Cormorant-induced shifts in littoral communities

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ABSTRACT: The great cormorant (*Phalacrocorax carbo sinensis*) population in the Baltic Sea has increased rapidly since the 1990s. As cormorants nest in high densities on islands, they can affect benthic communities through nutrient runoff from colonies and may also induce trophic cascades through fish predation. Here, we describe fish, invertebrate, and algal communities, as well as algal growth and biomass accumulation, around colony and control islands along the Finnish coast to determine how cormorants affect communities through top-down and bottom-up processes. While cormorants did not affect the species richness or biodiversity of any trophic levels, there were differences in the community composition of pelagic fish between colony and control islands, and mesopredators perch *Perca fluviatilis* and ruffe *Gymnocephalus cernua* were less abundant near colonies. The abundance of several species correlated with cormorant abundance, density and colony age, indicating that these are essential factors in determining the strength of colony impacts. Filamentous algae tended to be more abundant and primary production was higher near older, denser colonies, likely due to nutrient enrichment from the colonies, which overwhelms top-down control. Consequent increased competition by filamentous algae probably explains the decrease in biomass of the foundation algal species *Fucus vesiculosus* near denser, more populated colonies. Cormorants can thus affect benthic communities through both top-down and bottom-up processes, with bottom-up impacts being locally concentrated near colony islands. The impacts can become more pronounced over time and with increasing cormorant populations, potentially leading to shifts in community composition and ecosystem functioning around cormorant colonies.

KEY WORDS: Top-down · Trophic cascade · Bottom-up · Nutrient enrichment · Benthic communities · Cormorants · Baltic Sea

INTRODUCTION

Regulation of community assemblages and consequent biodiversity can be affected by multiple factors, including both top-down and bottom-up processes. In benthic marine systems, top-down processes often dominate, as the link between producers and herbivores is typically very strong (Poore et al. 2012), making communities vulnerable to trophic cascades, in which high trophic-level consumers affect producers (Pace et al. 1999, Shurin et al. 2002, Borer et al. 2005, Heck & Valentine 2007, Estes et al. 2011). Top-down control can become evident when a top predator is removed, leading to shifts in community composition and con-

sequent function (e.g. Estes & Palmisano 1974). In simple, linear trophic networks such as these, the links between trophic levels are evident and it can be easy to predict trophic cascades. However, in more complex systems, where linear food chains are replaced by food webs and many overlapping trophic levels, predictions become more difficult (Pace et al. 1999). In addition, bottom-up processes are always present (though their relative importance varies) and may affect the strength and detection of trophic cascades (Heck et al. 2000, Borer et al. 2006, Elmhagen & Rushton 2007, Eriksson et al. 2012, Jochum et al. 2012) through antagonistic or synergistic interactions with top-down processes (Crain et al. 2008).

When present at high densities, seabirds can remove large amounts of fish, therefore altering fish abundance and potentially triggering cascading effects on lower-trophic levels such as invertebrates and producers. In addition, guano from bird colonies can have eutrophying effects on lower trophic levels due to nutrient enrichment (Bosman & Hockey 1986, Wootton 1991, Kolb et al. 2010, Gagnon et al. 2013). Seabird colonies thus offer an excellent opportunity to study the joint effects of top-down and bottom-up impacts on ecosystems, and so we have taken advantage of the recent population growth of the great cormorant *Phalacrocorax carbo sinensis*, a colony-nesting seabird, in the Baltic Sea to investigate its effects on lower trophic levels in the littoral environment.

After having disappeared in the 19th century, great cormorants returned to the Baltic Sea in the mid-1990s, and their population has since grown exponentially (Van Eerden & Gregersen 1995, Lehikoinen 2006, Beike 2014), now standing at nearly 170 000 breeding pairs (Bregnballe et al. 2014), with 20 000 breeding pairs along the Finnish coast (2014; unpubl. monitoring data from Finnish Environmental Institute SYKE). The rapid increase, large population size, and high-density colonies of cormorants have raised questions regarding their impacts on coastal benthic communities. With an average daily intake of 1 kg of fish per breeding pair during the breeding season (Glahn & Brugger 1995, Ridgway 2010), predation could potentially diminish local fish populations, thus inducing increases in herbivorous invertebrates and consequent effects on the producer trophic level (Reiss et al. 2014).

In northern Europe, cormorant diet typically includes roach *Rutilus rutilus*, ruffe *Gymnocephalus cernua*, and perch *Perca fluviatilis*, with smaller amounts of eelpout *Zoarces viviparous*, pike-perch *Sander lucioperca*, Baltic herring *Clupea harengus membras*, and smelt *Osmerus eperlanus*, although the proportion of prey species differs by time and place (Dirksen et al. 1995, Engström 2001, Lehikoinen 2005, Žydelis & Kontautas 2008, Pūtys & Zarankait 2010, Östman et al. 2012, Salmi et al. 2015). Boström et al. (2012) found increased consumption of sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*) along the Swedish coast, coinciding with increasing populations of sticklebacks in the Baltic Sea, indicating that cormorants are likely opportunistic feeders which choose appropriately sized fish that are readily available.

Studies on the impacts of cormorants have mostly focused on fish communities and fisheries conflicts, showing that while cormorants can locally remove fish on the same scale as fisheries (Dirksen et al. 1995, Engström 2001, Žydelis & Kontautas 2008), there seems to be very little direct overlap in catch, as cormorants preferentially remove species with low commercial value and smaller-sized individuals than commercial fisheries (Rudstam et al. 2004, Žydelis & Kontautas 2008, Pūtys & Zarankait 2010, Salmi et al. 2015). However, little is known about how this can affect ecosystem functioning and trophic interactions. Because the most consumed prey species and size classes are also important invertebrate predators, the removal of these species in large numbers by cormorants (i.e. an average-sized colony of 500 breeding pairs could remove 60 000 kg of fish during the breeding season) could lead to higher numbers of herbivorous invertebrates, thus increasing herbivory and causing shifts in community structure (Eriksson et al. 2012).

However, trophic networks are complex systems, and species may not all respond in the same way, i.e. some species may benefit and others may be disadvantaged by shifts in trophic interactions due to changes in competitive hierarchies (Chase et al. 2002). In particular, different species of invertebrates have differing feeding behaviours, which could lead to different outcomes for algal species (Eriksson et al. 2011). In the northern Baltic Sea, one of the most abundant herbivorous invertebrates is the isopod *Idotea balthica*, which mostly feeds on the brown alga *Fucus vesiculosus* (hereinafter referred to as *Fucus*), an important foundation species in rocky littoral assemblages, as it provides habitat for other species (Salemaa 1987, Jormalainen et al. 2001, Leidenberger et al. 2012). Shifts in the abundance of this isopod could thus have a substantial impact on *Fucus* (Haavisto & Jormalainen 2014). However, another abundant grazer, the gastropod *Theodoxus fluviatilis*, feeds mostly on filamentous algae and periphyton (Jacoby 1985, Eriksson et al. 2011), and therefore, changes in the abundance of *T. fluviatilis* would have very different impacts on the algal community than changes in *I. balthica* abundance.

As previously mentioned, cormorants can also have bottom-up effects on littoral communities due to the runoff of nutrient-rich guano from colonies (Kolb et al. 2010, Gagnon et al. 2013). Increased nutrient availability generally leads to blooms of fast-growing filamentous algal species, thus instigating changes in productivity, algal species composition, nutrient cycling, and associated biodiversity (e.g. Valiela et al. 1997, Karez et al. 2004, Antón et al. 2011). Previous studies have shown that these bottom-up effects can

interact with top-down trophic processes; for example, the loss of top predators seems to exacerbate algal blooms caused by eutrophication, due to decreased herbivory (e.g. Eriksson et al. 2012, Hughes et al. 2013). Around cormorant colonies, nutrient enrichment could favour the growth and recruitment of ephemeral and filamentous algae, thus further harming *Fucus* populations (Berger et al. 2003, Steen & Rueness 2004, Korpinen & Jormalainen 2008).

