Relationships between off-bottom bivalve aquaculture and the Magellanic steamer duck *Tachyeres pteneres* in southern Chile

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ABSTRACT: The interactions between aquaculture farms and endemic marine birds in the Northern Hemisphere have been a recurrent topic in the past decades. In the Northern Hemisphere, shellfish aquaculture farms have diverse effects on wildlife populations, and the substantial predation on mussels by birds can lead to culling of the birds by farm managers. In this work, we assessed the interaction between Chilean blue mussel *Mytilus chilensis* farms and the Magellanic steamer duck *Tachyeres pteneres*, an endemic duck of southern Chile whose population is thought to be declining. In particular, we assessed the importance of the Chilean blue mussel in the Magellanic steamer duck's diet, and we estimated the magnitude of losses to aquaculture due to predation by the ducks. Between March 1988 and February 1989, observations and sampling collections were performed around a bivalve aquaculture farm in Yaldad Bay (Chiloé Island, Chile). In contrast to what happens in the Northern Hemisphere, we infer that Chilean blue mussel farms do not promote the increase of the Magellanic steamer duck population in Chile: the population dynamics appear to be responding to other habitat variables. Moreover, our estimate for the losses due to predation was less than 1.6% of the annual farm production in Chile. Despite the fact that sampling was done almost 30 years ago, this study is the most recent one investigating the ecology and social behaviour of the Magellanic steamer duck and its relationship with bivalve aquaculture.

KEY WORDS: Chilean blue mussel aquaculture · Magellanic steamer duck · Losses · Quality feeding strategy

1. INTRODUCTION

Shellfish aquaculture in Chile, as in other regions of the world, occurs in the intertidal-subtidal shallow nearshore waters, which also tend to harbour the highest densities and diversity of marine birds (Connolly & Colwell 2005, Dionne et al. 2006, Žydelis et al. 2009). Amongst the marine birds, sea ducks are a group of birds that are particularly likely to interact with shellfish aquaculture, as they are inherently linked to the same areas where most shellfish aquaculture occurs. Sea duck diets include a high proportion of bivalves and crustaceans and some small fish (Del Hoyo et al. 1992), making them potential predators of farmed shellfish, which would consequently negatively affect the economic success of the farm. However, shellfish aquaculture may negatively affect shorebird populations through habitat transformation or exclusion, or by disturbances arising from farming activities and boat traffic (Caldow et al. 2003, Smith & Shackley 2004, Connolly & Colwell 2005, Gallardi 2014). Indeed, the interaction between birds and marine farms is a well-documented problem in the Northern Hemisphere (e.g. Dzimbal & Jarvis 1982, Žydelis et al. 2009, Varennes et al. 2013).

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Despite the fact that the southern region of South America is recognized as having a high marine invertebrate biodiversity, only 1 bird genus is adapted to feed on these: *Tachyeres*. In contrast, in the Northern Hemisphere, there are at least 8 other genera with such adaptations (e.g. Sanger & Jones 1982, Whitlach 1982). In southern Chile, the largest *Tacherys* species is the Magellanic flightless steamer duck *T. pteneres*, Förster 1844. This marine bird is distributed from Valdivia (40° S) to Cape Horn (55° S) and is linked to nearshore intertidal and shallow subtidal habitats (Martínez Piña & González Cifuentes 2004). It is classified as 'Least Concern' by the IUCN Red List (http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T 22680033A92839660.en). Although there are no scientific publications about the relationship between birds and shellfish aquaculture in Chile, some studies have investigated the diet of several related coastal birds (e.g. Cursach et al. 2011, Tobar et al. 2011). In Chile, it has been officially accepted that the populations of Magellanic steamer sucks are declining (www.mma.gob.cl/clasificacionespecies/fichas12proceso/pac/Tachyeres_pteneres_12RCE_INICIO.pdf). Therefore, the aim of this study was to: (1) assess the importance of the Chilean blue mussel in the diet of the Magellanic steamer duck, providing information about population dynamics, and (2) estimate the magnitude of aquaculture losses due to duck predation.

