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Amphipod-supported food web: *Themisto gaudichaudii*, a key food resource for fishes in the southern Patagonian Shelf

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ABSTRACT

The trophic role of the hyperiid amphipod *Themisto gaudichaudii* in the southern Patagonian shelf food web was assessed from the analysis of stomach contents of the local fish assemblage. A total of 461 trawl samples were collected during seven seasonal cruises. A total of 17 out of 38 fish species were found to ingest *T. gaudichaudii*. This amphipod was a main prey item in five of these species, showing high values of alimentary index: *Seriolella porosa* (99.9%), *Macruronus magellanicus* (68.8%), *Micromesistius australis* (59.1%), *Patagonotothen ramsayi* (48.6%), and *Merluccius hubbsi* (10.9%). The contribution of *T. gaudichaudii*, in weight, to their summer diet was 60%, on average. This contribution was minimal in winter and maximal in summer. Fisheries studies have indicated that these five species, mainly *M. magellanicus*, account for almost 85% of the fish biomass in the area. Although the remaining 15% did not feed heavily on *T. gaudichaudii*, they are known to prey on the main hyperiid predators. Our study shows that *T. gaudichaudii* contributes greatly, both directly and indirectly, to supporting the fish community. We thus proposed that *T. gaudichaudii* plays a key role as a "wasp-waist" species in the sub-Antarctic region, similar to that of krill in Antarctic waters, channeling the energy flow and enabling a short and efficient food chain.

1. Introduction

In many food webs, most higher-level consumers depend either directly or indirectly on a single species as their main food source. These are considered key species due to both their high abundances and position in the food web (Jordán, 2009). A well-known case in the pelagic food web of upwelling zones are the small planktivorous pelagic fish represented by sardines and anchovies. These species function as forage fish, being the main prey of numerous top predators such as large pelagic and demersal fish, as well as marine birds and mammals (Cury et al., 2000).

In the Southern Ocean, the Antarctic krill (*Euphausia superba*) is considered a key species in Antarctic marine food webs. Krill are the main food source for most high level predators, from demersal fish to whales. However, krill abundance shows significant interannual variability and it has been reported that during krill-poor years, many predators feed on other crustaceans such as the hyperiid amphipod *Themisto gaudichaudii* (Collins et al., 2008; Everson et al., 1999).

T. gaudichaudii is the most common pelagic amphipod and a major component of the macrozooplankton community of the Southern Ocean (Vinogradov et al., 1996). It inhabits mainly neritic rather than oceanic areas, around islands and continents of sub-Antarctic and northern Antarctic regions (Bocher et al., 2001; Piatkowski et al., 1994; Sabatini and Álvarez Colombo, 2001; Siegfried, 1965), where highest abundances have been observed. Because of its high abundance in those areas, it has been suggested that in certain sectors of the sub-Antarctic region where krill are scarce or absent, *T. gaudichaudii* could play a role in the food webs similar to that of *E. superba* further south, in Antarctic waters (Bocher et al., 2001; Zeidler, 2004). However, although this hyperiid has been repeatedly recorded in the diet of a variety of top predators including fish (Kock et al., 1994; Shreeve et al., 2009), squid (Ivanovic and Brunetti, 1994; Mouat et al., 2001), seabirds (Cherel et al., 2002; Lescroël et al., 2004; Ridoux, 1994), and whales (Budylenko, 1978; Nemoto and Yoo, 1970), most works up to date mention the role of *T. gaudichaudii* only as a prey item for individual predators (see review of Dauby et al. (2003) and references therein). Only few studies have analyzed the incidence of this hyperiid in the diet of the seabird community as a whole, in waters around the Crozet and Kerguelen Islands (Bocher et al., 2001; Ridoux, 1994). These studies, which showed the primary trophic importance of *T. gaudichaudii* in peri-insular ecosystems, encouraged us to extend the analysis to a larger portion of the sub-Antarctic region.

