

Diel feeding rhythm of copepod size-fractions from Coliumo Bay, Central Chile*

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SUMMARY: The feeding behaviour of the size fractionated copepod assemblage was studied over a diel cycle in Coliumo Bay. In this shallow environment the photic layer reached the bottom and salinity, temperature, and food availability were fairly homogeneous throughout the water column. All four size-fractions (250-500 μm , 500-1000 μm , 1000-2000 μm , >2000 μm) showed a period of high feeding activity during the night and low feeding activity during the day. The persistence of nocturnal feeding in the presence of high food concentration over the 24-h cycle is interpreted as a predator avoidance strategy: empty guts by day make copepods less conspicuous to their visual daytime predators.

Key words: zooplankton, copepods, size-fractions, feeding rhythms, Chile.

INTRODUCTION

The vertical migration of zooplankton between deeper layers during the day and shallow layers at night is generally thought to occur when the water column is stratified into a shallow, lighted, food-rich layer and a deep, dark, oligotrophic layer. Under such conditions, the coupling of nocturnal feeding (NF) and diel vertical migration (DVM) would permit surface feeding at night when exposure to visual predators there is minimized (Gauld, 1953; Zaret and Suffern, 1976; Ohman *et al.*, 1983; Verity and Smetacek, 1996). A question arises in the field for shallow areas where zooplankton are unable to migrate out of surface area by day (to avoid predators). In such areas, will NF persist in spite of the inability to migrate by day, and in spite of persis-

tently available food? or will zooplankton feed continuously when food is available to make fastest use of available resources?. The results of studies addressed to answer these questions would give an indication of the importance of the pressures exerted on zooplankton, be they either food limitations or predation.

The typical Spring conditions of Coliumo Bay (36°32' S, 72°57' W, Fig. 1) provided an opportunity to analyze in situ the coupling between diel feeding and food availability in the absence of large scale diel vertical migration. In a shallow environment with a well mixed water column and high food concentration, the feeding activity of copepods was studied over a 24-hr cycle. The copepod community was fractionated in four size categories since metabolic rates and the extent of vertical migration are positively associated with size (Steele and Frost 1977; Hu, 1978; Cyr and Pace, 1993).

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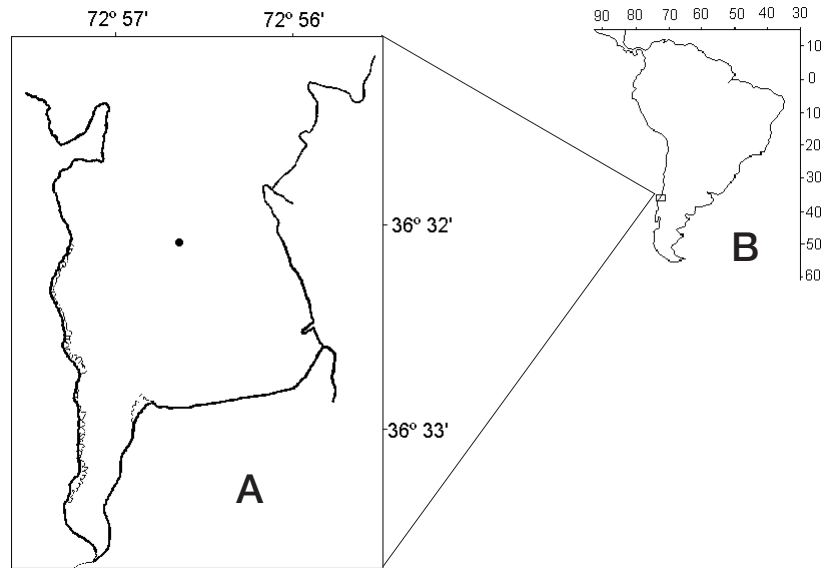


FIG. 1. – A. Map of Coliumo Bay. The black dot indicates the sampling station. B. Location of the study site in a general scale (South America).

