

Somatic and molt production in *Euphausia mucronata* off central-southern Chile: the influence of coastal upwelling variability

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ABSTRACT: Seasonal and inter-annual variability in population abundance, biomass, and somatic and molt production of the Humboldt Current krill *Euphausia mucronata* were studied during a monthly time series (August 2002 to June 2007) at Stn 18 (36° 30' S, 73° 07' W) off central-southern Chile. Experimental measurements in krill were performed at Stn 18 (in 2007 and 2008) and northern Chile (2010) in order to estimate vital rates for use in *E. mucronata* secondary production calculation at Stn 18. Coastal upwelling intensity was the main oceanographic process found to control *E. mucronata* population abundance and biomass production on seasonal and inter-annual time scales. Spawning peaks and population structure indicate that *E. mucronata* produces at least 2 generations per year. The main spawning period occurs during the austral spring when phytoplankton concentration is high. A second, less intense spawning period occurs at the end of the austral summer and early autumn. *E. mucronata* had a mean biomass of 100 mg C m⁻³ and an integrated annual secondary production of 2432 mg C m⁻³ yr⁻¹, with an overall production/biomass ratio (P/B) ratio of 24. In May 2007, a maximum daily integrated biomass of 5 g C m⁻³ and total daily secondary production of 63 mg C m⁻³ d⁻¹ were observed. These estimates are considerably higher than those reported for other krill species in coastal upwelling regions. Multivariate analyses indicate that upwelling-favorable winds promote high *E. mucronata* biomass and secondary production, but higher abundance and biomass were found during the transition periods from upwelling to downwelling conditions. Results suggest that *E. mucronata* has a highly efficient behavioral strategy to attain high production rates and recover rapidly from potential offshore losses due to advective processes in a highly productive coastal upwelling ecosystem.

KEY WORDS: Euphausiids · Biomass · Secondary production · Coastal upwelling · Time series · Humboldt Current System

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INTRODUCTION

Euphausiids (krill) contribute ~5 to 10% to total zooplankton biomass in the marine pelagic ecosystem, making them key components of the pelagic food web (Mauchline 1980). They feed on phytoplankton, protozoans, marine snow, zooplankton (mostly copepods), and fish eggs and larvae (Antezana & Brinton 1981, Dilling et al. 1998, Krautz et al. 2007). They are

in turn significant prey items for multiple predators, such as fish (Nicol 1984), sea birds (Abraham & Sydesman 2006), and marine mammals (Pérez et al. 2006).

There are relatively few krill species in the world ocean for which secondary production has been estimated (e.g. Ritz & Hosie 1982, Stuart & Pillar 1988, Lavaniegos 1995, Tanasichuk 1998). The estimation of biomass production is a key factor for quantifying carbon transfer to higher trophic levels.

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In the Humboldt Current System (HCS) there have been no studies to date of euphausiid dynamics, biomass, and vital rates; therefore no estimates of krill production are currently available. The lack of studies of krill dynamics in the HCS is a critical limitation in assessing and understanding secondary production and the potential for fish production in this large eutrophic marine ecosystem.

The euphausiid *Euphausia mucronata* G.O. Sars, 1883 is endemic, widely distributed, and the numerically dominant euphausiid species in the HCS (Antezana 2010, Riquelme-Bugueño et al. 2012). This species is an important prey item for fish populations in the Eastern South Pacific (ESP), such as jack mackerel *Trachurus murphi* and the Chilean hake *Merluccius gayi*, which are target species of a large regional fishing industry (Arancibia et al. 1995, Arcos et al. 2001). Previous studies of *E. mucronata* have examined its role as a prey item for multiple predators (Antezana 1970), its biogeography (Antezana 1976) and feeding (e.g. Antezana 2002, Krautz et al. 2007), its spatial-temporal and vertical distribution, daily vertical migration patterns (e.g. Linacre & Palma 2004, Escribano et al. 2009), and the morphological description of its larval stages (Antezana & Melo 2008). However, little is currently known about the population dynamics of *E. mucronata*, although it likely comprises most of the euphausiid biomass in the HCS.

The zooplankton dynamics in central-southern Chile are highly dependent on upwelling variability (Escribano et al. 2007) and depth of the upper boundary of the oxygen minimum zone (OMZ) (Escribano et al. 2009). In this region, the upwelling–downwelling cycle imposes strong seasonal variability in circulation patterns, thermohaline properties, and primary productivity (Sobarzo & Djurfeldt 2004, Montero et al. 2007, Sobarzo et al. 2007). This environmental seasonality causes temporal variability in zooplankton abundance, biomass, and population dynamics, which are characterized by greater aggregations of *Euphausia mucronata* over the continental shelf during the upwelling season (austral spring/summer) (Escribano et al. 2007, Riquelme-Bugueño et al. 2012). However, how oceanographic processes affect the population dynamics, and, most importantly, the magnitude of variability in secondary productivity of *E. mucronata* in the HCS, remains a critical gap in knowledge about this species.

One objective of the Center for Oceanographic Research in the eastern South Pacific (COPAS; <http://copas.udec.cl/eng>) is to understand how climate and ocean variability impact marine ecosystems and re-

gional productivity. As part of this research program, the present work focuses on the seasonal and inter-annual variations of *Euphausia mucronata* abundance, biomass, and secondary production rates. We analyzed a monthly time series (2002 to 2007) of oceanographic information and zooplankton samples collected off central-southern Chile at the oceanographic Stn 18 (36° 30' S, 73° 07' W, ~90 m seafloor depth) (Escribano & Schneider 2007). In addition, we did experimental incubations at Stn 18 in order to estimate *E. mucronata* vital rates. These incubations were complemented later with additional experiments carried out in northern Chile (Bahía Mejillones). Our goal was to assess the influence of coastal upwelling events on seasonal, annual, and inter-annual variability in population structure, abundance, biomass, and productivity rates of *E. mucronata*. We specifically aimed to test the hypothesis that population dynamics of this species are significantly coupled to upwelling–downwelling variability over seasonal and inter-annual time scales at Stn 18.

MATERIALS AND METHODS

Field sampling and environmental data

The COPAS time series program collects oceanographic information and zooplankton samples every month at Stn 18. We assumed that this location is representative of the environmental conditions in the neritic coastal upwelling region off Concepción, Chile (Fig. 1). This assumption is robustly supported by evidence from several interdisciplinary investigations carried out in this region (Sobarzo & Djurfeldt 2004, Escribano & Schneider 2007, Aguirre et al. 2012). The COPAS time series started in August 2002 and has continued sampling at an average interval of 28 d (± 12 d SD) (Escribano & Schneider 2007). Monthly *Euphausia mucronata* abundance and biomass variability was recorded from August 2002 to June 2007. Zooplankton was collected with a 1 m² mouth Tucker Trawl net (200 μ m mesh size) equipped with a calibrated digital General Oceanic flowmeter. Oblique net tows sampling the upper 80 m of the water column were done at a speed of 0.5 m s⁻¹ for 15 to 20 min. Zooplankton samples were preserved with 10% formalin buffered with saturated sodium borate solution.

Wind stress is an index of coastal upwelling intensity. Daily alongshore wind stress (τ , Pa) data recorded at 38° S (representative of the region where Stn 18 is located) were obtained from the QuickSCAT satellite (25° spatial resolution, <http://opendap.jpl>).

