

## Marine effect of introduced salmonids: Prey consumption by exotic steelhead and anadromous brown trout in the Patagonian Continental Shelf

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### Abstract

On the basis of stable isotope analysis, we estimated the marine diet of the most abundant anadromous salmonid species in Patagonian Atlantic basins. The results were coupled with bioenergetic and population models to estimate the consumption of food by salmonids and was compared with that by seabirds, the most abundant top predators in the area. Amphipods were the main salmonid prey, followed by sprat, silversides, squid, and euphausiids. The total consumption, even assuming large anadromous salmonid populations, represented < 5% of the total consumption by seabirds. We also identified the particular seabird colonies and artisanal fisheries with which salmonid trophic interactions at a more local scale could be significant.

Freshwater salmonid populations have been established in several river basins of the Southern Hemisphere, whereas most worldwide attempts to establish anadromous populations have failed (Pascual and Ciancio 2007). Southern Patagonia provides an exception to this rule: both Pacific and Atlantic rivers have self-sustaining populations of anadromous salmonids. Some species, such as Chinook salmon (*Oncorhynchus tshawytscha*), are actively colonizing rivers after introductions with established populations in virtually all Pacific river basins and at least one Atlantic river basin (Ciancio et al. 2005; Correa and Gross 2007). Anadromous rainbow trout (*Oncorhynchus mykiss*, hereafter steelhead) and anadromous brown trout (*Salmo trutta*, hereafter brown trout) are already established in Atlantic Patagonian basins.

The effects of resident salmonid populations on receiving freshwater communities have been studied in some depth in places around the world (McDowall 2006), including Patagonia (Aigo et al. 2008; Vigliano et al. 2009). Much less is known about the ecological effects of anadromous salmonids in marine habitats in general, and no information is available for populations inhabiting the southwestern Atlantic Ocean. Anadromous salmonids are highly valued, both as recreational and commercial species, but are also top predators that could affect host communities. Because of their complex life cycle, anadromous species could project their effects to native communities in rivers, lakes, and marine areas. Salmonid smolts are prey of other fish and seabirds during their initial entry to the ocean but rapidly grow to become top predators. Considering that salmonids have high feeding rates (Quinn 2002), the prey consumed by salmonids at sea, and in particular in confined areas such as fjords or estuaries, could exert considerable predation demand on localized food resources.

Anadromous salmonids could compete for food with other upper trophic level predators in the Atlantic Patagonian Shelf. Stable isotope analysis revealed that steelhead showed the same trophic level as other macrozooplankton feeders in this ecosystem, including the rockhopper penguin (*Eudyptes chrysocome*). Brown trout and Chinook salmon fed at the same trophic level as the piscivorous Magellanic Penguin (*Spheniscus magellanicus*), feeding mainly on schooling fish such as sprat and silversides (Ciancio et al. 2008b). In the present work, we focused on potential competition between trout and seabird, because of their conservation concern, and restricted feeding range and high food demand during the breeding season.

During the past 20 yr, bioenergetics models have provided an effective tool for quantifying trophic interactions between predators and their prey (Ney 1993; Hartman and Kitchell 2008). This tool has been used to evaluate conservation and management questions regarding factors limiting the production of fish populations (Hartman and Margraf 1993), including the effects of nonnative species (Ruzycski et al. 2003; Vigliano et al. 2009). Because these models are based on energy balance equations, they are frequently used to estimate consumption or growth for fish while accounting for changes in body mass, thermal experience, diet, and energy density of prey (Chipps and Wahl 2008) and are less time consuming than traditional methods. Species-specific models parameterized for salmonids have been particularly successful at estimating seasonal or annual consumption rates, with published corroborations typically reporting predictions within  $\pm 10\%$  of independent estimates of consumption (Madenjian et al. 2004).

In this work, we proposed to (1) describe the ontogenetic marine dietary patterns of anadromous steelhead and brown trout that spawn in Atlantic rivers basins of Patagonia; (2) use population-specific data on diet, growth, and thermal experience in bioenergetics models to estimate their consumption of marine prey; and (3) compare

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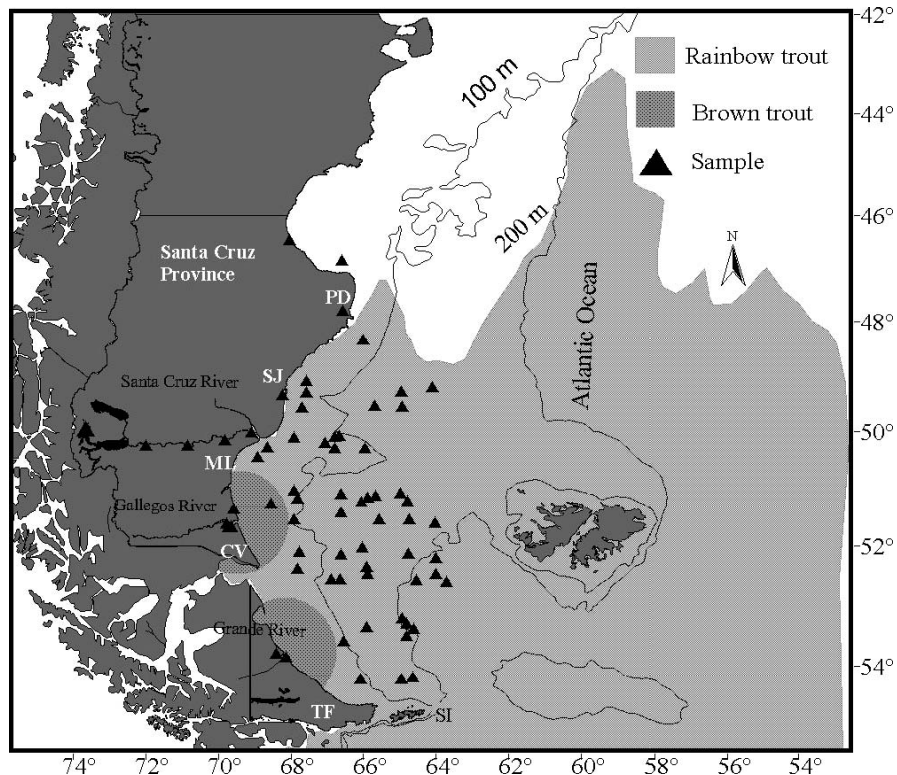


