

Effects of exotic fish farms on bird communities in lake and marine ecosystems

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Abstract Salmon farming is a widespread activity around the world, also known to promote diverse environmental effects on aquatic ecosystems. However, information regarding the impact of salmon farming on bird assemblages is notably scarce. We hypothesize that salmon farming, by providing food subsidies and physical structures to birds, will change their local community structure. To test this hypothesis, we conducted a seasonal monitoring of bird richness, abundance, and composition at paired salmon pen and control plots in two

marine and two lake sites in southern Chile, from fall 2002 to summer 2004. Overall, salmon farming had no significant effects on species richness, but bird abundance was significantly and noticeably higher in salmon pens than in controls. Such aggregation was mainly accounted for by the trophic guilds of omnivores, diving piscivores, carrion eaters, and perching piscivores, but not by invertebrate feeders, herbivores, and surface feeders. Species composition was also significantly and persistently different between salmon pens and controls within each lake or marine locality. The patterns described above remained consistent across environment types and seasons indicating that salmon farming is changing the community structure of birds in both lake and marine habitats by promoting functional and aggregation responses, particularly by favoring species with broader niches. Such local patterns may thus anticipate potential threats from the ongoing expansion of the salmon industry to neighboring areas in Chile, resulting in regional changes of bird communities, toward a less diverse one and dominated by opportunistic, common, and generalist species such as gulls, vultures, and cormorants.

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Introduction

Fish aquaculture, and particularly salmon farming, is an increasing worldwide economic activity, with documented environmental impacts (Buschmann et al. 2006; Wu 1995). Coastal and freshwater eutrophication derived from salmon farming has an outstanding impact on biodiversity and ecosystem services (Worm et al. 2006; Lotze et al. 2006; Carroll et al. 2003). Additionally, salmon farms may exert indirect effects at the community level because they constitute an attraction source for opportunistic species (Rosenberg 2001; Dempster et al. 2009) due to increased resource availability.

Birds prey on farmed fish, and also use aquaculture infrastructure as perching and nesting sites (Andelt et al. 1997). Consequently, avian effects on farm and game fisheries have been amply documented (e.g., Harris et al. 2008), and many lethal and non-lethal techniques have been developed to control such birds and reduce economic losses that they cause (e.g., Sullivan et al. 2006). However, very little attention has been given to the potential effects of fish farms on avian communities (e.g., Glahn et al. 2000; Glahn et al. 2002; Buschmann et al. 2006), particularly in countries like Chile where salmon (*Salmo salar* and *Oncorhynchus kisutch*) and trout (*Oncorhynchus mykiss*) farming have had an unprecedented growth over the past two decades (Camus and Jaksic 2009).

Despite the large scale of this industry, nonetheless, the effects of salmon farming on the biota remain largely understudied (Buschmann et al. 2006). The high biomass concentrations of these culture systems are known to reduce benthic community diversity underneath salmon pens (Rosenberg 2001), and promote disease and parasite outbreaks in fish (Boxaspen 2006; Costello 2006; Molinet et al. 2011). However, their impacts on local bird species are virtually unknown. In that sense, aiming to fill this knowledge gap we assessed the effects of salmon farming on bird assemblages of the Los Lagos District of southern Chile, in the face of an ongoing, massive expansion of this industry southwards of this area where salmon farms are widely distributed in lakes and marine shores, and are also located in habitats of high avian diversity (Gonzalez-Gajardo et al. 2009). We hypothesized that salmon farming produces a widespread local alteration of the structure of avian assemblages in both lake and marine environments. Specifically, we predicted that the distribution of birds within localities should exhibit a high between-site variation caused by a concentration of individuals and species in salmon farming sites, which should in turn lead to compositional differences between sites with presence or absence of salmon farming.

Materials and methods

Study environments and their bird assemblages

The study was conducted in four localities including two marine areas and two lakes of the Los Lagos District in southern Chile (Fig. 1). The localities of the same habitat type were selected due to their similarities in habitat structure to minimize potential differences related with factors other than the presence-absence of salmon farms (see Appendix S1, available online at Supplementary Material).

