophora* spp. (hard; 0-5 m), *Ulva* spp. (hard; 0-2.5 m), *Chorda filum* (hard; 0-5 m), *Dictyosiphon* spp. (hard; 0-5 m), *Ectocarpus/Pilayella* (hard; 0-10 m), *Fucus* spp. (hard; 0-5 m), *Ceramium* spp. (hard; 0-10 m), *Furcellaria lumbricalis* (hard; 5-10 m),

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Polysiphonia spp. (hard; 0-10 m), *Ceratophyllum/Myriophyllum* (soft; 0-5 m), charophytes (soft; 0-5 m), *Potamageton/Ruppia/ Stuckenia/Zannichellia* (soft; 0-5 m), *Zostera marina* (soft; 0-5 m), and total cover of submerged vegetation (SAV, including *Z. marina* and freshwater macrophytes) (soft; 0-5 m). For analyses involving *Fucus* spp. *and Z. marina*, we only used data points from the areas where these species are known to occur (*Fucus* spp. BOTS, ARC, WGF, EGF; *Z. marina*: ARC, WGF). For each taxon, we used a generalized-linear mixed model (GLMM) with quasibinomial distribution (glmmPQL function in the MASS package in R version 3.6.2), incorporating SiteID as a random factor, all environmental variables as fixed factors (Area, Year, Month and Treatment as categorical, all others as continuous), to test whether abundance differed significantly between treatments. For the foundation species *Fucus* spp. and *Z. marina*, we also transformed the data into presence/absence data, and used a GLMM with binomial distribution, as above, to test whether there was a difference in probability of occurrence between treatments.

For *Fucus* spp. (hard; 0-5 m; in BOTS, ARC, WGF, EGF), *Z. marina* (soft; 0-5 m, in ARC, WGF), and filamentous algae (hard and soft; 0-10 m; all areas), we also used the same GLMM method as above (with quasibinomial distribution and the same variables) to perform a regression of near-colony points and determine whether cormorant index had a significant effect.

3. Results

3.1. Multivariate analyses (communities)

Community structure was significantly different between near-colony and control points for the whole dataset, as well as two of eight habitats (2.5-5 m and 5-10 m hard substrate habitats; Table 1, Table S4), while Cormorant index had a very small, but significant effect on community structure in near-colony sites in the overall analysis of all habitats, as well as the analyses of all habitat subsets except the deep hard substrate habitat (Fig. 2, Fig. S5, Table 1, S5). Spatial and temporal variation were important factors in all habitats, as SiteID, Month,

and Year were included in all the best models, and present in all the top ten models across all habitats (Fig. 2, Table S5, S6). Depth and Salinity were included in the best models in seven of eight habitats, Substrate, Exposure, and Nitrogen were included in six of eight habitats, and Temperature and Secchi depth were included in five of eight habitats (Fig. 2, Table S5, S6)

Environmental variables explained 25-50% of variation in community structure of the near-colony points, though most of this explained variation was included in the 'SiteID' term. Thus, measured environmental variables only explained ~10% of the variation. In general our models explained more variation in hard substrate than soft substrate habitats of the same depth, except in the deeper habitats (>10 m depth), where explanatory power was low in both habitats (Fig. 2, Table S5). Adding Cormorant index to the model significantly increased the explanatory power of the model in hard substrate communities from 0-10 m depth and in all soft substrate communities (Fig. 2, Table 1). However, the relative contribution of Cormorant index to the model was extremely small (i.e. the proportion of explained variance after other factors were accounted for in the model was < 1%, Table 1, S5).