2. MATERIALS AND METHODS

2.1. Study area

Yaldad Bay is located in the south of Chiloe Island, Chile (43° 08′ S, 73° 44′ W; Fig. 1). Average depth is around 13.4 m, with a maximum of 32 m. The average slope is 2.3 % (maximum 12 %). The tidal cycle is semidiurnal, with amplitudes ranging from 3 to 5 m. The bay receives freshwater input from 4 rivers (approximately 25 m wide) and 17 streams, and includes 3 islands (Captuno, Pichiguapi and Linagua; Fig. 1). The mean annual temperature and salinity in the bay are 11.8°C and 29.9 %. An extensive area of the bay is used for cultivation of Chilean blue mussel *Mytilus chilensis* (Navarro & Winter 1982, Ribeiro et al. 2007). Between 1988 and 1989, the aquaculture farm at Yaldad consisted of 84 rafts of 16 × 16 m, 1 raft of 8 × 8 m and 64 floating longlines, each 100 m long. Seeded long lines are installed in October and moved in early March onto grow-out ropes. Harvesting of commercial mussels occurs 8 to 12 mo later,
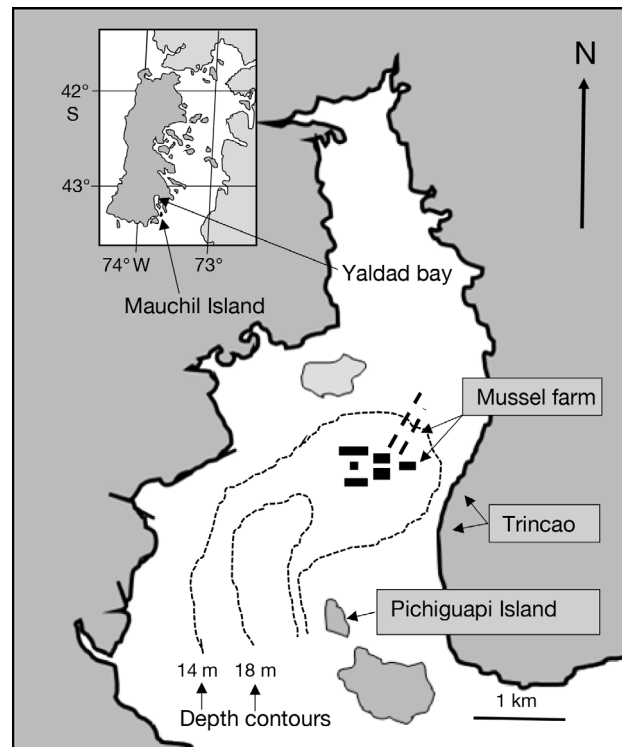

Fig. 1. Geographic location of Yaldad Bay and Mauchil Island, Chile, and the 3 study polygons: mussel farm, Trincao seashore and Pichiguapi Island

when they are >5 cm long. The most productive growth period of the year is between September and February, a period that includes gamete formation and spawning (December–January) (Navarro & Winter 1982). The seashore intertidal area is mostly stony and muddy, and the sea bottom at the mussel farm is soft sediment. All sites are characterized by a temperate-humid-cool climate with 2000–3000 mm of precipitation yr^{-1}, and an average humidity around 90 %. The average annual temperature is <10°C (Toledo & Zapater 1989). As control study sites, the area surrounding Mauchil Island and the south section of the Coldita channel were selected (Fig. 1); the island extension is 1.2 km^2, it is located 15 km south of Yaldad Bay (43° 15′ 26″ S, 73° 40′ 19″ W) and is accessible by navigating the Coldita channel waterway.

2.2. Assessment of the Magellanic steamer duck population

Three trips to select the study sites, determine the observation methods and choose rafts to be monitored were made between December 1987 and February 1988. Thereafter, from March 1988 to February

1989, 12 censuses at the *M. chilensis* farm in Yaldad Bay and the closed seashores of Pichiguapi Island and Trincao were made. A total of 292 h of observations were completed: 102 at Trincao, 102 in the farm area and 88 at Pichiguapi Island.

Duck surveys within Yaldad Bay were conducted once per month from 06:00–18:00 h. Ducks were observed during daylight from a moving inflatable boat following the bay contour at no more than 100 m from shore at medium speed (3 knots h^{-1}), with 7 × 42 binoculars and with a team of 1 driver/observer with a data recorder (Žydelis et al. 2009). An appropriate distance from the birds and suitable vessel speed were maintained to reduce the probability of ducks moving away. A total distance of 8.5 nautical miles was covered daily within, on average, 3 h (08:00–11:00 h). Thereafter, within the study area at Yaldad Bay, 3 study polygons were selected: (1) the mussel farm (2) the Trincao seashore and (3) the Pichiguapi Island seashore (Fig. 1). The observations in these 3 polygons were performed on 3 consecutive days on the rafts at the mussel farm, and hiding in the vegetation close to the sea at Trincao (Trincao polygon) and Pichiguapi Island (Pichiguapi polygon).

All birds in those polygons were counted, and their activity (feeding, agonistic, resting and moving) was recorded. On 5 occasions (May, June, November, January and February), a census at the control study site Mauchil Island (Fig. 1) was performed by walking the entire perimeter, counting all birds at no more than 200 m from shore with 7 × 42 binoculars. Each census was completed between 08:00 and 11:00 h. No steamer duck observations were performed in October 1988 and December 1989 due to poor weather conditions.