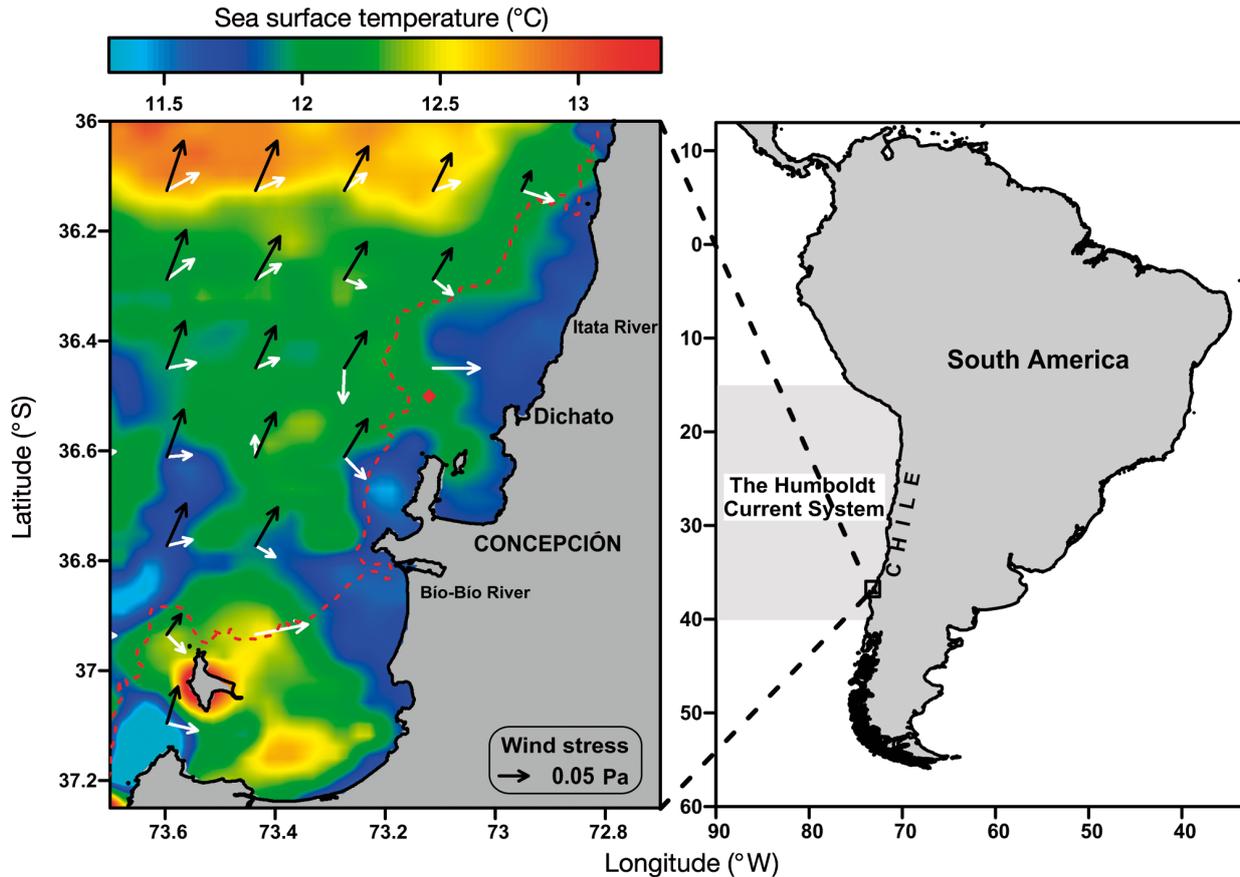


Fig. 1. Satellite sea surface temperature (SST) for November 2007 in the coastal upwelling region off Concepción, Chile, located in the Humboldt Current System. Wind stress vectors: upwelling (black arrows, November 2007) and downwelling (white arrows, June 2007) conditions. Red diamond: Stn 18. Monthly composite satellite data were processed by Pathfinder v5 and QuikSCAT for SST and wind data, respectively. Red dotted line: 100 m isobath

nasa.gov/opensdap/hyrax/OceanWinds/quikscat). The τ was re-calculated using 10 d of mean τ before each zooplankton sampling date. We used a period of 10 d to calculate accumulated τ prior to the sampling day because winds that favor coastal upwelling in central-southern Chile exhibit their spectral maximum over a synoptic time scale between 3 and 15 d (Rutllant et al. 2004, Sobarzo et al. 2007). On the seasonal time scale, winds favorable to coastal upwelling occur during austral spring/summer (September to April) and downwelling occurs during austral autumn/winter (May to August). April–May (upwelling to downwelling) and August–September (downwelling to upwelling) are considered transition periods (Sobarzo et al. 2007). Integrated 10 d τ data were later associated with *Euphausia mucronata* biological variables.

Physical and biological oceanographic sampling accompanied Tucker zooplankton tows. A CTD (Sea-bird Electronics, model 19 plus) or CTDO (model 25) mounted to a water sampling carousel (model 32C) was deployed down to 85 m depth to obtain vertical profiles of temperature (Temp), salinity (Sal), and dis-

solved oxygen (DO) concentration. DO profiles were obtained from an oxygen sensor (model 43) mounted to the CTDO. Discrete water samples were collected at 9 depths (0, 5, 10, 15, 20, 30, 40, 50, and 80 m) using Niskin bottles to measure chlorophyll *a* (chl *a*) and DO concentrations. From each depth, 200 ml of seawater was filtered onto a GF/F glass fiber filter and the filter was frozen in liquid nitrogen. Chl *a* concentration was measured after extraction with acetone using fluorometric analysis with a Turner Designs TD-700 fluorometer (Holm-Hansen et al. 1965). DO from Niskin bottle seawater samples was measured using the standard Winkler method (Carpenter 1965) to calibrate the CTDO oxygen concentration data set. Oceanographic data from the CTDO profiles and discrete depth measurements were used to map vertical profiles of Temp, Sal, DO, and chl *a* throughout the time series. We calculated mean water column values at monthly, seasonal, and inter-annual time scales using these 4 environmental variables. The depth of the upper boundary of the OMZ was defined as the depth where concentrations $<1 \text{ ml O}_2 \text{ l}^{-1}$ were recorded.

We related these oceanographic variables to the monthly, seasonal, and inter-annual changes in *Euphausia mucronata* abundance, biomass, and secondary production.

Laboratory procedures

All euphausiids were removed from zooplankton samples. Samples that contained large numbers of euphausiids were divided into aliquots of $\frac{1}{4}$ to $\frac{1}{8}$ from whole samples using a Folsom splitter. *Euphausia mucronata* was identified and counted using a stereoscope, and the abundance was standardized to number of individuals per m^3 (ind. m^{-3}) using the estimated filtered seawater volume of each tow.

Euphausia mucronata larvae (calytopis and furcilia stages), juveniles, and adults were identified using available taxonomic descriptions (Baker et al. 1990, Brinton et al. 1999, Antezana & Melo 2008). Currently there are no taxonomic keys to identify the eggs, nauplii, and metanauplii stages of *E. mucronata*. Total length (TL, mm) of each larval, juvenile, and adult specimen was measured from the tip of the rostrum to the end of the telson.

Nighttime euphausiid abundance using daylight zooplankton samples

Because most zooplankton samples were collected during daylight hours (14:00 to 18:00 h), we were concerned about potential net avoidance by *Euphausia mucronata*. If euphausiids are avoiding the net in the daytime, results based on these samples would underestimate their abundance (Brinton 1967, Shaw & Robinson 1998). Therefore, daytime and nighttime zooplankton samples were collected at Stn 18 at each sampling date during 1 yr (June 2008 to May 2009) in order to compare the krill abundance and biomass collected during day and night samples. We calculated the proportion of nighttime:daytime *E. mucronata* abundance as reported by Shaw & Robinson (1998). Specifically, we tested *E. mucronata* abundance differences between daytime and nighttime catches for 5 TL intervals: 4–8, 9–13, 14–18, 19–23 and ≥ 24 mm. These TL intervals were selected to increase degrees of freedom for statistical purposes, but they roughly correspond to larval (<6.6 mm), juvenile (mean 7.4 mm) (Antezana & Melo 2008), and adult ontogenetic phases that likely represent different swimming capabilities. The Mann-Whitney test was used to test statistical differences between day

and night *E. mucronata* abundances. Thus, we calculated a net avoidance index per TL interval, taking into account euphausiid size-dependent net-avoidance capabilities and/or vertical migration patterns that cause size-dependent abundance biases in the field (Barange 1990, De Robertis et al. 2000, Décima et al. 2010). The *E. mucronata* night/day avoidance proportion (N/DAP) for each TL interval (i) was calculated as follows:

$$N/DAP_i = \frac{\overline{NA}_i}{\overline{DA}_i} \quad (1)$$

where NA is the nighttime *E. mucronata* abundance (ind. m^{-3}) and DA is the daytime *E. mucronata* abundance at the same sampling site and day. These N/DAPs were used to correct daytime catches in the entire time series analyzed (2002 to 2007). Daytime abundances were multiplied by the N/DAP values at each TL interval.

Biomass and secondary production

We calculated an *Euphausia mucronata* biomass–total length regression model using TL and dry weight (DW) measurements of juvenile and adult euphausiids. Individual euphausiids were measured and dried for 24 h at 60°C on a pre-weighed fiberglass filter. Dried euphausiids were weighed on an analytical balance (precision: 0.1 mg). The DW–TL regression model was calculated as follows:

$$DW = 0.0019 \text{ TL}^{2.961} \quad (2)$$

This regression model was highly significant for animals between 10 and 25.5 mm TL ($r^2 = 0.901$, $F_{1,67} = 1009.2$, $p < 0.0001$, $n = 67$). The lack of individuals <10 mm TL did not affect our analysis because the entire observed size range of animals that we used to estimate secondary production fell within the 95% prediction intervals. *Euphausia mucronata* DWs were transformed to carbon content using a factor of 0.4 (Escribano et al. 2007).

Euphausia mucronata secondary production was estimated using the growth increment summation method from size-frequency data (Rigler & Downing 1984, Kimmerer 1987). This method does not require recognition and tracking of individual cohorts (Rigler & Downing 1984). Secondary production was computed as the sum of the daily somatic and molt production. We did not estimate *E. mucronata* egg production rates because their eggs cannot be identified from field samples and a probable underestimation of egg abundance. However, we used the occurrence of

krill egg peaks to qualitatively define main spawning seasons, assuming that a large proportion of the eggs collected at Stn 18 were spawned by *E. mucronata*. This is a reasonable assumption since *E. mucronata* accounts for >80% of the total krill abundance in the continental shelf region off Concepción (Riquelme-Bugueño et al. 2012). Abundances of *E. mucronata* larvae, juveniles, and adults were grouped into twenty-five 1 mm TL intervals and somatic production rates were estimated as follows:

$$P_g = \sum_{i=1}^s \left(\frac{CW_{i+1} - CW_i}{D_i} \right) \times N_i \quad (3)$$

where P_g is the daily somatic growth production ($\text{mg C m}^{-3} \text{ d}^{-1}$), CW_i and CW_{i+1} are carbon weight (mg C) at the beginning and end of each TL interval i , D_i is the number of days required to grow from TL interval i to $i+1$ (derived experimentally, see details below), N_i is the abundance (ind. m^{-3}) in each size class, and s is the number of the 25 TL intervals.

