

Seasonal size variation and growth of *Calanus chilensis* Brodsky in northern Chile

Variación estacional en tamaño y crecimiento de
Calanus chilensis Brodsky en el norte de Chile

RUBEN ESCRIBANO and LUIS RODRIGUEZ

Instituto de Investigaciones Oceanológicas, Universidad de Antofagasta,
Casilla 170, Antofagasta, Chile

ABSTRACT

Seasonal size variation of marine copepods has long been noted in the literature. Such variation is thought to be mostly determined by temperature and food availability throughout the year. Monthly samples of *Calanus chilensis* Brodsky, obtained at a fixed station in Bay of San Jorge, Antofagasta, along with vertical profiles of temperature, were used to analyze seasonal variation of prosome length, "structural dry weight" (SW) (lipid-discounted) and nutritional condition of adult females, copepodites CV and CIV. Previous studies suggest that body length may be more affected by temperature than food. Individual weight, on the other hand, seems to be more affected by food condition, although this weight may show a certain stability despite growing condition if lipids are discounted, i.e. SW. In this study body length of adults "♀♀" and stage CV were negatively correlated to mean temperature of the water column, although length of CIV did not show such correlation. SW and a condition index (Ci) show a seasonal pattern not associated with temperature. Therefore we found no support for the hypothesis of stability of SW. However, this species appears to continuously reproduce through the year, so that there is a possibility that a seasonal pattern of SW estimates in adult "♀♀" may result from differences in amounts of reproductive material, even although SW might still remain stable in nature. Measured and estimated mean SW were plotted against stages of development resulting an exponential-like curve. This suggests that growth may be exponential and hence not limited by food conditions. However such conclusion needs to be tested by having estimates of stage durations, or the time required to reach these values of SW.

Key words: Copepod, growth, size, temperature, individual variation.

RESUMEN

Variación estacional en el tamaño de copépodos marinos ha sido extensamente documentada. Se piensa que esta variación es primordialmente determinada por la temperatura y la disponibilidad de alimento a través del año. Muestras mensuales de *Calanus chilensis* Brodsky obtenidas en una estación fija en la Bahía de San Jorge, Antofagasta, junto a perfiles verticales de temperatura, se utilizaron para analizar la variación estacional en talla corporal (longitud del prosoma), "peso estructural" (SW) (lípidos descontados) y condiciones nutricionales de hembras adultas y estadios copepoditos CV y CIV. Estudios previos sugieren que la talla corporal puede ser más influida por la temperatura que el alimento. El peso de los individuos, por otra parte, parece estar más afecto a la disponibilidad de alimento, aunque el peso podría poseer cierta estabilidad frente a cambios ambientales, si es que los lípidos son descontados (SW). En nuestros resultados la talla corporal de adultos "♀♀" y estadios CV se correlaciona negativamente a la temperatura media integrada de la columna de agua, pero no la talla de estadio CIV. SW y un índice de condición (Ci) muestran un patrón estacional, no asociado a la temperatura. Estos resultados no apoyan la hipótesis de estabilidad de SW. Sin embargo esta especie presenta una reproducción relativamente continua en el año. De manera que no se puede descartar la posibilidad de que un patrón estacional en las estimaciones de SW en adultos "♀♀" pueda resultar por diferencias en las cantidades de material reproductivo, aun cuando SW sea realmente estable. Al graficar las mediciones y estimaciones de SW versus estadios de desarrollo se obtiene una curva tipo-exponencial. Este resultado sugiere que el crecimiento de los individuos puede ser exponencial y por lo tanto no limitado por el alimento. Esta sugerencia, sin embargo, necesita ser sometida a prueba obteniendo estimaciones de la duración de los estadios, o el tiempo necesario para alcanzar estos valores de SW.

Palabras clave: Copépodo, crecimiento, tamaño, temperatura, variación individual.

INTRODUCTION

A considerable amount of research on ecophysiology of marine copepods has accumulated in the last few decades. The major interest for these organisms results from the recognition of their importance as a link between primary producers and higher trophic levels of more direct interest for man.