METHODS

A sampling station was situated near the center of the Bay, where the water column is *ca.* 10 m deep. Zooplankton collections were carried out at 3-h intervals over a 24-h cycle on board the R/V Kay-Kay on November 4 and 5, 1996. A bongo net 35 cm mouth diameter and 250 μm mesh was obliquely towed from bottom to surface, slowly (0.2-0.5 knots) and quickly (*ca.* 5 min) to minimize stress to zooplankters. Immediately after the tow, the sample was mixed with carbon dioxide saturated water in equal parts in order to anaesthetize the organisms and prevent the loss of gut contents (Cervetto *et al.*, 1993). Samples were then quickly and gently filtered through a battery of sieves of 200, 500, 1000 and 2000 μm . Resulting size-fractions were placed in a dark and cold (0°C) insulated thermal box for *ca.* 1 h before laboratory analysis.

The zooplankton assemblage of Coliumo Bay and adjacent waters is strongly dominated by copepods (Arcos, 1975; Bernal *et al.*, 1985; Peterson *et al.*, 1988, Calliari 1999) of which the most abundant are: *Calanus chilensis*, *Calanus australis*, *Calanoides patagoniensis*, *Centropages brachiatus* and *Rhincalanus nasutus* in the two larger size-fractions (1000 - 2000 μm and > 2000 μm), and *Acartia tonsa*, *Paracalanus parvus*, *Oithona spp*, *Oncaea spp* and copepodites in the two smaller size-fractions (250 - 1000 μm).

Temperature and salinity measurements were taken every 6 h using a CTD (Sensordata 202).

Water samples for chlorophyll *a* (chl *a*) determination were collected at 12-h intervals and at 0, 2, 5 and 8 m with a Niskin bottle. Chl *a* concentration was estimated following Holm-Hansen *et al.* (1965) from 50 ml sea water sub samples filtered on GF/F (0.7 μm) filters. Pigments were extracted in 90% acetone and fluorescence was measured before and after acidification in a Turner Designs 10-005 R fluorometer. Light intensity in the water column was measured (Li-Cor, Li-193 sensor) (at 16:00 and 18:45) to estimate the extinction coefficient (*k*) and the depth of the photic layer.

Chl *a*-eq gut content in zooplankton was estimated following Mackas and Bohrer (1976) and used as an index of feeding activity. Given that zooplankton samples from Coliumo Bay are overwhelmingly comprised of copepods, only these organisms were sorted out for feeding estimates; and so all subsequent considerations refer to copepods. Zooplankton samples were processed as follows: 30 or more copepods from the smaller size-fractions and 15 from the larger ones were sorted out under a dissecting microscope and dim light, and transferred to a 90% acetone solution for pigment extraction during 12 h at -20°C in darkness. Fluorescence was then measured with a Turner Designs fluorometer before and after acidification. Total gut pigment values (chl *a*-eq) were corrected by adding 33% to compensate for losses of fluorescence (Dam and Peterson, 1988; Lopez *et al.*, 1988; Downs, 1989; Cervetto *et al.*, 1993; Peterson and Dam, 1996) and by subtracting the background fluorescence of animal tissues (estimated from cope-

pods representative of Coliumo Bay assemblage starved for 24 h in GF/F filtered sea water). Background fluorescence values were less than 0.1 ng chl *a*-eq. ind.⁻¹ for smaller species *A. tonsa* and *P. parvus*, and around 0.25 ng chl *a*-eq. ind.⁻¹ for larger species *Calanus spp* and *C. brachiatus*.