Typical resident birds in the study localities are *Larus* spp., *Phalacrocorax* spp., *Podiceps major*, and *Pelecanus thagus* in marine shores, and *Podiceps rolland*, *Podiceps occipitalis*, *P. major* and *Fulica armillata* in lakes. Most of these species

show peaks in abundance during the summer (Garay et al. 1991; Cursach et al. 2010). Also, there are some migratory species (e.g., *Tachyeres pteneres*) that spend the summer at this latitude and migrate northwards in winter. Additionally, some ecologically important species, such as *Larus dominicanus*, *Milvago chimango*, and *Nycticorax nycticorax*, are habitat generalists occurring at both marine and lake environments. In trophic terms, however, as a group, the piscivores (mainly *Phalacrocorax* spp., *Podiceps* spp.) are the most common bird species in both ecosystems in southern Chile, accounting for about 70 % of the total abundance of birds (Cursach et al. 2011).

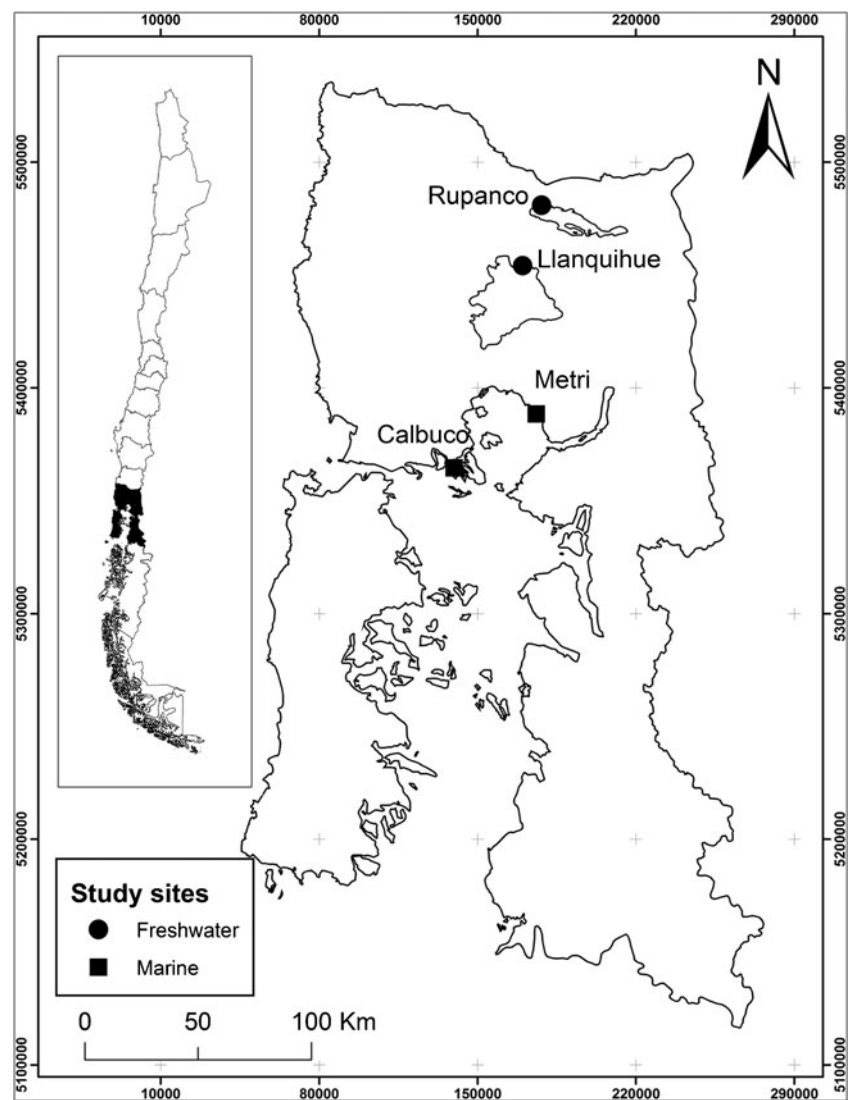
According to their feeding habits and ecological functions, we classified birds into the following trophic guilds (nomenclature after Jaramillo (2003)): (1) omnivores (gulls, chimangos, and caracaras), (2) carrion eaters (vultures), (3) diving piscivores (cormorants, pelicans, boobies, and grebes), (4) surface feeders (terns, skimmers, and kingfishers), (5) perching piscivores (herons and egrets), (6) shorebirds or marine invertebrate feeders (whimbrels, oystercatchers, sandpipers, plovers, and dotterels), (7) terrestrial invertebrate feeders (lapwings, ibises, cinclodes, and negritos), (8) aerial invertebrate feeders (swallows), and (9) herbivores (coots and dabbling ducks). All of these guilds were represented in both lake and marine environments, excepting the exclusively marine guild of invertebrate feeders.