2.3. Diet assessment of *Tachyeres pteneres*

Duck diet was inferred by identifying potential food sources for ducks in each polygon. For this purpose, relevant data were obtained by diving and searching for duck prey at the sea bottom in the intertidal and subtidal zones, by observing the feeding behaviour of the ducks and by shooting randomly selected ducks in the different study polygons. Fifteen ducks were shot and transported to the mussel farm laboratory at Yaldad Bay to be dissected and prey items found in the gullet, proventriculus and gizzard were then recorded. Shooting was done with a licence from the Servicio Agricola y Ganadero, Ministry of Agriculture, Chile. Dissections were performed according to Wobeser & Spraker (1987). The

number and size of mussels eaten was inferred by counting the total number of umbos and by measuring the shell length of uncrushed mussels found in the digestive tracts.

According to the farm workers, ducks did not predate the inside vertical ropes of rafts, only the exterior ones; this was also the case for the hanging submerged ropes or seed collectors of the longlines. These observations were confirmed during our study. To assess the losses from predation, we measured the weight of selected hanging submerged ropes from 2 randomly selected rafts. Among all hanging submerged ropes in each raft, we tagged 100 external ropes, all of which were located within 4 parallel lines from outside to inside; 20 intermediate ropes were considered as barriers, and 10 internal ropes were used as controls. Each vertical rope was weighed 6 times during the study to compare weight gained or lost. Furthermore, in each month, we collected randomly selected mussel samples from natural populations and from the longline population within Yaldad Bay in order to compare their size and resistance to compression (kg cm^{-2}) with calibrated equipment at the College of Engineering, Universidad Austral de Chile. Mussels were sampled from a section of 30 × 30 cm width at a depth of about 1 m below low tide.

2.4. Duck feeding behaviour

A main assumption was that Magellanic steamer ducks are diurnal, so in order to support this assumption, flocks at the mussel farm were followed all night long on 4 occasions. No birds were seen foraging after sunset, similar to what has been observed in other species of marine birds (Guillemette 1998). To estimate the proportion of time that ducks dedicate to feeding, observations started after first light, starting in general at 08:00 h and finishing at 18:00 h. Ducks within the polygons were observed every 10 min, and their activity (feeding, resting and interacting) was registered in intervals of 2 min. Feeding time was described as the proportion of total time (h) that ducks were feeding (diving, probing the substrate in search of prey, ingesting, searching or eating around seaweed banks at the sea or in ground) in relation to the the total time that ducks were observed. Tide times and depth were determined using the tide table of the Nautical Almanac of the Instituto Hidrográfico de la Armada de Chile. These observations were repeated for Mauchil Island on 5 occasions (May, June, November, January and February).

2.5. *M. chilensis* losses

To estimate *M. chilensis* losses at the mussel farm due to Magellanic steamer ducks between March 1988 and February 1989, we built up a simple mathematical model that considered (1) an estimate of the number of single blue mussels a duck can eat per day taking into account the growth pattern of *M. chilensis* at the farm in Yaldad Bay; (2) the number of ducks that visited the farm per month and (3) the wet weight of a blue mussel when harvested.

The growth pattern of *M. chilensis* at the farm was inferred from the data presented in Table 1, which represent random samples from the submerged ropes at the farm at no more than 50 cm depth; this sampling was performed for 1 yr, from March 1988 to February 1989. Using allometric principles (e.g. see Von Bertalanffy 1969), the average wet weight per month (W, g) and the average length per month (L, cm) were correlated using:

$$W = kL^\alpha \quad (1)$$

where the constants k and α must be determined. This equation has been successfully used in physiological investigations and applied in the management of mussel production (Gosling 1992, Mondol et al. 2016). Once the allometric relation is established, shell measurement or growth is sufficient to estimate biomass and flesh production. In turn, according to the data in Table 1, the average length behaves as a linear function of time, namely:

Table 1. Average length and weight of blue mussels *Mytilus chilensis* haphazardly collected from March 1988 to February 1989 from the rafts' hanging ropes at no more than 50 cm depth and Magellanic steamer ducks counted at the farm in Yaldad Bay in the corresponding month. Comparison length: for comparison, first-year lengths of *M. chilensis* at the Yaldad farm from 1982 are shown (data from Navarro & Winter 1982). N: number collected

