Quantifying Predation on Galaxiids and Other Native Organisms by Introduced Rainbow Trout in an Ultraoligotrophic Lake in Northern Patagonia, Argentina: a Bioenergetics Modeling Approach

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Abstract.—Exotic rainbow trout *Oncorhynchus mykiss* support an economically valuable recreational fishery in Patagonia but also create concern for impacts on native organisms. These concerns are intensified by the possibility of hatchery release programs in this region. We estimated losses of different prey from predation by rainbow trout in Lake Moreno, Río Negro Province, Argentina, using a bioenergetics model combined with input data from directed sampling on growth, seasonal diet, distribution, and thermal experience. The fish community was sampled seasonally using gill nets, hydroacoustics, and ichthyoplankton

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nets. Pelagic galaxiid larvae and benthic juvenile and adult small puyen *Galaxias maculatus* were the most important components of the diet. Bioenergetics simulations showed that over a 6-year life span in the lake (ages 1–7), rainbow trout attained a body mass of 2.3 kg and consumed 74.7 kg of food, of which 20% consisted of galaxiid larvae and 16% consisted of adult small puyen. Based on an estimated abundance of 29,000 rainbow trout of ages 1–7, this predator exerted significant but sustainable mortality on the native prey populations, consuming 44 metric tons or an estimated 23% of the annual larval galaxiid production and 35 metric tons of adult small puyen, which represented an unknown fraction of the postlarval population. Galaxiids supported the estimated predation demand under current conditions. However, simulations of stocking strategies normally proposed for this region showed that consumption demands on prey would increase to unsustainable levels, reducing native fish populations and likely reducing growth of rainbow trout. It is also probable that the fish community composition would shift further in response to the increased demand for prey by stocked predators. This implies that in some cases, stocking could jeopardize sport fisheries; stocking strategies should be evaluated on a case-by-case basis to be consistent with specific objectives for native fish conservation and sustainable food web interactions.

Introductions of exotic species are among the most serious human challenges to natural ecosystems (Lodge 1993; Moyle 1997; Rainbow 1998; Meador et al. 2003). Predation by exotic fish is frequently one of the main causes for decline of native fishes throughout their geographic ranges (Zaret and Paine 1973; Ogutu-Ohwayo 1990; Ogutu-Ohwayo and Hecky 1991; Townsend and Crowl 1991). Thus, piscivorous fish are expected to have higher impacts on local communities than other functional groups of exotics (Moyle and Light 1996).

Starting in 1904, Argentine Patagonia received 10 salmonid species, six of which persist in different water bodies (Macchi et al. 2008). Of these nonnative salmonids, rainbow trout *Oncorhynchus mykiss* are the most abundant and widely distributed throughout Patagonia (Pascual et al. 2002; Vigliano and Darrigran 2002; Macchi et al. 2008). The numbers and species of stocked hatchery fish have shifted through time (Macchi et al. 2008). Most existing salmonid populations are sustained by natural reproduction, but some lakes are supplemented with hatchery stocking (Pascual et al. 2007; Macchi et al. 2008).

The annual economic value of the salmonid sport fishery in the San Carlos de Bariloche region of Nahuel Haupi National Park has been conservatively estimated at US$8 million based on license sales and estimated average expenditures per angler (Vigliano and Alonso 2000), with sportfishing constituting one of the main tourist activities in the park. Constant demand to enhance the sport fishery by stocking hatchery salmonids has raised concern about conservation of native species, sustainability of desirable salmonid fisheries, and stability of the lake food webs.

The exotic salmonids interact with native fish communities that are characterized by low diversity but a high proportion of endemic species (Arratia et al. 1983). The direct and indirect effects of interactions between native fishes and salmonids could potentially alter the abundance, ontogenetic distribution, habitat use (Townsend and Crowl 1991; McIntosh et al. 1992, 1994), survival, growth, reproduction, behavior, and feeding (Edge et al. 1993) of the native species. However, the lack of relevant data on the host communities prior to salmonid introductions makes it difficult to determine the consequences of these introductions in Argentine Patagonia. Information about native species abundance and distribution before the introductions is at best contradictory (Marini 1936; Gonzáles Regalado 1945).

Although salmonid introductions have been related to the disappearance or declines of native fish in different parts of the world (McDowall 1990; Minns 1990; Fernando 1991; McIntosh 2000; Murillo and Ruiz 2003), information about their relationship with native fish species in southern South America is scarce and mostly circumstantial. Two closely related species, the small puyen *Galaxias maculatus* and big puyen *Galaxias platei*, are the primary prey for introduced salmonids and native Creole perch *Percichthys trucha* in many freshwater basins of Patagonia (Macchi et al. 1999, 2007; Milano et al. 2002, 2006). Galaxiids play a key role as the primary planktivores and prey fishes in lake food webs of this region. Landlocked populations of small puyen show ontogenetic and seasonal shifts in distribution and diet; a protracted pelagic larval stage feeds on zooplankton during spring and summer, and then postlarval stages settle into benthic habitats and shift to benthic-littoral prey and zooplankton (Battini 1997). Most Andean lakes are oligotrophic, and food web processes are influenced by nutrient levels and planktivory by small puyen (Balseiro and Modenutti 1998; Reissig et al. 2003). Small puyen can regulate the zooplankton community, creating seasonal fluctuations in its composition (Modenutti et al. 1993; Reissig et al. 2003). The main plankton consumers are larval and juvenile galaxiids and atherinids (Cussac et al. 1992; Cervellini et al. 1993; Battini 1997). In particular, larvae and juvenile small puyen reduce crustacean biomass, which could influence nutrient

dynamics (Reissig et al. 2003). In Lake Moreno, Lake Gutiérrez, and many other lakes of the region, larval small puyen are much more abundant than big puyen (Barriga et al. 2002; Barriga 2006). Peak larval density and biomass coincide with peak zooplankton abundance (Barriga et al. 2002; Barriga 2006). Larval small puyen exhibit diel vertical and horizontal migrations in these lakes (Lindegren 2003) and thus offer a temporally and spatially dynamic food supply for piscivorous salmonids and Creole perch.

The type of interactions between nonnative salmonids and galaxiids and the degree of salmonid impact on galaxiids in Argentine Patagonia are unknown. Initial identification and quantification of critical interactions between salmonids and the native fish fauna of Patagonia were reported by Macchi et al. (2007); however, an assessment of the degree of impact upon key prey species (e.g., galaxiids) and other prey has not been undertaken.

As part of a long-term program to understand trophic relationships between salmonids and native species, our objective was to quantify rainbow trout predation on galaxiids and other native organisms and to conduct an initial evaluation of whether this level of predation was sustainable (both in terms of conserving native species and supporting a desirable sport fishery) with the existing rainbow trout population and under likely hatchery stocking scenarios. We combined diet, distribution, and abundance data with a bioenergetics model to simulate temporal patterns of individual and population-level consumption on invertebrate and fish prey by rainbow trout in a characteristic Patagonian ultraoligotrophic lake.

Study Area

Lake Moreno (41°05′S, 71°32′W) is a small (10.6 km²), monomictic, ultraoligotrophic lake of glacial origin. The lake is divided into eastern and western basins (Figure 1). Both basins have average Secchi depths of 17 m, mean depths of approximately 60 m, and maximum depths of approximately 120 m. The lake is located within Nahuel Huapi National Park near the city of San Carlos de Bariloche, Río Negro Province. The lake stratifies during November–April, with epilimnetic (0–30-m depths) temperatures ranging from 12°C to 19°C (average = 14.7°C) during summer stratification and from 5°C to 8°C throughout the water column during the destratification period. Dissolved oxygen concentration remains above 7 mg/L, and the surface elevation of the lake fluctuates up to 3 m throughout the year. The lake is fed by snowmelt and rain through numerous small tributaries and two main streams and drains via a small outlet into the larger
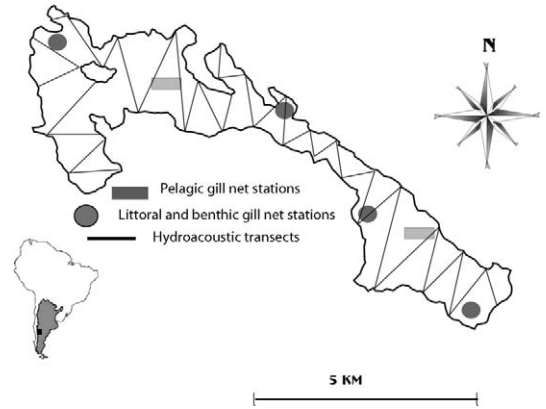

FIGURE 1.—Map of Lake Moreno, Argentina, depicting gill-net sampling stations and hydroacoustic transects.