3.2. Univariate analyses (species)

The abundance of most algal and plant taxa did not differ between near-colony and control points (Fig. 3, Table 2, Table S7). Only the abundance of two species differed: both *Ceramium* spp., and *Zostera marina* were more abundant in control than near-colony points (Fig. 2, Table 2, S8), and there was also significantly higher probability of finding *Z. marina* (Fig. 3; Table 1, Table S8) in control than near-colony points. Within the near-colony data points, Cormorant index had a significant effect on the abundance of *Fucus* spp. and filamentous algae in soft substrate, but no effect on the abundance of *Z. marina* filamentous algae in hard substrate (Table 2, S9), though we note that *Z. marina* was only present in six near-colony data points in total. The effect of Cormorant index was negative on *Fucus* spp. abundance, and positive on filamentous algae abundance (Fig. S6).

4. Discussion

Overall, very small, if any, differences in producer community structure could be detected between near-colony and control data points. Through a close analysis of the near-colony data points, we found that abiotic environmental conditions explained approximately 25-50 % of the variation in community structure across the whole Finnish coast, as well as within habitats. Spatial and temporal variation seemed to be the most important factors, though as not all geographic areas and sites were sampled in all years, some of the variation due to these two factors may be confounded. Despite this limitation, it is clear that both spatial and temporal (between and within year) differences in environmental conditions are important sources of variation in community structure over a seascape scale. The analysis of the pooled data from all habitats revealed that depth and substrate explained an additional 8% and 2% variation, respectively, when added (in that order) to the spatial and temporal variables, suggesting that these factors are especially important. Our subsequent analyses of data subsets which took into account these two variables suggested that the variation explained by additional abiotic environmental factors (temperature, exposure, salinity, etc.) was relatively low, though it is likely that these were at least partially included in the spatial variation factors (SiteID and geographic area).

The very large size of this dataset provided high statistical power to detect even miniscule differences in community structure and abundance after accounting for as many sources of variation as possible. Though statistically significant in most habitats, adding cormorant index to statistical models only infinitesimally increased the explanatory power of these models by 0.1-0.7% (i.e. less than most of the environmental variables), and are likely ecologically insignificant. Though previous studies have shown important and noticeable impacts of cormorants on producer communities in the immediate vicinity of colonies, the results of this study suggest that the importance of cormorants over the entire seascape is dwarfed by other

environmental variables.

While cormorant colonies seem to have little overall effects on vegetation communities, there might be some potentially ecologically-relevant effects on a limited number of individual species and functional groups, including foundation species and filamentous algae. These results support those of previous study in which we found higher abundances of filamentous algae and lower abundance of bladderwrack in hard substrate habitats in the immediate vicinity of cormorant colonies compared to control islands (Gagnon et al. 2015), as well as reduced bladderwrack recruitment around colony islands (Gagnon et al. 2016). These differences were mostly attributed to bottom-up effects caused by nutrient enrichment from guano which facilitates filamentous algal growth and can thus reduce bladderwrack growth and recruitment (Cederwall & Elmgren 1990, Bonsdorff et al. 2002, Bergström et al. 2003, Isæus et al. 2004). Here, the negative effect of cormorant index on *Fucus* abundance in near-colony data points and the positive effect on filamentous algal cover suggest that bottom-up nutrient enrichment may extend beyond the immediate vicinity of the colony. However, cormorant-induced changes in top-down pressure is likely to modify any effects of nutrient enrichment (e.g. Korpinen et al. 2007), potentially limiting the overall impacts of cormorant colonies as we found no differences between near-colony and control sites.

In this study, we also explored the effects of cormorant colonies on vegetation in soft-substrate habitats for the first time, and found that eelgrass meadows were both less abundant, and less likely to occur in near-colony than in control data points. Eelgrass, like most seagrasses, is especially sensitive to increased turbidity and filamentous algal blooms caused by nutrient enrichment (Short et al. 1995, Gustafsson & Boström 2014). For example, local nutrient enrichment caused by aquaculture can lead to reduced eelgrass cover and higher epiphyte loads near fish farms (Cullain et al. 2018), and the increased filamentous algal loads in soft-substrate near-colony points indicates that nutrient enrichment around colonies may similarly impact eelgrass presence and cover. Filamentous algae in soft-substrate

habitats may also benefit from nutrient enrichment, as they were more abundant in near-colony than control points. In Baltic Sea soft-substrate habitats such as eelgrass meadows, top-down effects may be less important as invertebrate grazers (amphipods, isopods, and gastropods) are less abundant than in hard-substrate algal beds (Gagnon et al. 2019) and therefore less able to counteract the effects of nutrient enrichment.