Fig. 1. Potential distribution area of steelhead and brown trout, seabird colonies, and sampling locations. The hypothesized marine distribution for steelhead consists of waters with average sea surface temperature within the range 6–14°C between October and March. Potential distribution areas for brown trout consist of the area with a 100-km radius around the outflow of natal rivers. Sea bird colonies: PD, Puerto Deseado; SJ, San Julián; ML, Monte León; CV, Cabo Virgenes; TF, Tierra del Fuego Island; SI, Staten Island.

consumption of shared marine prey resources between seabird populations and anadromous steelhead and brown trout.

## Methods

**Study area**—For the present study, we chose the two most abundant anadromous salmonid species that inhabit Atlantic river basins in Patagonia and focused on the biggest runs of these two species: steelhead from Santa Cruz River (mean flow = 700 m<sup>3</sup> s<sup>-1</sup>; 50°S) and brown trout from Gallegos (38 m<sup>3</sup> s<sup>-1</sup>; 52°S) and Grande Rivers (40 m<sup>3</sup> s<sup>-1</sup>; 54°S) (Fig. 1). We assumed that trout were distributed over the Patagonian Continental Shelf (one of the widest in the world) on the basis of several indicators: both species have stable isotope signatures similar to other predator species feeding over this area (Ciancio et al. 2008b) and are enriched compared with off-shelf top predators (e.g., female elephant seals; Lewis et al. 2006), both species have a short migration to the ocean (on average 6 months for the Santa Cruz river steelhead; Pascual et al. 2001; Table 1), brown trout is considered a species that remains close to the estuaries (Elliott 1994), and, finally, no marine catches of brown trout have been reported further than 50 km from the estuary in 10 yr of fisherman surveys (Ciancio 2009). Considering this, we

assumed a potential marine distribution for steelhead to be located within shelf waters with sea surface temperatures (SST) of 6–14°C (Burgner et al. 1992; Welch et al. 1998) during the warm period, October–March, when they actively feed in the ocean. For brown trout, which typically remain within 80 km of the estuary (Elliott 1994), we assumed that their marine distribution was confined within a 100-km radius around the outflow of natal rivers (Fig. 1).

**Sample collection**—During 2001–2006, we sampled 55 adult steelhead from the Santa Cruz River and brown trout from the Gallegos River (14 adults) and Grande River (eight adults) using a combination of rod and reel, gill nets, and electrofishing. Fork length (FL) and mass of adult fish were recorded, except in the Grande River, where FL was back-calculated from scale measurements and body mass estimated from a length–weight regression for Grande River trout (O’Neal et al. 2007). The estimated initial and final weights-at-age for each year of marine growth were used as inputs for bioenergetics model simulations of marine consumption described below.

We focused on five primary prey species (amphipods *Themisto gaudichaudii*, euphausiids *Euphausia lucens*, small and large sprat *Sprattus fuegensis*, silverside *Odontesthes smitti*, and Patagonian longfin squid *Loligo gahi*) on the basis of a multiple step analysis. First, potential prey in the

Atlantic Ocean were selected after a bibliographic review of preferred marine food items of trout in other regions of the world and prey distribution in the water column in Patagonia (Ciancio et al. 2008b; Ciancio 2009). Second, the spatiotemporal overlap between prey distribution and the potential distribution of trout on the Continental Shelf was examined, discarding prey that did not overlap with the hypothesized trout distribution (Ciancio 2009). Finally, we considered the stomach contents of a few brown trout captured at sea (M. Amaya pers. comm.; D. Fernandez pers. comm.). The spatiotemporal overlap analysis was also done to detect seabird colonies with potential trophic interactions with trout (Ciancio 2009). Prey were captured between October and March by commercial trawlers and artisanal fishermen and during austral research cruises of the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP; Fig. 1).

*Stable isotope analysis and diet determination*—Approximately 50 g of dorsal muscle (or muscle from the head in the case of the Grande River fish) was extracted from each individual trout and preserved frozen during transport to the laboratory. For ecotype and age determination, scales were removed from both sides of the fish from an area located below the anterior margin of the dorsal fin (for 10 Gallegos River brown trout, no scales were collected). Fish were assigned to resident and anadromous ecotypes on the basis of scale growth patterns and stable isotope signatures (Ciancio et al. 2008a), which allowed us to discard resident fish from the diet analysis.

Stable isotope analysis for C and N was conducted on dorsal muscle from trout and from whole prey organisms. Samples were dried at 60°C for 48 h and ground to a fine powder. To avoid bias in <sup>13</sup>C determination, lipids were extracted on samples with high lipid content (i.e., sprat and salmon caught in the ocean). All samples were analyzed for C and N content and stable isotopic signatures at the Stable Isotope Facility, University of California, Davis. The stable isotope ratios were expressed as  $\delta$  values as ‰:  $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ , where  $X$  is <sup>13</sup>C or <sup>15</sup>N and  $R$  is the corresponding ratio <sup>13</sup>C:<sup>12</sup>C or <sup>15</sup>N:<sup>14</sup>N. Standards used were Vienna Peedee belemnite for C and N<sub>2</sub> for N.

