

Carbon flow through the pelagic food web in southern Chilean Patagonia: relevance of *Euphausia vallentini* as a key species

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ABSTRACT: The southernmost Patagonian region constitutes a major glaciated area with a high freshwater input loaded with particulate and dissolved matter. We assessed the relevance of the terrestrial (allochthonous) and marine (autochthonous) matter that permeates into the fjord and channel system and their possible impact on the euphausiid-based food web. A research cruise (CIMAR 16) was conducted from 18 October to 13 November 2010 (austral spring) in the area between Magellan Strait and Drake Passage to study the physical-chemical and biological characteristics of the pelagic food web, as well as the main biological processes linked with the food web. The dominance of phytoplankton within the autochthonous fractions of particulate organic carbon (POC) and the high abundance and bacterivory rate shown by the heterotrophic nanoflagellates suggest an interplay between microbial and classical food webs. *Euphausia vallentini* showed a moderate grazing impact (3% of the gross primary production) and a daily ration of 18.6%, and the fecal pellet production rate corresponded to 24.5% of the ingestion rate. This species removed heterotrophic prey (67.5%) preferentially over diatoms (32.5%), and the ingested diet was mainly dinoflagellates, tintinnids, crustacean nauplii and centric diatoms. Overall, euphausiids fed preferentially on marine matter, which showed a tight link with the pelagic food web. Congeneric species of the genus *Euphausia* shared the condition of 'key species' as they constitute a major carbon and energy flow from lower to higher trophic levels and an important part of the POC flux through their active vertical migration and passive fecal-carbon export.

KEY WORDS: Chilean Patagonia · *Euphausia vallentini* · Pelagic carbon flux · Euphausiid diet

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INTRODUCTION

Southern Chilean Patagonia is an entangled area of fjords and channels that receives a high volume of

freshwater from river and glacial discharge. Overall, the freshwater is nutrient depleted (except of silicic acid), but very rich in total suspended particles and high in concentrations of particulate and dissolved

organic matter (POM and DOM, respectively) (González et al. 2013). Thus, the cold and oligotrophic water of glaciers and rivers mixes with the nutrient-rich Sub-Antarctic Water (SAAW) that penetrates the fjord region as part of the Antarctic Circumpolar Current (ACC). When the ACC approaches the coastal area of the southernmost part of Chilean Patagonia its name changes to Cape Horn Current, constituting one of the least studied systems in the eastern southernmost Pacific Ocean. The Sub-Antarctic system of the Magellan Strait and Cape Horn is unique because it is fed by one of the largest freshwater reserves on Earth (the North and South Patagonian Ice Fields), which is highly vulnerable to global warming (Rignot et al. 2003, Rivera et al. 2012). The presence of sill-constrictions has been mentioned as a key topographic feature in the regulation of water mass flow, which defines sub-basins within central (González et al. 2011) and southern (i.e. Strait of Magellan) Patagonian channels and fjords. The latter authors proposed dividing the Strait of Magellan into 3 basins: (1) from the Pacific entrance to Carlos III Island, an area dominated by Pacific SAAW, (2) from Carlos III Island to Segunda Angostura, an area dominated by a mixture of Pacific SAAW and glacial-fluvial freshwater and (3) from Segunda Angostura to the Atlantic entrance, an area dominated by Atlantic SAAW (Capello et al. 2011). These water masses set up a variety of biological, chemical and physical scenarios along west–east gradients in the study area (Mazzocchi et al. 1995). Thus, the mixture of terrestrial and oceanic environments inside fjords and channels affects the physical structure of the water column, setting a strong saline stratification that impinges on the structure and functioning of the pelagic and benthic ecosystems in southern Patagonia (Silva & Palma 2008). For example, the presence of a strong pycnocline may function as a ‘natural barrier’ for the vertical distribution of plankton, affecting the vertical migration of zooplankton, e.g. the euphausiid species *Euphausia vallentini*. Also, the particle and particulate organic carbon (POC) export flux to the deeper layers of fjords and channels and to the sediments may be reduced.

The multiple origins of POM and DOM in southern Patagonia include input from terrestrial, riverine, estuarine and marine systems. These materials may subsidize the autochthonous production and enhance the microbial food web, particularly in winter (González et al. 2010, Vargas et al. 2012, Lafon et al. 2014), as a transition from large diatoms in spring to small flagellates in winter has been reported (Iriarte et al. 1993, Marino et al. 1993). Thus,

a more complex trophic web (e.g. increase in mixotrophic nanoplankton, Czypionka et al. 2011) and a more conspicuous decoupling of the carbon export from the local primary production (PP) (González et al. 2013) may result from an exacerbated input of POC and dissolved organic carbon (DOC) of allochthonous origin.

The distribution of *E. vallentini* is circumglobal from the subtropical convergence from ~38–42° S to the Polar Front at ~60° S (or southern Cape Horn in the study area) (Antezana 1981). It is a key species and is the most abundant euphausiid in Chilean Patagonian waters (Palma & Silva 2004), and constitutes an ecological bridge between microplankton and the upper trophic levels (i.e. fishes, penguins and whales). On an annual cycle, its feeding activity reaches the highest level from August to early October in the Southern Indian Ocean, which is concurrent with maturation and the beginning of its breeding season (Ridoux 1988). In addition, this species seems to play a pivotal role in the pelagic–benthic coupling through active (diel vertical migrations) and passive fluxes of carbon (i.e. production of fast-sinking fecal strings) (González et al. 2013).

The objectives of the present study were to study the overall biological, chemical and physical characteristics of the southern Patagonia region and to assess the concentration, provenance (allochthonous versus autochthonous) and distribution of the POC and DOC pools. In addition, the carbon export towards the sediments and its flow through the pelagic food webs will be assayed (with emphasis on the dominant euphausiid species *E. vallentini*) in the sub-Antarctic region of the Chilean Patagonia. We hypothesize that *E. vallentini* is an important member in this highly diverse environment, influencing the food web structure and the carbon flux. We focused our study on the most comprehensive transects in terms of spatial coverage (T2 and T5; Fig. 1), the Magellan Strait and the Beagle Channel—down to Cape Horn—as these are the transects that, through different disparate microenvironments, connect the Pacific and Atlantic Oceans.

MATERIALS AND METHODS

Samples were collected during the CIMAR 16 research cruise, which took place during austral spring, from 18 October to 13 November 2010, on board the RV ‘Abate Molina’ in the area between Magellan Strait and the Drake Passage (Fig. 1). Two research approaches were implemented.

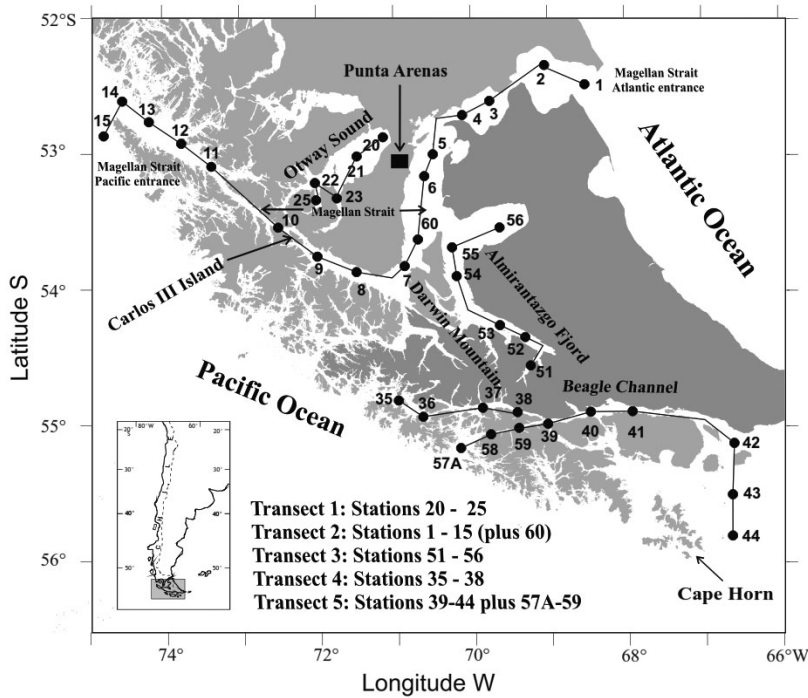


Fig. 1. Study area, showing the stations sampled along 5 different transects (T1–T5) and the process station 21 (located in Otway Sound as part of T1). Segunda Angostura is located between Stns 4 and 5

Approach 1: Five transects of oceanographic stations

A total of 44 oceanographic stations were distributed along 5 transects located in southern Chilean Patagonia: T1 (Otway Sound), T2 (Magellan Strait between the Pacific and Atlantic Oceans), T3 (Inutil Bay to Almirantazgo Bight), T4 (Cook Bay) and T5 (Beagle Channel to Cape Horn) (Fig. 1). At these stations, water samples for bacterioplankton, phytoplankton and microzooplankton (1, 5, 10, 25, 50 m depth) and dissolved inorganic nutrient analyses (1, 5, 10, 25, 50, 75, 100, 150, 200, 250, 300, 350 and 400 m) were collected using a bottle-rosette system equipped with fifteen 10-l Niskin bottles and a CTD (Seabird 19 CTD-O) to determine the physical structure of the water column (temperature, salinity, depth and dissolved oxygen). Salinity and dissolved oxygen sensors were calibrated by measuring salinity (with an Autosal salinometer) and dissolved oxygen (Winkler method) in discrete water samples. At these stations, POC and DOC concentrations as well as size-fractionated chlorophyll *a* (chl *a*) were measured. We also determined the abundances and carbon-based biomasses of phytoplankton, bacteria, heterotrophic and autotrophic nanoflagellates (HNF and ANF, respectively), dinoflagellates and ciliates (see below). In addition,

the fatty acid composition of the key species, *Euphausia vallentini*, was measured at several stations along the five transects.

Approach 2: A process-oriented time-series station

Stn 21 (53°04'S, 71°37'W), located in the middle of T1 in Otway Sound, was used for a process-oriented study for a period of 3 to 4 d (Fig. 1). This station was chosen because it represents a typical Patagonian semi-enclosed area affected by freshwater from glacier melt and marine water from the eastern and western sides (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m557p091_supp.pdf). The fate of photosynthetically generated organic carbon through the classical and microbial food webs was studied. In addition to the biological, chemical and physical measurements recorded for the oceanographic stations, we estimated gross primary production (GPP), *E. vallentini* grazing and vertical particulate matter fluxes.

Chl *a* and phytoplankton analysis

For chl *a* determination, 200 ml of seawater was filtered (GF/F Whatman glass fiber filters, 0.7 µm nominal pore size) in triplicate and immediately frozen (−20°C) until later analysis via fluorometry (Turner Design TD-700), using acetone:water (90:10% v/v) for pigment extraction according to standard procedures (Parsons et al. 1984). Chl *a* size fractionation was done in 3 sequential steps: (1) for the nanoplankton fraction (2–20 µm), seawater (125 ml) was pre-filtered using a 20 µm Nitex mesh sieve and then particles were collected on a 2 µm Nuclepore filter; (2) for the picoplankton fraction (0.7–2.0 µm), seawater (125 ml) was pre-filtered using a 2.0 µm Nuclepore filter and particles were collected on a 0.7 µm GF/F glass fiber filter; and (3) for the whole phytoplankton community, seawater (125 ml) was filtered through a 0.7 µm Whatman glass fiber filter. The amount of chl *a* of the microphytoplankton fraction was obtained by subtracting the chl *a* values of the nano- and picoplankton fractions from that of the whole plankton fraction.