Species of the genus *Calanus* have particularly been the focus for experimental studies under both laboratory (e.g. Paffenhöfer 1970, Mullin & Brooks 1970, Vidal 1980a, 1980b) and field conditions (e.g. Marshall et al. 1934, Diel & Klein Breteler 1986). Studies on these species are largely justified because of their larger size and higher numerical abundance in zooplankton samples, as compared to other copepod species. Such abundance also suggests that *Calanus* spp. comprise the key species controlling secondary production of the pelagic ecosystem.

Most *Calanus* species have been well studied. In ecophysiological aspects there is information for *C. finmarchicus* (Marshall & Orr 1955 for review), *C. glacialis* (e.g. Grainger 1961), *C. pacificus* (Vidal 1980a, 1980b), *C. hyperboreus* (Conover 1965), *C. helgolandicus* (Paffenhöfer 1970), *C. sinicus* (Uye 1988), and *C. marshallae* (Frost 1974).

C. chilensis, however, and endemic species of the Chilean coast, has not received much attention and only a few references to its taxonomy and distribution have been made (e.g. Brodsky 1959, Vidal 1976, Fagetti 1962, Heinrich 1970). Such descriptive studies suggest that this copepod might be numerically dominant and widely distributed along the Chilean coast (e.g. Vidal 1976), but no attempt has been made to evaluate its real importance for secondary production and system functioning of the Perú-Chile current. Such studies require information on dynamical processes of the species, including its fundamental life cycle, cohort development and population growth, and the relative importance of ambient variables in controlling population growth.

Within the above context, we have initiated ecophysiological studies of this species

in Bay of San Jorge, near Antofagasta. A description of the annual life cycle has been published elsewhere (Escribano & Rodríguez 1994). In this work we provide information on body size variation on a seasonal scale. Using field data we address some questions that may be highly relevant to elucidate aspects of secondary production of this species.

Although it has been recognized that many variables affect organisms' size (e.g. Roff 1981), previous studies have confirmed the importance of temperature and food availability in producing size variation of marine copepods (e.g. Deevey 1964, McLaren 1969, Klein-Breteler & Gonzalez 1988). These two factors, however, may affect differently two components of body size, namely body length and body mass (Escribano & McLaren 1992a). On the other hand, it is evident that observed variability in body size results from the interaction between rates of development and growth. These physiological rates, although subjected to allometric constraints (e.g. Smith 1980, Peters 1983), may be strongly altered by environmental conditions. Given spatial and temporal changes in the physical environment a consequent variation in body size is expected, of which seasonal variation is the most remarkable (e.g. Botrell & Robins 1984).

With respect to temporal changes in body size, the question we attempt to answer is, which of the body size components, body length or body mass, shows more variation associated with seasonal changes in the physical environment? This question is a critical one to determine to what extent growth in body mass or body volume is dependent on growing conditions. From laboratory experiments with *Calanus* Escribano and McLaren (1992a) concluded that variation in body length is rather determined by temperature, while body mass would be more affected by food condition. Furthermore these authors observed that the lipid store is the body component more affected by food quantity, such that the "structural weight" (lipid discounted) may remain unaffected. Stability of SW in nature may indicate that individuals can grow under not limited conditions through seasons, despite

eventual changes in food availability. This hypothesis, however, needs to be tested and it constitutes one of the major goals in this study.

Some further evidence supporting the above hypothesis is the fact that the coastal area of the Humboldt Current is known to be subject to intermittent upwelling throughout the year (e.g. Rodríguez et al. 1991). This might partially sustain a system widely recognized as one of the most productive in the world. A very rich coastal zone, and a copepod which appears to have a continuous reproduction the year around (Escribano & Rodríguez 1994), allow us to postulate that the growth rate of *C. chilensis* is not food-limited in waters off northern Chile.

