

Trophic relationships of exotic anadromous salmonids in the southern Patagonian Shelf as inferred from stable isotopes

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Abstract

On the basis of their thermal preferences, salmon introduced in South America can distribute over the whole Southern Patagonian Shelf Ecosystem (SPSE). Stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) data show that the SPSE is dominated by zooplanktivorous species (15 of 37), and its community is distributed over six trophic levels (TL), with salmonids occupying levels 4.2 to 4.9. A dual isotope mixing model was used to estimate diet proportions of adult salmonids (validated with stomach content analyses) and showed that chinook salmon (TL 4.9) and brown trout (TL 4.7) feed largely on sprats (96% and 79% predicted by the model) and were clustered together with intermediate size fish and cephalopod predators (TL 4.6–5), a diet similar to that in their native ranges (North Pacific and North Atlantic Oceans). Adult anadromous rainbow trout clustered together with zooplanktivorous species (TL 3.2–4.4), and the model predicted a diet dominated by planktonic crustaceans (55%), very different from the diet dominated by fish and squids characteristic of adult steelhead in the North Pacific Ocean. Diet predictions based on stable isotopes for Chinook salmon were indistinguishable from direct assessments of stomach contents of fish captured by bottom trawlers and overlapped widely with the diet of Magellanic penguins. The lack of reports on captures of anadromous rainbow trout by bottom trawlers suggests that this species has a shallower distribution. Stable isotope data for rainbow trout are very similar to those of rockhopper penguins, which feed on planktonic crustaceans, fish larvae, and juveniles.

The introduction of nonindigenous species constitutes one of the major environmental and economic threats to the structure and functioning of ecosystems worldwide (Lodge 1993). Yet the number of introduced species

continues growing everywhere, especially in marine and estuarine systems. There are several examples in which the ecological effects of a particular invasive species are very important (e.g., the Asian clam *Potamocorbula amurensis* to the San Francisco Bay). However, recent evidence shows that often the effects of invasions are additive (Sax and Gaines 2003). In general, our full understanding of the nature and magnitude of the ecological effects of multiple exotic species is limited to a few cases. Thus, predicting whether effects of an invasion will be important is still extremely difficult.

Salmonids are among the most widely introduced fish around the world (MacCrimmon 1971). Their effects on receiving freshwater communities are associated with competition for food and habitat, predation, and habitat alteration (e.g., Crowl et al. 1992). Little attention has been given to the potential effects of exotic anadromous salmonids (i.e., those that spend part of their life in the

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ocean) on receiving marine communities. Competition and predation at sea might not be negligible if we consider that anadromous salmonids are increasingly introduced into new marine areas around the world as a result of expanding aquaculture and that they are top predators with characteristically high feeding rates. In fact, salmon of the genus *Oncorhynchus* are the most significant pelagic predator species in their native North Pacific Ocean (Groot et al. 1995). Nevertheless, formal analyses of exotic salmonids in the ocean are restricted to one study on the distribution and food of chinook salmon (*Oncorhynchus tshawytscha*) in New Zealand (James and Unwin 1996) and another on the feeding behavior of anadromous rainbow trout (*Oncorhynchus mykiss*), atlantic Salmon (*Salmo salar*), and coho Salmon (*Oncorhynchus kisutch*) escaped from net pens in coastal Chile (Soto et al. 2001).

In Patagonia, the tip of South America, salmonids have been widely introduced and have been very successful at colonizing lakes and rivers (Pascual et al. 2002). In addition to these non-anadromous populations, evidence has started to accumulate in recent years that salmonids have been establishing anadromous populations in southern Patagonia, in contrast to limited success outside their native range elsewhere in the world (Pascual and Ciancio 2007). For instance, chinook salmon spawn in several river basins, both Pacific (Soto et al. 2001) and Atlantic (Ciancio et al. 2005); anadromous rainbow trout inhabit the Santa Cruz River of Argentina (Pascual et al. 2001); and sea-run brown trout (sea trout *Salmo trutta*) sustain world class fisheries in the continent, Tierra del Fuego, and Malvinas Islands (McDowall et al. 2001). Thus, they are already incorporated into the southwest Atlantic food web, although their status and effects on these communities are unknown.

The introduction of exotic anadromous salmon is likely to continue and increase as Chile moves forward to become the largest salmon producer in the world. Today, marine net pen aquaculture handles millions of salmonids in fjords of the Northern Patagonian Pacific Coast (primarily coho and Atlantic salmon, as well as rainbow trout) and is moving southward to the clean waters around the Strait of Magellan and Tierra del Fuego. The ecological effects of salmon aquaculture expanding south could reverberate on the southern Atlantic Ocean. Old and new information indicates that the southern portion of the Patagonian Shelf (Fig. 1) could constitute an important feeding ground for anadromous salmonids. Based on the oceanographic characteristics of the southern Pacific and Atlantic Oceans, together with general aspects of salmon biology, Donaldson and Joyner (1983) recommended developing salmon ranching experiments in Chile south of 45°S, a location that would facilitate migrations toward the Atlantic Ocean and into the highly productive waters of the Patagonian Shelf. The recent discovery of a spawning population of chinook salmon in the Santa Cruz River (50°S), an Atlantic drainage in Southern Argentina (Ciancio et al. 2005), and the corroboration with molecular techniques of their origin from ocean ranching experiments in southern Chile during the 1980s (Becker et al. 2007) provide the first concrete evidence of such a Pacific–Atlantic connection by migrating anadromous salmon. In southern Argentine Patagonia,

