FEEDING AND REPRODUCTIVE ACTIVITY OF THE COPEPODS *Drepanopus forcipatus* AND *Calanus australis* DURING LATE SUMMER ON THE SOUTHERN PATAGONIAN SHELF (ARGENTINA, 47°-55°S)

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ABSTRACT

Drepanopus forcipatus and *Calanus australis* are key planktonic copepods on the southern Patagonian shelf. Their feeding and reproductive patterns and population status were investigated during late summer, when environmental conditions may be critical. The presence of food in the gut and food-pellet length were recorded in adult females and the most abundant copepodite stages. Diet composition was also studied in adult females. Female reproductive status was evaluated by gonad staging. Despite generally low feeding conditions and decreasing seasonal temperature, both copepods fed to some degree. The most numerous copepodites and adult females of both species showed similarly low feeding activity. About half of the adult females of the two species and C5s of *C. australis* contained food in their guts, but the proportion of fed C4-females of *D. forcipatus* was much lower. All copepods were generally feeding at low or intermediate levels. Gonad stage distribution and population structure showed low but still ongoing reproduction in both species. Gut content findings suggest a preference for smaller nanoplanktonic particles, especially dinoflagellates by *D. forcipatus,* and for autotrophic prey, particularly large diatoms by *C. australis*. The feeding and reproduction patterns of the two copepods were likely influenced by the distributions of potential food resources and temperature.

RESUMO

Drepanopus forcipatus e *Calanus australis* são copépodos planctônicos relevantes na plataforma da Patagônia Austral. Seus padrões de alimentação, reprodução e status populacional foram investigados durante o fim do verão, quando as condições ambientais podem ser críticas. A presença de alimento no abdomen e o tamanho das pelotas alimentares foram registados em fêmeas adultas e nos estágios mais abundantes de copepodito. A composição da dieta também foi estudada em fêmeas adultas. O status reprodutivo das fêmeas foi avaliado através do estágio gonadal. De modo geral, apesar das baixas condições alimentares e diminuição sazonal da temperatura, ambos os copépodos se alimentaram. Os copepoditos mais numerosos e as fêmeas adultas de ambas espécies mostraram baixa atividade alimentar. Cerca de metade das fêmeas adultas das duas espécies e C5s de *C. australis* apresentaram alimento em seu intestino, porém a proporção de fêmeas *D. forcipatus* C4 alimentadas foi consideravelmente menor. De modo geral, todos os copépodos se alimentaram entre níveis baixo e intermediário. A distribuição do estágio gonadal e a estrutura populacional apresentaram reprodução baixa, mas contínua para ambas as espécies. Os alimentos encontrados no intestino sugerem uma preferência por partículas nanoplanctônicas, especialmente dinoflagelatos em *D. forcipatus,* e por presas autotróficas, particularmente grandes diatomáceas em *C. australis*. Os padrões de alimentação e reprodução dos dois copépodos foram provavelmente influenciados pela distribuição de recursos alimentares e temperatura.

Descriptors*: Drepanopus forcipatus; Calanus australis*; Feeding; Reproduction; Southern Patagonian shelf.
Descritores: *Drepanopus forcipatus; Calanus australis*; Alimentação; Reprodução; Plataforma da Patagônia Austral.

INTRODUCTION

Food availability acts as a bottom-up control of the size of populations. In particular, timing of reproduction by marine copepods inhabiting high latitudes is mainly governed by seasonality in food availability and water temperature (e.g. NORRBIN, 1994; PLOURDE; RUNGE, 1993). Calanoid

copepods are mostly omnivorous (KLEPPEL, 1993), but some species are predominantly herbivorous, and the availability of phytoplankton is likely the main factor influencing their life cycles (e.g. ATTWOOD; PETERSON, 1989; PETERSON et al., 1990). Temperature, in turn, controls the conversion of assimilated food into oocytes and oocyte maturation, along with metabolic rates (NIEHOFF, 2007). In subarctic and subantarctic marine ecosystems, both phytoplankton stocks and temperature have strong seasonal cycles with high values in spring and summer and low values in winter. Therefore, trophic flexibility, energy storage and occurrence of resting (diapause) stages coupled with ontogenetic vertical migrations are the usual strategies by which these copepods cope with harsh winter conditions (e.g. CONOVER, 1988; VARPE, 2012).

Mesozooplankton play a crucial role in the productivity and trophodynamics of the southern Patagonian shelf (SABATINI; ÁLVAREZ COLOMBO, 2001; CIANCIO et al., 2008; PADOVANI et al., 2012; SABATINI et al., 2012). At the end of summer and beginning of autumn the system becomes less productive. Larger nanoplankton and microplankton abundances diminish, and food availability is low in the size fraction mainly grazed by copepods (>10 μm). Studies in the shelf area off Patagonia between ca. 50° and 55°S during late summer/early autumn indicate that dinoflagellates, diatoms and silicoflagellates are scarce (OLGUÍN et al., 2005; CEFARELLI et al., 2010). Microplanktonic ciliate abundances also are low in the entire region (e.g. SANTOFERRARA; ALDER, 2009a and b, 2012) and small ultraplanktonic cells prevail (ALMANDOZ et al., 2007). These results suggest that during late summer, the inner area of the southern Patagonian shelf is characterized by a microbial trophic web sustained by pico- and nanoeukariotes and bacterioplankton, which could constitute food limiting conditions for copepods.

Two copepod species, the medium-sized clausocalanid Drepanopus forcipatus and the large calanid Calanus australis, together make up most of the mesozooplankton biomass and are currently considered key species in the local planktonic food web. This is due not only to their abundance but also to their wide occurrence and trophic position (e.g. SABATINI et al., 2000; SABATINI, 2008). Recent studies with fine plankton nets (66 μm) suggest, nonetheless, that the co-occurring small sized species Oithona helgolandica, Ctenocalaus vanus and Microsetella norvegica may be more relevant to the food web than was previously thought (ANTACLI et al., 2010; ANTACLI et al., 2014).

Drepanopus forcipatus and C. australis are both endemic to the southern hemisphere (HULSEMANN, 1985; RAMÍREZ; SABATINI, 2000

and references therein). Over the southern Patagonian shelf, both species are distributed across the entire region, occurring most abundantly at ~51°S in the Grande Bay area over the inner- and mid-shelf during late summer (SABATINI et al., 2000; SABATINI, 2008). Although at variable densities, they appear to be concentrated in that area all year long, D. forcipatus occurring always in much higher numbers than C. australis. Average values of the former increase from ca. 10,000 ind m^{-2} in winter to ca. 60,000 ind m^{-2} in early spring and to about 400,000 ind m^{-2} by late summer, while numbers of C. australis range from about 30-90 ind m^{-2} in winter and early spring to ca. 700 ind m^{-2} in late summer (SABATINI et al., pers. comm.*). For all their importance, however, there is no information concerning either the feeding and reproductive patterns of both copepods or their relation to lower trophic levels.

The overall objective of this study was to examine the feeding and reproduction of D. forcipatus and C. australis during late summer. We expected to find reduced or even no feeding or reproductive activity of either population due to food limitation and seasonally decreasing temperature over the study area. Therefore, we studied for both species: (i) the composition and abundance of potential food resources, (ii) the population structure and feeding activity of adult females and prevailing copepodites, and (iii) the reproductive status of adult females. Lastly, we explored the relationships between the feeding and reproductive patterns and the overall food and thermal conditions of the water column.

MATERIAL AND METHODS

Sampling

Sampling was conducted over the continental shelf off southern Patagonia (Argentina) from ~47° to 55°S in the period of 18 March to 2 April 2004 onboard RV "Dr. E. L. Holmberg".

Copepods were sampled at 32 stations arranged in four sections by vertical tows from just above the seafloor or from a maximum depth of approximately 100 m with a small Bongo sampler, 20 cm mouth opening, fitted with 66 and 150 μm mesh nets (Table 1). Filtered volumes were measured with digital flowmeters (Hydro-Bios). Samples were preserved in 4% buffered formalin. Sampling time was conditioned by the arrival at the stations depending on the route of the cruise.

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To analyze the potential food for copepods, the composition representative of the upper layer was determined at 18 stations from samples collected with Niskin bottles at three discrete depths (surface, maximum *in situ* fluorescence and below) (Table 1). Samples were preserved with 25% glutaraldehyde, 0.3% final concentration, to ensure optimal preservation of athecate dinoflagellates and aloricate ciliates.

Vertical profiles of temperature, salinity and fluorescence were recorded at all sampled stations using a Sea-Bird 9-11 CTD and a Sea Point fluorometer.

Table 1. Sampling overview of cruise RV "Dr. E.L. Holmberg" (18 March – 2 April 2004). Sampling dates, times and depths, sampled organisms and assessed variables for each station. D/N, daytime or nighttime; Df, *Drepanopus forcipatus*; Ca, *Calanus australis*; C6-F, adult females; C4-F, copepodite 4-female; C5, copepodite 5; Tupp, mean temperature upper layer; Tlow, mean temperature lower layer.