Euphausia mucronata molt (exuviae) production rates were calculated as follows:

$$P_e = \sum_{i=1}^s \left(\frac{\alpha DW_i N_i}{\text{IMP}_i} \right) \quad (4)$$

where P_e is the molt production rate ($\text{mg C m}^{-3} \text{ d}^{-1}$), α is the percent loss in DW per molting event (assumed to be 4% as measured for *E. pacifica*: Iguchi & Ikeda 1999) multiplied by carbon content of molts (assumed to be 23% of DW of complete krill specimen as determined for *E. pacifica*: Iguchi & Ikeda 1999), IMP_i is the time (d) between 2 consecutive molting events (defined below). We estimated the production/biomass ratio (P/B) as an index of population turnover (Rigler & Downing 1984).

Intermolt period

We estimated the *Euphausia mucronata* intermolt period (IMP_i) of juvenile and adult individuals using the 1/MR standard method (Tarling et al. 2006) from animals collected during austral spring 2007 and summer 2008 at Stn 18, and during autumn 2010 in northern Chile (Bahía Mejillones, $\sim 23^\circ \text{S}$). These experimental estimations were obtained in both locations and they were used in *E. mucronata* secondary production calculation at Stn 18. Animals were captured at night and transported in a cooler to a land-based cold-room laboratory. Euphausiids were incubated individually in 1 l plastic jars containing 200 μm filtered seawater. We used *in situ* surface seawater for further incubation experiments (up to 16 d). Sea-

water was changed every 2 d assuming that *E. mucronata* fed mainly on natural phytoplankton and microzooplankton assemblages. Animals were incubated at 7.5, 11.2, 16, and 18.5°C because these temperatures represent the temperature range in the *E. mucronata* habitat throughout its cross-shelf, along-shore, and vertical distribution range (Antezana 2002, Escribano et al. 2009, Riquelme-Bugueño et al. 2012). During the incubations, we checked each euphausiid every 12 h to detect when an individual molted. The TLs of molted animals were measured as defined previously. Thus, the IMP per experimental temperature (T) group was estimated as follows:

$$\text{IMP} = \frac{N \times t}{m} \quad (5)$$

where N represents the total number of krill that were alive at the end of the experiment plus those that molted during the incubation period, m is the number of individuals that molted, and t is the duration of the incubation (d) (Tarling et al. 2006). These estimated IMPs were used to fit a logarithmic equation to IMP as a function of TL and T , as key variables that influence euphausiid body growth rates and IMP (Iguchi & Ikeda 1995, Kawaguchi et al. 2006, Tarling et al. 2006) using the following equation:

$$\log_{10} \text{IMP}_i = a \text{TL}_i + 10^{b-cT} \quad (6)$$

where IMP and TL were defined above at i incubation temperature, and a , b and c are constant values from the regression model of \log_{10} IMP as a function of TL for each experimental T (see Fig. S1a in the supplement at www.int-res.com/articles/suppl/m476p039_supp.pdf). Slopes from these regression models were averaged (excluding data from 16°C incubations because their pattern was inconsistent). Mean slope (a) was 0.022 ± 0.004 (SD). Constants b and c were obtained from a regression analysis of \log_{10} -intercepts at each T (Fig. S1b).

Population growth rate

The population growth rate in TL (G_{L_i} ; mm d^{-1}) and DW (G_{W_i} ; mg d^{-1}) of each 1 mm TL interval was calculated by:

$$G_{L_i} = \frac{\text{TL}_{i+1} - \text{TL}_i}{\text{IMP}_i} \quad (7a)$$

$$G_{W_i} = \frac{\text{DW}_{i+1} - \text{DW}_i}{\text{IMP}_i} \quad (7b)$$

The weight-specific growth rate (g ; d^{-1}) was estimated as follows:

$$g_i = \frac{\ln\left(\frac{DW_{i+1}}{DW_i}\right)}{IMP_i} \quad (8)$$

In calculations of G_L , G_W and g , DWs and IMPs were estimated from Eqs. (2) & (6) (afterwards Eq. 10), respectively. D_i at each TL interval as a function of T was later calculated as the inverse of g_i . Thus, in order to estimate realistic D_i for *Euphausia mucronata*, we corrected our D_i values with D_i derived from *E. mucronata* early stage growth factors reported by Antezana & Melo (2008) (from calyptopis to juvenile). These growth factors were derived from an exponential function fitted to *E. mucronata* stage-specific TL. Since the derived growth factors above were nearly constant from ≥ 6 mm TL, we assume a constant D_i for euphausiids from this TL interval upwards.

The sum of accumulated D_i from 1 to 7 mm TL intervals was defined here as the generation time of *Euphausia mucronata* because this is the time elapsed between calyptopis and juvenile phases. The TL ranges of each development stage described by Antezana & Melo (2008) were used in order to assign approximate stages to our TL intervals.

In order to calibrate the population growth rate derived from Eqs. (7a), (7b) and (8) in the Stn 18 zooplankton time series, we did experimental incubations using the standard instantaneous growth rate (IGR) technique (Quetin & Ross 1991, Nicol et al. 1992, Tarling et al. 2006). IGR experiments were carried out in Bahía Mejillones ($\sim 23^\circ$ S) during austral autumn 2010. A conical net (1 m diameter mouth, 300 μ m mesh net) with a non-filtering codend (~ 32 l, 22 cm diameter, 50 cm length) was used to collect euphausiids at night. Healthy animals were gently placed in a container of filtered seawater. Euphausiids were randomly selected from this container to incubate them (usually ≥ 30 individuals). One euphausiid was placed in each ~ 800 ml plastic bottle filled with 100 μ m filtered seawater. We assumed that growth rates detected during incubations were driven by the food ingested in the field before collection (Shaw et al. 2010, Gómez-Gutiérrez et al. 2012). Krill incubations were set up in the cold room on shore ~ 1 to 2 h after the euphausiids were collected. Incubations were carried out in dark conditions at 11 to 12°C, which is close to the mean sea surface temperature at Stn 18 (Escribano et al. 2007). Incubations lasted 48 h and animals were checked every 12 h (eventually every 24 h). When a krill molted, it was preserved along with its molt in 10% formalin. IGR was measured as the difference of the TL of the animal and molt using the following equation:

$$IGR = \frac{TL_a - TL_m}{IMP} \quad (9)$$

where TL_a and TL_m denote the estimated TLs of the animal and molt, respectively. $TL_a - TL_m$ is the difference in length (or weight from Eq. 2) that can include positive (growth), zero (no size increment) or negative (shrinking) values. Since the TL of molt cannot be measured directly due to the molting process, we measured the telson length for each animal and molt, and converted this value to TL using the *Euphausia mucronata* TL-telson length equation from Melo & Antezana (1980). All length measurements were done using a stereomicroscope equipped with a calibrated micrometer. Only positive growth values were used to calculate somatic and molt production of the *E. mucronata* population.

Statistical analysis

We used non-parametric statistical analyses to compare *Euphausia mucronata* abundance, biomass, and production rates among seasons, years, and upwelling–downwelling cycles. Datasets were tested for normality using the Kolmogorov-Smirnov test. Normality was accepted for most of the oceanographic variables, but not for *E. mucronata* biological variables. Fourth-root transformation was used for biological variables to decrease variance (Clarke & Warwick 2001). To compare *E. mucronata* variables among different upwelling and downwelling conditions, we grouped our time series into 4 periods according to variation in the upwelling–downwelling cycle based on τ data and published oceanographic information (Sobarzo et al. 2007) as follows: upwelling (UPW), downwelling (DOW), transition from UPW to DOW (TR1), and transition from DOW to UPW (TR2) periods. An analysis of similarity (ANOSIM) and a permutational multivariate analysis of variance (PERMANOVA) were used to compare resemblance matrices of *E. mucronata* variables among upwelling–downwelling periods (Clarke & Warwick 2001, Anderson et al. 2008). In addition, we used a generalized nonlinear model (GNM) to determine the factors and covariates (wind stress, SST, chl *a*, etc.) that best predicted a dependent *E. mucronata* variable along the time series. We used GNM because it was expected that the effects of the predictors on the *E. mucronata* dependent variables were non-linear and had non-normal distributions. GNMs were fitted to a Poisson response distribution and log-link function. The best GNM was selected using the probability and Akaike Information Crite-

tion (AIC) values. Statistical analyses were done using E-Primer v6.1.1.5 (Clarke & Gorley 2006, Anderson et al. 2008) and Statistica 8 software.

