



Vertical diel migration and feeding of *Euphausia vallentini* within southern Chilean fjords

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ABSTRACT

E. vallentini is a circumpolar vertical migrator in the open ocean that enters the Chilean fjords through the sills to become the most common and abundant euphausiid. The diel migratory and feeding patterns of this species are studied in this distinct, enclosed and bathymetrically variable environment. The main goal was to determine the ability of *E. vallentini* to alter its vertical diel range in order to avoid shallow depths, or to maintain its depth migratory range and take advantage of benthic environment during daytime.

Multiple opening closing nets sampled the water column in several basins along the Strait of Magellan. Fluorometrically determined stomach pigments along with on board experiments of evacuation rates allowed estimation of ingestion and consumption rates. Samples of stomach content were microscopically examined to compare day and night diet.

E. vallentini migrated between the surface at night and 100–200 m in daytime. Surface night dwellers had higher chlorophyll stomach content than deep daytime dwellers. Diet composition changed from dinoflagellates and tintinnids at night, to a polychaeths-dominated diet in daytime. Stomach content, ingestion rates and consumption rates of phytoplankton were higher at night than in daytime, and accounted for an impact of 0.17% upon phytoplankton biomass.

Changes of diet of *E. vallentini* imply unique adaptations to take advantage of both pelagic and demersal environments, which could explain its high abundance and high frequency of encounter within the southern Chilean fjords.

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1. Introduction

Euphausia vallentini is a subantarctic circumpolar species ranging from the Polar Front to the subtropical convergence between 42° and 60° S in the Pacific, Atlantic and Indian Ocean (John, 1936). Throughout this very wide geographic distribution, the species forms swarms of very high densities (Ragulin, 1969), becoming an attractive prey for large size predators. In fact it is an important item of the diet of blue whales (Nemoto, 1959) and gentoos penguins (*Pygoscelis papua*) off the subantarctic Marion Island (Adams and Klages, 1989), the Falkland Islands (Bingham, 1998), and Crozet Islands (Ridoux, 1988).

In the open ocean, *E. vallentini* shows a strong diel vertical migration (Perissinotto and McQuaid, 1992), linked to a feeding rhythm characterized by high phytoplankton ingestion rates in dark hours and low feeding activity in day time (Gurney et al., 2002). Life cycle of *E. vallentini* was described from a seasonal

series of stomach content samples of planktivore Macaroni (*Eudyptes chrysolophus*), rockhopper (*E. chrysocome*) and gentoos penguins of Crozet Island (Ridoux, 1988). They concluded that *E. vallentini* has a life span of two years, larval recruitment occurs in summer and growth is fast until late fall.

Off South America, as the West Wind Drift approaches the coast, subantarctic waters diverge in two major branches: the Cape Horn Current and the Humboldt Current. Geographic distribution of *E. vallentini* closely follows these water masses extending to and around the tip of South America to the South and to about 36°S to the North (Antezana, 1978; 1981). The southern Chilean coast is broken into an extensive fjord region (ca. 1400 km in latitude) that is exposed to these subantarctic waters, where it mixes with fresh water inputs from glaciers and runoff. Water circulation driven by tidal currents, wind stress, internal waves and bottom friction, together with topography and bathymetry determines very complex and heterogeneous characteristics (Antezana, 1999a, 1999b; Silva and Calvete, 2003; Valdenegro and Silva, 2003). Hence, the open-ocean zooplankton that is advected into the fjords (Antezana et al., 2002; Mazzocchi and Ianora, 1991; Guglielmo et al., 1997; Fernandez-Severini and Hoffmeyer, 2005) encounters a very different environment

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compared to the open ocean. The extent of the mixing and the genetic isolation occurring between the open ocean and the inland population is unknown. The severe restriction of water exchange due to bathymetry and topographic constrictions (Antezana, 1999a), decreases the species richness within the fjords (Mazzocchi and Ianora, 1991). Trapped zooplankters may become vagrant or expatriates from the open-ocean population, and eventually adapt to live and take advantage of this uniquely different environment.

E. vallentini is the most dominant and frequent euphausiid of these fjords (Antezana, 1976; Guglielmo et al., 1997; Palma and Silva, 2004). It is uncertain, how adapted is *E. vallentini* to live in the fjords and how self sustained the population is. Deviation of basic behavior patterns may imply adaptation to such unique environment. Therefore the aim of this study focused on the diel vertical migration and feeding of *E. vallentini* in a representative isolated basin of the Chilean fjords.

2. Material and Methods

2.1. Sample collection

Zooplankton samples were collected as part of the “Italian Antarctic National Research Program (PNRA) in periantarctic areas”. Eight stations were studied along the Strait of Magellan (Fig. 1) in early fall (25th March - 1st April 1995). Stratified samples were obtained in day and/or night hours at each station, through the entire water column to 5–10 m near the bottom, as acoustic sensors at the mouth of the system made it feasible. A series of stratified day and night samples were also taken for four consecutive days at station 8 in the middle of the Strait of Magellan (Table 1). The EZNET-BIONESS multi-net system used had 11 nets of 230- μ m mesh size with a square mouth of 1 m² that could be opened and closed from deck at desired depth. In a typical multinet haul, strata were sampled every 10–20 m depth in the upper 100 m and every

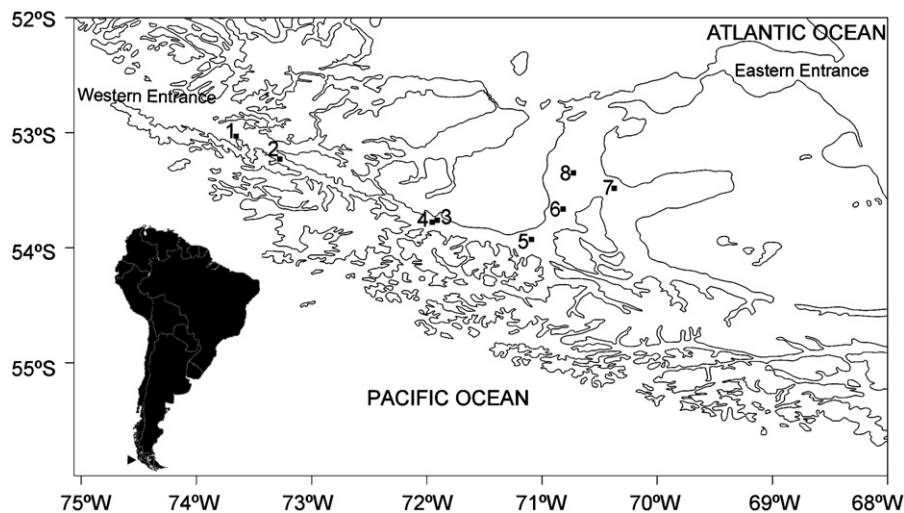


Fig. 1. Locations of sampling stations along the Strait of Magellan in early fall (March 25–April 1) 1995.

Table 1

Vertical stratified sampling (EZNET-BIONESS multi-net system) along the Strait of Magellan in early fall (March 25–April 1) 1995.

