

Short-term changes in the plankton of a highly homogeneous basin of the Straits of Magellan (Paso Ancho) during spring 1994*

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SUMMARY: Changes in nutrients, chlorophyll and zooplankton were followed for 11 d in a basin of the Straits of Magellan (Paso Ancho), characterized by a homogeneous water column during a spring event defined by a drastic change in wind stress and direction. Conditions hardly seemed conducive to a phytoplankton bloom. Initial conditions were characterized by SW gales, low nutrients as well as by *Chaetoceros* spp. and *Thalassiosira* spp. dominated phytoplankton. Wind switched abruptly to calm-weak northerlies by the middle of the study period, a subsurface chlorophyll peak developed and extended to the end of the study while nitrates decreased. Zooplankton was dominated by copepods, nauplii and a diverse meroplankton assemblage. Zooplankton composition was rather uniform, except for diel changes in some taxa. Gut contents of zooplankton size fractions (including *Euphausia vallentini* as the largest fraction) were measured. Grazing rates accounted for 0.5 % of the available chlorophyll. Phytoplankton blooming may be explained by transient water stratification resulting from the relaxation of wind stress and eventual retention of the phytoplankton in the photic layer. Minor variability in zooplankton implied the existence of a permanent and distinct assemblage in a strongly homogeneous environment.

Key words: Estuaries, homogeneous water column, bloom, size fraction, zooplankton grazing

RESUMEN: CAMBIOS DE PEQUEÑA ESCALA EN EL PLANCTON DE UNA CUENCA MUY HOMOGÉNEA DEL ESTRECHO DE MAGALLANES (PASO ANCHO) DURANTE LA PRIMAVERA DE 1994. – Se siguieron los cambios en nutrientes, clorofila y zooplancton durante 11 días en una cuenca del Estrecho de Magallanes (Paso Ancho), caracterizada por una columna de agua homogénea durante un evento de primavera definido por un cambio drástico en la dirección y velocidad del viento. Las condiciones no permitían prever una proliferación del fitoplancton. Las condiciones iniciales fueron de ventarrones del SW, bajos nutrientes y fitoplancton dominado por *Chaetoceros* spp. y *Thalassiosira* spp. El viento cambió abruptamente a calma y vientos débiles del Norte cerca de la mitad del período de estudio, se desarrolló un máximo subsuperficial de clorofila que perduró hasta el fin del estudio, mientras que los nitratos disminuyeron. El zooplancton estuvo dominado por copépodos, nauplii y un conjunto diverso de meroplancton. La composición del zooplancton fue uniforme, excepto por los cambios diurno-nocturnos de algunos taxones. Se midió el contenido estomacal de fracciones de tamaño del zooplancton (la fracción mayor correspondió a *Euphausia vallentini*). Las tasas de ingestión alcanzaron al 0.5% de la clorofila disponible. La proliferación del fitoplancton puede explicarse por una estratificación transitoria de la columna de agua debida a la relajación del viento y la consecuente retención del fitoplancton en la capa fótica. La escasa variabilidad del zooplancton implica la permanencia de un conjunto característico en un ambiente homogéneo.

Palabras clave: Estuarios, columna de agua homogénea, proliferación algal, fracciones de tamaño, ingestión del zooplancton.

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INTRODUCTION

Different factors must generally work together to produce a phytoplankton spring bloom in shelf and open ocean environments. Increasing radiation, sufficient nutrients, diminished grazing and the formation of a pycnocline to ensure that turbulence does not persistently transport cells out of the photic zone (Sverdrup, 1953) are determining factors. In temperate and boreal latitudes however, blooms can occur in non-stratified waters as well (Eilertsen, 1993), and can even take place in late winter, in absence of wind-induced vertical mixing when light penetration is deep (Townsend *et al.*, 1992).

Alternatively, when winds of short duration mix dividing cells below the compensation depth, a sequence of minor unsuccessful blooms, and a delay or a lengthening of the time period for spring bloom development may occur (Wassmann *et al.*, 1996). Variability in the wind regime combined with variability in solar radiation may result in changes of water column stratification within hours-days, and consequently either reinforces or disrupts the development of a phytoplankton bloom (Mann and Lazier, 1991).