MATERIAL AND METHODS

Sampling

Zooplankton samples from a fixed station ($23^{\circ} 39'05''$ S and $70^{\circ} 33'30''$ W), about 10 miles from the seashore in Bay of San Jorge (Fig. 1), were collected between January and December 1992, on a nearly monthly scale. Two types of plankton nets were used, one of $450 \mu\text{m}$ mesh-size and another $64 \mu\text{m}$ mesh-size, with opening diameters of 0.7 m and 0.5 m respectively. The nets were vertically towed from 50 to 0 m using an oceanographic wire and winch. Samples were always obtained in the same manner, keeping a constant speed (ca. $0.5 \text{ m} \times \text{s}^{-1}$) and with the wire as vertical as possible. Samples were preserved in neutralized formalin (5%) for sorting, identification and biometric measurements. At each sampling a vertical profile of temperature, from about 180 to 0 m (bottom depth ca. 210 m), was obtained using a bathythermograph, previously calibrated with discrete measurements of temperature using inverted thermometers attached to Nansen bottles at various depths. Bathythermographic measurements were corrected with the value of -0.972°C . This unique value did not show variation with depth. Since the bathythermograph showed a slow response at the surface, temperature at 0 m was always measured with the inverted thermometer.

Body size measurements

Prosome length of copepodite stages CI to adult was obtained using a dissecting microscope and micrometer, with measurements made to the nearest 0.005 mm. Depending on numerical abundance, between 5 and 40 individuals were measured per stage and per sample. In most cases early stages, such as CI and CII were either absent or in low number, so that more measurements were made for late stages. The total number of individual measurements for adults (230) may describe most of the length variability through the year.

According to Harris (1983), McLaren (1986) and Escribano and McLaren (1992a), the weight of a copepod can be divided into "structural weight" (SW) and weight of the "lipid store". The lipid component, mostly accumulated inside the oil sac may form a significant part of the total animal weight, up to 40% (Escribano 1990). In formalin pre-

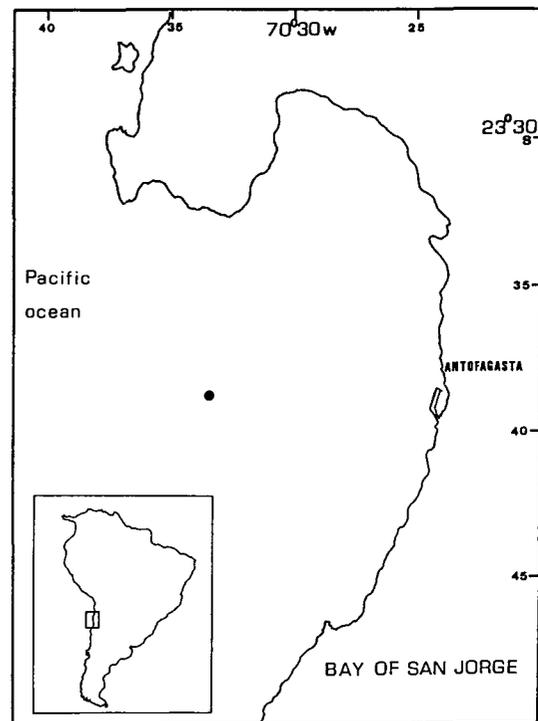


Fig. 1. Bay of San Jorge, Antofagasta, showing the fixed station for collection of zooplankton and other oceanographic variables.

Bahía San Jorge, Antofagasta, mostrando la estación fija para la colecta de zooplancton y otras variables oceanográficas.

served copepods an important part of the lipids is lost and the remaining fraction can be readily removed by squeezing the body with fine forceps (McLaren 1986). To obtain SW's as dry weight we followed this procedure. From each sample between 5 and 20 individuals were randomly chosen from the samples, of which usually 6 having the same or very similar body length (less than 5% difference), were quickly rinsed with distilled water to remove saltwater. On a concave slide they were softly squeezed with an insect fine forceps, allowing lipids to float on the remaining distilled water, which was rapidly extracted with a microsyringe (e.g. Escribano & McLaren 1992a). Thereafter, groups of 5 or 6 animals were placed in minuscule aluminum pans (average weight = 800 µg), dried in an oven at 70 °C and weighed using an analytical balance Precisa Model 120A. Constant weight was generally obtained in about 1 h. This short time necessary to reach constant dry weight has also been described when weighing other small copepods individually (McLaren & Corkett 1981, Escribano 1990). Measurements were repeated at least four times to increase precision, not finding variation of more than 10% among replicated readings. This method was applied to adult females, usually the most abundant stage in the samples, but some weights in the same manner were also obtained for stages, CIV and CV, using individuals obtained from different samples. In the case of stages CIV, the animals were weighed in groups of 12 individuals, given their smaller size. No corrections were made for loss of tissue due to preservation in formalin. As pointed out by McLaren (1986) preserved specimens tend to mostly lose lipids, i.e. the material to be discounted. In any case, eventual underestimates of SW because of loss of material is assumed to equally affect all measurements, such that data are comparable.