Plankton abundance and biomass

For counting bacterioplankton (pooled bacteria and archaea), protozoans and phytoplankton, 25, 100 and 250 ml of seawater were preserved with a glutaraldehyde 2% (bacterioplankton) or Lugol's (protozoan and phytoplankton) 1% final solution. For bacterioplankton abundance (cells ml⁻¹), 2 ml of seawater was filtered on polycarbonate membrane filters (Nuclepore 0.2 µm), stained with the fluorochrome DAPI (Porter & Feig 1980) and counted by epifluorescence microscopy. Bacterial biomass was estimated using a factor of 20 fg C cell⁻¹ (Lee & Fuhrman 1987). For the enumeration of nanoflagellates, 20 ml seawater from sub-samples were filtered on a 0.8 µm polycarbonate membrane filter and stained with Proflavine (0.033% w/v in distilled water) according to Haas (1982). Sub-samples for diatom counts (250 ml) were preserved in an acidic Lugol's solution (2% final conc.). Sub-samples of 20 to 50 ml were placed in settling chambers for 30 h before analysis under an inverted microscope (Zeiss Axiovert 200, 400× magnification) using the standard methodology (Utermöhl 1958); a carbon:plasma volume ratio of 0.11 pg C µm⁻³ was applied for diatom carbon estimates (Edler 1979).

For counting microzooplankton (dinoflagellates, ciliates and crustacean nauplii), 10 to 30 l of seawater from different depths (0, 5, 10, 25 and 50 m) were filtered gently through a sieve (10 µm mesh size), then concentrated to a final volume of ~100 ml and preserved with buffered formalin (5% final concentration). Carbon:plasma volume ratios of 0.30 and 0.19 pg C µm⁻³ were used for heavily thecate and athecate dinoflagellate forms, respectively (Gifford & Caron 2000), and 0.148 pg C µm⁻³ was applied for ciliates (Ohman & Snyder 1991).

Zooplankton samples were collected by oblique tows using a Tucker trawl net (1 m² catching area, 300 µm mesh size) within the upper 75 m of the water column during day and night sampling. Thus, as euphausiids perform daily migration, their abundance data should be treated with care because they represent a mean of integrated day and night distributions. Samples were preserved in borax buffered formalin (10% final concentration) for later species and stage identification and counting of euphausiids.

POC, DOC, stable isotopes and nutrients

Water samples for the determination of POC concentrations including δ¹³C were collected at some se-

lected oceanographic stations. The samples (0.5 to 1.0 l) were filtered through GF/F filters (pre-combusted for 4 h at 450°C) and stored frozen in liquid nitrogen until later analysis following standard procedures (von Bodungen et al. 1991). The autochthonous POC was estimated as the sum of the phytoplankton, bacterial and microzooplankton carbon. The carbon estimates were based on carbon to plasma volume ratios. The allochthonous POC (POC_{alloch}) was estimated by using a 2-source-mixing model (Bianchi 2007):

$$\% \text{POC}_{\text{alloch}} = \frac{(\delta^{13}\text{C}_{\text{sample}} - \delta^{13}\text{C}_{\text{marine}})}{(\delta^{13}\text{C}_{\text{terrestrial}} - \delta^{13}\text{C}_{\text{marine}})} \quad (1)$$

where δ¹³C_{sample} is the isotopic composition of the sample, δ¹³C_{marine} is the marine end-member from the most oceanic station (Stn 15, 25 m depth) and δ¹³C_{terrestrial} is a riverine/lake end-member value for POC as reported by Lafon et al. (2014).

For DOC determination, water samples were filtered (0.2 µm pore size filters, Swinnex), acidified (300 µl trace metal grade HCl) and stored in 40 ml amber I-Chem vials with septum caps. Prior to analysis, DOC samples were bubbled with CO₂-free nitrogen for 7 min to ensure complete removal of dissolved inorganic carbon.

All POC samples were run on an OI Analytical TIC-TOC Analyzer (model 1030). The first run was to determine the organic carbon concentration, the second for the δ¹³C isotope. The TIC-TOC analyzer was interfaced to a Finnegan Mat Delta Plus isotope ratio mass spectrometer for analysis by continuous flow. Data were normalized using internal standards. Analyses were conducted at the G. G. Hatch Isotope Laboratories at the University of Ottawa, Canada (www.isotope.uottawa.ca/techniques/water.html).

For nutrient analyses (nitrate, ortho-phosphate and silicic acid), 50 ml of water sample were stored at -20°C in acid-cleaned high-density polyethylene bottles and analyzed with a nutrient autoanalyzer (Technicon) according to Atlas et al. (1971).

Fatty acid analyses of *Euphausia vallentini*

After collection, euphausiids were immediately sorted and measured (total length [TL] in mm from tip of rostrum to end of telson), briefly rinsed with deionized water and stored in liquid nitrogen. Fatty acid analyses were performed according to a slightly modified protocol of Kattner & Fricke (1986). Briefly, euphausiids were homogenized with a Potter homogenizer and an internal standard (23:0) was added. The lipids were extracted with dichloromethane/

methanol (2:1, v/v), transesterified to fatty acid methyl esters with 3% sulphuric acid in methanol. The resulting fatty acid methyl esters were analyzed by gas-liquid chromatography (Hewlett Packard 6890 GC) on a 30 m wall-coated capillary column (inner diameter 0.25 mm, film thickness 0.25 μm ; liquid phase DB-FFAP). The compounds were identified with standard mixtures and, if necessary, confirmed by mass spectrometry.

Analysis of biological processes

Nanoflagellate ingestion rate. The bacterivory experiments were performed using the size-fractionation method (Sato et al. 2007, Vargas et al. 2008). Water samples were collected from the fluorescence maximum depth (10 and 15 m). Seawater was size-fractionated into 2 fractions by reverse filtration using polycarbonate filters: $<2 \mu\text{m}$ (mostly bacteria and also cyanobacteria) and $<10 \mu\text{m}$ (mostly bacteria, cyanobacteria, HNF and photosynthetic nanoflagellates). Triplicate batch cultures (500 ml bottles) were incubated on-board for 18 to 20 h in an incubator rack on deck (with running surface seawater to maintain the ambient water temperature of $1\text{--}2^\circ\text{C}$). Initial control bottles were immediately preserved in glutaraldehyde (2.0% w/v in $0.2 \mu\text{m}$ prefiltered seawater) for bacteria and nanoflagellate counts. At the end of the incubation period, sub-samples (20 ml) were taken from all bottles and preserved in glutaraldehyde for cell counts. Following Gifford (1993), grazing rates were estimated by comparing prey growth rates in the presence ($<10 \mu\text{m}$ filtered water sample) and absence ($<2 \mu\text{m}$ filtered water sample) incubation bottles. A minimum of 500 bacteria and 100 nanoflagellates were counted per bottle.

Gross primary production estimation rate. Incubations for GPP were performed with water samples obtained from different depths in the photic zone (2, 5, 10 and 25 m). Water was transferred into 125 ml borosilicate bottles (gravimetrically calibrated) using a silicone tube. Five control bottles, 5 light bottles and 5 dark bottles were used for each incubation depth. Water samples were collected at dawn and were incubated during the entire light period (average light period was 12 ± 1.3 h). Control bottles were preserved at the beginning of each experiment, while the incubation bottles were attached to a fixed mooring system. Dissolved oxygen concentrations were determined according to the Winkler method (Strickland & Parsons 1968), using an automatic Metronom burette (Dosimat plus 865) and visual end-point detection. The variation

coefficient was $0.03 \pm 0.02\%$. Rates of GPP were calculated on a per-hour basis and were extrapolated to a daily rate, considering a constant GPP rate during 12 h natural light period. GPP values were converted from oxygen to carbon using a conservative photosynthetic quotient of 1.25 (Williams & Robertson 1991). GPP discrete-depth estimates were integrated down to 25 m ($\sim 1\%$ light depth), using a polynomial method.

Euphausiid ingestion rate. For *E. vallentini* grazing estimates, animals were collected by slow vertical hauls in the upper 50 m of the water column using a WP-2 net (mesh size $200 \mu\text{m}$) with a large non-filtering cod end (~ 40 l) to avoid damage. Undamaged euphausiids were placed in 5-l acid-washed polycarbonate bottles. These bottles were filled with ambient water with natural food assemblages of microplankton pre-screened through a $200 \mu\text{m}$ net to remove most large grazers. Three control bottles without animals and 3 bottles with 2 to 3 animals each ($17\text{--}20$ mm TL) were placed in an incubator rack on deck (with a top lid maintain a twilight environment) for approximately 19 to 25 h. The seawater incubation was mixed by hand every hour and, to some extent, by the ship's motion. Initial control bottles were immediately preserved with 2% acidic Lugol's solution, and a sub-sample was also preserved in glutaraldehyde. At the end of the incubation, sub-samples were taken from all bottles and preserved in glutaraldehyde for nanoflagellate counts (20 ml) and acidic Lugol's solution (60 ml) for counting of the other cells. Ingestion rates, measured as cell removal, were calculated according to Frost (1972), as modified by Marin et al. (1986). Additional experiments to estimate the fecal-string production rate were conducted in parallel using a similar experimental setup, but reducing the incubation time to ca. 2 h. All feces was gently collected, and the carbon content was measured with a CHN elemental analyzer as used for POC measurements.

Carbon flux. The vertical flux of POC was estimated using surface-tethered, cylindrical sediment traps (122 cm^2 area and 8.3 aspect ratio) deployed at 50 and 100 m water depth for periods of 1 to 1.5 d. Sub-samples were taken for microscopic determinations; for POC, 0.5 to 1.0 l were filtered, stored frozen and analyzed as described above.

RESULTS

Hydrological conditions

The Magellan western zone is characterized by heavy rain, which fluctuates between 2000 and

5000 mm per year, whereas the eastern zone is characterized by light rain, ranging from 200 to 700 mm per year (Panella et al. 1991). Because the western zone consists mainly of steep, medium-sized islands, it has no watersheds to generate large rivers. According to the Chilean national water administration (DGA 2015), the major local rivers are: Río Grande 1, located on Riesco Island with a mean flow of $18 \text{ m}^3 \text{ s}^{-1}$, draining into Otway Sound; and Río Grande 2, located in Tierra del Fuego Island with a mean flow of $23 \text{ m}^3 \text{ s}^{-1}$, draining into the Atlantic Ocean. The eastern zone is flat without important rivers (e.g. mean flow $< 5 \text{ m}^3 \text{ s}^{-1}$). Therefore, the freshwater supply into the local channels and fjords comes from rain, snow, runoff and glacier melting from the Darwin Mountain Range (see Fig. 1 from Aracena et al. 2015 for a detailed distribution of the location of the Darwin Mountain Range and melt water flow).