We used the software IsoSource to estimate marine diet along the ontogeny of trout (Phillips and Gregg 2003). The software estimates the frequency of proportions of the collection of prey that satisfy the observed mixing conditions of the isotopic signatures. To run the model, we used published stable isotope concentrations of trout and prey in previous articles (Ciancio et al. 2008a,b) plus those generated during the present study. Sprat are the most abundant pelagic forage fish species in the area considered; size classes are geographically segregated (Sánchez et al. 1995) and have distinct stable isotopic signatures. For these reasons, sprat were separated into two size classes (small sprat < 90 mm FL; and large sprat > 90 mm FL). We first ran the model with the six prey categories and discarded those prey that showed low proportion in diet (< 5%).

Diet composition inputs for bioenergetic simulations of marine consumption by steelhead were expressed as the

median diet proportions with 5% and 95% percentiles resulting from the isotope mixing model (Fig. 2). Both age-3 and age-4 steelhead showed the same stable isotope signatures, so their diets were grouped together. Diets for older age classes were analyzed separately. Coastal silversides were excluded as prey for bioenergetic simulations of steelhead consumption because the mixing model indicated they contributed < 5% of the diet.

Diets for brown trout were combined for the Gallegos and Grande Rivers and were analyzed by size classes instead of by age because scales were not available to age-10 individuals from Gallegos River (Fig. 3). Euphausiids were not included in the brown trout model because the mixing model indicated they were a small proportion of the diet. The offshore distribution of euphausiids (Sabatini et al. 2004) was somewhat spatially segregated from the more coastal distribution of brown trout; moreover, euphausiids represented a low proportion of the marine diet for brown trout from other regions of the world (Knutson et al. 2001; Rikardsen and Amundsen 2005).

*Bioenergetic modeling*—We used population-specific data on annual marine growth increments, diet (from stable isotopes), and energy density as inputs to the Wisconsin bioenergetics model (Hanson et al. 1997) to estimate consumption of marine prey by steelhead and anadromous brown trout. This model has been widely used on fish populations, as reported in more than 250 scientific publications (Hartman and Kitchell 2008). Physiological parameters for steelhead were taken from the default values in the Wisconsin software (Rand et al. 1993) and from Dieterman et al. (2004) for brown trout (brown trout is not included in the set of species available in the software menu). Age-specific daily rates of consumption (g d<sup>-1</sup>) for all prey were computed. For steelhead, model runs began in the spring (months 9, 10, or 11, depending on age class; Table 1) and started in late winter for brown trout (month 8; Table 1). Daily consumption rates of individuals of each age class were expanded to population-level consumption estimates using initial abundance estimates for each age class, which were reduced by the daily mortality rate throughout the simulation. Indigestible proportions used for prey were 15% for crustaceans, 3% for fish, and 1% for cephalopods (Hanson et al. 1997).

*Energy density*—The energy density (ED, J g<sup>-1</sup> wet weight) of prey and consumers was estimated by bomb calorimetry (Parr model 1241). Brown trout ED was estimated by the relationship between ED and percent dry mass (Ciancio et al. 2007). ED of trout entering the ocean was estimated from fish at the end of the spawning season (remaining eggs were removed before ED estimation on females), and ED of returning fish was estimated from fish from the main run.

*Life histories*—Populations (age structure and survival; Table 1) and growth data were taken from our own database, Grupo de Estudios de Salmónidos Anádromos (GESA), for steelhead, from the Dirección de Pesca y Actividades Portuarias de Santa Cruz database for the

Table 1. Parameters used for bioenergetics simulations of the marine growth phase for different life history types and ages of anadromous steelhead and brown trout. Ages are presented as years in freshwater, saltwater. ED, energy density ( $\text{J g}^{-1}$  wet wt); *S*, survival (annual %); *N*, duration of the marine growth phase (d).  $^{13}\text{C}$  and  $^{15}\text{N}$  are stable isotope concentrations of C and N, respectively. Marine temperatures are average monthly thermal experiences ( $^{\circ}\text{C}$ ); temperatures are only presented for months when fish were in marine waters. Prey diet proportions and prey energy density are expressed on a wet weight base. Values in first row of diet proportion section indicate energy density (left) and stable isotopes (right) ( $^{13}\text{C}$ ;  $^{15}\text{N}$ ) of prey. Species river combinations: STSc, steelhead Santa Cruz River; BTGa, brown trout Gallegos River; BTGr, brown trout Grande River. Prey species: Euph., euphausiids; Amphip., amphipods; Sprat s., small sprat; Sprat l., large sprat.