RESULTS AND DISCUSSION

Temperature and salinity were quite homogeneous through the water column during the study period (Fig. 2a,b). The light extinction coefficient *k* estimated from the equation (Parsons *et al.* 1984):

$$I_z = I_0 \cdot e^{-k \cdot z} \quad (1)$$

where I_0 is light intensity at the surface, z is the depth and I_z is light intensity at depth z , indicated that the photic depth was greater than the water column depth. The percentage of incident light that reached the depth of 10 m at 16:00 and 18:45 was 4% ($k = 0.323 \text{ m}^{-1}$, $r^2 = 0.99$, photic depth 14.4 m) and 3% ($k = 0.354 \text{ m}^{-1}$, $r^2 = 0.97$, photic depth 13.2 m), respectively (Fig. 2c). Chl *a* vertical distribution was highly variable and fairly homogeneous too, with a smooth peak at around 5 m depth (Fig. 2d).

Gut pigment content of the larger size fractions (1000-2000 μm and $> 2000 \mu\text{m}$) ranged between 0.5 and 11.7 ng chl *a*-eq. ind.⁻¹. Such values are close to those obtained by Peterson *et al.* (1988) for *Centropages brachiatus* (0.14 - 14.20 ng chl *a*-eq. ind.⁻¹) and for *Calanus chilensis* (0.21 - 9.50 ng chl *a*-eq. ind.⁻¹) outside Coliumo Bay. Our gut content esti-