Oceanographical conditions

A conspicuous gradient in temperature (5 to 8°C) was found along T2, from the Atlantic to the Pacific entrance to the Magellan Strait. By contrast, at Otway Sound (T1), temperature was almost homothermal, ranging between 6.8 and 7.2°C along T1. The lower temperatures were measured from the Atlantic entrance up to the head of Almirantazgo Fjord (6.0 to 6.5°C from Stns 1 to 60), and the highest temperature was found in the Pacific Ocean (Stns 14 and 15), close to the western end of Magellan Strait (8.0°C) (Fig. 2).

In the surface layer (0 – 50 m) of all transects, salinity ranged from 28 to 33 , with the lowest values at the head of Almirantazgo Fjord (Stn 51; Fig. S2 in the Supplement), an area that receives melt water from the Darwin Mountain Range, and the highest values at the western end of Magellan Strait. Dissolved oxygen ranged from 6.0 to 7.5 ml l^{-1} . Nutrients ranged from 0.1 to $12 \text{ } \mu\text{M}$ (nitrate), 0.4 to $0.8 \text{ } \mu\text{M}$ (phosphate) and 0 to $4 \text{ } \mu\text{M}$ (silicic acid), with the lowest values in the Beagle Channel (Fig. 3) and the highest at the western end of Magellan Strait (Fig. 2).

In the deep layer (50 m to bottom) of all transects, salinity ranged from 30 to 33 , being lowest in Almirantazgo Fjord and highest in the western end of Magellan Strait and in Cook Bay. Dissolved oxygen ranged from 5.5 to 7.0 ml l^{-1} , being lowest at the head of Almirantazgo Fjord (Fig. S2) and Balleneros Channel (Fig. S3 in the Supplement) and highest in Cook Bay. Nutrients ranged from 8 to $16 \text{ } \mu\text{M}$ (nitrate), 0.8 to $1.4 \text{ } \mu\text{M}$ (phosphate) and 0 to $8.0 \text{ } \mu\text{M}$ (silicic acid), with the lowest values in the Beagle Channel (Fig. 3) and

the highest values at the head of Almirantazgo Fjord (Fig. S2).

Chl *a* and phytoplankton abundance and composition

Integrated (upper 25 m) chl *a* concentration averaged 206 ± 127 ($\pm\text{SD}$) mg m^{-2} , with a maximum value of $411 \pm 153 \text{ mg m}^{-2}$ along T5, and a minimum of $83 \pm 22 \text{ mg m}^{-2}$ along T1. The chl *a* biomass was dominated by the large size fraction (microphytoplankton $> 20 \text{ } \mu\text{m}$) along all transects (Fig. 4C).

Phytoplankton abundance and composition were recorded along T2 (Magellan Strait) and T5 (Beagle Channel–Cape Horn), where the averaged and integrated phytoplanktonic abundance ranged between 100 and $140\,000 \text{ cells l}^{-1}$ and between $500\,000$ and $4\,000\,000 \text{ cells m}^{-2}$, respectively (Fig. 5). Centric diatoms were dominant with $>70\%$ of the total abundance, while pennate diatoms and autotrophic dinoflagellates contributed considerably only at a few stations in the Magellan Strait and Cape Horn (Fig. 5). The most abundant taxa (mean \pm SD) in the Magellan Strait (T2) and Beagle Channel (T5) were represented by the diatom genera *Chaetoceros* spp. ($13\,700 \pm 16\,100$ and $57\,700 \pm 37\,700 \text{ cells l}^{-1}$, respectively) and *Thalassiosira* spp. ($17\,700 \pm 13\,000$ and $12\,800 \pm 10\,900 \text{ cells l}^{-1}$). Both taxa contributed $27 \pm 21\%$ and $56 \pm 21\%$ at T2 and $72 \pm 16\%$ and $14 \pm 7\%$ at T5 to total diatoms (Fig. 5). Other less abundant taxa (not shown) in the Magellan Strait were the diatoms *Thalassionema* sp. and *Cylindrotheca* sp., as well as the seldom-abundant dinoflagellate taxa *Protoperdinium* spp. and *Ceratium* spp. In the Beagle Channel area, the diatom *Pseudonitzschia* spp. and the dinoflagellates *Gyrodinium* spp. and *Ceratium* spp. were also observed. The overall POC:chl *a* ratio was 66 ± 55 , with a maximum value along T3 (116 ± 105) and a minimum along T5 (25 ± 8 ; Fig. 6).

Plankton biomass (bacteria and microzooplankton)

Integrated (upper 25 m depth) bacterioplankton carbon biomass showed maximum and minimum integrated values along T1 of 301 ± 101 and $169 \pm 36 \text{ mg C m}^{-2}$ and along T2 of 12.1 and $6.8 \text{ } \mu\text{g C l}^{-1}$, respectively. High ANF and HNF biomass were found along T4, with integrated average concentrations of 9.6 ± 15.7 and $25.7 \pm 20.4 \text{ mg C m}^{-2}$, respectively, and a maximum biomass range of 0 – 33 and

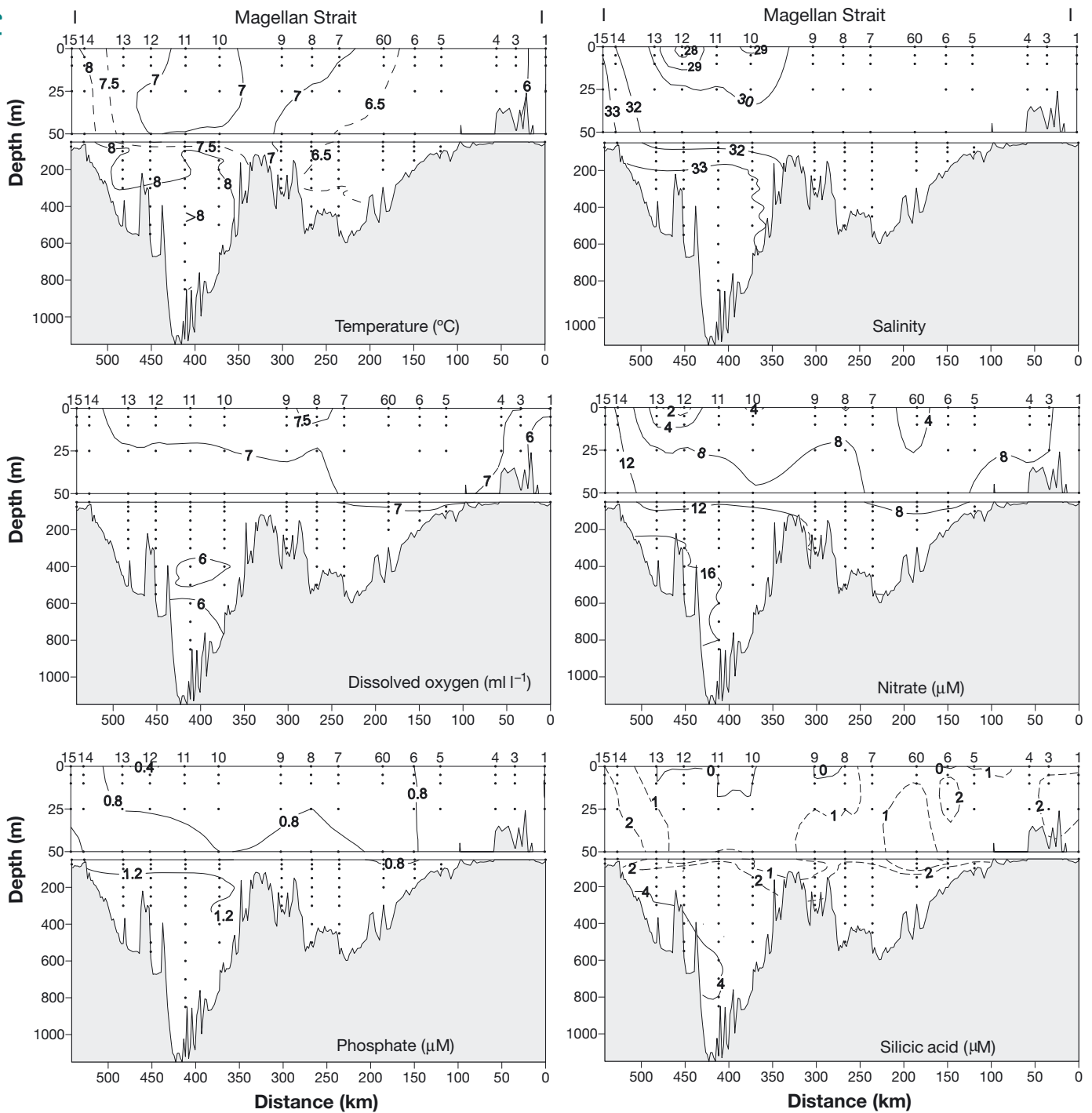


Fig. 2. Vertical distribution of temperature ($^{\circ}\text{C}$), salinity, dissolved oxygen (ml l^{-1}), nitrate, phosphate and silicic acid (μM) along the Magellan Strait transect (T2). Note that the y-axis scale changes at 50 m

$8\text{--}54 \text{ mg C m}^{-2}$ for ANF and HNF, respectively. In addition, low biomasses of ANF and HNF were found along T5 and T1, with 0.4 ± 0.8 and $9.7 \pm 7.0 \text{ mg C m}^{-2}$, respectively (Fig. 4E).

Bacterivory by HNF was empirically determined at the chl *a* maximum depth (10 and 15 m) at Stn 21, and averaged between 42 and 77 bacteria $\text{HNF}^{-1} \text{ h}^{-1}$. Considering a mean bacterial carbon value of ca. 20 fg