RESULTS

Variability in oceanographic conditions

The τ and the seasonal variability of τ were more intense during the austral summer (January to February) than during the rest of the year (Fig. 2a, see Fig. S2 in the supplement). This increase in wind intensity induced seasonal changes in oceanographic conditions, mainly in the upper 30 m layer of the water column. These changes, which are forced by coastal upwelling events, are typically manifested as slight sea surface warming during the austral summer and subsurface cooling during spring (Fig. 2b). Salinity showed sharp decreases (<33) near the surface during winter in association with intense regional rainfall and Itata river runoff (Fig. 2c). During the upwelling season (spring/summer), surface and subsurface salinity increased (>34.5) as a consequence of the intrusion of the deeper and more saline equatorial subsurface water mass (ESSW). Coastal upwelling pulses modified the vertical DO concentration gradients and the upper boundary of the OMZ was considerably shallower (<30 m) during the spring/summer upwelling season than during the rest of the year (>50 m) (Fig. 2d). Seasonal upwelling events coincided with a large increase in chl *a* concentration (>20 mg m⁻³ at surface) during the austral spring/summer. This spring/summer chl *a* peak pattern occurred consistently every year, although the 2006–2007 phytoplankton bloom was considerably less intense than in previous years, and the phytoplankton peak only occurred during the late austral summer in February 2007 (Fig. 2e).

There were subtle inter-annual anomalous conditions in the time series, such as an abrupt subsurface warming during August 2006 (Fig. 2b) associated with a significant increase in DO concentrations at >60 m depth. The upper boundary of the OMZ remained deeper (>50 m) than usual during most of the austral spring/summer 2006–07 (Fig. 2d).

The upwelling–downwelling intensity was highly correlated with seasonal variability in all environmental variables, indicating that τ is one of the most significant sources of environmental variability in the coastal pelagic ecosystem off Concepción (see Fig. S2 in the supplement). Surface warming events occurred during the austral summer, but the SST

range was narrow (~2.5°C) (Fig. S2). The lower sea surface salinity during the austral winter was likely due to rainfall and the runoff from the Itata river, sea surface DO concentrations increased during summer, likely due to oxygen oversaturation in seawater after phytoplankton blooms (Fig. S2).

Annual means of all variables exhibited considerable year-to-year variability, as evidenced by their standard error bars (Fig. S3). However, the higher seasonal variability signal masked the smaller inter-annual variability because no statistically significant inter-annual changes in mean τ were detected. A 2-way ANOVA showed that seasonality explained most of the variability in the environmental conditions recorded during the study period, but annual variation influenced the depth of the upper boundary of the OMZ and SST (Table 1). We detected significant differences in all environmental variables between UPW and DOW conditions (ANOVA, $p \leq 0.001$; Kruskal-Wallis test for chl *a*, $p \leq 0.02$).

Night/day abundance

The *Euphausia mucronata* N/DAPs as a function of TL were significantly >1 (more abundant during nighttime sampling) for krill in the 9 to 23 mm TL intervals (Mann-Whitney test, $U = 432$, $p = 0.017$), and not significantly different for furciliae and juveniles (4–8 mm, N/DAP = 1, $p > 0.05$) or adults ≥ 24 mm TL (N/DAP = 1, $p > 0.05$). This means that only *E. mucronata* in the 9–13, 14–18, and 19–23 mm TL intervals were significantly underestimated using daytime zooplankton samples. We calculated the following size-dependent N/DAP conversion factors (TL intervals): 3.5 (9–13 TL), 6 (14–18), and 55 (19–23). These factors were applied to the daytime samples in the time series to estimate nighttime krill abundance (Fig. S4).

Temporal changes in abundance and biomass

Nighttime estimates of abundance and biomass varied considerably throughout the time series. Median *Euphausia mucronata* abundance was 1.09 ind. m⁻³ (q_1 0.00 and q_3 11.25 ind. m⁻³, where $q_1 = 25\%$ quartile, $q_3 = 75\%$ quartile), with a maximum of ~860 ind. m⁻³ (May 2007). The median biomass was 3.34 mg C m⁻³ (q_1 0.00 and q_3 44.14 mg C m⁻³), with a maximum of 4.7 g C m⁻³ (May 2007). It was common to find positive correlations between abundance and biomass during the 5 yr time series (Fig. 3). This par-

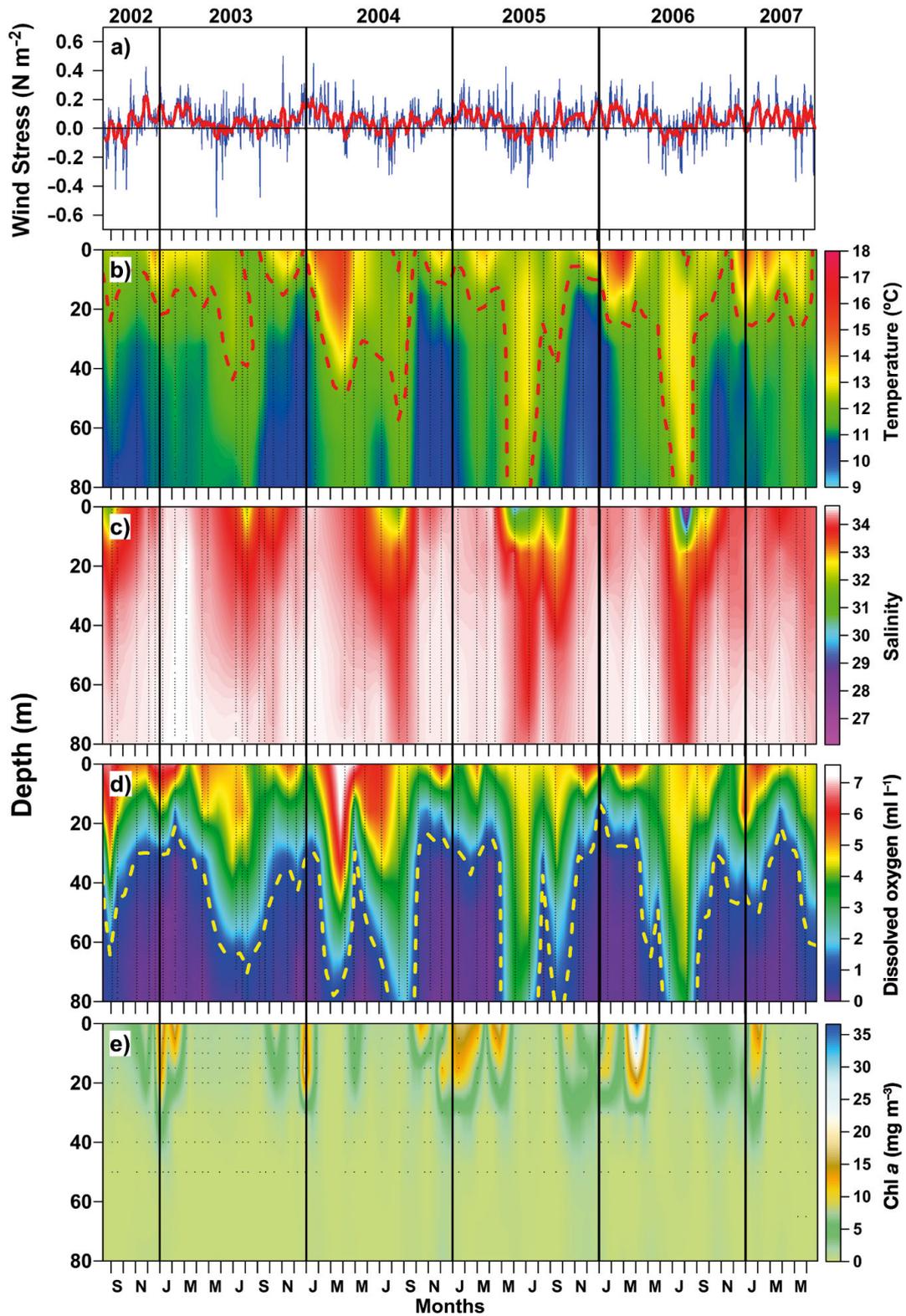


Fig. 2. Temporal variability of environmental conditions recorded at Stn 18 between August 2002 and June 2007. (a) Satellite daily alongshore wind stress (positive values = upwelling-favorable winds, negative values = downwelling events; red line: 10 d moving average filter). Hovmöller (time/depth) plots for (b) temperature (dashed red line: 12°C isotherm), (c) salinity, (d) dissolved oxygen concentration (dashed yellow line: upper boundary of oxygen minimum zone, $<1 \text{ ml l}^{-1}$), and (e) chl a concentration. Black points on plots (b–e) indicate depths at which each of the variables was recorded

Table 1. Factorial ANOVA to test inter-annual and seasonal effects on environmental and oceanographic conditions at Stn 18 during the zooplankton time series in the coastal upwelling zone off Concepción. Wind: alongshore wind stress; OMZ: depth of oxygen minimum zone; Chl *a*: surface chl *a* concentration; SST: sea surface temperature; SSS: sea surface salinity; DO: sea surface dissolved oxygen concentration. * $p < 0.05$, ** $p < 0.01$

	df	SS	MS	F	p
Wind					
Season	1	3.76	3.76	14.49	0.0005**
Year	3	0.35	0.12	0.45	0.7171
Season × Year	13	4.09	0.31	1.21	0.3069
Error	40	10.38	0.26		
Total	61	20.99			
OMZ					
Season	1	1617.14	1617.14	8.65	0.0054**
Year	3	2373.86	791.29	4.23	0.0109*
Season × Year	13	3025.80	232.75	1.24	0.2861
Error	40	7481.70	187.04		
Total	61	16393.44			
Chl <i>a</i>					
Season	1	262.17	62.17	4.32	0.0442*
Year	3	47.75	15.92	0.26	0.8523
Season × Year	13	777.58	59.81	0.98	0.4826
Error	40	2429.39	60.73		
Total	61	3748.04			
SST					
Season	1	26.13	26.13	29.83	0.0000**
Year	3	7.69	2.56	2.93	0.0453*
Season × Year	13	23.01	1.77	2.02	0.0444*
Error	40	35.04	0.88		
Total	61	93.29			
SSS					
Season	1	25.68	25.68	11.68	0.0015**
Year	3	9.09	3.03	1.38	0.2635
Season × Year	13	15.27	1.17	0.53	0.8889
Error	40	87.94	2.20		
Total	61	152.95			

tially explains why *E. mucronata* abundance varied seasonally with no consistent inter-annual pattern (Fig. 3a) and biomass was typically low, except for infrequent biomass peaks dominated by juveniles or adults (May and October 2003, September 2006, and April 2007).