Sampling locations, bird survey, and study variables

In each lake and marine locality, birds were monitored in each of two sites for comparison, one having a salmon farm and the other lacking it ("control"). Paired sites were located ≥ 1 km away. The study localities and sites were: (1) Metri Bay: a salmon farm operated by the Experimental Aquaculture and Marine Sciences Center of Universidad de Los Lagos (41°35'45"S, 72°42'07"W), and its control site 1.0 km away (41°35'59"S, 72°41'49"W); (2) Calbuco Bay: a salmon farm owned by Marine Harvest (41°47'46"S, 73°08'59"W), and its control site 1.1 km away (41°48'19"S, 73°09'10"W); (3) Rupanco Lake: the Experimental Aquaculture and Limnology Center of Universidad de Los Lagos (40°45'55"S, 72°37'37"W), and its control site 1.3 km away (40°45'47"S, 72°36'45"W); and (4) Llanquihue Lake: a salmon farm owned by Multiexport (41°00'10"S, 72°44'21"W), and its control site 1.6 km away (41°00'25"S, 72°43'14"W). Logistic constraints prevented the use of more localities. In addition, our sampling faced two constraints to be dealt with in statistical analyses: first, some salmon farms did not grant us access to their facilities, limiting our site selection to only one salmon farm per locality, and second, the saturation of the Los Lagos District with farming activities forced us to choose control sites within the same lakes and bays.

Between fall 2002 and summer 2003–2004, birds were monitored during each austral season to include seasonal and

Fig. 1 Location of the study localities in southern Chile



migratory species (Gonzalez-Gajardo et al. 2009; Garay et al. 1991). In each farming and control site, birds were monitored at one sampling plot of 200×200 m (with the shoreline as one of its sides) and 50 m of aerial space, using 10×25 binoculars and a 10×36 spotting scope, from visual vantage points located on the shore (100–150 m; distances were measured with a laser rangefinder). Plots at farming sites, which included floating salmon pens, are hereafter referred to as farming plots. In each season, birds were monitored hourly at each plot from dawn to dusk on two consecutive days, yielding a total monitoring effort of 128 days (2 days×two plots×four localities×eight seasons). Each bird that entered, exited, or remained within a monitoring plot was recorded to the species level and classified into one trophic guild. Given that the seasonal variation in day length was related to the duration of the monitoring periods, we based our analyses on the largest daily range available for all of the sampling days of 11 h per day (from 0700 to 1800 hours), which in turn maximized the number of samplings (98 % of the

samples were retained for further analyses) effectively recording the maximum activity level of birds each day.

To avoid biases derived from recording the same individuals more than once in the same plot and day, we used our day-long records for obtaining single, indirect estimates of our response variables for each plot, considering the following two variables: (a) maximum activity level of birds, defined as the highest modal value of the number of individuals of each species per hour; (b) species richness, defined as the total number of distinct species recorded per day, standardizing day length as described in the previous paragraph. As the two sampling days per season represent temporal pseudoreplicates, both activity level and species richness were expressed as the average of their corresponding two daily values.

For evaluating the variation in taxonomic composition of bird species, we analyzed the 64 available combinations of data (two plots×four sites×eight seasons) by generating a species-per-plot matrix, including the average number of individuals per species for each farming and control plot in

lake and marine environments. On a more general level, we complemented the above information by considering the number of individuals per trophic guild, averaged through all seasons for each farming and control plot. In this latter case, lake and marine environments were analyzed independently because the invertebrate feeder guild was composed exclusively by marine species.