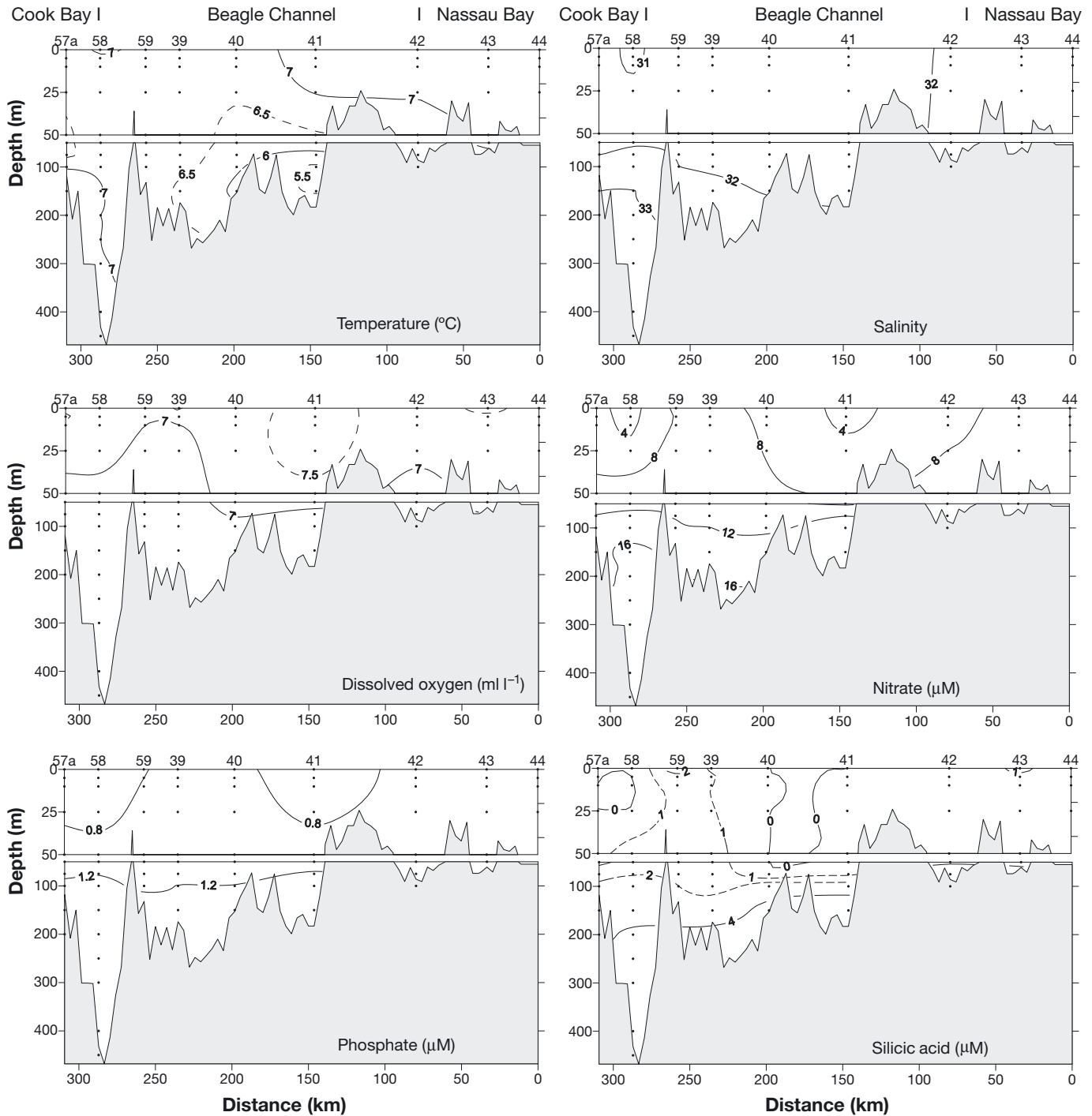


Fig. 3. Vertical distribution of temperature ($^{\circ}\text{C}$), salinity, dissolved oxygen (ml l^{-1}), nitrate, phosphate and silicic acid (μM), along the Beagle Channel to Cape Horn transect (T5). Note that the y-axis scale changes at 50 m

C bacteria^{-1} (Lee & Fuhrman 1987), such a bacterivory rate implies a carbon ingestion rate between 20 and $37 \text{ pg C HNF}^{-1} \text{ d}^{-1}$.

Heterotrophic dinoflagellates, tintinnids, aloricated ciliates and crustacean nauplii were the most important groups of the microzooplankton, with heterotro-

phic dinoflagellates being dominant in terms of abundance and carbon biomass. The maximum and minimum average microzooplankton biomass recorded along transects T1 and T3 were 806 ± 363 and $381 \pm 165 \text{ mg C m}^{-2}$, respectively (Fig. 4F). We saw the highest biomasses of microzooplankton at Stn 25

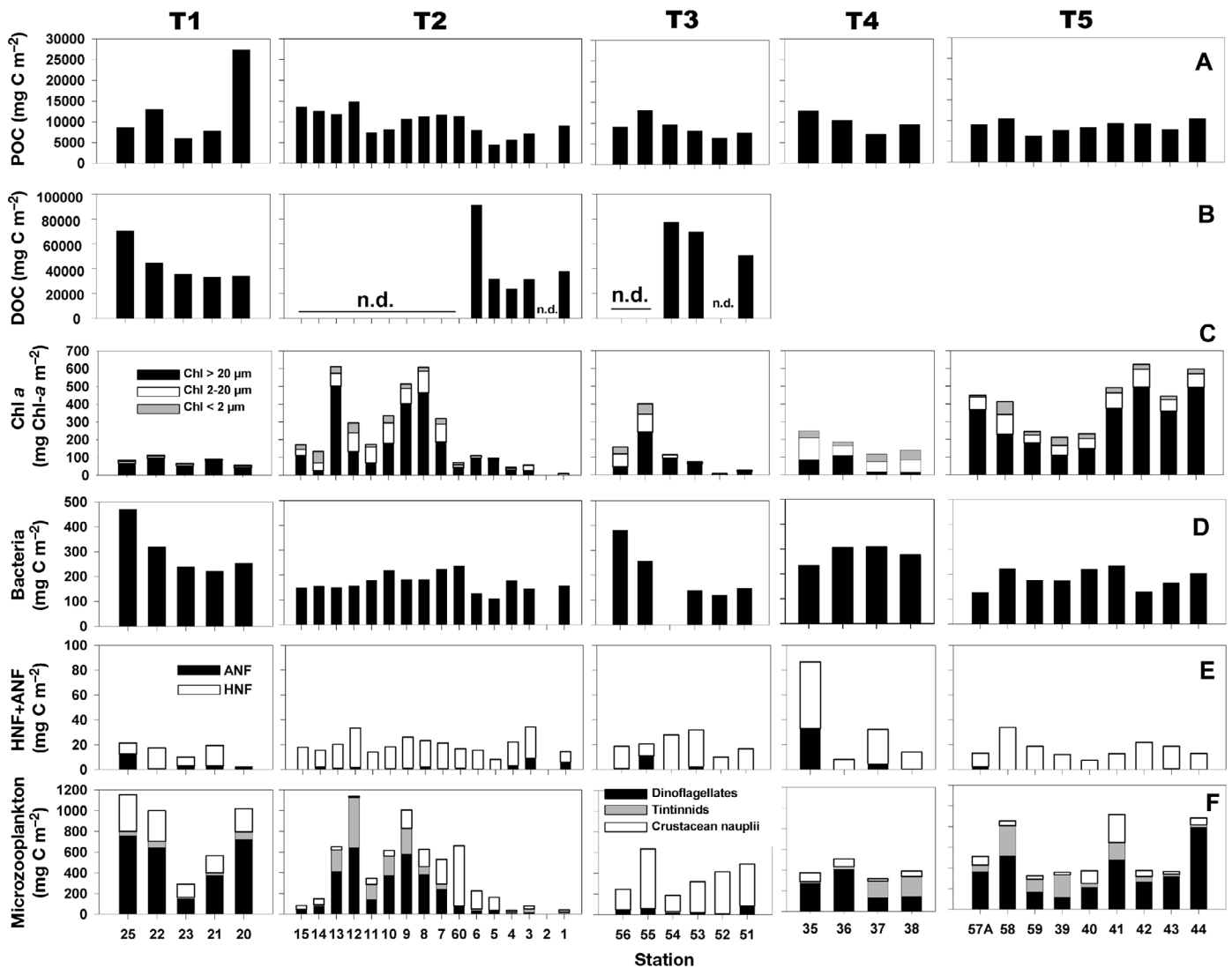


Fig. 4. (A–C) Integrated (upper 25 m water column) concentrations of (A) particulate organic carbon, (B) dissolved organic carbon and (C) fractionated chlorophyll *a* (chl *a*), and (D–F) integrated biomasses of (D) bacteria, (E) heterotrophic and auto-trophic nanoflagellates (HNF and ANF, respectively) and (F) microzooplankton functional groups (thecate dinoflagellates, tintinnids and crustacean nauplii) along the 5 transects sampled in Chilean Patagonia. n.d.: not determined

in T1 (1153 mg C m^{-2}), dominated by thecate dinoflagellates, and Stn 12 in T2 (1139 mg C m^{-2}), dominated by tintinnids and tecate dinoflagellates. Overall, biomasses were lowest at T3 and T4 (average of 391 mg C m^{-2}), and were dominated by nauplii of crustaceans and dinoflagellates, respectively (Fig. 4F).

POC, DOC and stable isotopes

The integrated POC concentrations showed higher values along T2 ($9.8 \pm 3.0 \text{ g C m}^{-2}$) and lower values

along T5 ($8.7 \pm 1.4 \text{ g C m}^{-2}$; Fig. 4A). The total average POC concentration in the upper 25 m of the water column of the study area was $248 \pm 102 \text{ } \mu\text{g C l}^{-1}$ with a range of $81\text{--}773 \text{ } \mu\text{g C l}^{-1}$ ($n = 245$). DOC showed little spatial variability in concentration along transects T1 and T2 ($43 \pm 0.3 \text{ g C m}^{-2}$), and higher concentrations at T3 ($66 \pm 14 \text{ g C m}^{-2}$). The average integrated value for the whole study area was $49 \pm 21 \text{ g C m}^{-2}$ (or $1.7 \pm 1.0 \text{ mg C l}^{-1}$; Fig. 4B). A combination of the highest integrated chl *a* ($411 \pm 152 \text{ mg m}^{-2}$; Fig. 4C) and diatom abundance ($79 \pm 47 \times 10^3 \text{ cells l}^{-1}$; Fig. 5), and lowest POC:chl *a* ratio (24 ± 18) occurred at T5 (Fig. 6).