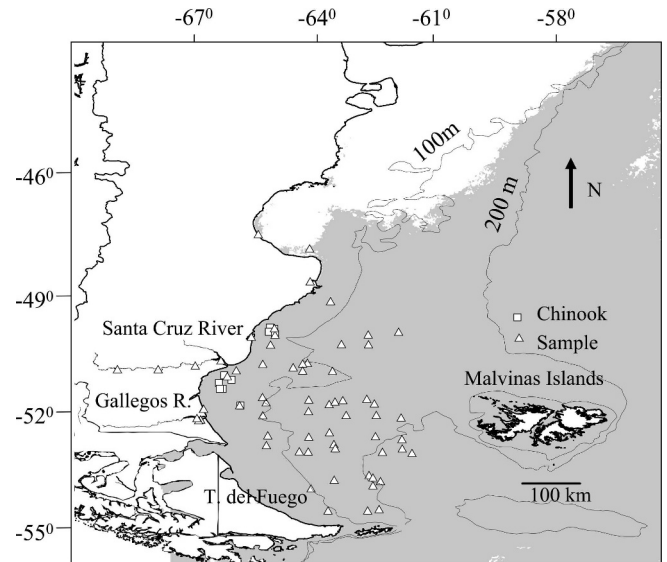


Fig. 1. Southern Patagonian Shelf Ecosystem Area. The grey area indicates potential distribution area for salmon at sea (mean temperatures between 4°C and 14°C from September to May). Triangles indicate sample collection locations and squares indicate chinook salmon (OT) captured at sea by commercial bottom trawlers.

exotic salmonids are potential competitors with several native marine species of conservation concern, such as penguins during their breeding season (Frere et al. 1996) and marine mammals. They are also potential predators of commercially or ecologically important species, such as the king crab larvae (*Lithodes antarcticus* and *Paralomis granulosa*), important economic resources in the fueguinean channels, or the fueguinean sprat (*Sprattus fuegensis*, Sánchez et al. 1995).

It is therefore relevant to ponder the trophic status of exotic anadromous salmon in the southern Patagonian shelf (hereafter called the Southern Patagonian Shelf Ecosystem [SPSE]; Fig 1). Whereas it is increasingly clear that the SPSE constitutes a productivity hotspot within the Argentine shelf (Rivas et al. 2006), there are very few community-wide studies, and food web structure remains poorly known.

In this work we generate sea surface temperature (SST) images to infer salmon distribution at sea and use stable isotope analysis (SIA) to (1) characterize trophic relationships among a large collection of species of the SPSE, (2) determine the trophic status of three species of exotic anadromous salmonids with spawning populations in Atlantic rivers of the region, and (3) discuss some of the potential effects of salmonids on the food web of the SPSE.

Methods

Study area and sample collection—We collected samples of marine organisms of the SPSE (Fig. 1) that were likely to interact directly with salmonids as prey, predators, or competitors, as well as key forage species in the region. To limit our effort within this large area, we concentrated on a section of the shelf where anadromous salmonids were

more likely to occur during their marine life stages. Ocean temperature has been the most extensively studied habitat variable in relation to the distribution of salmonids in the North Pacific. For instance, during summer months, steelhead on feeding grounds concentrated in waters with SSTs between 6°C and 12°C, rarely occurring at temperatures below 4°C or above 14°C (Burgner et al. 1992; Welch et al. 1998). Individual chinook salmon in coastal waters of the California Current implanted with archival tags consistently used waters with SST between 8°C and 12°C throughout the year (Hinke et al. 2005). A range of 4–14°C, therefore, includes temperature preferences of steelhead and chinook salmon in their native range. We mapped the occurrence of those waters in the Southeastern Atlantic Ocean based on SST extracted from NOAA (National Oceanic and Atmospheric Administration) AVHRR (Advanced Very High Resolution Radiometer) satellite images (Fig. 1). We processed 65 NOAA 14 satellite and 16 satellite (1 km × 1 km resolution) images of the period 1998–2003. A map of mean SST was generated for the period September–May, when salmon actively feed at sea (Groot et al. 1995), when Santa Cruz River anadromous rainbow trout reside at sea (Pascual et al. 2001), and when interactions with breeding seabirds are more likely to occur.

We limited our study to the shelf portion of the larger region with waters between 4°C and 14°C because available data suggest that exotic salmonids of Patagonia would not move beyond the shelf. All chinook salmon captures occurred close to the coast over the continental shelf, a behavior similar to that of the same species introduced in New Zealand (James and Unwin 1996). Santa Cruz rainbow trout, unlike typical long-range migrating steelhead from the Northern Hemisphere that spend between 2 and 4 years in the ocean (Burgner et al. 1992), have a reduced marine residency of 4–5 months (Riva Rossi et al. 2007), more similar to coastal rainbow trout from Kamtchatka (Pavlov et al. 1999). Sea trout typically perform short-distance migrations as compared to *Oncorhynchus* species, remaining closer to estuaries (Knutsen et al. 2004; Olsen 2006). Finally, female elephant seals (*Mirounga leonina*), top predators that forage in off-shelf waters (distances of up to 1,200 km from shore as depicted by satellite tracking), have contrastingly different stable isotope signatures from continental shelf top predators (Lewis et al. 2006). In particular, $\delta^{15}\text{N}$ values for female seals (11.2‰) are much less enriched than those of their shelf counterpart. Meanwhile, the isotope values we recorded for salmonids are consistent with likely trophic levels within the shelf food web, but inconsistent with off-shelf signatures.

Within the area selected, we collected samples corresponding to 30 different species of invertebrates and fish from the catch of artisanal fisheries, commercial bottom trawlers, and research cruises (0–341 m depth) in 2001–2005 and 7 species of seabirds and 2 of marine mammals collected on shore locations (Table 1). Zooplankton (euphausiids, amphipods, ctenophores, myctophids fish, and copepods) were obtained from stomach contents of fish and by nackthai net samples collected during a research cruise in March 2005. Seabird samples included recently dead chicks found on colonies, which are expected to reflect the trophic

status of parents during the breeding period within reach from colonies, and adult petrels and albatrosses incidentally caught by fishing boats. Chinook salmon samples were collected using gillnets in the Caterina River located within Estancia Cristina in Los Glaciares National Park (50°S 73°W; for details see Ciancio et al. 2005) and from incidental catches by bottom trawlers at sea from locations shown in Fig. 1 in 2002–2004. Sea trout samples were collected in the Gallegos River (52°S; Fig. 1) in 2004–2005 from sport fisheries catches, and rainbow trout/steelhead samples were collected in the Santa Cruz River (50°S 69°W; see Pascual et al. 2001; Fig. 1) during years 2001–2005 using gillnets and from catches by sport fishermen.