Month	N	Length (mm) Mean	SD	Weight (g) Mean	SD	Comparison length (mm)	No. of ducks
Mar	26	11.8	0.23	1	0.10	No data	9.9
Apr	32	13.8	0.34	1	0.15	No data	17.1
May	36	15.8	0.20	2	0.19	No data	33.9
Jun	45	17.8	0.21	2	0.30	No data	7.5
Jul	74	19.7	0.12	3	0.22	No data	4.2
Aug	48	29.5	0.10	4	0.14	24.2	1.8
Sep	32	39.4	0.35	5	0.24	27.1	17.3
Oct	34	44.9	0.40	9	0.33	33.4	10.6[a]
Nov	22	50.3	0.25	20	0.30	41.4	3.8
Dec	45	55.5	0.46	20	0.22	47.9	2.1[a]
Jan	76	60.7	0.12	20	0.12	48.8	0.4
Feb	12	66.9	0.48	30	0.42	No data	2.5

[a]Estimated results as no censuses were made in those months

$$L(t) = A + Bt \quad (2)$$

where the constants A and B must be determined, t is measured in months, and $t = 0$ corresponds to the beginning of the first month of the farming season, namely March. Combining both relations, an equation for the average wet weight as a function of time can be obtained:

$$W(t) = k(A + Bt)^\alpha \quad (3)$$

The average wet weight of a 1 yr old blue mussel at harvest is given by $W(12)$.

Regarding the number of ducks and the amount of *M. chilensis* (weight in grams) that they can consume daily during different months of the year at the farm, no global reasonable function of time t seemed to be available, since the feeding behaviour of Magellanic steamer ducks in relation to *M. chilensis* depends on many factors. To circumvent these difficulties, an estimate of the number of ducks present at the farm during each day of month t, which we denote by $D(t)$, was inferred from the observations (Table 1). The weight (g) of *M. chilensis* that a single bird can eat per day was assumed to be $C = 97.4$ g d^{-1}, the maximum recorded in 1 digestive tract (Table 2). With these considerations, the estimate for the annual *M. chilensis* losses at the farm is indeed an upper bound, *a priori* a pessimistic scenario for the economic success of the farm.

The upper bound for the number of *M. chilensis* eaten by a duck at the farm during month t is given by the function:

$$\varphi(t) = 31 \int_{t}^{t+1} \frac{C}{W(s)} ds \quad (4)$$

where we considered 31 to be the average number of days in a month. Note that $\varphi(t)$ is a decreasing function of t; indeed, the amount of *M. chilensis* equivalent to $C = 97.4$ g decreases since the average weight function $W(t)$ is increasing. We infer that the number of *M. chilensis* eaten by all ducks present at the farm during month t is at most:

$$N(t) = D(t) \times \varphi(t) \quad (5)$$

and the total number of *M. chilensis* eaten by the ducks in 1 yr is:

$$M = \sum_{t=0}^{11} N(t) \quad (6)$$

Finally, the upper bound for the annual *M. chilensis* losses in grams at the farm is the number $W(12) \times M$.

2.6. Data analysis

Data from the observations on duck feeding behaviour were neither normally distributed nor independent. Non-parametric Kruskal-Wallis and Mann-Whitney statistics tests were used to assess significance between study variables (duck population trends, time spent feeding, weight variations and differences in hanging submerged ropes); significance was set at $\alpha = 0.05$. Thereafter, a Pearson correlation matrix was used to assess correlations between tide, agonistic events and feeding time. Regarding the strength of the shells, a non-parametric Mann-Whitney U-test was used, since even after log10 transformation, the data did not correspond to a normal distribution (skewness −0.91, kurtosis −0.89). Log−log and linear regressions were used to model the growth of mussels (that were haphazardly and independently chosen) with an excellent correlation. Data processing and analysis were performed in SYSTAT 12 and Excel.

3. RESULTS

We counted (mean ±SD) 19 ± 3.6 ducks at Pichiguapi Island, 6.4 ± 4.2 at Trincao and 10 ± 4.5 at the farm. The Pichiguapi Island study site significantly concentrated the major number of ducks (68.6 ± 43.5); instead of Yaldad bay (55.3 ± 16.6) (Kruskal-Wallis test: $H_2 = 6.226$, p = 0.04). Only the Trincao study polygon recorded variation throughout the year ($H_2 = 6.0$, p < 0.05; Pichiguapi: H_2: 4.4, p = 0.11; farm: $H_2 = 3.7$, p = 0.15; Fig. 2). Nevertheless, the largest number of steamer ducks was recorded between March and May 1988, declining towards the rest of the year ($H_2 = 8.8$, p = 0.01). The population recorded at Yaldad Bay was 55.3 ± 16.6 ducks while at Mauchil Island it was 68.6 ± 43.5 ducks, with no significant variations during the year. This low variation of the population over time at the study sites shows a pattern of low mobility, mostly associated with a territorial and non-migrant species (Martínez Piña & González Cifuentes 2004).