Euphausia mucronata abundance varied seasonally, but abundances differentially peaked for eggs, calyptopis, furcilia and adults stages (Fig. 4a–d). Krill egg abundance peaked in the austral spring and summer (Fig. 4a), but calyptopis (Fig. 4b) and furcilia (Fig. 4c) phases were more abundant in early spring, less abundant during summer and autumn, and absent in winter. Juveniles and adults were collected during all months, with relatively low abundances during March, June, and November when smaller

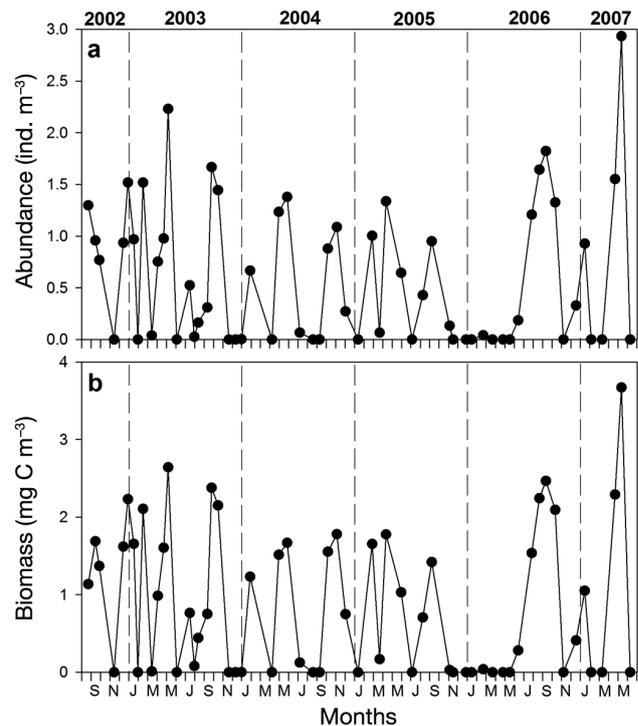


Fig. 3. *Euphausia mucronata*. Log-transformed (a) abundance and (b) biomass recorded during the time series study. All life phases, except eggs, were pooled

animals dominated (Fig. 4d,e), but higher abundances were always detected during April and May (transition period) of each year (Fig. 4d). Size composition seems to reflect broadcast spawning in spring and summer (Fig. 4e). The largest adult individuals were collected during the main reproductive period, as qualitatively defined by peaks in euphausiid egg abundances (spring to summer) (Fig. 4a,e).

IMP, growth, and biomass production

The median *Euphausia mucronata* IMP observed during incubations was 5.8 d (range: 2.3 to 16.2 d, $n = 52$). IMP had a negative correlation with T and a positive correlation with TL (Fig. S5) with a significant correlation fitted to the following regression model:

$$\text{Log}_{10}\text{IMP}_i = 0.0224 \text{ TL}_i + 10^{-0.0632 - 0.0219 T} \quad (10)$$

We estimated a mean population somatic growth rate for *Euphausia mucronata* of 0.23 ± 0.01 mm TL d^{-1} (or 0.003 ± 0.002 mg DW d^{-1}) (mean \pm SD) for calyptopis, 0.23 ± 0.01 mm TL d^{-1} (or 0.02 ± 0.01 mg DW d^{-1}) for furcilia, and 0.13 ± 0.04 mm TL d^{-1} (or 0.13 ± 0.05 mg DW d^{-1}) for juveniles and adults. Mean population weight-specific somatic growth

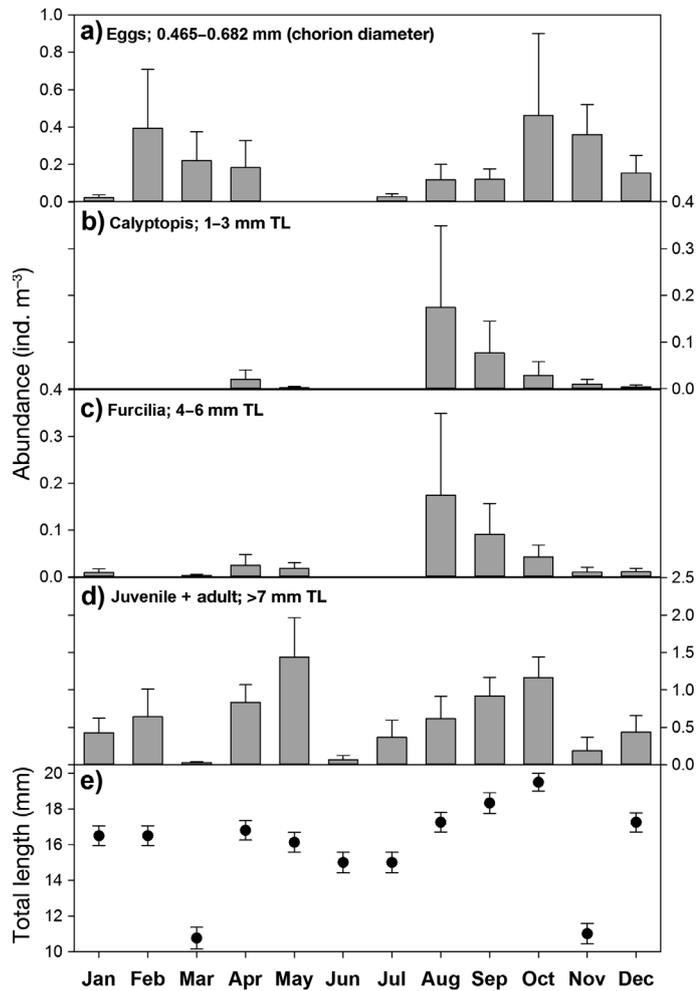


Fig. 4. *Euphausia mucronata*. Mean \pm SE monthly abundance (log-transformed) of (a) eggs from broadcast spawning krill, (b) calyptopis, (c) furcilia, (d) juvenile and adult phases, and (e) interannual mean modal total length (TL)

rates were 0.30 ± 0.06 d⁻¹ for calyptopis, 0.10 ± 0.05 d⁻¹ for furcilia, and 0.01 ± 0.01 d⁻¹ for juveniles and adults combined.

For IGR experiments, we incubated 100 *Euphausia mucronata* specimens (10.2 to 18.1 mm TL), but only a small proportion of them molted in <48 h incubations ($n = 43$). Observed IGR ranged from -0.23 to 0.31 mm TL d⁻¹ (or -0.20 to 0.28 mg DW d⁻¹) and weight-specific growth rates ranged from -0.05 to 0.07 d⁻¹. However, because negative values (shrinking) or zero growth (no change in TL) were obtained in IGR experiments, we used only positive growth increments ($n = 15$) for comparisons of somatic growth rates estimated using both methodological approaches (comparing specimens with equal TL range). Based on positive growth increments, mean somatic growth rate was 0.07 ± 0.07 mm TL d⁻¹ (or 0.08 ± 0.07 mg DW

d⁻¹) and weight-specific growth rate was 0.01 ± 0.02 d⁻¹. Somatic growth rates estimated mathematically were typically higher than observed IGR. However, they were never >2 times greater than observed IGR. Table 2 shows the *E. mucronata* vital rates (IMP, G_L , G_W , g , D_i) estimated per TL interval. The estimated generation time for *E. mucronata*, based on the cumulative D_i from calyptopis to juvenile phases, was 51 d.

The median somatic production rate for *Euphausia mucronata* was 0.051 mg C m⁻³ d⁻¹ (maximum, q_1 , and q_3 : 49.91, 0.000, and 0.49 mg C m⁻³ d⁻¹, respectively) and median molt production rate was 0.01 mg C m⁻³ d⁻¹ (maximum, q_1 , and q_3 : 12.81, 0.000, 0.12 mg C m⁻³ d⁻¹). Somatic and molt production rates were typically low with sporadic peaks of high productivity (December 2003 and May 2007) (Fig. 5a). The integration of biomass and somatic (80%) + molt (20%) production rates (by extrapolating to the days elapsed between sampling dates) yielded an annual biomass of 100.26 mg C m⁻³ and a total annual production of 2432 mg C m⁻³ yr⁻¹. The estimated *E. mucronata* annual P/B ratio, interpreted as the turnover population ratio, was 24.3. The monthly P/B ratio did not show a clear temporal pattern, but greater P/B values were found during the austral spring and summer when larvae and juveniles dominated euphausiid abundances (Fig. 5b).