Stable isotope analysis—SIA is a useful tool for food web analysis (Van Der Zanden et al. 1997). SIA has been extensively used in salmon (Satterfield and Finney 2002; Schindler et al. 2003), marine mammal, and seabird ecology studies (Hobson et al. 1996; Forero et al. 2002). In aquatic environments, stable isotopes of carbon (C) and nitrogen (N) can identify food chains and trophic position (Cabana and Rasmussen, 1994). Several authors (e.g., Welch and Parson 1993; Satterfield and Finney 2002) pointed out the importance of SIA to assess competitive overlap among different species of Pacific salmon and used SIA to describe the trophic position of salmonids feeding on the North Pacific Ocean. We conducted C and N stable isotope analyses on 36 marine species and 3 anadromous salmonids. Whole organisms for small species, dorsal muscle of large fish species, and pectoral muscle of recently dead seabirds were removed and tissues were stored frozen for transport to the laboratory, where samples were dried at 60°C for 48 h and ground to a fine powder. Carbonates were extracted from small crustaceans by fuming HCl. All samples were analyzed for C and N content and stable isotope signatures (Stable Isotope Facility, University of California, Davis). The stable isotope ratios are expressed as δ values in ‰: $\delta X = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1,000$, where X is ^{13}C or ^{15}N , and R is the corresponding ratio $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$. Standards used were Vienna Pee Dee belemnite for C and N_2 for N.

The food web analysis—In order to assign a trophic level to all species, we considered euphausiids to have the lowest trophic level of all groups considered, and this was supported by their $\delta^{15}\text{N}$ values. This group is generally recognized as omnivorous but *Euphausia lucens* has been reported to feed entirely on phytoplankton under condition of high ambient chlorophyll (Gibbons et al. 1991). We assigned a value of 2.0 to this group, which should be considered as a relative rather than an absolute trophic level. Using the mean trophic fractionation (TF) factor for ^{15}N for marine carnivores (3.4‰) and herbivores (2.52‰; Van Der Zanden and Rasmussen 2001), we calculated trophic level by:

$$\text{TL}_{\text{predator}} = 2 + (\delta^{15}\text{N}_{\text{predator}} - \delta^{15}\text{N}_{\text{euphausiid}})/\text{TF} \quad (1)$$

To determine general trophic relationships among all species considered, including salmonids, we used a cluster analysis of mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Species with small sample

Table 1. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (one SD) and trophic level (TL) estimated assuming that zooplankton (euphausids) were entirely herbivorous and constitute trophic level number 2 (Gorokhova et al. 2005).

Group	Species n=39	Abbreviation	Common name	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	TL	
Zooplankton	Copepods (<i>Calanus australis</i>)	CO	Copepods	7	-20.0(1.8)	9.27(1.1)	2.57	
	Euphausid (<i>Euphausia lucens</i>)	EL	Euphausid	7	-19.8(0.7)	7.33(0.8)	2.00	
	<i>Themisto gaudichaudii</i>	TG	Amphipods	17	-20.9(1.5)	10.5(1.8)	2.94	
	<i>Ctenophores</i>	CT		1	-22.3	10.7	2.99	
Benthos	<i>Peisos petrunkevitchi</i>	PP	Patagonian shrimp	3	-18.0(0.2)	13.0(0.4)	3.67	
	<i>Munida gregaria</i>	MG	Lobster crab	4	-16.6(0.4)	7.92(0.7)	2.18	
Fish	Mictophids	MIC	Lanternfish	5	-21.9(0.7)	11.7(0.9)	3.29	
	<i>Sprattus fuegensis</i>	SF	Patagonian sprat	25	-20.2(1.0)	13.1(0.9)	3.72	
	<i>Patagonotothen ramsayi</i>	PR	Notothenids	5	-19.3(0.6)	14.8(1.0)	4.22	
	<i>Engraulis anchoita</i>	EA	Anchovy	6	-18.1(0.0)	14.9(0.6)	4.25	
	<i>Genypterus blacodes</i>	GB	Kingklip	5	-17.5(0.2)	17.7(0.2)	5.06	
	<i>Eleginops maclovinus</i>	EM	Haddock	6	-14.9(0.3)	17.2(0.4)	4.92	
	<i>Odontesthes smitti</i>	OS	Silverside	6	-14.0(0.8)	16.7(0.2)	4.76	
	<i>Macroronus magellanicus</i>	MM	Hoki	17	-18.2(0.7)	13.9(0.7)	3.95	
	<i>Merluccius hubbsi</i>	MH	Hake	6	-18.2(0.9)	17.0(0.1)	4.85	
	<i>Merluccius australis</i>	MAU		3	-17.4(1.0)	15.6(0.6)	4.43	
	<i>Micromesistius australis</i>	MA	Southern blue whiting	8	-18.3(0.7)	11.7(0.5)	3.29	
	<i>Salilota australis</i>	SA	Tadpole codling	3	-17.7(0.2)	15.3(0.3)	4.35	
	<i>Coelorhynchus fasciatus</i>	CF	Grenadier	2	-17.2	12.9	3.66	
	<i>Stromateus brasiliensis</i>	SBR	Butterfish	3	-20.4(0.3)	14.7	4.19	
	Sharks	<i>Scheowsweichthys bivius</i>	SB	Narrowmouthed catshark	3	-16.9(0.4)	16.7(0.3)	4.76
		<i>Squalus acanthias</i>	SAC	Spiny dogfish	3	-19.3(0.7)	15.2(0.8)	4.18
Salmonids	<i>Oncorhynchus mykiss</i>	OMS	Rainbow trout	51	-19.8(0.4)	14.9(0.4)	4.23	
	<i>Oncorhynchus tshawytscha</i>	OT	Chinook salmon	40	-18.7(0.4)	17.0(0.7)	4.87	
	<i>Salmo trutta</i>	ST	Sea trout	7	-18.9(0.8)	16.4(0.8)	4.68	
Cephalopods	<i>Loligo gahi</i>	LG	Patagonian longfin squid	10	-19.0(0.6)	13.6(0.7)	3.86	
	<i>Moroteuthis ingens</i>	MI		2	-18.7(0.4)	13.5(1.1)	3.84	
	<i>Illex argentinus</i>	IA	Patagonian squid	12	-18.1(0.3)	13.1(0.9)	3.70	
	<i>Semirosoia tenera</i>	STE	Lesser bobtail squid	1	-20.4	12.3	3.47	
	<i>Enteroctopus megalocyathus</i>	ETM		2	-15.2	17.5	5.02	
Sea birds	<i>Eudyptes chrysolome</i>	EC	Rockhopper penguin	4	-19.4(0.6)	15.2(0.3)	4.32	
	<i>Spheniscus magellanicus</i>	SM	Magellanic penguin	36	-18.2(0.4)	16.9(0.4)	4.82	
	<i>Phalacrocorax olivaceus</i>	PO	Neotropical cormorant	4	-15.9(0.8)	20.0(0.6)	5.74	
	<i>Phalacrocorax gaimardi</i>	PG	Red legged cormorant	4	-17.3(0.2)	17.5(0.1)	4.99	
	<i>Phalacrocorax atriceps</i>	PA	Imperial cormorant	5	-15.8(0.3)	19.0(0.4)	5.45	
	<i>Thalassarche melanophris</i>	TM	Black-browed Albatross	9	-18.0(0.4)	15.0(1.1)	4.28	
	<i>Procellaria aequinoctialis</i>	PAE	White-chinned Petrel	8	-18.6(0.2)	15.5(0.2)	4.40	
Mammals	<i>Otaria flavescens</i>	OF	Southern sea lion	1	-17.3	22.5	6.46	
	<i>Cephalorhynchus commersonii</i>	CC	Commerson's dolphin	2	-16.4	19.2	5.50	
			Total	341				