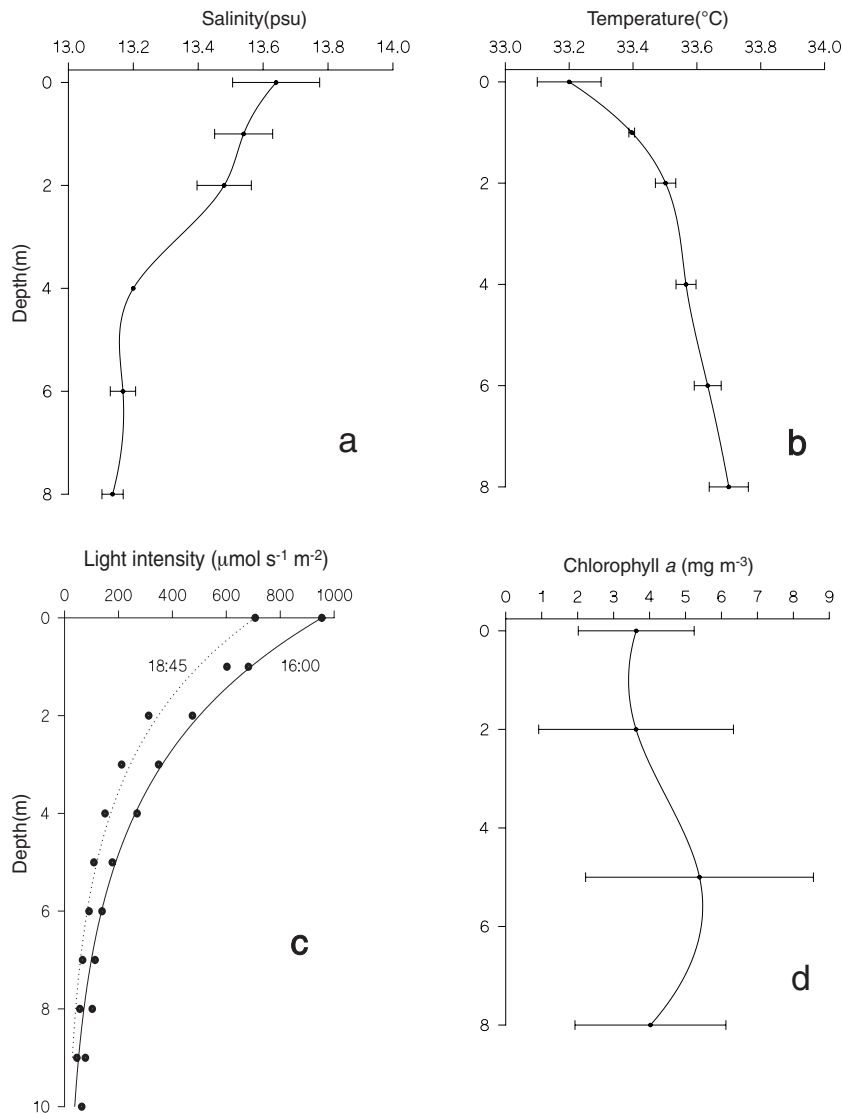


FIG. 2. – Vertical profiles of salinity (a), temperature (b), light penetration through the water column (c) and chlorophyll *a* (d) recorded in Coliumo Bay during the diel study (November 1996). In a, b and d error bars are standard deviations.

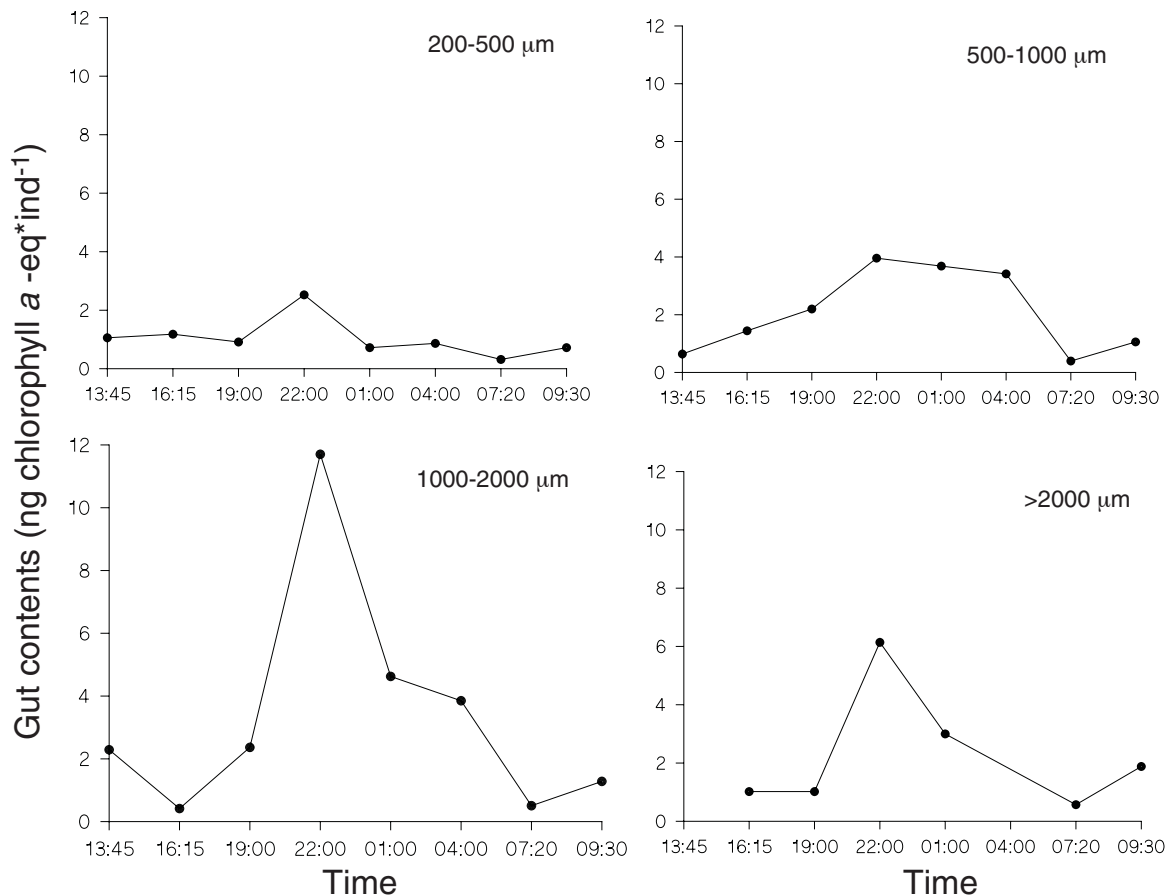


FIG. 3. – Gut contents of the four size-fractions of the copepods over a diel cycle.