Paso Ancho is the largest intermediate basin between the Pacific and Atlantic entrances of the Straits of Magellan. The presence of obstructive sills or shallow shelves and horizontal narrows in both

entrances to Paso Ancho likely isolate the plankton assemblage there (Antezana, 1999). Complete mixing of the water column in this basin in spring (Panella *et al.*, 1991; Figueroa and Yuras, 1996) has been associated with persistent and strong westerly winds and tidal currents (Magazzù *et al.*, 1996), abundant phytoplankton, and a much lower proportion of picoplankton in spring than summer through the Straits of Magellan, specially in Paso Ancho in Spring 1989 (Magazzù *et al.*, 1996). At the time of the RV "Victor Hensen" cruise in the middle of the austral spring, the water column was completely homogeneous and net phytoplankton was dominated by the chain-forming diatoms *Chaetoceros* spp. and *Thalassiosira* spp., which suggested that spring blooming conditions were occurring.

The first objective of this work was to describe vernal conditions for the development of a spring bloom in a homogeneous basin where an abrupt change in the wind regime took place. Abrupt changes in the wind conditions often determine the occurrence of oceanographic events leading to significant changes in phytoplankton production.

The second objective of this work was to estimate the relative impact of zooplankton grazing over the phytoplankton biomass. Rather than analyze the day to day changes in grazing rates during this wind-induced event, attention was focused on changes in composition and abundance of the zoo-

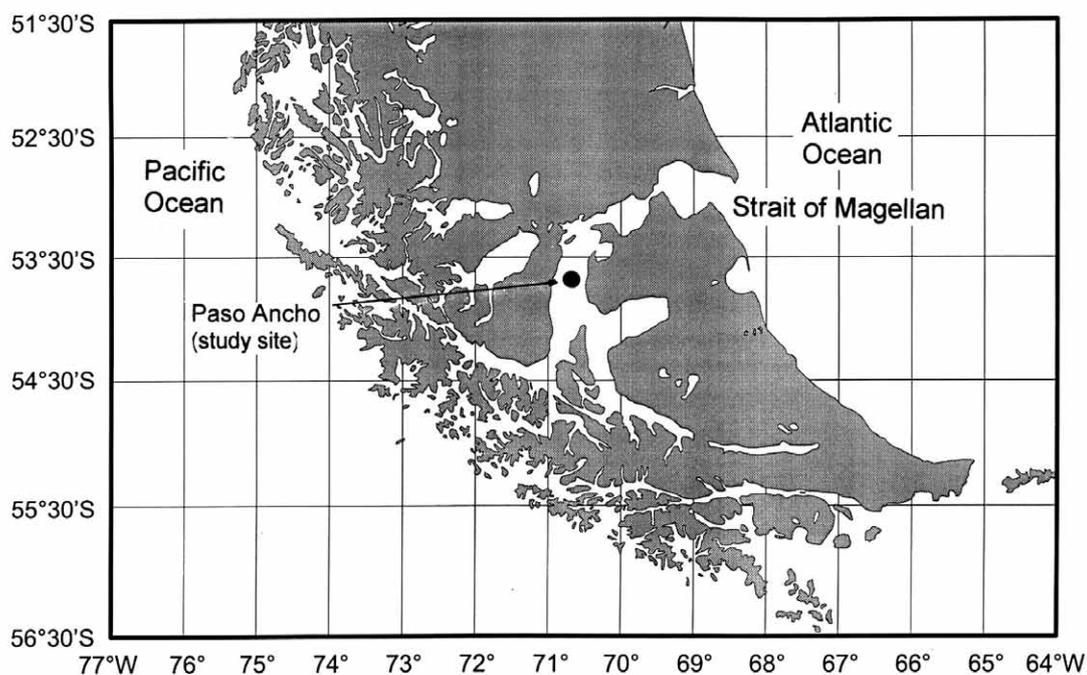


FIG. 1. – Location of the study site.

plankton assemblage, and the partitioning of the grazing effect among its size fractions.