sizes ($n < 3$) or sampled in only one location were excluded from this analysis. We report results corresponding to the average linkage clustering method, but we found no major differences between our results and those from other clustering algorithms (nearest neighbor, furthest neighbor, group average, and Ward methods).

In order to validate cluster results and to interpret the actual trophic status and model-predicted diets of different species of salmonids (see next paragraph) within the SPSE, we compared their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures with those of two reference species in the database for which diets were well known by direct methods and foraging areas were known by satellite tracking (Wilson et al. 2005) and which were clustered close to salmonids (see Results): rockhopper penguin, *Eudyptes chrysolome* (EC), a zooplanktivorous (mainly crustaceans and fish larvae) species (Putz et al. 2001), and magellanic penguin, *Spheniscus magellanicus* (SM), which in Southern Patagonia locations feeds primarily

on fish (mostly sprat *Sprattus fuegensis* [SF]) and squid (Frere et al. 1996). One-dimensional comparisons of $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values can lead to incorrect conclusions about whether two groups are statistically different, unless the covariance between isotopic values is also taken into account. We therefore used a Hotelling's T^2 for testing hypotheses concerning mean values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for salmon and reference species. We tested for normality in the isotope data by residual inspection using QQ (Quantile Quantile) plots. To test for the existence of inter-annual effects on a salmon stable isotope signature we applied a t -test to values recorded for chinook in two different years and an analysis of variance (ANOVA) to steelhead data for 4 years.

Salmonid trophic relationships—We estimated the most likely diet of salmonids based on a simple linear mixing model incorporating both C and N isotopes (Phillips 2001). The model relates the stable isotope composition of a

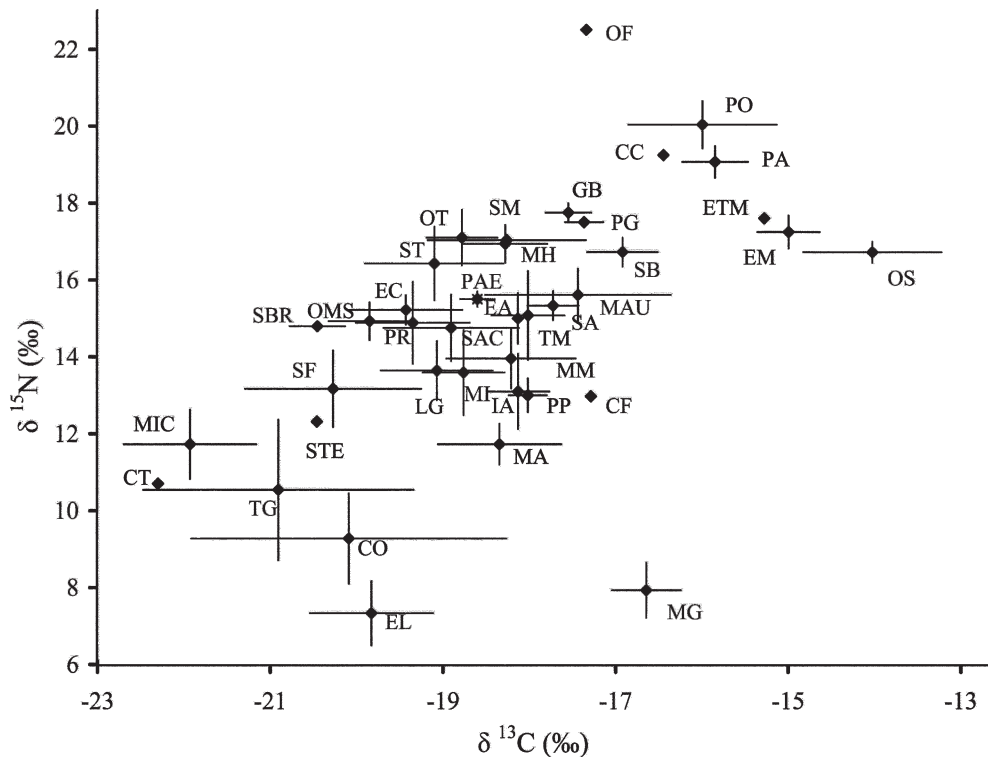


Fig. 2. Stable carbon and nitrogen isotopes in the food web of the Southern Patagonian Shelf Ecosystem (± 1 SD). The $\delta^{13}\text{C}$ values on the x-axis reflect potential carbon sources (more depleted in more offshore-pelagic waters), whereas $\delta^{15}\text{N}$ on the y axis generally can be interpreted as proportional to trophic level. See Table 1 for species code key.