Using data on length and SW a condition index was calculated for adult females as follows,

$$Ci = 0.1 \text{ SW}/\text{length}^3 \quad (1)$$

where, CI = Condition index (µg x mm⁻³), and 0.1 is a constant estimated by trial and

error to obtain a value for Ci close to unity (Escribano 1990). Ci, originally proposed by LeCren (1951), has proven to be a good indicator of body density and hence the nutritional condition of individuals.

RESULTS

From the total number of measurements made for body length and weight, Ci was estimated only for adult females. Table 1 shows a summary of size measurements. It should be noted that no direct measurements of weight were obtained for early stages CI, CII and CIII. Since early stages at several times of the year were either in very low numbers or absent, only adult females and stage CV were considered to analyze the seasonal pattern of body size. It is indeed expected, as it will be shown later, that late stages may better integrate environmental effects on their body sizes.

Since zooplankton samples were integrated from 50 to 0 m, integrated mean temperature (MT) and its variance were calculated for that layer (50-0 m). For most of the year the 50-0 m layer was the one that reflected seasonal changes in water temperature, while the deeper-layer was much more stable, with temperature ranging between 12 and 13 °C.

TABLE 1

Summary of biometric measurements in *Calanus chilensis* from monthly samples obtained at a fixed station in Bay of San Jorge 1992. n is the number of individuals and number of groups of individuals for body length and weight respectively

Resumen de las mediciones biométricas en *Calanus chilensis* desde muestras obtenidas mensualmente en una estación fija en la Bahía de San Jorge durante 1992. n representa el número de individuos y el número de grupos de individuos para la talla corporal y el peso respectivamente

Stage	Prosome Length (mm)		n	Individual Weight (µg)		n
	mean	S.D.		mean	S.D.	
ADULT "♀♀"	2.426	0.114	231	140.30	34.755	34
CV	1.928	0.130	196	81.95	4.829	12
CIV	1.491	0.112	85	36.65	4.738	7
CIII	1.220	0.078	28	16.75 (*)	-	-
CII	1.103	0.069	11	12.32 (*)	-	-
CI	0.990	0.051	10	8.87 (*)	-	-

(*) Estimated from equation (3) in the text.

Sea temperature shows a typical seasonal pattern well represented by surface temperature (ST), although having a notable anomaly during the months of March and April (Fig. 2), reflecting the presence of a warm water mass derived from the "El Niño current" (Escribano et al. 1992). The presence of a superficial warm-water mass at that time is evident from the sharp sinking of the 14 °C isotherm, down to 150 m (Fig. 2).

Consistent with temporal changes in water temperature, body size of females *C. chilensis* also show a seasonal pattern of variation. The relationship, however, it is not very clear. For instance, the maximal lengths of females are observed during the spring (October) and the minimal during winter (July) (Fig. 3a). Although there was an apparent positive relationship between the mean length of females and the surface temperature (ST), the correlation is not significant ($F_{1,8} = 1.81, P > 0.05$). Lack of correlation between length of CV's and ST was also obtained ($F_{1,8} < 1, P > 0.05$). However, mean length of females and the integrated mean temperature (MT) of the water column (50 to 0 m) were negatively

correlated ($F_{1,8} = 9.32, P < 0.05$). A similar negative correlation was found for stage CV ($F_{1,8} = 7.41, P < 0.05$), although not for stage CIV ($F_{1,8} = 1.33, P > 0.05$). The negative correlation between body length of females and CV's and temperature is consistent with the well documented negative relationship between copepod size and sea-water temperature (e.g. Deevey 1964, McLaren 1969).

