Dietary overlap among native and non-native fish in Patagonian low-order streams

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Abstract – The diet composition and feeding strategy of native and exotic fish species were studied from May 2005 to February 2006 in three Patagonian low-order streams. A total of 464 fish were caught, which belonged to the exotic species Oncorhynchus mykiss (270), Salmo trutta (177) and the native species Hatcheria macraei (17). The analysis of 336 stomach contents indicated that at the individual level, the three species had a generalized feeding strategy based on benthic invertebrates (Plecoptera, Trichoptera, Coleoptera and Diptera). In the three streams, the widest population niches were observed in winter. There was, however, also a slight tendency toward an increased between-phenotype contribution to the niche width in same season, indicating that a small proportion of individuals within the fish populations specialized by predominantly feeding on a few specific prey species. Hence, the wide population niche widths observed throughout the year were partly a result of mixed individual feeding strategies within the populations. The higher diet overlaps were registered between exotics O. mykiss – S. trutta at Glyn and Carbón, and O. mykiss and the native H. macraei at Manguera, but it changed markedly through the year, perhaps depending on temporal changes in food availability suggesting a competitive coexistence of these species. This is mainly related to the fact that both species changed their food preferences in spring and foraged almost exclusively on Aubertoperla illiesi. This implies that in order to reduce the predation risk or the inter-specific competition for food, the fish species might partition the feeding habitats.

Key words: Hatcheria macraei / salmonids / feeding strategies / Patagonia / Argentina

Introduction

The introduction of non-indigenous fish is considered one of the most important anthropogenic impacts on freshwater ecosystems (Kolar and Lodge, 2000). Fishes of the Salmonidae family have been widely introduced in the Southern Hemisphere and their ecological impacts have been substantial (Townsend, 2003). To understand the magnitude and implications of such impacts multi-species approaches are required.

In the last century Patagonia was affected by a continuous salmonid species stocking (Pascual et al., 2007). Thirteen salmonid species were introduced in the Argentinean Patagonia and among them the most widely distributed are Oncorhynchus mykiss, Salmo trutta and Salvelinus fontinalis. Recently, the anadromous Chinook salmon Oncorhynchus tshawytscha was observed spawning in headwaters of Pacific and Atlantic basins in Argentina (Pascual and Ciancio, 2007; Soto et al., 2007; Di Prinzio and Pascual, 2008). There is evidence indicating that the exotic O. mykiss feed intensively on native fishes (McDowall, 2003; Arismendi et al., 2009; among others).

The native fish species are widespread, being distributed throughout most of the region’s high-order rivers (Pascual et al., 2007). Their status in low-order streams is, however, poorly understood. In consequence, the understanding of the role of fish in freshwater ecosystems is important given that when species with similar feeding behaviors co-occur and the resource availability is limited in quantity or diversity some degree of food competition might be expected (Odum, 1971). In that situation, different feeding strategies may help to reduce interspecific competition. Thus, under some circumstances, competition may become an important force.

*Corresponding author: cydiprinzio@yahoo.com.ar
The study was conducted in three streams located in northwest Patagonia (Glyn 43°27'S, 71°33'W; Manguera 43°33'S, 71°26'W and Carbón 43°32'S, 71°28'W) in the Andean-Humid and the Sub-Andean Sub-humid biozones (Fig. 1). The landscape is strongly influenced by glacial action and strong fluvial erosion. River discharge is bimodal and determined by rainfall, which occurs mainly in winter and by the snowmelt in spring (Coronato and del Valle, 1988). The streams under study are second (Glyn) or third (Manguera and Carbón) order and belong to the Carrenleufú basin. The streams are 15 km (Manguera), 25 km (Glyn) and 30 km (Carbón) long. Catchments are surrounded by sub-Antarctic forest characterized by perennial (Austrocedrus chilensis, Nothofagus dombyei and Maytenus boaria) and deciduous (Nothofagus pumilio and Nothofagus antarctica) species.

**Measurement of physical and chemical variables**

Samples were obtained in May (autumn), September (winter) and December (spring) 2005 and in February 2006 (summer). In each sampled site, flow velocity, water depth, dry widths of channel, water discharge, water temperature, conductivity, pH, dissolved oxygen, turbidity, total suspended solids, soluble reactive phosphate, nitrate plus nitrite nitrogen and ammonia were calculated to determine whether environmental conditions were similar between rivers and stable. Statistical comparisons of values obtained for physical and chemical variables at each site were conducted by applying the Kruskal–Wallis test (Sokal and Rohlf, 1995).