Most pairs with ducklings were registered between December and March. These stable pairs of adult males and females concentrated along seashores near freshwater streams that provide a defense against flocks of solitary individuals; in fact, only on a few occasions did stable pairs come close to the farm area. In Yaldad Bay, stable pairs constituted 38% of the population, solitary adult males 2% and flocks 60%. Similarly, at Mauchil Island, stable pairs

comprised 44% of the population, solitary adult males 2% and flocks 54%. Those steamer ducks using the mussel farm polygon belonged mostly to flocks, which permanently moved in and out of the installations; only rarely were ducks from flocks observed resting at the seashore, and this occurred only at Pichuhuapi Island. In contrast, pairs of adult ducks associated with seashores were resting and preening on land every day.

The daily average time spent feeding at the mussel farm was 16% (1.3 h d^{-1}), of which 4% (0.1 h d^{-1}) was at the rafts, 30% (2.4 h d^{-1}) at Trincao and 42% (3.2 h d^{-1}) at Pichiguapi Island. When ducks in the farm area were not feeding, they were either moving or resting on the longline buoys. Moreover, from the total time that a single pair of ducks was followed at Yaldad Bay (250 additional hours), they spent 16 h (6%) feeding at the mussel farm, 24 h (10%) at Trincao and 38 h (15%) at Pichiguapi Island, showing a significant difference between the 3 studied polygons ($H_3 = 11.3$, p = 0.01). In comparison, at Mauchil Island, the observed time that the ducks spent feeding was 41%, very similar to Pichiguapi Island.

We recorded 521 diving events, lasting an average of 29 s (5−71 s) and no significant differences between the studied polygons.

Regarding the total population per day and the time birds spent feeding (predation intensity: population × hours spent feeding), it was higher at Pichiguapi Island ($H_2 = 11.9$, p < 0.01) than in the other 2 studied polygons (Fig. 3). In addition, the results from the farm showed no preferences of ducks for feeding either on the submerged ropes hanging on the rafts or those hanging on the longlines. Predation within the farm area was not constant during the year.
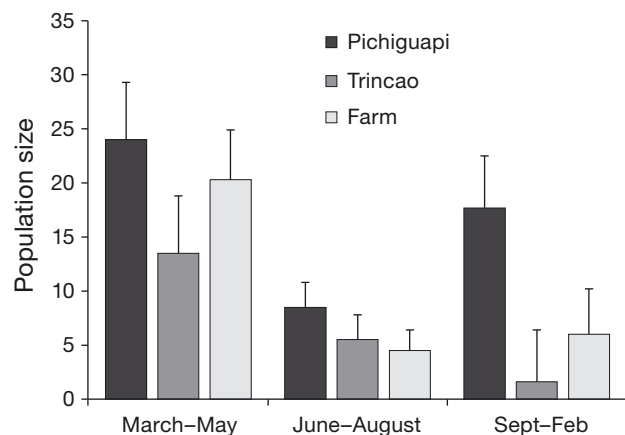

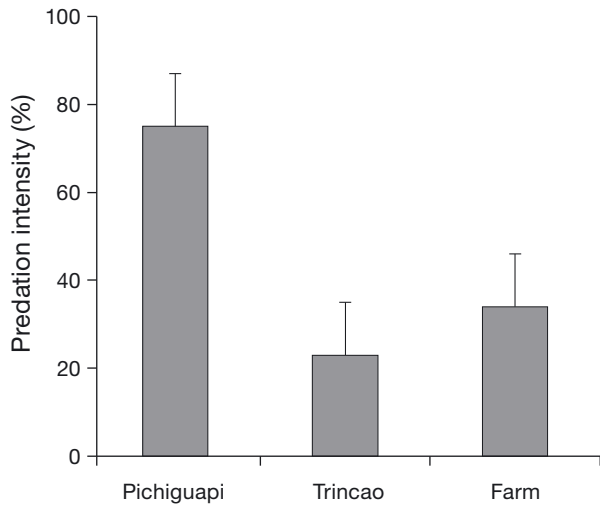Fig. 2. Mean ± SE population size of flightless steamer ducks counted at the 3 study polygons within Yaldad Bay

Fig. 3. Mean ± SE predation intensity (population × hours spent feeding) as a percentage of the total observation time that steamer ducks spent at the 3 study polygons within Yaldad Bay between March 1988 and February 1989

Fig. 4. Mean ± SE of total observation time that flightless steamer ducks dedicated to feeding during high and low tide at each study site within Yaldad Bay between March 1988 and February 1989