In this study, we investigated the effects of cormorants by comparing differences in communities of fish, invertebrates, and algae between colony and control islands along the Finnish coast of the Baltic Sea. We were particularly interested in whether we could detect shifts in community structure and biodiversity, and whether there were differences in the abundances of common species due to cormorant-triggered trophic cascades. We also determined if body-size distributions of fish differed between colony and control islands due to size-selective predation by cormorants. Finally, we measured algal biomass, growth, and herbivory to determine whether the combined effects of nutrient runoff from the colonies (bottom-up) and a presumed increase in grazing pressure (top-down) affected producers.

Based on previous studies of cormorant diets, we hypothesized that there would be lower abundance of fish species such as roach, perch, and ruffe near colony islands, leading to higher populations of invertebrates (especially mobile invertebrates such as isopods and amphipods), and thus increased grazing pressure on algae. However, we expected this to be somewhat counteracted by higher growth rates near colonies due to nutrient runoff, especially for fast-growing filamentous species.

MATERIALS AND METHODS

Study area and sites

We selected 9 pairs of islands along the southwestern Finnish coast, each pair consisting of 1 cormorant colony island and 1 control island without cormorants (Table 1, Fig. 1), essentially setting up a random block design (where each pair is a block, and each site an independent replicate). In cases where there were multiple samples from within a site, these were treated as subsamples in the statistical analyses (see 'Statistical analysis' below).

Table 1. Colony and control site characteristics, including area, number of breeding pairs (BPs) of *Phalacrocorax carbo sinensis* in 2012, and 2013, and year of colony establishment (for colony islands), as well as the types of sampling and experiments done at each site (including the year sampling occurred). Data from the colony islands were provided by the Finnish Environment Institute. Locations of study sites are shown in Fig. 1. y = yes; invert. = invertebrates; *Fucus* = *Fucus vesiculosus*

Block (Pair)	Site name	Colony or Control	BPs in 2012	BPs in 2013	Area (ha)	Year establ.	Fish 2012	Benthic invert. 2012	*Fucus* invert. 2012	*Fucus* biomass 2012	Algae 2012	Algal biomass 2013	*Fucus* growth 2013	Light intensity 2013
A	Marjakari	Colony	1171	1581	1.93	2003	y	y	y	y	y	y	y	y
A	Matinkari	Control					y	y	y	y	y	y	y	y
B	Puskakarta	Colony	996	780	3.64	2005	y	y	y	y	y	y	y	y
B	Kuuskajaskari	Control					y	y	y	y	y	y	y	y
C	Urpoinen	Colony	686	1160	4.18	2010	y	y	y	y	y	y	y	y
C	Päiväkarit	Control					y	y	y	y	y	y	y	y
D	Kluppi	Colony	81	70	5.18	2003	y	y	y	y	y	y	y	y
D	Korra	Control					y	y	y	y	y	y	y	y
E	Äggskär	Colony	1402	952	2.42	2003	y	y[a]	y	y	y	y[b]	y	y[b]
E	Orhisaari	Control					y		y	y	y	y[b]	y	y[b]
F	Måsgrund	Colony	210	265	0.13	2009	y	y			y			
F	Högholm	Control					y	y			y			
G	Svartbåden	Colony	200	250	0.23	2008						y[b]	y	y[b]
G	Tallholm	Control										y[b]	y	y[b]
H	Kumpelkari	Colony	344	477	1.24	2012						y[b]	y	y[b]
H	Iso-Suini	Control										y[b]	y	y[b]
I	Iso-Mustiletto	Colony	85	189	0.46	2009						y[b]	y	y[b]
I	Säärenkari	Control										y[b]	y	y[b]

[a]Samples from corresponding control site were lost, so site was not used in community or single-species analysis. It was, however, used in the regression analyses
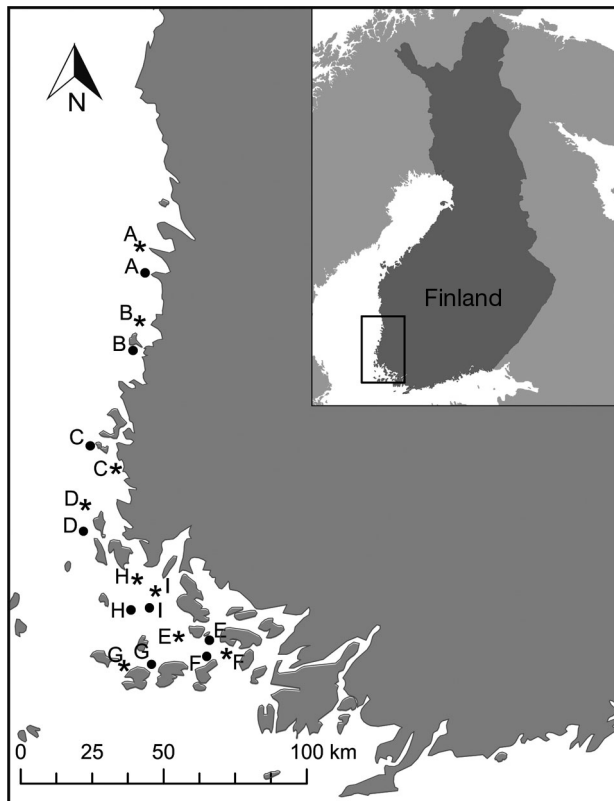[b]Measurements taken at 2 depths: 1 and 2 m

Fig. 1. Sites used for sampling and experiments. Inset: Archipelago Sea and Gulf of Bothnia areas of the Baltic Sea. Control sites (●) and *Phalacrocorax carbo sinensis* colony sites (*) are marked, and letters indicate the block (names and characteristics of the islands corresponding to the letters are listed in Table 1). All sites were located on islands and their positions on the map are approximate; therefore, distances between sites are not necessarily to scale

The distance between islands within pairs ranged from 2 to 10 km, and the distance between pairs was >10 km, with the exception of islands in pairs H and I, which were all within 10 km. The size, age, and number of nests varies widely throughout cormorant colonies in the Baltic Sea (unpubl. data from Finnish Environmental Institute SYKE); therefore, our colony sites represent a range of cormorant influences of different magnitudes (Table 1).

Fish

We used 2 methods to sample fish around 6 pairs of islands in late May 2012. We first used NORDIC survey gill nets, each consisting of twelve 1.5 m high and 2.5 m long panels of different mesh sizes (5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, and 55 mm), set up in 2 sets of 3 nets around the island in 2–4 m of

water (20–30 m from the shore), and left overnight including dusk and dawn (i.e. fishing time was 11–13 h). We counted and identified all fish in the nets, and recorded the mesh size in which they were caught. We measured the length and weight of the first 10 individuals of each species from each mesh size, and then calculated the average length and mass of each fish species for each mesh size.

To more accurately sample fish with a more benthic lifestyle, we also counted fish during SCUBA diving transects on the same nights. The diving was done at night using diving flashlights. Two 50 m long transect lines were marked in early evening at 2–4 m depth; these transect lines were located at least 100 m from the gill nets. After sunset, 2 divers swam alongside the lines, each diver counting and identifying all fish within a 2 m wide transect (i.e. each transect covered approximately 200 m^2). The results of this sampling were analysed separately from the results of the gill net sampling above (see 'Statistical analysis' below).

Invertebrates

For benthic invertebrate species (especially slow-moving or sessile species such as molluscs and barnacles), we placed 8 invertebrate traps at each island in late May 2012 (at the same islands as the fish sampling). The traps were placed at 1–1.5 m depth on rocky substrate within 10 m of the shoreline. A trap consisted of a ceramic tile (15 × 30 cm) with a mesh net (mesh size: 1 mm) rolled up under the tile. In late August 2012, we collected the traps by unrolling the mesh net underwater around the tile and tying the top to avoid losing any individuals, then counted and identified all fauna to species or genus level.