**Fish sampling**

Fish were sampled seasonally, in May (autumn), September (winter) and December (spring) 2005 and in February 2006 (summer) using a portable backpack electrofishing gear (Coffelt Mark-10 CPS, output 350 V) along reaches of 100 m long. The width of the sampling area was coincident with the stream width, except for those sections presenting non-wadeable sites with swift currents (Carbón stream). The sampled area was estimated considering the length and width of the reach. Thus, for each stream the density and biomass were estimated and expressed as the number of individuals (individuals.m⁻²) and biomass (g.m⁻²) per area sampled, respectively. The development of a sampling program may affect the fish populations under study (Casaux and Barrera-Oro, 2002), thus only up to 30 individuals (selected randomly) per species were dissected in the field at −10°C and at the laboratory were dissected for diet analysis.

**Dietary analyses**

Fish were dissected and the stomachs were separated for diet analysis. The stomach fullness was assessed using a five-point scale method employing a percentage scale ranging from empty (0%) to full (100%) (Amundsen et al., 1996). Food items were removed and identified to the lowest taxonomic level possible. The composition of the diet was calculated in terms of percent abundance (Ai),

![Fig. 1](location of the three sampled streams at Northwest Chubut, Patagonia, Argentina.)

**Material and methods**

**Study area**

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frequency of occurrence \((F_i)\) and prey-specific abundance \((P_i)\) following Amundsen et al. (1996):

\[
A_i = \left( \frac{\sum S_i}{\sum S_i} \right) \times 100
\]

\[
F_i = \frac{N_i}{N}
\]

\[
P_i = \left( \frac{\sum S_i}{\sum S_i} \right) \times 100
\]

where \(S_i\) is the contribution of prey \(i\) to stomach fullness, \(S_{Tk}\) is the total stomach fullness of fish with prey \(i\) in their stomach and \(S_i\) is the total stomach fullness of the fish, \(N_i\) is the number of fish with prey \(i\) in their stomach and \(N\) is the total number of fish with stomach contents.

The diet width \((B)\) was calculated using Levins (1968) index:

\[
B = 1 - \sum p_i^2
\]

where \(p_i\) is the proportion of each prey type \(i\) in the diet and equals \(A_i\) expressed as fraction rather than percentage.

**Diet overlap**

Dietary overlap between the fish species was calculated as an index expressed as a percentage overlap (Krebs, 1989):

\[
P_{jk} = \left[ \sum_{i} \min(P_{ij}, P_{ik}) \right] \times 100
\]

where \(P_{jk}\) is the percentage overlap between species \(j\) and species \(k\), \(P_{ij}\) are the proportions of resource \(i\) in relation to the total resources used by species \(j\) and \(k\), respectively, and \(n\) is the total number of prey categories. The overlap is considered to be significant when the index value exceeds 60% (Wallace, 1981).

**Feeding strategy and phenotype contributions to the niche width**

Food-niche characteristics were analyzed by the graphical method of Amundsen et al. (1996). For each prey type, the prey-specific abundance \((P_i)\) is plotted against the frequency of occurrence \((F_i)\) on a two-dimensional graph. Prey importance, feeding strategy and phenotype contribution to the niche width can be interpreted along the diagonals and axes of the diagram (see Amundsen et al., 1996). The diagonal from the lower left to the upper right corner provides a measure of prey importance for the whole population with dominant prey at the upper, right corner and rate and unimportant prey at the lower end. The vertical axis represents the feeding strategy in terms of specialization or generalization: specialists have prey points positioned in the upper part of the graph, whereas generalists have all prey points in the lower part. Points located in the upper left indicate specialization by subgroups of the predator population, whereas points in the upper right indicate specialization by the whole predator population on given prey. Hence, if one or a few points are located in the upper right, this reflects a predator population with a narrow niche width. When there are no prey points in this part of the diagram this reflects a predator population with a broader niche width. Prey points in the upper left and lower right corner represent the same percent abundance in the diet of the population as a whole, but illustrate totally different feeding strategies among the individual predators. Prey with high specific abundance and low occurrence (upper left) have been consumed by a few individuals displaying specialization, whereas prey with a low specific abundance and a high occurrence (lower right) have been eaten occasionally by most individuals. These differences are related to the between- and within-phenotype contributions to niche width, respectively. Points in the upper right part of the graph (i.e., above the diagonal from lower left to upper right) reflect a population with a high between-phenotype component (high BPC) with individuals specializing on different prey categories. Points in the opposite part (below the diagonal from lower left to upper right) represent a high within-phenotype component (high WPC) and the individuals utilize many common preys none of which dominate the diet (Roughgarden, 1972; Amundsen, 1995). In practical terms, a high WPC occurs when all prey categories have been eaten by most predators, but in small proportions, whereas a high BPC occurs when each prey category has been subjected to specialization, but only by a small fraction of the predator population.