Structural weight (SW) of adult females shows a variation pattern similar to that of length. That is to say, heavier animals were observed during the spring, while during the winter lighter individuals were found (Fig. 3b). However no significant correlation was found between SW and either ST or MT ($F_{1,8} < 1, P > 0.05$). This indicates that SW is not apparently affected by temperature, but it is also evident from the seasonal pattern (Fig. 3b), that it cannot be said that SW remains stable through the year. No attempts were made to obtain seasonal patterns of SW of stages CV and CIV, because they were not present at all the sampling dates and the estimates were obtained using pooled individuals from different samples.

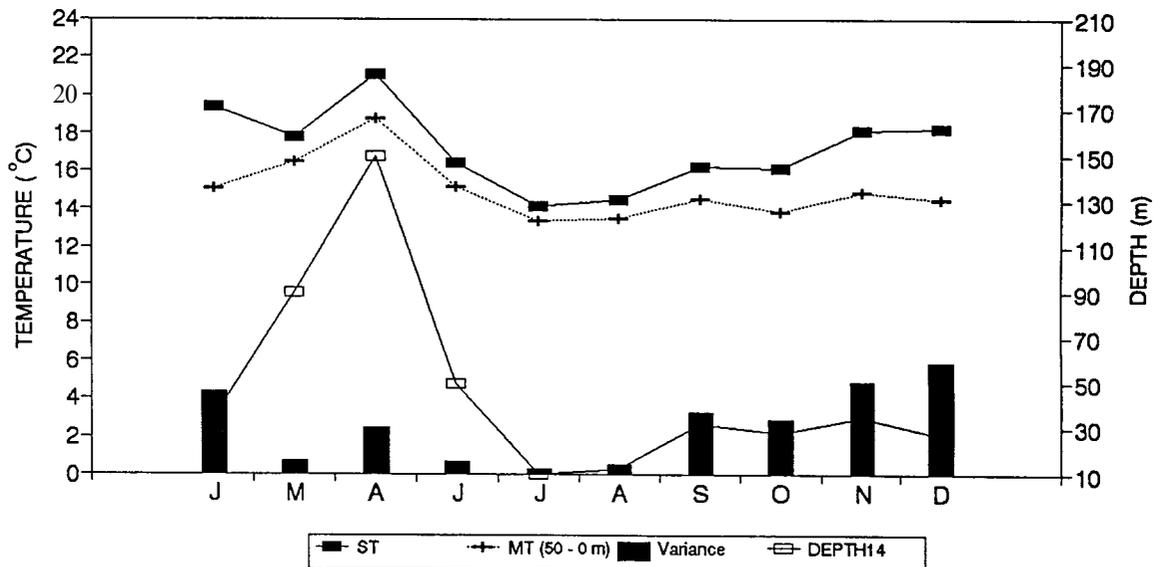


Fig. 2: Temperature conditions in the water column during 1992 in Bay of San Jorge, Antofagasta. ST = surface temperature, MT = integrated mean temperature of the water column (50 - 0 m), Depth 14 = depth (m) of 14 °C isotherm and Variance represents the integrated variance of temperature between 50 and 0 m.

Condiciones de temperatura en la columna de agua durante 1992 en Bahía San Jorge, Antofagasta. ST = Temperatura superficial, MT = Temperatura media integrada de la columna de agua (50 - 0 m), Depth 14 = Profundidad (m) de la isoterma de 14°C y Variance representa la varianza integrada de la temperatura entre 50 y 0 m.