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Most of the neritic areas of the sub-Antarctic region are composed of small island shelves. At this latitude range, the southern Patagonian shelf is the widest continental shelf, constituting a large ecosystem of the southwest Atlantic Ocean (hereafter called the Southern Patagonian Shelf Ecosystem, SPSE). The SPSE occupies an area of 284 680 km^2 south of 47°S bounded by the south American continent, Tierra del Fuego, Isla de los Estados, and the Malvinas (Falkland) Current flowing northward along the shelf break (Ciancio et al., 2008; Sabatini et al., 2004). The area is characterized by a high primary productivity (Romero et al., 2006) that supports an extraordinarily abundant and diverse community of species of major regional and global commercial importance (Food and Agricultural Organization, 1994). These species constitute the so-called "austral species assemblage", which is strongly dominated by hoki, *Macruronus magellanicus*, the most abundant fish species (Table 1), and the squid *Illex argentinus* (Angelescu and Prenski, 1987; Wöhler et al., 1999).

T. gaudichaudii is particularly abundant in the SPSE, where high densities are often found (Ramírez and Viñas, 1985; Sabatini, 2008; Sabatini and Álvarez Colombo, 2001). Some preliminary studies in the SPSE have reported that this crustacean is a frequent prey in stomach contents of the main zooplanktivorous taxa, including hoki and squid (Brickle et al., 2009; Ivanovic and Brunetti, 1994; Sánchez, 1999; Wöhler et al., 1999). On the other hand, based on stable isotope analysis of the food web, Ciancio et al. (2008) proposed that *T. gaudichaudii* may largely support the SPSE predator community.

To our knowledge, no attempt has been made, either in the SPSE or any other large ecological area, to estimate the importance of this or any other hyperiid species in the diet of the fish community as a whole. In this work, an extensive analysis of the stomach contents of the austral fish assemblage was performed with data from several research cruises. Both the importance of *T. gaudichaudii* as a food source for each species and the seasonal and spatial variability in the intake of this hyperiid were examined in order to establish the extent to which it represents a key species in the SPSE.

2. Methods

A program monitoring the stomach content of demersal and pelagic fishes was carried out during 1992–1994 by the Trophic Ecology Laboratory of the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) of Argentina. This study included data from 461 trawl samples collected during seven seasonal research cruises carried out in the SPSE (45°–55°S), Argentine Sea, on board the RVs. "Capitán Oca Balda" and "Eduardo Holmberg" (Table 2 and Fig. 1). Fish were captured using a bottom trawl with 200 mm mesh in the wing and 103 mm mesh in the codend. All trawls were made during day-time. A random sample from the total catch, representative of the size structure of the different species, was taken for the analysis of stomach contents. All fish in the sample were identified to species level whenever possible.

Specimens were dissected on board and their stomach contents analyzed. Individuals with apparent regurgitation or everted stomachs were excluded from this analysis. *T. gaudichaudii* was identified and its frequency of occurrence (%F) was recorded for all caught fish species as:

$$\%F = \text{No stomachs with } T.\,gaudichaudii/\text{No non-empty stomachs} \times 100.$$

Fish species showing a %F of *T. gaudichaudii* higher than 30% ("main hyperiid feeders" hereafter) were analyzed in more detail in order to evaluate the relative importance of this hyperiid as regards other prey items. %F was calculated for the main prey items, which were also weighed to the nearest 0.1 g (wet weight) to calculate the percent contribution (%W) to the diet:

$$\%W = T.\,gaudichaudii \text{ weight(or other prey item)/total stomach content weight} \times 100.$$

Additionally, the alimentary index (AI) was calculated as the product between %F and %W, expressed in percentage for each prey item:

$$\%AI = 100AI_i / \sum_{i=1}^{n} AI$$

where n is the total number of prey items considered (Griffiths, 1997; Lauzanne, 1975; Rosecchi and Nouaze, 1987).

Table 1
Estimated biomass in tons (t), and percentages (%), of the major fish species of the austral assemblage in summer of 1997. Modified from Wöhler et al. (1999).

Species	Biomass (t)	%
Macruronus magellanicus	3,209,120	67.04
Merluccius hubbsi	589,700	12.32
Patagonotothen ramsayi	230,169	4.81
Salilota australis	208,517	4.36
Genypterus blacodes	188,017	3.93
Squalus acanthias	40,834	0.85
Bathyraja spp.	37,599	0.79
Merluccius australis	34,445	0.72
Seriolella porosa[a]	18,255	0.38
Micromesistius australis	7315	0.15
Others spp.	222,754	4.65
Total	4,786,725	100.00

[a] From Wöhler (1997).

Table 2
List of cruises included in the present study carried out in SPSE (45°–55°S). (N) Number of trawl stations.