predator and a set of candidate prey, assigning a relative proportion of each prey to the diet. The model assumes that isotopic values of all the prey items considered are significantly different from each other and that an individual predator consumes all available prey items. It also assumes that the partitioning of food sources is the same for both C and N, an assumption less likely to be a problem when sources are all animal tissues (Phillips 2001). Estimating model parameters (i.e., proportion of prey, herein F_s) requires solving a system of linear equations. With data for two isotopes, C and N, a maximum of three prey can be considered (i.e., two free parameters):

$$\delta^{15}\text{N}_{\text{predator}} = F_a \delta^{15}\text{N}_{\text{prey a}} + F_b \delta^{15}\text{N}_{\text{prey b}} + F_c \delta^{15}\text{N}_{\text{prey c}} \quad (2)$$

$$\delta^{13}\text{C}_{\text{predator}} = F_a \delta^{13}\text{C}_{\text{prey a}} + F_b \delta^{13}\text{C}_{\text{prey b}} + F_c \delta^{13}\text{C}_{\text{prey c}} \quad (3)$$

$$1 = F_a + F_b + F_c \quad (4)$$

We selected five candidate species (in three groups) that appear as the most likely candidate prey based on their stable isotope signatures, relative abundance, and importance in the SPSE (e.g., Angelescu and Prenski 1987; Wohler et al. 1997; Sabatini et al. 2004), together with salmon food preferences in the Northern Hemisphere (Table 4) and New Zealand (James and Unwin 1996): Sprats (*Sprattus fuegensis* [SF]), cephalopods (*Illex argentinus* [IA] and *Loligo gahi* [LG]), and coastal zooplankton (copepods [CO] and *Themisto gaudichaudii* [TG], the most

abundant zooplankton components of coastal waters; Table 1). The choice of items and the estimation of diet composition were validated and compared with the diet of 12 of the 28 chinook salmon caught by bottom trawlers (16 fish had empty stomachs) between 2002–2004 in waters between latitude 47°S and 51°S (Fig. 1). Stomach contents were quantified through gravimetric and frequency analysis. Prey items were separated, counted, and wet weighed.

Results

Distribution area—Water temperatures preferred by salmonids during spring, summer, and fall occur immediately offshore of Atlantic rivers of Patagonia where salmonids were able to establish anadromous populations (Fig. 1). This marine area overlaps with an oceanographic region named the Atlantic Patagonian Cold Estuarine Zone by Acha et al. (2004, Fig. 1). This is a highly productive area, with ocean fronts generated by the inflow into the Patagonian Shelf of low salinity water through the Le Maire Strait, the Strait of Magellan, and Southern Atlantic rivers, readily identified on SeaWiFS (Sea-viewing Wide Field-of-view Sensor) images (Rivas et al. 2006). In this paper we propose the name Southern Patagonian Shelf Ecosystem (SPSE) to designate the biotic and abiotic components and processes characteristic of this oceanographic region.

The food web analysis—Plots of $\delta^{13}\text{C}$ against $\delta^{15}\text{N}$ provide a quick look at food web structure and can be

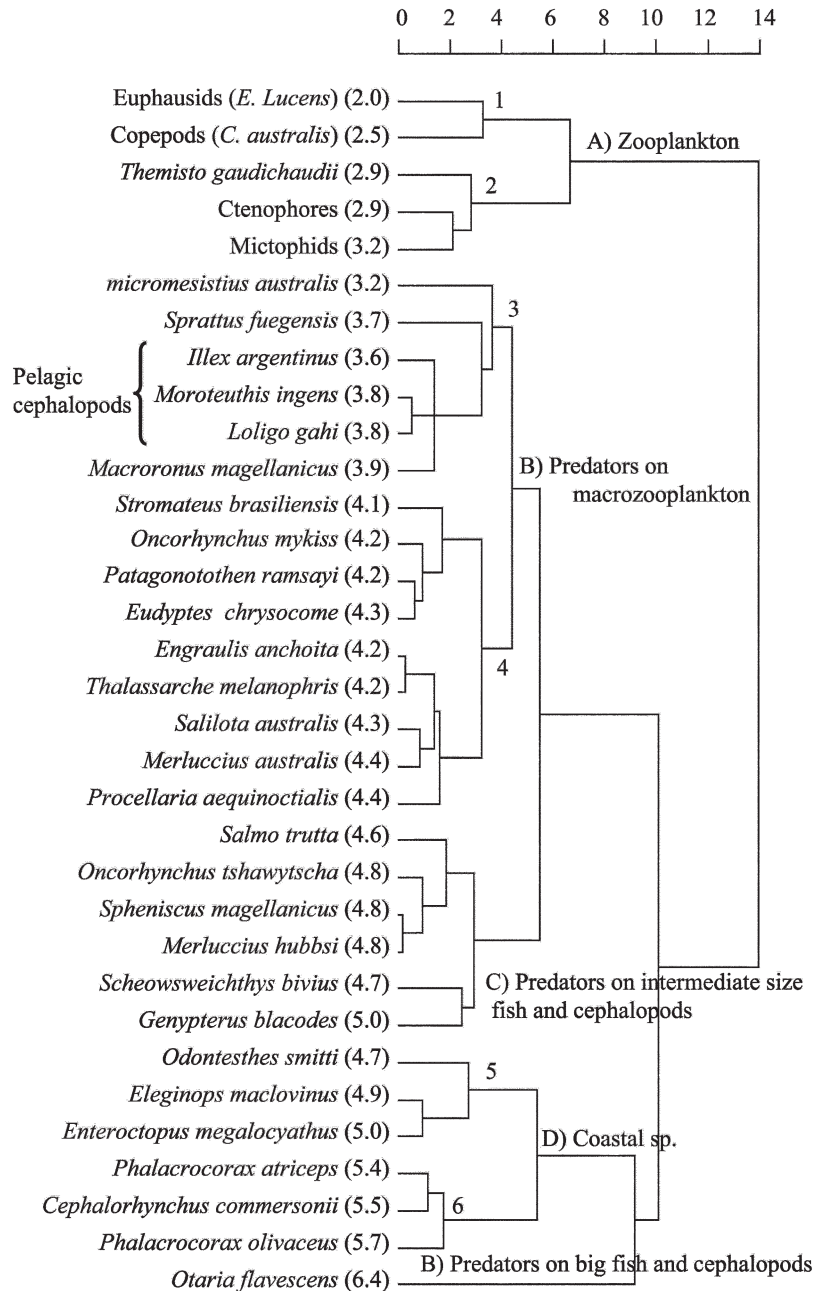


Fig. 3. Cluster analysis (Euclidean distances and average method) using $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for the whole SPSE. Species with less than three samples or those that were sampled in only one location were excluded from the analysis; trophic level is indicated between brackets.