For invertebrates associated with *Fucus*, we used mesh nets (mesh size: 1 mm) to randomly collect 8 adult *Fucus* thalli per island from 1–2 m depth in late August 2012. We rinsed and weighed each *Fucus* thallus, then counted and identified all fauna to species or genus level.

Algal and plant communities

To quantify algal and aquatic plant communities, we established transects perpendicular to the shore of each island in June 2012. These transects were separate from the dive transects used for counting fish, and were located in lightly sloping areas with rocky substrate, avoiding sandy and soft-bottom

areas. We then set up four 1 m² quadrats at 4 depth zones (zone 1: 0.3–0.8 m, zone 2: 1–2 m, zone 3: 2–3 m, zone 4: 3–4 m; at some islands, however, there were no algae present in the deeper depth zones). In each quadrat, we assessed the percent cover of all species (to either species or genus level). If necessary, we first estimated the percent cover of the top layer of filamentous algae and then moved this layer aside to measure the underlying species (i.e. total percent cover in 1 quadrat could be >100%).

Algal biomass

We measured the accumulation of algal biomass in the littoral zone to determine whether colonies affected primary production. We used small, rough ceramic tiles (50 × 50 × 4 mm) as settlement substrate for algae, and attached 3 of these tiles to a brick, so that the brick would act as an anchor, and placed them in the littoral zone in late May 2013. At 8 islands (pairs E, G, H, and I), 3 bricks were placed on the bottom at 1 m and another 3 bricks at 2 m. At the 8 other islands (pairs A, B, C, and D), 3 bricks were placed on the bottom at 2 m depth only. We collected the bricks in mid-August 2013. We washed off sediment from the tiles by rinsing with a pipette, and scraped off all the algae from the top and sides of the tiles, then calculated dry biomass for each tile after 2 d of drying at 60°C.

Fucus vesiculosus growth and herbivory

We measured the growth of *Fucus*, in terms of biomass change, as well as herbivory by isopods, in the same littoral zone of the same islands as the biomass tiles. We used small *Fucus* fragments (approximately length: 6–8 cm; approximate mass: 1 g; 8–12 apical tips) to measure growth and to detect possible herbivory by invertebrates. We placed the *Fucus* fragments into 15 × 6 × 6 cm mesh cages (mesh size: 1 × 1 cm) that allowed herbivores to graze on the algae. To increase the power of the test, we reduced variation in growth by using *Fucus* fragments taken from 3 different *Fucus* individuals, and split each individual into 16 fragments so that each site had 1 fragment from each individual. We placed the cages at 1 m depth in early July 2013 and collected them after 6 wk. We photographed and weighed the fragments before and after the experiment, and counted the number of grazing marks left by the isopod *Idotea balthica* (the main grazer of *Fucus*, which leaves easily identifiable grazing marks) from the photographs.

Light intensity

We measured light in 2013 using temperature/light data loggers (HOBO Pendant©, model UA-002-64) attached with the light sensor facing upwards just above 1 of the 3 bricks used in the biomass experiments (so that all islands had 1 data logger at 2 m depth, and 8 islands also had a data logger at 1 m depth, as with the algal tiles described above). The data loggers were programmed to record light intensity at 30 min intervals over the whole experimental period. We deployed the data loggers along with the bricks in May 2013, and used the daytime (07:00–20:00 h) data from 4 wk in June 2013 in the analysis (as they became fouled by epifauna and epiphytes after this time).

Statistical analysis

Communities

We used the statistical program PRIMER v.6 for all community analyses, using non-metric multidimensional scaling (NMDS) to visualize variation in community structure and PERMANOVA to test for differences between communities in colony and control islands.

For the fish data, we only had 1 replicate per site and thus we used the total amount of fish caught or seen on nightly diving censuses per site in the analyses. Prior to analysis, we applied a square-root transformation to reduce the contribution of highly abundant species. The occurrence of the colony on the island (colony or control) was treated as a fixed factor, while the block (i.e. pair) was treated as a random factor to account for local environmental conditions (e.g. salinity, nutrients, or temperature).

For benthic invertebrates, each tile provided a replicate measurement of the abundance within the site. For *Fucus*-associated invertebrates, each *Fucus* individual provided a replicate, but in this case we standardized the data prior to analysis (i.e. all counts were converted to relative percentages, as per Clarke & Gorley 2006), because the weight of the sampled thalli and thus the substrate volume varied substantially among the *Fucus* individuals (a factor which is highly correlated with invertebrate abundance; Schagerström et al. 2014). Thus, the community analysis of *Fucus*-associated invertebrates focused on species assemblage alone without taking into account absolute densities of species. We used a PERMANOVA design with colony

occurrence as a fixed factor and block as a random factor. Replicates within the site allowed for testing of the interaction between colony occurrence and block.

For algal communities, we used a similar PERM-ANOVA design but added the depth zone as a fixed factor (colony occurrence and depth zone: fixed factors; block and block × colony occurrence: random factors), and then also analysed each depth zone separately.

We also calculated the species richness and biodiversity (Shannon diversity index) for fish, invertebrate, and algal communities at each island. We then used mixed ANOVA (MIXED procedure in SAS 9.3) with colony occurrence as a fixed factor, and block and block × colony occurrence as random factors.

Single species

We used generalized linear mixed models to test differences in the abundance of single species (GLIMMIX procedure in SAS 9.3), with a negative binomial error distribution. In the model, we defined colony occurrence as a fixed factor, and block and block × colony occurrence as random factors to account for the subsampling of tiles or thalli (for fish species, we did not include the block × colony occurrence as there were no subsamples). We only ran this analysis on the most abundant species: (gill net fishing: Baltic herring *Clupea harengus membras*, perch *Perca fluviatilis*, roach *Rutilus rutilus*, ruffe *Gymnocephalus cernua*, and three-spined stickleback *Gasterosteus aculeatus*; diving transects: eelpout *Zoarces viviparous*, ninespine stickleback *Pungitius pungitius*, sand goby *Pomatoschistus minutus*, and three-spine stickleback; benthic and *Fucus*-associated invertebrates: *Gammarus* spp., *Idotea* spp., *Hydrobia* spp., *Mytilus trossulus*, and *Theodoxus fluviatilis*). For the *Fucus*-associated invertebrates, the mass of the thallus was included as a weighting variable since substrate volume influences associated fauna (Schagerström et al. 2014).

We performed a similar analysis for the most abundant algal species (*Ceramium tenuicorne*, *Cladophora glomerata*, *Ectocarpus siliculosus*, *Fucus vesiculosus*, *Pilayella littoralis*, *Ulva* spp.). While plants such as eelgrass *Zostera marina* and aquatic angiosperms (including *Myriophyllum* spp., *Potamageton* spp. and *Ruppia* spp.) are common in the area, they tend to grow over the summer and become

more important in later summer, rather than during our sampling period, and so we did not include separate analyses for plants (although they were included in the community analysis). For the algae, we analysed each depth zone separately, but we did not analyse the depth zone if the species in question was present in <10% of quadrats (as this was likely not the ideal depth for the species). The percent cover values were first converted to proportions and fitted with a quasi-binomial error distribution using the GLIMMIX procedure (SAS Institute Inc. 2008), with colony occurrence as a fixed factor, and block and block × colony occurrence as random factors to account for subsampling (in this case, each quadrat within a site was treated as a subsample).

In the colony sites, we also checked whether the abundance of these species varied with the total number of breeding pairs in the colony, and the colony age. As nutrient enrichment is strongly correlated with cormorant density (Kolb et al. 2010, Gagnon et al. 2013), we also checked whether invertebrate and algae abundances correlated with cormorant density (i.e. the number of breeding pairs divided by the area of the colony island). For these analyses, we used the GLIMMIX procedure with the same error distributions as mentioned above, also including thallus biomass as a weighing variable for the *Fucus*-associated invertebrates).