We randomly collected 482 blue mussels from the farm and 290 blue mussels from natural populations over 7 mo. On average, their length varied from 20.3 to 54.3 cm, and strength varied from 7.3 to 30.3 kg cm^{-2}. Among all samples, there was no difference between the length of the mussels collected at the farm (35.5 cm average) and those collected from natural populations (34.7 cm average). However, shells of mussels collected from natural populations were significantly ($U_1 = 0.0$, p < 0.01) more resistant to compression (45.6 kg cm^{-2} on average) than those from the farm (20.4 kg cm^{-2} on average). There was a close to significant negative correlation between the population of *Tachyeres pteneres* at the farm and the *Mytilus chilensis* growth pattern during the year (Pearson correlation matrix: −0.6; p = 0.07): the larger the mussels were, the smaller the number of ducks using the farm area. Moreover, the larger *M. chilensis* were at the farm, the less time *T. pteneres* spent feeding (Pearson correlation matrix: −0.7; p < 0.01): indeed, the intensity of predation at the longlines decreased from March to February (Fig. 3).

Regarding tidal effects (Fig. 4), ducks spent significantly more time feeding at low tide outside the farm area at Trincao (Mann-Whitney $U_1 = 18.0$, p = 0.02) and Pichuguapi Island ($U_2 = 0.0$, p < 0.01). In contrast, at the farm, a longer time feeding was registered at high tide, with a close to significant difference ($U_1 = 73.5$, p = 0.07).

Within all analysed digestive tracts, 51 undigested blue mussels were found, with an average length of 16.6 mm (range: 5–65 mm). In 5 birds, there were no
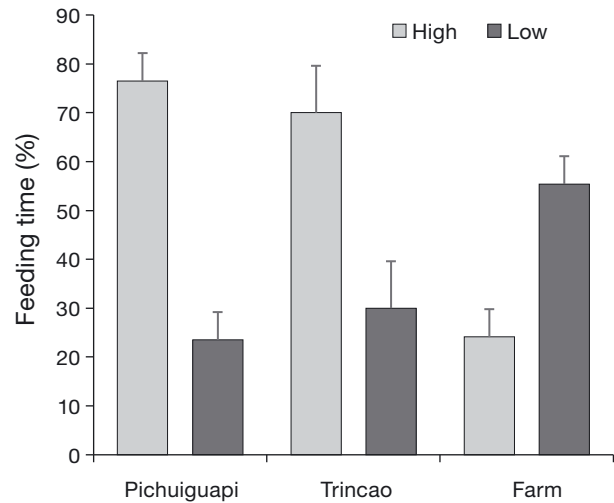
mussels inside their digestive tracts, but crustacean remains were found instead. The heaviest bivalve content (97.4 g) in a single *T. pteneres* was recorded at the farm. The average wet weight of the digestive tract contents was 45.3 g, of which 23.8 g (53%) corresponded to bivalves. In individual digestive tracts with mussel content, 1 to 68 *M. chilensis* were recorded (Table 2).

With respect to the hanging submerged ropes at the selected study rafts, all increased their initial weights by 5.8 to 5.9 times, with no significant difference between the outside, middle and inside ropes.

Mussels were the most predominant dietary item recorded in the digestive tracts at every location: at Trincao, 78% of the total wet weight were mussels and only 22% crustaceans, giving a ratio of 3.54, compared to a ratio of 6.14 at Mauchil Island and 1.63 at the mussel farm. The digestive contents included several species of crustaceans (*Munida subrugosa*, *Cancer edwardsi*, *C. coronatus* and undetermined amphipods), as well as mussels (*M. chilensis*, *Aulacomya ater*, *Tagelus dombeii* and undetermined species).

We found no relationship between human activity at the farm and the time the ducks spent feeding therein. As explained in Section 2.5, we provide an equation based on allometric principles for the average wet weight, $W(t)$, of *M. chilensis* (Eq. 3), where k, A, B and α must be determined from the data randomly collected from the vertical ropes at the farm (see Table 1). In the first step, assuming Eq. (1), we performed a log–log-linear regression to obtain $k = 1.314 \times 10^{-3}$ and $\alpha = 2.3813$ ($R^2 = 0.946$).