Data analysis

The maximum activity level and species richness of birds were both analyzed by means of a balanced ANOVA design (GLM approach, using type II SS and an overparameterized model), including: treatment (control vs. farming plots) as the focal factor, environment (lake vs. marine) as a secondary factor nested within treatment, and quarterly samplings as a repeated measure ($n=8$). For simplicity, we hereafter refer to the presence–absence of salmon farming as “treatment,” noting that salmon farms cannot be randomized or manipulated within a locality. While lake and marine units do not represent a random selection from a larger set of conditions, environment type is not a factor of primary interest and we lack a clear basis to state some explicit hypothesis about its effects. Thus, we treated environments as subgroups that could potentially account for some unspecified variation. Similarly, the potential relevance of seasonality cannot be clearly inferred from the current information, and therefore, we defined seasonal samplings as a repeated measure to assess the consistency of treatment effects throughout the study. Normality and homoscedasticity were assessed with Kolmogorov–Smirnov and Levene tests, respectively, and sphericity with the Mauchly test. The analysis of species richness did not meet the sphericity assumption; therefore, we applied the Greenhouse–Geisser and Huynh–Feldt corrections. ANOVAs were conducted using Statistica 7.0 (StatSoft 2004).

The compositional variation of bird species was examined by using a non-metric multidimensional scaling (nMDS) ordination (Fasham 1977; Legendre and Gallagher 2001), based on a Bray–Curtis dissimilarity matrix; this multivariate procedure has been extensively used in avifauna studies (Jansen and Robertson 2001; Naidoo 2004; Radovic and Tepic 2009). Then, we applied a nested analysis of similarity (ANOSIM) for assessing differences between localities and treatments (nested within locality) applying global and pairwise permutation tests (corrected for multiple comparisons when required), and finally a sample discrimination analysis (SIMPER) for assessing the contribution of particular species. These analyses were conducted using PRIMER 6.0 (Clarke 1993; Clarke and Gorley 2006). Complementarily, the number of birds per trophic guild was analyzed separately for lake and marine environments (due to their different number of guilds) using two-way ANOVAs with guild and treatment as factors, with

localities serving as replicates, and log-transformed data for achieving homoscedasticity.

Results

We recorded a total of 42 bird species (Supplementary Table S1, available online) belonging to nine orders: Charadriiformes (14 species), Pelecaniformes (6), Passeriformes (6), Ciconiiformes (5), Falconiformes (4), Podicipediformes (3), Anseriformes (2), Coraciiformes (1), and Gruiformes (1). Of these 42 species, 38 (91 %) and 28 (67 %) were found in marine bays and lakes, respectively, and 16 (38 %) occurred in both environments and in all seasons each year. Likewise, 26 (68 %) and 21 (75 %) species of marine and lake assemblages, respectively, were presumably residents as they occurred through all the study period. The remaining species were either absent or not detected in at least one season each year, suggesting that some fraction of them would be migrants.

Bird activity level (abundance)

The maximum activity level of birds was significantly different between salmon farming and control plots, and this effect showed a significant interaction with the repeated measure, involving also a significant contribution of the environment type (Table 1a). The variation of activity through time (Fig. 2a) evidenced a consistently higher number of birds in farming plots, including a strong peak in spring 2002 with a significantly greater (nearly twice) value than in the remaining seasons (Tukey, $P<0.0002$ in all cases). In contrast, the activity level in controls was nearly half that of farming plots in most seasons, excepting winter 2002 when it showed a small increase that was not significantly greater than the values in other seasons, or than those recorded in farming plots. Excluding the above peaks, the number of birds in the rest of the study period exhibited a small temporal variation and followed a similar trend in both farming and control plots. Additionally, birds always occurred at significantly higher numbers in marine environments than in lakes, although in both cases the activity was consistently higher in farming plots (Fig. 2b).