Fish size analysis

For the fish caught in gill nets, we calculated the mean length for each species and island (as we had measured 10 individuals of each species in each mesh size, for the remaining individuals we assigned a random length drawn from a normal distribution with the mean and standard deviation of the 10 measured fish), and tested for differences using a mixed ANOVA (MIXED procedure; colony occurrence: fixed factor; block and block × colony occurrence: random factors to account for subsampling) for herring, perch, ruffe, roach, and three-spined stickleback.

To detect body-size differences around colonies, we grouped individuals of the most common species with a large size range (herring, perch, ruffe, roach; all three-spined stickleback individuals were ≤10 cm and thus not analysed) into size classes (≤10 cm, 11–12 cm, 13–14 cm, 15–16 cm, 17–18 cm, 19–20 cm, ≥21 cm), and ran the generalized linear mixed models for each size class of each species separately (as detailed above for species-specific analyses of fish abundance).

Algal biomass and growth, and light intensity

We performed a mixed ANOVA on the algal biomass on the tiles, with lognormal error distribution (GLIMMIX procedure; colony occurrence, depth, and their interaction: fixed factors; block, block × colony occurrence, and brick ID: random factors to account for subsampling), with each tile as a subsample. We also used a mixed ANOVA (colony occurrence: fixed factor; block, block × colony occurrence, and *Fucus* individuals: random factors to account for subsampling) to test the effect of cormorant colonies on the growth of *Fucus* fragments.

Using the biomass of adult *Fucus* thalli collected during the invertebrate sampling in 2012, we then analysed whether this differed between colonies and controls. For the analysis of the number of grazing marks, we used a similar model with negative binomial distribution of error variance (as above for single species).

We also used a mixed ANOVA (GLIMMIX procedure) with lognormal error distribution to test for differences in weekly average daylight intensity. We analysed each depth separately with colony occurrence, week (repeated), and their interaction as fixed factors, and block and block × week as random factors. In the colony sites, we conducted a regression of colony characteristics (number of breeding pairs, their density, and colony age) on algal biomass, *Fucus* growth and biomass, and light (analysing each depth separately for the algal biomass and light), and also checked whether algal biomass and growth were correlated with light intensity, but found no significant correlations.

RESULTS

Fish

A total of 23 species were counted in the gill nets (Table S1 in the Supplement at www.int-res.com/articles/suppl/m541p015_supp.pdf). The community structure of fish caught in gill nets differed between colony and control islands (Table S2 in the Supplement; Fig. 2a), and there were significant differences between blocks. Species richness or biodiversity of fish did not differ between colony and control sites (Table S2). When comparing the abundance of individual fish species, there were significantly fewer perch and ruffe near colony islands (Fig. 2b, Table S3 in the Supplement), while the only significant correlation was
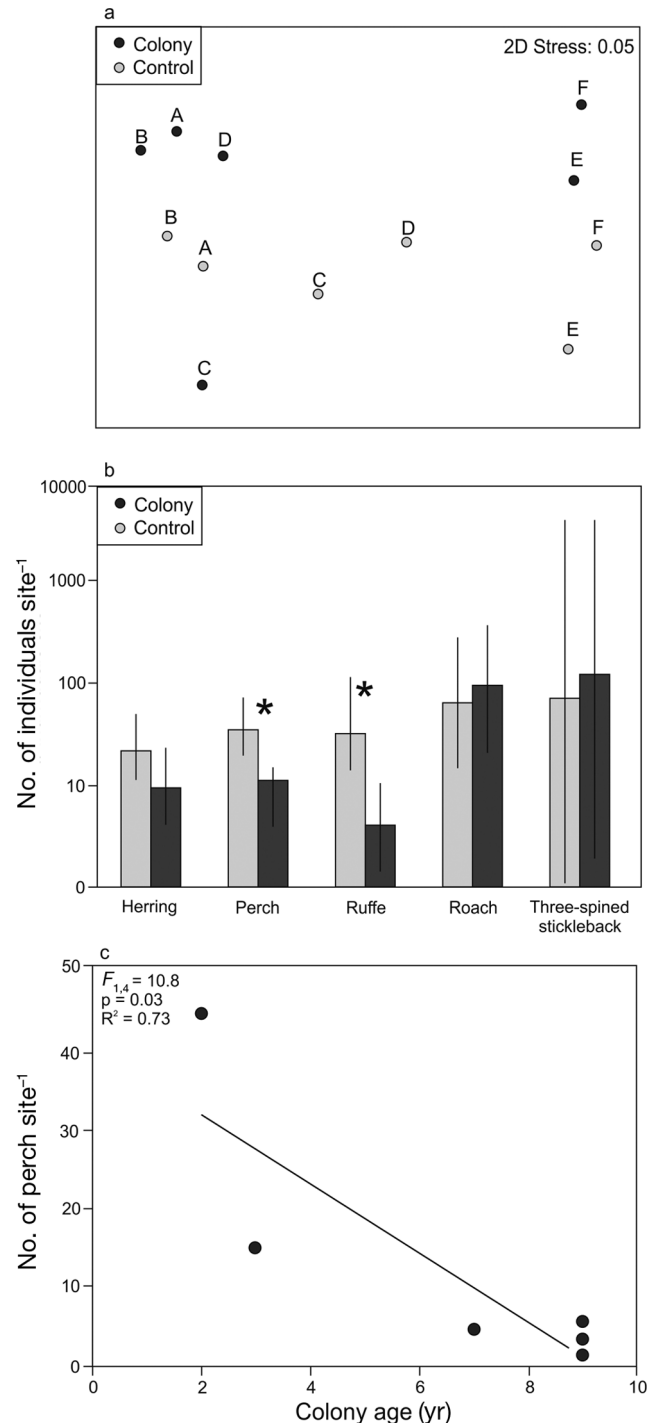

Fig. 2. (a) Non-metric multidimensional scaling (NMDS) plots of fish caught in gill nets. *Phalacrocorax carbo sinensis* colonies and control sites are indicated, while letters indicate the block (see Table 1, Fig. 1). Distance between circles is an indication of similarity in community composition. (b) Abundance (mean ± 95% confidence limits) of fish in colony and control sites. *Significant difference (p < 0.05) as determined from a general linear mixed model. (c) Effect of colony age on perch (*Perca fluviatilis*) abundance. The line represents the slope as determined from general linear mixed models

Table 2. Significant (p < 0.05, in **bold**) and marginally significant (p < 0.10) regression coefficients derived from generalized linear mixed models, between colony characteristics (cormorant density, number of breeding pairs, and colony age) and densities of: fish caught in gill nets, benthic invertebrates, *Fucus*-associated invertebrates, algal species, algal biomass, *Fucus vesiculosus* biomass; and light intensity. Numbers in parentheses after the algal species indicate the depth zone. Degrees of freedom (df) are given as numerator df, denominator df. Variables are presented as dependent variable–independent variable. b: slope