Basin	Station	Latitude	Longitude	Date	Hour	Sampled depth (m)	Bottom depth (m)
Pacific	1	53°01.77'	73°39.31'	26 March	09:00	600	638
	2	53°13.80'	73°16.67'	26 March	16:30	750	1000
Transition	3	53°45.64'	71°54.56'	25 March	19:15	200	230
	4	53°46.72'	71°57.25'	27 March	11:00	380	420
	5	53°55.60'	71°05.61'	27 March	19:00	440	480
	6	53°39.87'	70°49.10'	27 March	23:00	400	430
Paso Ancho	7	53°29.00'	70°22.45'	28 March	11:10	110	113
	8	53°20.51'	70°43.61'	28 March	17:30	160	173
	8A	53°21.00'	70°43.77'	28 March	23:45	165	176
	8B	53°20.71'	70°44.12'	29 March	06:45	155	165
	8C	53°20.73'	70°44.04'	29 March	12:15	160	170
	8D	53°20.84'	70°43.79'	29 March	18:45	165	170
	8E	53°21.83'	70°43.60'	30 March	10:15	180	203
	8F	53°21.07'	70°43.28'	30 March	15:00	190	200
	8G	53°21.14'	70°43.65'	30 March	19:45	175	187
	8H	53°21.49'	70°43.78'	31 March	11:30	175	180
	8I	53°20.78'	70°43.78'	31 March	17:45	160	166
	8J	53°21.04'	70°43.70'	31 March	23:45	168	176
	8K	53°21.00'	70°43.41'	1 April	04:00	165	170
8L	53°20.26'	70°43.56'	1 April	08:15	155	162	
8M	53°20.19'	70°43.48'	1 April	18:30	158	167	

50–100 m from 100 to 400–750 m. It took ca. 1 h and covered ca. 2–3 km. The system was equipped with temperature, salinity and fluorescence sensors, and others which determined water flux and filtered volume, speed and depth of the net and bottom depth. Hydrographic and chlorophyll data (Budillon et al., 1996; Carrada et al., 1996) were obtained along with plankton collections. Estimations of euphausiid abundance were based on stereomicroscopy counts of individuals and flowmeter-based filtered volumes. Filtered volumes ranged between 50 and 800 m³ as a function of depth strata sampled and towing time.

Adults of *E. valleritini* were sorted out for gut content analysis from fresh plankton samples immediately after collection. Gut pigment was estimated in specimens collected in 10 vertical strata at night (04:00 h) and day (18:30 h) at Paso Ancho (St. 8 K and 8 M, respectively). Additionally, adults of *E. valleritini* were separated from live plankton samples for two evacuation rates experiments at Paso Ancho. Samples were collected in 10 minutes tows between 0 m and 50 m at midnight with a Bongo net (70 cm mouth diameter and 300 µm mesh),

2.2. Identification of diel patterns

In order to describe the vertical migration of *E. valleritini* population Weighted Mean Depths (WMD) were estimated at each station according to Barange (1990):

$$WMD = \frac{\sum(n_i \times d_i)}{N}$$

where, n_i corresponds to the number of individuals in the i strata; d_i , corresponds to sample depth (mean depth of the sample stratum, e.g. 30 m for a 20–40 m depth stratum); and N , is the sum of individuals of all sampled strata. The WMD was used when the distribution of abundances with depth was close to normal, otherwise (*i.e.* bimodal distribution with depth) the chosen depth was at the population peak. In order to compare diel abundances, a randomization method (Manly, 1991) was applied.

2.3. Estimation of feeding rates and Carbon flux

2.3.1. Gut Content

Specimens from preserved samples at the WMD in daytime and nighttime (*i.e.* deep and surface layers, respectively) were sorted out for microscopic analysis of stomach content. During dawn hours, when population was actively migrating, samples were analyzed from both upper and deeper layers (Table 2).

Stomach content was examined as follows: (1) the stomach of each specimen was dissected using a stereoscopic microscope (Zeiss STEMI SV8), and transferred to a slide with a drop of filtered sea water, (2) the degree of gut fullness was estimated by transparency and expressed as percentage of the entire stomach volume in a scale of four equal ranks, (3) identification and counting of items was made using an inverted microscope (Olympus CH-2) after removing the stomach walls, and spreading items by the vibration of two interacting needles.

Items were identified to species level whenever possible, and otherwise to families for phytoplankton, and suborders or orders for zooplankton. Relative abundances of items were estimated according to various criteria. The number of copepods was estimated from the number of mandibles (*i.e.* two mandibles for one copepod) or large fragments of their body parts (*i.e.* legs, urosoma and furca for one copepod). The number of polychaeths was estimated from the number of setae (*i.e.* more than 40 setae for one polychaeth). The number of diatoms was estimated by counting undamaged valves only. Grinded material was recorded to account for its occurrence but ignored from quantitative

Table 2

Number of *E. valleritini* stomachs (n) examined at the weighted mean depth (WMD) in early fall (March 25–April 1) 1995.

Basin	Station	Stratum	n
Pacific	1	150–200	10
	2	100–150	10
Transition	3*	20–40; 140–160	9; 20
	4	100–150	10
	5*	0–20	20
	6*	0–20	20
Paso Ancho	7	90–110	6
	8	140–160	20
	8A*	20–30	20
	8B	140–155	18
	8C	140–160	20
	8D*	20–30; 140–165	9; 20
	8E	140–180	20
	8F	160–190	20
	8G*	20–30	20
	8H	120–140	20
	8I	140–160	20
	8J*	20–30	29
	8K*	20–30	20
8L	140–155	20	
8M	140–158	15	
Total	21 stations		396 stomachs

*Night sampling.

analysis. Twenty specimens per station with total of 209 for daytime and 187 for nighttime were examined.

Dominance of a given item at a particular sample combined the percentage of occurrence (*i.e.* the number of stomachs containing an item relative to the total number of stomachs containing all food items, expressed as percentage); and the average abundance of each item (excluding empty stomachs).

Statistical comparison between daytime and nighttime diet was established using a new approach for detecting difference in fish diets (Somerton, 1991). The method combines the Hotelling's T² statistics (Morrison, 1976) and a randomization test (Edgington, 1987) to produce a probability level per prey category; both were incorporated in a computer program modified from the original created by Somerton (DIETTEST). These statistics are valuable when prey abundances, expressed as numeric proportions of the total food consumed, do not fulfill requirements for a parametric method.

2.3.2. Ingestion rates

Ingestion rates of *E. valleritini* were estimated (in ng pig ind⁻¹ d⁻¹) by the fluorescence method (Mackas and Bohrer, 1976), which involved measurements of gut content (G) and its evacuation rate (k).

(a) Gut Pigment Content (G)

Immediately upon retrieval of EZNET-BIONESS system, carbon dioxide saturated water was poured into the plankton sample to anesthetize the animals (Kleppel et al., 1988). Gut pigments were fluorometrically determined in aliquots of three individuals (with three replicates) sorted out at random. Individuals were stored in darkness at –20 °C for 6–12 h for gut pigment extraction in acetone (90%), following standard procedure (Mackas and Bohrer, 1976; Dagg and Wyman, 1983). Pigments were measured in a Turner Design Fluorometer and computed as the sum of chloro- and phaeopigments (in µg pig ind⁻¹). Diel differences were established by non-parametric Mann-Whitney U test.