**Results**

**Environmental features**

Sites were located between 403 m. a.s.l. (Carbón) and 699 m.a.s.l. (Manguera) (Table 1). Flow velocity was comprised between 0.8 m.s\(^{-1}\) (Carbón) and 1.1 m.s\(^{-1}\) (Glyn). The streambed wet width ranged from 4.2 to 18.8 m in Glyn and Carbón, respectively. The lowest dissolved oxygen content was observed at Carbón (11.9 mg.L\(^{-1}\)) and the highest one at Glyn (12.4 mg.L\(^{-1}\)). Carbón stream presented the highest conductivity (70.3 \(\mu S_{20,cm}^{-1}\)), whereas the highest concentrations of soluble reactive phosphate (0.8 \(\mu g.L^{-1}\)) and total suspended solid (5.1 mg.L\(^{-1}\)) were registered at Manguera stream. Wet width and mean discharge was significantly higher (Kruskal–Wallis, \(P < 0.05\)) in Carbón stream than in the remaining sites.

**Fish analysis**

A total of 464 fish was caught and the individuals belonging to exotic species (\(O.\ mykiss\) and \(S.\ trutta\)) largely
Table 1. Locations of the three sampled streams and environmental features during the study period (n = 4). Values are presented as mean values (± SD).

<table>
<thead>
<tr>
<th>Feature</th>
<th>Glyn</th>
<th>Manguera</th>
<th>Carbón</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude (°S)</td>
<td>43°27’33.7’</td>
<td>43°33’25’</td>
<td>43°32’12.5’</td>
</tr>
<tr>
<td>Longitude (°W)</td>
<td>71°33’25’</td>
<td>71°26’35.1’</td>
<td>71°28’20.3’</td>
</tr>
<tr>
<td>Altitude (m a.s.l)</td>
<td>615</td>
<td>699</td>
<td>403</td>
</tr>
<tr>
<td>Stream order</td>
<td>2</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Wet width (m)</td>
<td>4.2 ± 0.8</td>
<td>5.8 ± 0.7</td>
<td>18.8 ± 3.7*</td>
</tr>
<tr>
<td>Depth (m)</td>
<td>0.2 ± 0.1</td>
<td>0.2 ± 0.0</td>
<td>0.3 ± 0.1</td>
</tr>
<tr>
<td>Water temperature (°C)</td>
<td>7.4 ± 2.2</td>
<td>7.1 ± 1.4</td>
<td>8.1 ± 2.1</td>
</tr>
<tr>
<td>Flow velocity (m.s⁻¹)</td>
<td>1.1 ± 0.5</td>
<td>0.9 ± 0.4</td>
<td>0.8 ± 0.2</td>
</tr>
<tr>
<td>Discharge (m.seg⁻¹)</td>
<td>1.1 ± 1.1</td>
<td>1.0 ± 0.8</td>
<td>4.8 ± 2.9*</td>
</tr>
<tr>
<td>pH</td>
<td>7.2 ± 0.1</td>
<td>7.4 ± 0.4</td>
<td>7.2 ± 0.2</td>
</tr>
<tr>
<td>Dissolved oxygen (mg.L⁻¹)</td>
<td>12.4 ± 3.7</td>
<td>12.3 ± 2.0</td>
<td>11.9 ± 3.6</td>
</tr>
<tr>
<td>Conductivity (µS.cm⁻¹)</td>
<td>56.8 ± 15.8</td>
<td>65.0 ± 21.6</td>
<td>70.3 ± 18.4</td>
</tr>
<tr>
<td>Turbidity (NTU)</td>
<td>10.3 ± 17.9</td>
<td>8.5 ± 12.4</td>
<td>7.0 ± 6.8</td>
</tr>
<tr>
<td>Ammonia (µg.L⁻¹)</td>
<td>0.9 ± 0.8</td>
<td>1.0 ± 0.8</td>
<td>1.0 ± 0.7</td>
</tr>
<tr>
<td>Nitrate + nitrite nitrogen (µg.L⁻¹)</td>
<td>0.3 ± 0.2</td>
<td>0.2 ± 0.3</td>
<td>0.3 ± 0.2</td>
</tr>
<tr>
<td>Soluble reactive phosphate (µg.L⁻¹)</td>
<td>0.4 ± 0.2</td>
<td>0.8 ± 0.6</td>
<td>0.5 ± 0.1</td>
</tr>
<tr>
<td>Total suspended solids (mg.L⁻¹)</td>
<td>1.1 ± 0.6</td>
<td>5.1 ± 7.3</td>
<td>2.6 ± 1.31</td>
</tr>
</tbody>
</table>