St.	Date	Time	D/N	Bottom depth (m)	Bottles depth (m)	Plankton 2-200 μm	Copepods	Small Bongo depth (m)	Feeding, diet, reproduction		Feeding		Tupp (°C)	Tlow (°C)
									Df C6-F	*Ca* C6-F	*Df* C4-F	*Ca* C5		
262	02/04/2004	00:30	N	59	0,10,40	x	x	45	x		x		13.3	13.3
264	02/04/2004	04:00	N	92	0,10,40	x	x	70		x	x	x	12.3	11.7
266	02/04/2004	06:40	N	95	0,10,40	x	x	73	x	x				
267	02/04/2004	08:46	D	106			x	81						
269	02/04/2004	12:59	D	110	0,25,35	x	x	84				x	12.2	7.9
271	02/04/2004	17:45	D	120	0,15,35	x	x	92						
273	02/04/2004	22:45	N	128	0,21,30	x	x	98	x		x		11.2	6.0
250	31/03/2004	10:00	N	69			x	53						
251	31/03/2004	14:40	D	98			x	75						
254	31/03/2004	20:20	N	59	0,10,25	x	x	45	x	x	x	x	12.1	10.9
255	31/03/2004	22:50	N	100			x	77						
256	01/04/2004	00:35	N	94	0,20,40	x	x	72	x		x	x	12.5	9.4
257	01/04/2004	03:20	N	105			x	80						
258	01/04/2004	05:20	N	107	0,20,40	x	x	82	x		x		11.5	7.8
182	18/03/2004	15:30	D	84			x	64						
183	18/03/2004	21:45	N	22	0,10,20	x	x	17						
184	19/03/2004	00:15	N	90			x	69						
185	19/03/2004	02:00	N	88	0,15,50	x	x	67	x	x	x	x	11.4	7.8
186	19/03/2004	04:45	N	94			x	72						
187	19/03/2004	07:30	D	104	0,20,50	x	x	80	x	x	x	x	11.6	8.2
188	19/03/2004	09:30	D	103			x	79						
189	19/03/2004	11:20	D	115	0,23,50	x	x	88	x	x	x	x	10.9	8.8
191	19/03/2004	15:45	D	120	0,18,40	x	x	92						
193	19/03/2004	20:25	N	120	0,24,40	x	x	92						
244	30/03/2004	07:30	D	50			x	38						
216	23/03/2004	22:30	N	118	0,30,65	x	x	90						
228	27/03/2004	10:45	D	86			x	66						
229	27/03/2004	13:15	D	78			x	60						
230	27/03/2004	15:50	D	81			x	62						
231	27/03/2004	18:45	D	63			x	48						
236	29/03/2004	01:45	N	33	0,15,25	x	x	25	x	x	x	x	10.6	10.6
240	29/03/2004	11:30	D	68			x	52						
209	22/03/2004	11:40		295	0,15,40	x		failed						
						N=18	N=32		N=11	N=7	N=10	N=8		

Assessment of Potential Food Resources

The abundance and spatial distribution of the plankton <200 μm were estimated by microscopy (UTERMÖHL, 1958). Particles in the size range 2-10 μm and >10-200 μm were counted with an inverted microscope (Olympus IX 70) at 1000x and 200x magnification, respectively, after sedimentation in 100 mL chambers during at least 48 h to ensure the precipitation of smaller organisms. Cell counts were performed either across the entire, a half or a quarter of the chamber surface depending on sample concentration. An average of between 250 and 300 cells in the size range 2-200 μm were counted for each sample (VENRICK, 1978; EDLER; ELBRÄCHTER, 2010). Organisms were photographed with a digital camera (Olympus DP 71) fitted to the microscope and measured with image analysis software (Image Pro Plus v.6.0). Plankton communities were classified by size (ultraplankton 2-5 μm, smaller nanoplankton >5-10 μm, larger nanoplankton >10-20 μm, and microplankton >20-200 μm) and trophic category (autotrophs and heterotrophs). Trophic sorting was based on taxonomic identification and the trophic modality reported in the literature for a given taxon. Mixotrophs were not classified separately because experimental procedures with labeled prey are needed for their accurate estimation. Concentrations (cells L^{-1}) at the three sampling depths were integrated by trapezoidal interpolation to obtain a single value (cells m^{-2}) for each station.

Copepod Counting and Staging

Stage-specific identification of *D. forcipatus* and *C. australis* was performed in accordance with descriptions by Hulsemann (1991) and Bradford et al. (1988), respectively. Adult (C6) and copepodite stages (C1-C5) of both species were counted under a stereomicroscope (Leica M8). Copepods were enumerated in a number of successive aliquots (POSTEL et al., 2000) until at least 200 individuals of the most abundant stage were classified, or the entire sample was analyzed when animals were scarce. Counting was performed separately focusing on one species at a time because of their different abundance in the samples. Adults and late copepodites were also sexed. While separation of sexes in pre-adult *D. forcipatus* is clearly defined by externally visible sexual characters, this is not the case in the genus *Calanus*. Although in some *Calanus* species C4 and C5 can be separated on the basis of differences in the genital system (e.g. TANDE; HOPKINS, 1981) or by the bimodal distribution of prosome length in the C5 population (GRIGG et al., 1987), this information seems to be unavailable for *C. australis* (Dr. J. BRADFORD-GRIEVE, Wellington, pers. comm.). In fact, the distribution of prosome length of C5 in the summer population off southern Patagonia is unimodal (SABATINI, 2008), and no specific studies on gonad development have been conducted to date. Nauplii were not identified at the species level and were excluded from population analysis.

For the 32 sampled stations, abundance estimates (individuals m^{-3}) were obtained from the 66 µm net. Depth-integrated values (individuals m^{-2}) were calculated by multiplying the concentration per cubic meter by the sampling depth (m) at each station in order to compare with the overall food and thermal conditions of the water column. Catches by the fine net were preferred because this appears to be more efficient than the coarser 150 µm mesh in sampling the younger stages of the locally most representative copepod species, without biasing the catchability of the older and larger copepodites of *Calanus australis* (ANTACLI et al., 2010). However, we cannot rule out completely the possibility that these latter may have avoided the 20 cm opening of the small Bongo sampler because of a greater escape response (ANDERSON; WARREN, 1991).

Copepod Sorting and Treatment

Feeding, diet and reproduction of *D. forcipatus* and *C. australis* were analyzed only at those locations where both populations were abundant (Table 1). Many stations had to be left out of these analyses because adult females and/or prevailing late copepodites were there absent or too few (see below

'Copepod abundance and age structure'). For each station, 30 preserved adult females (C6-F) of each species as well as 30 individuals of the most abundant copepodite stage, that is, C5 of *C. australis* and female C4 (C4-F) of *D. forcipatus* (ANTACLI et al., 2010) were randomly selected under a stereomicroscope from homogeneously stirred samples and carefully washed with bi-distilled water to remove formaldehyde and residuals. A total of 1080 copepods were examined individually: 210 C6-F (7 stations) and 240 C5 (8 stations) of *C. australis*, 330 C6-F (11 stations) and 300 C4-F (10 stations) of *D. forcipatus*. With a few exceptions, analyzed animals were collected mostly during nighttime (Table 1). Guts and gonads were inspected straight through the cuticle when that was transparent enough. Otherwise, animals were cleared with glycerin for 24 h.

Feeding Activity

Feeding condition was examined by inspection of guts with a light microscope prepared for image analysis (Zeiss Axioskop with a Sony CCD-IRIS/RGB camera) at 400x magnification. For each individual, the presence or absence of food inside the gut was recorded, and the lengths of the prosome and the food-pellet inside the gut were measured on micrographs with image analysis software (KS300 v.2.0). A total of 30 adult females and 30 individuals of the most abundant copepodite stage of each species were analyzed for every selected station.

Feeding activity was estimated by the combination of the proportion of individuals with food inside the gut (P_k) and mean pellet length ($\overline{PelL_k}$). While this would account for 'how many' specimens within the population were actually feeding, it would also be an approximate measure of 'how much' they were feeding. Thus, the mean feeding activity at station k was estimated by the index. To compare FI_k values among species and developmental stages, the dependency of food-pellet length on body size was removed by standardizing the values as $PelL_S = PelL / proL$, where $proL$ is the prosome length. Independence of the standardized values from body size was then graphically corroborated (Statistica v.8.0). Pellet lengths were associated with feeding levels (low, intermediate, and high) by calculating the 33.33% and 66.66% percentiles of the standardized pellet length distributions ($PelL_S$) of both species and stages.

Diet

Diet composition was approached by microscopic inspection of gut contents. Ten to fifteen adult females of both *D. forcipatus* and *C. australis* were sorted from the sample from each station selected for feeding examination (Table 1), and their

guts were dissected. A total of 110 guts of *D. forcipatus* from 11 sampling stations and 79 guts of *C. australis* from 7 stations were analyzed.

The food-pellet was extracted, preferably from the mid gut, and its content spread on a slide for analysis. Inspecting the contents of the whole gut may be biased because of the increased proportion of completely degraded particles from the posterior gut (urosome) and of post capture meals in the anterior gut (esophagus). Food items were identified to the lowest possible taxonomic level, counted, and measured with a light microscopy imaging system at 1000x magnification. Food items were sorted into three approximate size categories: <10 μm, 10-20 μm and >20 μm. The presence of quartz/clay particles and fragmentary items was also recorded but not quantified. The average contribution of a given food item to all gut contents analyzed (relative abundance), and the percentage of copepods containing a given food item (frequency of occurrence) were then calculated.

We are aware that gut content analysis underestimates consumption of soft, naked forms, such as fragile phytoplankton, aloricate ciliates and athecate dinoflagellates, which very often dominate the plankton community. Also large but rare food items might be underestimated compared with those smaller and more numerous. Thus, the suggestions on selectivity patterns should be regarded only as tentative. On the bright side, gut inspection does provide information about what is truly ingested from the resources available *in situ.*

Reproductive Activity

The occurrence of mature oocytes is indicative of the end of gonad maturation and thus a good clue to spawning activity in calanoid copepods (NIEHOFF, 2007). Therefore, the reproductive status of both copepod populations was approximated to by the gonad developmental staging of adult females.