Season	Date	Cruise	R.V.	N
Summer	10–28 Jan 93	EH-01/93	Dr. E. Holmberg	81
Summer	22 Jan–16 Feb 93	OB-01/93	Cap. Oca Balda	49
Fall	21 Mar–09 May 94	OB-04/94	Cap. Oca Balda	109
Fall	05–15 May 93	OB-06/93	Cap. Oca Balda	30
Winter	22 Jul–16 Aug 93	OB-08/93	Cap. Oca Balda	89
Spring	07–22 Nov 92	EH-09/92	Dr. E. Holmberg	84
Spring	27 Nov–12 Dec 92	OB-01/92	Cap. Oca Balda	19

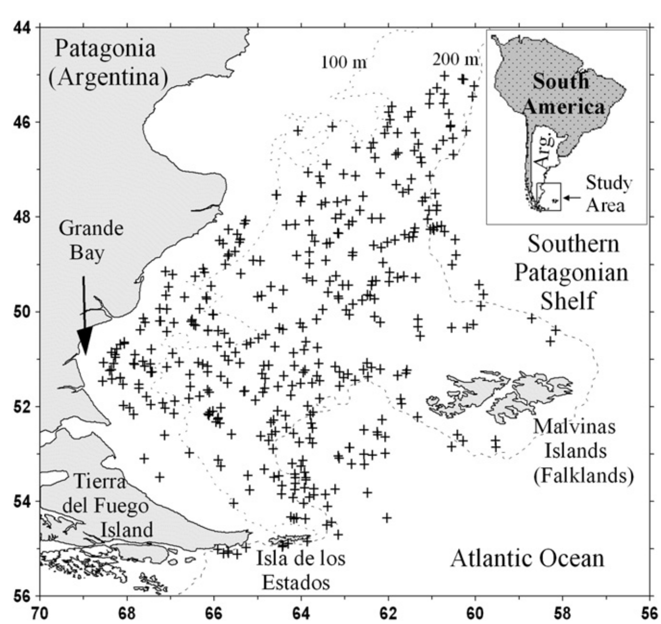

Fig. 1. Study area and 461 trawl stations from 7 seasonal research cruises.

The seasonal variability in *T. gaudichaudii* consumption by the main hyperiid feeders was assessed based on the %W data, but considering only those trawl stations located south of 48°S, due to the highly variable sampling effort in the study area.

In order to identify spatial variations in *T. gaudichaudii* consumption, we also analyzed the distribution of the AI per trawl station for this species. Because the AI takes into account both the frequency and weight of a particular prey item, it can be used as an indicator of local prey availability.

3. Results

A total of 22,981 stomachs, corresponding to 38 fish species (21 osteichthyes and 17 chondrichtyes) were analyzed. The number of individuals sampled during each season was 5920 in summer, 9363 in fall, 3886 in winter, and 3812 in spring. More than half (54.9%) of the stomachs contained food (Table 3). Specimens of *T. gaudichaudii*, ranging in size from 3 to 23 mm, were found in more than 30% (4007 individuals) of those stomachs, which corresponded to 17 fish species (Table 4).

These 17 fish species can be divided into two groups in relation to the annual %F of *T. gaudichaudii* in their stomachs. The first group, the main hyperiid feeders, included six osteichthyes species with frequencies higher than 30%: *Seriolella porosa* (94.3), *M. magellanicus* (48.8), *Patagonotothen ramsayi* (37.5), *Micromesistius australis* (35.8), *Merluccius hubbsi* (32.0) and *Austrophycis marginata*; the latter showed the highest frequencies, but, as it was poorly represented (six individuals), it was not considered in further analyses (Table 4).

The second group, the occasional hyperiid feeders, included 11 species of osteichthyes and chondrichtyes, with frequencies lower than 10%. Two of these species, *Salilota australis* and *Squalus acanthias*, showed seasonal increases in frequency. *T. gaudichaudii* was rarely found in the stomachs of the other fish species: *Bathyraja brachyurops*, *Bathyraja macloviana*, *Coelorhynchus fasciatus*, *Congiopodus peruvianus*, *Dissostichus eleginoides*, *Merluccius australis*, *Schoederichthys bivius*, *Sebastes oculatus* and *Stromateus brasiliensis* (Table 4).