*Indicates significant differences between values (Kruskal–Wallis test, P < 0.05).

Table 2. Fish abundance, in terms of density (ind.m⁻²) and biomass (g.m⁻²), at the three sampled sites at Northwest Patagonia, Argentina. – indicates no captures.

<table>
<thead>
<tr>
<th>Specie</th>
<th>Glyn (ind.m⁻²)</th>
<th>(g.m⁻²)</th>
<th>Manguera (ind.m⁻²)</th>
<th>(g.m⁻²)</th>
<th>Carbón (ind.m⁻²)</th>
<th>(g.m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autumn</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>O. mykiss</td>
<td>0.19</td>
<td>4.40</td>
<td>0.17</td>
<td>1.95</td>
<td>0.16</td>
<td>2.33</td>
</tr>
<tr>
<td>S. trutta</td>
<td>0.18</td>
<td>1.84</td>
<td>–</td>
<td>–</td>
<td>0.10</td>
<td>2.28</td>
</tr>
<tr>
<td>H. macraei</td>
<td>0.00</td>
<td>–</td>
<td>0.02</td>
<td>0.05</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Total</td>
<td>0.37</td>
<td>6.24</td>
<td>0.19</td>
<td>2.01</td>
<td>0.26</td>
<td>4.61</td>
</tr>
<tr>
<td>Winter</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>O. mykiss</td>
<td>0.13</td>
<td>0.20</td>
<td>0.03</td>
<td>0.42</td>
<td>0.23</td>
<td>3.35</td>
</tr>
<tr>
<td>S. trutta</td>
<td>0.17</td>
<td>0.64</td>
<td>–</td>
<td>–</td>
<td>0.11</td>
<td>0.99</td>
</tr>
<tr>
<td>H. macraei</td>
<td>0.00</td>
<td>–</td>
<td>0.01</td>
<td>0.04</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Total</td>
<td>0.30</td>
<td>0.84</td>
<td>0.04</td>
<td>0.45</td>
<td>0.34</td>
<td>4.34</td>
</tr>
<tr>
<td>Spring</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>O. mykiss</td>
<td>0.04</td>
<td>0.87</td>
<td>0.01</td>
<td>0.09</td>
<td>0.07</td>
<td>0.63</td>
</tr>
<tr>
<td>S. trutta</td>
<td>0.09</td>
<td>3.15</td>
<td>–</td>
<td>–</td>
<td>0.09</td>
<td>2.03</td>
</tr>
<tr>
<td>H. macraei</td>
<td>0.01</td>
<td>0.12</td>
<td>0.006</td>
<td>0.03</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Total</td>
<td>0.15</td>
<td>4.15</td>
<td>0.02</td>
<td>0.12</td>
<td>0.16</td>
<td>2.66</td>
</tr>
<tr>
<td>Summer</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>O. mykiss</td>
<td>0.38</td>
<td>4.26</td>
<td>0.06</td>
<td>1.29</td>
<td>0.28</td>
<td>3.62</td>
</tr>
<tr>
<td>S. trutta</td>
<td>0.30</td>
<td>3.03</td>
<td>–</td>
<td>–</td>
<td>0.30</td>
<td>2.57</td>
</tr>
<tr>
<td>H. macraei</td>
<td>0.01</td>
<td>0.02</td>
<td>0.01</td>
<td>0.06</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Total</td>
<td>0.69</td>
<td>7.31</td>
<td>0.07</td>
<td>1.36</td>
<td>0.58</td>
<td>6.19</td>
</tr>
<tr>
<td>Annually (mean)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>O. mykiss</td>
<td>0.19 ± 0.14</td>
<td>2.43 ± 2.21</td>
<td>0.07 ± 0.07</td>
<td>0.94 ± 0.85</td>
<td>0.18 ± 0.09</td>
<td>2.48 ± 1.35</td>
</tr>
<tr>
<td>S. trutta</td>
<td>0.19 ± 0.09</td>
<td>2.17 ± 1.18</td>
<td>–</td>
<td>–</td>
<td>0.15 ± 0.10</td>
<td>1.96 ± 0.69</td>
</tr>
<tr>
<td>H. macraei</td>
<td>0.01 ± 0.01</td>
<td>0.07 ± 0.07</td>
<td>0.01 ± 0.00</td>
<td>0.05 ± 0.02</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

