

Seasonal vertical distribution, abundance, biomass, and biometrical relationships of ostracods in Golfo Dulce, Pacific coast of Costa Rica

Alvaro Morales-Ramírez^{1,2} & Jens Jakob³

1. Centro de Investigación en Ciencias del Mar y Limnología (CIMAR), Universidad de Costa Rica, 2060 San Pedro de Montes de Oca, Costa Rica.
2. Escuela de Biología, Universidad de Costa Rica, 2060 San Pedro de Montes de Oca, Costa Rica; alvaro.morales@ucr.ac.cr
3. Institut für Zoologie, Berlin Frei Universität, Berlin, und das Zentrum für Marine Tropenökologie (ZMT), Universität Bremen, Germany

Received 09-X-2007. Corrected 10-IV-2008. Accepted 12-V-2008.

Abstract: The abundance, biomass, and vertical distribution of ostracods, as well as some biometrical relationships, were investigated during a 24h cycle over a period of two days, both in May and September 1995 in Golfo Dulce, on the Pacific coast of Costa Rica. The sampling was performed according to the tidal cycle, in addition to vertical sampling at depths of 0-10-20-30-40-50-70-80 and 100m to determine temperature, salinity, oxygen concentration, and Secchi depth. Zooplankton samples were taken using a close-up Nansen net in three sampling layers: 0-20m, 20-50m and 50-100m. Ostracod abundance (adults and developmental stages) and total dry weight biomass were estimated from one aliquot obtained with a Folsom Plankton Splitter. Ostracod dry weight biomass was measured by taking between five and fifty organisms of a single development stage. Four ostracod species were found: *Cypridina americana*, *Euchonchoecia chierchiae*, *Porroecia spinirostris*, and *Porroecia* sp.. Biometrical relationships for the former two species revealed significant differences between all stages both in average length and season ($p < 5 \cdot 10^{-7}$), and seasonal differences in the size between males and females for both species, with strong sexual dimorphisms in the males. Seasonal differences in biomass were found in *C. americana* due to the fact that ovigerous females weighed twice as much in May than in September. Species dominance in ostracod abundance alternated between *E. chierchiae* and *C. americana*, depending on the season. In general terms, both species were primarily found at depths within the first 20m in May, while at depths greater than 50m abundance was only 2% and 0.4% for *C. americana* and *E. chierchiae*, respectively. In May, some differences in the day/night rhythms were detected in *C. americana* in all developmental stages, except the first stages, which were always found at depths within the first 20m, in contrast to *E. chierchiae*, where all development stages, except stage I, remained in the first sampled layer, regardless of circadian periodicity. Differences in vertical patterns may be related to a predator avoidance behavior or to utilization of food resources related to ontogenetic components, at least for *C. americana*. Ostracod abundance in Golfo Dulce, in comparison with the oceanic environment, is extraordinary high in spite of the oceanic features of this gulf. Both species play an important role in the trophic ecology of Golfo Dulce, where *C. americana* is a detritivorous species and a facultative predator, whereas *E. chierchiae* grazes on organic matter. This is the first ecological study on ostracods from Costa Rican coastal waters. Rev. Biol. Trop. 56 (Suppl. 4): 125-147. Epub 2009 June 30.

Key words: ostracods, Golfo Dulce, Pacific, abundance, biomass, distribution, *Cypridina americana*, Costa Rica.

Marine pelagic ostracods have received scant attention from marine ecologists despite their relatively high numerical abundance (often outnumbered only by copepods), and more or less ubiquitous occurrence at all oceanic depths (Angel 1999). They are the second

most dominant zooplankton group in tropical and sub-tropical areas after copepods (Angel 1999). For example, Poulsen (1977) reported that out of 100 species found in three oceans, seventy common tropical-subtropical species are distributed between 39°N and 39°S. They

are considered omnivorous, including a few specialist and opportunistic species (Jacob 1996) feeding on detritus (Angel 1999) and preying on living organisms (Kornicker *et al.* 1976). Pelagic ostracods form a significant part of the diets of chaetognaths (Segura *et al.* 1992), decapods (Guerao 1995), sergestids (Hopkins *et al.* 1994), thysanopods (Kinsey & Hopkins 1994), and also tropical and subtropical fishes (Hopkins & Baird 1985, Lancroft *et al.* 1988, Elorduy-Garay & Caraveo-Patiño 1994, Sazar & Glova 1998). Several ostracod species carry out a diel vertical migration as is the case for *Conchoecia* spp. (Angel 1984), *Macrocypridina castanea*, and *Gigantocypris muelleri* (Kornicker *et al.* 1976). Many species have often been found at the surface at night, while few have been encountered at the surface during the day (Poulsen 1977), the bioluminescence of many species being one of their salient ecological features (Shimomura 2006). In addition, marine and brackish ostracods are being considered relevant sentinel species of anthropogenic impact (Ruiz *et al.* 2005). However there is very little information available about the life histories of most pelagic ostracods, except for the prominent works of Kock (1992), regarding the life cycle of two endemic *Alacia* spp. of the South Ocean, and of Ikeda (1990, 1991, 1992) on *Conchoecia pseudodiscophora* from the Japan Sea. Consequently, important ecological features of tropical and sub-tropical ostracod species are practically unknown. Few works including aspects of distribution and composition, have been published from the Indian Ocean (Vijayalakshmi & Madhupratap 1984), Adriatic Sea (Brautovic *et al.* 2006), and the Red Sea (Cornils *et al.* 2005).