Sp. and river	Age (yr.yr)	Initial weight (g)	Final weight (g)	Initial ED	Final ED	<i>S</i> (%)	$^{13}\text{C}$	$^{15}\text{N}$	<i>N</i> (d)	Marine temperature ( $^{\circ}\text{C}$ )											
										1	2	3	4	5	6	7	8	9	10	11	12
STSc	2.1	40	931	4793	8125	27	-19.7	14.9	240	10	11	10	10	9			6	8	9	9	
STSc	2.2	890	2083	5398	8125	27	-19.7	14.9	210	10	11	10	10					8	9	9	
STSc	2.3	1702	3503	6512	7999	30	-20	14.9	150	10	11	10							9	9	
STSc	2.4	2605	4243	6996	8728	67	-19.5	15	150	10	11	10							9	9	
STSc	2.5	3514	4586	6900	9178	60	-19.9	15.4	150	10	11	10							9	9	
STSc	2.6	4273	5150	6900	9178	60	-19.9	15.4	150	10	11	10							9	9	
STSc	2.7	4482	6050	6277	9178	60	-19.9	15.4	150	10	11	10							9	9	
STSc	≥9	4373	5975	5940	9178	60	-19.9	15.4	150	10	11	10							9	9	
BTGa	2.1	40	840	4631	7610	39	-18.3	16.2	450	12	13	12	11	10	4	3	6	6	8	12	12
BTGa	2.2	840	2568	5479	7610	39	-18.3	16.2	210	12	13						6	6	8	12	12
BTGa	2.3	2568	5212	5479	7610	39	-17.4	16.2	210	12	13						6	6	8	12	12
BTGa	2.4	5212	5831	5479	7610	36	-17.4	16.2	210	12	13						6	6	8	12	12
BTGa	2.5	5831	6635	5479	7610	76	-17.4	16.2	210	12	13						6	6	8	12	12
BTGa	3.1	547	1050	4631	7610	39	-18.3	16.2	450	12	13	12	11	10	4	3	6	6	8	12	12
BTGa	3.2	1050	2750	4790	7610	39	-18.3	16.2	210	12	13						6	6	8	12	12
BTGa	3.3	2750	3304	4790	7610	76	-17.4	16.2	210	12	13						6	6	8	12	12
BTGr	2.1	40	1999	4631	7610	42	-18.3	16.2	450	12	12	11	11	10	4	2	5	5	6	11	12
BTGr	2.2	1999	2843	4790	7610	42	-18.3	16.2	210	12	12						5	5	6	11	12
BTGr	2.3	2843	4411	4790	7610	42	-17.4	16.2	210	12	12						5	5	6	11	12
BTGr	2.4	4411	5031	4790	7610	42	-17.4	16.2	210	12	12						5	5	6	11	12
BTGr	2.5	5031	6691	4790	7610	36	-17.4	16.2	210	12	12						5	5	6	11	12
BTGr	2.6	5031	6970	4790	7610	11	-17.4	16.2	210	12	12						5	5	6	11	12
BTGr	2.7	5031	6970	4790	7610	11	-17.4	16.2	210	12	12						5	5	6	11	12
BTGr	3.1	200	2151	4631	7610	43	-18.3	16.2	450	12	12	11	11	10	4	2	5	5	6	11	12
BTGr	3.2	2151	2921	4790	7610	43	-17.4	16.2	210	12	12						5	5	6	11	12
BTGr	3.3	2921	3858	4790	7610	43	-17.4	16.2	210	12	12						5	5	6	11	12
BTGr	3.4	3858	5089	4790	7610	25	-17.4	16.2	210	12	12						5	5	6	11	12
BTGr	3.5	5089	7286	4790	7610	25	-17.4	16.2	210	12	12						5	5	6	11	12

Gallegos river brown trout, and from information provided by Sarah O'Neal (Flathead Lake Biological Station, University of Montana) for the Grande River fish. The modeled age classes were selected from life history patterns observed for these populations. Santa Cruz River steelhead have a dominant life history type (90%) that spends 2 yr in freshwater before migrating to the ocean as smolts. Brown trout have a more complex life cycle. Gallegos River brown trout exhibited four life history types, with the dominant strategies spending 2 (66%) or 3 yr (17%) in freshwater. Brown trout from the Grande River exhibited the same dominant life histories but different proportions (54%, 2 yr; 33%, 3 yr, in freshwater).

*Growth*—The growth achieved during the annual ocean feeding migration was estimated by subtracting the mass of spawners at the end of the spawning season (used as the initial mass) from the mass of the next older age class at the beginning of the spawning run. Because of the extended spawning period for brown trout, the time spent in freshwater was unknown, so the difference between mean

body masses of consecutive age classes was used to estimate marine growth. Body mass of the age-2 or age-3 smolts was inferred from resident fish of the same age (Table 1).

*Survival*—Annual survival rates were estimated from the age class structure (Chapman and Robson 1960) found in the databases mentioned above for the three populations. Mortality rates of Santa Cruz steelhead were similar to those estimated for steelhead for lakes Ontario and Michigan (Rand et al. 1993; Table 1).

*Population sizes*—Abundance estimates only exist for brown trout in the Grande River. With the use of mark recapture methods, O'Neal et al. (2007) estimated that a population of 55,000 anadromous adult brown trout recruited to the sport fishery (95% CI between 44,700 and 71,400 individuals). Assuming a marine mortality rate of 58% (the same as for the next age) during their first year at sea, these adults should have originated from a population of 17,183 age-2.1 (first value represents the number of years [2] spent in freshwater, second value is the number of



Table 2. Total consumption ( $\times 10^3$  kg yr<sup>-1</sup>) by prey item for three abundance scenarios of trout and for the three river populations (brown trout in Grande and Gallegos; steelhead in Santa Cruz). The population levels ( $N$ ) indicated in the first column represent different abundance scenarios for smolts + adults for each of the three river populations.

$N$	Squid	Silversides	Sprat, small	Sprat, large	Amphipods	Euphausiids	Total
10,000	11.8	19.2	20.5	17.6	67.0	1.8	148.1
50,000	59.0	96.4	102.6	88.1	335.4	9.3	690.8
100,000	118	192.8	205.2	176.2	670.8	18.6	1381.6

with foraging areas that overlapped potential trout distribution areas. Wilson et al. (2007) estimated daily requirements of 664 g of food for a Magellanic penguin breeding two chicks at Cabo Virgenes. Brown (1989) estimated a daily consumption of 530 g for rockhopper penguins breeding at the Prince Edwards Islands. We used these estimates to calculate the total amount of food consumed by the birds breeding along the coast. We assumed that the cormorants consumed the same fraction of their body mass per day as estimated for the penguins during egg incubation (12% of body mass) and during chick rearing (18% of body mass). The daily ingestion was estimated as 198 g for rock cormorant and 165 g for imperial cormorant during egg incubation, 284 g for rock cormorant and 287 g for imperial cormorant during chick rearing (average body mass from Punta et al. [2003]). Consumption was estimated by adding up adult daily food requirements over the incubation period, plus daily food

requirements during chick rearing over the rearing period (Frere 1993; Frere et al. 2005; Raya Rey 2005).