Dietary analyses

The diet composition of the three fish species (336 stomachs) was diverse and benthic organisms largely dominated in the samples. A total of 88 prey taxa were identified from the stomach contents (Fig. 2). Depending on the season and site, the most important prey species of O. mykiss were Aubertoperla illiesi, Antactoperla michaelseni, Nousia delicata, Sinicridea annulicornis, Parasericostoma ovale, Simulidae larvae and vegetable fragments. Similarly, A. michaelseni, Limnoperla jaffueli, N. delicata, A. illiesi, S. annulicornis and Athericidae predominated samples (96.34%). O. mykiss was the most abundant fish (270 individuals, 0.44 ind.m⁻²), followed by S. trutta (177 individuals, 0.34 ind.m⁻²) and Hatcheria macraei (17 individuals, 0.02 ind.m⁻²) (Table 2). A similar pattern was observed in the contribution of the different species to the samples by biomass: O. mykiss 5.85 g.m⁻², S. trutta 4.13 g.m⁻² and H. macraei 0.12 g.m⁻². The size of the fish caught ranged between 3.0 (H. macraei at Manguera) and 27.0 cm (S. trutta at Carbón), whereas their weight ranged between 0.1 (H. macraei at Manguera) and 378.8 (O. mykiss at Glyn) g (see details in Table 3).
Table 3. Seasonal changes in the total length (TL in cm) and weight (in g), represented as mean ± standard deviation and range, observed in the fish sampled at three streams in Northwest Patagonia, Argentina. – indicates no captures.

<table>
<thead>
<tr>
<th>Species</th>
<th>Winter</th>
<th>Spring</th>
<th>Summer</th>
</tr>
</thead>
<tbody>
<tr>
<td>O. mykiss</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total length</td>
<td>Range: 12.5–14.1</td>
<td>14.1–16.4</td>
<td>13.8–24.5</td>
</tr>
<tr>
<td>Mean: 16.0</td>
<td>1.4–2.8</td>
<td>1.6–3.2</td>
<td>2.1–4.9</td>
</tr>
<tr>
<td>Weight</td>
<td>Range: 9.5–12.3</td>
<td>12.3–15.4</td>
<td>9.6–19.2</td>
</tr>
<tr>
<td>Mean: 11.5</td>
<td>1.1–1.5</td>
<td>1.2–1.7</td>
<td>1.5–2.4</td>
</tr>
<tr>
<td>O. mykiss</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total length</td>
<td>Range: 12.5–14.1</td>
<td>14.1–16.4</td>
<td>13.8–24.5</td>
</tr>
<tr>
<td>Mean: 16.0</td>
<td>1.4–2.8</td>
<td>1.6–3.2</td>
<td>2.1–4.9</td>
</tr>
<tr>
<td>Weight</td>
<td>Range: 9.5–12.3</td>
<td>12.3–15.4</td>
<td>9.6–19.2</td>
</tr>
<tr>
<td>Mean: 11.5</td>
<td>1.1–1.5</td>
<td>1.2–1.7</td>
<td>1.5–2.4</td>
</tr>
<tr>
<td>S. trutta</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total length</td>
<td>Range: 3.8–5.1</td>
<td>5.1–6.5</td>
<td>5.0–7.5</td>
</tr>
<tr>
<td>Mean: 4.6</td>
<td>0.5–1.2</td>
<td>0.7–1.4</td>
<td>0.8–1.9</td>
</tr>
<tr>
<td>Weight</td>
<td>Range: 3.0–5.0</td>
<td>5.0–7.0</td>
<td>5.0–7.5</td>
</tr>
<tr>
<td>Mean: 4.5</td>
<td>0.5–1.2</td>
<td>0.7–1.4</td>
<td>0.8–1.9</td>
</tr>
<tr>
<td>H. macraei</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total length</td>
<td>Range: 5.0–7.5</td>
<td>7.5–10.0</td>
<td>7.5–10.5</td>
</tr>
<tr>
<td>Mean: 6.5</td>
<td>0.5–1.2</td>
<td>0.7–1.4</td>
<td>0.8–1.9</td>
</tr>
<tr>
<td>Weight</td>
<td>Range: 3.0–5.0</td>
<td>5.0–7.0</td>
<td>5.0–7.5</td>
</tr>
<tr>
<td>Mean: 4.5</td>
<td>0.5–1.2</td>
<td>0.7–1.4</td>
<td>0.8–1.9</td>
</tr>
</tbody>
</table>