As cormorant colonies are known to be significant local sources of nutrients and to impose high predation pressure on fish, we expected them to have considerable impacts on producer communities through both nutrient enrichment and cascading effects on the food web. Instead we found that though large-scale cormorant effects are detectable and significant with the high statistical power of a large dataset, they are mostly ecologically insignificant. This is likely due to the far greater importance of spatial and temporal variation as well as abiotic and biotic environmental factors. Below we discuss reasons why cormorant impacts may be difficult to detect or are relatively unimportant over large seascape scales:

(1) We condensed cormorant effects into a single index based on distance and size of the cormorant population, and the data did not allow us to distinguish between bottom-up and top-down effects. In addition, the cormorant index was based on evenly decreasing magnitude with increasing radius, but prevailing wind-driven currents and local hydrography likely result in nutrients, and thus bottom-up effects, distributed unevenly in different directions rather than homogeneously based only on distance. Top-down effects may also not correlate directly with distance since cormorants favour foraging in certain food-rich sites (Quintana et al. 2011).

(2) Cormorant foraging range during the breeding period is relatively poorly known, and the only Baltic estimate suggests that cormorants fish mostly within 10 km of the colony (Hentati-Sundberg et al. 2018). Estimates from lake-nesting populations have also found that cormorant seem to prefer foraging within 5 km of their colony (Thaxter et al. 2012, Paillisson et al. 2014), but will travel up to 40 km from colonies when food is scarce (Platteuw & Van

Eerden 1995). Since we have no data on the food availability around the different colonies in this study, there remains a possibility that at least some cormorants are foraging over long distances. Top-down pressure from cormorants may be an important factor regulating vegetation communities, but if they are predominantly spatially widespread due to large-scale cormorant foraging, our comparisons in this study would be unable to reveal them.

(3) In our seascape-scale approach, it was not possible to consider the age of the colony, which has been shown to affect the strength of the bottom-up effects in the immediate vicinity of the colonies (Gagnon et al. 2015). Some colonies studied here were in their second year, while others had been continuously used for 10 years. Cormorant effects, be they bottom-up or top-down, likely take time to build up and are probably cumulative over the years as the colony grows.

(4) Anthropogenic eutrophication (mostly caused by terrestrial nitrogen and phosphorus input) has greatly impacted the Baltic Sea since the 1980s (Andersen et al. 2017, Reusch et al. 2018), so increased nutrient concentrations around cormorant colonies may have little substantial impact as it may be masked by large scale nutrient enrichment. This is especially true as cormorants essentially redistribute and concentrate nutrients around colonies, rather than adding new nutrients into the sea, while anthropogenic eutrophication is due to the increased input of terrestrial nutrients into the sea over a much larger scale.

(5) Top-down effects of fish removal by cormorants may be masked by fisheries: commercial fisheries annually remove ~138 million kg of fish from Finnish marine waters (Finnish Game and Fisheries Research Institute 2014), while recreational fisheries remove ~7.5 million kg (Natural Resources Institute Finland 2016). By contrast, cormorants remove ~3 million kg of fish (based on 1 kg daily fish consumption per breeding pair; Grémillet et al. 1995, Ridgway 2010) over the four-month breeding season. Similarly, predation by other avian predators (such as eagles, ospreys, gulls, and diving ducks) and seals pose an order of magnitude higher predation pressure on fish than cormorants do (Hansson et al. 2018).

Though cormorants likely have local effects on the abundance of certain fish species (e.g. Vetemaa et al. 2010, Östman et al. 2013), large-scale top-down cascading effects of cormorants may therefore be masked by fisheries and natural predation by other predators.

