

Production of *Calanus chilensis* in the upwelling area of Antofagasta, northern Chile

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ABSTRACT: Salinities, temperatures, chlorophyll *a* (chl *a*), and quantitative samples of *Calanus chilensis* were obtained at ~17 d intervals from June 1996 to June 1997 at 3 stations in the Bay of Mejillones, northern Chile, and from 53 stations in a broad-scale survey of surrounding waters from 17 to 21 December 1996. Temporal variability in cohort structure precluded direct estimates of production from samples. However, lack of relationship of eggs per female and stage-frequency distribution with chl *a* in the broad survey, the apparently continuous development (and presence of adult males) during the time series, and the seasonal correlation of female body size with temperature, but not chl *a*, all suggest that food supply did not determine production rates. Therefore, temperature-dependent production was estimated, from sample biomasses and from laboratory rearings of *C. chilensis* and other species, as 45 mg C m⁻³ yr⁻¹. This is substantially lower than comparable estimates for *C. finmarchicus* off eastern Canada and northeastern USA. However, broad-scale production in December 1996 was much higher than that at the 3 time-series stations. A production:biomass ratio of 45, compared with 8 for *C. finmarchicus* off eastern Canada, is compatible with the general view that the upwelling area off northern Chile is part of one of the world's most productive marine systems.

KEY WORDS: *Calanus* · Temperature · Growth · Development · Humboldt Current · Chlorophyll

INTRODUCTION

Herbivorous zooplankton production may have a crucial influence on the variability of pelagic fish in the Humboldt Current ecosystem. Among the planktonic herbivores, the copepod *Calanus chilensis* is very abundant (Heinrich 1973) and this has prompted studies of factors that may control its development and growth rates (e.g. Escribano & Rodriguez 1995, Escribano et al. 1997). The importance of food in limiting zooplankton production is debated. Huntley & Lopez (1992) concluded in a wide-ranging review that temperature alone might account for variation of growth rates among copepod species. This suggestion, however, has been challenged by Kleppel et al. (1996), who argued that Huntley & Lopez's (1992) conclusions were based on inappropriately long time scales for the underlying causal relationships. It seems that the evi-

dence for food-limited growth ought to be examined for every particular situation.

The area off Antofagasta, northern Chile (23°S), is known to be an actively upwelling zone (Fonseca & Farias 1987, Rodriguez et al. 1991, Marin et al. 1993), providing high rates of primary production in nearshore waters (Marin et al. 1993). Upwelling may occur year round in the area (Fonseca & Farias 1987), suggesting that phytoplankton production is high in all seasons and consequently may promote continuous growth of zooplankters like *Calanus chilensis*. In the upwelling area off Antofagasta this species is present through the year and has a multigenerational life cycle (Escribano & Rodriguez 1994), suggesting that its population growth is not food-limited (Escribano & Rodriguez 1995). On the other hand, it may show retarded development rates in the laboratory at food levels likely to be found in nature (Escribano et al. 1997).

In some temperate localities where seasonality imposes initial synchrony, so that cohorts are distinguishable in successive samples, it is possible to estimate

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development rates (e.g. McLaren 1978) and production (e.g. McLaren et al. 1989a) directly from nature and compare these with expectations for prevailing temperatures. However, if patterns of development are complex in space and time so that cohorts cannot readily be followed in samples, indirect evidence for independence from food supply must be found before temperature-dependence of production is assumed. Here, we examine such indirect evidence and then estimate production rates of *Calanus chilensis*, based on field samples and on published work on development of *C. chilensis* and other *Calanus* species under food-satiated conditions in the laboratory. We also conclude that, because of great local variability in population abundances and structures, local estimates of production are not widely applicable in such upwelling systems.

METHODS

Sampling and sample processing. A 1 yr time series of samples was obtained at 3 stations in the northern Bay of Mejillones (northern Chile) (Fig. 1). In addition, a broad-scale survey of 53 stations was carried out from 17 to 21 December 1996 from Mejillones to Antofagasta (Fig. 1) to assess the wider patterns of distribution and production at this spring-summer season.

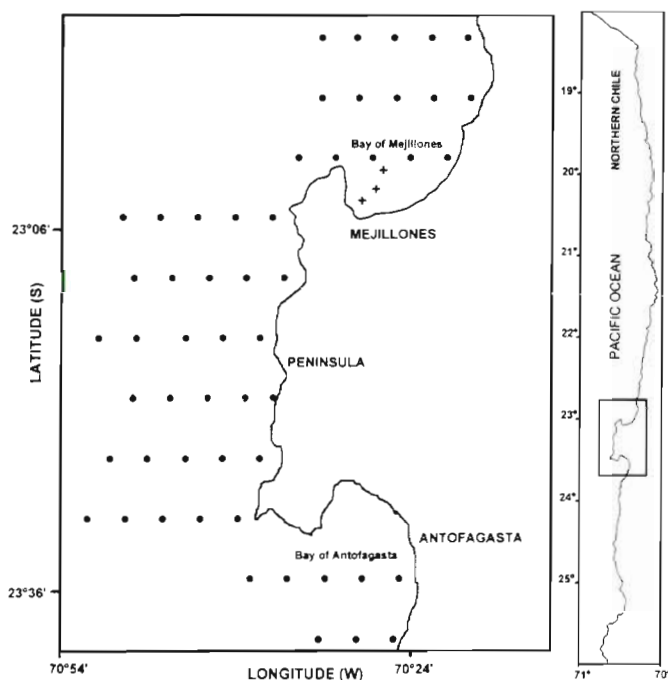


Fig. 1. Peninsula Mejillones (northern Chile), indicating the stations used for a *Calanus chilensis* broad-scale survey (●) and a time series sampling at 3 stations (+) in the northern Bay of Mejillones

During the cruise of December 1996, each station was sampled as follows: a Hensen-type net, with 200 μ m mesh, equipped with a double closing-opening mechanism and a General Oceanics flowmeter, was used to sample the upper 200 m strata. Nearshore stations (<100 m) were sampled from near the bottom to the surface. Nets were vertically towed at about 1 m s⁻¹. Zooplankton samples were preserved in 5% neutralized formalin. At each sampling station, from 200 m (or bottom) to surface, Conductivity-Temperature-Depth (CTD) profiles were obtained with a SeaBird SBE-19. An additional CTD, Ocean Sensor CTD model OS200, equipped with a Westar fluorometer, was deployed down to 100 m.