Overall, only minor dietary overlap was observed in winter between all three species (Table 4). The dietary overlap observed between the introduced O. mykiss and S. trutta at Glyn exceeded 60% in autumn, spring and summer (Table 4). The dietary overlap between O. mykiss and H. macraei at Manguera exceeded 60% only in spring (Table 4). The dietary overlap between O. mykiss and S. trutta exceeded 60% only in autumn, but in spring such value approached significance (Table 4).

Diet overlap

The maximum value of diet-width index varied with the season and site. Thus, at Glyn O. mykiss showed the maximum value of this index in autumn, while in S. trutta this occurred in winter. At Manguera, the maximum value of diet-width index of O. mykiss showed the maximum value of this index in autumn, whereas in S. trutta was in winter. At Carboñ the maximum value of diet-width index of O. mykiss and H. macraei occurred in spring and autumn respectively. At Carboñ the maximum value of diet-width index of O. mykiss was in spring, whereas in S. trutta was in autumn (Table 5).

Most of the prey types had very similar contributions to the diet of the three fish species both in terms of frequency of occurrence and prey-specific abundance (Fig. 3), and the three fish species exhibited a remarkable similarity in their feeding strategies and prey utilization patterns. At the individual level, there was a clear generalized feeding strategy within the three species as the prey points were mainly located in the lower half of the diagram and the prey-specific abundance only occasionally exceeded 50% (Fig. 3(A, E, G, H, I, L)). The prey species that showed high specific abundance and low occurrence (upper left) have been consumed by a few individuals displaying specialization were Lymnaea sp. for S. trutta and Limnephilidae for O. mykiss in Glyn (autumn) (Fig. 3(A)). In the same way, in Manguera the
Fig. 2. Diet overlap pattern between *O. mykiss* (black bars), *S. trutta* (white bars) and *H. macraei* (hatched bars) through the year sampled in three Northwest Patagonian streams (Argentina). %D.C.: Diet contribution percentage. Values scales of Y-axes are represented to easy the interpretation graphs.
prey species that showed high specific abundance and low occurrence for *O. mykiss* were *Mastigoptila longicornuta* (autumn), *Metrichia patagonica* and *S. annulicornis* (spring) and Coleoptera sp.1 (summer), while for *H. macraei* was *Paratrichocladius* sp. (autumn and summer) and *A. illiesi* in spring (Fig. 3(E, G, H)). In Carbón, Dermaptera and *Oxyethira bidentata* were the most consumed prey in autumn by *S. trutta* (Fig. 3(I)) and *Aegla aff nequensis* for *O. mykiss* (summer) (Fig. 3(L)).

At the population level, both *H. macraei* (Manguera) and *O. mykiss* (Glyn) showed two different feeding strategies by specialization in spring, summer (Fig. 3(G, H)) and winter (Fig. 3(B)), respectively and a generalization at the rest of the year. The population specialization of the two species was exposed by one prey point being located toward upper right of the diagram. In contrast, no prey types emerged as particularly important in the diet of these species and all prey points were located along or below the diagonal from the upper left to the lower right corner (Fig. 3(E, F, A, C, D)). In spring, the population specialization of *H. macraei* was directed toward the Plecoptera *A. illiesi*, whereas in summer with the Diptera *Paratrichocladius*. The population specialization in *O. mykiss* was related to the Diptera Simuliidae larvae. Thus, a large number of prey types were utilized, but all had a low contribution to the diet, resulting in pronounced population generalizations and large niche widths of both species during the rest of the year (Table 5).