Gonads of 30 adult females of each species were examined individually for each selected station with the same image analysis system used for inspection of guts. The gonad macroscopic structure and developmental stages of both *D. forcipatus* and *C. australis* adult females (Figs. 1 and 2; Table 2) were in agreement with former descriptions for *Pseudocalanus* spp. and *Calanus* spp. Therefore, determination of the gonad developmental stages (GS) of *D. forcipatus* was based on the classifications developed for *Pseudocalanus* spp. by NIEHOFF (2003), and GS of *C. australis* were based on descriptions for *Calanus finmarchicus* by NIEHOFF and HIRCHE (1996) and Niehoff and Runge (2003). *Drepanopus forcipatus* females in GS1 were considered immature, either prior

to their first spawning event or between spawning events, and females in GS3 and GS4 corresponded to mature individuals ready to spawn. In *C. australis,* females in GS4 were regarded as mature animals ready to spawn.
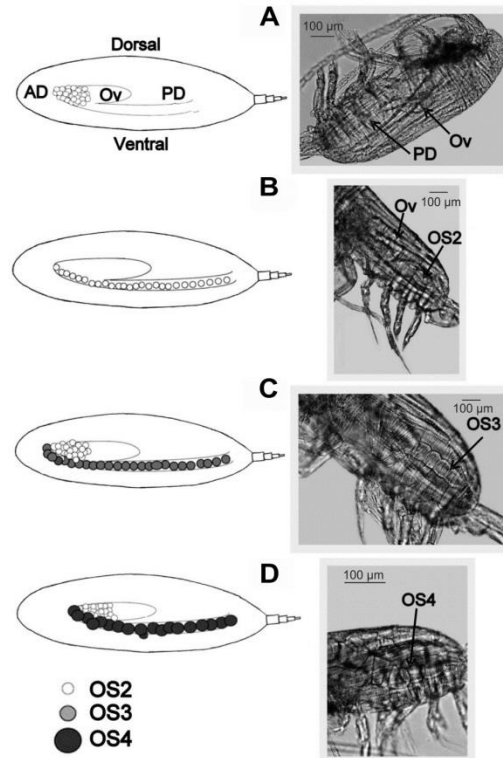

Fig. 1. Gonad developmental stages (GS) of *Drepanopus forcipatus* adult female. To the right: lateral views, this study. Non-spawning or immature females, (A) GS1 and (B) GS2; mature females ready to spawn, (C) GS3 and (D) GS4. To the left: schematic drawings of morphological changes in the *Pseudocalanus*-type gonad throughout the spawning cycle (modified from Niehoff, 2003, 2007). OS = oocyte developmental stage. AD = anterior diverticulum. PD = posterior diverticulum. Ov = ovary.

Relationship between Feeding and Reproductive Patterns and Ambient Food and Temperature Conditions

An indirect, principal component analysis (PCA, CANOCO v.4.5) was performed to portray the variability in feeding and reproductive activity of the two species versus food and temperature conditions prevailing during late summer 2004 over the southern Patagonian shelf. The environmental variables in an indirect analysis are passively projected onto the resulting ordination space and can suggest interpretations for the principal components (LEPŠ; ŠMILAUER, 2003).
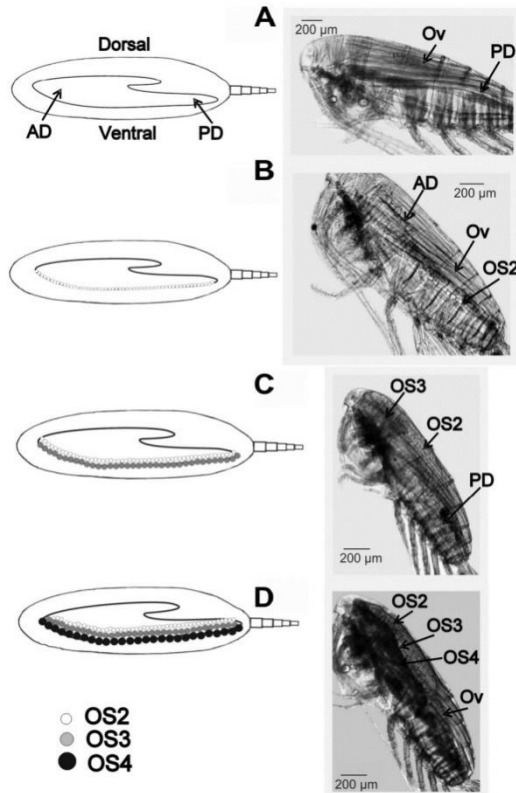
Fig. 2. Gonad developmental stages (GS) of *Calanus australis* adult female. To the right: lateral views, this study. Non-spawning or immature females, (A) GS1, (B) GS2 and (C) GS3; mature females ready to spawn, (D) GS4. To the left: schematic drawings of morphological changes in the *Calanus*-type gonad throughout the spawning cycle (modified from Niehoff, 2003, 2007). OS = oocyte developmental stage. AD = anterior diverticulum. PD = posterior diverticulum. Ov = ovary.

The primary data for each species was a rectangular matrix, where the rows represented the individual samples (8 sampling stations for *C. australis* and 10 for *D. forcipatus*) and the columns represented the response variables. The samples in which missing values occurred were removed ("case-wise deletion", LEPŠ; ŠMILAUER, 2003). The response variables for each sample/station were: (1) the mean standardized pellet length ($\overline{PelL_k}$) of adult females of the two species, C5 of *C. australis* and C4-F of *D. forcipatus*, and (2) the stage-specific copepodite abundances of both species (individuals m^{-2}). Adult females were further classified according to their maturity condition (mature or immature) and their feeding status (with or without food in the gut). Copepodites C5 of *C. australis* and C4-F of *D. forcipatus* were also sorted according to their feeding

status. Abundance of early copepodites C1 to C3 were pooled and considered a signal of active reproduction. For each sample/station, the actual input values into the matrix were averages of 30 animals for the standardized pellet lengths of dominant copepodites and females, the number of dominant copepodites with/without food in the gut, the number of mature females with/without food and the number of immature females with/without food. Total numbers were estimated by multiplying the stage-specific abundances at the station by the respective proportion of feeding and reproductive categories as found in the samples of 30 individuals. Copepod abundances and pellet lengths were log-transformed (log x+1) before the PCA analysis.

Table 2. Classification of gonad developmental stages of females of *Drepanopus forcipatus* and *Calanus australis* based on the classifications developed for *Pseudocalanus* spp. by Niehoff (2003) and for *Calanus finmarchicus* by Niehoff and Hirche (1996) and Niehoff and Runge (2003).

	Drepanopus forcipatus	*Calanus australis*
GS1	Diverticula and oviducts are empty.	Diverticula and oviducts are empty; only ovary is visible.
GS2	Large opaque oocytes in the diverticula.	Small either transparent or slightly opaque oocytes in one layer in both anterior and posterior diverticula. In late GS2, multiple layers of oocytes are found in the anterior diverticulum.
GS3	Oocytes in the diverticula are large and nuclei are clearly visible. Oocytes are darker and their nuclei less-visible as development advances.	Several layers of small oocytes in both diverticula.
GS4	Brown oocytes over the length of the diverticula, whose nuclei are no longer visible, and with small opaque oocytes in the anterior part.	Small opaque oocytes located dorsally, and medium to dark brown oocytes undergoing final maturation in the most ventral layer.

The matrices with the response variables of both species were accompanied by two other data sets containing the environmental variables for the same stations. Potential food was represented by eight taxa (diatoms, dinoflagellates, chlorophytes, haptophytes, cryptophytes, 'other autotrophs', ciliates and 'other heterotrophs') and four size groups (2-5 μm ultraplankton, >5-10 μm and >10-20 μm nanoplankton and >20-200 μm microplankton). Food categories recorded at less than 50% of sampling stations were omitted. Because of the strong thermal stratification at the time (see below 'Summary of hydrographic conditions'), the ambient temperature likely experienced by copepods in the water column was

represented by the mean values in the layers above and below the thermocline (*ca.* 50 m depth). In homogenous or weakly stratified waters, the average temperatures of the upper and lower layers were indeed the same or very close (Table 1). All environmental variables were centered and standardized to bring their means to zero and their variances to one (LEPŠ; ŠMILAUER, 2003).

Strictly speaking, in the PCA above the ambient food and temperature variables should be regarded as potential or the assumed to be *in situ* conditions for the copepod populations. In the context of the methods, copepod samples were representative of the whole water column, while food availability was representative of the upper layer and the temperature was not vertically homogeneous. This potential mismatch in their distribution may have introduced some bias in the results.

RESULTS

Hydrographic Conditions

Surface temperature over the study area decreased gradually with increasing latitude from 14.5°C to 8.4°C, while the bottom field varied longitudinally from 13°-9.5°C near the coast to lower values ranging 9°-5.5°C over the mid shelf. Except for some coastal areas, the water column was strongly stratified southward to *ca.* 52°S, with a sharp thermocline occurring at 40-50 m. Thermal vertical gradients weakened southwards until disappearing completely (Fig. 3). Therefore, in March/April 2004 the region was characterized to the north and to the south of *ca.* 52°S by two different hydrographic scenarios in terms of vertical stratification and temperature (mainly the surface field).
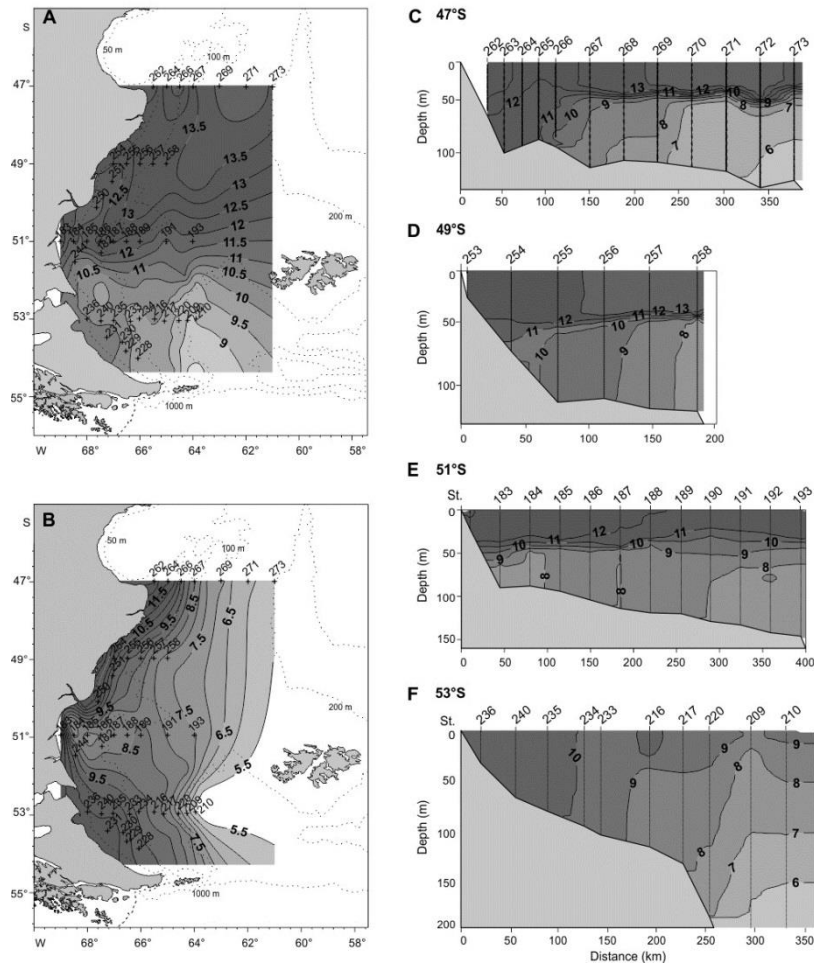