(b) Evacuation rates (k)

Gut evacuation rates were estimated experimentally on board at Paso Ancho. Freshly caught individuals (*ca.* 90) were sorted out at random, transferred to filtered sea water at 8.5 °C and kept on deck on a covered plastic container in darkness for successive

sampling. The experiment lasted three hours. Sub-samples of three individuals were taken at the beginning of the experiment (*i.e.* time 0), every five minutes during the first 20 minutes, every 10 minutes during the following hour and every 30 minutes during the remaining two hours. Samples were transferred to 90% acetone for pigment extraction and kept refrigerated (– 10 °C) in

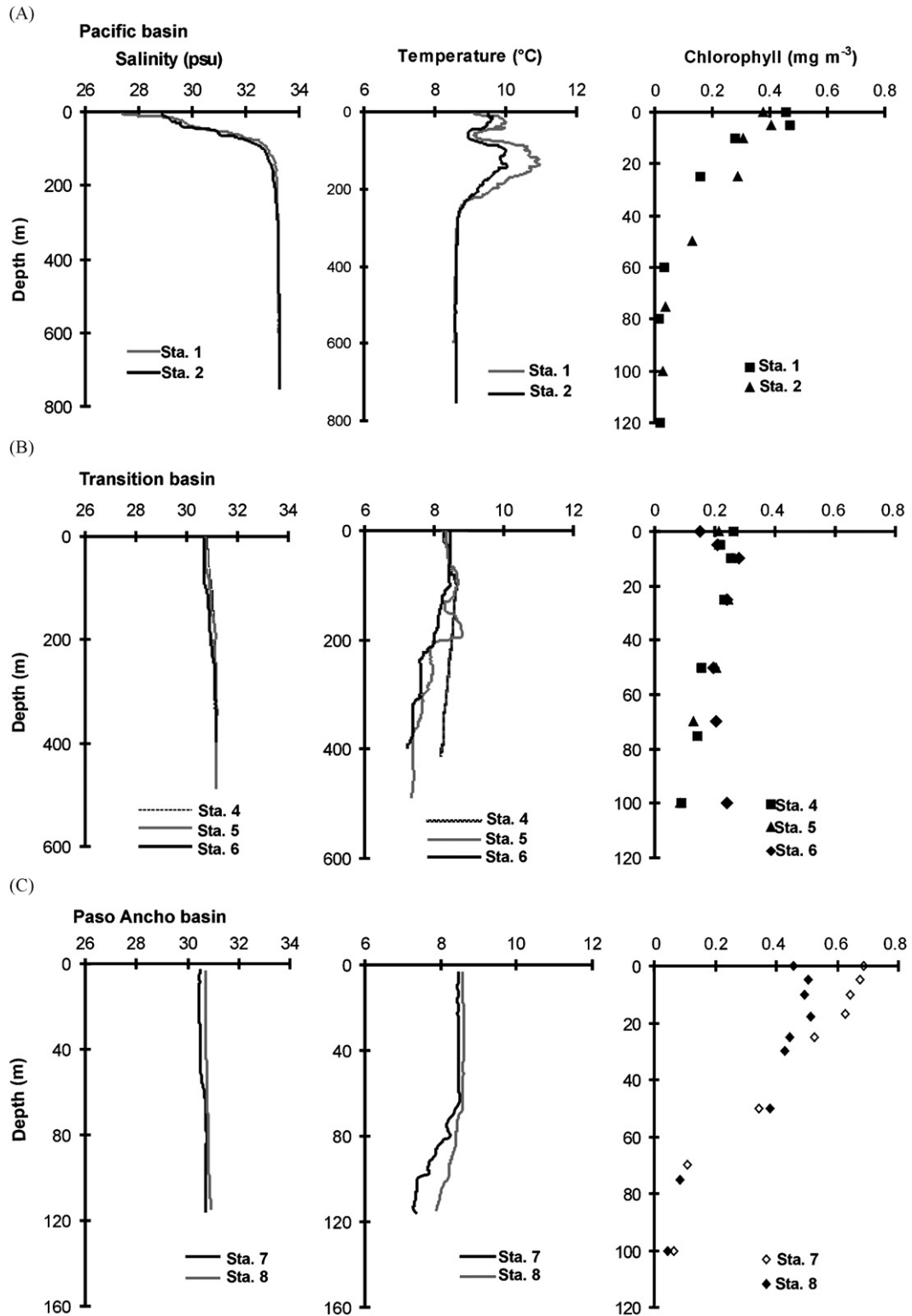


Fig. 2. Vertical Profiles of Temperature (°C), Salinity (psu) and Chlorophyll (mg m⁻³) in (A) Pacific basin (stations 1 and 2), (B) Transition basin (stations 3, 4, 5 and 6) and (C) Paso Ancho basin (stations 7 and 8) in early fall (March 25–April 1) 1995.

darkness, and analyzed fluorometrically (Mackas and Bohrer, 1976). Evacuation rates were estimated using both the exponential (Wang and Conover, 1986) and potential model (Huntley et al., 1987).

2.3.3. Feeding Impact

The daily feeding impact of *E. vallentini* on phytoplankton biomass was calculated as the ratio between total consumption rate (obtained from ingestion rate, $\mu\text{g pig ind}^{-1} \text{d}^{-1}$, and abundance, ind m^{-3}), and chlorophyll concentration in sea water ($\mu\text{g chl m}^{-3}$).

The feeding impact on phytoplankton biomass and on primary production was estimated at the stations where gut content was estimated (i.e. St. 8 K and 8 M). It was calculated for the upper layer for the day (12 h) and night (12 h) periods separately. The sum of both periods gave the daily impact on phytoplankton biomass.

Feeding impact of *E. vallentini* on copepod abundance (St. 8, 8 A to 8 M) was estimated as well. The feeding impact on the copepod population was estimated for the upper layer at night and for the deep layer in daytime.

The daily impact on primary production was calculated as the ratio between consumption rate ($\mu\text{g chl m}^{-3} \text{d}^{-1}$) and primary production ($\text{mg C m}^{-3} \text{d}^{-1}$). In order to convert Chlorophyll units to Carbon units, a 86.6 Carbon:Chlorophyll ratio calculated for the region was used (Carrada et al., 1996; Povero et al., 1996).

The impact on copepod population was calculated as the ratio between consumption rate (number of copepods $\text{m}^{-3} \text{d}^{-1}$) and

copepod abundance (ind m^{-3}). Evacuation rate ($k=0.46 \text{ h}^{-1}$) of copepod prey was taken from *Euphausia lucens* a closely related species (after Stuart and Pillar, 1990) with a temperature correction of a $Q_{10}=2$ (Ohman, 1984).