Table 2. Characteristics and wet weight of digestive tract contents of Magellanic steamer ducks captured in Yaldad Bay and Mauchil Island between March 1988 and February 1989. Total body length includes tail length

Month	Site	Sex	Body weight (kg)	Total body length (cm)	Tail length (cm)	Digestive tract content (g) Crustaceans	Bivalves	No. of blue mussel umbos	Minimum no. of blue mussels
March	Farm	Male	5.2	77.0	8.3	38.2	0		
		Female	2.1	64.3	1.5	12.3	9.1	82	41
April	Trincao	Male	5.9	74.0	9.6	21.1	27.6	12	6
	Farm	Female	4.4	74.0	8.8	22.2	21.5	136	68
		Female	5.3	77.0	8.7	8.3	55.5	85	43
	Trincao	Male	6.1	80.0	10.0	29.7	33.7	2	1
May	Mauchil	Male	4.2	25.5	9.8	35.1	0		
	Trincao	Male	5.0	29.3	7.5	30.1	16.2	2	1
	Farm	Male	5.0	76.5	5.5	6.3	51.7	13	7
	Trincao	Female	4.1	71.5	6.0	10.2	33.6	20	10
July	Mauchil	Female	3.9	71.0	8.7	42.1	0		
	Trincao	Male	4.8	73.5	6.8	6.3	97.4	11	6
	Farm	Male	5.4	80.1	9.2	30.4	11.2	76	38
November	Mauchil	Male	4.9	76.5	9.2	18.3	0		
		Female	4.5	74.5	9.7	12.4	0		
Mean			4.7	68.3	8.0	21.5	23.8		22
SD			1.0	17.1	2.2	12.0	27.7		23

In the second step, assuming (Eq. 2), we get $A = 5.6218$, $B = 5.4339$ ($R^2 = 0.968$). Then, solving the integral involved in $\varphi(t)$, we get a formula for an upper bound for the number of *M. chilensis* that 1 *T. pteneres* can eat during month *t*:

$$\varphi(t) = \frac{31C}{kB(1-\alpha)}\left\{\left[A+B(t+1)\right]^{(1-\alpha)} - (A+Bt)^{(1-\alpha)}\right\} \quad (7)$$

recalling that $C = 97.4$ g is the heaviest bivalve content found in a single duck. Using the estimated number of *T. pteneres* present at the farm during month *t* from Table 1, we use Eq. (5) to calculate the upper bound for the number of *M. chilensis* eaten by all the ducks at the farm during month *t*. Then adding the values of $N(t)$ from March 1988 ($t = 0$) to February 1989 ($t = 11$), the upper bound for number of *M. chilensis* predated by the ducks during the year is obtained, namely $M = 342\,571$. Finally, using $W(12) = 33.5$ g as the average weight of *M. chilensis* at the end of February 1989, the upper bound for the yearly *M. chilensis* losses in the farm between March 1988 and February 1989 is 11.5 t.

4. DISCUSSION

Several studies have shown that bivalve aquaculture structures (rafts and longlines) provide good conditions for recruiting and growing mussels, additionally offering refuge to invertebrate predators, which, in turn, provide higher densities of better-quality prey for sea ducks than otherwise available in intertidal areas (Dionne et al. 2006, Žydelis et al. 2009, Cursach et al. 2011, Varennes et al. 2013). In fact, shellfish aquaculture offers a rare example in which the introduction of an industry leads to positive effects on wildlife populations (Žydelis et al. 2009). However, the negative effect of predation on mussels and the resulting losses to the industry might lead to control measures of duck populations by managers. In this context, Winter et al. (1980) described predation by *Tachyeres pteneres* as one of the main causes of major losses in *Mytilus chilensis* aquaculture: more precisely, Winter et al. (1982, 1988) asserted that depredation by this bird is the reason for major losses of shellfish less than 2.5 cm long from rafts and longlines, especially in austral spring (August to November), during the *T. pteneres* breeding season, suggesting that these birds should be controlled. Their conclusion was probably influenced by what happens in the Northern Hemisphere, where small mussels (average length 20 mm) harvested on collectors are generally the most affected by predation due to the selective behaviour of some sea ducks, such as common eider *Somateria mollissima* (Galbraith 1992, Varennes et al. 2015). As an

example, stock losses due to predation by eiders and scoters (*Melanitta* spp.) in Scotland and Canada varied between 10 and 30% of the total stock (Ross & Furness 2000, Varennes et al. 2015). The most widely represented prey classes in the diet of sea ducks of North America are bivalves (50.1%), followed by crustaceans (23.7%) and gastropods (13.7%) (Ouellet et al. 2013). Ouellet et al. (2013) estimated an increasing contribution of bivalves with increasing body mass and the opposite trend for crustaceans, concluding that, for the larger common eiders, prey preference is driven by an issue different from energy value (see also Bustnes & Erikstad 1990, Bustnes 1998); moreover, common eiders in North America significantly vary their daily feeding time between winter and spring (Guillemette et al. 1996).