Fig. 3. Surface and bottom temperature fields on the Southern Patagonian shelf (Argentina) during the March/April 2004 cruise. (A) Surface temperature; (B) Bottom temperature; (C-F) Average vertical distribution of water temperature (°C) along transects.

Food Resources for Copepods

Cells 2-5 µm were highly abundant over the southern Patagonian shelf in March/April 2004 and dominated to a large extent the 2-200 µm size range in the plankton communities (Figs. 4A and 5A). Within this size fraction, autotrophs predominated over heterotrophs, the former being mainly represented by chlorophytes, diatoms, haptophytes, cryptophytes, chrysophytes and unidentified cells. Chlorophytes largely dominated at 51°S and 53°S, diatoms at 47°S and unidentified autotrophs at 49°S.

Nanoplankton >5-10 µm, which includes organisms at about the lower size limit for efficient copepod consumption, showed relatively higher numbers over the outer shelf at 47°S. Within this size fraction, heterotrophs, mainly represented by ciliates, flagellates, dinoflagellates, and unidentified cells (pooled as 'Other heterotrophs') were twice as abundant as autotrophs (Fig. 4B).
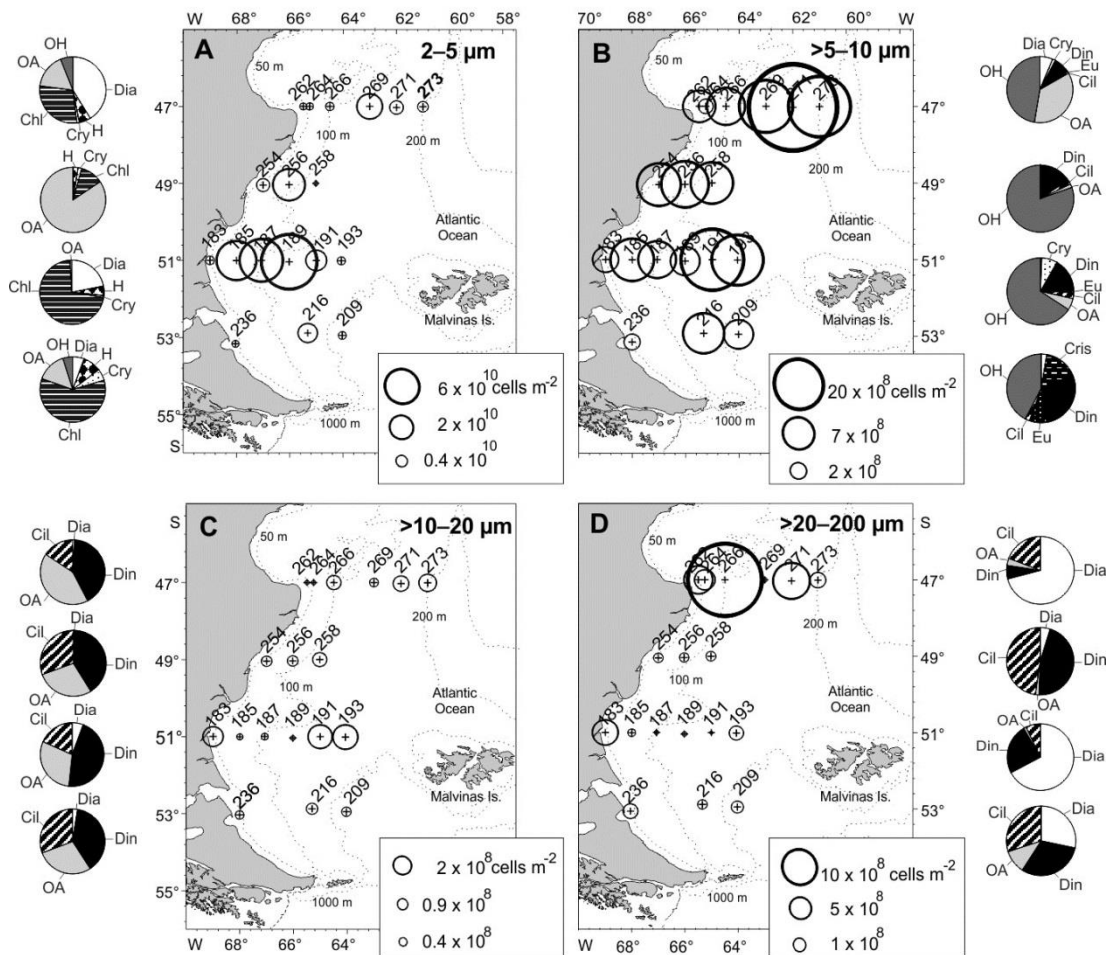
Fig. 4. Spatial distribution and abundance of phyto- and protozoooplankton size-fractions. (A) Ultraplankton 2-5 µm, (B) nanoplankton >5-10 µm, (C) nanoplankton >10-20 µm, and (D) microplankton >20-200 µm. Note the different scales of the panels. Pie-diagrams indicate the average relative abundance of major groups for each section to show latitudinal differences. Dia = diatoms; Din = dinoflagellates; OH = other unidentified heterotrophs; OA = other unidentified autotrophs; Chl = chlorophytes; Cry = cryptophytes; Cris = chrysophytes; H = haptophytes; Cil = ciliates; Eu = euglenophytes.
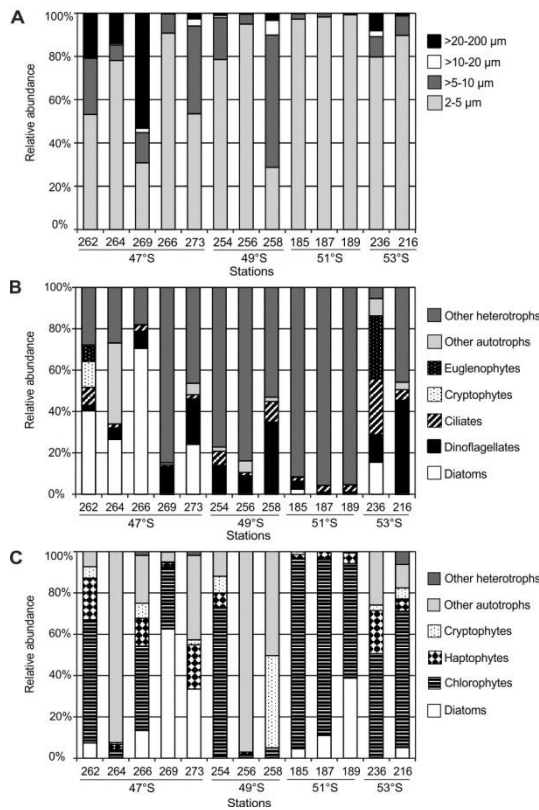
Fig. 5. Potential food availability for copepods at stations where feeding and reproduction were studied. (A) Composition by size-classes, (B) contribution of taxonomic groups to the >5 μm size fraction, (C) contribution of taxonomic groups to the 2-5 μm size-class.

Nanoplankton >10-20 μm and microplankton >20-200 μm, which are the size classes mostly grazed by copepods, were the least abundant classes over the entire region, with the >10-20 μm fraction slightly less abundant than the 20-200 μm fraction (Figs. 4C and D). Relatively higher values of the >10-20 μm size class were found at the outermost stations in the Grande Bay area, where dinoflagellates largely dominated. Unidentified autotrophs, dinoflagellates and ciliates predominated on all latitudinal sections, while diatoms were present at much lower abundances (Fig. 4C). Diatoms, dinoflagellates, and ciliates were the predominant groups in the microplanktonic size fraction along all sections. In particular, diatoms occurred in low numbers but showed relatively higher abundances at three locations at 47°S (Sts. 262 and 266) and 51°S (St. 183). *Rhizosolenia setigera* occurring at 10 m depth was responsible for the highest concentration at St. 266, while *R. fragilissima*, *R. delicatula*, *Pseudonitzschia*, and *Thalassiosira* cf. *decipiens* dominated at

the other two stations. Dinoflagellates also occurred in low abundances along all sections but were relatively more abundant from 49°S to 53°S. The dinoflagellate *Prorocentrum minimum* occurred frequently over the entire area at relatively high concentrations, as well as several species of *Protoperidinium*, such as *P. bispinum*. Ciliates were also relatively abundant through all sections, except for 47°S. Among them, aloricate ciliates and tintinnids (identified only as morphotypes) were numerous and commonly recorded in the area (Fig. 4D).