3. Results

3.1. Vertical Distribution and Diel migration

In order to compare vertical distribution and diel patterns along the Strait, the stations were grouped according to hydrographic and bathymetric characteristics into three basins: (a) Pacific basin (St. 1 and 2); (b) Transition basin (St. 3, 4, 5 and 6) and (c) Paso Ancho basin (St. 7, 8, 8 A to 8 M). Depth became progressively shallower and water column progressively mixed from the Pacific Entrance towards the Atlantic Entrance (Fig. 1). The Pacific basin has a bottom depth of 600–1000 m; was well stratified, with a halocline at ca. 100–125 m and a thermocline at 150–200 m (Fig. 2). The Transition Basin and Paso Ancho basin have bottom depths of 200–500 m and 100–200 m, respectively, and were fully mixed. The Atlantic basin has a bottom depth of 30–50 m and was also fully mixed. Strong tidal current and very shallow depth of this basin made biological sampling unfeasible.

E. vallentini vertical range was independent of the bottom depth. It extended from the surface at night to the deep layers during daytime (Fig. 3). In the Pacific basin, daytime WMD was

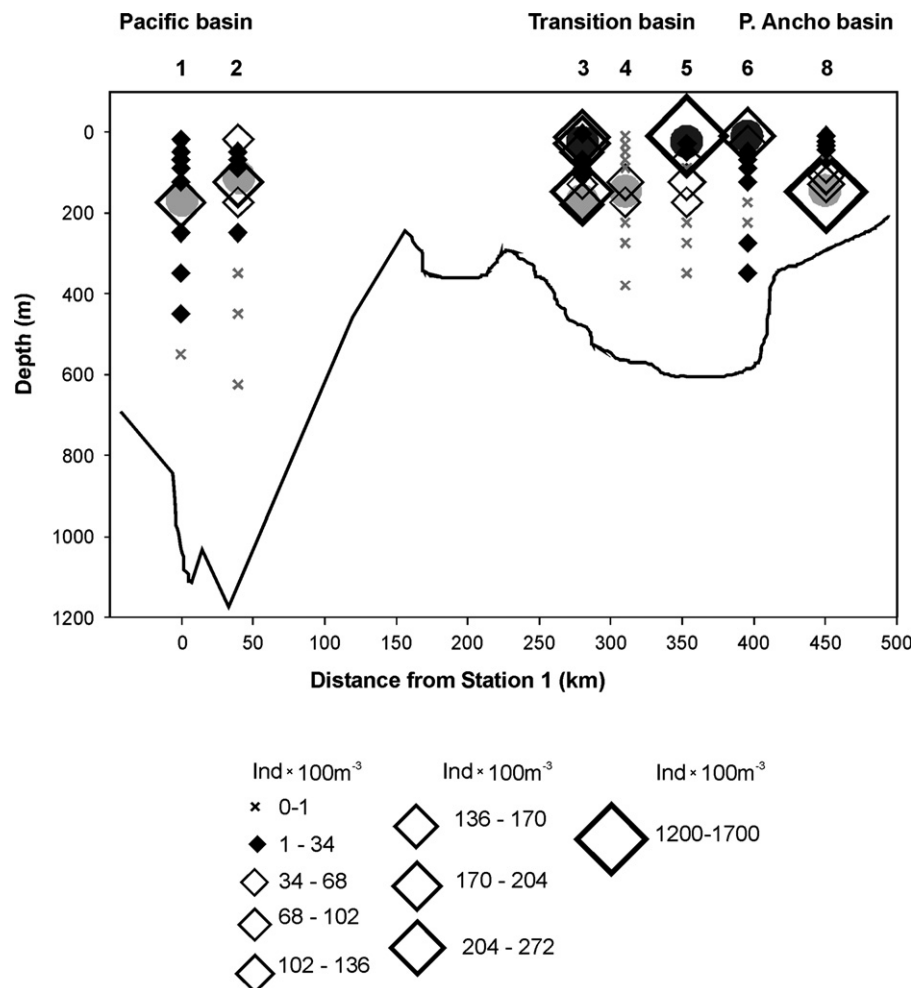


Fig. 3. Horizontal and vertical distribution of *E. vallentini* along the Strait of Magellan in early fall (March 25–April 1) 1995. Black and grey circles represent the weighted mean depth (WMD) during night and day, respectively. (For Interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

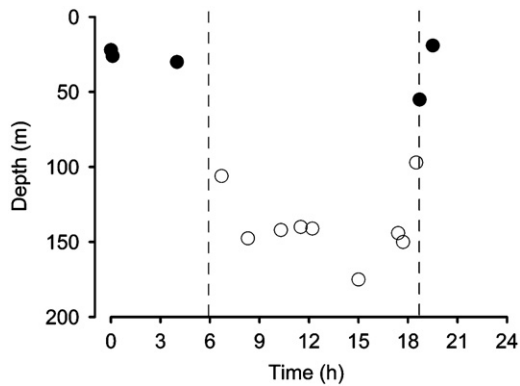


Fig. 4. Weighted mean depth (WMD) during a 24 hr diel cycle at Paso Ancho basin. Data were integrated from a 4 d sampling period. Black and white circles represent night and day WMDs, respectively.

112 and 168 m (St. 1 and 2, respectively), but some individuals at station 1 (bottom depth 638 m) occurred at the deepest sampled stratum (*i.e.* 500–600 m). In the Transition basin, daytime WMD was 170 and 140 m (St. 3 and 4, respectively), but organisms were found at station 3 (bottom depth 230 m) in high abundance at the deepest sampled stratum (160–200 m). In Paso Ancho basin, the daytime WMDs were at the deepest sampled stratum, which was in some cases 5–10 m from the bottom. On St. 8 L, which had a bottom depth of 162 m, the WMD was found between 140 and 155 m. On St. 8 I, which has a bottom depth of 166 m, the WMD was found between 140 and 160 m.

WMD of the population showed a clear diel vertical migration (Fig. 4). Significant differences in abundance from surface and deep layers during the day (Randomization test, $p=0.002$) and night (Randomization test, $p=0.0002$) were found. The population was in the upper layer at night (WMD=22 m), and remained there until 4:00 h at least, since no pre-dawn or dawn sampling were performed. Approximately one hour after dawn (6:45 h), the population reached 106 m, and at 8:15 h reached 148 m. The downward velocity of the migrating population, estimated from the differences in WMDs between 4:00 and 8:15 h was 26–28 m h^{-1} .

During daytime, the core of the population descended to a WMD of 150 m, stayed there until 17:45 h (with the exception of a single finding at 175 m), when it began an abrupt ascent to the upper most layers, around sunset (18:30 h), reaching the shallowest night level of 19 m at 19:45 h. The upward velocities for the 18:30 to 19:45-h period fluctuated from 45 to 78 m h^{-1} , two to three times higher than the downward velocity.

3.2. Items of the diet

Stomach content analysis of 396 specimens chosen at the WMD in day and night times along the Strait of Magellan showed a wide range of items in terms of taxa and size (Table 3). Among the microplankters, the most frequent and abundant taxa were dinoflagellates and tintinnids (Fig. 5) and among mesozooplankters, polychaeths and copepods were frequent items, but of low abundance.