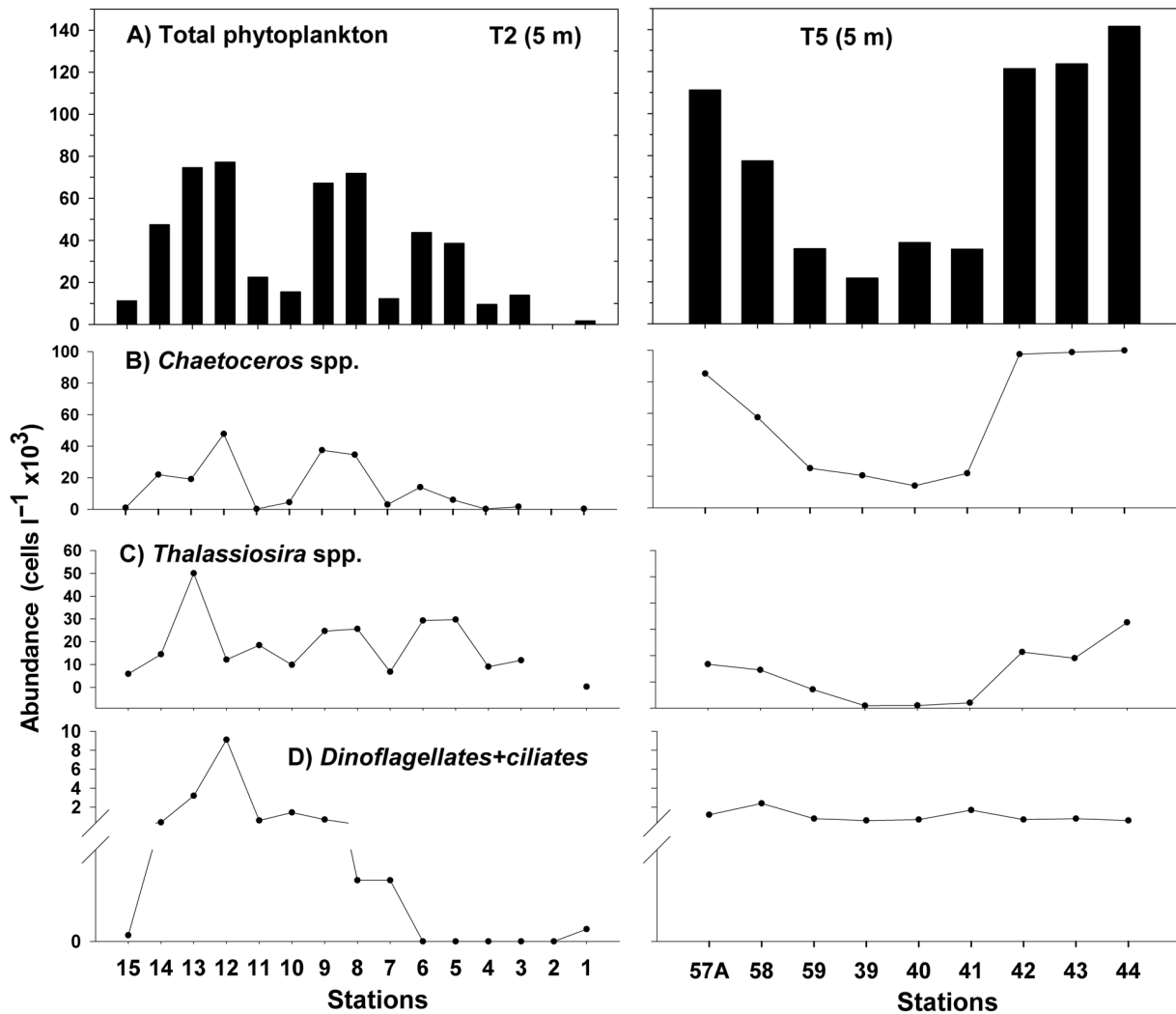


Fig. 5. (A) Total phytoplankton abundance at 5 m depth in thousands of cells per liter, and (B–D) the contribution of the 3 most important functional groups: species of the genera *Chaetoceros* (B) and *Thalassiosira* (C) and total thecate dinoflagellates + ciliates (D) at stations located along the transects of Magellan Strait (T2) and Beagle Channel to Cape Horn (T5)

The largest differences in $\delta^{13}\text{C}$ -POC were found at the surface between Stns 13 and 41, with -18.7 and -25.8 ‰, respectively, and at 25 m depth between Stns 35 and 38, with -18.4 and -26.0 ‰, respectively (Fig. 7B, Table 1). A clear outside–inside fjord gradient in $\delta^{13}\text{C}$ -POC was found at Cook Bay (T4), with values most enriched at Stn 35 (-18.6 ‰) and most depleted at Stns 37 and 38 (-24.6 ‰); at these stations, the relative contribution of allochthonous POC to total POC was on average 14 and 74%, respectively (Table 1). Along T1, $\delta^{13}\text{C}$ at the surface showed little fluctuation between -22.2 and -23.4 ‰ from Stns 25 to 20, a region that also encompassed a significant contribution of allochthonous POC to total POC of 49 to 61% (Table 1).

Along T2, the most enriched value (-17.1 ‰) was found at 25 m depth of the more oceanic station (Stn 15) on the Pacific Ocean side (used as marine end-member) and the most depleted value was found at Stn 41 (-25.8 ‰) in the inner part of the Beagle Channel. Maximum differences were found at Stns 14 and 10 (25 m depth), where the allochthonous POC contributed 17.8 and 48.4%, respectively. Comparing the outermost stations of all transects on the Pacific Ocean side (Stns 14–15, 35, 57A and 43–44), their $\delta^{13}\text{C}$ values at 25 m depth remained similarly high between T2 and T4 (-18.9 to 18.4 ‰) but decreased at the highest latitude stations (Stns 43 and 44) of T5 (-22.0 and -22.2 ‰; Table 1, Fig. 7B).

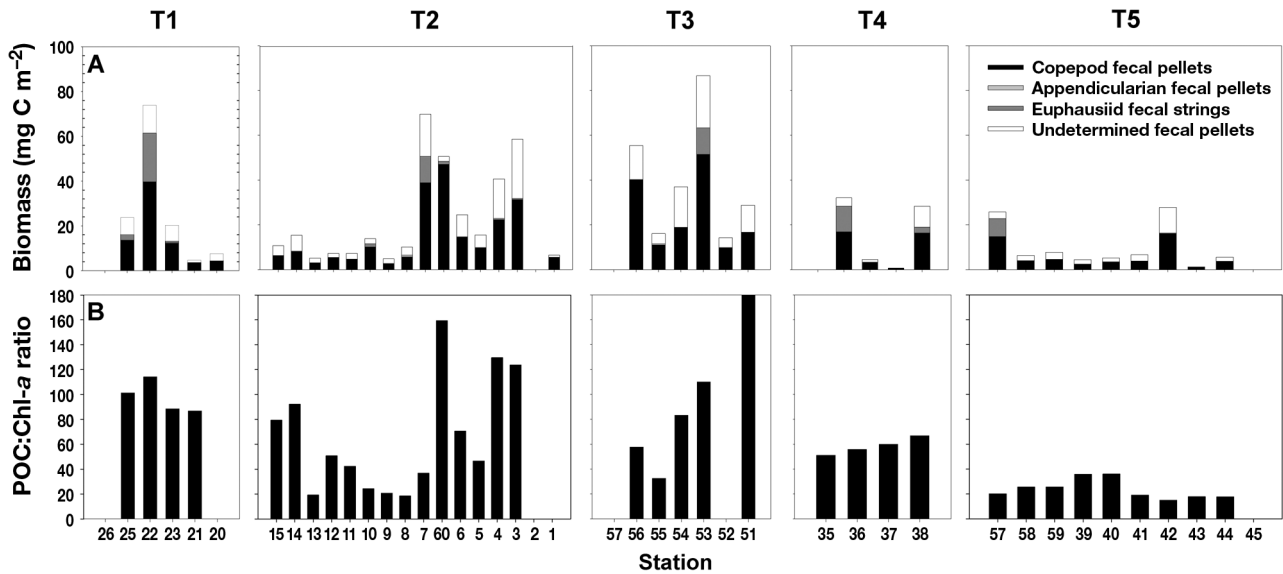


Fig. 6. (A) Integrated carbon-based biomass of copepod, appendicularian, euphausiid and undetermined fecal pellets in the upper 25 m water column of the stations along the 5 transects. (B) Particulate organic carbon to chlorophyll a ratio at the stations located along the 5 transects. At T3 Stn 51, the POC:chl a ratio bar was truncated and represents a ratio of 296

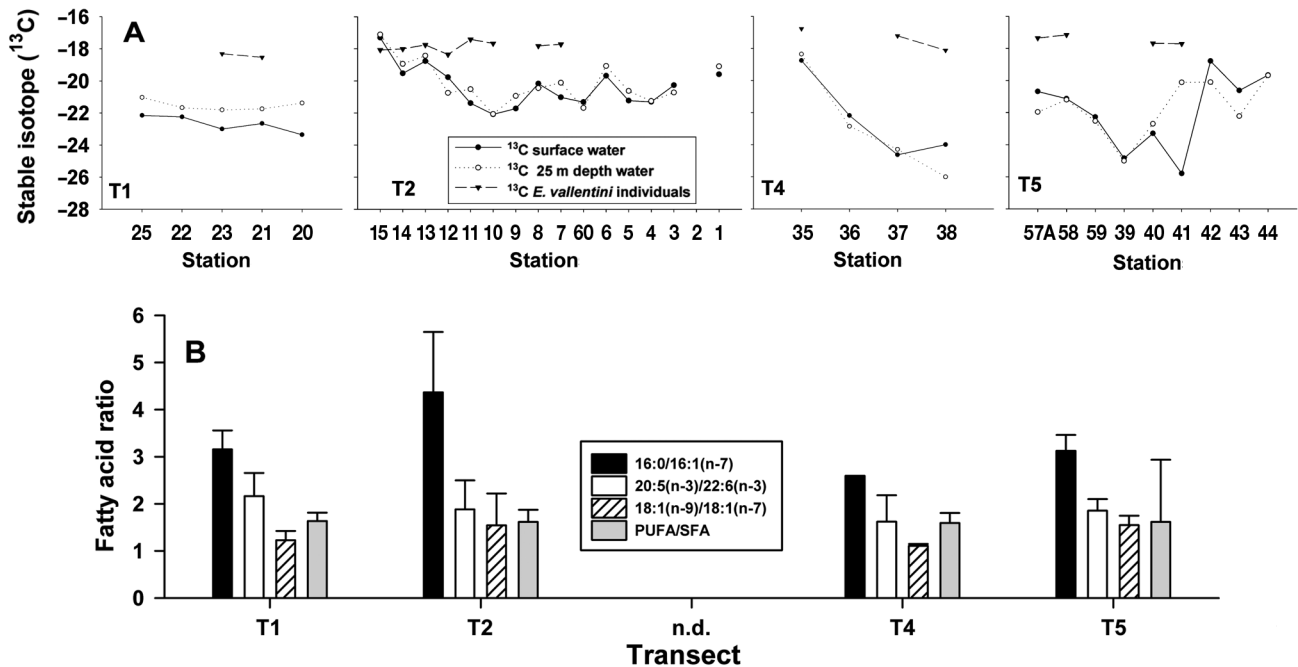


Fig. 7. (A) Stable isotope (¹³C) in water samples collected close to the surface (black circles) and at 25 m depth (white circles) and measured in *Euphausia vallentini* adults/juveniles tissue (1.8 to 2.0 cm TL). (B) Average fatty acid ratios in *E. vallentini* adults/juveniles tissue (1.8 to 2.0 cm TL) in the 5 transects sampled in the study area. PUFA: polyunsaturated fatty acids; SFA: saturated fatty acids. Error bars represent 1 SD. n.d.: no data

Abundance, biomass, feeding rates, stable isotopes and fatty acid composition of *Euphausia vallentini*

The total abundance of adult *E. vallentini* ranged from 0.1 to 9.1 ind. m⁻³ or from 5 to 455 ind. m⁻², integrated over the upper 50 m of the water column

(Fig. 8). The carbon content of individuals from 18 to 22 mm TL averaged $492 \pm 75 \mu\text{g ind.}^{-1}$ ($n = 63$). Grazing experiments showed an average ingestion rate of $92 \pm 79 \mu\text{g C ind.}^{-1} \text{d}^{-1}$, which is equivalent to 18.6% of body carbon (daily ration). The average ingestion of heterotrophic (microzooplankton) and autotrophic

Table 1. Percentage of allochthonous particulate organic carbon (%POC_{alloch}) in suspended POC along the transects sampled in the southernmost part of Chilean Patagonia. For these estimates, we used the following end-members: Riverine/lake ($\delta^{13}\text{C}$ -27.35), marine from Stn 15 at 25 m depth ($\delta^{13}\text{C}$ -17.12)