Nahuel Huapi Lake (557 km²), which is part of an extensive Atlantic watershed.

Methods

We used bioenergetics model simulations to estimate the daily, seasonal, and annual consumption rates by each rainbow trout age-class on galaxiids and other major prey. Field sampling was used to obtain data on annual growth, size structure, abundance, size-specific seasonal distribution and diet, and thermal experience for use as inputs to the bioenergetics simulations. Individual daily consumption rates for each age-class of rainbow trout were multiplied by age-specific abundance estimates (modified by daily survival rates) to expand to a population-level consumption rate.

Fish sampling.—Fish community composition and distribution were determined from catches in sinking horizontal gill nets. The nets were 60 m long and 2 m tall, with 10-m-long panels of 15-, 20-, 30-, 50-, 60-, and 70-mm bar mesh sizes that were randomly located in each net. This net configuration has shown to be nonselective in the size range of salmonids sampled (fork length [FL] $\geq$ 200 mm; P.H.V., unpublished data). Four littoral-benthic and two limnetic sites (Figure 1) were fished once per season starting in March 1999 (summer) and ending in August 2000 (winter). At each littoral-benthic site, one sinking gill net was set perpendicular to shore at the shallowest depth, and one sinking gill net was set parallel to shore along each of six depth contours at 2, 10, 20, 30, 40, and 50 m. At each limnetic site, one horizontal gill net was suspended at each of three depths (0, 10, and 15 m). A detailed description of gill-net construction and deployment is provided by Vigliano et al. (1999). Peak catch per unit effort (CPUE) in the gill nets coincided with summer stratification for all fish species except

small puyen, which were too small to be captured in gill nets. During this period, the relative abundance of each species was calculated separately for limnetic and benthic habitats and was estimated by the ratio of the CPUE for the individual species relative to the CPUE for all species. Effort was defined as the product of soak time (effort) times the total area of each gill net used, standardized to an overnight, 15-h set of a 100-m^2 area of gill net. Because juvenile and adult small puyen were invulnerable to gill nets, we sampled their presence–absence in benthic-littoral habitats using minnow traps and beach seining at the benthic gillnetting locations, but quantitative ichthyoplankton sampling was conducted for larval galaxiids in limnetic regions (Barriga et al. 2002; Barriga 2006).

The limnetic abundance of rainbow trout and other large-bodied fish (FL $\geq$ 200 mm) like Creole perch and Patagonian silversides *Odontesthes hatcheri* was calculated through hydroacoustic assessment conducted on November 2000. Data were collected on 34 zig-zag transects crossing the lake at regular intervals by use of a BioSonics DE 4000 scientific echosounder with a 208-kHz, single-beam (3° half angle) transducer mounted on the side of the boat and towed at 2 m/s. A 20 log R (range of transducer in meters) time-varied gain was used for echo integration, and 40 log R was used for echo counting. Hydroacoustic transects were monitored visually on the display screen of a microcomputer, and data were stored on the hard drive for subsequent analysis. Hydroacoustic data were analyzed with the program EchoView version 4.1 from sonar data collected from 1.00 m below the surface to 0.50 m above the bottom in 10-m depth intervals and 100-m-long transect segments for a total of 1,037 insonification bins. The hydroacoustic abundance estimates were stratified into slope zone and limnetic regions because the echograms indicated qualitative differences in depth and density patterns of fish in close proximity to the slope versus targets that were further offshore. Based on inspection of the echograms, transect segments were visually assigned to either slope zone or limnetic strata. The influence of the slope zone varied depending on the steepness of the bottom slope, and individual slope zone strata extended anywhere from 10 to 200 m from shore (mean of approximately 50 m from shore). Within the slope strata, the species composition of acoustic targets was allocated according to the relative abundance of fishes captured at corresponding depth intervals in the sinking gill nets. In the limnetic zone, rainbow trout were the only large fish (FL > 200 mm) captured in the suspended gill nets; therefore, all larger acoustic targets in the limnetic strata were assumed to be rainbow trout. To estimate density (fish/m^3) of trout-sized targets, the average backscattering cross-section was set to 5.07 $\times$ 10^{-15}, which corresponded to a fish of 224 mm in total length (or 200 mm FL for rainbow trout) according to equations by Love (1971, 1977). This target size threshold excluded the small puyen and juvenile fish. Bottom-dwelling fishes like the big puyen and velvet catfish *Diplomystes viedmensis* were excluded from this acoustic estimate because their detections were unlikely due to the blanking zone within 0.5 m of the bottom. Estimates of the total number of non-bottom-dwelling fish in the slope and limnetic strata were each computed separately by multiplying the average target density for all insonified bins in each 10-m depth stratum times the total volume of each stratum.

Data on FL (nearest mm), weight (nearest g), age, and diet composition of rainbow trout were recorded. Ages were assigned by reading mounted scales (Wootton 1990). We estimated annual survival rates (S) for rainbow trout of ages 2–6. Although age-1 rainbow trout immigrated to the lake at 120–150 mm FL during late spring and early summer, they were only captured in littoral habitats and were not fully recruited to gill nets because of size selectivity (P.H.V., unpublished data). Rainbow trout were fully recruited to the gill nets at age 2 (mean $\pm$ SD = 234 $\pm$ 44 mm FL), and age-2 fish occupied both slope and limnetic habitats during summer stratification. The S for rainbow trout was computed by regressing $\log_e(C_y)$ against age y (where C_y is the catch of age-y fish, y = 2–6), and the resulting slope of the regression was the instantaneous annual mortality rate (Z), calculated as $-\log_e S$ ($Z = 0.3856$, $S = 0.68$; $r^2 = 0.846$, $N = 5$ age-classes).

Seasonal diet composition was estimated from rainbow trout caught in gill nets by dissecting the section of the digestive tract extending from the esophagus to the beginning of the duodenum. Prey items were identified to the lowest possible taxon. For the seasonal diet composition used as inputs for the bioenergetics model, the proportional weight contribution of each prey category was computed for each stomach individually and then averaged across all nonempty stomachs within the same season and rainbow trout size-class (Chipps and Garvey 2007). Prey items that represented low, sporadic contributions to the diet were pooled into an "other prey" category. Larval small puyen and big puyen were visually indistinguishable and were thus grouped into one category; however, small puyen represented over 98% of the larval galaxiids in the lake (Barriga 2006).

We used bomb calorimetry to measure energy density (J/g wet mass) of the major prey items. Prey samples were dried in an oven at 60–70°C for 24–72 h and then were ground to a powder. One-gram pellets

were formed and burned at 30 atmospheres of oxygen in a bomb calorimeter (Parr Model 1241); galaxiid larvae were burned in a micro-calorimeter (Parr Model 1425) to determine gross energetic content. Ash weight was measured after combustion. When prey body size was small (i.e., insects and gastropods), a sampling unit consisted of whole-body samples of numerous individuals. When prey body size was large (i.e., fish), a sampling unit consisted of a whole-body sample from one individual. Prey energy densities were also compared with energy densities of analogous species from North America (Probst et al. 1984) and Patagonia (Ciancio and Pascual 2006; Ciancio et al. 2007). For model simulations, conventional assumptions were used for indigestible fractions (i.e., 3% for fish and 15% for invertebrates; Hanson et al. 1997).