3.3. Diel changes in the diet

Visual observations of stomach fullness showed significant diel differences (Mann-Whitney U test, $p < 0.05$) with greater percentages at night than in day time (79 and 19% grand average, respectively; Table 4).

Table 3

Items of *E. vallentini* diet from pooled stomach samples ($n=396$) along the Strait of Magellan in early fall (March 25–April 1) 1995.

Major taxa and size ranges of identified items	
Dinophyceae (38–120 μm)	<i>Dinophysis</i> sp. <i>Protoperdinium</i> sp. <i>Alexandrium</i> sp.
Bacillariophyceae (20–63 μm)	<i>Pennada</i> spp. <i>Thalassiosira</i> sp. <i>Pseudonitzschia</i> sp. <i>Coscinodiscus</i> sp. <i>Leptocilindrus</i> sp. <i>Thalassionema</i> sp.
Tintinnina (33–200 μm)	<i>Salpingella</i> sp. <i>Acanthostomella</i> sp. <i>Dictyocystis</i> sp. <i>Parundella</i> sp. <i>Helicostomella</i> sp. <i>Protorhabdonella</i> sp. Xystonellidae Codonellopsidae Cyttarocylidae <i>Tintinnus</i> sp.
Foraminiferida (100 μm)	unidentified
Polychaeta (150–200 μm)	unidentified
Copepoda (50–200 μm)	Most unidentified <i>Oncaea</i> sp. <i>Lubbockia</i> sp. <i>Oithona</i> sp.

Diel changes in the diet were significantly different (Somerton test, $p < 0.005$) for dinoflagellates, tintinnids and polychaeths at the Transition and Paso Ancho basins. Nighttime diet was characterized by dinoflagellates and tintinnids (Fig. 5) and the daytime diet, by polychaeths. Copepods were more frequent in daytime than at night, although their abundances were equally low in both periods (Table 5). Diatoms occurred in greater percentages at night than in daytime. The Pacific basin was only sampled during daytime so no diel comparison was possible.

Individuals collected during dusk hours (St. 3 and 8 D) had also a distinctive diet. There was a high occurrence and abundance of polychaeths at depth (140–160 m) and of dinoflagellates and diatoms at the upper layer (20–40 m). Nevertheless, in this latter layer stomachs presented a high content of unidentifiable grinded material.

3.4. Feeding rates and impacts on the environment

Chlorophyll content in the stomachs of pooled layers was significantly higher at night time than in daytime (Mann-Whitney U test, $p < 0.05$). Gut pigment content at nighttime showed maxima in two layers: an upper one at 0–20 m (58.7 ± 36.4 ng pig ind^{-1}) and a subsurface or intermediate one, with highest concentrations spread between 50 and 120 m (36.9 ± 10.7 ng pig ind^{-1}) (Fig. 6). During daytime gut pigment content presented steadily low values throughout the water column (5.2 ± 4.9 ng pig ind^{-1}). Gut evacuation data fitted the exponential model better than the potential model. The estimated evacuation rate amounted to 0.16 h^{-1} (Fig. 7). Ingestion rates showed a trend which was consistent to stomach contents: daytime rates (1.02 ± 0.84 ng pig $\text{ind}^{-1} \text{d}^{-1}$) were significantly lower (Mann-Whitney U test, $p < 0.05$) than nighttime rates (4.82 ± 2.6 ng pig $\text{ind}^{-1} \text{d}^{-1}$).

Consumption rates showed two maxima at nighttime: a peak of 40.1 ± 14.9 ng pig $\text{m}^{-3} \text{d}^{-1}$ between 0 and 40 m, and a much lower one of 2.8 ± 1.3 ng pig $\text{m}^{-3} \text{d}^{-1}$ between 80 and 158 m.

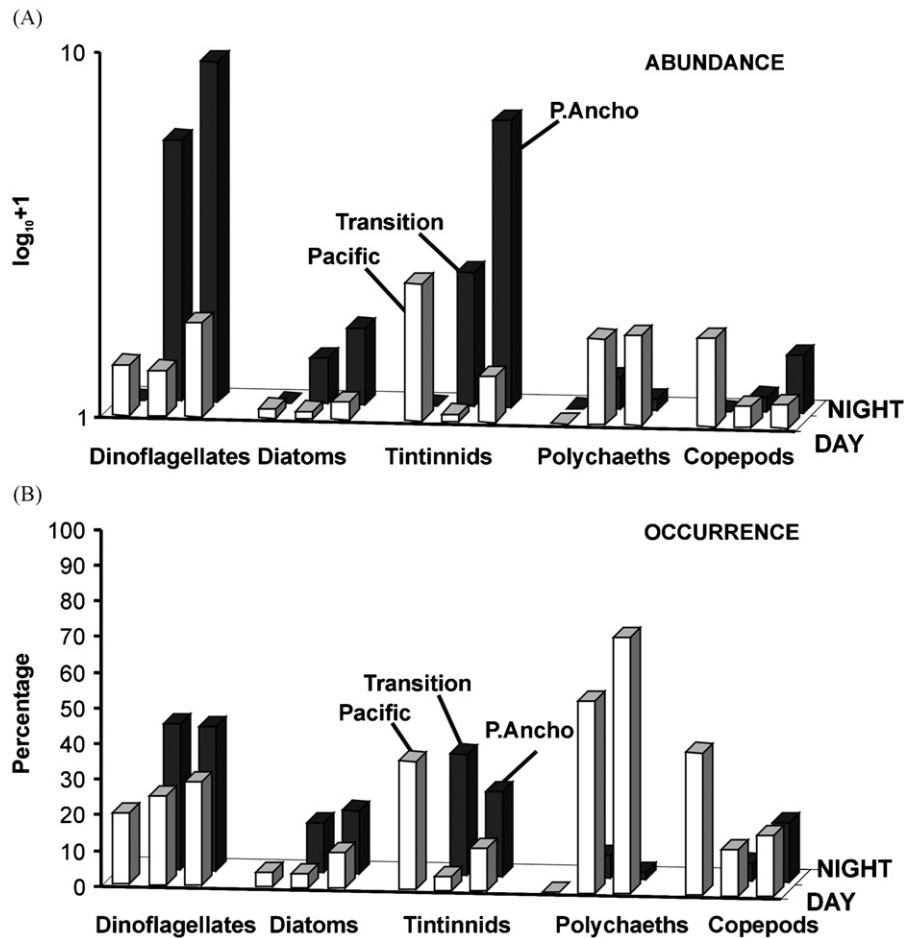


Fig. 5. Items of the diet of *E. vallentini* along the strait of Magellan in early fall (March 25–April 1) 1995. (A) Average abundance as given by $\log_{10}(\text{abundance}+1)$ and (B) Frequency of occurrence at night and day in the Pacific, Transition and Paso Ancho basins.

Table 4

Day and night stomach fullness (%) of *E. vallentini* along the Strait of Magellan in early fall (March 25–April 1) 1995.