Transect	Station	$\delta^{13}\text{C}$		POC _{alloch} (%)	
		1 m	25 m	1 m	25 m
1	25	-22.15	-21.03	49.2	38.2
	22	-22.24	-21.68	50.1	44.6
	23	-23.00	-21.81	57.5	45.9
	21	-22.66	-21.75	54.2	45.3
	20	-23.36	-21.39	61.0	41.8
	Mean (\pm SD)				48.8 \pm 7.1
2	1	-19.60	-19.09	24.3	19.3
	3	-20.27	-20.73	30.8	35.3
	4	-21.30	-21.26	40.9	40.5
	5	-21.23	-20.63	40.2	34.3
	6	-19.69	-19.08	25.1	19.2
	60	-21.32	-21.69	41.1	44.7
	7	-21.02	-20.12	38.1	29.4
	8	-20.17	-20.46	29.8	32.7
	9	-21.72	-20.94	45.0	37.4
	10	-22.08	-22.07	48.5	48.4
	11	-21.39	-20.52	41.8	33.3
	12	-19.78	-20.75	26.0	35.5
	13	-18.77	-18.43	16.2	12.8
	14	-19.53	-18.94	23.6	17.8
Mean (\pm SD)				31.5 \pm 11.4	
4	35	-18.76	-18.36	16.0	12.1
	36	-22.18	-22.18	49.5	56.0
	37	-24.63	-24.29	73.4	70.1
	38	-23.99	-26.01	67.2	86.9
Mean (\pm SD)				53.9 \pm 27.0	
5	57A	-20.68	-21.96	34.8	47.3
	58	-21.13	-21.20	39.2	39.9
	59	-22.28	-22.52	50.5	52.8
	39	-24.84	-25.01	75.5	77.1
	40	-23.29	-22.70	60.3	54.6
	41	-25.79	-20.12	84.8	29.4
	42	-18.79	-20.10	16.4	29.2
	43	-20.62	-22.22	34.2	49.9
	44	-19.66	-19.68	24.9	25.1
Mean (\pm SD)				45.9 \pm 19.4	

(phytoplankton) prey was on average 67.4 and 32.6%, respectively. The average fecal-string production rate was $22.5 \pm 11.2 \mu\text{g C ind.}^{-1} \text{d}^{-1}$, equivalent to 24.5% of the ingestion rate.

The $\delta^{13}\text{C}$ signals of the euphausiids were very similar along all transects (Fig. 7B). The most depleted value (-18.5%) was found at Stn 21 (process station in the inner Otway Sound) and the most enriched value (-16.8%) was found at Stn 35, located at the Pacific end of T4.

The fatty acid composition of *E. vallentini* (juvenile and adult individuals) was similar along all transects. Multivariate statistics gave no clear differentiation

according to more oceanic or riverine influenced regions. Highest percentages were determined (in descending order) for 16:0 (21–25%), 20:5(n-3) (23–27%), 22:6(n-3) (12–14%), 18:1(n-9) and 18:1(n-7) (7–11%) and 16:1(n-7) (5–8%) (Table 2). A small difference was found between the stations along T3 and the other transects. This was due in particular to higher proportions of 18:1(n-9) and 16:1(n-7) and lower proportions of 20:5(n-3). The proportions of 16:1(n-7), a typical fatty acid of diatoms, were clearly higher in all samples than that of 18:4(n-3), a flagellate marker. The ratio between 18:1(n-9) and 18:1(n-7), indicative of feeding behavior, also showed only small differences, ranging between 1.2 and 1.6. Odd chain-length fatty acids, indicative of bacterial activity, were also minor, with slightly higher values along T2 and T4.

Productivity, pelagic food web and carbon export flux

Average GPP rates at Stn 21 showed values of $1.5 \pm 0.13 \text{ g C m}^{-2} \text{d}^{-1}$, which was slightly higher than the total microbial community respiration (CR) ($1.1 \pm 0.13 \text{ g C m}^{-2} \text{d}^{-1}$), resulting in a GPP:CR ratio of 1.4 (autotrophic system). The vertical flux of POC at 50 and 100 m depth showed values of 73 and $100 \text{ mg m}^{-2} \text{d}^{-1}$, respectively, where the lithogenic and organic matter fraction fluxes were relatively similar, with 204 and $182 \text{ mg m}^{-2} \text{d}^{-1}$ at 50 m depth, and 215 and $150 \text{ mg m}^{-2} \text{d}^{-1}$ at 100 m depth. The sediment traps collected mainly zooplankton fecal pellets, microphytoplankton and microzooplankton. The dominant type of particles that contributed to the POC flux were zooplankton fecal pellets, with values of 7.9 and $6.3 \text{ mg m}^{-2} \text{d}^{-1}$ at 50 and 100 m depth, respectively (Fig. 9), which correspond to ~95% of the total flux that could be identified by microscopy methods. Fecal pellets from euphausiids, copepods, appendicularians and unidentified, semi-degraded fecal material were recorded, and the amorphous unidentified fecal material predominated with 92 and 97% at 50 and 100 m depth, respectively. This type of fecal material corresponds to what we found in the water column in all transects (Fig. 6, upper panels).

DISCUSSION

The SAAW penetrates the Magellan Strait from the Pacific and Atlantic Ocean sides, although the more prominent sill-constriction at the western side deter-

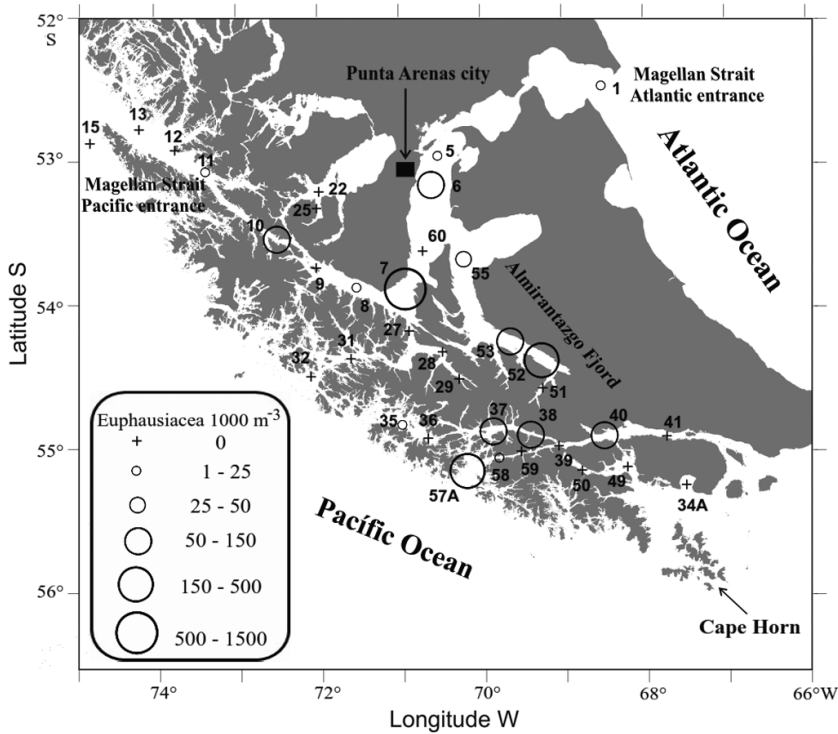


Fig. 8. Average abundance of *Euphausia vallentini* (ind. per 1000 m³) within the study area

ern Reloncaví Fjord (200–600 mg C m⁻³; González et al. 2010).

The composition of POC being on average half allochthonous and half autochthonous, the latter predominated by phytoplankton, suggests a classical spring food web in our study area. The allochthonous and autochthonous proportions were, however, highly variable, in particular along T2, T4 and T5, ranging from 13 to 87% in the upper water column. The presence of rivers and glaciers usually corresponds to areas with intense allochthonous POM input, as along transects around the Darwin Mountain Range (T3 and inner part of T4). This was also evident in the nearby Chiloé and Aysén channels and fjords, where surface sediments contain up to 50% of terrestrial material (Sepúlveda et al. 2011, Silva et al. 2011). In central Patagonia, rivers with freshwater discharges close to 1000 m³ s⁻¹ enter the fjords with a sus-

mines a more conspicuous presence of the Pacific SAAW up to the Beagle Channel (Silva & Palma 2008). In addition, freshwater from glaciers extending all along the Darwin Mountain Range creates an upper (50 m) brackish layer of slightly modified SAAW (salinity of 31–33) in the oceanic region of the fjords and channels and a heavily modified SAAW (salinity of <28–31) in the inner regions and areas closer to the Darwin Mountain glacier.

Particulate and dissolved organic matter

Our average POC concentrations in the upper 25 m of the water column (248 mg C m⁻³) were higher than previous values reported for the Magellan Strait (76 mg C m⁻³, Fabiano et al. 1999; 150 mg C m⁻³, Povero et al. 1996), but were comparable with those from the north-

Table 2. *Euphausia vallentini*. Fatty acid composition (mass % of total fatty acids) averaged for the different transects (T1–T5). Data are means ± SD. n: number of replicates (specimens from different depth ranges and stations). SFA: saturated fatty acids; PUFA: polyunsaturated fatty acids; MUFA: monounsaturated fatty acids. Asterisk indicates that the data are the sum of several isomers

	T1 (n = 21)	T2 (n = 14)	T3 (n = 6)	T4 (n = 37)	T5 (n = 28)
14:0	3.3 ± 0.5	3.0 ± 0.9	2.9 ± 0.4	3.6 ± 0.9	3.0 ± 0.7
16:0	21.4 ± 0.7	22.7 ± 1.6	24.8 ± 1.6	20.9 ± 1.1	21.9 ± 1.4
16:1(n-7)	7.0 ± 1.0	5.4 ± 0.8	8.2 ± 1.3	6.2 ± 1.0	5.9 ± 1.0
16 PUFA	4.3 ± 1.1	4.6 ± 1.5	2.3 ± 0.8	3.9 ± 1.5	4.5 ± 2.1
Odd chain FA	0.2 ± 0.1	1.5 ± 1.8	0.3 ± 0.1	1.6 ± 1.6	0.6 ± 0.6
18:0	2.1 ± 0.3	2.0 ± 0.3	1.7 ± 0.8	1.9 ± 0.3	1.9 ± 0.4
18:1(n-9)	8.1 ± 1.2	8.6 ± 1.1	10.5 ± 1.9	8.7 ± 1.1	9.1 ± 1.6
18:1(n-7)	6.7 ± 0.4	5.7 ± 0.3	6.7 ± 0.5	6.8 ± 0.4	6.5 ± 0.4
18:2(n-6)	0.9 ± 0.3	0.8 ± 0.2	0.7 ± 0.1	1.3 ± 0.2	1.0 ± 0.3
18:3(n-6)	0.3 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.3 ± 0.0	0.3 ± 0.1
18:4(n-3)	1.0 ± 0.5	1.6 ± 0.7	0.9 ± 0.4	1.3 ± 0.3	1.0 ± 0.3
20:1*	0.9 ± 0.2	0.8 ± 0.4	1.3 ± 0.7	1.1 ± 0.3	1.0 ± 0.3
20:2(n-6)	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
20:4(n-6)	0.9 ± 0.3	1.2 ± 0.8	0.6 ± 0.3	2.3 ± 0.4	1.7 ± 0.5
20:4(n-3)	0.3 ± 0.1	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.1	0.2 ± 0.1
20:5(n-3)	26.5 ± 1.7	25.4 ± 2.4	23.3 ± 3.5	22.9 ± 1.8	25.2 ± 1.9
22:1*	0.3 ± 0.1	0.3 ± 0.2	0.6 ± 0.3	0.4 ± 0.2	0.4 ± 0.2
22:5(n-3)	1.3 ± 0.3	1.1 ± 0.2	1.1 ± 0.3	1.1 ± 0.2	1.0 ± 0.2
22:6(n-3)	13.1 ± 3.1	13.6 ± 3.7	12.2 ± 1.8	14.0 ± 2.2	13.9 ± 2.1
SFA	26.7 ± 1.2	27.6 ± 2.2	29.4 ± 1.8	26.4 ± 1.0	26.8 ± 1.5
MUFA	23.0 ± 2.1	20.9 ± 2.0	27.4 ± 3.6	23.3 ± 1.2	22.7 ± 1.4
PUFA	49.2 ± 3.0	49.4 ± 3.3	42.0 ± 5.6	48.2 ± 2.5	49.4 ± 2.7