Variables	b	R^2	df	*F*	p
Fish					
Perch – Colony age	−4.48	0.73	1, 5	10.8	**0.03**
Benthic invertebrates					
Gammarus spp. – Colony age	3.97	0.25	1, 34	14.2	**0.0006**
Gammarus spp. – no. of breeding pairs	0.0006	0.14	1, 34	3.06	0.09
Hydrobia spp. – Cormorant density	0.0005	0.20	1, 34	3.09	0.088
Hydrobia spp. – no. of breeding pairs	0.0006	0.14	1, 34	3.62	0.066
Idotea spp. - no. of breeding pairs	0.0025	0.08	1, 34	6.22	**0.017**
Mytilus trossulus – Cormorant density	0.002	0.63	1, 34	8.51	**0.0062**
***Fucus*-associated invertebrates**					
Gammarus spp. – Cormorant density	0.0010	0.01	1, 38	2.89	0.098
Gammarus spp. – no. of breeding pairs	0.0009	0.03	1, 38	11.36	**0.0017**
Gammarus spp. – Colony age	−0.065	0.10	1, 38	3.42	0.072
Idotea spp. – Cormorant density	−0.0037	0.25	1, 38	44.9	**<0.0001**
Idotea spp. – no. of breeding pairs	−0.0013	0.14	1, 38	16.3	**0.0003**
Mytilus trossulus – Cormorant density	0.0021	0.12	1, 38	4.8	**0.035**
Mytilus trossulus – no. of breeding pairs	0.0015	0.10	1, 38	12.6	**0.0011**
Theodoxus fluviatilis – Cormorant density	−0.0028	0.16	1, 38	37.2	**<0.0001**
Theodoxus fluviatilis – no. of breeding pairs	−0.001	0.06	1, 38	17.2	**0.0002**
Algae					
Cladophora glomerata (2) – Cormorant density	0.0003	0.66	1, 20	3.64	0.071
Ectocarpus siliculosus (3) – Cormorant density	0.0005	0.77	1, 18	5.24	**0.034**
Ectocarpus siliculosus (4) – Cormorant density	0.0005	0.73	1, 22	5.27	**0.032**
Pilayella littoralis (2) – Colony age	0.076	0.56	1, 20	4.21	0.053
Pilayella littoralis (3) – Colony age	0.085	0.47	1, 18	3.64	0.072
Algal biomass (1 m depth) – Colony age	0.048	0.25	1, 31	8.24	**0.007**
Algal biomass (2 m depth) – Colony age	0.072	0.19	1, 67	48.71	**<0.0001**
***Fucus vesiculosus* biomass** – no. of breeding pairs	−0.092	0.15	1, 24	6.60	**0.014**
Light intensity (2 m depth) – Cormorant density	−4.7	0.21	1, 30	6.94	0.074

that perch abundance decreased colony age (Table 2, Fig. 2c).

Most fish of the common species caught in the gill nets were <20 cm in size (mean ± SD: herring: 15.8 ± 0.2 cm; perch: 14.6 ± 0.2 cm; ruffe: 12.5 ± 0.1 cm; roach: 13.1 ± 0.1 cm; three-spined stickleback: 6.3 ± 0.01 cm). While there were no significant differences in the mean body-size of any species between control and colony islands, the abundance of perch and ruffe was significantly or marginally significantly lower around the colony islands than around control islands over most body-size classes (perch: 11–12, 15–16, 17–18, and ≥21 cm; ruffe: ≤10, 13–14, 15–16, 17–18; Fig. 3, Table S4 in the Supplement).

Fourteen species of fish were counted during the night diving transects (Table S1) and there were no differences in community composition between colony and control islands, though there was a significant block effect (Table S2). There were also no differences in species richness, biodiversity, or abundance of any species between colony and control islands (Tables S2 & S3).

Invertebrates

We found 29 and 27 taxa of benthic and *Fucus*-associated invertebrates, respectively (Table S1), and in both cases the main effect of colony occurrence on community structure was not significant, though the block effect and block × colony occurrence interaction were significant for both (Table S2), indicating that colony effects varied spatially. There were also no significant differences in the species richness or diversity of benthic invertebrates, while for *Fucus*-associated invertebrates, species richness was significantly lower near colony islands (mean ± SE for colonies: 8.3 ± 0.8; controls: 10.8 ± 0.8), but diversity did not differ (Table S2). Most species were rare, with only 1–2 individuals, and the invertebrate communities were dominated by few species, which may have masked any community-level effects. Near colonies, the abundance of benthic *Idotea* spp. (Table 2, Fig. 4a) increased with the number of breeding pairs, while *Mytilus*
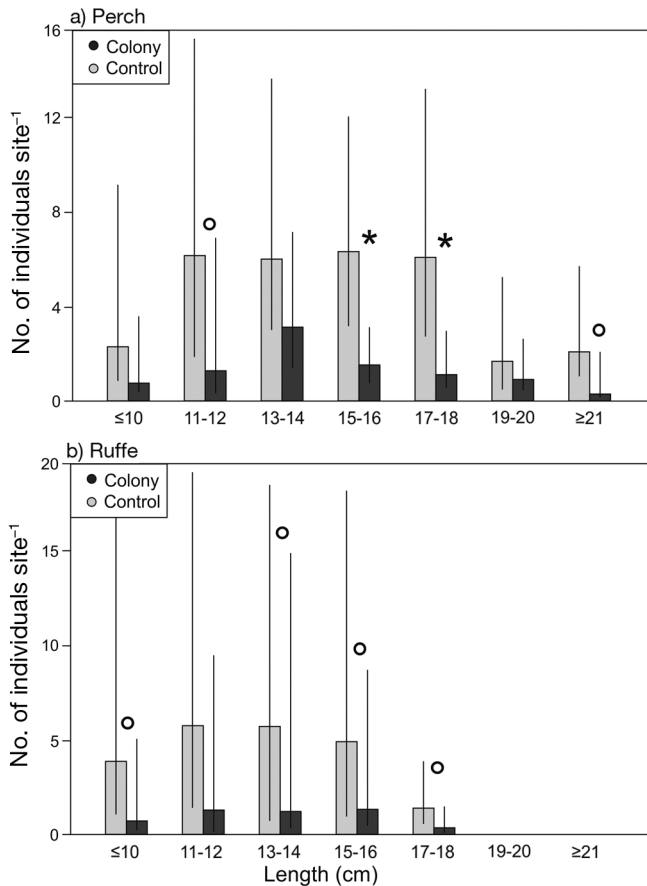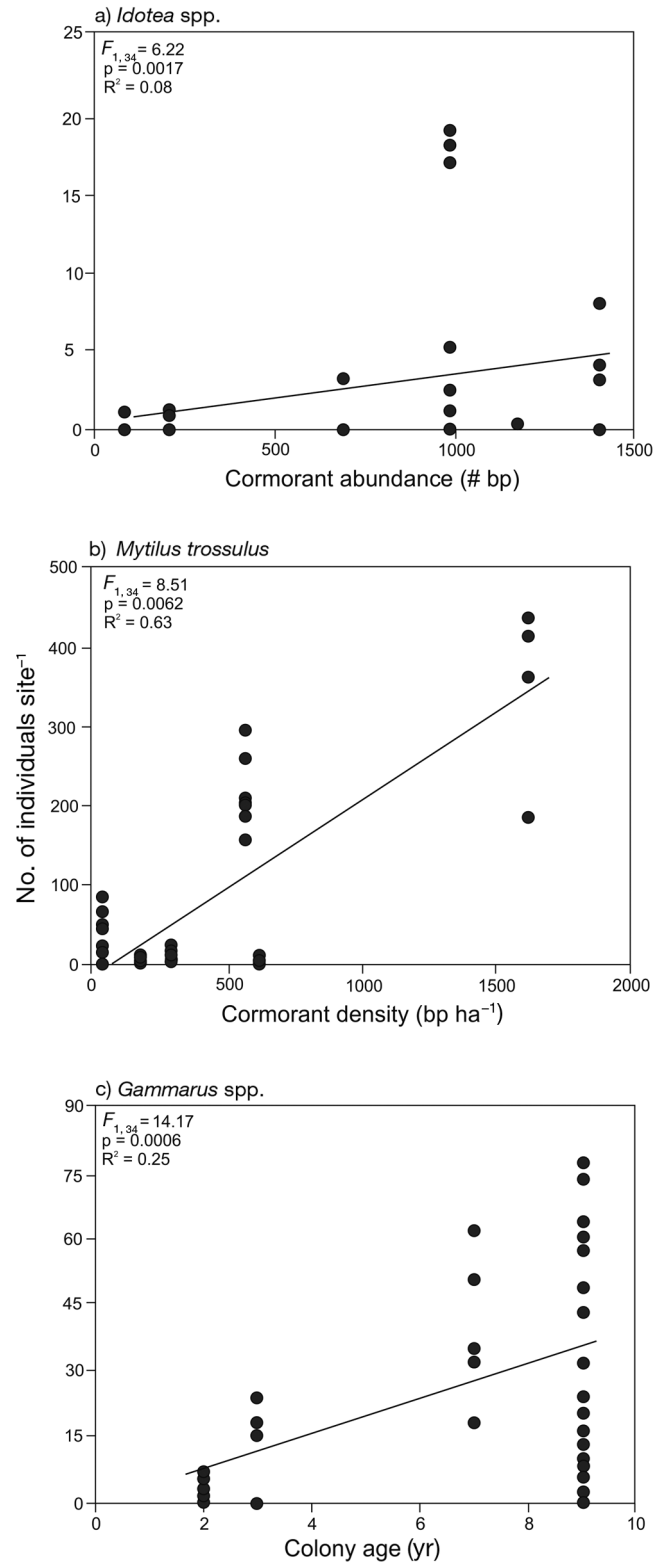
Fig. 3. Abundance (mean ± 95% confidence limits) of (a) perch *Perca fluviatilis* and (b) ruffe *Gymnocephalus cernua* of different size classes in *Phalacrocorax carbo sinensis* colony and control sites. *Significant difference (p < 0.05), and an open circle indicates a marginally significant difference (p < 0.10), as determined from a general linear mixed model