We inferred thermal experience for rainbow trout from the seasonal depth distribution according to gill-net catches. Annual growth increments were calculated by fitting length-at-age data to the von Bertalanffy growth equation and converting length (FL, mm) to body mass (g) using a length–weight regression derived from this population (weight $W = 0.000025 \cdot \text{FL}^{2.9}$; $r^2 = 0.92$, $N = 384$, $P = 0.001$).

Bioenergetics modeling.—Age-specific daily rates of consumption (g/d) by rainbow trout for all prey groups were computed using steelhead (anadromous rainbow trout) functions and parameters (Rand et al. 1993) in the Wisconsin Bioenergetics Model (Hanson et al. 1997). The average proportion of the maximum consumption rates were fit to the annual growth increments from the von Bertalanffy curve by using the p-fit routine in the Wisconsin Bioenergetics Model. Model runs began in spring (1 November 1999) and ended the subsequent winter (31 October 2000). Separate simulations were run for each age-class (ages 1–6). Spawning losses of 8% body mass were applied to ages 3 and older on simulation day 335 (1 October). Daily consumption rates for individuals of each age-class were expanded to population-level consumption estimates using initial abundance estimates for each age-class, which were reduced daily by the daily mortality rates throughout the 365-d simulation.

Predation estimates were first generated in terms of consumption by a size-structured population of 1,000 rainbow trout (ages 1–7). Assuming a constant S of 68% for all ages in the lake, the age-specific abundance was iteratively fit to an initial abundance of age-1 rainbow trout such that the total abundance of ages 1–7 in the lake summed to 1,000 on day 1 of the simulation. Abundance was reduced by applying the instantaneous daily mortality rate.

Because salmonid stocking is still a common practice in the Patagonia region, we simulated the potential predation effects of different stocking strategies on key prey types. Levels of age-1 rainbow trout stocking were assumed to equal an additional 1.0, 1.5, and 2.0 times the estimated current abundance of all age-1 and older rainbow trout in Lake Moreno (i.e., the population would increase to 2.0×, 2.5×, and 3.0× the current lake population of 29,000 age-1 and older rainbow trout). The simulations assumed consistent annual stocking rates and spanned a period of 6 years, equal to the observed life span of feral rainbow trout, under the assumption that feral and stocked fish would experience the same S as estimated for the current population in the lake.

Larval galaxiid abundance, biomass, and production estimates.—To provide an approximation of the predation impact imposed by rainbow trout on galaxiid larval life stages, we compared estimates of predation by rainbow trout with (1) the annual production of age-0 galaxiids and (2) the peak abundance and biomass of premetamorphic and metamorphic galaxiid larvae during the summer (Barriga et al. 2002; Barriga 2006). Because the density of the littoral-benthic juvenile and adult small puyen could not be quantified, we could not compare predation with the availability of these older life stages. The limnetic abundance of larval galaxiids was dynamic through time, but peak production occurred during summer and was composed of at least two major cohorts that developed through the premetamorphic and metamorphic life stages (the pelagic stages consumed by rainbow trout); these stages cycled through the limnetic population at different times during the summer. Additional, much smaller cohorts appeared sporadically throughout the year (Barriga et al. 2002). Abundances of the galaxiid free embryo, premetamorphic, and metamorphic larval stages were estimated using seasonal and diel depth-stratified sampling with ichthyoplankton nets. Two 50-cm-diameter, 300-cm-long, conical nets (500- and 1,500-μm mesh) were towed simultaneously. Catches were averaged to compute densities (larvae/m^3; Barriga 2006), and abundance was computed by multiplying the depth-specific densities by the volume in the corresponding depth intervals. Depth-stratified tows were deployed over the upper 20 m at dawn, day, dusk, and night periods. More recent acoustic surveys during 2008 indicated that a high-density layer of larvae extended down to 40-m depth during the summer (M.R., unpublished data); therefore, the densities recorded from the ichthyoplankton samples at 20 m were also applied to the 20–40-m depth interval. We used a mean body mass of 0.16 g (20 mm standard length [SL]) for the predominant larval form available during summer (Barriga et al. 2002) for the purposes of

converting predation losses and prey availability between biomass and numbers.

Seasonal biomass and production rates of age-0 galaxiids were estimated from the seasonal abundance estimates and from SLs reported by Barriga et al. (2002) for November (5 mm SL), February (20 mm), May (40 mm), and November (45 mm). The SLs were converted to approximate weights using a generalized length–weight regression with the intercept selected from the range specified for fishes with "elongated" body morphology, producing an observed body mass of 0.16 g for 20-mm SL premetamorphic larvae (Fish Base website, 5 May 2009; www.fishbase.org/PopDyn/):

$$W = 0.00002 \cdot SL^{3.0},$$

where W is in grams and SL is in millimeters.

Annual production was calculated as the sum of the seasonal production rates (P_t) using the following equation:

$$P_t = B_t \times G_t,$$

where B_t = mean biomass during season t (calculated as $W_t \times N_t$; W_t = estimated mean body weight of age-0 galaxiids during season t; N_t = estimated abundance of age-0 galaxiids during season t) and $G_t = \log_e(W_t / W_{t-1})$.

Results

Species Composition, Distribution, and Abundance

Catches from sinking gill nets in littoral and slope habitats totaled 545 fish, with Creole perch (43%) as the most abundant species, followed by rainbow trout (38%), brook trout *Salvelinus fontinalis* (12%), big puyen (4%), Patagonian silversides (1.2%), brown trout *Salmo trutta* (1.2%), and velvet catfish (0.2%). Rainbow trout and Creole perch were the most abundant predators in the lake, but the rainbow trout was the only significant limnetic predator. Although salmonids were found over the entire depth range, catch rates were concentrated in littoral and benthic zones (Figure 2). The highest catch rates for rainbow trout were consistently in the upper 10 m of the littoral and slope regions during all seasons, with a second mode also appearing in deep water during winter. Creole perch concentrated in 10–30-m depths throughout the year. Brook trout were caught at all depths, while the small numbers of brown trout were caught above 30 m. Adult big puyen were only caught in the silty substrate below 30 m, whereas velvet catfish were only caught in the eastern basin and were always associated with bottom silts above 30 m. Patagonian silversides were only caught in littoral areas associated with dense macrophyte cover. Minnow traps showed that small puyen were widespread in benthic habitats throughout the lake, but catches were highest in the littoral region.

Limnetic catch rates in the suspended gill nets were much lower than catch rates in sinking gill nets in the littoral and benthic habitats. However, lower catch rates were expected in the suspended gill nets because of the large dilution factor of pelagic habitats and the capture inefficiencies inherent in passive sampling for less-abundant, larger fishes in three-dimensional habitats that lack solid boundaries (e.g., slopes) to concentrate and guide fish into the nets. The only fish captured in the suspended gill nets were rainbow trout in the 0–10-m depth stratum. This was consistent with hydro-acoustic data, which showed that the only pelagic targets large enough to be rainbow trout occurred in low densities at 0–10-m depths. Samples from both sinking and suspended gill nets indicated that rainbow trout were generally caught at depths of 0–10 m throughout the year but also in 30–50-m depths during winter.

Proportional allocation of gill-netted fish larger than 224 mm total length to the hydroacoustic-estimated abundance of 47,900 (±4,800 SD) fish consisted of 19,041 rainbow trout from the limnetic and slope strata combined and 21,800 Creole perch, 6,147 brook trout, and 651 brown trout confined to the slope strata.