For the time series in the Bay of Mejillones, zooplankton samples were obtained at an average 17 d interval at 3 stations (Fig. 1) between June 1996 and June 1997. Two nets were used: one with 200 μ m mesh, and the other with 100 μ m mesh, both with openings of 0.5 m. Between them, the nets were assumed to be able to capture all stages of *Calanus chilensis*. The nets were vertically towed from near the bottom (ca 90 m at the deepest station) to surface. General Oceanics flowmeters were used to estimate volume filtered by each net. Samples were preserved in 5% neutralized formalin for later analysis. CTD profiles were also obtained at each station, as described above. In addition, at the central station, 1 l Nansen bottles were deployed at 5 depths to obtain samples to measure chlorophyll *a* (chl *a*) concentration, using the spectrophotometric method (Strickland & Parsons 1972). Samples for chl *a* were filtered through 0.45 μ m Millipore filters and kept overnight in the dark at low temperature (6°C). The extracts were then used to estimate chl *a* by measuring absorbance at wavelengths of 680, 750 and 630 nm using a Spectronic 20 spectrophotometer. Measurements of chl *a* were used for an *in situ* calibration of the fluorometer.

In the laboratory, preserved samples were sorted, and all stages including eggs and nauplii were identified and counted from each net. Copepodids and adults were assumed to be equally well sampled by the 100 and 200 μ m nets, but nauplii and eggs were assumed to be fully retained only by the 100 μ m mesh net. Dry weights were obtained for copepodids CI to adult. Individuals were first measured in prosome length under the microscope (to the nearest 0.1 mm), using a calibrated micrometer, then rinsed in distilled water, dried for 12 h at 70°C and weighed by 3 or 4 readings to the nearest 10 μ g, using a Denver 250D microbalance. Copepodids CV and adult males and females were individually weighed, while earlier stages were weighed as small groups of individuals. Stages CI were weighed in groups of 8 to 10, CII in groups of 5 to 8, CIII in groups of 3 to 5 and CIV as 2 or 3 individuals. All copepodid weights were increased by

30% to compensate for potential losses after formalin preservation (Omori & Ikeda 1984). Dry weight of eggs was estimated as 0.46 µg using diameter measurements and assuming the relation between egg volume and egg carbon given by Huntley & Lopez (1992). Carbon content was taken as 0.40 of dry weight. The dry weight of combined naupliar stages was estimated as 1.95 µg, the logarithmic mean value of egg and CI.

Estimating production. Copepod production was estimated from weight-specific growth rates (g_i) of copepodids and nauplii and biomasses obtained from mean dry weights and numbers per m³ of developmental stages for each sampling date. Growth between successive stages was assumed to be exponential. Thus g_i between stages could be estimated as

$$g_i = (\ln(W_{i+1}/W_i))/D_i \quad (1)$$

where W_{i+1} and W_i are mean dry weights (µg) of 2 successive stages, and D_i is midpoint development time (d) between the 2 stages. D_i was assumed to be a function of temperature. According to the equiproportionality rule of development (Corkett et al. 1986), at any temperature the proportion of time occupied by each stage remains constant, when food and other conditions are not limiting. Thus, embryonic durations can be used to specify relative responses to temperature of other developmental stages.

The temperature-dependent development embryonic duration of *Calanus chilensis* was empirically derived by Escribano et al. (1998) as

$$D = 747.7(T + 11.0)^{-2.05} \quad (2)$$

where D = embryonic time (d) and T is temperature (°C). The value 747.7 represents the parameter a of the Beléhrádek model. Escribano et al. (1998) also estimated that the median time from egg hatching to copepodid CI was 7.4 d at a constant temperature of 15°C. Although Escribano et al. (1998) were able to rear *C. chilensis* from egg to adult at a constant temperature of 15°C and supposedly satiating food conditions, there was evidence of severe retardation of some individuals after CI. Late stages are known to be more susceptible to laboratory conditions (e.g. Lopez 1991, Carlotti & Nival 1992) giving rise to large variances and presence of abnormally slow-developing individuals (McLaren et al. 1989b). Thus, development times of later stages of copepods in the laboratory may not represent those possible in the field. The equiproportional rule of development, on the other hands, yields quite uniform relative durations of copepodid stages among several *Calanus* species (Corkett et al. 1986). In order to avoid uncertainty of development times of later copepodids in the laboratory, we decided to use the Beléhrádek equation (Eq. 2) to estimate development from hatching to the mean time to reach CI as follows.

From Eq. (2) the parameter a of the Beléhrádek equation for development from hatching to CI is

$$a = 7.4 (15 + 11)^{+2.05} = 5887$$

Thus the time between hatching and CI could be estimated as

$$D_i = 5887(T + 11.0)^{-2.05}$$

Then the time between hatching and subsequent copepodid stages can be estimated as

$$D_i = p_i[5887(T + 11.0)^{-2.05}] \quad (3)$$

where p_i is the average proportion of time to each copepodid mid-stage relative to the time from hatching to CI, as the average for several species of *Calanus* as tabulated by Corkett et al. (1986).