Overall, in the three streams, the wider population niches observed was in winter (Fig. 3(B, F, J)), spring (Glyn and Carbón) (Fig. 3(C, J)) and summer (Glyn) (Fig. 3(D)). This is illustrated in the diagram by most of the prey points being located to the lower right of the

### Table 4. Prey overlap (%) among fish represented in three streams located in Northwest Patagonia Argentina. – indicates no captures.

<table>
<thead>
<tr>
<th></th>
<th>Glyn</th>
<th>Manguera</th>
<th>Carbon</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autumn</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>O. mykiss–S. trutta</em></td>
<td>61.16</td>
<td>–</td>
<td>60.96</td>
</tr>
<tr>
<td><em>O. mykiss–H. macraei</em></td>
<td>–</td>
<td>15.73</td>
<td>–</td>
</tr>
<tr>
<td>Winter</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>O. mykiss–S. trutta</em></td>
<td>30.55</td>
<td>–</td>
<td>43.74</td>
</tr>
<tr>
<td><em>O. mykiss–H. macraei</em></td>
<td>–</td>
<td>29.03</td>
<td>–</td>
</tr>
<tr>
<td>Spring</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>O. mykiss–S. trutta</em></td>
<td>73.39</td>
<td>–</td>
<td>57.23</td>
</tr>
<tr>
<td><em>O. mykiss–H. macraei</em></td>
<td>–</td>
<td>1.24</td>
<td>62.50</td>
</tr>
<tr>
<td><em>S. trutta–H. macraei</em></td>
<td>2.85</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Summer</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>O. mykiss–S. trutta</em></td>
<td>62.89</td>
<td>–</td>
<td>46.81</td>
</tr>
<tr>
<td><em>O. mykiss–H. macraei</em></td>
<td>–</td>
<td>14.74</td>
<td>–</td>
</tr>
</tbody>
</table>

### Table 5. Population niche width (Levins index, B) of the three species presented in the three streams studied in the Northwest Patagonia, Argentina. – indicates no captures.

<table>
<thead>
<tr>
<th></th>
<th>Autumn</th>
<th>Winter</th>
<th>Spring</th>
<th>Summer</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glyn</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>O. mykiss</em></td>
<td>0.27</td>
<td>0.06</td>
<td>0.22</td>
<td>0.24</td>
</tr>
<tr>
<td><em>S. trutta</em></td>
<td>0.29</td>
<td>0.50</td>
<td>0.22</td>
<td>0.26</td>
</tr>
<tr>
<td><em>H. macraei</em></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Manguera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>O. mykiss</em></td>
<td>0.30</td>
<td>0.45</td>
<td>0.71</td>
<td>0.22</td>
</tr>
<tr>
<td><em>H. macraei</em></td>
<td>0.96</td>
<td>–</td>
<td>–</td>
<td>0.16</td>
</tr>
<tr>
<td>Carbon</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>O. mykiss</em></td>
<td>0.31</td>
<td>0.23</td>
<td>0.32</td>
<td>0.31</td>
</tr>
<tr>
<td><em>S. trutta</em></td>
<td>0.61</td>
<td>0.34</td>
<td>0.43</td>
<td>0.27</td>
</tr>
</tbody>
</table>

![Fig. 3. Feeding strategy of *O. mykiss*, *S. trutta* and *H. macraei* through the year sampled in three Northwest Patagonian streams (Argentina). The most important prey categories are identified by shortened names. % PSA: prey-specific abundance percentage. *S. trutta* ● *O. mykiss* ○; *H. macraei* △.](image-url)
diagonal from the origin to the upper right corner. There was, however, also a slight tendency toward an increased between-phenotype contribution to the niche width parti-
cularly in autumn (Glyn and Carbón) (Fig. 3(A, I)), in spring (Manguera for O. mykiss) (Fig. 3(G)) and in sum-
er (Carbón) (Fig. 3(D)), as a few prey types were skewed
toward the upper left of the diagram. This indicates that
small fractions of individuals within the fish populations
tended to specialize by predominantly feeding on a few
specific prey.