used to visually identify likely predator-prey relationships as well as pairs of competing species (Fig. 2). The SPSE food web is triangular, with marine mammals (*Otaria flavescens* [OF] and *Cephalorhynchus commersonii* [CC]) and birds (*Phalacrocorax olivaceus* [PO], *Phalacrocorax atriceps* [PA], and *Phalacrocorax gaimardi* [PG]) at the apex and zooplankton (*Euphausia lucens* [EL], CO, and TG) forming the broader base. There was a wide range of $\delta^{15}\text{N}$ values (7.3–22.5‰) from invertebrates to top predators, whereas $\delta^{13}\text{C}$ values ranged from –22.3‰ at the base of the food web to –16.4‰ on top predators. The overall arrangement of species in the C and N gradient reflects

different source areas: Coastal species (fishes *Odontesthes smitti* [OS], *Eleginops maclovinus* [EM]; benthic cephalopods *Enteroctopus megalocyathus* [ETM]), coastal sea birds (PO, PA, and PG), offshore sea birds (*Spheniscus magellanicus* [SM], EC, *Thalassarche melanophris* [TM], *Procellaria aequinoctialis* [PAE]), marine mammals (OT, CC), and zooplankton (EL, CO, myctophids [MIC], ctenophores [CT], and TG) (Figs. 1, 2). Relatively enriched $\delta^{13}\text{C}$ values were found in coastal (OS, EM) and benthic (MG, ETM) organisms in agreement with general patterns observed in other ecosystems (Michener and Schell 1994). Using our isotopic model to calculate average trophic level,

we determined that the marine food-web of the SPSE is composed of approximately six trophic levels with salmonids occupying levels 4.2 to 4.9 (Table 1).

The cluster analysis detected functional ecological groups (Fig. 3). Zooplankton species (group A) were classified in two groups: (1) less carnivorous species, including our basal species EL and CO (trophic levels [TL] = 2–2.5) and (2) more carnivorous species (TG, CT, and MIC; TL = 2.9–3.2). Macrozooplankton feeders (group B) were classified as: (3) small crustacean predators (*Micromesistius australis* [MA], *Sprattus fuegensis* [SF], *Macroroncus magellanicus* [MM], and all the pelagic cephalopods *Loligo gahi* [LG], *Moroteuthis ingens* [MI], and *Illex argentinus* [IA]; TL = 3.2–3.9), and (4) large crustaceans, fish larvae, and small cephalopod feeders, including rainbow trout (*Stromateus brasiliensis* [SBR], *Onchorhynchus mykiss* [OMS], *Patagonotothen ramsayi* [PR], EC, *Engraulis anchoita* [EA], *Thalassarche melanophris* [TM], *Salilota australis* [SA], *Merluccius australis* [MAU], *Procellaria aequinoctialis* [PAE]; TL = 4.1–4.4). Consumers of intermediate size fish and squid (group C) clustered in a relatively homogeneous group and include sea trout and chinook salmon (*Salmo trutta* [ST], *Onchorhynchus tshawytscha* [OT], *Spheniscus magellanicus* [SM], *Merluccius hubbsi* [MH], *Scheowweichthys bivius* [SB], *Genypterus blacodes* [GB]; TL = 4.6–5.0). Coastal species clustered together (group D) and are divided into: (5) nearshore sp. (OS, EM; TL = 4.7–4.9) and (6) nearshore schooling fish predators (PA, CC, PO; TL = 5.4–5.7). Sea lions (group E) are top predators that feed on big fish and cephalopods and are in a group by themselves (OF; TL = 6.4).

Salmonid trophic relationships—Although size, sex, and feeding area can affect isotope values, we found no relationship between size and $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ for salmonid species (range: rainbow trout = 420–830, chinook = 380–1040, sea trout = 390–550 mm). Moreover, we did not find differences between years in stable isotope signatures of anadromous rainbow trout (ANOVA $\delta^{15}\text{N}$ $p = 0.57$, $\delta^{13}\text{C}$ $p = 0.57$) or chinook salmon (ANOVA $\delta^{15}\text{N}$ $p = 0.41$, $\delta^{13}\text{C}$ $p = 0.057$). There were significant differences in the trophic status of salmonid species, with sea trout and chinook salmon displaying significantly higher values of both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ than rainbow trout (Fig. 4). Isotope values of chinook OT and sea trout ST (group C) were more similar to those of the more piscivorous magellanic penguin (Frere et al. 1996; Wilson et al. 2005), whereas values of rainbow trout OMS (group 4) were comparable to those of rockhopper penguins from Penguin Island (47°S), feeding mainly on crustacean (TG and EL 60%) and fish larvae and juveniles (40%) (Frere pers. obs.). The N and C bi-variate analysis for all pair-wise species comparisons supports the general patterns just presented (Table 2): Sea trout and chinook salmon had similar trophic status ($p = 0.32$), and both were significantly different from rainbow trout ($p < 0.001$ for both), which in turn had a trophic status similar to that of rockhopper penguins ($p = 0.62$). Whereas chinook salmon were clearly differentiated from all the plankton feeders, sea trout could not be differentiated from rockhopper penguins.