Eq. (3) was applied using field temperatures through the sampling year. Temperature at 10 m was chosen as better representing the habitat temperature experienced by the population. The thermocline as well as chlorophyll maxima were located near this depth for most of the year. It is well known that adult body size is negatively correlated to temperature through seasons (e.g. Deevey 1964), and female prosome lengths of *Calanus chilensis* showed the highest correlation with temperature at 10 m, as compared to SST and mean temperature of the water column.

After application of Eq. (1) to estimate instantaneous growth rates between stages, the daily production rates (PR) per stage were estimated as

$$PR = B_i (e^{g_i} - 1) \quad (4)$$

where B_i is the observed biomass (µg dry weight m⁻³) for stage i and g_i is as defined in Eq. (1).

Annual production was calculated by integrating the year cycle as

$$P = \sum_{i=1}^n PR_i t_i \quad (5)$$

where P is annual production (mg dry weight m⁻³ yr⁻¹), i is the time interval and t is the number of days between time intervals.

To analyze spatial variability of PR during the December 1996 survey, g_i was estimated for each sampling station from mean dry weights of stages and application of Eq. (3), again using observed temperatures at 10 m depth to estimate D_i .

RESULTS

Spatial distributions during December 1996

During the cruise of December 1996, the sea surface temperature (SST) measured *in situ* ranged from 16.0 to 20.9°C. As shown by a satellite image obtained dur-

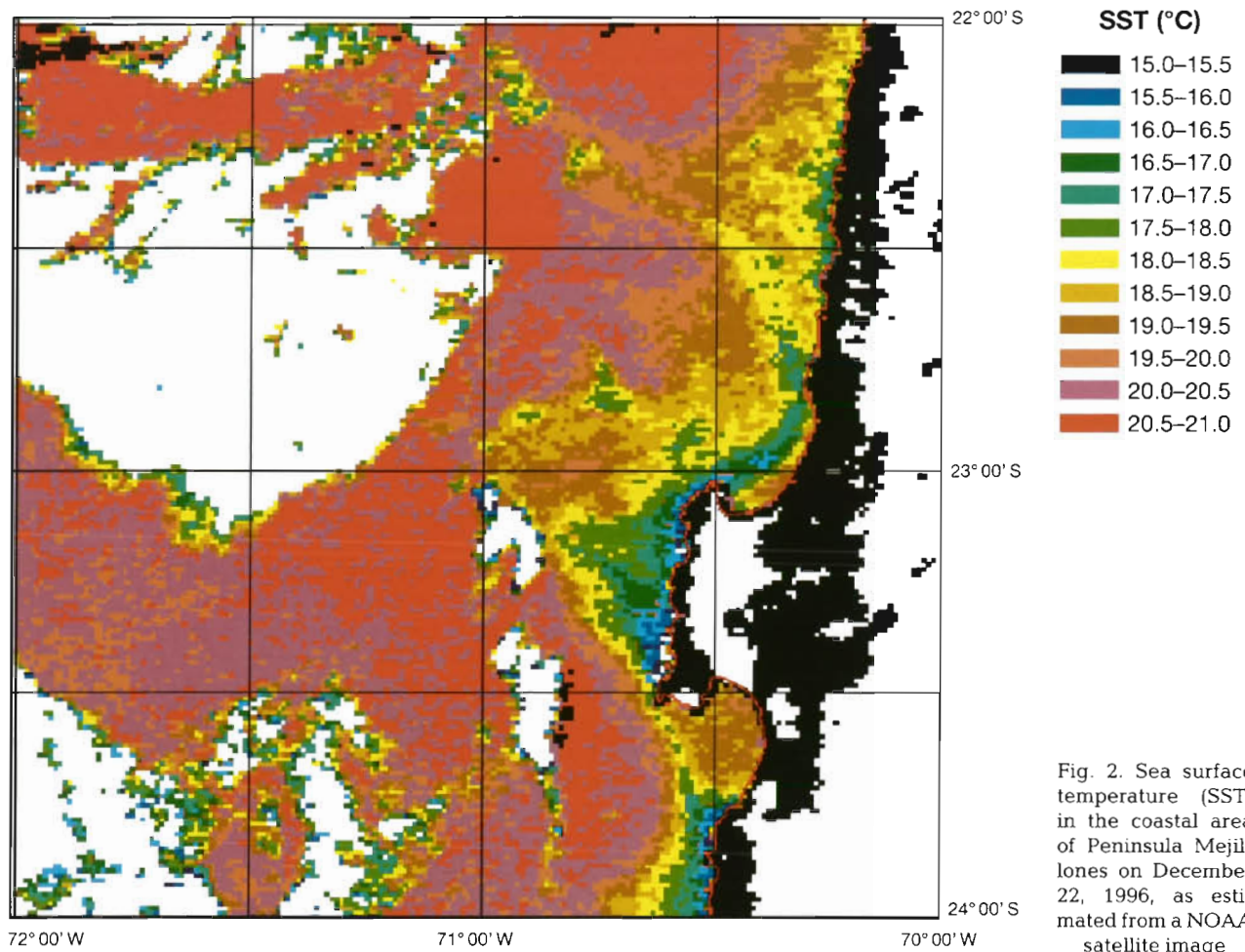


Fig. 2. Sea surface temperature (SST) in the coastal area of Peninsula Mejillones on December 22, 1996, as estimated from a NOAA satellite image

ing the sampling (Fig. 2), cold water was mostly located nearshore, indicating that upwelling was active at the time. Although somewhat weakened by high chl *a* levels 'downstream' of the cool, upwelled water in the Bay of Mejillones, the negative correlation of surface chl *a* with SST was highly significant ($r = -0.607$, $p < 0.001$). The correlation of the water-column maximum chl *a* with temperature at 10 m was considerably weaker ($r = -0.334$, $p = 0.014$). It can be seen (Fig. 1) that the 3 stations chosen for the time-series sampling were outside the area of upwelling and high chl *a* levels in December 1996 (Fig. 2).