Station	Mean	SD
DAY		
1	41.8	44.3
2	23.2	34.1
4	29.8	33.9
7	33.5	38.6
8B	30.1	38.9
8L	11.3	19.1
8H	2.4	6.1
8C	27.5	31.7
8F	10.3	21.5
8I	7.0	8.9
8	11.3	19.2
8M	3.7	6.0
Grand average	19.2	
NIGHT		
5	92.8	16.2
6	79.6	31.6
8D	73.3	26.9
8G	65.0	31.6
8A	86.5	21.3
8J	74.3	26.5
8K	84.5	23.6
Grand average	79.4	

SD: standard deviation.

Table 5

Mean abundances (and standard deviations) of items in stomachs of *E. vallentini* collected at night and day in the Pacific, Transition and Paso Ancho basins of the Strait of Magellan in early fall (March 25–April 1) 1995.

Items	Basin	Average	
		Night	Day
Dinoflagellates	Pacific	–	0.38 (0.62)
	Transition	4.19 (2.44)	0.33 (0.58)
	Paso Ancho	7.53 (6.13)	0.80 (2.24)
Diatoms	Pacific	–	0.06 (0.25)
	Transition	0.33 (0.53)	0.05 (0.22)
	Paso Ancho	0.62 (0.88)	0.12 (0.41)
Tintinnids	Pacific	–	1.38 (2.68)
	Transition	1.33 (1.15)	0.05 (0.22)
	Paso Ancho	5.11 (9.48)	0.33 (1.33)
Polychaeths	Pacific	–	0.00 (0.00)
	Transition	0.22 (0.72)	0.71 (0.72)
	Paso Ancho	0.07 (0.38)	0.76 (0.55)
Copepods	Pacific	–	0.75 (0.77)
	Transition	0.11 (0.32)	0.14 (0.36)
	Paso Ancho	0.46 (0.67)	0.16 (0.37)

During daytime, consumption rates were low ($1.6 \pm 1.5 \text{ ng pig m}^{-3} \text{ d}^{-1}$) along the entire water column.

Feeding impact (%) of the population upon phytoplankton biomass reached 0.002% in daytime and 0.17% in nighttime, with an overall daily value of 0.17% of environmental chlorophyll

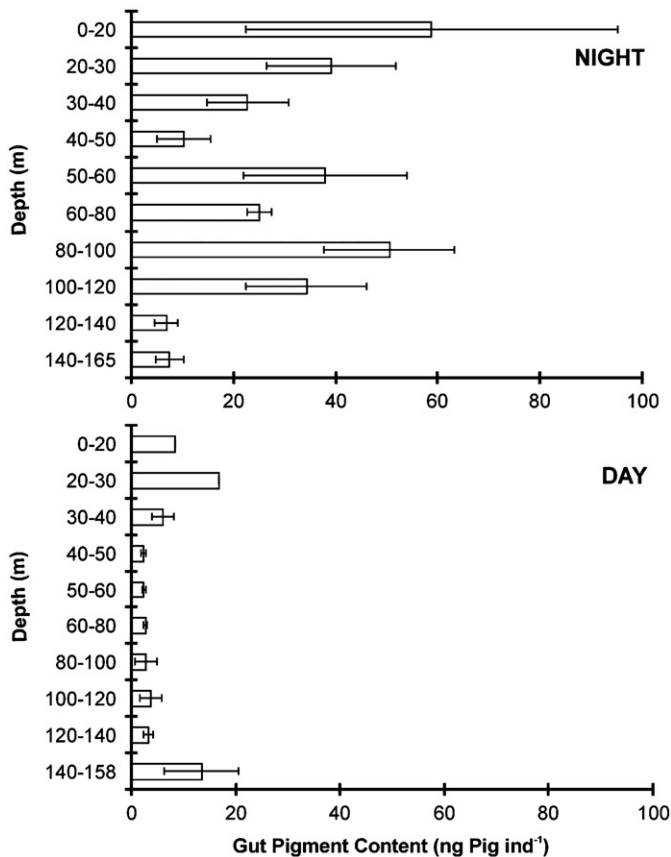


Fig. 6. Gut pigment content (ng ind⁻¹) of *E. vallentini* (n=3) in Paso Ancho basin at (a) Night (station 8 K at 03:57 h) and (b) Day (station 8 L at 18:30 h).

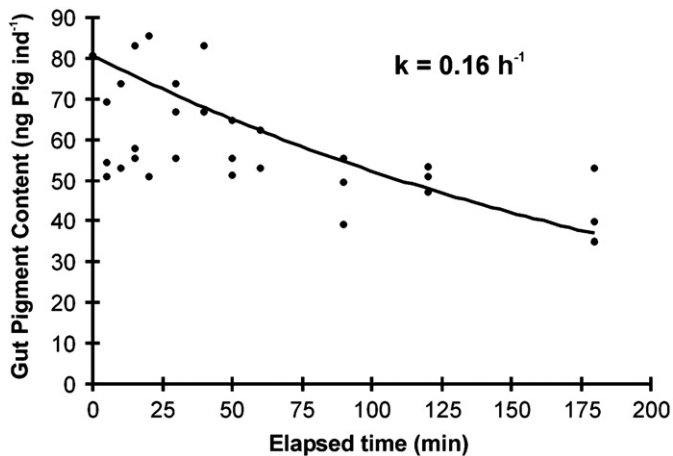


Fig. 7. Evacuation rate (h^{-1}) of *E. vallentini* (n=3) in early fall (March 25–April 1) 1995.

concentration. The impact of *E. vallentini* population upon daily primary production reached 17–45%.

The daily impact of predation of *E. vallentini* population upon copepods abundance reached $8.5 \pm 4.1\%$.

4. Discussion

E. vallentini, an open ocean circumpolar species, has colonized the Chilean fjords to become one of the most abundant species in

the zooplankton community (Antezana, 1976; 1999a; Guglielmo et al., 1997; Antezana and Hamame, 1999; Palma and Silva, 2004). It is also found near other subantarctic islands and archipelagos, where it occurs in such densities to become a food item for large vertebrates (Gurney et al., 2002; Perissinotto and McQuaid, 1992; Ridoux, 1988).

Our results tested for peculiarities in the behavior of the species within the fjords. Diel vertical migration was examined, since it is considered to be specific and to follow an endogenous rhythm.

The diel vertical migratory pattern of *E. vallentini* within the Strait of Magellan was similar to the open ocean, with population displacement between the surface at night and the deep in daytime. Nevertheless, the extent of the migration differed. While daytime depth in the open ocean reached 300–400 m (Perissinotto and McQuaid, 1992; Pakhomov et al., 1994; Pakhomov and Froneman, 1999), the core of the population in the Strait of Magellan remained at 100–200 m layer during the day, independently of the bottom depth. In fact, in shallow locations, the deepest tow was purposely done as close as 5–10 m to the bottom.

Other evidence of adaptation to this fjord environment comes from peculiarities in food and feeding behavior associated with migratory patterns. Our results indicate that *E. vallentini* is actively feeding on phytoplankton in dark hours, as it does in the vicinity of Prince Island (Gurney et al., 2002). Yet throughout the diel migration in the Strait of Magellan, *E. vallentini* was a facultative omnivore, with a broad spectrum diet dominated by dinoflagellates, tintinnids, copepods and polychaeths.