Species richness

Unlike the activity level, the number of bird species only revealed a significantly higher richness in marine bays than in lakes, but no treatment effects were found (Table 1b). Contrasting with the lack of difference between farming and control plots in lakes (Fig. 3), birds in marine bays showed a higher (non-significant) average richness in farming plots. However, such trend could be related with the high response shown by only two trophic guilds, and the richness

Table 1 Analysis of variance for (A) the maximum activity level of birds, and (B) species richness

Response	Effects	<i>df</i>	<i>F</i>	<i>P</i>
(A) Activity level	<i>T</i>	1	163.2	0.0002
	<i>E (T)</i>	2	44.3	0.0019
	Error	4		
	RM	7	13.9	<0.0001
	RM× <i>T</i>	7	11.4	<0.0001
	RM× <i>E (T)</i>	14	1.59	0.1433
	Error	28		
	(B) Species richness	<i>T</i>	1	1.92
	<i>E (T)</i>	2	40.9	0.0022
	Error	4		
	RM	1.73	1.44	0.2959
	RM× <i>T</i>	1.73	1.45	0.2934
	RM× <i>E (T)</i>	3.47	2.54	0.1372
	Error	6.94		

T treatment: presence vs. absence of salmon farms, *E* environment: lake vs. marine, *RM* repeated measure

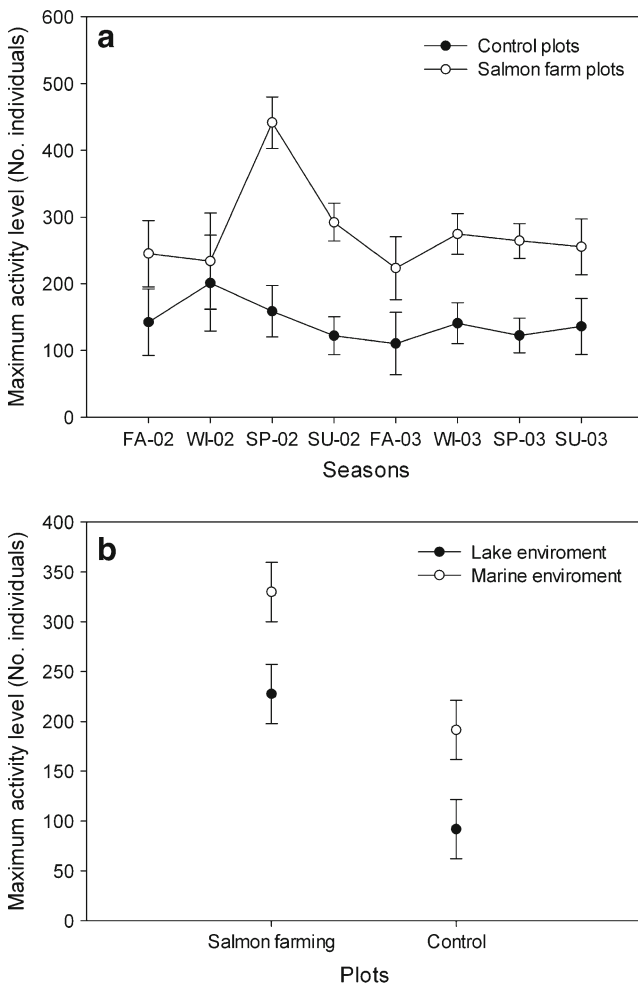


Fig. 2 Maximum daily activity level of birds in marine and lake environments from southern Chile. **a** Temporal variation in salmon farming and control plots. **b** Variation between environments in farming and control plots. Values: mean±95 % confidence interval

of birds at the assemblage level was clearly not influenced by the presence of salmon farms.

Species composition

Twenty-four of the recorded species were common to both environments, whereas 14 species occurred exclusively in marine bays and 4 species were exclusive of lakes. Consequently, the overall similarity between marine and lake assemblages was only 36.4 %. The nMDS ordination of species composition (Fig. 4) showed an obvious segregation between lake and marine environments, as expected due to their different suites of resident species, but more importantly, it showed a clear distinction between treatment levels, virtually overriding any difference between localities. This