Within the main hyperiid feeders, the relative importance of *T. gaudichaudii* and other major prey items present in the stomachs was assessed by the percentage of the AI. The results show that this species was by far the most important prey item for *S. porosa*, *M. magellanicus*, *M. australis*, and *P. ramsayi* (AI: 99.9%, 68.8%, 59.1%, and 48.6%, respectively), and the third prey item for *M. hubbsi* (10.9%) (Table 5). Other major prey items were euphausiids, the notothenid *P. ramsayi*, and squid. Benthic invertebrates were significant only in the diet of *P. ramsayi*. These five prey items made up the bulk of the hyperiid feeders' diet (between 63.2% and 98.1% in weight). Other minor prey items were found occasionally.

Although the number of species feeding on *T. gaudichaudii* remained relatively constant seasonally (8–10 species), the %F of this prey item in the stomachs was minimum in winter (14.3) and maximum in summer (48.5) (Table 4). Particularly, for the main hyperiid feeders, the %W followed the same pattern (Fig. 2). In fact, the peak of hyperiid intake was recorded in summer for all five species and its contribution was highest for *S. porosa*, *M. australis*, *P. ramsayi*, and *M. magellanicus* (98%, 97.5%, 58.3% and 44.4% respectively), and lowest for *M. hubbsi* (6.7%).

Considering the main hyperiid feeders together, the distribution of the AI per trawl station was not evenly distributed in the study area. High values appeared to be located between 49° and 53°S. Particularly, feeding on *T. gaudichaudii* was highest in a smaller coastal sector of this area (50°–52°S), even in winter (Fig. 3).

4. Discussion

Our results demonstrate the significant role played by *T. gaudichaudii* in the food web of the SPSE, the largest continental shelf of the sub-Antarctic region. The analysis of stomach contents of a large number of fish species and individuals, allowed a comprehensive assessment of the importance of this hyperiid as a main food source for the austral fish assemblage.

T. gaudichaudii was one of the main prey items for 5 of the 17 fish species that ingested this hyperiid. Although in terms of number of species this may seem moderate, biomass assessment data for the SPSE have shown that these main hyperiid feeders may account almost 85% of the estimated fish biomass (see Table 1). One species in particular, *M. magellanicus*, reached 67% of fish biomass, well above the other four species (Table 1). *T. gaudichaudii* was by far the main prey item for this fish, constituting almost 45% of its diet in summer (Fig. 2). In fact, during summer, *M. magellanicus* usually concentrates on the Patagonian shelf to feed actively (Giussi et al.,

Table 3
List of fish species caught and number of stomachs analyzed each season. Tot.: total No. of stomachs analyzed, w/food: No. of stomachs with food, T.g.: presence of *T. gaudichaudii* (1), absence (0).

Fish species	Summer	Fall	Winter	Spring	Total		
					Tot	w/ food	T.g.: 1/0
Chondrichthyes							
Squalus acanthias	123	441	121	353	1038	464	1
Schroederichthys bivius	168	233	205	184	790	673	1
Bathyraja macloviana	41	95	117	19	272	244	1
Bathyraja albomaculata	54	89	35	54	232	210	0
Psammobatis spp.	5	113	15	36	169	144	0
Bathyraja brachyurops	32	45	57	12	146	113	1
Bathyraja magellanica	19	47	34	26	126	100	0
Psammobatis scobina	50	6	65	5	126	101	0
Dipturus spp.	0	35	0	0	35	28	0
Dipturus chilensis	3	3	19	6	31	21	0
Bathyraja scaphiops	2	0	18	7	27	18	0
Sympterygia acuta	0	26	2	0	26	21	0
Sympterygia bonapartii	2	13	1	0	14	13	0
Dipturus trachyderma	8	1	5	0	14	11	0
Bathyraja multispinis	0	8	0	0	8	5	0
Callorhynchus callorhynchus	0	0	8	0	8	5	0
Psammobatis bergi	5	0	2	0	7	7	0
Bathyraja spp.	2	3	0	0	5	5	0
Psammobatis extenta	0	0	3	0	4	3	0
Atlantoraja castelnaui	1	0	0	0	4	2	0
Osteichthyes							
Macruronus magellanicus	3123	4910	1104	2149	11,286	6121	1
Patagonotothen ramsayi	750	328	461	169	1708	1140	1
Merluccius hubbsi	353	786	496	27	1662	838	1
Micromesistius australis	149	980	228	32	1 389	495	1
Genypterus blacodes	155	174	124	466	919	256	0
Stromateus brasiliensis	318	196	8	76	598	217	1
Cottoperca gobio	152	123	224	67	566	375	0
Salilota australis	98	128	138	16	380	309	1
Merluccius australis	83	179	100	1	363	159	1
Dissostichus eleginoides	34	170	31	10	245	138	1
Coelorhynchus fasciatus	12	91	88	0	191	69	1
Congiopodus peruvianus	74	0	53	35	162	96	1
Seriolella porosa	43	18	1	55	117	70	1
Sebastes oculatus	16	2	74	1	93	24	1
Macrourus holotrachys	0	84	0	0	84	49	0
Iluocoetes fimbriatus	21	0	9	3	31	10	0
Macrourus spp.	16	10	7	0	30	15	0
Helicolenus dactylopterus l.	0	0	15	0	15	1	0
Austrophycis marginata	0	13	0	0	13	6	1
Macruronus whitsoni	0	0	4	0	4	3	0
Austrolycus laticinctus	0	2	1	0	6	2	0
Xystreurys rasile	0	0	3	0	5	2	0
Total	5920	9363	3886	3812	22,981	12,610	17