In summary, the >5 μm size fraction, expected to be palatable for larger copepods, was in general dominated by >5-10 μm unidentified heterotrophs and dinoflagellates and, at lower concentration, ciliates, unidentified autotrophs, and euglenophytes. Cells in the size 2-5 μm, which absolutely dominated the plankton communities over the study area, could be important to the feeding of nauplii and small copepodites, thus influencing the overall population structure. The most important contributors to the smallest size class were chlorophytes and diatoms (Figs. 5B and C).

Copepod Abundance and Age Structure

Drepanopus forcipatus outnumbered *C. australis* over the entire area; the average abundances were 600×10^3 and 10×10^3 ind m^{-2}, respectively. Highest numbers of *D. forcipatus* were recorded in Grande Bay at 51°S, while the maximum abundance of *C. australis* occurred in coastal waters at 49°S. Both species were concentrated over the inner shelf, mainly in the Grande Bay area and northward, decreasing in the offshore direction. The population of *D. forcipatus* was relatively much less abundant at both the northernmost (47°S) and southernmost (53ºS) stations, while *C. australis* was nearly absent in the southern area (Fig. 6A and D). Adult females of both species were particularly scarce over the whole area (Fig. 6B and E) and prevailing copepodites C4-F of *D. forcipatus* and C5 of *C. australis* were mainly distributed in inner and mid areas of Grande Bay and coastal waters at 49°S (Fig. 6C and F).

The population of *D. forcipatus* was on average dominated by lipid-storing copepodites C4 and C5 (69%). Stocks of *C. australis* were largely dominated by C5 (43%), with most C5 individuals carrying well-developed oil sacs and small, undifferentiated gonads. Stage C3 composed about 20% of the two populations. The occurrence of adult females was markedly low (~5%), and adult males and C1-C2 were also scarce in both species.

Although in very low numbers, copepodites C1 to C3 of *D. forcipatus* were relatively more abundant at 47° and 49°S. Young stages were also present in Grande Bay (51°S) and on 53°S, but C4

prevailed at those locations (Fig. 7A). The population structure of *C. australis* clearly changed with latitude: C1 to C3 predominated overall at 51°S and northward, while to the south those stages were absent and C5 largely dominated the population, followed by adult females and males (Fig. 7C).

Feeding Activity

About half of the *C. australis* adult females (49% of 210 individuals examined) and of C5 (42% of 240) contained food in their guts. While this was also true for adult females of *D. forcipatus* (42% of 330 individuals examined), the percentage of feeding C4-F was much lower (26% of 300) (P_k, Fig. 8A-D).

The amount of ingested food, roughly approached by the (standardized) pellet length (PelL$_S$), was on average less in adult females of both *D. forcipatus* and *C. australis* than in their C4-F and C5, respectively. In comparison, *C. australis* adult females

were ingesting much less food (smallest average PelL$_S$), whereas late copepodites of both species and *D. forcipatus* adult females were all consuming about the same amount (Fig. 8 E-H).

The interplay between the proportion of individuals with a pellet in the gut and the approximate amount of ingested food (pellet length) would roughly characterize the grazing realized by the populations in the field ($\overline{FI}_k$). The overall feeding activity of adult females of *D. forcipatus* in late summer was rather variable spatially and relatively higher than in *C. australis*. In contrast, grazing by C4-F of *D. forcipatus* was consistently low over the study area, except for one station at 53°S (Fig. 9A). The feeding activity of adult females of *C. australis* was also low and relatively constant among all stations, whereas the C5 showed a more variable pattern and in general slightly higher values (Fig. 9B).
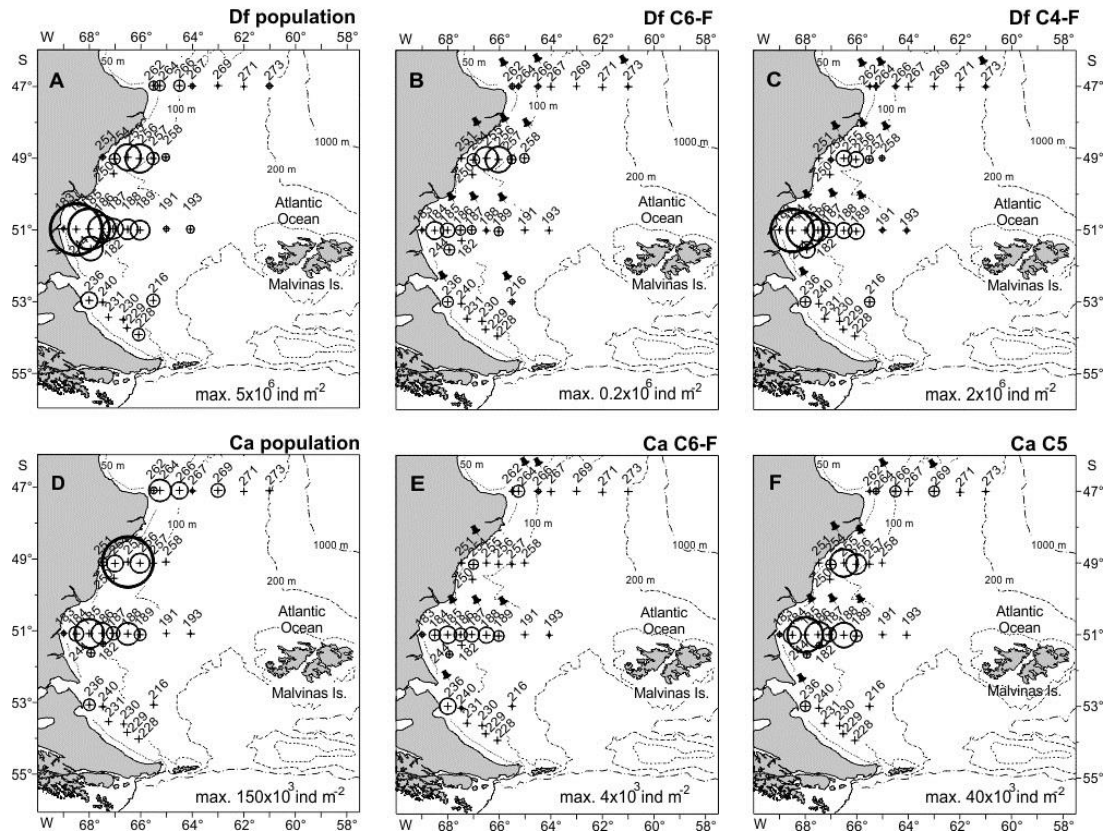

Fig. 6. Spatial distribution and abundance of (A) all copepodite stages of *Drepanopus forcipatus*, (B) C6-F *Drepanopus forcipatus*, (C) C4-F *D. forcipatus*, (D) all copepodite stages of *Calanus australis*, (E) C6-F *C. australis*, and (F) C5 *C. australis*. Maximum abundances are indicated. Locations where feeding and reproduction activity were studied are tagged with a special character (✺). Abundances correspond to the small Bongo net 66 µm mesh-size (for details see Material and Methods). Df = *Drepanopus forcipatus*; Ca = *Calanus australis*; C6-F = adult female; C5 = copepodite stage 5; C4-F = copepodite stage 4-female. Note different scales for the abundance of the two species.
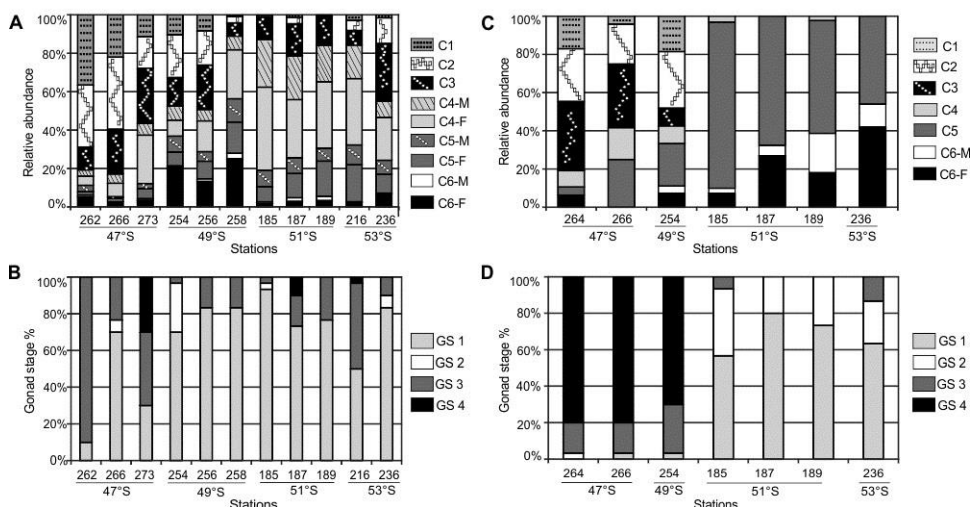
Fig. 7. Population structure and gonad stage distribution of *Drepanopus forcipatus* (A and B) and *Calanus australis* (C and D). F = female; M = male; C6 = adults; C1-C5 = copepodite stages 1 to 5.
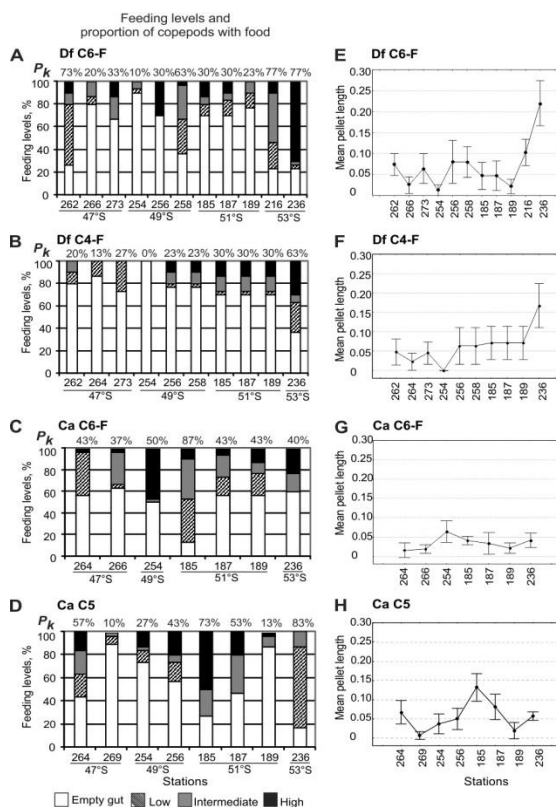