Survival and Size Structure of Rainbow Trout

Seven age-classes of rainbow trout were found, and age 2 was the most abundant (Figure 3). The size range for each age-class was within the normal limits observed for other rainbow trout populations in this area (Vigliano et al. 2008). The von Bertalanffy growth function fit to FL-at-age (FL$_t$) data was

$$FL_t = 629[1 - e^{-0.32(t-0.35)}].$$

Values of S and Z computed from the completely recruited age-classes (age-2 and older fish) were 68% and 0.3856, respectively. The rainbow trout in Lake Moreno grew from an average FL of 118 mm (26.3 g) at age 1 to 554 mm (2,349 g) at age 7. Assuming constant Z across all age-classes in the lake, an age-structured population of 1,000 rainbow trout of ages 1–7 would be composed of 343 age-1 fish and 34 age-7 fish (Table 1). Based on the hydroacoustic estimate of 19,041 age-2 and older pelagic rainbow trout, the age-specific hydroacoustic abundances declined from 6,762 age-2 individuals to 983 age-7 individuals on day 1 of the bioenergetics model simulation. Age-1 rainbow trout were not found in the pelagic zone and were thus not detectable to hydroacoustics, so their abundance was not accounted for in the hydroacoustic abundance
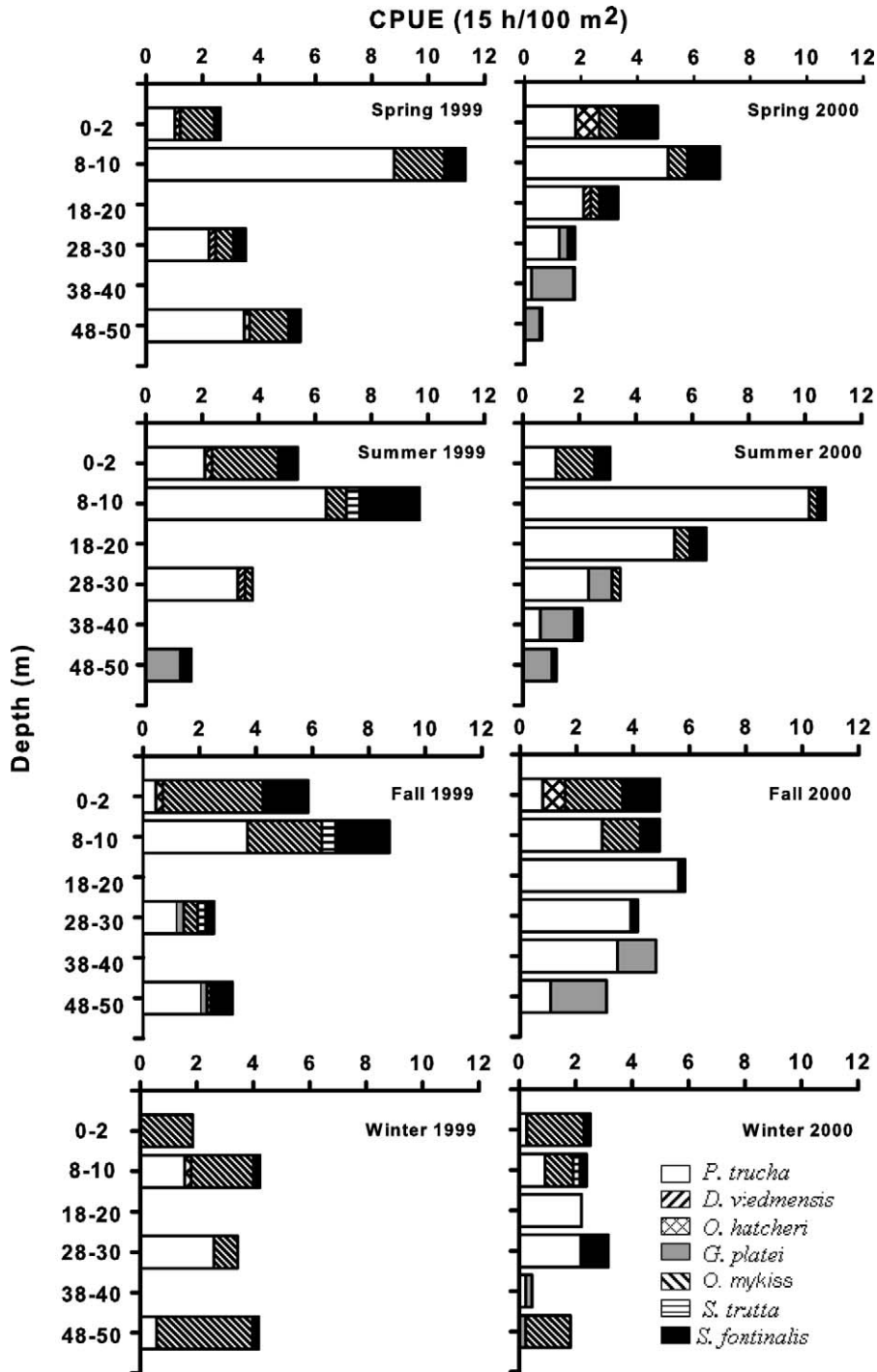
FIGURE 2.—Fish catch per unit effort (CPUE; number of fish per 15-h set of a 100-m² area of gill net) by depth and season in Lake Moreno, Argentina. Species are Creole perch *Percichthys trucha*, velvet catfish *Diplomystes viedmensis*, Patagonian silverside *Odontesthes hatcheri*, big puyen *Galaxias platei*, rainbow trout *Oncorhynchus mykiss*, brown trout *Salmo trutta*, and brook trout *Salvelinus fontinalis*.
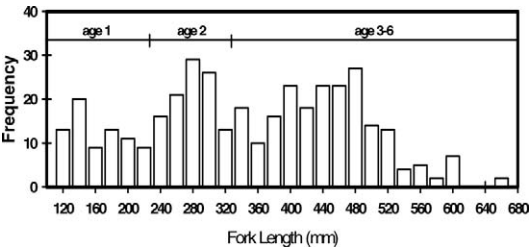
FIGURE 3.—Catch frequencies and fork length and age distributions of rainbow trout caught via gillnetting in Lake Moreno, Argentina, 1999–2000.

estimate of 19,041 pelagic rainbow trout. The corresponding abundance of age-1 rainbow trout in the littoral zone was back-calculated to 9,944 based on the S of 68% (Table 1).

Rainbow Trout Seasonal Diet Composition

Out of 150 rainbow trout stomachs analyzed, only 129 contained food; 10 different prey categories were represented in the diet. Although diet composition differed among three size-classes of rainbow trout (corresponding to ages 1, 2, and ≥3), galaxiids were the most important prey item for all predator sizes. Only proportions of insect larvae and pupae differed significantly among size-classes (Kruskal–Wallis nonparametric test: $H = 10.131$, df = 2, $P = 0.006$); these prey categories became less important as rainbow trout grew.

All predator size-groups exhibited seasonal shifts in prey selection (Table 2). Age-1 rainbow trout primarily ate insect larvae and pupae (predominantly dragonflies Anisoptera and damselflies Zygoptera), followed by adult insects and adult small puyen during spring and summer; larval galaxiids also became important prey during summer. During autumn, the diet shifted to larval and adult galaxiids, anomurans *Aegla* spp., and insect larvae or pupae, whereas the diet during winter was composed primarily of adult small puyen (58%)

and aquatic insect larvae or pupae. The diets of age-2 and older rainbow trout generally contained larger fractions of larval and adult galaxiids and smaller fractions of insects and other invertebrates, although insects (predominantly Trichoptera and Anisoptera) were still seasonally important, especially during spring and summer.

Thermal Experience

The seasonal vertical distribution patterns for rainbow trout showed that all size-classes utilized similar depths (Kruskal–Wallis test: all $P > 0.05$) and were concentrated in 0–20-m depths. The resulting seasonal thermal history corresponded to a sinusoidal pattern, with the highest temperatures during February (17.6°C) and the lowest in September (8.1°C; Table 3).

Prey Energy Density

The composite energy density of the diet for rainbow trout was relatively low despite the relatively high degree of piscivory (Table 4). Energy densities of the primary prey fishes, larval galaxiids (2,879 J/g) and adult small puyen (3,540 J/g), were low compared with those of the other fishes, which averaged 6,040 J/g but represented a small fraction of the diet.

Larval Galaxiid Abundance and Production

The point estimates of larval galaxiid abundance were highest during spring, with an estimated 1.16×10^9 free embryos and premetamorphic larvae; abundance estimates declined to 1.92×10^8 (primarily premetamorphic larvae) during summer, 1.05×10^8 during autumn, and 7.55×10^6 during winter. The estimated production of age-0 galaxiids was 3.93×10^4 kg during mid-November to February, peaked at 1.34×10^5 kg during February–May, and then declined dramatically to 1.53×10^4 kg during May to early November. Total annual production was 1.89×10^5 kg of age-0 galaxiids in limnetic regions of the lake.