MATERIAL AND METHODS

The study site was located in the middle of Paso Ancho (Fig. 1), the largest basin of the Straits of Magellan extending for ca. 90 km in an approximately north-south direction in the intermediate passage between the Pacific and the Atlantic entrances. Except for the immediate west coast, the entire basin is fully exposed to strong winds during most of the year and particularly in spring and summer; gales over 15 msec^{-1} are not uncommon (Santana, 1991). The bottom profile showed maximum depths in the southern sector (300 m) decreasing toward the northern sector (100 m) and beyond where a shallow shelf (30-50m) extends onto the Atlantic (Antezana *et al.*, 1992).

A homogeneous water column is a typical feature of Paso Ancho in the spring and summer (Budillon *et al.*, 1996) with the occasional occurrence of a shallow lens of slightly warmer and less saline water (Panella *et al.*, 1991). Predominant semidiurnal tides encompassing the whole water column, in conjunction with atmospheric forcing (wind) and the geomorphology of Paso Ancho determine a clockwise gyre (Budillon *et al.*, 1996).

The study site at the reference station had a bottom depth of 120 m; it was repeatedly occupied for a period of 11 days in the spring of 1994 on board R.V. "Victor Hensen" (Arntz and Gorny, 1996). The water column to 50 m was homogeneous, as recorded in an hour to hour variability study carried out during the same cruise where temperature (6.08 to 6.18 °C) and salinity (30.73-30.75 psu) varied little (Figuroa and Yuras, 1996). Vertical profiles of light intensity were obtained near midday (11 hr-14 hr) using a LiCor submersible spherical quantummeter. Niskin bottle casts at fixed depths of 0, 2, 5, 10, 15, 50 m followed. Water samples were drawn for determination of photosynthetic pigments, nutrients and phytoplankton taxa. Additional phytoplankton surface hauls were made with a conical net 70 μm mesh size for 5 minutes to determine a qualitative rank order of abundance of major taxa.

Photosynthetic pigments were fluorometrically measured on board from GF/F filtered sea water (50 cc) and extracted for 12-24 hr in 90% acetone. Water samples for nutrient determinations (nitrates and silicates) were deep frozen, stored at -40°C for 4

months and analyzed on an autoanalyzer Alpkem on board R.V. "Italica", by standard procedures (Catalano and Goffart, 1991). Temperature, salinity and depth profiles were occasionally done and observed on deck, using a CTD SeaBird (SBE19 / MKII). Unfortunately, most CTD data were lost during processing.

Wind velocity and direction were estimated every hour by ship officers according to the Beaufort scale (Bft) which, although qualitative, provided a reliable trend of wind stress during the study period. Rough conditions prevailed during the first half of the study period with winds reaching 9 Bft at times, which often kept the ship out of port; calmer conditions prevailed during the second half of the study (Arntz and Gorny, 1996).

An oblique net haul 0-50 m with a Bongo net 70 cm mouth opening and 300 μm mesh size and provided with a digital flow-meter followed and ended the station. Samples were preserved in buffered formaline, major taxonomic groups were counted under the stereomicroscope and densities were determined and standardized to filtered water volume.

Zooplankton gut contents were measured every 1-2 hr for 24 hr on October 27th. Immediately upon retrieval and washing of the Bongo net, sea water saturated with carbon dioxide was poured into one of the plankton samples to anesthetize the animals; zooplankton was then wet sieved through a stack of strainers with 2000 μm , 1000 μm , 500 μm and 200 μm meshes. Gut pigments on these 4 size fractions (average 2500 individuals for the smallest size fraction, 800 individuals, 100 individuals and 20 individuals for the medium, large and very large size fractions, respectively) were determined on board after 12-42 hr extraction in acetone 90% following standard procedure (Mackas and Bohrer, 1976; Dagg and Wyman, 1983) using a Turner Design Fluorometer. Fluorescence was computed as the sum of chlorophyll a and phaeopigments and expressed as nanograms of pigments per individual. The sample from the other cod end was preserved in buffered formalin (10%) for estimation of densities of the major groups. Samples were classified in day and night according to sunrise and sunset times, ignoring samples from transition periods.