## Results

*Steelhead diet*—We found ontogenetic changes in the diet of steelhead, which agreed with general patterns described for salmonids (Keeley and Grant 2001; Fig. 2). The contribution of macrozooplankton (euphausiids and amphipods) in the diet declined with age, from a median value of 66% of the diet for age-3 and age-4 individuals to 42% for age-7 and older individuals. Coastal zooplankton (amphipods) eaten by younger steelhead were replaced by euphausiids that inhabited offshore waters in the diet of older fish. Sprat of all sizes increased from 30% to 45% and became the dominant prey in the diet of older steelhead. Small sprat were the dominant prey eaten by all ages, but the proportion of large sprat increased with age (8–19%). Consumption of

Table 3. Population numbers ( $N$ , number of pairs), total consumption ( $C$ ,  $\times 10^3$  kg), diet proportions of prey (by weight), prey biomass ( $\times 10^3$  kg) consumed by seabirds for prey items that were also eaten by trout, and prey stocks. Trout consumption is assuming population sizes of 50,000 individuals per river. References (Ref.) are: (a) Wilson et al. 2005, (b) Raya Rey 2005, (c) Sclaro et al. 1999, (d) Frere 1993, (e) E. Frere pers. comm., (f) mean proportion between M. León and C. Virgenes colonies, (g) Schiavini et al. 2005, (h) Millones et al. unpubl., (i) Ferrari et al. 2004, (j) Arkhipkin et al. 2004, (k) Sánchez et al. 1995. Prey: SF, sprat; OS, silverside; LG, Patagonian longfin squid; TG, amphipods; and EL, euphausiids.

Region/sp./colony	$N$	$C$	Diet proportion of prey					Prey consumption ( $\times 10^3$ kg)					Ref.
			SF	OS	LG	TG	EL	SF	OS	LG	TG	EL	
Santa Cruz province													
Rockhopper penguin	180	16	0.4			0.4	0.2		7		7	3	e
Magellanic penguin													
Deseado-S. Julián	98,190	7038	0.4	0.2	0.2			2745	1267	1337			a,d
Santa Cruz River-M. León	99,200	7111		0.3	0.7			36	1849	5148			c
R. Gallegos	3560	255	0.5	0.4	0.1			128	102	25			f
Cabo Virgenes	89,200	6394	0.65	0.35	0.1			4156	1598	511			a,c,d
Imperial cormorant	19,238	496	0.15	0.31	0.53			74	154	262			h,i
Rock cormorant	1513	39			0.3					12			h,i
Del Fuego Staten islands													
Rockhopper penguin	174,000	7924	0.1		0.3	0.1	0.1	792		2219	436	872	b
Magellanic penguin	120,919	8667	0.3		0.5			2600		4334			g
Imperial cormorant	16,485	425	0.15	0.31	0.53			64	132	225			h,i
Rock cormorant	2191	56			0.3					16.9			h,i
Total birds	624,496	38,406						10,601	5102	14,092	442	875	
Brown trout/Gallegos River													
		195						45	45	19	85		
Brown trout/Grande River													
		223						54	51	23	94		
Steelhead/Santa Cruz River													
		273						90		17	156	9	
Total trout		690						190	96	59	335	9	
Prey stock								320,000		30,000			j,k