TABLE 1.—Estimated age-specific fork length, weight, and abundance of nonnative rainbow trout in Lake Moreno, Argentina. Abundance is presented for (1) an age-structured population of 1,000 fish of ages 1–7 and (2) ages 2–7 calculated from hydroacoustic assessment and age-1 abundance back-calculated using an annual survival rate of 68%.

Age t	Fork length (mm)	Initial weight (g)	Final weight (g)	Spawning loss (%)	Age-structured population of 1,000	Estimated lakewide abundance
1	118	26.3	254.8	0	343	9,944
2	258	254.8	668.7	0	233	6,762
3	360	668.7	1,150.0	8	158	4,598
4	433	1,150.0	1,613.6	8	108	3,127
5	487	1,613.6	2,017.3	8	73	2,126
6	526	2,017.3	2,348.6	8	50	1,446
7	554	2,348.6		8	34	983
Total					999	28,986

TABLE 2.—Seasonal diet composition for different age-classes of nonnative rainbow trout in Lake Moreno, Argentina, and the associated sample sizes (*N*) of nonempty stomachs examined. The diet entries represent the proportional weight contribution of each prey category in terms of blotted-dry wet weight. The diet compositions on days 1 and 365 were taken from the closest, most appropriate sampling date for that age or from an adjacent age-class and were used as inputs for the bioenergetics model simulations. Other fishes were a mix of the non-galaxiids without any predominant species. Other food was composed of fish eggs and a smaller fraction of miscellaneous prey.

Date	Simulation day	Adult galaxiids	Larval galaxiids	Other fish	Molluscs	Adult insects	Insect larvae, pupae	Anomurans *Aegla* spp.	Crayfish *Samastacus* spp.	Amphipods	Other food	N
Age-1 rainbow trout												
1 Nov	1	0.20	0.00	0.00	0.00	0.27	0.53	0.00	0.00	0.00	0.00	
15 Dec	45	0.20	0.00	0.00	0.00	0.27	0.53	0.00	0.00	0.00	0.00	3
1 Feb	91	0.12	0.26	0.00	0.00	0.30	0.32	0.00	0.00	0.00	0.00	5
1 May	182	0.11	0.33	0.00	0.00	0.00	0.23	0.33	0.00	0.00	0.00	4
1 Aug	273	0.59	0.00	0.00	0.00	0.00	0.35	0.06	0.00	0.00	0.00	4
31 Oct	365	0.24	0.00	0.02	0.13	0.24	0.27	0.00	0.09	0.01	0.00	
Age-2 rainbow trout												
1 Nov	1	0.24	0.00	0.02	0.13	0.24	0.27	0.00	0.09	0.01	0.00	
15 Dec	45	0.24	0.00	0.02	0.13	0.24	0.27	0.00	0.09	0.01	0.00	13
1 Feb	91	0.19	0.26	0.00	0.00	0.40	0.15	0.00	0.00	0.00	0.00	16
1 May	182	0.12	0.45	0.00	0.09	0.00	0.09	0.14	0.07	0.00	0.04	32
1 Aug	273	0.26	0.19	0.00	0.26	0.00	0.16	0.06	0.07	0.00	0.00	12
31 Oct	365	0.00	0.00	0.00	0.29	0.26	0.27	0.00	0.16	0.02	0.00	
Age-3 and older rainbow trout												
1 Nov	1	0.00	0.00	0.00	0.29	0.26	0.27	0.00	0.16	0.02	0.00	
15 Dec	45	0.00	0.00	0.00	0.29	0.26	0.27	0.00	0.16	0.02	0.00	7
1 Feb	91	0.18	0.38	0.14	0.15	0.14	0.01	0.00	0.00	0.00	0.00	7
1 May	182	0.06	0.30	0.04	0.28	0.00	0.11	0.15	0.06	0.00	0.00	16
1 Aug	273	0.44	0.11	0.07	0.00	0.00	0.25	0.13	0.00	0.00	0.00	18
31 Oct	365	0.00	0.00	0.00	0.29	0.26	0.27	0.00	0.16	0.02	0.00	

Predation by Rainbow Trout and Impacts of Different Stocking Scenarios

Model simulations showed that galaxiid premetamorphic larvae and adults represented 36–42% of the annual consumption for different age-classes of rainbow trout and totaled 37% of the prey consumed over the rainbow trout life span in the lake (Table 5). Rainbow trout consumed large per capita amounts of galaxiid larvae, ranging from 0.3 kg/year for an age-1 rainbow trout to 4.4 kg/year for an age-6 individual,

TABLE 3.—Thermal experience of nonnative rainbow trout in Lake Moreno, Argentina, based on seasonal vertical distribution patterns in gill-net catches during 1999 and 2000.

Month	Day	Temperature (°C)
Nov	1	12.5
Dec	30	14.8
Jan	60	16.4
Feb	90	17.6
Mar	120	16.3
Apr	150	15.2
May	180	11.7
Jun	210	10.2
Jul	240	9.2
Aug	270	8.4
Sep	300	8.1
Oct	330	9.3
Nov	365	12.5

and per capita consumption of galaxiid larvae totaled 15.3 kg over the life span. This lifetime consumption represented approximately 95,600 larvae based on the mean weight of 0.16 g for galaxiid larvae found in stomach samples. The lifetime consumption of other important items included small puyen adults (12.2 kg), other fishes (4.3 kg), molluscs (13.3 kg), insect larvae and pupae (11.9 kg), adult insects (8.3 kg), and benthos (9.5 kg; Table 5).

Model simulations indicated that a size-structured population of 1,000 age-1 and older rainbow trout consumed 1,516 kg of larval galaxiids annually, representing 0.5–2.1% of the estimated seasonal larval production and 0.8% of the estimated annual larval production in the limnetic region (Table 6). The pelagic predators (ages 2–6) consumed the largest biomass of larval galaxiids; larval predation peaked sharply during summer (704 kg/1,000 rainbow trout), reached intermediate values during both spring (383 kg/1,000 rainbow trout) and autumn (350 kg/1,000 rainbow trout), and declined to 79 kg/1,000 rainbow trout during winter (Figure 4). All ages of rainbow trout in the lake, including the littorally oriented age-1 fish, consumed relatively similar biomasses of the benthic adult galaxiids annually (160–225 kg/1,000 rainbow trout). Predation on adult galaxiids increased steadily

TABLE 4.—Energy density values (J/g wet weight; measured by bomb calorimetry) of prey consumed by nonnative rainbow trout in Lake Moreno, Argentina, and the indigestible percentage of prey, used as inputs in the bioenergetics model simulations. Other fish were a mix of the non-galaxiids without any predominant species. Other food was composed of fish eggs and other miscellaneous prey.

Variable	Adult galaxiids	Larval galaxiids	Other fish	Molluscs	Adult insects	Insect larvae, pupae	*Aegla* spp.	*Samastacus* spp.	Amphipods	Other food
Energy density (J/g), simulation days 1–365	3,540	2,879	6,040	1,705	5,296	2,062	3,731	3,974	4,429	6,000
Indigestible (%)	3	3	3	15	15	15	15	15	15	3

from spring (238 kg/1,000 rainbow trout) and summer (262 kg/1,000 rainbow trout) to autumn (379 kg/1,000 rainbow trout) and then declined slightly during winter (325 kg/1,000 rainbow trout).