Gut evacuation rate of *Euphausia vallentini* Stebbing 1900 was estimated from an evacuation constant obtained on board. Freshly caught individuals (20) were sorted out at random, transferred to filtered sea water and kept on a covered plastic container for successive sampling on deck. Replicate

samples of 3 individuals were obtained at time 0, every 10 during the first 20 minutes, every 20 minutes during the first hour and every hour during the following 3 hours. Samples were transferred to 90 % acetone and kept refrigerated (-10°C) at dark for extraction and further fluorometrical analysis. Gut evacuation rate of copepods was not measured on board, but instead, an evacuation constant was adopted from Morales *et al.* (1991), who found that evacuation was similar for all size copepods and was not size dependent.

Ingestion rate is the product of gut pigment ($\mu\text{g chlor ind}^{-1}$) and the evacuation constant (hr^{-1}). Diel ingestion rate was estimated as the product of the evacuation constant and the mean gut content over 24 hr for size fractions with no or minimal diel changes in gut content. For size fractions with significant diel changes in gut content (Mann Whitney U test; $p < 0.05$) diel rate was estimated using a mean value of gut content for night samples over 6 hr and for day samples over 18 hr. The consumption rate of a given size fraction assemblage ($\mu\text{g chlor m}^{-3} \text{d}^{-1}$) is defined as the product of individual diel ingestion rate ($\mu\text{g chlor ind}^{-1} \text{d}^{-1}$) and the density of individuals in the ocean (ind m^{-3}). Furthermore, grazing impact of the zooplankton assemblage over available

chlorophyll ($\% \text{ chlor d}^{-1}$) is a measure of the proportion of the available chlorophyll removed by grazers. It was estimated as the ratio of the diel consumption rate and the mean chlorophyll concentration in the 0-50 m layer (mg chlor m^{-3}).

RESULTS

Trends in chlorophyll, nutrients, wind and photic layer

Vertical distribution of chlorophyll (Fig. 2a) was rather homogeneous (*ca.* 1-2 mg m^{-3}) throughout the water column down to 50 m during the first half of the study period, October 23th-27th. On October 28th a subsurface maximum of 3.1 mg m^{-3} appeared at 2 m. In the next sampling period (November 1st) a more pronounced subsurface maximum (2.5-6.6 mg m^{-3}) layer extended between 0 m and 15 m with the core at 10 m. This chlorophyll maximum layer persisted until the end of the event with even higher values (4.3- 6.0 mg m^{-3} between 10 m and 15 m). Chlorophyll concentration decreased with depth, yet values as high as *ca.* 2 mg m^{-3} occurred at 50 m depth during most of the study period.