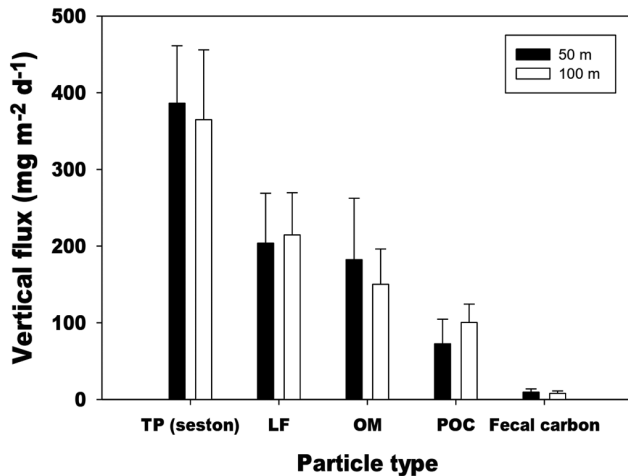


Fig. 9. Total particulate (dry weight) seston (TP), lithogenic fraction (LF), organic matter (OM), particulate organic carbon (POC) and fecal carbon flux as estimated using sediment traps deployed at 50 and 100 m depth at the process station 21. Error bars represent SD

pendent sediment load in the range of 50–100 g m⁻³ and diverse refractory remains, derived from terrestrial vascular plants and forest tree plantations (González et al. 2013). The Magellan Region is devoid of large rivers but is a major glaciated region, which may be an important site of storage and release of organic carbon (Hood et al. 2015). This organic carbon (dissolved and particulate) of allochthonous, mainly glacial origin, and autochthonous, mostly large diatom origin (Turner 2002), seems to set up favorable conditions for the growth of a diverse and abundant microbial community (Gutiérrez et al. 2015). The average integrated bacterioplankton biomass in our study area was similar to that in the Baker and Aysén fjords at 45.3°S (300 mg C m⁻²; González et al. 2011), and nearly half of what was found in the Reloncaví Fjord at 41.4°S (507 mg C m⁻²; González et al. 2010).

The high abundance of HNF and its high bacterivory rate resulted in a removal rate of 50 to 92 mg C of the total bacterioplankton by the HNF community per day, which corresponds to a loss of 24 to 44% of its biomass. Hence, it may be possible that the impact on bacterial production by the HNF bacterivory results in more autochthonous and allochthonous organic carbon from riverine DOC remains in the water column. This DOC may be available to lower trophic levels during winter, when phytoplankton growth is scarce, and then further carrying the terrestrial signal to higher trophic levels (Vargas et al. 2011), although several trophic flows and losses might obscure the signal up to euphausiids (Fig. 10).

The variability of the POC:chl *a* ratio was more related to the highly variable chl *a* than POC concentrations (Fig. 6). The POC:chl *a* ratio was higher along T3, where the large-size phytoplankton (>20 μm) contributed only about one-half to chl *a*, and the minimum was along T5, where these phytoplankton contributed approximately ¾ of the ratio. The predominance of the microphytoplankton (>20 μm) during this study seems to be a recurrent feature during spring, when the increase in solar radiation and sufficient nutrients seem to favor the development of large, chain-forming diatom blooms (genera *Thalassiosira* and *Chaetoceros*) in the northern (González et al. 2011) and southern Patagonian fjords and channels (Iriarte et al. 2001). It is possible that from the Beagle Channel up to Nassau Bay (Stns 40 to 44), the low silicic acid concentration (<1 μM; Fig. 3) might represent the aftermath of a diatom bloom because of the high chl *a* values in the microphytoplankton size fraction in this area (Fig. 4C).

Unexpectedly, low values of phytoplankton abundance and biomass were found at the Pacific and Atlantic entrances of the Strait of Magellan. This may be caused by the strong tidal fluctuation at the entrances (Medeiros & Kierfve 1988), resulting in a high turbidity (Zingone et al. 2011) and a strong mixing of the water column that together limit the development of phytoplankton (Magazzù et al. 1996). In general, low POC:chl *a* ratios have been related to productive areas during spring and autumn: for example, a ratio of 87 during early autumn in the Strait of Magellan (Povero et al. 1996), 108 during August–September in the Skagerrak (Maar et al. 2004) or a range of 29–207 in the coastal region off Concepción (Grunewald et al. 2002). By contrast, high values seem to characterize less productive areas during winter or periods when allochthonous organic matter input (probably loaded with refractory humic-like carbon) increases during the spring–summer period with high freshwater and seston (Table S1) inputs from rivers and glaciers, such as at T3 around the Darwin Mountain Range. Other fjord areas, such as the Reloncaví Fjord and the Interior Sea of Chiloé, located in northern Chilean Patagonia, showed low average values during spring (87) and high during winter (487) (González et al. 2010). DOC and POC from freshwater inputs by rivers and glaciers might support benthic (Connolly et al. 2009) and planktonic communities, making stable isotopes (δ¹³C) a suitable tracer for carbon export from terrestrial systems (West et al. 2006).

In the upper 25 m of the process study station (Stn 21), the average DOC value was almost 5-fold

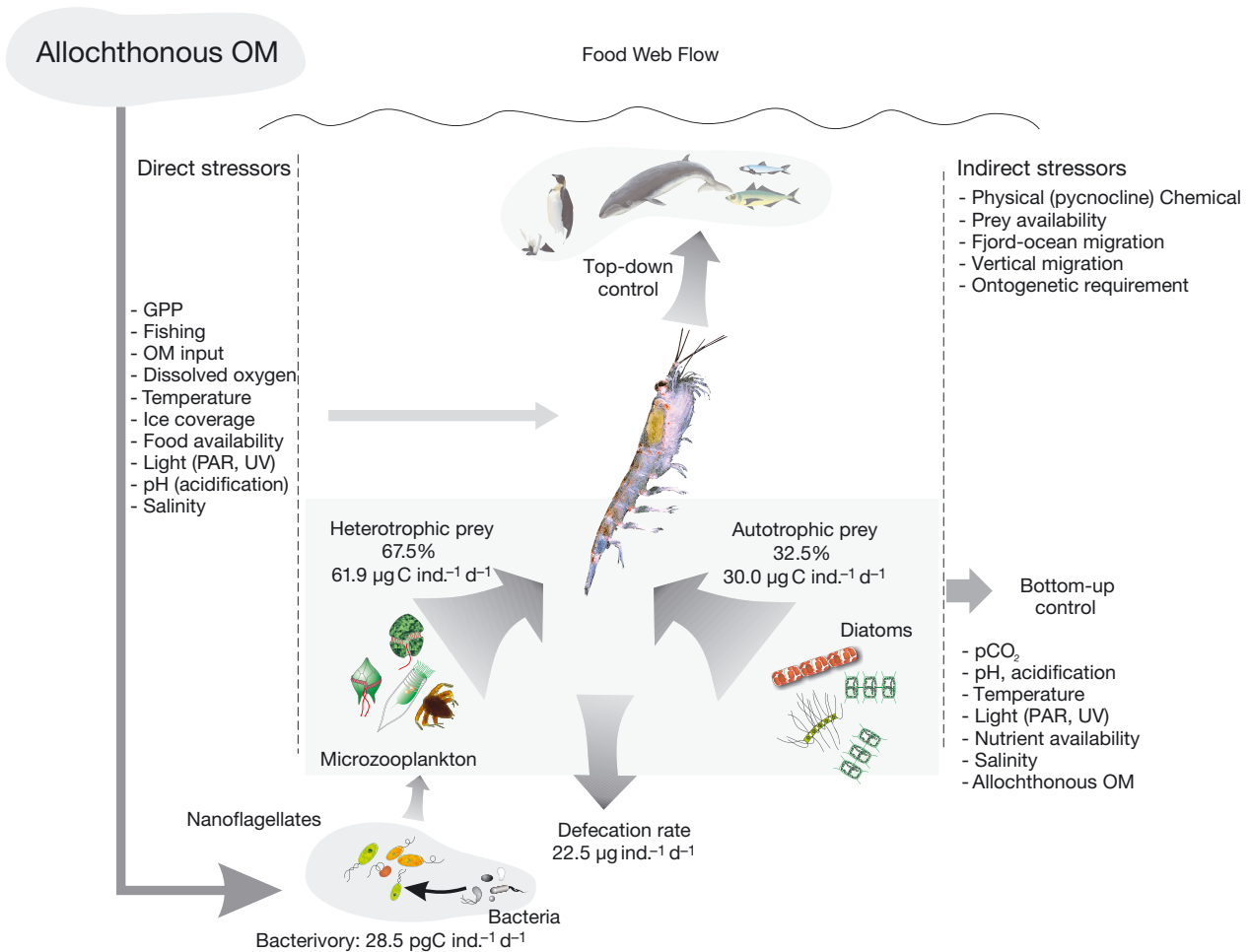


Fig. 10. Trophic flow of *E. vallentini* in Patagonian fjords. Direct stressors that affect the functional and ecological parameters of the krill and indirect stressors that affect the functional parameters of prey (bottom-up control) and predators (top-down control) are shown. GPP: gross primary production; OM: organic matter; PAR: photosynthetically active radiation; UV: ultraviolet

higher than the POC value. The DOC:POC ratios varied widely at the Atlantic side of the Magellan Strait. The ratio increased from 4.2 at the entrance (Stn 1) to 11.5 at the middle of the strait (Stn 6). While POC showed only little changes, DOC increased considerably towards the inner stations. Thus, we infer that the freshwater at stations close to glaciers (i.e. stations along the T3 in Almirantazgo Fjord) introduce additional DOC to the more autochthonous-dominated DOC from the oceanic stations. Smith et al. (2015) hypothesized that fjords from high latitudes might be hotspots of organic carbon input and burial. This supports that the allochthonous input of organic matter into estuarine systems is quantitatively important; however, autochthonous organic matter likely provides more readily available substrates for bacteria (Maranger et al. 2005). Various recent reports suggested that a significant proportion of organic

matter in Chilean fjords is of allochthonous origin, which may become available through the microbial food web to higher trophic levels (i.e. allochthonous DOC – bacteria – HNF – zooplankton) (González et al. 2010, 2011, Vargas et al. 2011, Lafon et al. 2014).