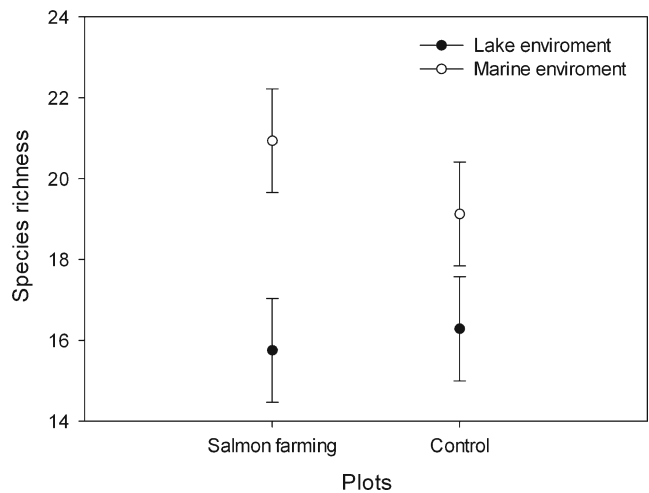


Fig. 3 Variation of bird species richness between environments and between salmon farming and control plots

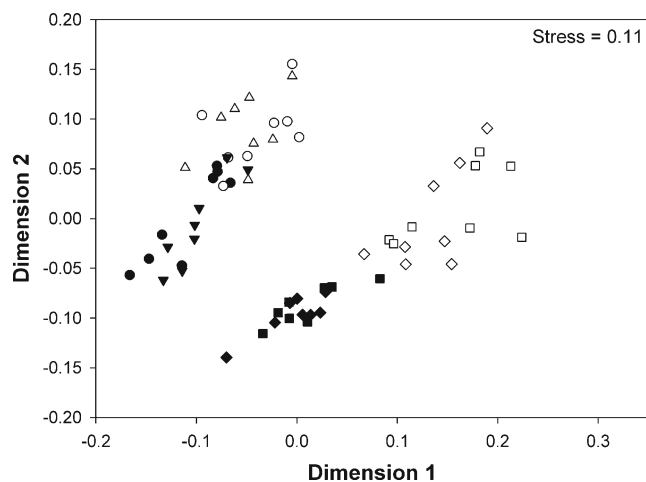


Fig. 4 Multivariate ordination results (nMDS, based on Bray–Curtis) of the seasonal composition of bird species in salmon farming (*open symbols*) and control (*filled symbols*) plots within marine (*circles* for Calbuco and *triangles* for Metri) and lake (*squares* for Llanquihue and *diamonds* for Rupanco) environments

pattern was supported by the statistical results showing a significant difference between farming and control plots within localities (ANOSIM; $R=0.67$; $P=0.001$), but no difference between localities ($R=0.33$, $P=0.171$). SIMPER results indicated that *L. dominicanus*, *Phalacrocorax atriceps*, and *M. chimango* were the main contributors (51.2 %) to the dissimilarity between farming and control plots (overall dissimilarity=52.3 %) because of their greater average abundance in the former. Accordingly, *L. dominicanus* and *M. chimango* were also the main contributors (64.5 %) to the similarity between salmon farming plots (overall similarity=60.9 %).

Trophic guilds

Both in marine and lake environments, the number of birds was significantly different among trophic guilds and significantly greater in salmon farming plots, with a significant interaction between guild and treatment (Table 2). In both environments, the interaction was largely explained by the differential importance of mainly three guilds: omnivores, diving piscivores, and carrion eaters, with a smaller contribution of other guilds (Fig. 5). In both environments, omnivores were by far the most abundant guild, and their number in farming plots was two and three times greater than in controls at marine bays and lakes, respectively (Tukey, $P=0.0002$ in both cases). In marine bays, diving piscivores and carrion eaters were the second and third guilds in importance, both of them more numerous in farming plots ($P\leq 0.0002$ in both cases), followed secondarily by perching piscivores and marine invertebrate feeders, this latter being the only guild more abundant in control plots ($P=0.0173$). In lakes, carrion eaters were the second guild in importance,

slightly ahead of diving piscivores, surface feeders, and terrestrial invertebrate feeders, all but the latter more abundant in farming plots ($P\leq 0.0139$). Two omnivores (*L. dominicanus*, *M. chimango*) and one diving piscivore (*P. atriceps*) made up the bulk of detected birds, representing 65 % of the community in 2002, and 54 % in 2003. On the other hand, species richness within trophic guilds followed the same trend than overall species richness, showing no significant differences between control and farming plots ($F_{1,1}=0.5$, $P=0.6$).