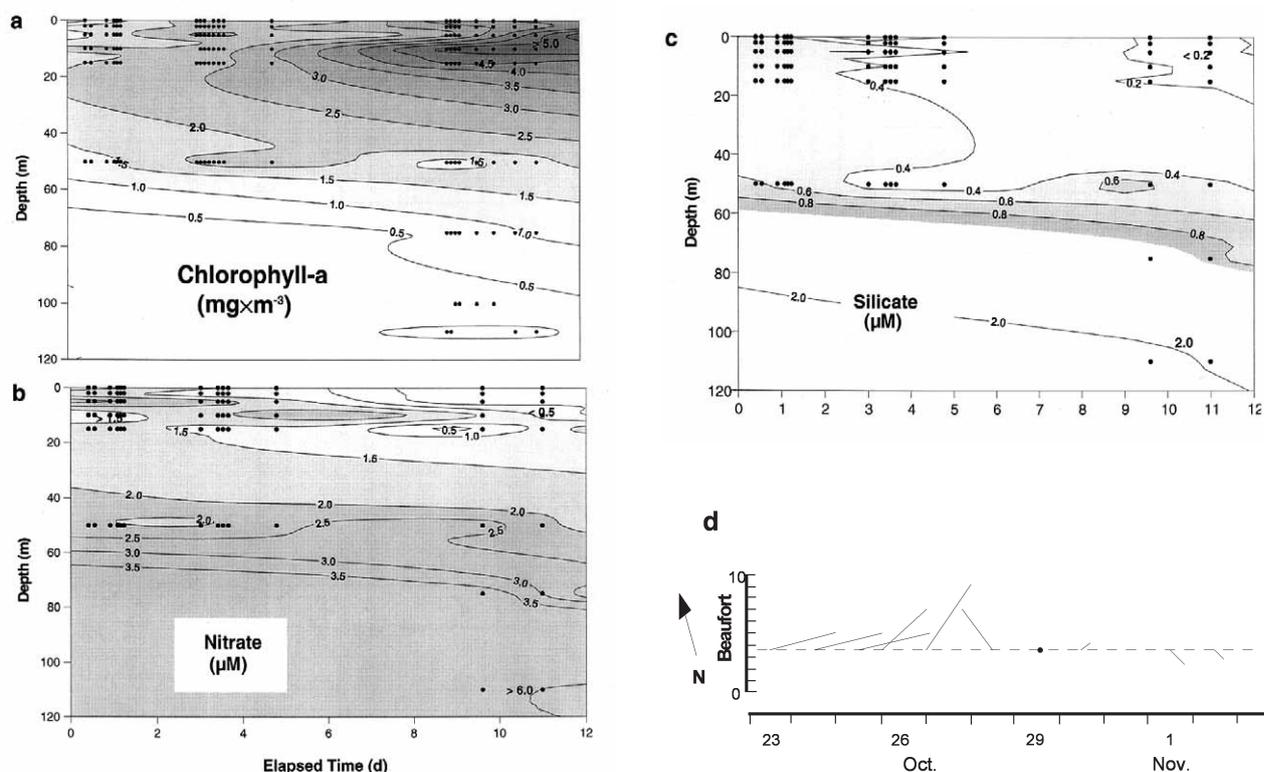


FIG. 2. – Short - term changes in Paso Ancho. a.- Chlorophyll a in mg m^{-3} ; b.- Nitrates in μM ; c.- Silicates in μM ; d.- Wind velocity and direction in daily average Beaufort units (Bft).

Integrated chlorophyll in the 0-50 m layer ranged between 60 to 130 mg m⁻² during 23-28 October and 138 and 228 mg m⁻² during 1-2 November. Significant differences were found between the first and second half of the period (Mann Whitney U test p=0.001).

Nitrate concentration (Fig. 2b) was lower than 1.5 μM in the upper 15 m and increased gradually with depth to 6.9 μM at 110 m. During the study period, nitrates varied inversely with chlorophyll, although replication of measurements was much lower in the last part of the study period. During the first half of the event ending on 28 October, a slight maximum was encountered at 5-10 m depth. Later, nitrate concentration in the 0-15 m layer decreased to 0.1-1.9 μM with a median value near 0.1 μM. The deeper 50-110 m layer had concentrations of 2.0-6.9 μM. Integrated nitrates for the 0-50 m layer ranged between 60 and 123 μmol m⁻² in the first half of the event and between 64 and 73 μmol m⁻² in the last part of the study period, when nitrates became more

stratified. However, integrated nitrates did not differ significantly between the first and the second phase (Mann Whitney U test p= 0.16).

Silicates were very low (less than 1 μM regardless of the time and depth) and were clearly depleted in the upper 15 m of the last 2 days of the study period (Fig. 2c).

The wind regime (Fig 2d) as typical of spring was dominated by westerlies at the beginning of the event (6-7 Bft), turned into south-westerlies (4-8 Bft) on October 27th, but abruptly decreased in intensity (2 Bft) and changed directions from the morning to the evening of October 28th; winds finally changed to much weaker northerlies (0-2 Bft) during the second part of the study.