Fig. 8. Feeding parameters of adult females and most abundant copepodites of *Drepanopus forcipatus* and *Calanus australis*. (A-D) Feeding levels and proportion of inspected individuals with food in the gut, P_k. (E–H) Mean standardized mean pellet length. Df = *Drepanopus forcipatus*; Ca = *Calanus australis*; C6-F = adult female; C4-F = copepodite stage 4-female; C5 = copepodite stage 5.
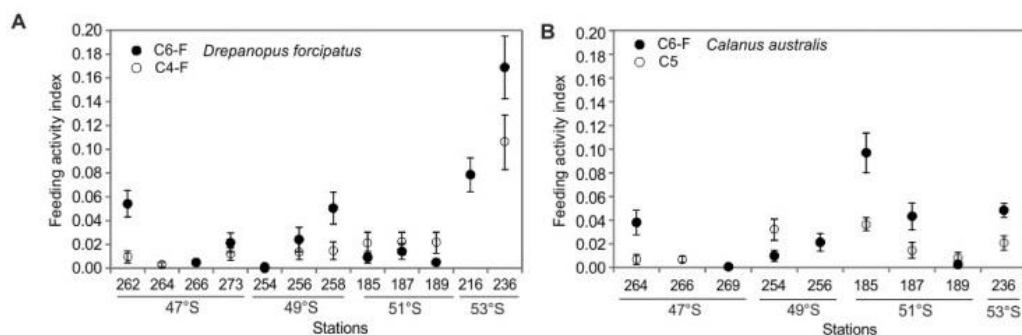
Fig. 9. Feeding activity index ($\overline{FI}_k$) of adult females and C4-F of *Drepanopus forcipatus* (A), and adult females and C5 of *Calanus australis*. C6-F = adult female (B); C4-F = copepodite stage 4-female; C5 = copepodite stage 5.

Diet

Most adult females of both *D. forcipatus* and *C. australis* inspected for diet composition carried a well-formed and compacted pellet inside the gut. The largest portion of the pellets was generally an unidentifiable mass of highly degraded particles. The items recognized in the guts are detailed in Table 3. Of the pellets examined for *D. forcipatus*, 100% contained trichocysts, 20% diatoms and 65%

prasinophytes in the smallest size class. Particles in the mid and largest size classes were also noticeable in this species (100% of pellets contained both dinoflagellates and tintinnids, 80% diatoms and 35% prasinophytes) (Fig. 10A). The largest and mid size classes mainly comprised the diet in *C. australis*: 98% of pellets contained diatoms and 100% tintinnids >20 µm; 97% contained dinoflagellates and 100% prasinophytes in the 10-20 µm class (Fig. 10C).

Table 3. Food items in gut contents of *Drepanopus forcipatus* and *Calanus australis* adult females sorted into size-classes.

| Size-class food-items in guts	*Drepanopus forcipatus*	*Calanus australis*
<10 µm	- Coccolithophorides 3-10 µm. - Trichocysts 5 µm (likely of dinoflagellates). - Unidentified cells 3-7 µm (likely coccolithophorides). - Unidentified diatoms ~10 µm.	- Trichocysts 5 µm (possibly of dinoflagellates). - Unidentified cells 3-10 µm (coccolithophorides or chrysophyte cysts).
10-20 µm	- Diatoms: *Paralia sulcata*. - Dinoflagellates: *Prorocentrum minimum, Prorocentrum* sp., unidentifiedspecies. - Prasinophytes: *Pterosperma cristatum, Pterosperma* spp., unidentified resting cells. - Silicoflagellates: broken skeletons.	- Diatoms: *Gyrosigma, Surirella*. - Dinoflagellates: *Prorocentrum minimum, Protoperidinium* sp., unidentified peridiniacean, cysts of peridiniaceans. - Prasinophytes: cysts of *Pterosperma* spp. And *P. cristatum*. - Silicoflagellates: *Distephanus speculum*,broken skeletons of unidentified species.
>20 µm	-Diatoms: *Paralia sulcata*,.*Fragilariopsis* sp., *Rhizosolenia* sp. - Dinoflagellates: *Prorocentrum minimum, Protoperidinium bispinum, Protoperidinium* sp., peridiniacean cysts. - Tintinnids: cf. *Salpingella*.	- Diatoms: *Paralia sulcata*, cf. *Fragilariopsis* sp., *Rhizosolenia* sp. - Dinoflagellates: *Prorocentrum minimum, Protoperidinium bispinum, Protoperidinium* sp., peridiniacean cysts. - Tintinnids: cf. *Salpingella*.
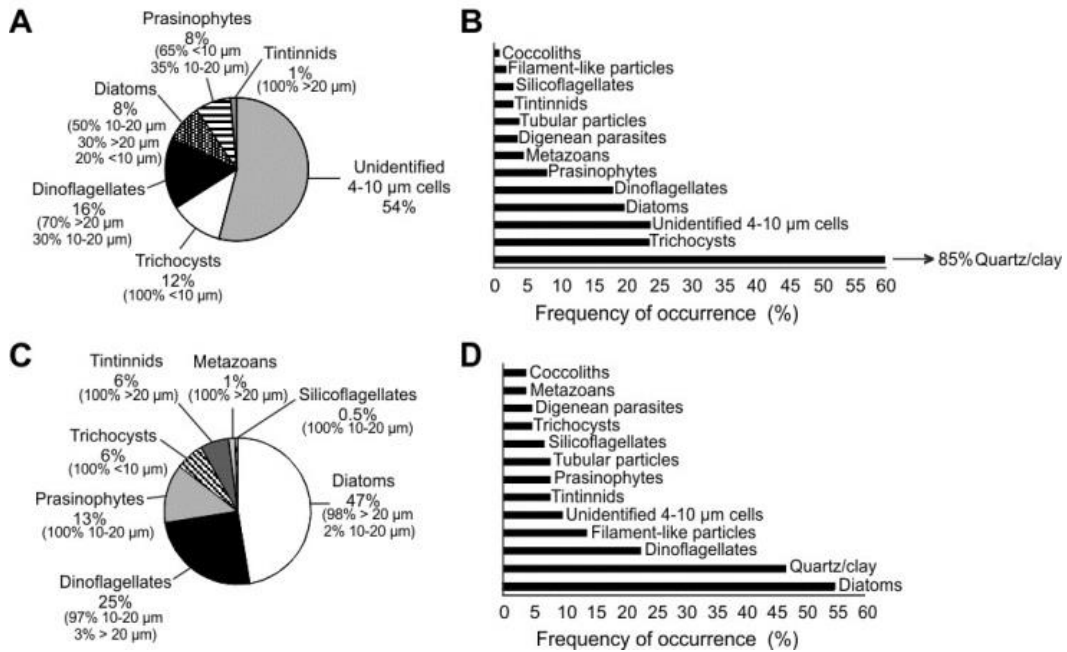
Fig. 10. Gut content of adult females of *Drepanopus forcipatus* (A and B) and *Calanus australis* (C and D). Relative abundance and frequency of occurrence of food items identified in mid guts (averages across all examined stations).

Diatoms (largely >10 μm) were more frequently and abundantly found in *C. australis* (Fig. 10C and D), while dinoflagellates occurred almost equally in pellets of both copepods, since trichocysts in *D. forcipatus* most likely represent the remnants of ingested dinoflagellates (Fig. 10A and B). Quartz/clay particles 5-50 μm were very frequent in both species, being in many cases the only recognizable item in the guts, particularly in *D. forcipatus* (Fig. 10B and D). Small amounts of prasinophytes, tintinnids, silicoflagellates, metazoans (nauplii, pieces of crustacean limbs) were occasionally found in guts of both species, but mainly in *C. australis*. Much less frequent items in the guts were large tubular and filament-like particles (possibly microcrustacean pieces), digenean parasites and coccolithophorids.

Reproductive Activity

Drepanopus forcipatus and *C. australis* showed low reproductive activity during March/April 2004. Most late summer females of both species had immature gonads, while mature females ready to spawn were only one third of the field populations (on average *D. forcipatus* 30% and *C. australis* 33%). At

some stations, female *D. forcipatus* were carrying spermatophores or eggs (1-4 eggs female^{-1}).

The distribution of gonad stages of *D. forcipatus* was rather homogeneous over the study area, with immature females (GS1) prevailing at almost all stations. The percentage of ovaries ready to spawn was high (70-90%) at only two stations in the north of the study area (Sts. 262 and 273 at 47°S) (Fig. 7B). A distinct latitudinal pattern was found in the proportion of mature females ready to spawn in *C. australis*, ranging from 70-80% at the 47° and 49°S stations to none at the 51° and 53°S stations (Fig. 7D).

Feeding, Reproduction and Population Structure in Relation to Potential Food Availability and Temperature

Results from the PCA indicate that the first two principal components explained together 83% of the total variation in the stage-specific copepodite abundances, feeding and reproductive activity of *D. forcipatus*. Selected environmental variables contributing the most to each ordination axis were assessed by their correlation values (Table 4). The ordination diagram for *D. forcipatus* and the variables representing the potential food and temperature likely experienced by the copepods show a weak segregation

among stage-specific copepodite abundances (Fig. 11A). All copepodite stages of *D. forcipatus* tended to be more abundant at higher concentrations of 2-5 μm chlorophytes, 2-5 μm and 10-20 μm diatoms, 2-5 μm haptophytes, 2-5 μm 'other autotrophs', and to lower water temperature (both T upp and T low). Along the Axis 2, the immature adult females with and without food, mature adult females and C4-F with empty guts, adult males, C5, C4M and C1-C3 were, on the one hand, related to higher abundances of 2-5 μm cryptophytes, 10-20 μm ciliates and 5-10 μm 'other heterotrophs', while on the other, feeding adult females and C4F as well as their pellet lengths, appear segregated from the former and were associated with lower abundances of those food items, and higher concentrations of 2-5 μm haptophytes, diatoms and 'other autotrophs'.