trossulus increased with cormorant density (Table 2, Fig. 4b), and *Gammarus* spp. increased with colony age (Table 2, Fig. 4c). In addition, there were also trends towards *Gammarus* spp. increasing with the number of breeding pairs and *Hydrobia* spp. increasing with cormorant abundance and density (Table 2, Table S5 in the Supplement).

For *Fucus*-associated invertebrates, the abundance of *Idotea* spp. and *Theodoxus fluviatilis* decreased with cormorant density (Fig. 5a,b) and the number of breeding pairs (Tables 2 & S5), while *M. trossulus* and *Gammarus* spp. showed the opposite pattern as they increased with cormorant density and the number of breeding pairs (though this pattern seemed to be driven mostly by 1 site in the case of *M. trossulus*; Table 2, Fig. 5c). *Gammarus* spp. also tended to decrease with colony age (Tables 2 & S5).

Fig. 4. Effect of (a) cormorant (*Phalacrocorax carbo sinensis*) abundance (number of breeding pairs, bp), (b) cormorant density, and (c) colony age, on the abundance of benthic invertebrates. Lines represent slopes derived from general linear mixed models
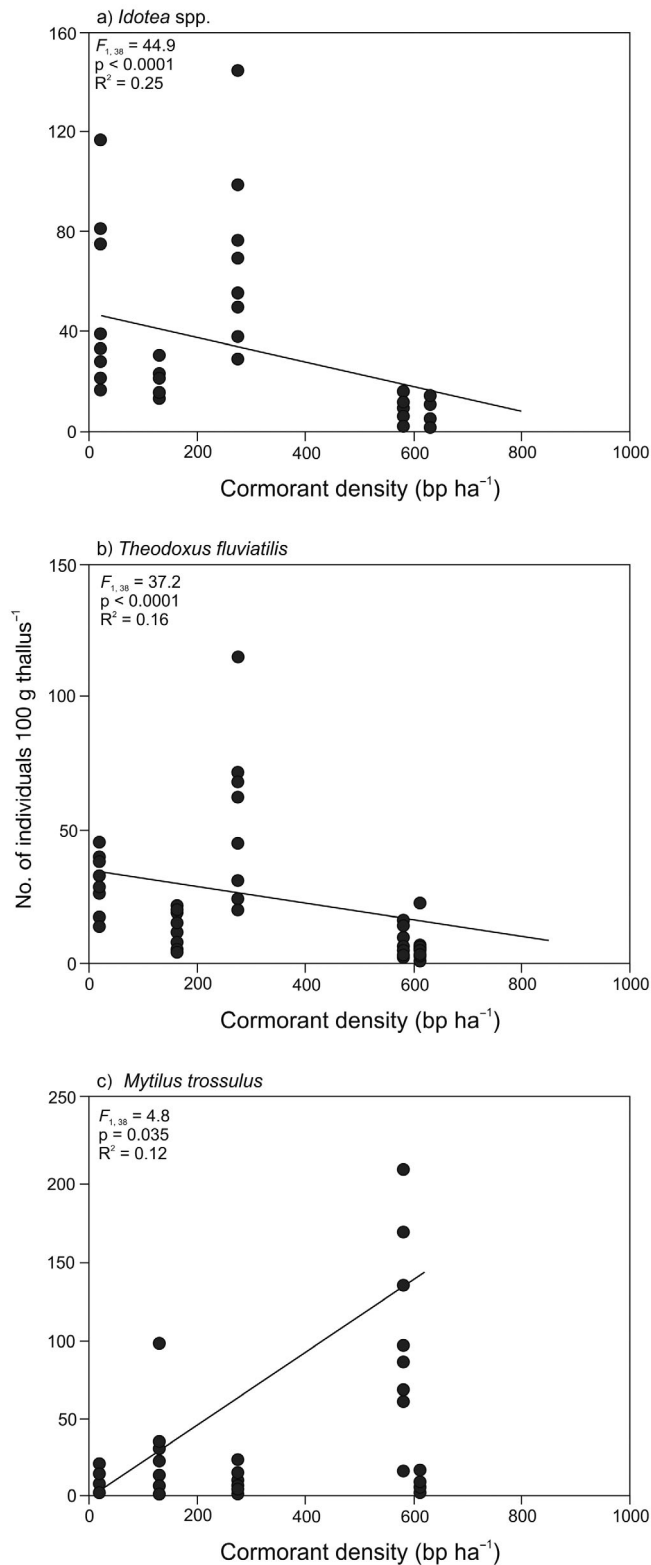
Fig. 5. Effect of cormorant (*Phalacrocorax carbo sinensis*) density on abundance of *Fucus*-associated invertebrates: (a) *Idotea* spp., (b) *Theodoxus fluviatilis*, (c) *Mytilus trossulus*. Lines represent slopes derived from general linear mixed models. bp = breeding pairs

Algal and plant communities

The vegetation communities were composed of 26 different species, including 6 plant species (Table S1); there was no effect of colony occurrence on the community composition, but the block and block × colony occurrence interaction were significant, and there was a significant effect of depth zone (Table S6 in the Supplement). When analysing each depth zone separately, we still found no overall differences in community structure between colony and control islands, though the block and block × colony occurrence interaction effects were significant in all cases. There was no difference in species richness between colonies and controls, although it did vary among depth zones, and the block × colony occurrence interaction was also significant (Table S6). Species richness was highest in depth zone 2 (mean ± SE: 6.2 ± 0.5), followed by depth zone 3 (5.7 ± 0.6), depth zone 1 (4.7 ± 0.5), and lowest in depth zone 4 (4.1 ± 0.6). Diversity varied by depth zone and was marginally higher in colonies than controls (Table S6). Diversity was highest in depth zones 2 and 3 (mean ± SE: 1.05 ± 0.10 and 1.11 ± 0.11, respectively), and lowest in depth zones 1 and 4 (0.75 ± 0.09 and 0.77 ± 0.13, respectively).

When focusing on coverage of the 6 most abundant individual algal species, we found that the block × colony occurrence interaction was significant for most species (Table S7 in the Supplement), indicating that colony effects varied between blocks. The only exception was that in the shallowest zone, *Ulva* spp. coverage was marginally higher in colonies than controls. Algal cover increased with cormorant density or tended to do so for *Cladophora glomerata* in zone 2 and *Ectocarpus siliculosus* in zones 3 and 4 (Fig. 6), while *Pilayella littoralis* cover tended to increase with colony age in zones 2 and 3 (Tables 2 & S5).

Algal biomass

Biomass accumulation did not differ between colonies and controls, though it was higher at 1 m than at 2 m (Fig. 7, Table S8 in the Supplement), but increased significantly with colony age at both depths (Tables 2 & S5).