Surface light intensity during the period changed considerably (ranging between 488 and 1100 μmol m⁻² sec⁻¹) but with no clear trend. Most days were cloudy or partially cloudy; sunny bright days were scattered throughout the study period. Light extinction was measured on October 21th, 27th, 29th and

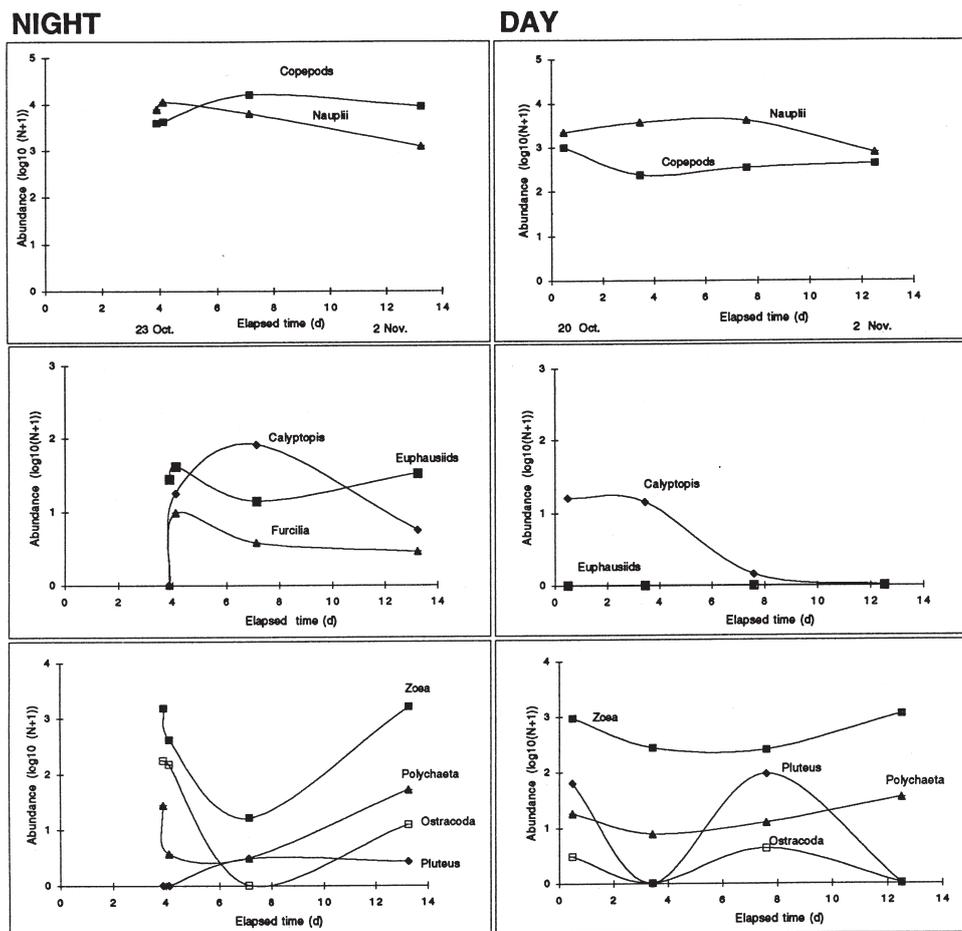


FIG. 3. – Short-term changes of dominant zooplankters from day and night sampling (n= number of individuals per 100 m³).

TABLE 1. – Day-night differences in density of dominant zooplankton groups in Paso Ancho during a short event in spring 1994. Probabilities for two-tailed Mann-Whitney U-test. (Day samples n=9, night samples n=6).

Groups	Probability	Significance
Amphipoda	0.007	s
Copepoda	0.001	s
Euphausiids	0.001	s
Furcilia	0.035	s
Pluteus	0.046	s
Calyptopis	0.162	ns
Ostracoda	0.072	ns
Polychaeta	0.555	ns
Nauplius	0.239	ns
Zoea	0.195	ns

November 2nd. Depth of the photic zone at the 1% level ranged between 26 m on 21st to 16m on 27th and showed no trend. In fact on November 2nd it fluctuated between 19 m and 23 m.