The annual cycle of abundance and biomass was characterized by greater values during late autumn and mid-spring (Fig. 6a). As expected, somatic and molt production rates were positively associated with the annual cycle (Fig. 6b,c), and the P/B ratio was negatively associated with somatic growth and molt production, co-varying over a semi-annual cycle but with no clear annual pattern (Fig. 6d). Meanwhile, over the seasonal scale, median *Euphausia mucronata* abundance, biomass, and somatic and molt production rates clearly peaked during spring and autumn (Fig. 7a–c), and the P/B ratio showed no clear trend (Fig. 7d). In turn, median interannual *E. mucronata* abundance, biomass, and somatic and molt production rates were high at the beginning and the end of the time series (Fig. 8a–c), whereas P/B ratios showed relatively constant values between 2003 and 2006 (Fig. 8d).

Population dynamics

Coastal upwelling–downwelling variability drives most of the strong seasonal environmental signals in the water column off central-southern Chile

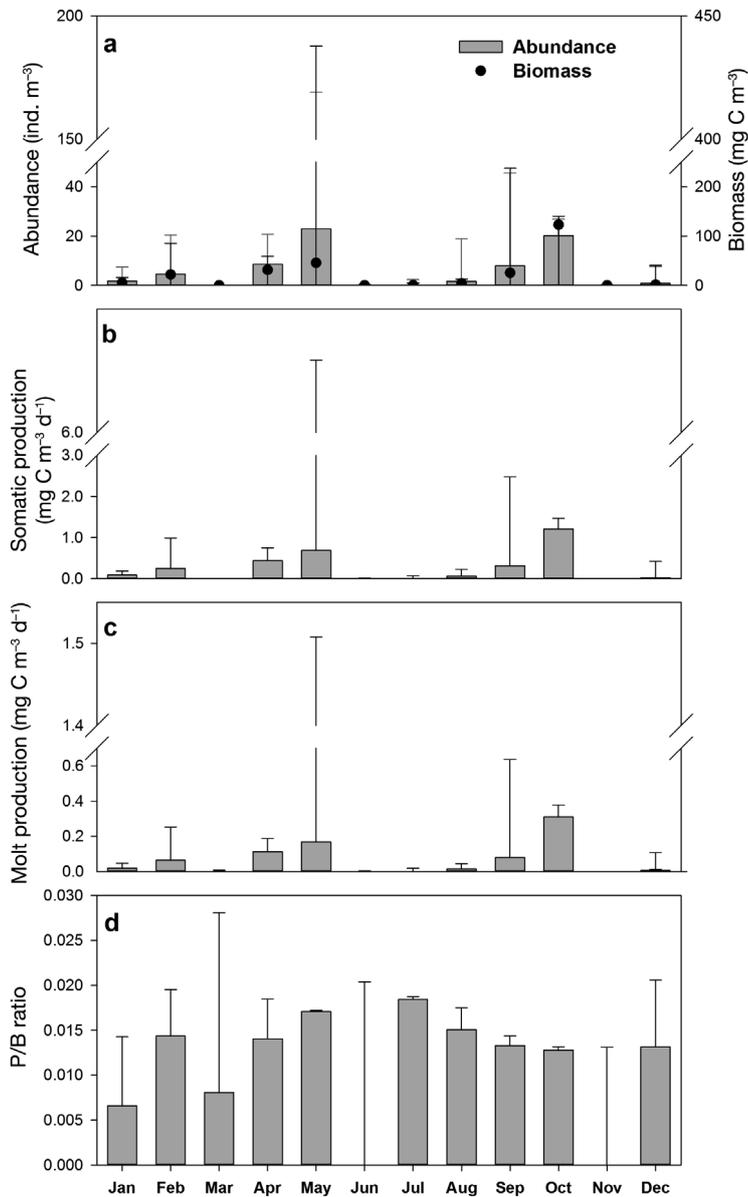


Fig. 6. *Euphausia mucronata*. Monthly medians for (a) abundance and biomass, (b) somatic production, (c) molt production, and (d) production/biomass (P/B) ratio recorded during the annual cycle of the time series study. Bars: upper quartiles

56 d interval reported for similar *E. mucronata* TL intervals, considering at least 2 of the most common furciliae I and II developmental pathways (Antezana & Melo 2008). *E. pacifica*, a krill species similar to *E. mucronata*, also has generation times (egg to juvenile stage) ranging between 50 and 60 d at similar seawater temperatures (10 to 12°C) (Ross 1981, Iguchi & Ikeda 1999, Feinberg et al. 2006). However, generation times can vary depending on water temperature (Ross 1981, Feinberg et al. 2006), furcilia develop-

mental pathways (Feinberg et al. 2006, Antezana & Melo 2008), and mortality rate (Bi et al. 2010).

We found a strong relationship among *Euphausia mucronata* IMP, *T*, and TL, as observed with *E. pacifica* in the Japan Sea (Iguchi & Ikeda 1995). We estimated a median IMP of 5.8 d for *E. mucronata* (9 to 25 mm TL), ranging from 2.3 to 16.2 d. This median IMP was slightly larger than the median of 4 d (range 4 to 6 d) reported for *E. mucronata* larvae and juveniles by Antezana & Melo (2008). In that study, they did not find a significant relationship between IMP and body size, probably because they included only *E. mucronata* calyptopis, furcilia and young juvenile phases, nor did they find a significant correlation with food supply. Thus, they assumed a constant IMP over the entire lifetime of the species. However, IMP is considered to be highly variable in euphausiids and seems to be strongly influenced by daily and seasonal environmental conditions (Iguchi & Ikeda 1995, Pinchuk & Hopcroft 2007). For example, mean IMP for *E. pacifica* off the Oregon coast was 8 d during upwelling and 11 d during downwelling, and showed no significant association with TL (Shaw et al. 2010). This could result from high individual variability imposed by food availability and prevailing environmental conditions prior to krill collection and/or life developmental phases. High variability in IMP (and in other vital rates) has been observed under laboratory conditions in individuals of the same species incubated under similar experimental conditions (Feinberg et al. 2007). We conclude that higher temperatures are negatively associated with *E. mucronata* IMP and that IMP becomes longer as *E. mucronata* get larger, resulting in a size-dependent molting rate throughout their life cycle.

Population somatic growth rate

Euphausia mucronata monthly size frequency distributions showed a highly variable pattern; therefore it was difficult to infer population growth rates by tracking successive modal TL intervals. Thus, we did not use classical cohort analysis to estimate somatic growth rates from field samples. We used Eqs. (7) to (9) to calculate, for the first time, *E. mucronata* mean somatic growth rates under field condi-

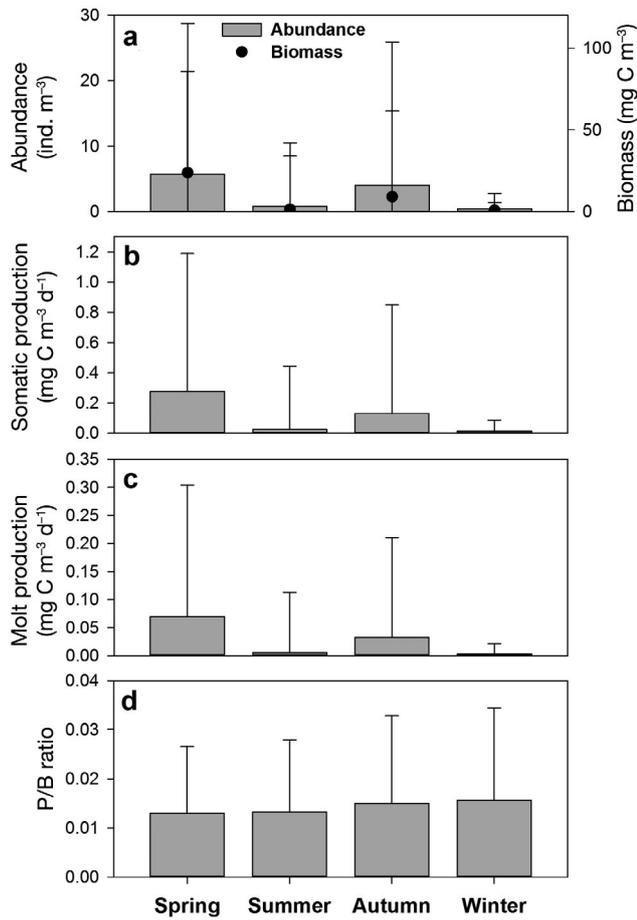


Fig. 7. *Euphausia mucronata*. Seasonal medians for (a) abundance and biomass, (b) somatic production, (c) molt production, and (d) P/B ratio recorded during the annual cycle of the time series study. Bars: upper quartiles

tions (i.e. mathematical calculation from the whole time series) and compared those growth rates with the first laboratory measurements of *E. mucronata* growth rates (i.e. IGR method). Comparison indicated that the mathematical calculation yielded a 2-fold overestimation of the growth rate with respect to the IGR-based growth rate estimation (omitting negative and no growth IGR values that do not contribute to *E. mucronata* somatic production). This difference is partially because the former method does not consider the possibility of shrinking or no growth between successive molts (Nicol et al. 1992, Shaw et al. 2010).