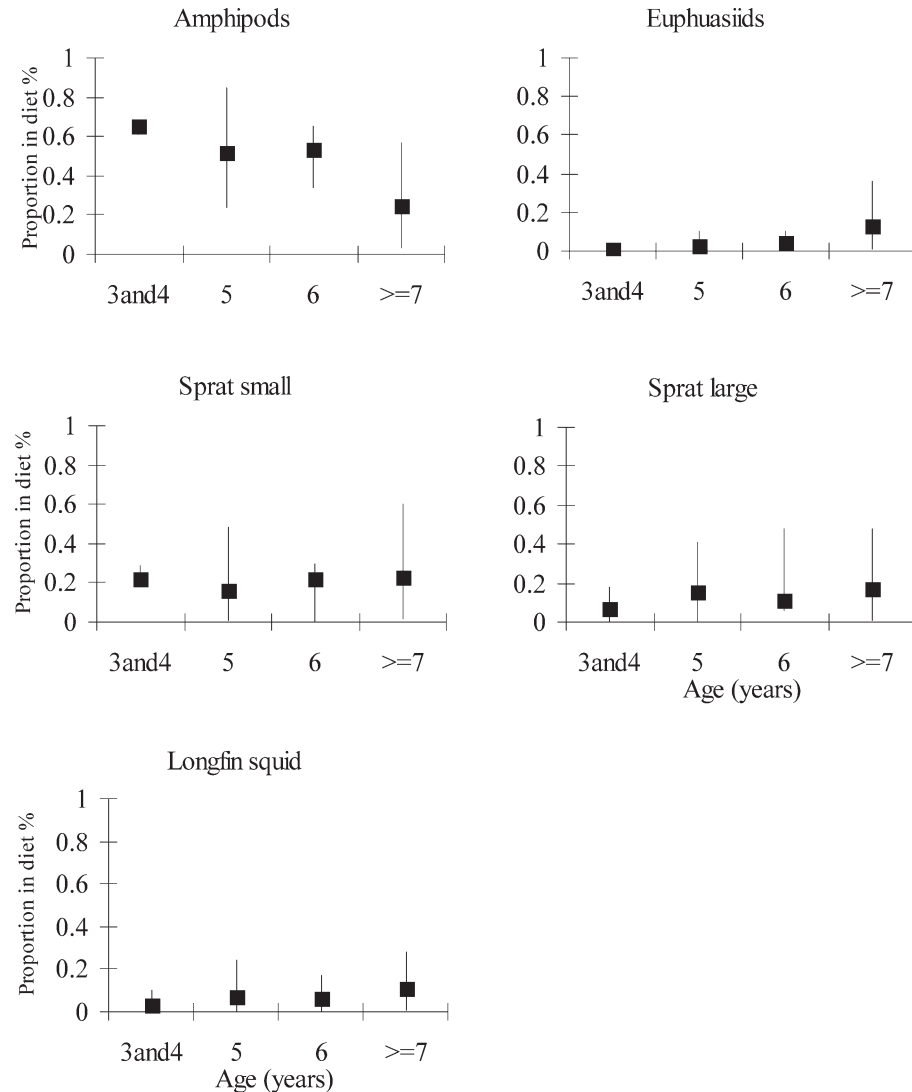


Fig. 2. Steelhead diet inferred from a stable isotopes mixing model. Values are the median and the 5% and 95% percentiles predicted by the model. Tolerances between 0.001 and 1.000 were used (Phillips and Gregg 2003).

longfin squid was low for all age groups (4–12%), but the proportions increased in the diets of older steelhead.

**Brown trout diet**—Amphipods (60%) and coastal silversides (27%) dominated the diet of smaller brown trout (400–700 mm), whereas sprat (9%) and squid (3%) were less important (Fig. 3). The diet of larger brown trout (> 700 mm) was dominated by sprat (small and large, 40%) and similar proportions of silversides (19%), amphipods (22%), and squid (18%).

**Consumption of marine prey by trout**—For a given population size, steelhead consumed more food than brown trout ( $273 \times 10^3$  kg yr<sup>-1</sup> for a population of 50,000 steelhead compared with  $195 \times 10^3$  kg consumed by a similar population of brown trout from the Gallegos River, and  $222 \times 10^3$  kg consumed by a similar population of brown trout from the Grande River; Fig. 4; Table 2). These differences resulted from several features of the model

simulations: brown trout consumed prey with higher ED and digestibility (thus requiring less food to attain a given growth rate) and exhibited a different age class structure (Table 1) and different physiological parameters (Dieterman et al. 2004).

Under the medium-sized population scenarios (50,000 individuals per river), the total biomass consumed by the three populations was  $690 \times 10^3$  kg (Table 2). Amphipods were the main prey, followed by sprat, then silversides, squid, and euphausiids.

Consumption by different age classes showed similar patterns between steelhead in the Santa Cruz River and brown trout in the Gallegos River (Fig. 4). In both populations, age-4 fish with 2 yr in freshwater (2.2) were the age classes that consumed the most biomass of marine prey (31% of the total biomass consumed by Santa Cruz River steelhead and 30% of the total consumption by Gallegos River brown trout). Age classes from 3- to 6-year-old consumed the bulk of the total biomass in both

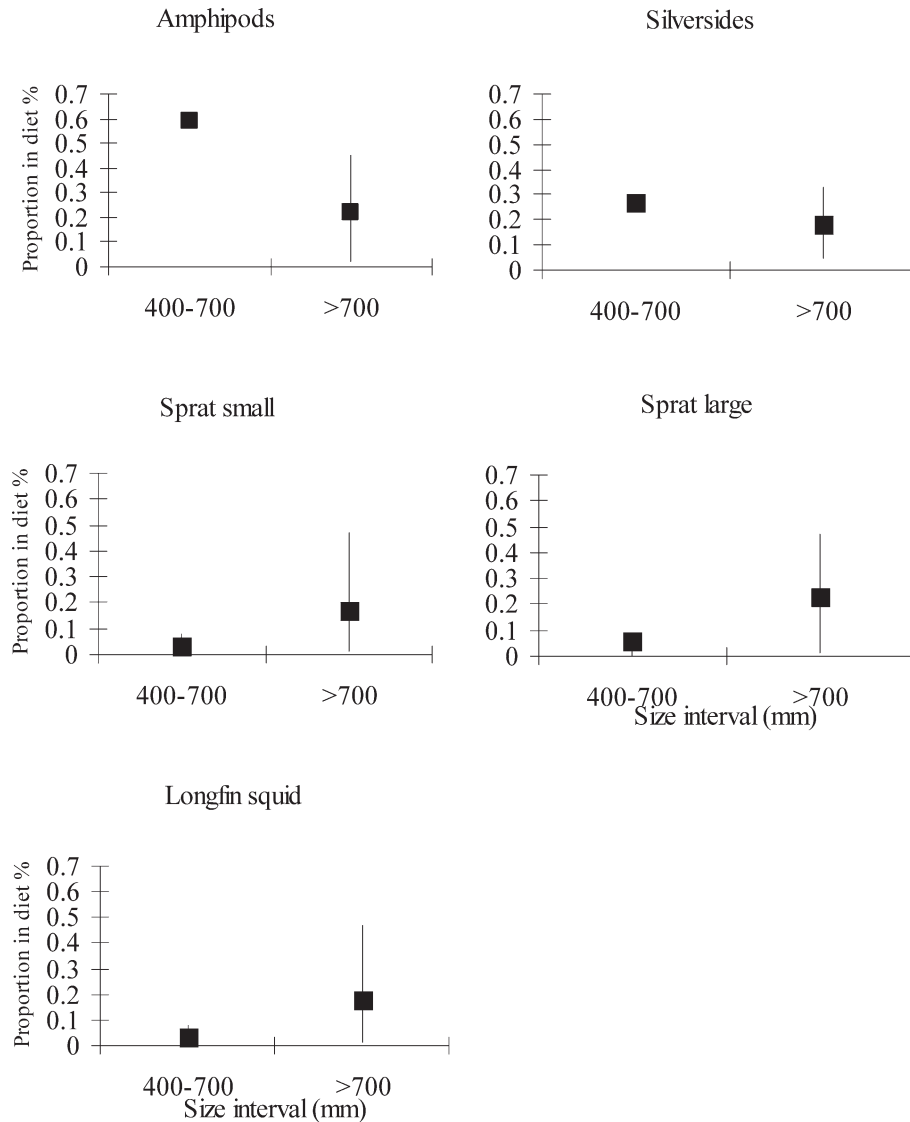


Fig. 3. Brown trout diet inferred from a stable isotopes mixing model. Values are the median and the 5% and 95% percentiles predicted by the model. Tolerances between 0.001 and 1.000 were used (Phillips and Gregg 2003).

population (91% of total biomass consumed by Santa Cruz River steelhead and 88% for Gallegos River brown trout).