However, those observations are notoriously different from what has been described for *T. pteneres* in Chile, whose diet does not include more than 2.6% bivalves; according to Tobar et al. (2011), gastropods comprise up to 13.2%, crustaceans up to 60.5% and chitons up to 7.9% of the diet. Moreover, in Argentina, the most frequent prey for the white-headed steamer duck *T. leucocephalus* are *Cyrtograpsus* spp., Nereididae and Mytilidae, but only up to 14%. So how important is *M. chilensis* for the Magellenic steamer duck? Any animal must balance energy intake with expenditures to maintain body condition and survive, and 2 standard strategies allow a forager to achieve energy intake maximization: one is the 'quality strategy', which avoids filling the gut with low-quality food, prioritizing opportunities to feed on highly energetic prey but usually requires a longer search time; the other strategy is the 'quantity strategy', which relies on food that ensures a high encounter rate and minimal search time, with little regard for energy value (Ouellet et al. 2013). Our observations suggest that *T. pteneres* adopts the quality strategy: indeed, a diet based solely on bivalves requires a larger intake and spending a longer time engaged in feeding activities than an alternative crustacean-based diet. For bufflehead ducks *Bucephala albeola* (mean body mass 492 g), Ouellet et al. (2013) estimated an intake of approximately 146% of their body mass if they were feeding on bivalves only, while they would need only 75% if they were feeding only on Malacostraca. However, for large sea ducks, in contrast to smaller species, the amount of food that meets their needs represents a smaller proportion of their body mass (Von Bertalanffy 1969, Ouellet et al. 2013). Since the average recorded body weight of *T. pteneres* was 4.7 kg, close to the 5.1 kg recorded by Weller (1976), it is

expected that prey abundance and caloric value, together with other exogenous and endogenous factors, must have an important effect on the time that *T. pteneres* spends feeding.

Guillemette et al. (1996) estimated that common eider consumption of mussels ranged between 1.78 kg (spring) and 2.1 kg (late winter) per day, spending 33–46% of their daily time on feeding, completely filling their gullet and stomach with 185 g of mussels in 6 min (Nyström & Pehrsson 1988). Player (1971) and Varennes et al. (2015) observed that this species prefers bivalves <30 mm long and cultivated ones over natural grown ones. Moreover, several authors have described common eiders feeding only during daylight and preferably during low tide (Player 1971). On the other hand, in southern Chile, *M. chilensis* (2.98 kJ g^{-1}), *Choromytilus chorus* (2.42 kJ g^{-1}), gastropods (2.2–5.4 kJ g^{-1}) and crustaceans (2.7–9.8 kJ g^{-1}) are available, and in the case of *M. chilensis*, the energy value decreases as the wet weight and length increase (Duarte et al. 1980). In our study, predation on *M. chilensis* at the mussel farm was concentrated in autumn (March–May), when mussels have thinner shells and higher flesh content. These observations support the idea that, in our study area, *T. pteneres* has a feeding strategy oriented towards higher-quality prey such as crustaceans (*Munida subrugosa*, *Cancer edwardsii*, *C. coronatus* and undetermined amphipods), choosing those places where alternative options to bivalves are abundant (Tobar et al. 2011).

Diving time is linearly related to the depth at which birds are foraging, thus dives between 20 and 40 s are in general below 10 m depth (Žydelis et al. 2009). During our study, dives by *T. pteneres* lasted on average 29 s (range: 5–71 s), hence at a depth below 5 m, in concordance with the bay depth in the study polygons (Fig. 1). This suggests that our observed ducks must have been foraging at the sea bottom searching for crustaceans, which have been observed in their diet (Tobar et al. 2011).

According to Winter et al. (1988), during 1988 the mussel farm production was approximately 720 t, and our upper bound for the *M. chilensis* losses due predation by *T. pteneres* is 11.5 t, i.e. <1.6% of farm production; hence in Chile, the losses due to predation by sea ducks appear insignificant compared to what has been recorded in Canada and Scotland (Ross & Furness 2000, Varennes et al. 2013).

We conclude that, in an extremely pessimistic scenario for the mussel farms' success, predation of blue mussels by Magellanic steamer ducks is at most 1.6% of the annual production. It should also be

noted that during the study, we observed boats coming during the night into the farm area several times to steal mussels from longlines. To be more efficient, the thieves harvested only the first 2 m of the hanging rope, just like a duck would do, a fact of which farm owners were informed.

We also conclude that blue mussel farms in southern Chile do not promote an increase in Magellanic steamer duck populations; although they seem to provide safe resting sites for flocks, population dynamics seem to be related to other habitat variables, such as the availability of freshwater streams, the presence of safe nesting sites for pairs along the seashore and convenience of higher-quality prey like crustaceans.

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