Average estimates from both methods were within a comparable and suitable range of values that should not affect the overall estimation of *Euphausia mucronata* somatic growth production rate in the field and its association with environmental conditions. Therefore, we believe that observed laboratory growth rates could be extrapolated, as an 'average' growth

rate, to the *E. mucronata* population sampled at Stn 18 because these estimates from experimental conditions were from temperatures similar to those observed in the HCS. *E. mucronata* juvenile and adult growth rates (field and laboratory estimates) were similar in magnitude to estimates using the IGR method for *E. pacifica* adults that inhabit a similar coastal upwelling–downwelling ecosystem in Oregon and California (Shaw et al. 2010) and Alaska (Pinchuk & Hopcroft 2007). However, *E. pacifica* growth rates were seasonally highly variable without apparently significant association with field food availability (Pinchuk & Hopcroft 2007, Shaw et al. 2010).

Environmental influences

We demonstrated that upwelling–downwelling processes modulate the *Euphausia mucronata* population, which displays higher abundance, biomass, and somatic and molt productivity rates during the austral autumn season when the transition from upwelling to downwelling conditions occurs (Figs. 4, 6 & 7) and upwelling intensity is generally low (Sobarzo et al. 2007). This relaxation in upwelling may explain the largest *E. mucronata* abundances collected throughout the time series.

The upwelling zone off central-southern Chile is a highly advective environment dominated by meso-scale eddies and upwelling filaments that extend long distances offshore (>100 km) (Correa-Ramírez et al. 2007). This highly dynamic ecosystem may partially explain the low abundances of *Euphausia mucronata* found in the zooplankton samples. For example, the lower abundances of *E. mucronata* were recorded from 2003 to 2006 (Fig. 8), when stronger southerly winds favorable to upwelling were detected, compared to 2002 when weaker winds and higher abundances co-occurred (Figs. 8 & S3). However, population losses driven by advective processes can be compensated for by vertical migration, which is likely the main mechanism that retains zooplankton nearshore (Barange & Pillar 1992, Peterson 1998, Lamb & Peterson 2005). *E. mucronata* is an active daily vertical migrator that regularly enters in the shallow OMZ (Escribano et al. 2009), making it reasonable to assume that they will be returned to the coastal zone by subsurface cross-shelf circulation during active upwelling events.

In the California Current System observations suggest that some instances of low krill abundances on daily to weekly time scales may be attributed to anomalously strong upwelling periods that induce

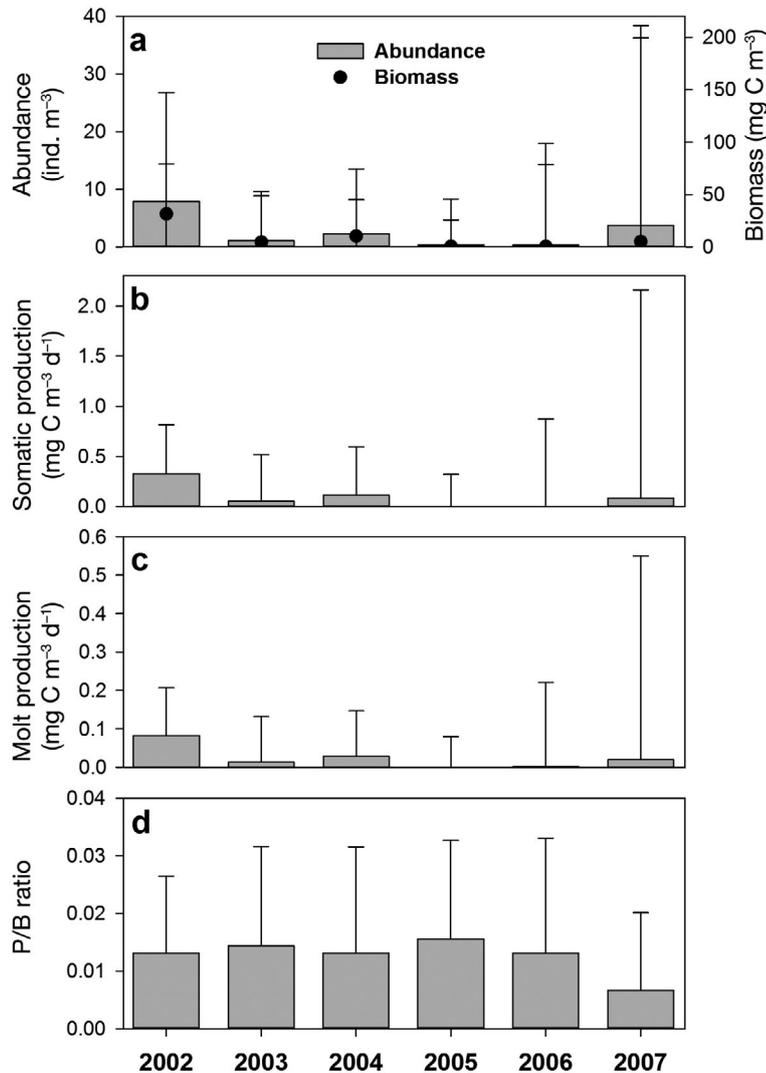


Fig. 8. *Euphausia mucronata*. Annual medians for (a) abundance and biomass, (b) somatic production, (c) molt production, and (d) production/biomass (P/B) ratio recorded during the annual cycle of the time series study. Bars: upper quartiles

offshore losses (Mackas et al. 2001, Dorman et al. 2005). However, over seasonal time scales, several studies suggest that increased upwelling intensity and duration enhances population growth rates and increases population abundances overall (Brinton 1976, Tanasichuk 1998, Feinberg & Peterson 2003).

The *Euphausia mucronata* population increased in abundance under weak upwelling conditions during the second half of 2006 and autumn 2007, when the thermocline was deep, the upper boundary of the OMZ was deep, and surface conditions were warm (Figs. 2b & S3). Warmer conditions in 2006 were likely caused by the weak El Niño event detected along the South American Pacific coasts (Fuentes et

al. 2012). This weak El Niño event may have also led to relatively less intense phytoplankton blooms in spring/summer 2006–2007, but conditions were apparently still favorable for *E. mucronata* spawning and growth, such that the population was sustained within the coastal zone. This suggests high *E. mucronata* resilience to El Niño environmental conditions and offshore surface advection.

The occurrence of higher *Euphausia mucronata* abundance and biomass during the austral autumn season (April to May), in comparison with other months/seasons, might be due to seasonal horizontal ontogenetic migration, as previously reported for the Antarctic krill *E. superba* (Nicol 2006). This hypothetical onshore transport may be supported by evidence of our zooplankton time series that shows high pulses in abundance and biomass every autumn from 2003 to 2007 (this study) and from a study carried out in 1991 in the Concepción region (Linacre & Palma 2004). Our ongoing time series at Stn 18 shows that this trend has persisted through the austral autumn (April of 2012).

The *Euphausia mucronata* biomass production estimation indicates that the population at Stn 18 may experience favorable food and environmental conditions even during winter when mesotrophic downwelling conditions prevail. *E. mucronata* seems able to adapt to these austral winter conditions, showing continuous somatic growth throughout the year in spite of potentially drastic changes in food quality during the year in this coastal region (Anabalón et al. 2007). The spring phyto-

plankton blooms (upwelling conditions) recorded at Stn 18 typically are dominated by large, chain-forming diatoms, whereas during the rest of the year (downwelling conditions) small nanoplankton and dinoflagellates are numerically dominant (Peterson et al. 1988, Vargas et al. 2006, Anabalón et al. 2007).