Table 4
Seasonal fish predation on *T. gaudichaudii* according to stomach content analysis. w/food: No. of stomachs with food, w/T.g.: No. of stomachs with *T. gaudichaudii*, %F: frequency of occurrence. Shaded rows show the main hyperiid feeders.

Predator	Summer			Fall			Winter			Spring			Total		
	w/food	w/T.g.	%F	w/food	w/T.g.	%F	w/food	w/T.g.	%F	w/food	w/T.g.	%F	w/food	w/T.g.	%F
Chondrichthyes															
Squalus acanthias	79	8	10.1	226	6	2.6	38	2	5.3	121	12	9.9	464	28	6.0
Bathyraja macloviana	35	0	0	84	0	0	109	4	3.7	16	0	0	244	4	1.6
Bathyraja brachyurops	25	0	0	36	0	0	44	1	2.3	8	0	0	113	1	0.9
Schroederichthys bivius	140	0	0	201	0	0	165	1	0.6	167	0	0	673	1	0.1
Osteichthyes															
Austrophycis marginata	0	0	0	6	6	100.0	0	0	0	0	0	0	6	6	100.0
Seriolella porosa	36	34	94.4	0	0	0	1	0	0	33	32	97.0	70	66	94.3
Macruronus magellanicus	1 933	1 156	59.8	2 224	1 151	51.7	514	126	24.5	1 450	554	38.2	6 121	2 987	48.8
Patagonotothen ramsayi	575	312	54.3	172	18	10.5	276	65	23.5	117	33	28.2	1 140	428	37.5
Micromesistius australis	66	64	97.0	292	86	29.4	111	10	9.0	26	17	65.4	495	177	35.8
Merluccius hubbsi	181	56	30.9	405	173	42.7	243	37	15.2	9	2	22.2	838	268	32.0
Salilota australis	77	18	23.4	107	3	2.8	112	7	6.2	13	0	0	309	28	9.1
Sebastes oculatus	2	0	0	1	0	0	21	1	4.8	0	0	0	24	1	4.2
Dissostichus eleginoides	30	0	0	87	2	2.3	18	0	0	3	1	33.3	138	3	2.2
Congiopodus peruvianus	42	0	0	0	0	0	37	0	0	17	2	11.8	96	2	2.1
Stromateus brasiliensis	145	3	2.1	70	1	1.4	2	0	0	0	0	0	217	4	1.8
Coelorhynchus fasciatus	8	0	0	30	1	3.3	31	0	0	0	0	0	69	1	1.4
Merluccius australis	32	2	6.2	82	0	0	44	0	0	1	0	0	159	2	1.3
Total	3407	1654	48.5	4023	1446	35.9	1766	253	14.3	1981	655	33.1	11 177	4 007	
Total spp.			9			10			10			8			17

2004), coinciding both temporally and spatially with the highest abundances of *T. gaudichaudii* in the field (Sabatini and Álvarez Colombo, 2001).