Stomach content of *E. vallentini* partly reflected prey abundance in the field. Tintinnids were most abundant in the upper layer both in daytime and at night (Guglielmo et al., 1997), and were also abundant in stomachs of individuals collected at night in the upper layer. However, field abundances of a given item of the diet may differ from abundances in the stomachs, implying prey preference. In fact, copepods abundance in the field (Guglielmo et al., 1997), which had a similar vertical distribution to *E. vallentini* (i.e. more abundant during the day in deep layers and during the night in upper layers), were nearly absent in stomachs collected at night in the upper layer. This difference suggests that *E. vallentini* preferred phytoplankton and tintinnids during nighttime.

The most remarkable adaptation occurred when the mostly oceanic *E. vallentini* encountered demersal habitats in daytime. In locations where the bottom was shallower than the common daytime depth range of the species, individuals did not avoid the bottom layer but rather stayed right near the bottom, and fed upon polychaeths. This item was absent in individuals reaching the daytime depths (ca. 100 m) at locations where the bottom was much deeper (ca. 1000 m). It is suggested that *E. vallentini* takes advantage of alternative food items of the benthic environment, particularly when phytoplankton is limiting, an opportunistic strategy to changing and unpredictable environments. Although identified as an herbivore (Mauchline, 1980), *E. vallentini* may change its diet according to available food (Gurney et al., 2002) as do other euphausiids (Antezana, 1978; Antezana et al., 1982; Price et al., 1988; Stuart and Pillar 1990; Gibbons et al., 1991).

In our study, quantitative estimates of consumption rate and impact upon phytoplankton were low due to low evacuation rates. Our estimate of evacuation rate (0.16 h^{-1}) was considerable lower than in other experimental studies performed for the same species (1.02 h^{-1}), when chlorophyll concentrations were much higher (Antezana and Hamame, 1999). Gut evacuation of *E. vallentini* near Prince Edward Island was also higher than in the present study ($0.45\text{--}0.99 \text{ h}^{-1}$ for adults and $0.47\text{--}1.36 \text{ h}^{-1}$ for juveniles), resulting in higher ingestion rates ($0.24\text{--}1.82 \mu\text{g}$ pigm

ind⁻¹d⁻¹ for adults and even higher for juveniles; Gurney et al., 2002). Therefore our estimation of population consumption and impact on phytoplankton and primary production may be underestimated and should be taken with caution. Impact on primary production of *E. vallentini* in Chilean fjords would increase three fold if higher evacuation rates (i.e. Gurney et al., 2002) are used to compute consumption rate and impact on phytoplankton. Furthermore, the abundance of *E. vallentini* was much lower (3–9 ind m⁻³) than previously encountered (Antezana, 1976), hence the impact on daily primary production may increase from the estimated 17–45% to 99.3%, when the population is more abundant (e.g. 40 ind m⁻³).

E. vallentini may play a key role in channeling primary production and also be an important prey of large predators when swarming. The occurrence of *E. vallentini* swarms was reported in the Chilean fjords (Antezana, 1976), and it may be associated with humpback whales recurrently feeding and nursing in the Strait of Magellan (Gibbons et al., 2003) and Gulf of Corcovado (Hucke-Gaete et al., 2004).

A last evidence of adaptation of *E. vallentini* to the fjord is the occasional encounter of large numbers of furcilia larvae in the Magellan and Fuegian fjords (Antezana et al., 2002), and the complete larval series found in enclosed fjords of Chiloe Archipelago. These larval occurrences are indications of a self sustained population and isolated from the parental open ocean population. The speciation history of *Euphausia* species and in particular of geographically overlapping *E. vallentini* and *E. lucens* is characterized by only minor and recent genetic differentiation, resulting in sympatric speciation (Jarman et al., 2000).

In conclusion, our results on feeding and migratory peculiarities of *E. vallentini* suggest an adaptive behavior to rather isolated and entrapped waters implying a degree of isolation and self sustenance of this population within the extensive Chilean fjords.

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References

Adams, J.N., Klages, N.T., 1989. Temporal variation in the diet of the Gentoo Penguin *Pygoscelis papua* at sub-Antarctic Marion Island. *Colonial Waterbirds* 12 (1), 30–36.

Antezana, T., 1976. Diversidad y equilibrio ecológico en comunidades pelágicas. In: Orrego, F (Ed.), *Preservación del Medio Ambiente Marino*. Universidad Técnica del Estado, Santiago, pp. 40–54.

Antezana, T., 1978. Distribution of euphausiids in the Chile-Peru Current with particular reference to the endemic *Euphausia mucronata* and the oxygen minima layer. PhD thesis, University of California, San Diego, California.

Antezana, T., 1981. Zoogeography of euphausiids of the South Eastern Pacific Ocean, *Memorias del Seminario sobre Indicadores Biológicos del Plancton*. UNESCO, Montevideo p 5–23.

Antezana, T., 1999a. Plankton of Southern Chilean Fjords: trends and linkages. *Scientia Marina* 63 (Supl. 1), 69–80.

Antezana, T., 1999b. Hydrographic features of Magellan and Fuegian inland passages and adjacent subantarctic waters. *Scientia Marina* 63 (Supl. 1), 23–34.

Antezana, T., Ray, K., Melo, C., 1982. Trophic behavior of *Euphausia superba* Dana in laboratory conditions. *Polar Biology* 1 (2), 77–82.

Antezana, T., Hamame, M., 1999. Short-term changes in the plankton of a highly homogeneous basin of the Strait of Magellan (Paso Ancho) during spring 1994. *Scientia Marina* 63 (Supl. 1), 59–67.

Antezana, T., Giraldo, A., Hamame, M., 2002. Clorofila y alimentación del zooplancton fraccionado por tamaño, en subcuencas del Sistema de Canales Magallánicos y Fueguinos durante la primavera de 1998. *Ciencia y Tecnología del Mar* 25 (1), 109–130.

Barange, M., 1990. Vertical migration and habitat partitioning of six euphausiid species in the northern Benguela upwelling system. *Journal of Plankton Research* 12, 1223–1237.

Bingham, M., 1998. The distribution, abundance and population trends of Gentoo, Rockhopper and King penguins at the Falkland Islands. *Orxy* 32 (3), 223–232.

Budillon, G., Hernández, J., Sobarzo, M., Spezie, G., 1996. Hydrodynamics of the Straits of Magellan (1995). In: Faranda, F.M., Guglielmo, L., Povero, P. (Eds.), *Nat. Progr. Ant. Res. Straits of Magellan Ocean. Cruise, March–April 1995*. Data Report, G. Lang-Arti Grafique, Genova, pp. 9–52.

Carrada, G.C., Mangoni, O., Sgrosso, S., Basualto, S., 1996. Spatial distribution of size fractionated phytoplankton pigments along the Straits of Magellan and their daily variation in the Paso Ancho area (autumn 1995). In: Faranda, F.M., Guglielmo, L., Povero, P. (Eds.), *Nat. Progr. Ant. Res. Straits of Magellan Ocean. Cruise, March–April 1995*. Data Report, G. Lang-Arti Grafique, Genova, pp. 107–120.