Euphausiids are omnivores (Ohman 1984, Dilling et al. 1998), and omnivorous feeding behavior by *Euphausia mucronata* could sustain development, somatic growth, and even spawning during the low chl *a* season. For example, *E. mucronata* actively preys on the eggs of the anchovy *Engraulis ringens* (Krautz et al. 2007), which spawns primarily during winter (Castro et al. 2000). Other zooplankton col-

Table 3. *Euphausia mucronata*. Oceanographic influence on *E. mucronata* population parameters based on generalized non-linear model. Wind: alongshore wind stress (Pa); OMZ: upper boundary of oxygen minimum zone (m); Chl *a*: (mg m⁻³); SST: sea surface temperature (°C); Temp: mean temperature of water column (°C); SSS: sea surface salinity; DO: dissolved oxygen (ml l⁻¹); UPW: upwelling condition; DOW: downwelling condition; TR1: transition from UPW to DOW; TR2: transition from DOW to UPW; AIC: Akaike Information Criteria. *p < 0.05, **p < 0.01, ***p < 0.0001

Dependent variable	Predictor variables	Factor	Estimate	p	AIC
Abundance		Wind	1.69	***	1897
		OMZ	0.03	***	
		Chl <i>a</i>	-0.05	***	
		SST	-0.16	*	
		SSS	-0.15	**	
		DO	0.10	*	
		UPW	-0.53	***	
	TR1	2.22	***		
Biomass		Temp	-0.47	***	8365
		Wind	1.78	***	
		OMZ	0.04	***	
		Chl <i>a</i>	-0.05	***	
		SST	0.08	**	
		TR2	0.15	**	
		UPW	-0.63	***	
	TR1	2.29	***		
Somatic production		Wind	1.82	***	152
		OMZ	0.03	*	
		TR1	2.48	***	
Molt production		Wind	1.83	**	64
		TR1	2.50	**	
Somatic + molt		Wind	1.82	***	177
		OMZ	0.03	**	
		TR1	2.49	***	
Eggs occurrence		Temp	-0.69	*	310
		Chl <i>a</i>	0.04	*	
		TR1	1.49	**	

lected at Stn 18, such as copepods, seasonally shift their diet from mostly diatoms in the spring to heterotrophic prey items during the periods when diatom concentrations are usually low (Vargas et al. 2006).

The most intense *Euphausia mucronata* reproduction periods at Stn 18 occurred during the austral spring and late summer, when high upwelling intensity is typically reached and the duration of the phytoplankton bloom leads to maximum chl *a* concentrations. The seasonal association of pulses of chl *a* concentrations and krill egg abundance reveals the close association with phytoplankton blooms induced by upwelling pulses. These peaks of eggs might reflect a behavioral strategy where adults release their eggs inshore to mitigate the impacts of offshore advection (Peterson 1998). Also, spawning

in nutrient-rich coastal waters may increase the chance of survival of first-feeding larval stages compared to spawning offshore. Although the presence of these major egg abundance peaks delimit the main reproductive season, we should keep in mind that spawning is highly variable spatially and inter-annually (Feinberg & Peterson 2003). Also, krill eggs may be found at any time during the year at Stn 18, suggesting that this numerically dominant euphausiid has continuous year-round production with a possible cohort overlap.

We found a positive and significant correlation between monthly averages of krill egg abundances and chl *a* concentration (results not shown), and this is consistent with previously reported observations in the study region (Riquelme-Bugueño et al. 2012). In *Euphausia* spp. distributed in other coastal upwelling regions, high chl *a* concentration seems to be the key factor that induces krill spawning events (Feinberg & Peterson 2003, Dorman et al. 2005), but spawning does not occur during winter when downwelling and low phytoplankton concentration conditions prevail (Gómez-Gutiérrez et al. 2007). We conclude that the strong seasonality of upwelling–downwelling conditions in the Concepción upwelling area does not seem to restrict *E. mucronata* reproduction during the austral winter when mean chl *a* concentrations are <2 mg chl *a* m⁻³.

Euphausia mucronata somatic and molt production, and P/B estimations were relatively high compared with those estimated for other euphausiid species distributed in other regions of the world ocean (see Table S1 in the supplement). Annual somatic and molt production of *E. mucronata* was several times higher than that estimated for *E. lucens* in the Benguela Current System. The mean *E. mucronata* P/B ratio estimation was near the upper limit of the range observed in other temperate and subtropical krill species because *E. mucronata* had a considerably higher biomass than was observed for other krill species. Year-round reproduction promoted by continuous food availability may partially explain the high *E. mucronata* biomass and production rates. Moreover, zooplankton production in this upwelling region must be high because it sustains an intensive industrial fishery that operates in this region, yielding up to 3 million t yr⁻¹ of a single pelagic fish species such as jack mackerel *Trachurus murphi* (Arcos et al. 2001). This fishery production is >15 times higher than in other coastal upwelling systems with similar characteristics, even though primary production rates are similar (Kudela et al. 2005). Thus, short and efficient carbon transfer and transformation

between primary producers and omnivores (e.g. krill) could explain the high population of small pelagics in the HCS compared to other regions of the world (Fréon et al. 2006).

Limitations and future research

Monthly sampling at a single oceanographic station during 5 yr may be considered as a 'Eulerian' sampling strategy. Several limitations and questions can arise from this zooplankton sampling design. First, even though sampling occurred at similar times of day and most of the water column was sampled, it is possible that differences in daily ontogenetic vertical migration, size-dependent patchiness (Décima et al. 2010), or epibenthic krill aggregations may not be sampled using these methods (Gómez-Gutiérrez & Robinson 2006). Second, along- and cross-shelf advection should have a principal role in the spatial variability of krill aggregations and temporal variability at a fixed oceanographic station, particularly in a highly dynamic circulation region (Tanasichuk 1998, Feinberg & Peterson 2003, Dorman et al. 2005). In fact, we observed a decoupling of seasonal abundance patterns of different ontogenetic stages, such as egg, calyptopis, and furcilia abundance peaks where peaks of larvae were sometimes detected earlier than peaks of eggs (Fig. 4). This fact may be attributable to an artifact of our Eulerian sampling design, which is unable to detect dynamic advective currents that would differently impact the abundance of eggs, larvae, and adults at the sampling site, as observed in other studies (Lu et al. 2003, Lamb & Peterson 2005, Dorman et al. 2005). Horizontal advection may partially explain very low egg densities in our zooplankton samples. However, temporal succession of different ontogenetic development stages can be a major challenge because *Euphausia mucronata* seem to spawn throughout the year, generating considerable cohort overlap.

Third, daytime net avoidance is another bias to estimating euphausiid abundance (Brinton 1967). The 1 m² Tucker Trawl system has been previously tested and suggested as suitable sampling gear for collecting euphausiids (Shaw & Robinson 1998). We clearly demonstrated that small *Euphausia mucronata* (<8 mm TL) and larger adults (>24 mm) seem not to show significant differences in day–night abundances when collected on the same date during a year sampling effort. Only *E. mucronata* juveniles and adults (>8 and <23 mm TL) seemed to avoid nets during the day, which is likely associated with envi-

ronmental light intensity, size-dependent diel vertical migration behavior, and escape swimming capabilities. Also, *E. mucronata* adults might migrate to regions with greater seafloor depths (farther offshore) during the day to avoid predators. This species is known to actively migrate to depths >200 m during daylight in the OMZ (Escribano et al. 2009).

We certainly confirmed previous observations that nighttime sampling was more efficient for capturing euphausiids, as reported in several other regions of the world (Brinton 1967, Stuart & Pillar 1988, Mackas et al. 2004). A recent study in the coastal upwelling zone off Concepción demonstrated that night versus day abundance estimation is perhaps the most critical source of variance in euphausiid abundance and biomass estimates (Manríquez et al. 2012). However, we tried to compensate for this bias by estimating an N/DAP ratio (June 2008 to May 2009) to obtain a more realistic estimation of available nighttime *Euphausia mucronata* abundance and biomass at Stn 18. This approach has been applied previously to other euphausiid species around the world with similar results (e.g. Mackas et al. 2004, Ware & Thomson 2005).

Greater and systematic scientific effort is still required to deal with methodological limitations. However, despite the limitations discussed above, the present study provides an unprecedented field and laboratory approach to examine and test the magnitude of temporal variability of *Euphausia mucronata* abundance, biomass, and production associated with environmental conditions in the continental shelf off Concepción. We should also consider that monthly sampling during a 5 yr time series may decrease inherent sampling biases at the population level (more precise at seasonal and interannual time scales but less precise at monthly time scales). Because we estimated that population cycles (generation times) are ~2 mo and oceanographic processes are systematically repeated throughout time, this 5 yr time series elucidated several significant seasonal patterns, such as the main *E. mucronata* reproductive season (Fig. 4). The time series sampling strategy also helped to delimit reproductive seasons and population dynamics of broadcast spawning euphausiids in Oregon (Feinberg & Peterson 2003) and the Mexican tropical coast (Ambriz-Arreola et al. 2012). Geographically extensive oceanographic cruises conducted in the region off Concepción show that Stn 18 is indeed representative of typical *E. mucronata* densities along the continental shelf — the region where higher densities of this endemic species occur (Riquelme-Bugueño et al. 2012).

One aspect of *Euphausia mucronata* total secondary production not considered here is egg production. Further studies could investigate egg production by this species, following the methods used for laboratory studies of *E. pacifica* egg production (Shaw et al. 2006, Feinberg et al. 2007, Gómez-Gutiérrez et al. 2007). Egg production rates from field-collected eggs cannot be estimated until the eggs can be identified to species level using biometrical criteria or genetic methods (Gómez-Gutiérrez et al. 2010). Egg production can also be measured by incubating gravid female euphausiids to measure brood size and inter-brood period (Gómez-Gutiérrez et al. 2007, 2012). Our previous attempts to incubate gravid *E. mucronata* females have been unsuccessful, but it would be extremely useful to have measurements of egg production rates and to determine how to identify the eggs of this species in preserved samples.

A systematic time series to estimate IMP (1/MR method) and IGR, along with simultaneous zooplankton and oceanographic sampling, would certainly improve estimations of *Euphausia mucronata* growth and molting rates and thus help to understand the precise role of this euphausiid in the food web of the HCS.

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