When predation was expanded to the estimated lakewide population of 29,000 rainbow trout of ages 1–7, model simulations estimated an annual population-level consumption totaling 211,000 kg for all prey, of which 44,000 kg were galaxiid larvae and 34,900 kg were galaxiid adults. The seasonal population-level consumption estimates on larval galaxiids represented 37% of the estimated larval production during November–February, 15% during peak production in February–May, and 60% during May–November; overall, the annual predation by rainbow trout totaled 23% of the estimated annual production of larval galaxiids (Table 6) and was considered to be a sustainable level of predation mortality. However, hatchery stocking scenarios that increased the existing predator population by two- to threefold (i.e., 58,000–87,000 rainbow trout of ages 1–7) resulted in predation rates that were 47–70% of the annual larval production, 30–45% of peak summer larval production, and excessive percentages of larval production during the other seasons (Table 6); these levels of predation were considered unsustainable. The stocking scenarios would similarly increase predation rates on other prey (e.g., for 58,000 predators, the impact would be 58 times the consumption rates presented in Table 6 for a size-structured population of 1,000 rainbow trout); however, the lack of information on the abundance, biomass, or production of these prey prevents an assessment of predation rate.

Discussion

Since the introduction of salmonids into Patagonia, their impact on native biota has been more a matter of speculation than of actual fact, giving rise to a series of ecological and management questions. By quantifying the temporal-spatial and size-structured predation by rainbow trout, we can now begin to evaluate the direct effects of exotic salmonids on the native galaxiids and explore the implications of other direct and indirect effects on the structure and function of the native fish and macroinvertebrate community. In general, galaxiids were the main prey for all sizes of rainbow trout, and predation varied seasonally on pelagic premeta-morphic larvae or on benthic juveniles and adults according to availability. Rainbow trout exerted seasonally high consumption demand on the pelagic premetamorphic larvae, removing an estimated 15% of the peak summer larval production and 23% of the annual larval production in Lake Moreno. The biomass of benthic juvenile and adult small puyen consumed by rainbow trout was nearly as high as the pelagic larval biomass consumed; however, we currently lack the

TABLE 5.—Annual age-specific and lifetime consumption rates of major prey categories (g/predator) by rainbow trout of ages 1–6 in Lake Moreno, Argentina.

Age	Adult galaxiids	Larval galaxiids	Other fish	Adult insects	Insect larvae, pupae	Molluscs	Other benthos	Total annual consumption	Adult and larval galaxiids (%)
1	604	302	8	274	677	54	264	2,183	42
2	1,031	1,415	13	1,021	1,034	869	820	6,205	39
3	1,763	2,211	692	1,139	1,693	2,021	1,395	10,913	36
4	2,412	3,090	968	1,602	2,320	2,819	1,916	15,127	36
5	2,960	3,839	1,203	1,999	2,851	3,498	2,357	18,708	36
6	3,400	4,444	1,392	2,320	3,278	4,047	2,711	21,592	36
Total lifetime consumption (g)	12,170	15,302	4,276	8,355	11,853	13,308	9,463	74,727	37
Percent of lifetime consumption	16	20	6	11	16	18	13		

TABLE 6.—Seasonal production of larval galaxiids in Lake Moreno, Argentina, and estimated predation of larval galaxiids by a size-structured population of 1,000 rainbow trout (ages 1–7), the estimated population of 29,000 rainbow trout, and increased rainbow trout populations under three hatchery stocking scenarios (populations that are 2.0, 2.5, or 3.0 × current abundance N).

Period	Larval production (kg)	Kilograms of larvae eaten/1,000	Kilograms of larvae eaten by 29,000	Percent production eaten/1000	Percent production eaten by 29,000	Percent production eaten by 2.0N	Percent production eaten by 2.5N	Percent production eaten by 3.0N
Nov–Feb	39,337	501	14,533	1.3	37	74	92	111
Feb–May	134,313	697	20,193	0.5	15	30	38	45
May–Nov	15,256	318	9,219	2.1	60	121	151	181
Annual	188,907	1,516	43,945	0.8	23	47	58	70

biomass and abundance estimates needed to translate these consumption estimates into predation rates on the older life stages. This current level of predation on galaxiids was considered high but sustainable given the persistent sympatry of galaxiids with introduced salmonids in lakes over the past century. Nonetheless, rainbow trout have likely altered the structure and function of these lake food webs, and further increases in rainbow trout abundance via hatchery stocking could quickly become unsustainable by removing too large a fraction of the larval galaxiid production and could potentially press production limits for other parts of the food web.

In Patagonia, the native freshwater fish species diversity is low, and the only major native piscivore is the Creole perch. The introduction of predatory salmonids (Macchi et al. 1999; Milano et al. 2002) has considerably altered the temporal-spatial and size-structured dimensions of predator–prey interactions in Patagonian lakes. Small puyen and big puyen are common prey for Creole perch and salmonids, and predation pressure dramatically influences the biology of these species (Milano 2003; Macchi et al. 2008). To understand the real impact of salmonids on these lakes, we must address predation by rainbow trout within the context of the additional predation by the other salmonids and native predators. Introduced rainbow trout have imposed significant, and perhaps novel, predation risk on the early pelagic life stages of galaxiids, whereas the native Creole perch and the
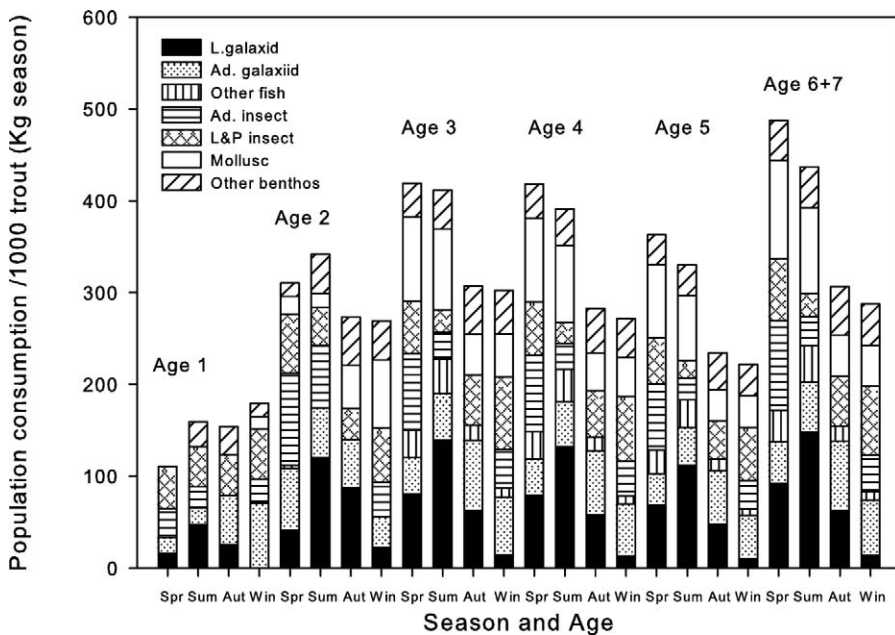

FIGURE 4.—Seasonal age-specific prey consumption (kg) by an age-structured population of 1,000 rainbow trout (ages 1–7) in Lake Moreno, Argentina. Seasons are spring (Spr), summer (Sum), autumn (Aut), and winter (Win). Prey groups are larval (L.) galaxiids, adult (Ad.) galaxiids, other fish, adult insects, insect larvae and pupae (L&P), molluscs, and other benthos.

other salmonids feed primarily on the older benthic juvenile and adult life stages of galaxiids. By reducing the recruitment of juvenile galaxiids to benthic habitats, rainbow trout predation could reduce the availability of these prey to Creole perch and the other benthic predatory salmonids. Moreover, rainbow trout eat a considerable biomass of juvenile and adult galaxiids, so they potentially compete directly with Creole perch and other salmonids in benthic habitats as well.

Although it is difficult to determine how benthic invertebrate communities and most of the fish populations might have changed in response to introduced salmonid predators and competitors, we can consider the case of the Patagonian silverside. According to historical records, beach seining in several lakes in the area (including Lake Moreno) historically yielded several hundred Patagonian silversides per tow (Macchi 2004). However, as shown by this study and extensive monitoring of 40 lakes in the region, catches of this species are currently low and restricted to highly vegetated habitats (P.H.V., unpublished data) or habitats that are unfavorable environments for salmonids (García Asorey 2001). The contemporary low catches of Patagonian silversides in Lake Moreno compared with past catch rates could be due in part to predation in an environment with low macrophyte cover. Recent reports of predation by larger Patagonian silversides (25–35 cm) on larval small puyen (Macchi et al. 1999, 2007) also imply that the rainbow trout might have usurped limnetic habitats from the Patagonian silversides, both as a competitor for limnetic larval galaxiid prey and as a predator on Patagonian silversides.