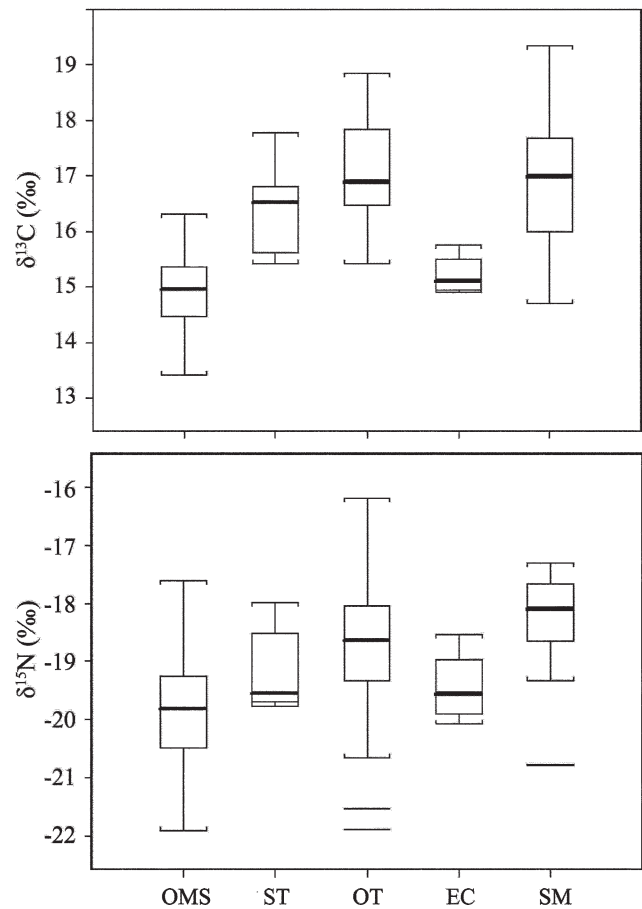


Fig. 4. Box and whisker plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for anadromous salmonids (*Oncorhynchus mykiss* [OMS], *Oncorhynchus tshawytscha* [OT], and *Salmo trutta* [ST]) and reference species of the SPSE (*Eudyptes chrysocome* [EC], *Spheniscus magellanicus* [SM]). Solid lines represent median values, limits of boxes contain 50% of data, and whiskers are 1.5 times the interquartile range. Outliers are individually shown.

Altogether, these results provide statistical support for the clustering of rainbow trout with zooplanktivorous species (group 4 in cluster analysis, Fig. 3) and of sea trout and chinook salmon with more piscivorous species predators on intermediate size fish and cephalopods (group C in cluster analysis). The pattern of trophic relationships for salmon is further supported by results from the dual isotope model (Table 3). Rainbow trout appeared again as primarily zooplanktivorous (crustaceans are 55% of diet), whereas chinook salmon and sea trout were primarily sprat feeders (96% and 79%, respectively).

The stomach content analysis of the 12 chinook salmon caught in the region showed similar proportions of the three candidate items as those estimated by the model (Table 3), providing strong support for our results.

Discussion

Temperatures preferred by salmon occur during warmer months in the southern portion of the Patagonian Continental Shelf. Using SIA, we made the first description

Table 2. *p* values of paired species Hotelling's T² test comparisons. Salmon species are *Onchorhynchus mykiss* (OMS), *Onchorhynchus tshawytscha* (OT), *Salmo trutta* (ST) compared with *Eudyptes chrysocome* (EC), and *Spheniscus magellanicus* (SM) penguins.

	OT	ST	EC	SM
OMS	<0.001	<0.001	0.62	<0.001
OT		0.32	0.001	0.056
ST			0.14	0.11
EC				0.003

of the food web of the species inhabiting this system, the SPSE. The SPSE appears to be dominated by zooplanktivorous species. The dual isotope mixing model provided accurate estimates of the diet proportion for the salmon species, supported by direct inspection of chinook stomachs. Whereas chinook salmon and sea trout diets resemble their preferences in the Northern Hemisphere, feeding mainly on sprats, anadromous rainbow trout feed on the abundant zooplankton crustaceans, a novel feeding behavior for the species.

The region inhabited by salmon, an area of 284,680 km² south of latitude 47°S with depths between 30 m and 200 m and bounded by the continent, Tierra del Fuego, Staten Island, and the Malvinas current, is inhabited by commercial species called the "austral species assemblage" (Angelico and Prenski 1987). This assemblage is characterized by the highly abundant hoki MM, squids (IA and LG) and, in coastal areas, sprats (SF). All these species are primarily zooplanktivorous (Ivanovic and Brunetti 1994), and their distribution overlaps widely with that of zooplankton "hot spots" characteristic of this area (Sabatini et al. 2004).

In our analyses, SIA emerges as a powerful and reliable technique to characterize trophic relationships within the SPSE. In general, our results are highly consistent with expected diets based on the literature and with links established by direct food web analysis. For instance, our group B-3 is composed by species that are recognized as predators of zooplankton crustaceans: MA (78% TG and 22% EL; Wohler et al. 1997), SF (CO, TG, and EL; Ramirez 1976), IA (72% G, 13% EL; Ivanovic and Brunetti 1994), or MM (60% TG and 20% EL; Wohler et al. 1997).

The SIA highlights the importance of zooplankton for the productivity of the SPSE, as zooplanktivorous taxa are very

abundant in terms of a number of species (15 out of 37 are included in group B), as well as biomass (MM in group B is the most abundant fish species in the SPSE, with an estimated abundance of over 3 million mt, Wohler et al. 1997). Among zooplankton species, the amphipod TG is very abundant and it is known to constitute a primary food item for major zooplanktivorous taxa (Wohler et al. 1997). A similar food web is supported by this same species in the Kerguelen Island, at about the same latitude (49–50°S) in the Indian Ocean, where TG is the major prey for all seabird species investigated (39–80% of total diet number of petrels, prions, and rockhopper penguins; Bocher et al. 2001).

Salmonids are generalist predators that can adapt to changes in prey abundances in time or space, but particular species display some characteristic behavior in their native ranges in the Northern Hemisphere (Quinn 2002). Comparing the trophic position of the three species analyzed in this paper with those displayed in the native range may serve as a test for the plasticity in feeding behavior as the fish are confronted with novel conditions. For example, chinook salmon, together with coho salmon, feed primarily on larger micronektonic prey, such as fishes and squids, whereas other species of the genus *Oncorhynchus*, such as sockeye (*O. nerka*), chum (*O. keta*), and pink salmon (*O. gorbuscha*), are more opportunistic feeders, feeding on smaller prey items such as zooplankton (Kaeriyama et al. 2004). This trophic hierarchy is also supported by SIA analysis (Welch and Parson 1993; Satterfield and Finney 2002; Kaeriyama et al. 2004). Adult steelhead in the North Pacific Ocean also feed primarily on fish and cephalopods (Table 4). Cluster analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for *Oncorhynchus* spp. in the Alaskan Gyre grouped steelhead with chinook and coho salmon (*O. kisutch*; Kaeriyama et al. 2004). In the North Atlantic Ocean, sea trout, which stay near estuaries, feed primarily on fish (*Sprattus sprattus* and *Clupea harengus*; Knutsen et al. 2001, 2004) a feeding behavior similar to that of coastal chinook populations in the North Pacific Ocean, whose diet in coastal waters from British Columbia to California consists mainly of fish (70–97% of diet, Table 4). The trophic position and prey selection by chinook salmon OT and sea trout ST in the SPSE do not differ much from those in their native ranges. Chinook salmon introduced in New Zealand have a diet composed 76% by weight by *Sprattus muelleri* (James and Unwin 1996), a species similar to *Sprattus sprattus* found in