Discussion

The streams considered in this study were dominated
by the exotic O. mykiss in terms of both density and bio-
mass, whereas the native H. macraei was scarcely re-
presented in the samples, similar to findings by Di Prinzio
et al. (2009). Hatcheria macraei is a rheophilic and negatively
phototactic catfish (Menni, 2004) which inhabits fast flow-
ing, clear, cold and well-oxygenated waters (Ringuelet
1975). This fish was widely distributed in Patagonia in
the past, but is currently considered as rare (López et al.,
2003). Their current restricted distribution could be
related to a variety of causes like habitat loss, predation
and competition from salmonids (Pascual et al., 2007).

According to the graphical method of Amundsen et al.
(1996), the three fish species showed to be considered
as generalist feeders. Overall, benthic invertebrates
(Plecoptera, Trichoptera, Coleoptera and Diptera) were
the main prey. These results are in line with those reported
for these fish species at other localities of Patagonia
(Ferriz, 1994; Arismendi et al., 2009; Barriga and Battini,
2009; Buria et al., 2009). The difference in the resource
niche between exotic and native species is agreed with the
competitive exclusion principle, which states that co-
existing species should segregate in resource use. Under
such circumstances, different feeding strategies may help
to reduce interspecific competition. The higher diet over-
laps were registered between O. mykiss and S. trutta at
Glyn and Carbón, which suggests that there is a com-
petitive coexistence of these species in spite of their
extensive niche overlap. Extensive niche overlap has been
suggested to occur between competitors that are similar
in their skills to compete for resources (Agrén and
Fagerström, 1984; Keddy, 1989), such as when consumers
differ in their foraging behavior toward the same renew-
able resource (Wilson et al., 1999). According to Agrén
and Fagerström (1984), competitors can survive by segre-
gating along a resource gradient if they have ample differ-
ences in their ecological niches, but they can also coexist
under conditions of extensive overlap if they are highly
similar in their niche utilization, and thereby equal com-
petitors (see also Keddy, 1989). It was observed that
O. mykiss and H. macraei reflected significant diet overlap
at Manguera in spring. It may be surprising that dissimilar
species such as salmonids and a freshwater catfish have
diets that are highly similar, as one should expect their
distinct morphological differences to be reflected in
segregated food niches. Hatcheria macraei is morpho-
logically adapted for living at the bottom of the river and
are regarded as strictly benthic fishes. The salmonoids are,
in contrast, morphologically adapted to adopt different
positions in the water column and may feed on either
benthic or drifting preys (Kalleberg, 1958). However, these
two species, showed different niche width in spring, while
O. mykiss reflected a broad niche width, H. macraei pre-
vented a narrow width wide with a specialization at popu-
lation level. This is mainly related to the fact that both
species changed their food preferences in spring and
foraged almost exclusively on the Plecoptera A. illiesi
(Fig. 3(G)). This pattern is similar to the one reported by
Gabler and Amundsen (2010) for the Atlantic salmon parr
and the alpine bullhead in a sub-Arctic river and by
Barriga and Battini (2009) who suggested that in order
to reduce the predation risk or the inter-specific competition
for food, H. macraei might partition the use of the feeding
habitat in a Patagonian river. Accordingly, Penaluna et al.
(2009) observed that three native fish species had niche
overlap with the introduced O. mykiss and S. trutta, and
that they changed their mesohabitat use after the reduc-
tion of salmonids abundance in two Patagonian rivers
(Chile).

The levels of prey overlap observed between O. mykiss
and S. trutta in Glyn and Carbón also changed markedly
through the year and may be a reflection of temporal
changes in food availability. However, some studies
have indicated that when prey overlap between species is
high, the resource competition is often low as a result of
high abundance of their principal prey (Klemetsen, 1993;
Höines and Bergstad, 2002; Barrera Oro, 2003). McIntosh
et al. (1992) observed in New Zealand streams that native
and exotic species temporally and spatially segregated the
use of food resources and observed a small proportion
of the fish populations specialising by predominantly
feeding on a few specific prey. Hence, the wide population
niche widths observed along the year were partly a result
of mixed individual feeding strategies within the popu-
lations.

The magnitude of the impact of introduced salmonids
on Patagonian native fish is difficult to determine due to
the absence of pre-introduction information (Pascual
et al., 2007). Similarly, Baiguín and Ferriz (2003) indicated
that it is not well understood how exotic fish have modified
the structure of the communities in different Patagonian
basins. Thus, the studies on food competition between
native and exotic species might help to understand the
co-adaptive process related to the salmonoids’ intro-
duction.

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Laboratorio de Investigaciones en Ecología y Sistemática
Animal (LIESA) No. 76.
References