Fucus vesiculosus growth and herbivory

Fucus fragments grew almost 30 % more near the colonies than near the control islands (Fig. 8a). How-
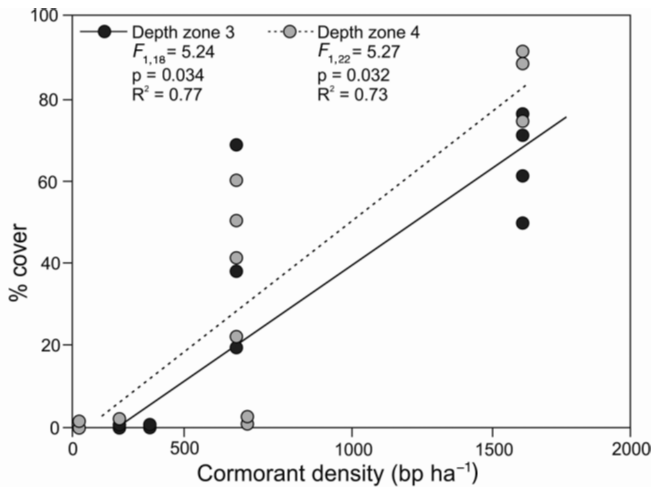
Fig. 6. Effect of cormorant (*Phalacrocorax carbo sinensis*) density on percent cover of *Ectocarpus siliculosus* at depth zones 3 and 4 (see 'Materials and methods' for details). Lines represent slopes determined by general linear mixed models. bp = breeding pairs
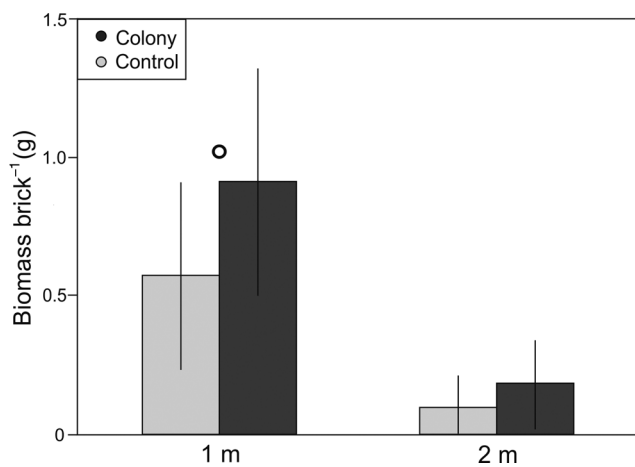

Fig. 7. Biomass accumulation (mean ± 95% confidence limits) of algae on settlement tiles (1 brick = 3 settlement tiles) around colony islands at depths of 1 m and 2 m. The open circle represents a marginally significant difference (p < 0.1; mixed ANOVA)

ever, the *Fucus* thalli collected while sampling invertebrates did not differ in size between colony and control islands (although the block × colony occurrence interaction was significant; Table S7), and thallus size decreased with cormorant abundance (Table 2, Fig. 8b). Herbivory on *Fucus* was very rare, as most algae had either no (42%) or only one (27%) isopod grazing mark, and there was no effect of colony occurrence or block on the number of grazing marks (Table S8).

Light intensity

At 1 m depth, there was a significant interaction of colony occurrence and week, with no differences between colonies and controls during the first 2 wk of June but decreased light intensity in colony sites during the last 2 wk (Table S8). Meanwhile, at 2 m depth, there was only a significant difference between weeks, as light intensity decreased over time in both colonies and controls (Table S7). Within colonies, light intensity at 2 m depth also tended to decrease with colony density (Table 2), but did not otherwise vary with colony characteristics (Table S5).
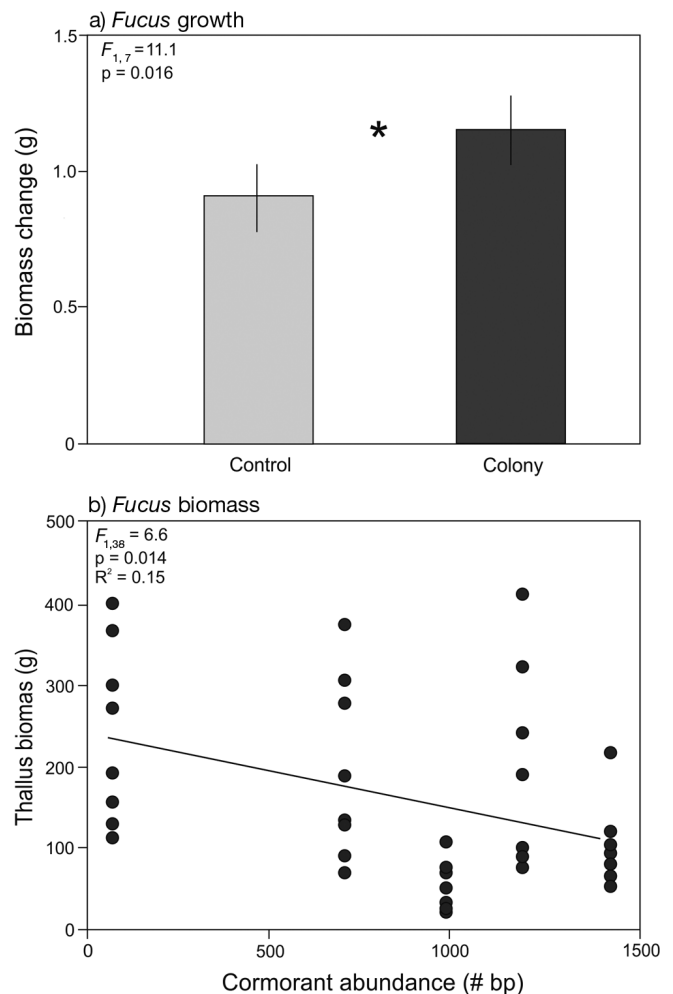

Fig. 8. (a) Growth (mean ± 95% CI) of *Fucus vesiculosus* fragments in colony and control sites. *Significant (p < 0.05) difference (result from mixed ANOVA). (b) Effect of cormorant abundance on biomass of adult *Fucus* thalli from colony sites, with the line representing the slope derived from a general linear mixed model. bp = breeding pairs

DISCUSSION

Our results show that cormorants can indeed affect coastal communities at multiple trophic levels, although the strength of these impacts is modulated by colony characteristics and local environmental conditions. Top-down cormorant effects seem to be species-specific rather than shifting community structure and species assemblages as a whole, suggesting that the trophic levels are abstractions rather than coherent hierarchical structures. In particular, direct effects of cormorant predation were limited to a small subset of fish species (perch and ruffe). However, these 2 species play an important role as meso-predators in this system, preying on a number of invertebrate species — especially those individuals in the size classes caught (e.g. the diet of littoral perch of size 10–20 cm consists of ~50 % macroinverte-brates; Mustamäki et al. 2014).

On the other hand, producers were directly affected by bottom-up cormorant effects in the form of nutrient enrichment from guano runoff, leading to higher biomass and density of filamentous algae near large, well-established colonies where nutrient en-richment is highest (Kolb et al. 2010, Gagnon et al. 2013). In these colonies, there was also some evi-dence of increased herbivore density, therefore suggesting that top-down processes may play a role. However, community structure at all trophic levels also showed high regional variability, likely due to large-scale environmental patterns (e.g. north-south gradients in salinity and temperature) and local conditions (e.g. substrate availability, turbidity, expo-sure, anthropogenic impacts, etc.). The impacts of colonies on most species thus varied locally, and that variation was often correlated with the magnitude of the cormorant effects, i.e. the number of breeding pairs, nest density, or colony age.