The remaining fish species (excluding the main hyperiid feeders), which may constitute 15% of the biomass (mainly *S. australis*, *Genypterus blacodes*, *S. acanthias* and *Merluccius australis*, Table 1), feed mostly on squid, fish and macrocrustaceans (Angelescu and Prenski, 1987). Although in this work these fish species did not feed significantly on *T. gaudichaudii*, it has been reported that they prey heavily on two major hyperiid predators: the nototheniid *P. ramsayi* and the squid *I. argentinus* (Arkhipkin et al., 2001; Ivanovic and Brunetti, 1994; Nyegaard et al., 2004). In turn, these two species are also a secondary food source for the main hyperiid feeders, as shown here. Thus, *T. gaudichaudii* contributes greatly both directly and indirectly to the food supply of the fish community.

The contribution of *T. gaudichaudii* to the diet of fish in the SPSE had a strong seasonal component, with a winter minimum and increasing values from spring to summer. Previous studies have pointed out the strong seasonality of *T. gaudichaudii* in stomach contents compared to other large zooplankton such as euphausiids, whose presence is more constant throughout the year (Brickle et al., 2009; Perrotta, 1982). Seasonality of this hyperiid has also been recorded in zooplankton studies in the SPSE (Ciechomski and Sánchez, 1983; Sabatini and Álvarez Colombo, 2001), and an analogous pattern has been described for the sub-Antarctic waters of the Kerguelen Islands, at a similar latitude (Labat et al., 2005). It appears that a seasonal signal of the environmental parameters controls the cycle of *T. gaudichaudii* through the temperature effect on the growth rate and food resource availability (Labat et al., 2005).

Although the spatial distribution of the sampling effort was highly variable seasonally, it was possible to delineate a zone of increased consumption of *T. gaudichaudii* by the main hyperiid feeders. This zone, over the coastal area of Grande Bay (50°–52°S) and up to *ca.* 200 km offshore, coincided roughly with a recurrent "hot spot" of zooplankton with biomass values well above the background mean (Sabatini et al., 2004). The contribution of *T. gaudichaudii* to the zooplankton biomass in this coastal area is very significant and most likely supported by the often co-occurring high copepod biomass

Table 5
Contribution of *T. gaudichaudii* and other prey items to the diet of the main hyperiid feeders. %F: frequency of occurrence, %W: percentage of weight, %AI: percentage of alimentary index.

Prey\predator	*S. porosa*			*M. magellanicus*			*M. australis*			*P. ramsayi*			*M. hubbsi*		
	%F	%W	%AI	%F	%W	%AI	%F	%W	%AI	%F	%W	%AI	%F	%W	%AI
T. gaudichaudii	94.3	98.1	99.9	48.8	36.1	68.8	35.8	37.6	59.1	37.5	38.1	48.6	32.0	5.1	10.9
Euphausiid	7.1	1.0	0.1	30.6	12.7	15.1	26.7	20.7	24.4	7.4	6.1	1.6	24.8	3.9	6.6
P. ramsayi	0	0	0	9.7	14.4	5.5	0	0	0	3.2	4.6	0.5	12.0	33.3	27.1
Squid	0	0	0	5.9	22.1	5.1	0.6	4.9	0.1	1.2	3.1	0.1	16.2	41.1	45.1
Benthic invert.[a]	0	0	0	0.7	0.4	<0.1	0	0	0	37.4	31.5	40.1	0.8	0.5	<0.1
Others [b]	1.4	0.9	<0.1	9.87	14.3	5.5	10.1	36.8	16.4	16.1	16.6	9.1	9.5	16.1	10.3

[a] Includes mainly echinoderms, polychaetes, coelenterates, gammarid amphipods, mollusks and isopods.
[b] Includes mainly gelatinous zooplankton, the sprat *Sprattus fuegensis*, the crustaceans munida spp., and myctophids fish.

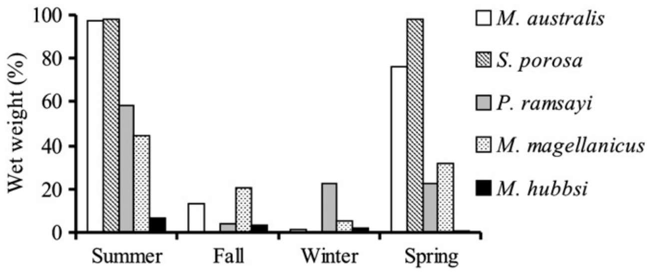

Fig. 2. Seasonal contribution of *T. gaudichaudii* expressed as percentage of wet weight (%W) to the diet of their more frequent fish predators (south of 48°S).