There were profound differences in abundances of copepods among the stations sampled in December 1996 (Fig. 3). Stepwise regression (with $p = 0.1$ to retain variables) using SST, temperature at 10 m, and surface and water-column maximum chl *a* indicate that overall abundance was related (positively) only to the chl *a* maximum, most strongly when log abundance was used ($F = 15.515$, $p = 0.0001$). The same positive relationships with chl *a*, with somewhat reduced p levels, apply to each population component: nauplii, copepodids, and adults.

There was no correlation of egg abundance with either temperature or food ($F < 2$, $p > 0.05$). Perhaps of greater interest, stepwise regression revealed a significant negative influence of chl *a* maximum on the distribution of eggs per female ($F = 5.143$, $p < 0.05$).

Among stations, there were large differences in stage-frequency distributions during the broad-scale survey. Average stage of development (assuming 12 stages, NI to adult, with grouped nauplii taken as stage 3) was not related (stepwise regression at p to retain = 0.1) to temperature or chl *a*. Nor did there appear to be spatial patterns in stage-frequency distributions among stations. On a larger scale, the stage-frequency distributions in each of the 3 broad localities (15 stations combined in the Bay of Mejillones, 30 stations off the Mejillones Peninsula, and 8 stations off Antofagasta—see Fig. 1) differed strongly (contingency $\chi^2 = 17746$, $p < 10^{-7}$). Even within a limited area of the Bay of Mejillones, there were large differences among stations (Fig. 4; contingency $\chi^2 = 7949$, $p < 10^{-7}$). Cluster analysis of the rank correlations among stations in the Bay of Mejillones revealed inconsistent groupings of nearby

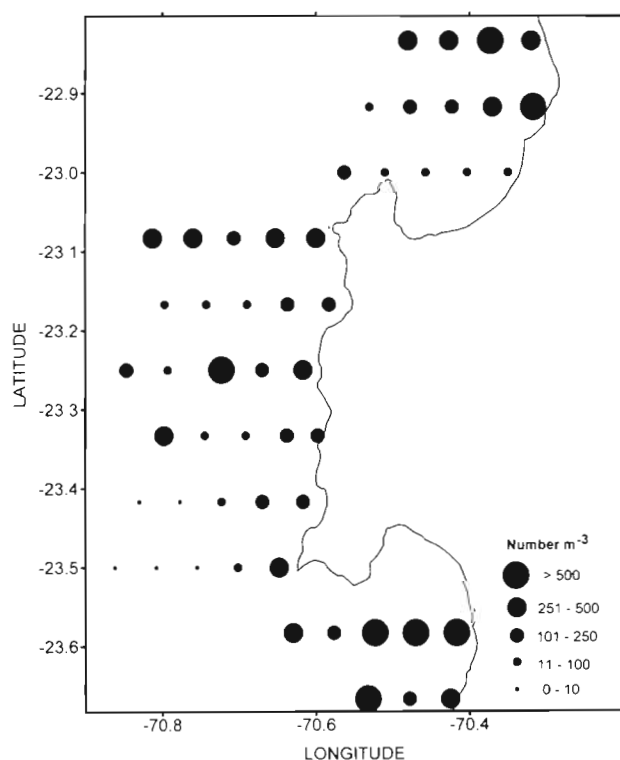


Fig. 3. Distribution of *Calanus chilensis* in December 1996 in the coastal area of the Mejillones Peninsula in the upper 200 m layer. Abundance for each station was obtained from mean values between the 2 sampling strata: 200 – 50 m and 50 – 0 m depth and includes all copepodites and nauplii stages

stations, and overall there was no relationship between similarities of stage distributions (rank correlations) and distances among stations ($r = 0.04$, $p > 0.05$).

In summary, while abundances of *Calanus chilensis* were positively related to chlorophyll concentrations, 2 potential measures of the effects of chl *a* on production (mean stages of development, eggs per female) were either negative or non-significant.

Annual cycles in the Bay of Mejillones

The annual cycles of temperature and chl *a* (Fig. 5) show the relatively high chl *a* levels through much of the year, and the usual development of stratification during the austral summer. However, Fig. 5 also shows that the normal seasonal pattern of temperature was altered by the onset of El Niño 1997, which produced an abrupt warming and deepening of the thermocline by May 1997, preceded by a sharp near-surface chlorophyll maximum.

Abundances and stage-frequency distributions of *Calanus chilensis* varied greatly through the year, although numbers were generally higher in winter and lower in the summer (Fig. 6). It might seem tempting to trace cohorts in the seasonal stage-frequency distributions (for example, suggesting that adults on June 23 produced the many eggs and nauplii observed on July 9, and in turn giving rise to the copepodites and adults