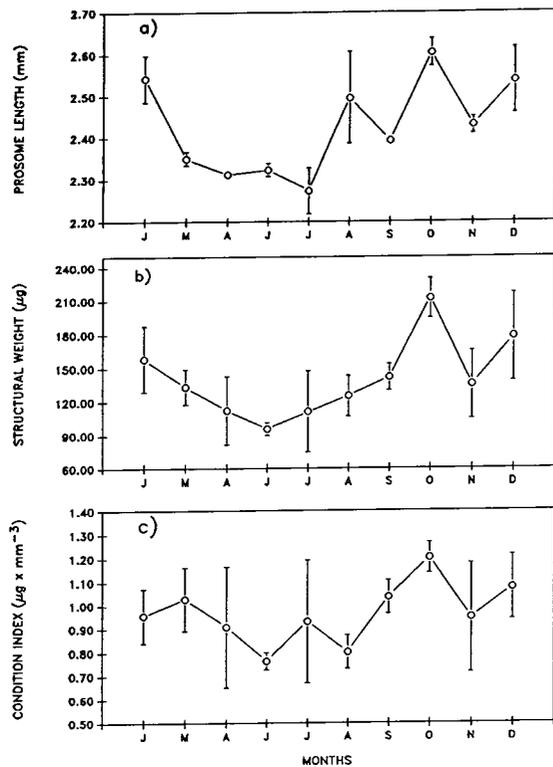


Fig. 3: Monthly changes in morphometric variables of individual adult "♀♀" *C. chilensis*. a) Prosome length, B) structural weight = lipid-discounted dry weight, c) Condition index = $0.1 \text{ SW}/\text{length}^3$. Vertical bars are the standard deviations from the mean values.

Cambios mensuales en variables morfométricas de individuos adultos "♀♀" *C. chilensis*. a) Longitud del prosoma, b) Peso estructural = Peso seco descontados los lípidos, c) Índice de condición = $0.1 \text{ SW}/\text{length}^3$. Las barras verticales son las desviaciones estándar desde los valores medios.

The seasonal pattern of Ci for adult females, on the other hand, was similar to that of length and SW, although it shows much more residual variation, reflecting the variety of physiological conditions of individuals, independent of seasonality (Fig. 3c). Thus, Ci variation was not associated with either ST, or MT ($F_{1,8} < 1$, $P > 0.05$).

In addition to seasonal changes in magnitude, the vertical gradient of temperature in the water column may also change with season. If *C. chilensis* performs vertical migration, then individuals are exposed to different vertical gradients depending on season. The periods of maximal thermal stratification were observed between the months of November and March. This is evident from the sharp increase in vertical

variance (integrated 50 to 0m) of temperature during this time (Fig. 2). In such periods a greater variance in body weight is observed (Fig. 3b).

For all the measurements in SW, independently of the developmental stage, a length-weight regression was constructed with loge transformed variables (Fig. 4). The fitted function was,

$$\log_e (\text{SW}) = \log_e (a) + b \log_e (\text{length}) \quad (2)$$

with SW (μg) and length (mm) and where the parameters a and b are the y-intercept and the slope of the well-known allometric equation (e.g. Smith 1980). Equation (2) was fitted through a non-linear regression (Wilkinson 1990) and the summary statistics for curve fitting is shown in Table 2. The estimated slope, $b = 3.04$, is not significantly different from 3 ($t_{0.05, \infty} < 1$, $P > 0.05$), the expected value for isometric growth. Even although the measurements of SW were mostly made for stages adult and CV, we have assumed that the fitted equation,

$$\log_e \text{SW} = 2.21 + 3.04 \log_e (\text{length}) \quad (3)$$

may represent the general length-weight regression for all developmental stages from CI to adult. Under this assumption SW for stages CI, CII and CIII was estimated from equation (3) for which we only had measurements of body length (Table 1).

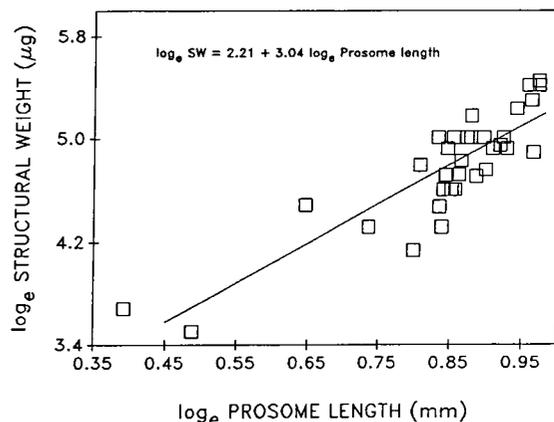


Fig. 4: The length-weight relationship of copepodites CI to adult *C. chilensis* monthly sampled from Bay of San Jorge. SW = structural weight (lipid-discounted).