Anglers and hatcheries frequently pressure regional managers to increase fish stocking and aquaculture activities, which could also lead to shifts in fish community composition. In Patagonia, stocking of salmonids is still seen by many resource administrators as the primary management tool for addressing a wide variety of fisheries needs. The most widely stocked salmonid is the rainbow trout (Macchi et al. 2008). However, as this study suggests, artificial addition of rainbow trout into a lake would impose additional demands on the vertebrate and invertebrate prey populations; these demands should be evaluated quantitatively as part of the decision-making process before any action is considered. It is unlikely that stocking strategies, such as those simulated here, could be sustained; rather, galaxiid recruitment would probably decline, with coincident declines in growth and perhaps survival of feral or stocked rainbow trout. It is also probable that the fish community composition would shift in response to the increased demand for prey by stocked predators.

The observed salmonid assemblages in northern Patagonia are probably the result of shifts in species stocking policy. Brook trout was initially the most widely stocked species, dominating until at least 1945 in an area extending from the Andean range into the Patagonian steppe. Historical records show that after 1945, brook trout dominance declined dramatically and retracted toward the Andean range. This shift seems to be the result of rainbow trout becoming the more widely stocked species during and after the 1930s (Macchi et al. 2008). Escapes from aquaculture facilities may also have a profound effect on fish community composition. In Argentina, salmonid aquaculture is mostly related to cage farming facilities for rainbow trout in the hydroelectric reservoirs of northern Patagonia. Temporetti et al. (2001) demonstrated that gill-net catches of rainbow trout in Alicura Reservoir shifted from 100% wild specimens prior to establishment of the first aquaculture facilities in 1990 to only 3% wild individuals and 97% escaped fish 8 years later.

With the exception of larval galaxiids, no estimates exist for the productivity of the major prey items of rainbow trout or for consumption of these taxa by other predators in Lake Moreno. Therefore, it is not yet possible to model the limits that food supply might impose on the carrying capacity for the fish community. Critical issues need to be resolved first. Foremost among these are (1) estimation of species-specific abundance and productivity of the other predators (Creole perch, brook trout, and brown trout) and their primary prey and (2) diet and stable isotope analyses for developing a more comprehensive picture of the critical food web relations in these lakes.

References

Arratia, G., M. B. Peñafort, and S. Menú-Marque. 1983. Peces de la región sureste de los Andes y sus probables relaciones biogeográficas actuales. [Fishes of the southeast region of the Andes and their probable actual biogeographic relationships] Deserta 7:48–107.

Balseiro, E. G., and B. E. Modenutti. 1998. Pelagic communities and ecosystem processes in Andean Patagonian lakes. Ecología Austral 8:183–189.

Barriga, J. P. 2006. Estudio comparado de la distribución espacio temporal, el crecimiento y la alimentación de larvas y juveniles de *Galaxias* (Pisces, Galaxiidae) en lagos y ríos Patagónicos. [Spatial and temporal distribution, growth and feeding of larvae and juveniles of *Galaxias* (Pisces, Galaxidae) in Patagonian lakes and rivers] Doctoral dissertation. Universidad Nacional del Comahue, Bariloche, Río Negro, Argentina.

Barriga, J. P., M. A. Battini, P. J. Macchi, D. Milano, and V. E. Cussac. 2002. Spatial and temporal distribution of landlocked *Galaxias maculatus* and *Galaxias platei* (Pisces, Galaxiidae) in a lake in the South American Andes. New Zealand Journal of Marine and Freshwater Research 36:349–363.

Battini, M. A. 1997. Los estadios tempranos de vida de *Galaxias maculatus* (Jenyns, 1842) y *Odontesthes hatcheri* (Eigenmann, 1909), con especial referencia a su alimentación y crecimiento. [Early life stages of *Galaxias maculatus* (Jenyns, 1842) and *Odontesthes hatcheri* (Eigenmann, 1909) with special reference to their feeding and growth] Doctoral dissertation. Universidad Nacional del Comahue, Río Negro, Argentina.

Cervellini, P. M., M. A. Battini, and V. E. Cussac. 1993. Ontogenetic shift in the diet of *Galaxias maculatus* (Galaxiidae) and *Odontesthes microlepidotus* (Atherinidae). Environmental Biology of Fishes 36:283–290.

Chipps, S. R., and J. E. Garvey. 2007. Quantitative assessment of food habits and feeding patterns. Pages 473–514 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Ciancio, J., and M. Pascual. 2006. Energy density of freshwater Patagonian organisms. Ecología Austral 16:91–94.

Ciancio, J. E., M. A. Pascual, and D. A. Beauchamp. 2007. Energy density of Patagonian aquatic organisms and empirical predictions based on water content. Transactions of the American Fisheries Society 136:1415–1422.

Cussac, V. E., P. M. Cervellini, and M. A. Battini. 1992. Intralacustrine movements of *Galaxias maculatus* (Galaxiidae) and *Odontesthes microlepidotus* (Atherinidae) during their early life history. Environmental Biology of Fishes 35:141–148.

Edge, K.-A., C. R. Townsend, and T. A. Crowl. 1993. Investigating anti-predator behaviour in three genetically differentiated populations of nonmigratory galaxiid fishes in a New Zealand river. New Zealand Journal of Marine and Freshwater Research 27:357–363.

Fernando, C. H. 1991. Impacts of fish introductions in tropical Asia and America. Canadian Journal of Fisheries and Aquatic Sciences 48:24–32.

García Asorey, M. I. 2001. Estructura de edades y crecimientos de *Oncorhynchus mykiss* Walbaum 1792 y *Salmo trutta* L. 1758 en embalses de la región Patagónica, Argentina. [Age structure and growth of *Oncorhynchus mykiss* Walbaum, 1792 and *Salmo trutta* L. 1758 in hydroelectric power reservoirs of Patagonia, Argentina] Licenciate thesis. Universidad Nacional del Comahue, Río Negro, Argentina.

Gonzáles Regalado, T. 1945. Peces de los Parques Nacionales Nahuel Huapi, Lanín y Los Alerces. [Fishes of the Nahvel Huapi, Lanin and Los Alerces national parks] Anales del Museo de la Patagonia 1:121–138.

Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish bioenergetics 3.0. Wisconsin Sea Grant Institute, WISCU-T-97-001, Madison.

Lindegren, M. 2003. Daily migration of fish: a complicated game of hide and seek in Patagonia. Honours thesis. Lund University, Lund, Sweden.

Lodge, D. M. 1993. Biological invasions: lessons for ecology. Trends in Ecology and Evolution 8:133–137.

Love, R. H. 1971. Dorsal aspect target strength of an individual fish. Journal of the Acoustical Society of America 49:816–823.

Love, R. H. 1977. Target strength of an individual fish at any aspect. Journal of the Acoustical Society of America 62:1397–1403.

Macchi, P. J. 2004. Respuestas de *Galaxias maculatus* a la depredación por parte de *Percichthys trucha* y los salmónidos introducidos en ambientes lénticos de la Patagonia norte. Doctoral dissertation. Universidad Nacional del Comahue, Río Negro, Argentina.

Macchi, P. J., V. E. Cussac, M. F. Alonso, and M. A. Denegri. 1999. Predation relationships between introduced salmonids and native fish fauna in lakes and reservoirs of northern Patagonia. [Responses of *Galaxias maculatus* to predation by *Percichthys trucha* and by salmonids introduced in lenthic water bodies of northern Patagonia] Ecology of Freshwater Fish 8:227–236.

Macchi, P. J., M. A. Pascual, and P. H. Vigliano. 2007. Differential piscivory of the native *Percichthys trucha* and exotic salmonids upon the native forage fish *Galaxias maculatus* in Patagonian Andean lakes. Limnologica 37:76–87.