Zooplankton was dominated by copepods which were more abundant at night, and nauplii and zoea larvae (Fig. 3). Several other taxa were one to two orders of magnitude, such as polychaetes and ostracods by day, and euphausiids (adults and furcilia larvae) and amphipods at night. Pluteus larvae were also abundant, but much more so during day than at night. Thus, diel changes in abundance were significant (Table 1) for holoplankters (e.g. copepods, euphausiids, adults and furcilia), meroplankters (e.g. pluteus) and tytoplankters (e.g. amphipods). Other taxa (calyptopis larvae and ostracods) showed no significant diel differences in densities.

On the contrary, no significant trends were found in other zooplankters, however replicated sampling in the last part of the event showed that overall abundances were much lower.

Gut content and grazing of zooplankton

Gut content per individual (Table 2) increased with the size of the zooplankton fractions. Day and night differences in gut content were strikingly

noticeable among size fractions; gut contents were greater in the day than at night for the medium (500-1000 μm) and large (1000-2000 μm) fractions. The opposite occurred (greater content by night than day) in the smallest (300-500 μm) and the largest (euphausiids) fractions. The gut content of *E. valentini* (as measured in the very few individuals caught in daytime) was one half times larger than all the other fractions combined in the day, and about 15 times larger at night. Grazing impact of the euphausiid population on available chlorophyll as measured through one 24 hr cycle was 0.008 % per day, with an evacuation constant of 1.02 hr^{-1} estimated during on board experiments at the same location and cruise. Grazing impact of copepods of all size fractions reached 0.5% per day with an evacuation constant of 1.26 hr^{-1} .

DISCUSSION

Our results indicate an inverse trend of increasing chlorophyll and decreasing nutrient concentration in the upper 50 m layer right after an abrupt change of the wind regime. Such changes were not associated with solar radiation (percentage of cloud coverage) or the depth of the photic layer. Rather these changes were associated with the commence of a spring phytoplankton bloom. It seems likely that this short term study (11 days) occurred when the spring bloom had already begun to develop in Paso Ancho because: 1.- chlorophyll concentrations (1-2 mg m^{-3}) were at least higher than in winter, early spring and late summer (Iriarte *et al.*, 1993; Magazzù *et al.*, 1996); 2.- the chain forming diatoms (*Chaetoceros* spp. and *Thalassiosira* spp). which are typical components of spring blooms (Uribe, 1988, 1991) rather than pico- and nanoplankton dominated the phytoplankton in early spring and late summer (Iriarte *et al.*, 1993; Saggiomo *et al.*, 1994; Carrada *et al.*, 1994; Magazzù *et al.*, 1996); 3.- the presence of a shallow photic

TABLE 2. – Gut content (ng Chlor ind.⁻¹) of size fractions of zooplankton. Paso Ancho, 27 October 1994.

	SMALL 300-500 μm	MEDIUM 500-1000 μm	LARGE 1000-2000 μm	Σ Fractions 300-2000 μm	Euphausiids > 2000 μm
DAY (n=3)					
Mean	1.50	6.21	7.01	14.71	21.80
SD	0.74	2.59	4.66	7.37	15.13
NIGHT (n=3)					
Mean	2.70	3.85	5.82	12.38	196.01
SD	1.30	2.52	1.13	1.49	44.33

layer (ca. 20 m) which in September and early October was comparatively much deeper than in late spring (Uribe, 1991) and in late summer (Iriarte *et al.*, 1993; Magazzù *et al.*, 1996), 4.- low values of nitrates and silicates, which were lower than in late summer (Catalano *et al.*, 1996), but not as high as one could expect for a shallow and well mixed basin. Curiously, low levels of nitrates and silicates during the study period, and only a minor decrease of nitrates in the second phase could not explain the increase in chlorophyll at the study site. The advection of chlorophyll into the area seems unlikely, but this possibility cannot be excluded.