(6) Though we discussed the potential negative effects of filamentous algae on bladderwrack and eelgrass abundance, we did not consider biotic interactions such as competition between species as a factor in structuring vegetation communities. Similarly, we did not explicitly consider predation pressure from either fisheries or natural predators (see above) as a separate factor in the analyses. Though our comparison of near-colony to control points should mitigate this to some extent, it is likely that these biotic interactions and their relative importance are highly variable over time, space, and according to the species present (including algal and plant species, as well as grazers, fish, and higher predators.

One interesting possibility remaining is that the establishment of colonies and the initial choice of their locations may not be random with respect to underwater habitat characteristics and vegetation community composition. Very little is known about the process of establishment of cormorant colonies and nothing about the role the underwater seascape plays in choosing a colony site. In general, the formation of a seabird colony is typically preceded by roosting at the site (Pyk et al. 2013, and references therein), at which stage the birds use environmental cues to assess the quality of the site (Oro and Ruxton 2002). While the availability of suitable nesting sites, predation risk, and proximity to human disturbances are probably important choice criteria, habitat quality, in particular prey availability (Kildaw et al. 2005) is likely an important factor in colony formation (Sandvik et al. 2016). We consider it highly likely that the choice of colony sites and colony establishment is not completely random with regards to environmental conditions. Thus, the underwater seascape, and initial vegetation community in near-colony and control data points may not have been equivalent prior to cormorant colony establishment.

5. Conclusions

This study quantifies, for the first time, the effects of cormorants beyond the immediate vicinity of their colonies. Overall, seascape-scale differences between producer communities between near-colony and control data points could not be detected in most habitats. Similarly, the cormorant index significantly contributed to explaining community structure in near-colony points, but its contribution was ecologically negligible (<1 %). Spatial and temporal variation accounted for most of the explained variation, along with abiotic environmental variables. We did find some effects of cormorant colonies on a limited number of species, including negative effects on the foundation species *Fucus* spp. and *Zostera marina*, and positive effects on filamentous algae. While our results may indicate some limited impacts of cormorants on Baltic Sea coastal benthic habitats at a seascape scale, we cannot rule out other explanations (e.g. non-random establishment of colonies) due to the correlative nature of our data. Overall, the impacts of colonies on benthic producer communities are negligible at the seascape scale when taking into account the scale and magnitude of other prevailing bottom up (eutrophication) and top-down (fisheries, natural predation) processes that structure Baltic Sea ecosystems.

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Table 1. Summary of multivariate results of (a) permutational manova (PERMANOVA) tests of differences between treatments (near-colony vs control points), and (b) distance-based linear-modelling (DistLM) determining the % contribution of cormorant index (near-colony points only) and associated p-value (i.e. whether adding the factor significantly improved the model, obtained from sequential tests, both separately for the different habitats and for the pooled data ("all habitats"). Degrees of freedom (df) are given as numerator df, denominator df, and values in bold indicate statistically significant ($p<0.05$) values. Complete PERMANOVA results with the significance of all environmental factors, are shown in Table S4, while the % contributions of all factors in the DistLM are shown in Figure 2 and Table S6.

Habitat	(a) Treatment (PERMANOVA of near-colony and control points)		(b) Cormorant index (DistLM of near-colony points only)	
	Pseudo-F $_{df}$	p	% contrib.	p
Hard 0-2.5 m	1.01 $_{1, 1692}$	0.4	0.32	**0.002**
Hard 2.5-5 m	3.19 $_{1, 1925}$	**0.002**	0.27	**0.001**
Hard 5-10 m	1.69 $_{1, 2549}$	**0.001**	0.66	**0.001**
Hard 10-15 m	0.76 $_{1, 1408}$	0.75	0.13	0.25
Soft 0-2.5 m	0.91 $_{1, 1692}$	0.6	0.23	**0.006**
Soft 2.5-5 m	0.47 $_{1, 1797}$	0.99	0.42	**0.001**
Soft 5-10 m	0.25 $_{1, 3223}$	0.99	0.12	**0.048**
Soft 10-15 m	0.18 $_{1, 3091}$	0.99	0.30	**0.013**
All habitats	6.20 $_{1, 17684}$	**<0.001**	0.08	**0.005**