(Sabatini and Álvarez Colombo, 2001). It has been suggested that the presence of several fronts at this location and the associated complex circulation patterns likely enhance zooplankton production and accumulation through increased primary production (Palma et al., 2004; Sabatini et al., 2004).

The key species status in an ecosystem may be due to different attributes (Begon et al., 2006), including species position in the food web. Certainly, there are food webs where the positional importance of certain species is of central relevance (Jordán, 2009). The best examples are probably the "wasp-waist" ecosystems of pelagic upwelling zones (Cury et al., 2000), where a large number of species at low and high trophic levels are linked by a single or a few species in the mid trophic levels. Wasp-waist species are often the regulators of both higher and lower trophic levels, channeling and modulating the energy flow through the food web (Cury et al., 2000; Rice, 1995).

In the Southern Ocean, krill plays this role in the Antarctic food webs (Ducklow et al., 2007; Jordán, 2009; Smith et al., 2007), acting not only as food for numerous top predators, but also as a dominant grazer on a variety of phytoplankton species (Ross et al., 1998).

We suggest that *T. gaudichaudii* could replace krill as a wasp-waist species further north in sub-Antarctic trophic webs. Indeed, in this region, the species not only is a main food source for higher trophic levels, as shown in the present work, but can also play a major role in the control of local mesozooplankton communities as an opportunistic predator, mainly on copepods (Pakhomov and Perissinotto, 1996).

Furthermore, a wasp-waist species must also have an appropriate body size. In fact, in size-structured food webs, the position of an organism depends on its body size, which increases with trophic level. The length of these food chains, on the other hand, is partially a function of the predator–prey size ratio (Post, 2002) and in turn directly affects the proportion of biogenic carbon that reaches higher trophic levels.

It could then be speculated that both the position in the food web and the body size of *T. gaudichaudii* make it a suitable vehicle for channeling part of the high primary productivity of the SPSE system, via mesozooplankton, to higher trophic levels. In this way, this key crustacean species facilitates a relatively short and efficient food web, supporting millions of tons of fish and squid.

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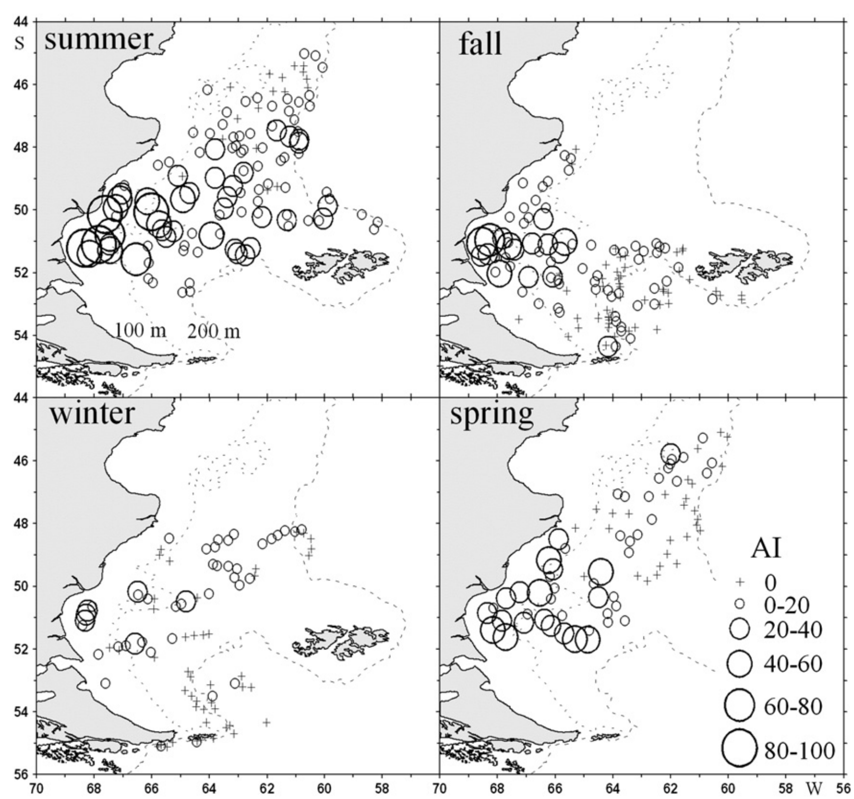

Fig. 3. Seasonal and spatial distribution of alimentary index (AI) of *T. gaudichaudii* in stomach contents of the main hyperiid feeders in southern Patagonia.

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