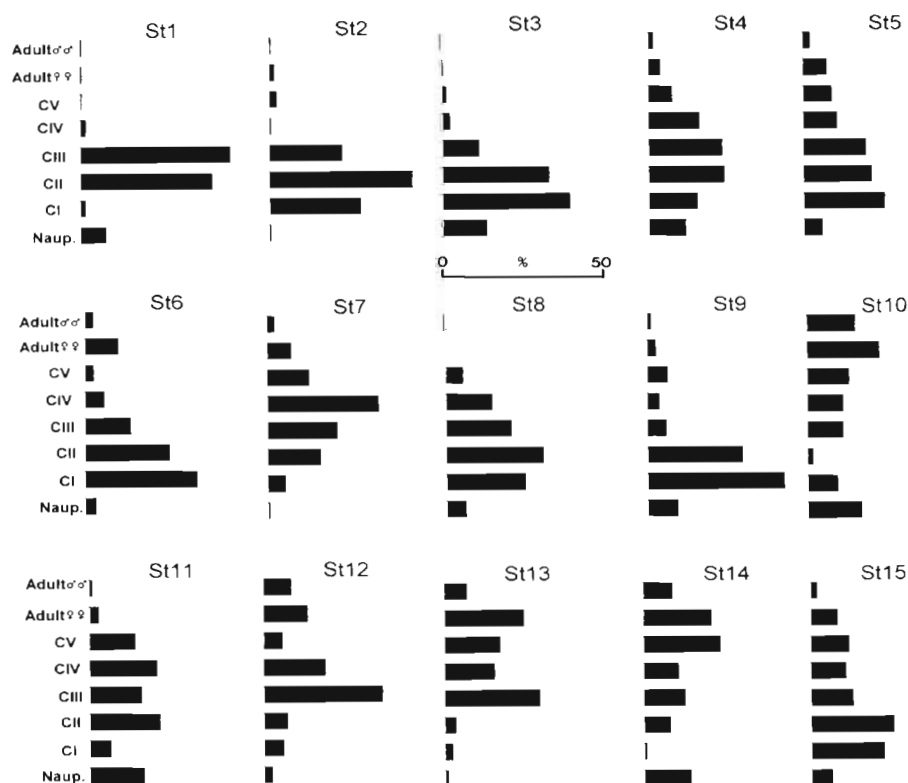


Fig. 4. Stage distribution of *Calanus chilensis* from 15 stations in the northern area of Peninsula Mejillones (see Fig. 1)

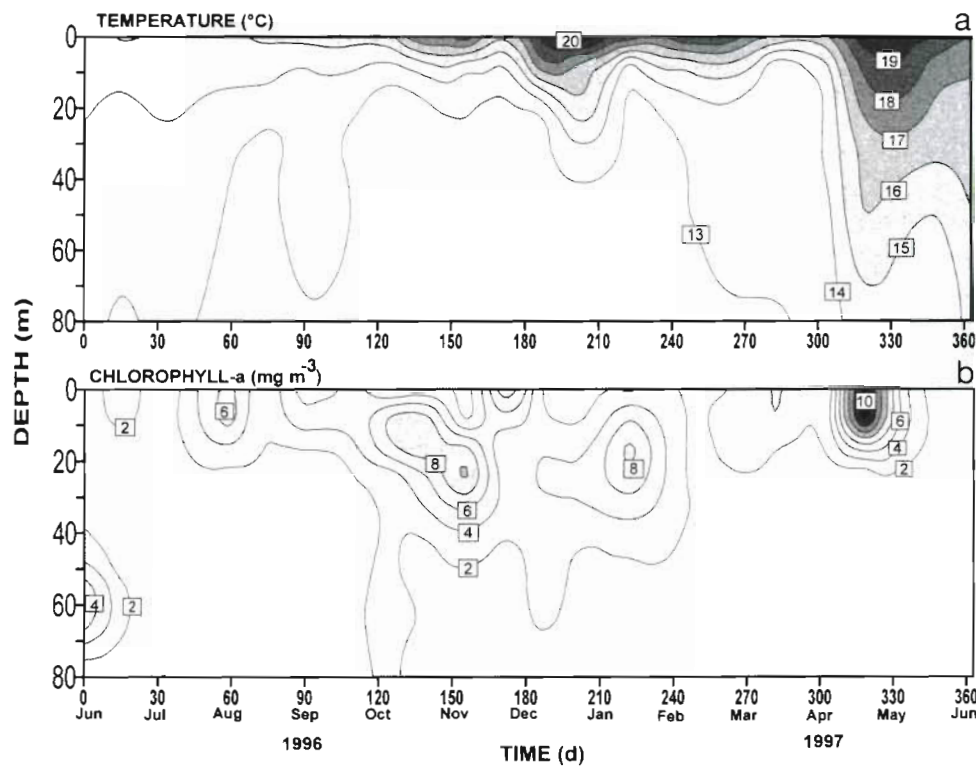


Fig. 5. The seasonal cycle of (a) temperature and (b) phytoplankton biomass in the Bay of Mejillones during June 1996 and July 1997, obtained from ~15 d interval profiles from 3 stations. Contours were constructed from every 5 m depth of resolution from surface to bottom