1 **Table 2.** Summary of univariate results showing the results of (a) generalised linear mixed
2 model (GLMM) analyses of the significance of treatment on (a) cover (using a quasibinomial
3 distribution) and (b) presence (using a binomial distribution, and (c) the significance of
4 cormorant index on cover (quasibinomial distribution) of selected ecologically-relevant
5 species. Degrees of freedom (df) are given as numerator df, denominator df, and values in
6 bold indicate statistically significant (p<0.05) values. Complete GLMM results with the
7 significance of all environmental factors, are shown in Tables S7, S8, S9, while the effects of
8 treatment and cormorant index on each species are shown in Figures 3 and 4, respectively.
9

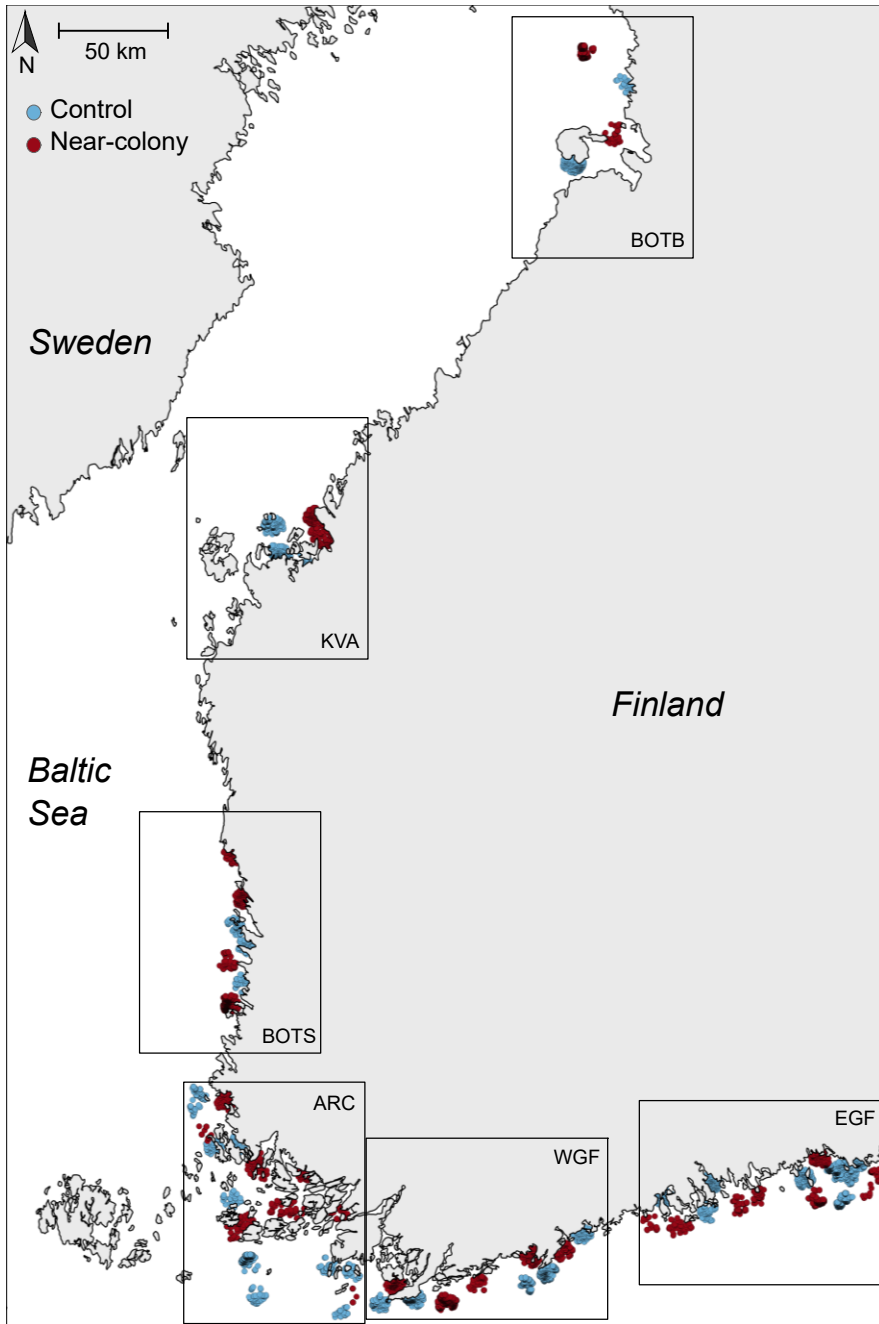|	(**a**) Treatment (near-colony and control points)		(**b**) Cormorant index (near-colony points)	
	F_{df}	p	F_{df}	p
Hard substrate				