Brown trout from Grande River showed a different pattern. Fish with 2 yr in freshwater and 1 yr of marine growth (2.1) and fish with 3 yr in freshwater and 1 yr of marine growth (3.1) were the age classes that consumed the most biomass of marine prey. Remaining age classes with 2 yr in freshwater exhibited very similar marine consumption rates (Fig. 4). Fish with 3 yr in freshwater and more than 2 yr of marine growth consumed a small fraction of the total consumption by the population.

*Diet and consumption of seabirds*—An estimated 624,496 seabird pairs breed in the area of interest (Table 3). The most abundant species were Magellanic penguin (411,069 pairs), rockhopper penguin (174,180 pairs), imperial cormorant (35,723 pairs), and rock cormorant (3704 pairs).

As revealed by the bibliographic review, Magellanic penguins fed on similar proportions of sprat, silversides, and squid in the northern area (Fig. 1; Table 3). In the central area (Cabo Vírgenes colony), sprat were the primary prey, and squids were the main prey in the southern colony (Staten Island). Rockhopper penguins fed mainly on larval sprat, macrocrustaceans, and zooplankton in the north, whereas squid were the main prey in the south.

Diets of imperial and rock cormorants in the north consisted mainly of notothenids and squid, but the rock cormorant fed more frequently on coastal prey (Table 3). In the central area, the imperial cormorant fed on notothenids, squid, sprat, and silversides.

From the seabird species identified as potential competitors of trout, Magellanic penguin were the main predator in the area, consuming  $25,836 \times 10^3 \text{ kg yr}^{-1}$  (37% sprat, 19% silversides, and 44% squid). Second in order was the



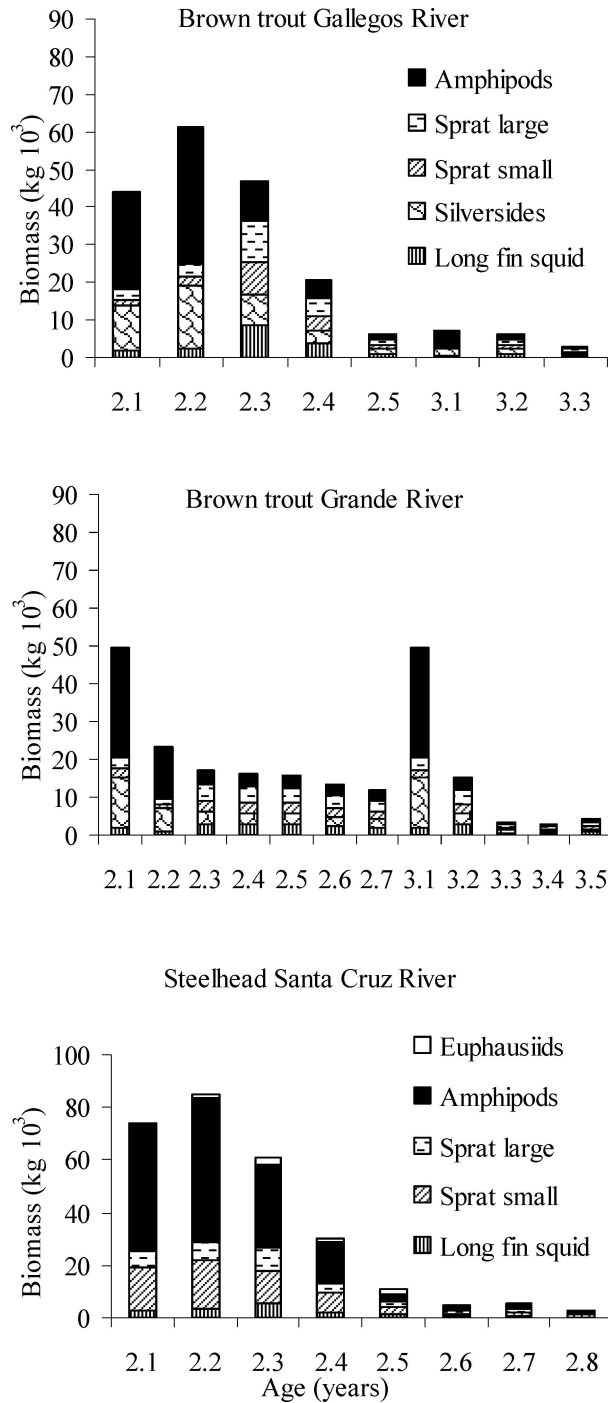


Fig. 4. Overall biomass consumed annually by 50,000 individuals of each of the three trout populations considered. Freshwater.marine ages, indicated as different life history stages, are indicated on the x-axis.

rockhopper penguin, which consumed  $4335 \times 10^3$  kg (18% sprat, 51% squid, 10% amphipods, and 20% euphausiids). Imperial cormorants were the third greatest consumers, but consumed far less than penguins ( $912 \times 10^3$  kg: 15% sprat, 31% silversides, and 53% squid). Rock cormorants consumed the least amount of food,  $29 \times 10^3$  kg (100% squid). For the marine prey resources shared by birds and

trout, birds consumed large quantities of squid ( $14,092 \times 10^3$  kg), sprat ( $10,601 \times 10^3$  kg), and silversides ( $5102 \times 10^3$  kg), but far less biomass of zooplankton (euphausiids and amphipods).