The homogeneous temperatures and salinities in the water column and transient stratification of densities in Paso Ancho (Figueroa and Yuras, 1996; Antezana, 1999) make it seem reasonable to assume that the sudden switch in the wind regime from westerly gales to calm and weak northerly winds (which defined this event, and took place from the early morning of October 28th through the end of the study), decreased mixing and likely reduced population loss below the compensation depth. The sudden change in the wind regime coincided with the appearance of a slight chlorophyll maximum hours later, which reached 6.6 mg m^{-3} at 10 m at the end of the event. As a result, the integrated chlorophyll in the upper 50 m increased just about twice as much by the end of the 11 d event, as it did in the first half of the event. Our spring values for Paso Ancho were similar to chlorophyll concentrations encountered in spring-summer season (Iriarte *et al.*, 1993; Magazzù *et al.*, 1996), suggesting that blooming conditions could occur throughout spring and summer seasons. Since Paso Ancho is a fully exposed and mostly mixed basin, it seems likely that the development of a spring bloom or the enhancement of on-going blooms there are more associated with abrupt changes in wind regime and slight transient stratification, than with differences in light intensity.

Grazing rates were not followed during the event, but those measurements made during the period of strong westerlies suggest that copepods and euphausiids, consumed about 0.5% of the available chlorophyll per day and probably did not limit phytoplankton growth during the wind relaxation phase. Even though grazing rates could not be carried out during the last part of the event, the fact that zooplankton densities remained fairly constant over the study suggests also that grazing was insufficient to control the chlorophyll increase.

The fact that the zooplankton assemblage maintained its rank order of abundance throughout the study period suggests that Paso Ancho basin harboured stable and rather isolated populations. The community of Paso Ancho has been characterized (Guglielmo *et al.*, 1996) by few species found in high densities (e.g. *Drepanopus forcipatus* Giesbrecht 1888, *Ctenocalanus citer* Heron and Bowman 1971, *Calanus simillimus* Giesbrecht 1902, *Calanus australis* Vidal 1968, *Paraeuchaeta antarctica* Giesbrecht 1902, *Metridia lucens* Boeck 1864, *Euphausia vallentini* Stebbing 1900, *Discochoecia elegans* Sars 1865 and *Sagitta tasmanica* Thomson 1947). Behavioural responses of zooplankters may counteract or be adapted to external dispersive forcing to maintain the structure of the community. Although tidal effect, wind induced mixing and eddies play a significant role in the temporal distribution of the zooplankton (Fernández *et al.*, 1993), zooplankters may behave as active drifters rather than passive drifters to maintain the same community structure even during periods of high turbulent mixing driven by wind stress (Wiafe and Frid, 1996). Species which were separated in space and are brought together by mixing, will remain in an area once the mixing intensity decreases. The restructuring of the community follows in a sequence which is dependent on the behaviour and swimming ability of the component species (Hauri *et al.*, 1990). Alternatively, typically Subantarctic or oceanic zooplankton may disperse into shallower areas and simply modify their vertical diel migratory patterns as suggested by Kaartvedt (1993) in other coastal regions.

Dispersive forces may also have prevented the formation of monospecific aggregations or swarms during this period. Swarming has been pointed out to be a common feature of the plankton in Chilean fjords and particularly in *Munida gregaria* (Fabricius 1793) and *E. vallentini* Stebbing 1900 (Tabeta and Kanamaru, 1970; Antezana, 1976; Kawamura, 1976). However, it may be said that swarming is likely a transient or occasional phenomenon or restricted to some species and to some environmental circumstances. In the presence of dense aggregations, grazing rates and grazing impact on blooming or patchy phytoplankton may drastically reverse the direct input of primary produced carbon to the bottom for a greater input to the food chain through nectonic predators or through a faeces loop. In any case, the rich benthic community of Paso Ancho (Gutt and Schickan, 1996) and the massive spawn-

ing, as evidenced by the diversified and large number of holo- and meroplanktonic larvae found during spring, indicate that strong benthic-pelagic coupling occurred during blooming conditions in this vertically homogeneous basin. As for those species unable to sit and wait at the bottom for the rain of pelagic organic matter, such as amphipods and polychaetes found in plankton samples, the alternative is to migrate from the bottom into the upper layers of the water column to search for food.

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