Cladophora spp. (0-5 m)	$0.18_{1,65}$	0.67		
Ulva spp. (0-2.5 m)	$0.81_{1,57}$	0.37		
Chorda filum (0-5 m)	$2.12_{1,65}$	0.15		
Dictyosiphon/Stictyosiphon (0-5 m)	$0.56_{1,65}$	0.46		
Ectocarpus/Pilayella (0-10 m)	$1.68_{1,66}$	0.20		
Fucus spp. (0-5 m)	$0.02_{1,56}$	0.88	$8.08_{1,1521}$	**0.0045**
Ceramium spp. (0-10 m)	$4.78_{1,66}$	**0.0323**		
Furcellaria lumbricalis (0-10 m)	$0.97_{1,66}$	0.33		
Polysiphonia spp. (0-10 m)	$0.03_{1,66}$	0.85		
Filamentous algae (0-10 m)	$1.09_{1,66}$	0.30	$0.34_{1,56}$	0.56
Soft substrate				
Charophytes (0-5 m)	$0.33_{1,62}$	0.57		
Ceratophyllum/Myriophyllum (0-5 m)	$0.06_{1,62}$	0.81		
Potamageton, etc. (0-5m)	$0.01_{1,62}$	0.92		
Zostera marina (0-5 m)	$5.38_{1,29}$	**0.028**	$0.01_{1,462}$	0.93
SAV (0-5 m)	$0.08_{1,62}$	0.78		
Filamentous algae (0-10 m)	$0.04_{1,65}$	0.84	$3.90_{1,29}$	**0.028**
Occurrence				
Fucus spp. (hard; 0-5 m)	$0.34_{1,56}$	0.56		
Zostera marina (soft; 0-5 m)	$3.90_{1,29}$	**0.028**		