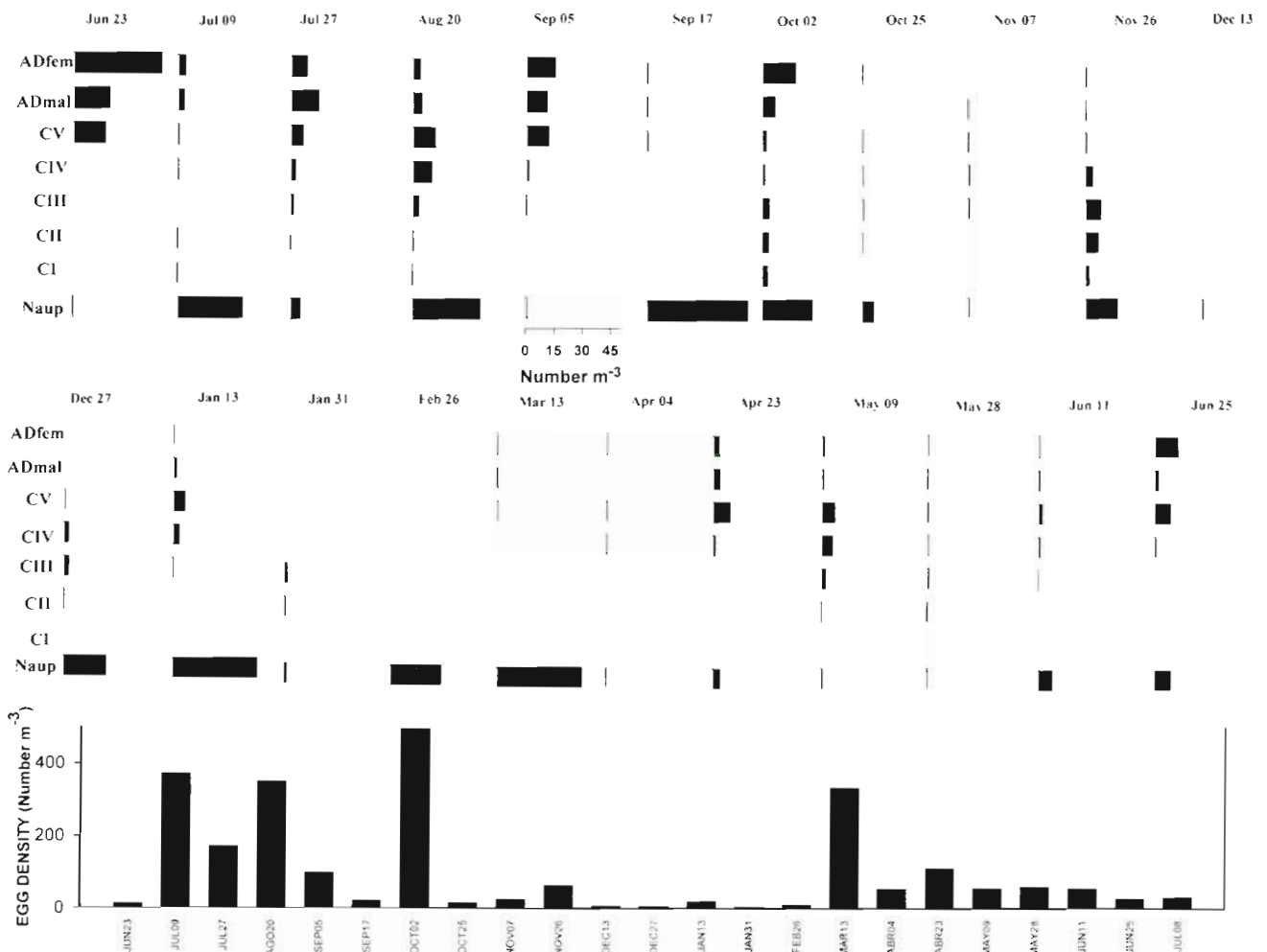


Fig. 6. Stage distribution and abundance of *Calanus chilensis* during a year cycle in the Bay of Mejillones. Stage abundances are estimated from mean values from 3 stations (Fig. 1), sampled from near the bottom (ca 90 m) to surface

found on July 27). This would be unwise for 2 reasons. First, the great spatial variation in stage-frequency distributions (Fig. 4) precludes assumption that cohorts are widely synchronous. Second, the mean sampling interval of ~17 d is not far short of generation times predicted from temperatures during the year (ca 22 d, Table 1). Much overlapping of cohorts must result from continuous production, because eggs were always present (Fig. 6). Moreover the number of eggs per female although variable remained high most of the year (Fig. 7).

At the end of May, the onset of El Niño 1997 was accompanied by an almost complete disappearance of *Calanus chilensis* from samples. However, by late June, numbers were restored to levels approaching those of the previous June.

Lengths, weights, and production

Here we estimate production on the assumption that it is determined by temperatures at the times of sampling. This procedure is justified in the discussion.

Dry weights and body lengths were obtained directly for copepodids and adults present on each sampling date, and weights of eggs and nauplii assumed as indicated in 'Methods'. Adult female dry weights and lengths were higher in winter-spring and declined sharply in summer (Fig. 8). Decline of body size was associated with increasing temperatures towards summer and fall (Fig. 5). Body length was negatively associated with temperature at 10 m depth (stepwise regression, $F = 13.051$, $p < 0.01$), but not with

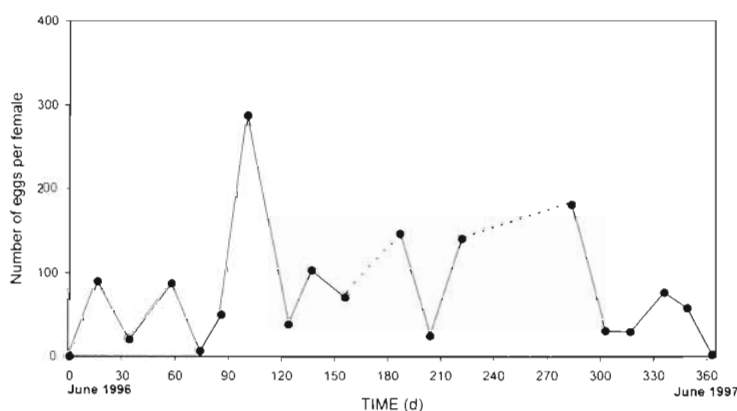


Fig. 7. The ratio between number of eggs and female abundance of *Calanus chilensis* during a year cycle 1996–1997. The sampling interval is roughly 15 d and dotted lines represent interpolations in periods when females were absent

mean chl *a* concentration in the upper 50 m, which was high in the spring, low in the summer, and again high in the fall (Fig. 5). Female dry weight showed no association with either temperature, or chl *a*.