La relación talla-peso de copepoditos CI a adulto *C. chilensis* muestreados mensualmente en Bahía San Jorge. SW = Peso estructural (lípidos descontados).

TABLE 2

Summary statistics after regression of structural dry weight (SW) on prosome length of individuals *Calanus chilensis* from stage CI to adult female. The equation $\log_e (SW) = \log_e (a) + b \log_e (\text{length})$, where a and b are the constants for the allometric model, was fitted using a non linear model. S.E. = standard error, C.L. = confidence limits, and MSR = mean square residuals

Resumen estadístico de la regresión del peso estructural (SW) y la longitud del prosoma de individuos *Calanus chilensis* desde el estadio CI a hembras adultas.

La ecuación $\text{Log}_e (SW) = \log_e (a) + b \log_e (\text{length})$, donde a y b son las constantes del modelo alométrico, se ajustó usando un modelo no lineal. S.E. = error estándar, C.L. = límites de confianza, y MSR = residuales medios al cuadrado

Parameter	Estimated value	S.E.	95% C.L.	r ²	MSR
log _e a	2.21	0.273	1.66 - 2.77	0.74	0.051
b	3.04	0.319	2.39 - 3.70		

The reason for attempting to estimate individual weight for all the copepodite stages was to obtain the weight increments through stages, and this might give us some insights on the pattern of growth in SW. In contrast to body length, growth in body mass may be continuous through time despite the discrete changes in length at each moulting. Thus, measured weights for individuals of a given stage may represent the weight of a recently moulted animal, as well as that of a ready-to-moult one. Since there is no chance of knowing at what stage the weighed animal is, we have assumed that the mean weight of all individuals for a given stage represents the weight of middle-stage. At this point we have no means for estimating stage durations, or even to examine whether development is isochronic (Miller et al. 1977), i.e. all the stages having the same durations. Nevertheless the pattern of SW increase through developmental stages resembles an exponential curve (Fig. 5a), as described in other *Calanus* species (e.g. McLaren 1986, Uye 1988). Body length, on the other hand, increases discretely through stages showing a similar pattern to that of weight. It is not clear if it is linear (Fig. 5b), as described in other copepod species (e.g. Escribano 1990,

Escribano 1992, Escribano & McLaren 1992b). In order for a linear pattern to occur late stages should last longer than early ones.

DISCUSSION

Size variation of copepods has long been documented from field samples. Body length is the most easily measured variable of body size and its variation has been attributed to factors, such as food quantity and quality (e.g. Klein-Breteler & Gonzalez 1982, Huntley et al. 1987, Klein Breteler et al. 1990), temperature (e.g. Deevey 1960, Corkett & McLaren 1978), size dependent predation (e.g. Warren et al. 1986). Even although numerous laboratory experiments have studied the effects of such factors, it has been difficult to evaluate their relative importance in producing length variation. Field data have generally shown a negative relationship between body length and temperature, but other correlated variables,

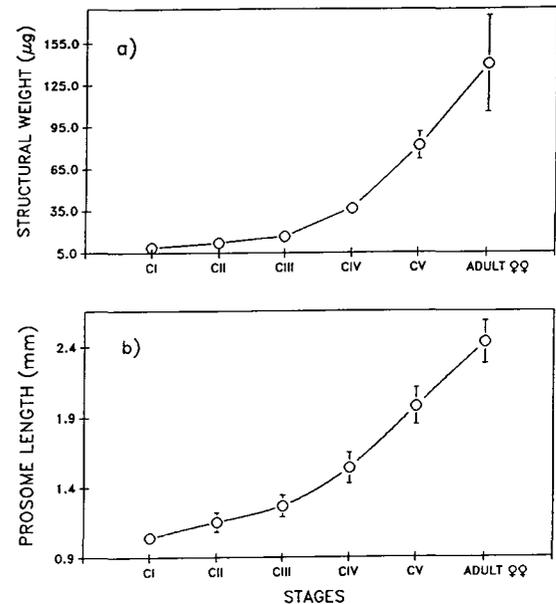


Fig. 5: Growth in *C. chilensis* from copepodites CI to adult female in Bay of San Jorge. a) "structural weight" (lipid-discounted) vs stages, b) length vs stages. No estimates of stage durations were made.