Assumed ambient food and water temperature, Axes 1 and 2, explained 88.3% of the total variation in the abundance of all copepodite stages, feeding and reproductive activity of *C. australis*. Their correlation values to the ordination axes are shown in Table 4. The main gradient in the biplot (Fig. 11B) occurs along Axis 1, with immature adult females and C5 (both with and without food in the guts) segregating from mature adult females (both C6F-m/f and C6F-m/e), C4 and C1-C3. Longer pellet lengths of adult females and C5, together with larger abundances of immature females and C5, were associated with higher values of 2-5 μm chlorophytes, 2-5 μm and10-20 μm diatoms, 2-5 μm haptophytes and 20-200 μm ciliates. These two stages actually separate along Axis 2: C5 tended to have larger abundances at higher concentrations of 2-5 μm haptophytes, 2-5 μm and10-20 μm diatoms, transitional temperatures of the upper layer and colder waters of the lower layer, while all females (mature and immature, feeding and with empty guts) were associated with higher abundances of 10-20 μm ciliates, 20-200 μm diatoms and 'other autotrophs' and higher temperature of the lower layer, while C4 and C1-3 were more closely associated with higher temperature of the upper layer and higher abundances of all sizes dinoflagellates, 2-5 μm and 10-20 μm 'other autotrophs' and 5-10 μm 'other heterotrophs'.

Table 4. Summary of copepod–environment PCA ordinations for *Drepanopus forcipatus* and *Calanus australis*. Eigenvalues of the correlation matrix and Pearson correlation coefficients between potential ambient food and temperature (environmental/explicatory variables) and PCA axes.

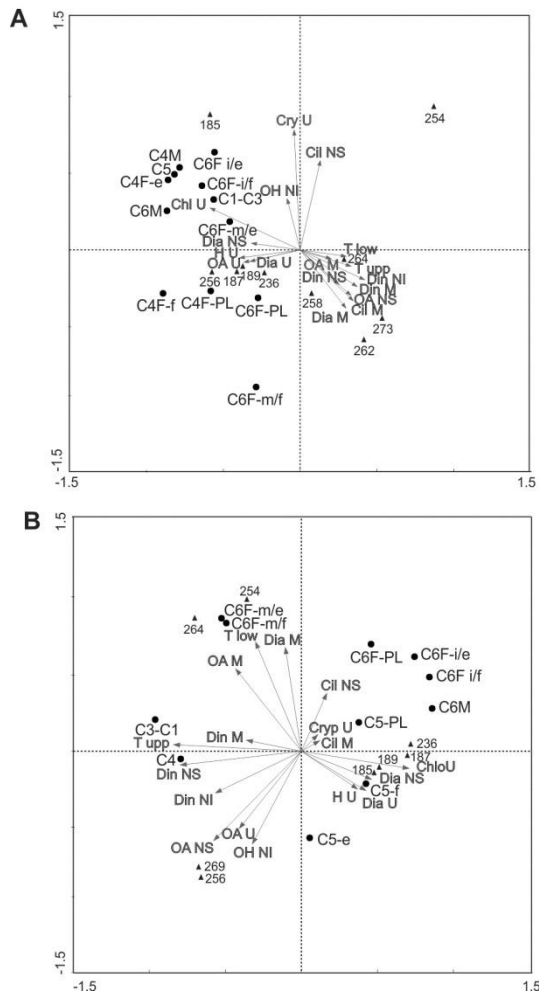|		Drepanopus forcipatus		Calanus australis	
		PCA Axis1	PCA Axis2	PCA Axis1	PCA Axis2
Eigenvalues		0.500	0.330	0.646	0.237
% Total variance		50.0	83.0	64.6	88.3
Variables	**Codes in PCA biplot**				
Diatoms >10-20 μm	Dia NS	-0.3169	0.0433	0.4623	-0.1857
Diatoms >20-200 μm	Dia M	0.2983	-0.3796	-0.1058	0.6836
Dinoflagellates >5-10 μm	Din NI	0.4197	-0.1946	-0.5663	-0.2755
Dinoflagellates >10-20 μm	Din NS	0.2544	-0.2270	-0.7975	-0.0911
Dinoflagellates >20-200 μm	Din M	0.3712	-0.2394	-0.3627	0.0725
Ciliates >10-20 μm	Cil NS	0.1320	0.5831	0.1672	0.3818
Ciliates >20-200 μm	Cil M	0.3462	-0.3323	0.1209	0.0697
Other autotrophs >10-20 μm	OA NS	0.3309	-0.2972	-0.5769	-0.5892
Other autotrophs >20-200 μm	OA M	0.2025	-0.0574	-0.4325	0.5425
Other heterotrophs >5-10 μm	OH NI	-0.0844	0.3343	-0.3226	-0.6110
Diatoms 2-5 μm	Dia U	-0.3274	-0.0754	0.4266	-0.2606
Haptophytes 2-5 μm	H U	-0.3951	-0.0526	0.3706	-0.2499
Cryptophytes 2-5 μm	Cry U	-0.0392	0.7811	0.1086	0.1097
Chlorophytes 2-5 μm	Chl U	-0.5867	0.2733	0.7095	-0.1137
Other autotrophs 2-5 μm	OA U	-0.3676	-0.0809	-0.4088	-0.5093
Temperature upper layer (0-50 m depth)	Tupp	0.3321	-0.1069	-0.8419	0.0430
Temperature lower layer (>50-100 m depth)	Tlow	0.3002	-0.0417	-0.3020	0.7195

Fig. 11. Copepods–environment biplot diagrams from the PCA. (A) *Drepanopus forcipatus*, (B) *Calanus australis*. Response variables (filled circles): C6= adults, C1 to 5= copepodites 1 to 5, F= female, M= male, PL= standardized pellet length, m = mature gonad, i = immature gonad, f = with food in the gut (feeding), e= empty gut (non-feeding). Environmental variables (arrows) passively projected into the resulting ordination space (see codes in Table 4). Stations are displayed as triangles.

DISCUSSION

Feeding and Reproductive Activity Patterns

The proportion of feeding animals and the length of food-pellets inside their guts have been used previously to describe feeding patterns of copepods from preserved samples (e.g. DRITS, 1985; PASTERNAK, 1995; PASTERNAK; SCHNACK-SCHIEL, 2007). These indices, however, can at best reflect satisfactorily the overall feeding activity but not the actual rate of the process. Potential drawbacks of

this approach are various, mainly from a trophodynamic standpoint. For instance, maximum standardized pellet length (100% of body size) may have different implications for differently sized animals due to their distinct nutritional needs and consumed prey sizes. On the other hand, food pellet length may not only be related to the amount of ingested food but also to the type of food ingested, i.e. hard bodied prey (diatoms, thecate ciliates, crustaceans) may yield larger pellets than soft bodied prey (flagellates, athecate ciliates). Also the proportion of feeding copepods estimated from the presence of food in the guts may be somehow biased because some animals could have defecated. These indices certainly do not account for feeding history or the underlying interactions between rates, temperature, gut passage times and food concentration.

For the purposes of our study, beyond all the shortcomings, the standardized pellet length did provide a rough estimate of the amount of ingested food relative to body size, enabling thus the comparison among species and stages. Pellet length in combination with the proportion of fed animals (i.e. with food in their guts) would account for the overall feeding activity of the two populations in the field.

After high production during spring and early summer, late summer marks the beginning of a less productive season on the southern Patagonian shelf (e.g. RIVAS et al., 2006; ROMERO et al., 2006). We found the abundances of phyto- and protozooplankton>10 μm to be markedly low, while small cells in the range 2-10 μm were highly dominant. That suggests the prevalence of a microbial trophic web during that season, long after the spring phytoplankton bloom of larger food particles. Likely because most potential food was below the optimal size for efficient consumption by larger copepods (>10-14 μm; e.g. FROST, 1972; BERGGREEN et al., 1988), adult females and late copepodites of *D. forcipatus* and *C. australis* showed in general low feeding activity.

The quantity of food consumed by copepods is typically related to the ambient concentration of prey (e.g. MAYOR et al., 2006; CASTELLANI et al., 2008), and food limitation is recognized as the factor mainly responsible for low feeding rates in the field (SAIZ; CALBET, 2011). Accordingly, we have found striking differences in the feeding activity of *D. forcipatus* and *C. australis* (at least in adult females) between seasons with low and high *in situ* food availability. The same feeding indices were estimated for adult females of *D. forcipatus* and *C. australis* during a monospecific phytoplankton bloom of the dinoflagellate *Prorocentrum minimum* in Grande Bay during early spring 2005 (SABATINI et al., 2012). During the bloom, the proportion of feeding females of *C. australis* doubled on average compared to that

during late summer 2004; the pellet size in the guts increased four-fold, and the overall feeding activity index was about eight-fold higher. In the case of *D. forcipatus*, the proportion of females actually feeding doubled on average and pellets in the guts were three-fold longer. Thus, the effective feeding by females in the field was about six times greater than in late summer. Most females of both species were feeding at high levels during the dinoflagellate bloom, while in summer they fed at low to intermediate levels. The shifts were about equal for the two species (ANTACLI, unpubl. data)

The gonad structure of *D. forcipatus* and *C. australis* corresponds well to the *Pseudocalanus* and *Calanus* types, respectively, as described by Niehoff (2007). To our knowledge this is the first verification of the *Pseudocalanus*-type structure for a member of the genus *Drepanopus*, which also belongs to the family Clausocalanidae. Gonad staging has been used similarly to our study to describe the reproductive patterns of marine copepods from preserved samples (e.g. PASTERNAK et al., 2004; CORNILS et al., 2007).