Table 3. Diet predicted by dual the stable isotope model (sex ratio order F:M:immature) and stomach-content diet of 12 chinook salmon captured at sea by bottom trawlers. Diet items are sprats (SF), cephalopods (IA and LG), and zooplankton (CO and TG), the most abundant zooplankton components of coastal waters). Mean weight is expressed in grams (expressed as % of weight) and fork length (FL) of fish is expressed in mm.

Species	<i>n</i>	Sex	FL	Weight	Diet predicted %		
					SF	CO+TG	IA+LG
<i>O. mykiss</i> OMS	51	31:20	621	2,884	41	55	4
<i>S. trutta</i> ST	5	2:3	535	2,528	79	5	16
<i>O. tshawytscha</i> OT	40	10:13:17	566	3,092	96	1	3
OT direct estimation	12		488	2,252	93	3	4

Table 4. Proportion (%) of diet items for salmon in the North Pacific Ocean, North Atlantic Ocean, and for the introduced populations of OT in New Zealand grouped by crustaceans (C), fish (F), and cephalopods (Ceph).

Species	C	F	Ceph.	Variable	Stage	Area	Author
OMS	6	63	31	Volume	Adult	Gulf Alaska	Taylor and LeBrasseur 1957
	0.4	59	39	Weight	Adult	Transitional W. Subartic	Light 1985
	1.1	13	39	Weight	Adult	Cent. Subartic	Light 1985
	2.4	89	6.5	Weight	Adult	Alaskan stream	Light 1985
	3	15	60	Volume	Adult	Subartic current	Kaeriyama et al. 2004
	5	40	30	Volume	Adult	Alaskan Gyre	Kaeriyama et al. 2004
	36	61		Weight	Juvenile	Oregon and Washington	Pearcy et al. 1990
Mean OMS	8	49	34				
OT		20	80	Volume	Adult	Alaskan Gyre	Kaeriyama et al. 2004
	9	88	2	Weight	Juvenile	Oregon and Washington	Brodeur and Pearcy 1990
	18	82		Weight	Adult	New Zealand	James and Unwin 1996
	3	97			Adult	British Columbia	Healey 1991
	10	85			Adult	Washington	Healey 1991
	15	80			Adult	Oregon	Healey 1991
	15	70	10		Adult	California	Healey 1991
Mean OT	12	75	31				
ST	7	71		Weight	Adult	Norwegian coast	Knutsen et al. 2004
	10	73		Weight		Ranafjord	Rikardsen et al. 2006*
	26	66		Weight		Balsfjord	Rikardsen et al. 2006*
Mean ST	11	70					

* Mean values of weight are between May and October.

native waters of the North Atlantic Ocean and to *Sprattus fuegensis*, the main schooling fish in coastal waters of the SPSE (Sánchez et al. 1995) and the main prey candidate for chinook salmon in the SPSE.

Adult anadromous rainbow trout is an exception. The dual isotope model (Table 3) showed zooplankton crustaceans as their main prey item, something that would have not been predicted from the behavior of the species in its native range (Table 4). This result is consistent with observations in coastal Chile (Soto et al. 2002), where crustaceans were the dominant prey item of anadromous rainbow trout escaped from net pens. Great abundances of copepods, amphipods (Sabatini et al. 2004), and sprat larvae and juveniles (Sánchez et al. 1995) are characteristic of SPSE coastal waters, particularly during the spring, when smolts and spawned adults go out to sea. Whereas in the Northern Hemisphere rainbow trout are characteristically less piscivorous than sea trout or chinook salmon (Table 4), in the SPSE its diet dominated by zooplankton is remarkable. The characteristically high density of crustaceans in the SPSE during spring and summer may make this particular feeding profitable for Santa Cruz River anadromous rainbow trout, while that may not be the case in waters with lower plankton densities.

The zooplanktivorous behavior of adult rainbow trout is consistent with its apparently shallower distribution as compared to that of chinook. The absence of rainbow trout catches by large bottom trawlers operating in the area (fishing gear capture fish within a few meters over the seafloor), which regularly catch chinook, points at a shallower distribution where zooplankton is dominant. This behavior has been previously described by Burgner et al. (1992), associated with surface foraging at night. While

the foraging behavior of rainbow trout in the SPSE substantiates the plasticity of feeding behavior in this species, differences between species indicate that they will interact at different trophic levels. Chinook and sea trout occupy higher trophic levels, interacting directly with different species than rainbow trout.

Chinook and steelhead/anadromous rainbow trout from the SPSE have enriched $\delta^{15}\text{N}$ compared with salmonids of the North Pacific Ocean (Welch and Parson 1993; Satterfield and Finney 2002) and off-shelf predators (Lewis et al. 2006). This may be explained by differences in ocean areas. North Pacific Ocean salmonids make extensive offshore migrations, whereas SPSE salmon appear to be more coastal, inhabiting one of the world's most extensive marine shelves. Variation in isotope ratios in consumers may result from the trophic level at which they feed, but also from spatial and temporal changes in the isotopic composition at the base of the food web. This may well be the case in the SPSE, where the $\delta^{15}\text{N}$ of primary consumers have values between 7‰ and 8‰.

We have presented the first large scale analysis of the food web status of introduced salmonids in southern oceans, a process of invasion that started 100 years ago that is being further driven by the explosive growth of aquaculture in southern Chile. Yet, the main question of whether these invasions are additive or are having a significant ecological effect remains virtually uncharted. This question will become even more critical if escapements from aquaculture continue to grow and wild populations continue to expand, colonizing new environments. In fact, there are hundreds of rivers suitable for salmon spawning and rearing in Patagonia, providing a fitting scenario for such an expansion.

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