Crecimiento en *C. chilensis* desde copepoditos CI a adultos hembras en Bahía San Jorge. a) "peso estructural" (lípidos descontados) versus estadios, b) talla corporal versus estadios. No se obtuvieron estimaciones de duración de los estadios.

such as food availability can also partly explain this variation.

Mean temperature (MT) appeared to better represent thermal condition of the water column than surface temperature (ST). This because of the negative correlation between body length of females and CV's and MT. Throughout the year the sharpest decrease in body size was observed during the presence of an anomalous warm water mass, as a consequence of the 1991-92 "El niño". At this time (April 1992), the thermocline was drastically deepened (Fig. 2) and very small females were present associated with high temperature. This would give support to Escrivano and McLaren's (1992a) suggestion that variation of body length may be rather determined by temperature in nature.

Weight variation might be more directly related to food quantity and quality. It is necessary, however, to make the distinction between lipid store and "structural copepod" (sensus Harris 1983). Such distinction may be useful to understand the relative importance of temperature and food in producing size variation. For instance, Escrivano and McLaren (1992a) found that even though the lipid store was greatly reduced under low food condition, SW remained unaffected. They also concluded that temperature mostly exerts its effect on body volume, such that at high temperature individuals are smaller, but heavier per unit of body volume. This result had also been reported by another laboratory experiment (Klein-Breteler & Gonzalez 1988), in which animals of *Temora longicornis*, reared at high temperature resulted in smaller and denser adults than other reared at lower temperature in similar food conditions.

Field data on body weight have not separated the lipid store from SW (e.g. Comita et al. 1966, Gatten et al. 1979, Botrell & Robins 1984). Therefore our work constitutes the first attempt to evaluate from field data Escrivano and McLaren's (1992a) plea that SW shows a certain stability, in spite of changing environmental conditions, and so that only the lipid store reacts to food conditions, such that the total weight results affected. Fig. 3b, however, clearly shows a seasonal pattern of SW, indicating that SW does not have such "stability". Nevertheless,

if we look at Fig. 3c it is evident that Ci has much more variation than length and SW. Since lipids have been removed, changes in body density, here reflected in Ci, may be attributed to either variation in the amount of structural tissue, or changes in amounts of reproductive material. It is relevant to note that the greatest values of Ci occurs during the spring-summer period, when reproduction is more intense (Escrivano & Rodríguez 1994). Furthermore a great variation in Ci might be explained by continuous reproduction of this species throughout the year (Escrivano & Rodríguez 1994). In their laboratory experiment Escrivano and McLaren (1992a) utilized females *Calanus glacialis* reared from stage CIII and virtually no males were obtained, such that it is unlikely that females were fertilized and hence not much reproductive material was present. This could have produced a more stable SW of females despite the various conditions of food and temperature. Therefore, it is still likely that SW shows a certain stability in nature if differential amounts of reproductive material, in addition to the lipid store are discounted. This possibility certainly deserves more study, perhaps using sufficient data of SW for a developmental stage earlier than mature females, such as stage CV, which may not yet accumulate reproductive material, and only lipids are to be taken into account.

Although weight data suggests that somatic growth may be exponential, it became clear that information on stage duration is crucial to examine to what extent the growth rate remains constant through development and is not limited by food availability. It is not surprising however that a nearly continuously reproducing species can have (Escrivano & Rodríguez 1994) can have an exponential growth. In fact, exponential growth of copepods has generally been described in species having continuous development of cohorts throughout the year, such as *Eurytemora herdmanni* (McLaren & Corkett 1981), *Acartia* (Miller et al. 1977), *Calanus sinicus* (Uye 1988). Continuous production, on the other hand, may be an indication that animals do not experience food-shortage periods. This would certainly confirm the high productive capacity of

the Humboldt upwelling ecosystem. Even though individuals *C. chilensis* are affected by anomalous situations, such those derived from "El Niño", an apparently short generational time and continuous production seem to be the population responses to allow rapid recovering of body size in successive cohorts.

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