Dagg, M.J., Wyman, K.D., 1983. Ingestion, gut passage and egestion by the copepod *Neocalanus plumchrus* and *N. cristatus* calculated from gut contents. *Marine Ecology Progress Series* 13, 37–46.

Edgington, E.S., 1987. In: *Randomization tests* 2nd ed. Marcel Dekker, NY 341 p.

Fernandez-Severini, M.D., Hoffmeyer, M.S., 2005. Mesozooplankton assemblages in two bays in the Beagle channel (Argentina) during January 2001. *Scientia Marina* 69 (Suppl. 2), 27–37.

Gibbons, M.J., Barange, M., Pillar, S.C., 1991. Vertical migration and feeding of *Euphausia lucens* (Euphausiacea) in the Southern Benguela. *Journal of Plankton Research* 13, 473–486.

Gibbons, J., Capella, J.J., Valladares, C., 2003. Rediscovery of a humpback whale (*Megaptera novaeangliae*) feeding ground in the straits of Magellan, Chile. *Journal of Cetacean Research Management* 5 (2), 203–208.

Guglielmo, L., Antezana, T., Crescenti, N., Granata, A., 1997. Euphausiids. In: Guglielmo, L., Ianora, A. (Eds.), *Atlas of Marine Zooplankton. Straits of Magellan: Amphipods, Euphausiids, Mysids, Ostracods, and Chaetognaths*. Springer-Verlag, Berlin, pp. 87–125.

Gurney, L.J., Froneman, P.W., Pakhomov, E.A., McQuaid, C.D., 2002. Diel feeding patterns and daily ration estimates of three subantarctic euphausiids in the vicinity of the Prince Edward Islands (Southern Ocean). *Deep-Sea Research II* 49, 3207–3227.

Hucke-Gaete, R., Osman, L.P., Moreno, C.A., Findlay, K.P., Ljungblad, D.K., 2004. Discovery of a blue whale feeding and nursing ground in southern Chile. *Proceedings of the Royal Society of London Series B (Suppl.) Biology Letters* 271, S170–S173.

Huntley, M.E., Marin, V., Escritor, F., 1987. Zooplankton grazers as transformers of ocean optics. I. Diel changes in zooplankton grazing. *Journal of Marine Research* 45, 911–945.

Jarman, S.N., Elliot, G., Nicol, S., McMinn, A., 2000. Molecular phylogenetics of circumglobal *Euphausia* species (Euphausiacea: Crustacea). *Canadian Journal of Fisheries and Aquatic Sciences* 57 (S3), 51–58.

John, D.D., 1936. The southern species of the genus *Euphausia*. *Discovery Reports* 14, 193–324.

Kleppel, G.S., Pieper, R.E., Trager, G., 1988. Variability in the gut content of individual *Acartia tonsa* from waters off Southern California. *Marine Biology* 97, 185–190.

Mackas, D., Bohrer, R., 1976. Fluorescence analysis of zooplankton gut contents an investigation of diel feeding patterns. *Journal of Experimental Marine Biology and Ecology* 25, 77–85.

Manly, B.F., 1991. In: *Randomization and Monte Carlo Methods in Biology*. Chapman and Hall, London.

Mauchline, J., 1980. The biology of mysids and euphausiids. *Advances in Marine Biology* 18, 1–681.

Mazzocchi, M.G., Ianora, A., 1991. A faunistic study of the copepod assemblages in the Strait of Magellan. *Bolletino Oceanografico Teoria Applicata* 9 (2–3), 163–177.

Nemoto, T., 1959. Food of baleen whales with reference to whale movements. *Scientific Report of the Whales Research Institute* 14, 149–290.

Morrison, D.F., 1976. In: *Multivariate statistical methods*. 2nd ed. McGraw-Hill, NY 105 p.

Ohman, M.D., 1984. Omnivory by *Euphausia pacifica*: the role of copepod prey. *Marine Ecology Progress Series* 19, 125–131.

Pakhomov, E.A., Perissinotto, R., McQuaid, C.D., 1994. Comparative structure of the macro-zooplankton/micronekton communities of the subtropical and Antarctic Polar fronts. *Marine Ecology Progress Series* 111, 155–169.

Pakhomov, E.A., Froneman, P.W., 1999. Macrozooplankton/micronekton dynamics in the vicinity of the Prince Edward Islands (Southern Ocean). *Marine Biology* 134, 501–515.

Palma, S., Silva, N., 2004. Distribution of siphonophores, chaetognaths, euphausiids and oceanographic conditions in the fjords and channels of southern Chile. *Deep-Sea Research II* 51, 513–535.

Perissinotto, R., McQuaid, C.D., 1992. Land-based predator impact on vertically migrating zooplankton and micronekton advected to a Southern Ocean archipelago. *Marine Ecology Progress Series* 80, 15–27.

- Povero, P., Tucci, S., Cisternas, M., Capello, M., Mistic, C., Fabiano, M., 1996. Distribution and composition of suspended particulate matter in the Straits of Magellan. In: Faranda, F.M., Guglielmo, L., Povero, P. (Eds.), Nat. Progr. Ant. Res. Straits of Magellan Ocean. Cruise, March-April 1995, Data Report. G. Lang-Arti Grafique, Genova, pp. 219–230.
- Price, H.J., Boyd, K.R., Boyd, C.M., 1988. Omnivorous feeding behavior of the Antarctic krill *Euphausia superba*. *Marine Biology* 97, 67–77.
- Ragulin, A.G., 1969. Underwater observations on krill. Tr. Vses. Nauchno-Issled. Inst Morsk Rybn Khoz Okeanogr 66, 231–234 (Engl. transl.).
- Ridoux, V., 1988. Subantarctic krill, *Euphausia vallentini* Stebbing, preyed upon by penguins around Crozet Island (Southern Indian Ocean): population structure and annual cycle. *Journal of Plankton Research* 10 (4), 675–690.
- Silva, N., Calvete, C., 2003. Características oceanográficas físicas y químicas de canales australes chilenos entre el golfo de Penas y el estrecho de Magallanes (Crucero Cimar Fiordo 2). *Ciencia y Tecnología del Mar* 25 (1), 23–88.
- Somerton, D.A., 1991. Detecting differences in fish diets. *Fishery Bulletin* 89, 167–169.
- Stuart, V., Pillar, S.C., 1990. Diel grazing patterns of all ontogenetic stages of *Euphausia lucens* and *in situ* predation rates on copepods in the southern Benguela upwelling region. *Marine Ecological Progress Series* 64, 227–241.
- Valdenegro, A., Silva, N., 2003. Caracterización física y química de la zona de canales y fiordos australes de Chile entre el estrecho de Magallanes y cabo de Hornos (Crucero Cimar Fiordo 3). *Ciencia y Tecnología del Mar* 26 (2), 19–60.
- Wang, R., Conover, R.J., 1986. Dynamics of gut pigment in the copepod *Temora longicornis* and the determination of *in situ* grazing rates. *Limnology and Oceanography* 31 (4), 867–977.