The temperature-dependent stage durations and instantaneous growth rates are shown in Table 1. Growth rate changed only moderately through time, although it does not closely follow the temperature pattern. Although the growth rates are driven by a positive effect of temperature on development rate, the apparent lack of effect on body weights (negative on body lengths, and perhaps on weights with larger sample sizes) obscures this positive effect development rates. Daily production rates on the other hand show drastic variability, according to differences of biomass, although there is a lack of any seasonal pattern associated with either temperature or food (Fig. 9).

Using the stage-by-stage growth rates and biomasses, estimated daily production rates and corresponding total biomasses for each time interval; integrated annual production was calculated as 45.4 mg dry weight m^{-3} , corresponding to ca 1.12 g C $m^{-2} yr^{-1}$, assuming 40% of carbon content from the dry weight and taking a mean depth of the 3 sampling stations as 62 m. The mean annual biomass of about 1 mg dry weight m^{-3} yields a P/B ratio of about 45.

The biomass of *Calanus chilensis* during December 1996 was unevenly distributed in the area, following the distributional pattern of adult females. Distribution of the daily production rates was, as expected, highly associated with that of biomass. The mean daily production of *C. chilensis* for the 53 stations was 1.57 mg dry weight $m^{-3} d^{-1}$, with a standard deviation of 1.706. Integrating in the water column down to 200 m, this yields 126 mg C $m^{-2} d^{-1}$ as an average for the 3 d sampling period.

Spatial variability of biomass in the whole area might explain the apparent low annual production in the Bay

Table 1. Temperature-dependent stage durations and instantaneous growth rates (g_i) of *Calanus chilensis* during the annual cycle in Bay of Mejillones, from June 1996 to June 1997. Mean values and standard deviations (SD) are from $n = 22$. Stages durations and g_i were estimated using Eq. (1) and (3) (see text) and using the mean temperature at 10 m depth measured at 3 stations in the Bay of Mejillones (Fig. 1)

Stage or phase of development	Stage duration (d)		g_i (d^{-1})	
	Mean	SD	Mean	SD
Hatching–CI	8.5	0.87	0.045	0.024
CI	1.9	0.19	0.335	0.177
CII	2.1	0.22	0.240	0.111
CIII	2.3	0.24	0.354	0.180
CIV	2.7	0.29	0.313	0.113
CV	4.7	0.50	0.092	0.049
Total	22.2			

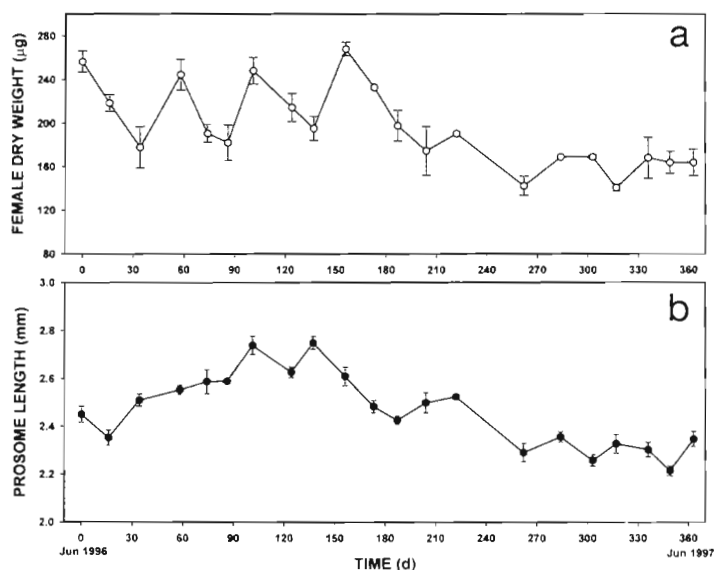


Fig. 8. (a) Female dry weight and (b) female prosome length of *Calanus chilensis* in the Bay of Mejillones during its annual cycle 1996–1997. Values are means from $n > 5$ for dry weight and $n > 20$ for length and vertical bars are standard errors

of Mejillones. For instance, on December 13, a few days prior to the survey, the estimate of daily production for the 3 stations inside the bay was extremely low, ca $0.9 \mu\text{g dry weight m}^{-3}$ when only nauplii were present (Fig. 6). This estimate is orders of magnitude lower than the average for the broad-scale survey. Low biomass of *Calanus chilensis* in the Bay of Mejillones is evident from Fig. 3, and this might well be a frequent situation in the area during the annual cycle.

DISCUSSION

The critical assumption in our estimates of production is that growth and development were determined by prevailing temperatures and unaffected by the quantity or quality of available food. The temperature-dependence of development rates could not be directly tested from successions of distinguishable cohorts in the time-series samples. However, there is some indirect evidence that food supply is unimportant.

(1) The lack of correlation in the broad-scale survey between levels of chlorophyll *a* and mean stage of development suggests that copepod development was locally neither retarded nor accelerated in relation to food supply.

(2) The year-long series revealed no evidence of possible responses of aspects of life

histories to food shortages. Development did not become stalled in particular stages (for example in copepodid resting stages) during the year-long study. Rather, nauplii, copepods, and adults were present in varying proportions in virtually all samples. In particular, adult males, which indicates recent maturation in other *Calanus* species because they are short-lived (e.g. Marshall & Orr 1955), were present in most samples (Fig. 6). Furthermore, the number of eggs per female in the samples (Fig. 7), while very variable, showed no seasonal patterns that might reflect food shortages and was not associated with either mean chl *a* in the upper 50 m, or temperature at 10 m (step-wise regressions, $F < 1$, $p > 0.05$). The weak negative relationship between number of eggs per female and chl *a* levels in the broad-scale survey again suggest that egg production was unaffected by food supply during that time. (The negative effect is inexplicable, without ad hoc explanations involving, perhaps, differential distribution of egg predation.)