Origin and fate of primary production

Our average values of GPP (Stn 21) during spring were clearly higher than those recorded in late summer for the Magellan Strait (Saggiomo et al. 1994), but similar to estimates for northern Patagonian fjords, such as Reloncaví and Aysén Fjords, highlighting the high productivity of the southernmost part of Chilean Patagonia (González et al. 2010, 2011). High GPP and the dominance of diatoms may result in high vertical POC fluxes. In general, its

seems that the POC export depends more on the variable input of both particulate and dissolved matter from terrestrial systems (Xing et al. 2011), and, as in coastal regions, is uncoupled from the local GPP.

In the Otway Sound (Stn 21), the total particulate material in the sediment traps at 100 m depth was composed of 41 % organic matter. The most conspicuous particles in the traps were fecal pellets from copepods and euphausiids. Thus, the high POC concentrations in the water column as well as in the sediment traps suggest that Patagonian fjords may behave as a net sink for organic carbon during the productive season. This is in line with reports that Chilean Patagonia behaves as a carbon export area during the productive period (Sepúlveda et al. 2011, Torres et al. 2011). A study of the carbonate system along the Magellan–Whiteside–Almirantazgo fjord section carried out during our cruise showed low alkalinity and low pH and high $p\text{CO}_2$ levels (C.A.V. unpubl. data). These levels were associated with low salinity waters in the upper 5 m at Stn 52 in Almirantazgo Fjord, and at Stn 11 (Magellan Strait), mostly associated with the freshwater contribution from ice-melting and/or river runoff. Low $p\text{CO}_2$ surface waters ($<400 \mu\text{atm}$, which means CO_2 undersaturation) were observed mostly along T3 (C.A.V. unpubl. data). This CO_2 undersaturation fits well with the dominance of the large microphytoplankton (Fig. 5) and the high carbon export flux found at Stn 21 (Fig. 9). In general, recent studies indicate that high latitude fjords are responsible for approximately 11 % of total modern global organic carbon burial and may play an important role in climate regulation on glacial–interglacial time scales (e.g. Smith et al. 2015).

Euphausiid ecology

E. vallentini was studied in more detail because it is the predominant euphausiid species in the Patagonian fjord food web and usually accounts for 98 % of total euphausiid abundance in the fjords (Palma & Silva 2004). Thus, it is an important member of the food web, influencing the overall ecosystem. In addition, other species, such as *Thysanoessa gregaria*, *Nematoscelis megalops*, *Euphausia lucens*, *Stylocheiron longicornis* and *S. maximum* have been occasionally found in the Magellan Strait (Zagami et al. 2011). The wide range of abundance of *E. vallentini* we found may be caused by diurnal and nocturnal sampling of this species, which performs conspicuous vertical (circadian) migration. Thus, the analysis of grazing impact of euphausiids (and probably also large cope-

pods) will be treated as minimum and maximum impacts, and considered with caution because their abundance may have been underestimated during daytime trawls due to the active migration.

E. vallentini showed a moderate daily ratio, which corresponded to 18.6 % of body carbon per day, and the fecal pellet production rate corresponded to 24.5 % of the ingestion rate. In contrast, very high assimilation efficiencies of 42–80 % have been reported for *Euphausia superba* (Schnack 1985, Pakhomov et al. 1997), which correspond to 35.8 % of defecated (non-assimilated) carbon. This difference may be due to the fact that *E. vallentini* had a higher assimilation efficiency (less defecation) and/or that very small fragments of euphausiid fecal strings were overlooked and not included for fecal carbon estimates. In addition, our grazing experiments showed that *E. vallentini* removed preferentially heterotrophic prey (67.5 %) over diatoms (32.5 %), where the ingested heterotrophic groups were mainly dinoflagellates (thecate and athecate) as well as loricated tintinnids and crustacean nauplii (Fig. 10). The removed phytoplankton comprised mainly centric diatoms such as the genera *Rhizosolenia*, *Chaetoceros* and *Leptocylindrus*. Ontogenetic changes in the diet of *E. vallentini* suggest an increase in carnivory from juveniles to adults, where the percentage of the autotrophic daily ration decreased from 65–100 % to 3–22 % (Gurney et al. 2002). These authors found a predominantly herbivorous and carnivorous feeding behavior for *E. vallentini* juveniles and adults, respectively, using gut content analysis and stable isotope approaches. Unfortunately, both methods may bias the results as the former technique overestimates the analysis towards hard, mineral-skeleton organisms (e.g. diatoms), and the latter only considers the autochthonous versus allochthonous origin of the food ingested.

Although *E. vallentini* is the predominant member of the euphausiids in this region, the estimated daily grazing impact during the productive season was low, with values up to 3 % of GPP and 0.02 % of the phytoplankton biomass. Estimates of grazing impact exerted by euphausiid in general, and *E. vallentini* in particular, have been low. When we compare grazing impacts of *E. vallentini* with its congeneric species in sub-Antarctic and Antarctic areas, a similar picture appeared. For example, 0.002 % (daytime sampling) and 0.17 % (nighttime sampling) of the phytoplankton biomass was removed daily by *E. vallentini* in the Magellan Strait (Hamame & Antezana 2010), and *E. superba* had a daily grazing impact of 0.2 % on the phytoplankton standing stock (Atkinson & Snýder

1997) and between 0.1 and 14% on primary production in the Southern Ocean (Holm-Hansen & Huntley 1984, Drits & Semenova 1989, Drits & Pasternak 1993). In addition, feeding of *E. valleritini* on terrestrial organic carbon, which might be an additional source, could be almost excluded by the carbon isotope signature. Both were clearly different, indicating the presence of terrestrial (allochthonous) carbon in the water column, but only a very low ingestion by *E. valleritini*.

Another way to investigate the diet of *E. valleritini* is through its fatty acid composition. So far, the lipids of this euphausiid have not been studied. The composition was clearly dominated by the fatty acids belonging to the phospholipids, the major membrane constituents. *E. valleritini* stores lipids in the form not of wax esters but probably of triacylglycerols, which is comparable to *E. superba* but different to many other euphausiids and copepods, which also or almost exclusively store wax esters (Falk-Petersen et al. 2000, Lee et al. 2006). Thus, the fatty acid composition of *E. valleritini* (present study) and that of *E. superba* (Hagen et al. 2001) was dominated by 16:0, 20:5(n-3) and 22:6(n-3). In the older stages of both species, the so-called fatty acid trophic markers 16:1(n-7) for diatoms and 18:4(n-3) for flagellates were not abundant, and thus they are only of limited use to reveal prey preferences. Because the proportions of the 16:1(n-7) fatty acid were clearly higher than those of 18:4(n-3), an ingestion of diatoms seems to be more plausible (Hagen et al. 2001). However, this is in contrast to our experimental results, which showed that *E. valleritini* ingested more heterotrophic prey (mainly dinoflagellates) than diatoms. The higher proportions of 18:1(n-9) are indicative of omnivorous and carnivorous feeding (Dalsgaard et al. 2003), probably on tintinnids and larval stages of copepods, which will indeed also influence the fatty acid composition. In addition, the 18:1(n-9) to 18:1(n-7) ratio also suggests a dominance of carnivory (Graeve et al. 1997, Cripps et al. 1999, Mayzaud et al. 1999, Cripps & Atkinson 2000), as the (n-9) isomer of 18:1 is a common fatty acid in metazoans (Falk-Petersen et al. 2000). The very low abundances of 20:1 and 22:1 fatty acids suggest that herbivorous copepodites and adults of calanoid copepods were not important prey (Hagen et al. 2001). The polyunsaturated fatty acid 22:6(n-3) has also been found to be abundant in fish (anchoveta) eggs (Castro et al. 2010) in times of increased dinoflagellate abundance. The presence of this fatty acid in *E. valleritini* (Table 2) suggests an ingestion of these type of eggs by *E. valleritini*, similarly to *E. mucronata* predation on anchoveta eggs in the Humboldt Current off central-northern Chile (Krautz et al. 2007), being an addi-

tional reason for fish mortality. In contrast, the fatty acids with a terrestrial signature, such as 18:2(n-6) and 18:3(n-3) (Harwood & Russell 1984, Dalsgaard et al. 2003), were very minor in *E. valleritini*, on average less than 1% (Table 2). The small proportions of odd chain-length fatty acids reveal that bacterial-derived material had no influence on the lipids of *E. valleritini*, and hence is not an additional food source.

The fatty acid composition confirms that in this type of fjord, subjected to a large freshwater and terrestrial input from rivers and glaciers, allochthonous detritus is weakly linked with the local pelagic food web. This situation has been found in different types of rivers and estuaries worldwide (Müller-Solger et al. 2002, van den Meersche et al. 2009, Delong & Thorp 2006, Martineau et al. 2004, Sobczak et al. 2005). The weak terrestrial signal in euphausiids, using stable isotopes and fatty acid fingerprints as proxies, probably results from a specific selection of autochthonous carbon prey and/or because terrestrial material is inefficiently consumed by *E. valleritini*. However, it seems more likely that *E. valleritini* avoids feeding on detrital material in general and on organic matter of terrestrial origin in particular. This results in a very weak flow of terrestrial organic matter towards upper trophic levels (Fig. 10). Even though the interaction between photochemical and biological processes might allow bacterial degradation of terrigenous DOM from the coastal environment (Miller & Moran 1997), the subsequent flow through the microbial food web only enables a minor percentage to reach medium trophic levels (such as euphausiids). The utilization of autochthonous organic matter as a main food source might be also favored by the reported presence of a pigment thin-layer formation, dominated by diatoms and dinoflagellates, in Otway Sound (Ríos et al. 2016), and the high abundance of microzooplankton (Fig. 4F). The high HNF bacterivory rate, and the important role exerted by heterotrophic dinoflagellates, both as prey for euphausiids (Fig. 10) and as diatom grazers (Carreto et al. 2016), highlights the importance of the microbial food web. In general, because of the high complexity of the food web, more information from integrative studies on end-to-end food web characteristics and organic carbon export in Patagonian fjords and channels is required. In this context, direct and indirect stressors, as well as top-down and bottom-up controls, would affect trophic flow and organic matter export (Fig. 10). The high variability in temporal and spatial physical processes and biological interactions would require a combination of tools and scientific studies to be able to capture that variability.

Overall, *E. vallentini* plays an important role in Patagonian fjords and channels, being able to remove a wide range of prey sizes that covers nanoplankton to microzooplankton and phytoplankton (Fig. 10). *E. vallentini* has been reported as the dominant prey found in guts of a wide range of predators such as myctophid and nothotenid fishes, and also prey for several species of penguins and whales (Perissinotto & McQuaid 1992, Ridoux 1988, Gibbons et al. 2003, Hucke-Gaete et al. 2004, Hamame & Antezana 2010). In summary, the trophic role of *E. vallentini* did not differ from that of its congeneric species *E. mucronata* from the Humboldt Current System of the Eastern South Pacific or from that of *E. superba* in the Southern Ocean. All of them share the condition of 'key species' because they constitute a major carbon and energy flow from lower to higher trophic levels and are important vehicles of POC flux to deeper layers of the ocean.

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