Discussion

Salmon farms represent discrete points in space that concentrate a great amount of food and structural resources, which exceed their normal availability at a given habitat (lake or marine), and act as attraction centers for native birds (Pitt and Conover 1996). Our results show that such discrete resource concentration caused a significant increase on the activity level (i.e., number of individuals registered in a given time) of birds at our study sites, by attracting nearby individuals that may take advantage of the large food supply and perching structures (Kloskowski et al. 2009). Such attraction, however, did not involve significant changes on species richness, and consequently, the primary effect of salmon farms so far is a strong aggregation response of bird populations, modulated by within-locality changes in bird composition. Albeit 28 % of the recorded species were migrants, they would have little influence on the variation in abundance and species richness over time since most migrants are present in spring, and the guilds showing stronger responses to salmon farming (omnivores, diving piscivores, and carrion eaters) are composed mainly by resident species.

Interestingly, marine and lake environments seemed to respond in the same way to salmon farming. At both environments, salmon farming facilities are capable to attract a large number of individuals of those species present in the surrounding area, but their influence is not strong or spatially wide enough to attract species from more distant locations. In addition, bird assemblages at both environments might be partly determined by the size-structure of fish (Webb et al. 2011). A greater abundance and size of prey may prevent birds with small gape size to ingest larger, more profitable fish, or may alter competition and predation interactions involving generalist bird species (Kloskowski et al. 2010; Kloskowski 2011a). However, potential effects derived from structural differences between lake and marine environments should not be discarded. For instance, the intensification of fish farming in pond systems in France was not correlated with bird species richness, but it had negative effects on macrophyte cover, which in turn explained the variation in bird richness (Broyer and Curtet 2012). At least for lake

Table 2 Analyses of variance for the number of bird individuals per trophic guild

Environment	Effect	<i>df</i>	<i>F</i>	<i>P</i>
Marine bays	<i>G</i>	8	775.0	<0.0001
	<i>T</i>	1	160.1	<0.0001
	<i>G</i> × <i>T</i>	8	36.4	<0.0001
	Error	18		
Lakes	<i>G</i>	7	426.0	<0.0001
	<i>T</i>	1	154.8	<0.0001
	<i>G</i> × <i>T</i>	7	34.0	<0.0001
	Error	16		

The two environments were assessed separately due to their different number of guilds. Effects are *T* treatment and *G* guild

environments, therefore, the apparent absence of farming effects on bird species richness in our study could be re-examined by considering indirect effects related with habitat properties.