In terms of overall average consumption across all species, age groups, and ranges, the total amount of food consumed by the three trout populations of 50,000 individuals each represented only 2.3% of the total biomass consumed by birds, suggesting a low potential for competition by the trout on the birds. Only amphipods were consumed at comparable levels by birds and trout. For the other prey types considered, trout consumption was never higher than 2% of the amount consumed by birds (Table 3). However, when examined in a more spatially explicit context, if we consider the consumption by trout in close proximity to bird colonies, then some potential competition scenarios could occur. Such is the case of brown trout feeding on silversides, restricted to coastal areas.

### Discussion

Our simulations indicated that the total biomass of shared marine prey resources consumed by trout represented a small fraction of the biomass consumed by birds and also represented a very small fraction of the available prey biomass. For example, the total biomass of sprat consumed by trout represented only 0.05% of available biomass ( $3.2 \times 10^8$  kg; Sánchez et al. 1995; Table 3). Amphipods were the only prey in which similar amounts were consumed by birds and trout, presenting a potential competition scenario for this prey. However the high abundance of amphipods in the region (densities have been reported in this region as high as  $3.5 \text{ g m}^{-3}$ ; Grande Bay, Sabatini et al. 2004) decreases the chances for this to occur. Amphipods are the main prey for the most abundant commercial fish and squid. Common hake *Merluccius hubbsi* alone consume  $8 \times 10^9$  kg of amphipods and euphausiids in this region (Prenski and Angelescu 1993). The continental Patagonian longfin squid stock has been estimated at  $3 \times 10^7$  kg (Arkhipkin et al. 2004; Table 3); seabirds consume nearly half of this stock ( $1.4 \times 10^7$  kg), potentially reducing squid densities around colonies. No biomass estimates are currently available for silversides, but regarding their restricted distribution to coastal waters (first 5 km from the coast), their abundance should be lower than the other prey considered, making this prey a candidate for potential competition and localized depletion.

Considering more localized competition based on specific species or locations, steelhead consumed more food than brown trout, but their zooplanktophagous feeding patterns and broader distributional range at sea could dilute their effects on marine ecosystems. In contrast, brown trout were a more typical coastal species, remaining in brackish waters in relatively close proximity to the estuary (Elliott 1994). Gallegos and Grande River brown trout could potentially consume nearly  $100 \times 10^3$  kg  $\text{yr}^{-1}$  of silverside, several times the amount of fish captured by artisanal fishermen or nearly the same amount of silversides consumed by penguins from a breeding colony in the Gallegos River estuary ( $102 \times 10^3$  kg; Table 3). Other potential effects were the consumption of pelagic

larvae of species in estuarine or coastal waters. Salmonid smolts remained in confined waters before their offshore migrations. Smolts and juveniles could feed on larvae of important economic resources such as king crabs (*Lithodes santolla* and *Paralomis granulosa*), potentially affecting the recruitment of this species.

Bioenergetic modeling scenarios are especially sensitive to estimates of annual survival, growth, and population abundance (Rand et al. 1993; Hartman and Kitchell 2008). We considered that our major sources of uncertainty in the population-level consumption estimates were related to the abundance estimates of the trout. For this reason, we postulated three population size scenarios. Even considering the highest abundance for the three trout populations (100,000 individuals), total consumption represented less than the 5% of the total biomass consumed by birds. We were able to estimate trout growth during marine migration with different accuracy for each population. We used our own large database for steelhead, selecting only fish that just arrived from the ocean (fish that have not been starving in freshwater). However, we estimated brown trout growth from body mass reported by sport anglers. Because we did not know the duration of the time spent in freshwater by fish, we used the difference between mean body mass values of subsequent ages. Consumption by brown trout could have been underestimated if either the initial mass was overestimated or the final mass was underestimated in the simulation.

To run the bioenergetics model, we assumed several behaviors for trout at sea (Hartman and Kitchell 2008). Whereas we consider seasonal changes in thermal experience by trout, we assumed a constant temperature experience throughout the day. Many salmonids perform daily vertical migrations in marine environments (Rikardsen et al. 2007; Walker et al. 2007) to follow prey, escape predators, or improve digestion efficiency. In the Patagonian Continental Shelf during the summer months, trout that migrated to deeper and colder waters could experience temperature changes, which could change the consumption estimates presented here.

Bioenergetic models often “borrow” energy density values from prey and predators from related species (Johnson et al. 2006; Vatland et al. 2008), incorporating an important source of error (Ney 1993; Hartman and Kitchell 2008). For our model inputs, both prey and predator energy densities were estimated by direct bomb calorimetry or by water content on tissues (Ciancio et al. 2007), reducing the potential error from the use of energy densities of related species.

The results presented in this work indicate that at the actual population numbers of trout are not important over all trophic players at the scale of the Patagonian Continental Shelf and might not be a threat, either as predators or as competitors. Further analysis will be needed to consider local effects in more restricted areas, including diet preferences of particular seabird and trout species and more realistic spatiotemporal dynamics of prey and potential competitors.

Here, we described a first attempt to estimate the effects of prey consumption by introduced steelhead and brown trout in the ocean. The methods described provide the basis

for future studies with other anadromous species that are expanding in the region, such as Chinook salmon. Chinook salmon populations are steadily expanding along the Pacific Coast of Patagonia (Correa and Gross 2007), being the most successful anadromous salmonid to invade and establish populations in rivers in the Southern Hemisphere. Chinook salmon also exhibit high growth and consumption rates. The effect of this species in the Southern Oceans remains unknown, this work constitutes a framework for future studies on the effects of expanding populations of exotic trout and salmon in Patagonia.

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