Top-down effects on fish and invertebrates

Previous studies have shown that roach, stickle-back, and herring can also make up a substantial part of cormorant diets (Engström 2001, Lehikoinen et al. 2011, Boström et al. 2012). We had therefore expected to find shifts due to cormorant predation in these species in addition to perch and ruffe. The reason for not finding such effects may be related to the high abundance and increasing population sizes of roach and sticklebacks in the Baltic Sea (Ådjers et al. 2006, Ljunggren et al. 2010). Cormorant predation effects would be very difficult to detect as they may

have a minimal effect on an immensely abundant prey. In addition, sticklebacks have a broad diet, including zooplankton and benthic invertebrates, and thus they may find more zooplankton food near colonies where nutrient enrichment from guano (Gagnon et al. 2013) could sustain higher production, thus mitigating any cormorant predation impacts. In addition, fishing in shallow littoral waters may also give a distorted picture of species with pelagic lifestyles, such as herring; therefore, these results may not represent actual herring abundances. In addition, we assumed the colony and control islands originally had similar fish species composition, which may not be true: it is not known if and how cormorants choose islands for colonies and it is thus possible that fish communities differed prior to colonization and the colony sites were actually chosen by cormorants due to their fish availability. However, if there is site choice by cormorants, they would likely choose islands with higher prey abun-dance, and thus we may actually be underestimating the impacts of cormorants on fish abundance.

On a more general note, fish communities were only sampled once — there can be variation in fish communities and abundance over time within a site, due to fluctuating environmental conditions such as weather, waves, turbidity, and water temperature. In addition, fish could potentially move away from cormorant colonies during the day and back at night when our sampling took place, while benthic species may have been missed due to the high algal cover at many sites. Therefore, a single sampling event hardly gives a complete picture of fish communities around islands. Cormorant fishing ranges in the Baltic Sea are unknown, but the highest predation pressure on fish may not actually be in the immediate vicinity of the colony (e.g. if waters around the colony are very turbid, visual predation may be difficult). It is known from other systems that cormorants can fly several tens of kilometres to reach richer fishing areas (e.g. Platteeuw & Van Eerden 1995, Paillisson et al. 2004), and therefore the top-down effects of cormorants may be diffuse across a regional scale, and not particularly confined to the immediate area around a colony.

Possibly due to this diffuse top-down effect, top-down impacts on invertebrates were difficult to detect, and when present, correlated with individual colony characteristics, as indicated by a significant block × colony occurrence effect. The mobile species (isopods and amphipods) are typical prey of many littoral fish species, including perch and roach (Segerstråle 1944, Salemaa 1978, Reiss et al. 2014),

and we thus expected to find higher abundances around colony sites due to lower fish predation. However, we found no overall difference in the mobile species' abundance between colony and control sites, though several increased with cormorant abundance, or colony age. On the other hand, the abundance of molluscs increased with colony density, indicating that bottom-up effects might be affecting invertebrate populations (possibly due to consuming nutrient-enriched algae; Gagnon et al. 2013).

Contrary to the above hypothesis, we found that the densities of *Fucus*-associated *Idotea* spp. and *Theodoxus fluviatilis* actually decreased with the increasing number and density of cormorants; however, the R^2 values of these correlations were very low, indicating that other factors also play a role. This may be due to altered dietary preferences (as these species consume more periphyton than *Fucus* near colony islands; Kolb et al. 2010, Gagnon et al. 2013), or decreased habitat availability causing an increase in invertebrate density per thallus (due to smaller *Fucus* size near the same colonies, which is likely also responsible for decreased invertebrate species richness near colonies). It is also possible that decreased fish abundance could cause behavioural changes, with these invertebrates spending less time hiding within the *Fucus* canopy (as evidenced by the increase of benthic and decrease of *Fucus*-associated *Idotea* with increasing cormorant abundance).

Algal responses to trophic cascades and nutrient enrichment

At the lowest trophic level, primary production (as measured either in terms of algal biomass accumulation or growth rate of *Fucus*) increased with colony age and/or density. In addition, several filamentous algal species showed positive correlations with cormorant density or colony age, likely due to increased nutrient enrichment around colonies. For example, the green ephemeral alga *Ulva* spp., which thrives in high-nutrient environments (Kamer et al. 2004, Kennison et al. 2011), was among those more abundant in colony sites. However, while the growth rate of *Fucus* fragments was higher in cormorant colonies, the biomass of adult *Fucus* thalli decreased with cormorant abundance and density, indicating that strong enrichment effects actually hinder *Fucus* and favour filamentous algae. Nutrient enrichment is likely be more beneficial to filamentous algae than to *Fucus*, as the former tend to respond more quickly to

nutrient enrichment, due to their higher growth rate and nutrient intake ability (Wallentinus 1984, Kennison et al. 2011). This could lead to future decreases in *Fucus* recruitment due to increased competition (Berger et al. 2003, Steen & Rueness 2004, Korpinen & Jormalainen 2008), as indicated by the higher biomass accumulation of filamentous algae in older colonies. Furthermore, while there was no overall difference in light intensity, the tendency towards decreased light around dense colonies, as well as the decreased light in colonies over time (likely due to higher levels of fouling by ephemeral algae on the light sensors) could further hinder *Fucus* growth. As we sampled algae in early summer (before the peak of guano runoff from the colonies; Gagnon et al. 2013), we would also expect differences in both nutrient enrichment and light intensity between colony and control islands to become more pronounced over the summer.

Increased grazing due to the trophic cascade, if it occurs, does not seem strong enough to completely counter this nutrient enrichment effect, despite predictions to the contrary (Eriksson et al. 2012), likely because cormorants do not completely eliminate predation on herbivores by fish (due to more diffuse top-down impacts as suggested above). In addition, remaining fish may compensate by consuming more due to decreased competition. While we might have expected high grazing due to increased palatability of enriched algae even without a trophic cascade (e.g. Hemmi & Jormalainen 2002), this also did not occur, possibly due to high nutrient levels along the coast in all sites and the relatively low isopod densities during the summer (as they typically peak in very late summer or early autumn; Salemaa 1987). Therefore, temporal variation in grazing pressure likely makes it more difficult to detect trophic cascades. Finally, environmental factors other than cormorants, such as salinity, turbidity, and exposure (Eriksson & Bergström 2005, Rinne et al. 2011), may be more important determinants of algal communities in some areas.

CONCLUSIONS

Overall, cormorants can affect benthic communities in 2 distinct ways. First, predation can decrease the abundance of some fish species, which frees, to some degree, certain mesograzer species from fish predation, especially when cormorant pressure is high and long-lasting. However, this top-down effect is difficult to detect, and likely occurs over a larger

geographical area rather than only within close vicinity of the colony. Secondly, nutrient enrichment from guano runoff affects algal growth, favouring filamentous algae, though the strength of this effect is also determined by the density and age of the colony. Contrary to the trophic cascade, this effect is locally concentrated in the immediate vicinity of the colony and thus has stronger effects on lower trophic levels around cormorant colonies. Cormorants have only been present in the Baltic Sea for <20 yr, and the colonies we studied were at most 10 yr old. Over time, cormorant impacts are likely to become more extensive, possibly resulting in locally eutrophicated ecosystems dominated by fast-growing filamentous algae, which could result in lower associated biodiversity and altered trophic functioning (Thiel & Watling 1998, Bolam et al. 2000, Green et al. 2014), though increased herbivory arising from the trophic cascade could counteract this to some extent (Korpinen et al. 2007, Eriksson et al. 2012).

There has been an increasing interest in the ubiquity of trophic cascading effects in many ecosystems, where a high trophic level can have important repercussions for the producer trophic level (Pace et al. 1999, Estes et al. 2011, Ripple et al. 2014, Sergio et al. 2014). However, the consequences are often far from straightforward to predict, even in relatively simple, species-poor systems such as the Baltic Sea, and seem to depend on local environmental conditions and the strength of the impacts. Here, we showed that concurrent top-down and bottom-up effects from cormorants could have multiple impacts, leading to shifts in the species composition of littoral communities, although the scale of their importance may vary. Our study demonstrates the importance of considering both top-down and bottom-up effects simultaneously, and, in particular, recognizing the species specificity of altered regulation pathways.

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