10

Figure legends

Fig. 1. Near-colony (dark red; (<5 km from a colony) and control (light blue; >10km from a colony) data points included in the study, and geographic areas (BOTB=Bothnian Bay, KVA=Kvarken, BOTS=Bothnian Sea, ARC=Archipelago Sea, WGF=Western Gulf of Finland, EGF=Eastern Gulf of Finland). See Fig. S1 for close-up maps of each geographic area.

Fig. 2. Contribution (%) to the explained variation in producer community structure of each environmental factor and Cormorant index in different habitats as well as in the pooled data ("all habitats"). Full results of the distance-based linear modelling analyses, showing % contribution of all factors, are shown in Table S5. Distance-based redundancy plots showing the ordination of data points are shown in Fig. S5.

Fig. 3. Percent cover of selected algal and plant species, filamentous algae, and probability of occurrence of *Fucus* spp. and *Zostera marina* in near-colony (dark) and control (light) points. Error bars indicate 95% confidence limits, and asterisks indicate significant differences (p<0.05). See Table 2 for data subsets and habitats in which each species was analysed. Means and confidence limits were derived from general linear models with quasibinomial distribution (or binomial distribution for occurrence) and including other environmental variables (Table S7, S8).
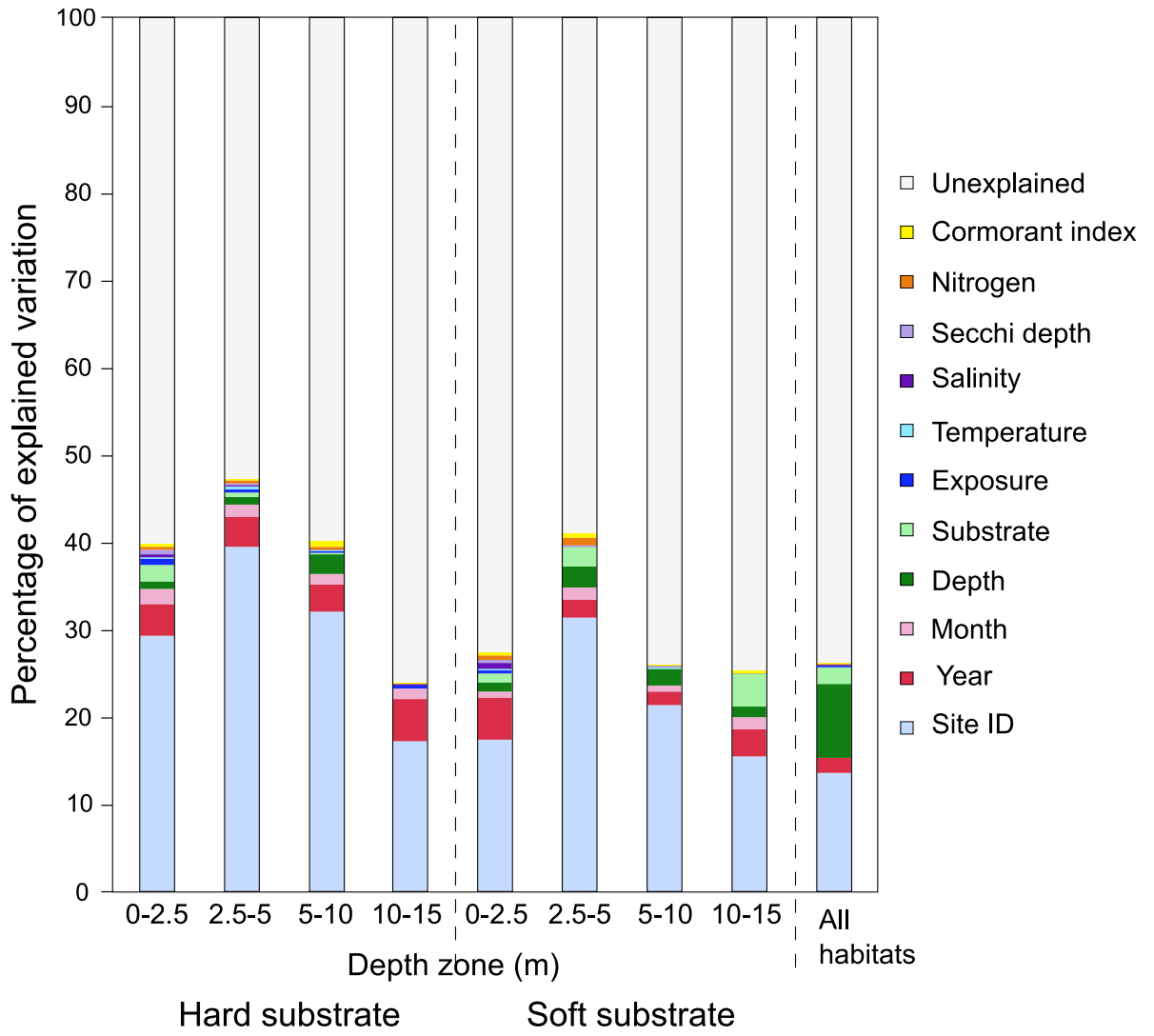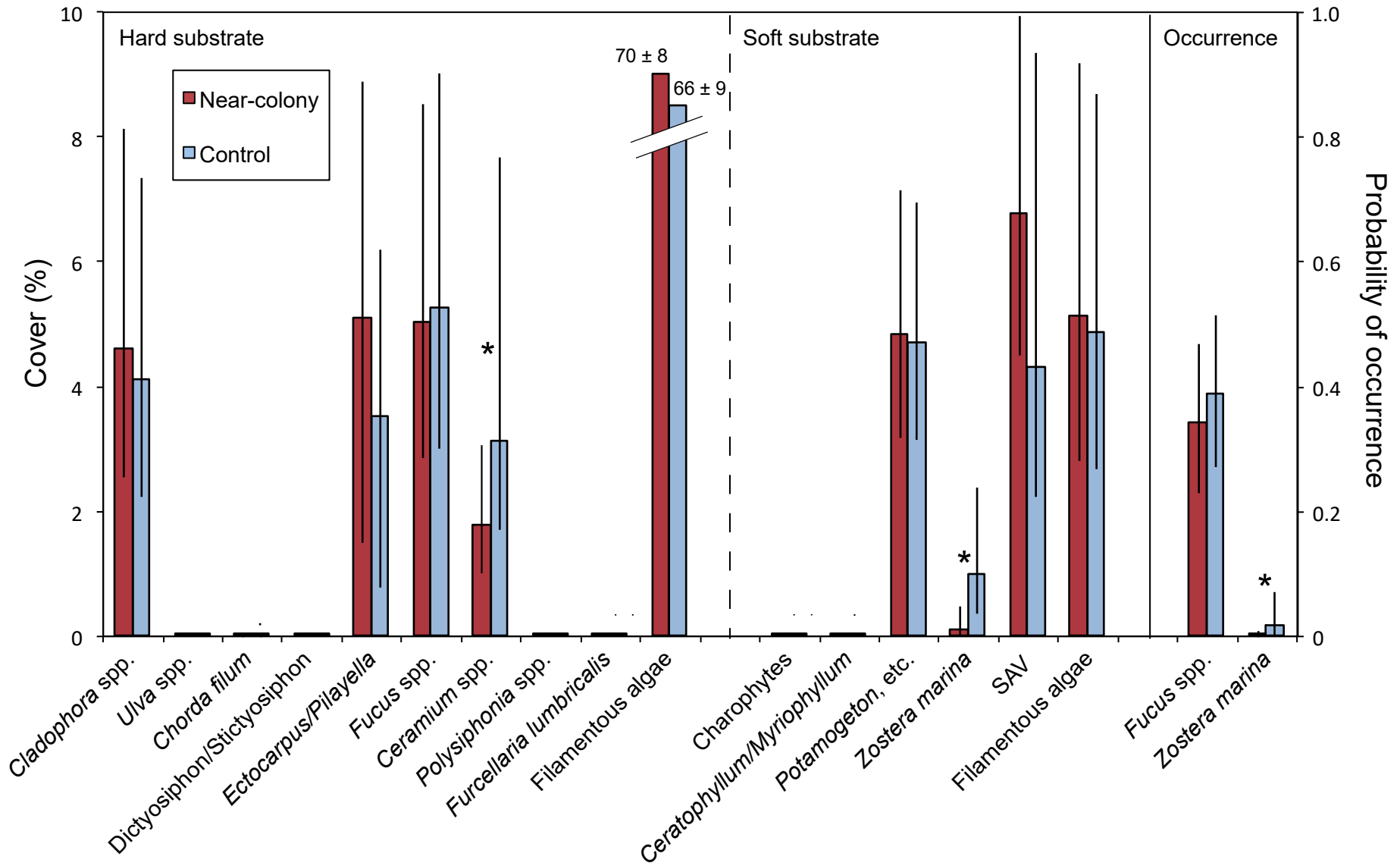
1 **Figure 1.**

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Figure 2.

1   **Figure 3.**

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