Macchi, P. J., P. H. Vigliano, M. Pascual, M. F. Alonso, M. A. Denegri, D. Milano, M. García Asorey, and G. E. Lippolt. 2008. Historical policy goals for fish management in Northern Continental Patagonia, Argentina: a structuring force of actual fish assemblages? Pages 331–348 *in* J. Nielsen, J. Dodson, K. Friedland, T. Hamon, N. Hughes, J. Musick, and E. Verspoor, editors. 2005. Reconciling fisheries with conservation: the challenge of managing aquatic ecosystems. Proceedings of the Fourth World Fisheries Congress. American Fisheries Society, Symposium 49, Bethesda, Maryland.

Marini, T. L. 1936. Los salmónidos en nuestros Parque Nacional de Nahuel Huapi. [Salmonids in our Nahuel

Huapi National Park] Anales de la Sociedad Científica Argentina 121:1–24.

McDowall, R. M. 1990. When galaxiid and salmonid fishes meet, a family reunion in New Zealand. Journal of Fish Biology 37:35–43.

McIntosh, A. R. 2000. Habitat- and size-related variations in exotic trout impacts on native galaxiid fishes in New Zealand streams. Canadian Journal of Fisheries and Aquatic Sciences 57:2140–2151.

McIntosh, A. R, T. A. Crowl, and C. R. Townsend. 1994. Size-related impacts of introduced brown trout on the distribution of native common river galaxias. New Zealand Journal of Marine and Freshwater Research 28:135–144.

McIntosh, A. R., C. R. Townsend, and T. A. Crowl. 1992. Competition for space between introduced brown trout (*Salmo trutta* L.) and a native galaxiid (*Galaxias vulgaris* Stokell) in a New Zealand stream. Journal of Fish Biology 41:63–81.

Meador, M. R., L. R. Brown, and T. Short. 2003. Relations between introduced fish and environmental conditions at large geographic scales. Ecological Indicators 3:81–92.

Milano, D. 2003. Biología de *Galaxias platei* (Pisces, Galaxiidae): especializaciones relativas a su distribución. [Biology of *Galaxias platei* (Pisces: Galaxiidae): distribution related specializations.] Doctoral dissertation. Universidad Nacional del Comahue, Río Negro, Argentina.

Milano, D., V. E. Cussac, P. J. Macchi, D. E. Ruzzante, M. F. Alonso, P. H. Vigliano, and M. A. Denegri. 2002. Predator associated morphology in *Galaxias platei* in Patagonian lakes. Journal of Fish Biology 61:138–156.

Milano, D., D. E. Ruzzante, V. E. Cussac, P. J. Macchi, R. A. Férriz, J. P. Barriga, J. Aigo, M. E. Lattuca, and S. Walde. 2006. Latitudinal and ecological correlates of morphological variation in *Galaxias platei* (Pisces, Galaxiidae) in Patagonia. Biological Journal of the Linnean Society 87:69–82.

Minns, C. H. K. 1990. Patterns of distribution and association of freshwater fish in New Zealand. New Zealand Journal of Marine and Freshwater Research 24:31–44.

Modenutti, B. E., E. G. Balseiro, and P. M. Cervellini. 1993. Effect of selective feeding of *Galaxias maculatus* (Salmoniformes, Galaxiidae) on zooplankton of a South Andes lake. Aquatic Sciences 55(1):65–75.

Moyle, P. B. 1997. The importance of an historical perspective: fish introductions. Fisheries 22:14.

Moyle, P. B., and T. Light. 1996. Biological invasions of freshwater: empirical rules and assembly theory. Biological Conservation 78:149–161.

Murillo, V. H., and V. H. Ruiz. 2003. El puye *Galaxias globiceps* Eigenmann 1927 (Osteichthyes Galaxiidae): ¿una especie en peligro de extinción? [The puye *Galaxias globiceps* Eigenmann 1927 (Osteichthys Galaxiidae): a species threatened with extinction?] Guyana Zoológica 43:10–20.

Ogutu-Ohwayo, R. 1990. Changes in prey ingested and the variations in the Nile perch and other fish stocks in Lake Kyoga and the northern waters of Lake Victoria (Uganda). Journal of Fish Biology 27:55–63.

Ogutu-Ohwayo, R., and R. E. Hecky. 1991. Fish introductions in Africa and some of their implications. Canadian Journal of Fisheries and Aquatic Sciences 48:8–12.

Pascual, M. A., V. Cussac, B. Dyer, D. Soto, P. H. Vigliano, S. Ortubay, and P. Macchi. 2007. Freshwater fishes of Patagonia in the 21st Century after a hundred years of human settlement, species introductions, and environmental change. Aquatic Ecosystem Health and Management 10:212–217.

Pascual, M., P. Macchi, J. Urbanski, F. Marcos, C. Riva Rossi, M. Novara, and P. Dell' Arciprete. 2002. Evaluating potential effects of exotic freshwater fish from incomplete species presence-absence data. Biological Invasions 4:101–113.

Probst, W. E., C. F. Rabeni, W. G. Covington, and R. E. Marteney. 1984. Resource use by stream-dwelling rock bass and smallmouth bass. Transactions of the American Fisheries Society 113:283–294.

Rainbow, P. 1998. Impacts of invasions by alien species. Journal of Zoology 246:247–248.

Rand, P. S., D. J. Stewart, P. W. Seelbach, M. L. Jones, and L. R. Wedge. 1993. Modelling steelhead population energetics in Lakes Michigan and Ontario. Transactions of the American Fisheries Society 122:977–1001.

Reissig, M., C. P. Queimaliños, and E. G. Balseiro. 2003. Effects of *Galaxias maculatus* on nutrient dynamics and phytoplankton biomass in a North Patagonian oligotrophic lake C. P. Environmental Biology of Fishes 68:15–24.

Temporetti, P., M. Alonso, G. Baffico, M. Diaz, W. Lopez, F. Pedrozo, and P. H. Vigliano. 2001. Trophic status, fish community and intensive production of salmonids in Alicurá Reservoir (Patagonia, Argentina). Lakes and Reservoirs: Research and Management 6:259–267.

Townsend, J. M., and T. A. Crowl. 1991. Fragmented population structure in a native New Zealand fish: an effect of introduced brown trout. Oikos 61:347–354.

Vigliano, P. H., and M. Alonso. 2000. Potencial económico de la pesca recreacional en la Argentina: una forma de pesca artesanal poco conocida y su posible impacto en economías regionales de países no desarrollados. Gayana Zoológica, Chile 64(1):109–114.

Vigliano, P. H., M. F. Alonso, P. J. Macchi, M. A. Denegri, M. García Asorey, G. E. Lippolt, and P. Alvear. 2008. Gill net and hydroacoustics fish resource evaluation of an ultraoligotrophic lake in northern Patagonia, Argentina. Pages 1745–1768 *in* J. L. Nielsen, J. J. Dodson, K. Friedland, T. R. Hamon, J. Musick, and E. Verspoor, editors. Reconciling fisheries with conservation: proceedings of the Fourth World Fisheries Congress. American Fisheries Society, Symposium 49, Bethesda, Maryland.

Vigliano, P. H., and G. Darrigran. 2002. Argentina's Freshwater Systems, Aliens in Wonderland. Pages 25–44 *in* Proceedings of the 11th International Conference on Aquatic Invasive Species, 25–28 February 2002,

Alexandria, Virginia. The Professional Edge, Pembroke, Ontario, Canada.

Vigliano, P., P. Macchi, M. Alonso, M. A. Denegri, D. Milano, G. Lippolt, and G. Padilla. 1999. Un diseño modificado y procedimiento de calado de redes agalleras para estudios cuali-cuantitativos de peces por estratos de profundidad en lagos araucanos. [A modified gillnetting and sampling procedure design for quali-quantitative studies by depth strata for deep araucanian lakes.] Natura Neotropicalis 30:1–11.

Wootton, R. J. 1990. Ecology of teleost fishes. Kluwer, London.

Zaret, T., and R. T. Paine. 1973. Species introduction in a tropical lake. Science 182:449–455.