As a result of limited feeding in late summer, reproduction was expected to be limited also. In fact, the low abundance of adults and young stages, the distribution of gonad stages and the dominance of older copepodite stages containing oil sacs suggest that the reproduction of both copepods was well below their maximum. A decline in the reproductive activity in response to decreasing food concentrations at the end of the productive season has been reported in particular for copepod species inhabiting cold temperate environments (e.g. PLOURDE; RUNGE, 1993). Although in low numbers, the occurrence of spawning females (30% in *D. forcipatus* and 33% in *C. australis*) indicated ongoing reproduction. The presence of some females of *D. forcipatus* carrying either spermatophores or egg sacs, and the occurrence in the population of C1 and C2, though also in low abundance, suggest that at least some GS1-females were actually between spawning events, rather than newly molted females before their first spawning (NIEHOFF, 2007). In contrast, during the early spring *Prorocentrum* bloom, about 90% of adult female *D. forcipatus* were ready to spawn and 57% of *C. australis* had mature gonads (ANTACLI, unpubl. data).

In other clausocalanids egg production can be relatively high at low food concentrations (MAZZOCCHI; PAFFENHOFER, 1998; NIEHOFF et al., 2002). Some species of genus *Pseudocalanus* seem to be not much affected by food limitation and can reproduce year round with fluctuating food conditions (RENZ et al., 2008). Egg production in *Pseudocalanus* spp. is generally sustained by lower food concentration than is required by large calanids

(FROST, 1985). As regards *Calanus* species, it has been found that the low summer concentrations of nanoplanktonic algae in temperate waters can sustain low but continuous reproduction of *C. finmarchicus* (e.g. BÅMSTEDT et al., 1999).

As are other *Calanus* species inhabiting high latitudes (e.g. PLOURDE et al., 2005; MADSEN et al., 2008), it is likely that *C. australis* is well adapted to seasonally variable trophic conditions. This is suggested by our findings in early spring 2005, when its reproductive activity was found to increase two-fold under the favorable food conditions offered by the *Prorocentrum* bloom in Grande Bay (ANTACLI, unpubl. data). This strategy would be useful to maximize exploitation of short pulses of food and to optimize population development during the growing season on the southern Patagonian shelf.

Diet

A large proportion of the late summer gut contents of both copepods consisted of a greenish-brown unidentifiable mass. Similarly, guts packed with material mostly impossible to identify have been reported for a variety of copepods (e.g. PASTERNAK, 1995; PASTERNAK; SCHNACK-SCHIEL, 2001, 2007; KOSOBOKOVA et al., 2002).

Quartz/clay particles in the size 5-50 μm were identified very frequently in the guts of both *C. australis* and *D. forcipatus*. These particles even made up the entire food pellet in many specimens, especially at the southern stations (53°S) in agreement with their overall high availability in the environment. Resuspension of detritus by tidal mixing and fluvial inflow are major sources of these particles in the study area. Like the intake of detrital aggregates by some mesozooplankton species (WILSON; STEINBERG, 2010), the unselective ingestion of quartz /clay particles by *C. australis* and *D. forcipatus* could be a secondary pathway by which ingestion of small-sized cells (picoplankton/ultraplankton) is enhanced in a food-poor environment.

Diatoms and dinoflagellates were important food items in the guts of both species. However, a preference for (large) diatoms by *C. australis* and for (small) dinoflagellates by *D. forcipatus* was apparent in late summer (Fig. 10A and B). Some experimental studies have shown that cell size seems to be the main selection factor for *C. finmarchicus* and *C. helgolandicus* when feeding on algal cells with no clear distinction in external morphology (MEYER et al., 2002). However, a slight preference particularly for diatoms has been observed in the field for both species, although there has been little evidence developed for selective feeding on different phytoplankton (MEYER-HARMS et al., 1999; IRIGOIEN et al., 2000). In our study, *C. australis* exhibited a more carnivorous diet than *D. forcipatus*.

Metazoan parts found in the guts of adult females may have been a supplement in their diets to maintain activity during periods with low phytoplankton. A switch from herbivory to a more carnivorous diet has been shown experimentally in *Calanus pacificus* (LANDRY, 1981). This change of behavior may be significant in nature during the decline of phytoplankton blooms. For example, *C. helgolandicus* seems to obtain most of its energy from phytoplankton during the spring bloom, while during non-bloom periods protozooplankton and especially ciliates become significant contributors to their diet (FILEMAN et al., 2007). Just as suggested by our findings from gut content of *D. forcipatus*, a preference for dinoflagellates and diatoms has been found in clausocalanid species (CORNILS et al., 2007). It is also likely that *D. forcipatus* feeds opportunistically on abundant particles, which seems to be a survival strategy under oligotrophic conditions (e.g. TURNER, 1991; CORNILS et al., 2007).

Feeding and Reproduction in Relation to Potential Food Resources and Temperature

Drepanopus forcipatus

Multivariate analysis (PCA, Fig. 11A; Table 4) along with diet results (Fig. 10A and B) would indicate for *D. forcipatus* an opportunistic feeding behavior on the smaller but more abundant particles in the environment. This is suggested by the fact that larger abundances of most copepodite stages and larger pellet lengths occurred in areas with high concentrations of ultraplanktonic and nanoplanktonic (<10 μm) particles (Fig. 11A).These cells were in turn the most numerous and frequently found items in the guts of this species (Fig. 10A and B). The ability to ingest small-sized food particles could be an important advantage over large copepods, and perhaps a reason for the overwhelming numerical abundance of *D. forcipatus* in some areas of the southern Patagonian shelf. Opportunistic feeding must be a supplement to energy storage for smaller copepod species occurring at high latitudes because of their higher metabolic rates and the limitation of storage space (NORRBIN et al., 1990). Grazing during a previous temporal window may explain that higher abundances of nearly all copepodite stages appeared to be related to low concentrations of most potential food items. This explanation is plausible when taking into consideration that our copepod data actually portray a photograph of a given temporal window rather than the real population response to current environmental conditions. As regards temperature, all stage-specific copepodite abundances and the pellet length of adult and C4 females seemed to be inversely related to the temperature of both the upper and lower layers. However, their low contribution to the axes formation

(Table 4) suggests a relatively minor influence of these variables in the distribution of *D. forcipatus* during late summer 2004.

Calanus australis

Our findings for *C. australis* suggest a likely higher ingestion of autotrophic prey, particularly large diatoms (Fig. 11B; Table 4).The greater abundance of mature adult females at high concentrations of >20-200 μm diatoms (Fig. 11B) corresponds well with our diet results suggesting that *C. australis* fed mostly on microplanktonic diatoms (Fig. 10C and D). Their further positive relation to high concentrations of 20-200 μm 'other autotrophs' (Fig. 11B) is in agreement with studies showing a preference for autotrophic prey in other *Calanus* species (e.g. KOSKI; WEXELS RISER, 2006). Although in lower numbers, other autotrophic items, such as 10-20 μm prasinophytes and silicoflagellates, also contributed to the diet of this species (Fig. 10C and D). Hence, it may be inferred that among all other potential food, autotrophic prey would be relatively more important items in the feeding of *C. australis.* This possibility is further supported by the occurrence of higher abundances of mature adult females of *C. australis* at low concentrations of the remainder of potential food categories (Fig. 11B). Considering the late date in the productive season and from the same perspective as explained above for *D. forcipatus*, those items may have been previously grazed by the copepods. This was likely the case of 10-20 μm diatoms, 10-20 μm dinoflagellates and ciliates (mostly tintinnids) in the 10-20 μm and 20-200 μm size classes, which were inversely related to the occurrence of mature adult females (Fig. 11B). These potential food items were relatively scarcer *in situ* (Fig. 4D) but contributed in some degree to the diet of *C. australis* (Fig. 10C and D). Despite their low concentrations *in situ*, also 10-20 μm ciliates were positively associated with the distribution of immature adult females and longer pellet lengths of both C6F and C5, although with a relatively lower contribution to axes ordination. On the other hand, some small-sized algae appeared only related to C5s but showed larger contributions to axes ordination (Table 4); this was probably due to their much higher abundances throughout the study area. Some *Calanus* species select food by size, with a preference for large phytoplankton cells (FROST, 1972; PETERSON; BELLANTONI, 1987; WALKER; PETERSON, 1991), likely because they are able to manipulate larger cells more efficiently than smaller ones (FROST, 1977). In particular, a preference for larger particles has been observed in species of the *helgolandicus* lineage that includes *C. australis*, such as *C. pacificus* (HARRIS, 1982), *C. helgolandicus* (MEYER et al., 2002; FILEMAN et al., 2007) and *C. agulhensis* (HUGGETT; RICHARDSON, 2000).

Differently from *D. forcipatus*, both the temperature of the upper and lower layers appeared to have largely influenced the distribution of *C. australis* (highest correlations to PC axis 1 and 2 respectively, Table 4). The former would have been relatively more important in view of the much higher percentage of variance explained by Axis 1. Thus, reproductive females and younger copepodite stages occurred in warmer waters than immature females, adult males and late copepodites C5 which were apparently associated with colder waters. This is further supported by the latitudinal patterns we found in the population structure and gonad stage distribution of *C. australis* (Fig. 7C and D). Our findings suggest that the population was still reproductive in warmer waters of the northern area (47° and 49°S), while in the colder southern waters (51° and 53°S) fewer females were present, all with immature gonads, and only older C4-C5 occurred. It follows that beyond food resources, temperature had an important influence on *C. australis* reproduction in late summer 2004.

Despite some caveats applying to the relationships described above, mainly regarding the sampling strategy and the small number of stations involved in the analyses, this approach offers preliminary but valuable information on the overall distinct distribution of the two copepods relative to their potential food resources and summer temperature fields on the southern Patagonian shelf.

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