mates for the larger size-fractions are also similar to those of *Calanoides patagoniensis* (0.5 - 5.5 ng chl *a*-eq. ind.⁻¹), but significantly lower than in *C. chilensis* (5 - 45 ng chl *a*-eq. ind.⁻¹) in Concepción Bay (Castro *et al.*, 1991). Gut contents varied between 0.3 and 4 ng chl *a*-eq. ind.⁻¹ for the smaller size-fractions (250-500 μm and 500-1000 μm), which are similar to those obtained *in vitro* for *A. tonsa* (0.41-6.97 ng chl *a*-eq. ind.⁻¹; Durbin *et al.*, 1990), and higher than those of *Acartia spp* in the Japan Sea (~0.1 - 0.5 ng chl *a*-eq. ind.⁻¹, Checkley *et al.*, 1992).

All size-fractions showed reduced feeding during the day and high feeding activity during the night hours, with a peak between 22:00 and 4:00 (Fig. 3), except for the smaller size-fraction (250 - 500 μm) which showed a more restricted peak around 22:00. The observed feeding rhythm was consistent with studies that describe circadian feeding rhythms in several species (i.e. Mackas and Bohrer, 1976; Baars and Oosterhuis, 1984; Durbin *et al.*, 1990; Castro *et al.*, 1991; Checkley *et al.*, 1992; Cervetto *et al.*, 1993), and also agrees with the persistence of circa-

dian feeding rhythms in copepods under non limiting food supply or constant illumination (Petipa, 1958 *vide* Stearns, 1986; Mayzaud *et al.*, 1984; Stearns, 1986; Dagg *et al.*, 1989).

In all these cases, NF seems to be the rule. The only exception seems to occur when limiting food conditions either alter or suppress the diel feeding rhythms (Daro, 1985; Gliwicz and Pijanowska, 1988). For example, *Acartia clausi* displayed flexible feeding, with maximum gut content in either day or night samples according to highest ambient food concentrations (Pagano and Saint-Jean, 1985 *vide* Cervetto *et al.* 1993). Other species like *A. tonsa*, though affected by ambient food concentration are primarily nocturnal feeders (Durbin *et al.*, 1990; Cervetto *et al.*, 1993). In the present study, the fact that NF persisted in the presence of abundant food suggests that, at least in Spring in Coliumo Bay, food was not the major concern, but that some other factor, namely predation, could be.

Feeding to zooplankton is costly in terms of predation risks incurred from non-visual predators (Gerritsen and Strickler, 1977; Kerfoot, 1982; Roth-

schild and Osborn, 1988; Tiselius *et al.*, 1997) and visual predators as well (Guiguere and Northcote, 1987). Tsuda *et al.* (1998) showed that visual predators fed at significantly higher rates on copepods with full guts than on copepods with empty guts. Then NF in itself, would be a strategy to reduce predation by visual predators in daylight hours. This strategy would emerge as a trade-off to reduce mortality at the cost of fasting during the day.

NF is usually associated with DVM, though most of the advantages attributed to both behaviors are hardly applicable in shallow mixed environments. In Coliumo Bay in Spring there are no energetic incentives to migrate vertically (Loose and Dawidowicz, 1994) because the temperature gradient is minimal and food is fairly homogeneous. Since currents are clockwise (Sobarzo, 1984), neither is there any incentive for migrating vertically into a layer for "hitch hiking" purposes (Hardy, 1956). In Spring, the photic layer reaches the bottom, so there is literally nowhere for zooplankton to go, nonetheless hide, so copepods remain in the photic zone, exposed to high food concentrations and predators. The persistence of NF for all size fractions is interpreted as an effective strategy by which to reduce predation by visual predators.

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