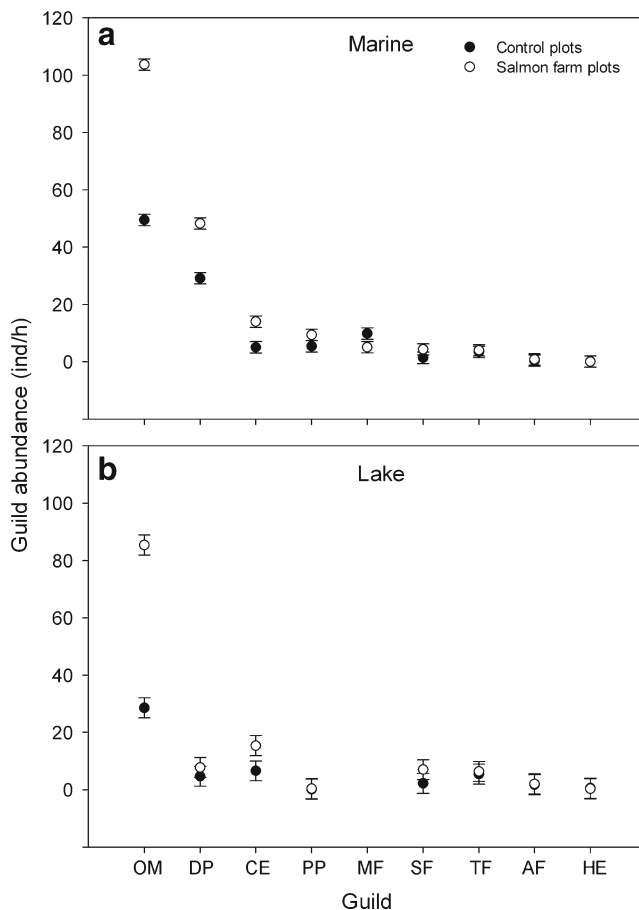


Fig. 5 Variation of the number of bird individuals per trophic guild found in salmon farming and control plots in marine bays (a) and lakes (b). *OM* omnivores, *DP* diving piscivores, *CE* carrion eaters, *PP* perching piscivores, *SF* surface feeders, *MF* marine invertebrate feeders, *TF* terrestrial invertebrate feeders, *AF* aerial invertebrate feeders, *HE* herbivores

The increase in bird activity represents a major problem for fish farming companies because it also increases bird predation and cause fish stock losses (Kloskowski 2011b). In consequence, many techniques (lethal and non-lethal) have been developed to control bird predation impact on farms (e.g., Kloskowski 2011b; Maricchiolo et al. 2011). However, those preventive actions have not considered that the main cause of fish predation would be farming itself, by generating a positive feedback on bird populations. Paradoxically, birds are attracted to densely aggregated fish stocks that impose high mortality risks and offer low reproduction opportunities, reasons why many fish farms could be acting as ecological traps (i.e., maladaptive habitats; Kloskowski 2012). On the other hand, it remains to be assessed whether the aggregation response of birds may conduct to an intensified predation on native species of fish and invertebrates. However, it is also likely that aggregated birds may contribute to reduce the impact of escaped salmonids, which are known to feed on native species and stay around fish pens (Soto et al. 2001).

From our results, resource concentration by salmon farming in southern Chile might be interpreted as a positive effect for waterbirds, in terms of increasing the total number of individuals locally. Nevertheless, such increase was uneven through the marine or lake communities, involving a strongly different distribution of species abundances, which would represent a negative effect. Generalist and opportunistic species such as the carrion eaters *Cathartes aura* and *Coragyps atratus*, the omnivores *L. dominicanus* and *M. chimango*, and the piscivore cormorant *P. atriceps*, were the most benefited since they are capable to consume and have a profit from large fish prey (i.e., salmon), and some gulls are also attracted by surplus food pellets floating nearby salmon pens (Habit et al. 2012). Conversely, other small-gaped piscivores or more specialized species (e.g., herbivores or aerial invertebrate feeders) had little or no profit of such prey increase (Kloskowski 2012) because their main food resources are largely independent of the presence of fish farms. In this

context, both the increased abundance of resources in salmon farms make little likely that narrow-niche species, especially if they do not depend on resources (or resource states) subsidized by salmon farms, are competitively excluded by broad-niche species in the long term. Likewise, strong competition for food among dominant species is not expected to occur owing to the constant renewal of these resources. Hence, salmon farms may not alter bird species richness, but they do promote dominance by a few common species, leading to decreased community evenness (i.e., increased homogeneity; see Fig. 4).

In conclusion, our predictions were partially supported because native birds have responded to salmon farms in an idiosyncratic way. Despite not affecting species richness, the concentration of resources triggered consistent aggregation responses of generalist species which greatly benefited from this new scenario, unlike trophic specialists or narrow-niche species which made little profit. Our results also show that subsidized communities undergo predictable and systematic changes in both lake and marine environments, closely associated with the increased dominance of three generalist and widely distributed species (*L. dominicanus*, *M. chimango*, and *P. atriceps*).

After a virtual collapse caused by a virus outbreak in 2008 (Godoy et al. 2008), the Chilean salmon industry has moved further southwards to the austral districts of Aysén and Magallanes (43 to 53°S), which have a particularly high diversity of freshwater and marine birds, receiving migrant species from Antarctica in winter. Thus, considering the scenario described in this study, we think likely that the massive presence of salmon farms in those austral districts might lead to the homogenization of biodiversity in bird communities (McKinnney and Lockwood 1999).

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