(3) The decline of both body length and weight of females towards the warm season might appear to suggest that cohorts were experiencing poor conditions for maximal growth and development rates. However, female body length in the time series was related to temperatures, not chlorophyll, and body weight (based on smaller sample sizes) was not related to either. It is known that higher temperatures may reduce final size in ectotherms (Atkinson 1994), including copepods (Uye 1988, Escibano & McLaren 1992, Carloti et al. 1993).

Assuming that production rates were indeed dependent on temperature alone, our estimation procedures can also be justified.

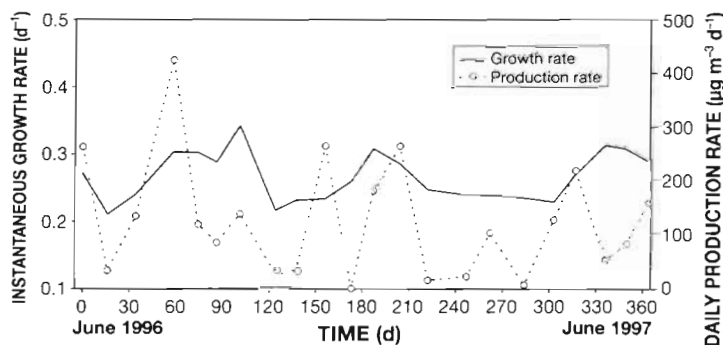


Fig. 9. Variability of the weight-specific growth rate and daily production rate of *Calanus chilensis* in B. Mejillones during its annual cycle 1996–1997. Weight-specific growth rate (g_t) was estimated as temperature-dependent and production rate by biomass estimated from dry weights of all developmental stages

(1) The Beléhrádek equation is simple in form and its parameters are related to some other features of animal responses to temperature (McLaren 1995). Here we have used it only as an empirical convenience when assuming the same relative stage durations found in other *Calanus* species. The production estimates would not be noticeably affected by choice of a particular temperature function.

(2) Because of the possible inadequacy of estimated development times of later copepodids of *Calanus chilensis* in laboratory experiments, we have used estimates based on the similarity of relative times among other *Calanus* species, as justified in our 'Methods' section.

There was great local variation in abundance of *Calanus chilensis*, and its correlation with surface chl *a* need not imply a direct, causal relationship. It could, for example, result from common hydrographic processes (e.g. Lindahl & Perissinoto 1987) or copepod motility in relation to small-scale concentrations of food (e.g. Garcia-Soto et al. 1990, Cowles et al. 1993). Abundances were generally smaller at stations inside the northern bay than elsewhere, and in particular in the southeast part of the Bay of Mejillones (Fig. 3). Upwelling with advection offshore may have produced some of the variation among stations. Advection is a relevant factor in upwelling zones (Smith 1968). Strong offshore currents of the surface Ekman layer may cause large displacement of passive populations (e.g. Wroblewski 1980). This seems to strongly affect distribution of *C. chilensis* in northern Chile (Gonzalez & Marin 1998). Although in vertically stratified systems zooplankton can use current shear to maintain vertical position (e.g. Peterson et al. 1979), *C. chilensis* copepodids tend to accumulate offshore because of advection (Gonzalez & Marin 1998). Younger copepodids were relatively more abundant at the outermost stations in the Bay of Mejillones, whereas older copepodids and adults predominated in the much smaller populations at stations in the inner and southern parts of the bay (Fig. 4). This is perhaps consistent with younger animals being swept out by the offshore currents, with older ones better able to take advantage of shear conditions for maintaining their positions.

The variation in stage-frequency distributions among samples from the December survey, and the lack of coherence of mean stage of development among nearby samples, suggests that cohorts were spawned and developed without the wide synchrony that is imposed by seasonality in some temperate localities (e.g. Solow & Steele 1995). The homogenizing forces of diffusion and advection were evidently not enough to eliminate the effects of local population histories in the area. Both abundances and stage-frequency distributions could also have been subjected to locally varying predation regimes.

Whatever the sources of the great local variation in abundance and population structure, it casts doubt on the wider applicability of the estimates of annual production at 3 stations in the Bay of Mejillones. The estimated annual production of *Calanus chilensis* at 45 mg dry weight m^{-3} , even though production is sustained through the year, is lower than that of *Calanus finmarchicus* on Georges Bank (Canada), estimated as 76.2 mg C m^{-3} (Davis 1984), equivalent (at C/dry weight = 0.40) to 190 mg dry weight m^{-3} , or on the Scotian Shelf, eastern Canada, estimated as 122 mg dry weight m^{-3} (McLaren et al. 1989a). If the relatively low biomasses of *C. chilensis* during December 1996 in southern Bay of Mejillones prevailed at other times of year, then annual production may have been much higher in the wider upwelling area off northern Chile. The annual P/B of 45 in the Bay of Mejillones, compared with P/B of ~8 on the Scotian Shelf (McLaren et al. 1989a), is more in keeping with the general view that the former is part of one of the world's most productive marine systems.

Acknowledgements. This work has been funded by FONDECYT-Chile, Grant 196/1265 to R.E. It is also a contribution to the FONDAP-HUMBOLDT Program of CONICYT-Chile, which provided additional support. I.M. research is supported by an operating grant from the Natural Science and Engineering Research Council of Canada. Valuable comments from anonymous reviewers have helped improved earlier versions of this work.

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Editorial responsibility: Otto Kinne (Editor),
Oldendorf/Luhe, Germany

Submitted: March 26, 1998; Accepted: September 19, 1998
Proofs received from author(s): February 3, 1999