For Costa Rican coastal waters, studies of ostracods are very scarce. In Golfo Papagayo, a small upwelling region in the North Pacific coast, ostracods show a seasonal dominance over copepods: they are the most abundant group during the rainy season (not upwelling, Bednarski & Morales-Ramírez 2004). In other upwelling regions in the Pacific, ostracods are more abundant during the seasonal absence of upwelling and during an El Niño event

(Castillo *et al.* 2007). It was observed during the *Victor Hensen* expedition on the Pacific coast of Costa Rica Wolff & Vargas (1994), and one of us (A. Morales), high abundances of pelagic ostracods, especially in the inner area of Golfo Dulce. It has now been established that ostracods contribute to 8% of the total abundance of non-gelatinous zooplankton in Golfo Dulce (Quesada-Alpizar & Morales-Ramírez 2006), being the third group after copepods and appendicularians. The goal of this study was to evaluate the vertical distribution, abundance, and biomass of ostracods, as well as some biometrical relationships of two ostracod species in Golfo Dulce, a fjord-like ecosystem on the Pacific coast of Costa Rica.

MATERIALS AND METHODS

The selected station was located in the northwest region of Golfo Dulce, near Rincon Bay (8°42' N and 83°27' W, Fig. 1), precisely where high densities of ostracods have been observed (Hossfeld *et al.* 1994).

Sampling program and analytical procedures: The sampling was carried out from an inflatable boat which was equipped with a hand winch for bottles and net. For the comparison of seasonal behaviors of ostracods, a sampling program was conducted for two days in May and September 1995 (Table 1), which reflects the dry and rainy seasons, respectively. Before each zooplankton haul, a vertical profile was conducted, sampling at 0-10-20-30-40-50-60-70-80 and 100m depth to determine the physical parameters. Temperature (°C) was measured with a thermometer and salinity with a hand refractometer. For oxygen content, a modified micro-Winkler set kit on board was employed (ISO 5813:1983). Secchi depth was also determined. Three sampling layers were defined: 0-20, 20-50 and 50-100m. Zooplankton samples were taken using a close-up Nansen net, with 70cm diameter and 100µm mesh size approximately every six hours following a tidal cycle, from an inflatable boat. Due to the weight of the net

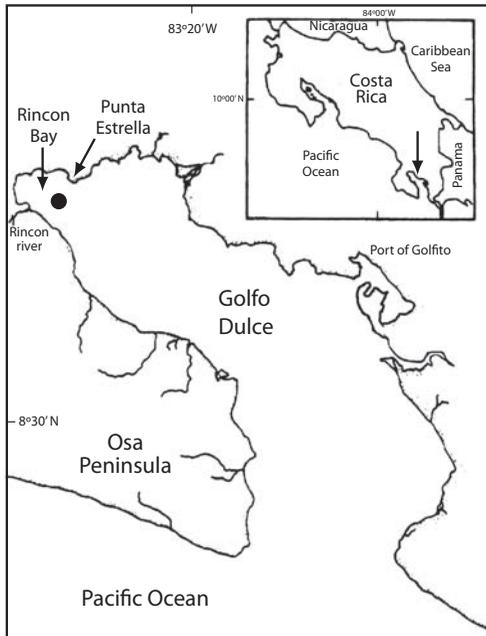


Fig. 1. Golfo Dulce, Pacific coast of Costa Rica. Location of the study site in Rincon Bay.

(30-35kg, with a weight base to give stability to the net during the trawl), it was not practical to take more than one sample from each sampling layer. Samples were preserved with 4% formalin.

In order to estimate ostracod abundance, for each depth layer one aliquot was obtained with a Folsom Plankton Splitter depending on zooplankton density, representing not more than 1/32 of the original sample. Homogeneous distribution was tested with a χ^2 . No significant deviations were observed. Adult ostracods and their corresponding developmental stages were identified and counted. The identification followed Kornicker (1967, 1968, 1970a,b, 1974, 1975, 1983, 1987, 1991), Heitkamp (1978), and Angel (1981). In addition, one fourth of the sample was filtered on a pre-weighed Whatman 55mm diameter GF/C glass filter for dry weight determination. The filters were dried at 60°C for 24 hours and then placed for one hour in a desiccator and weighed in an analytical balance (0.01mg). Ostracod dry weight biomass was measured by taking between five and fifty organisms of a single development stage and putting them into a small pre-weighed aluminum box. The same procedure mentioned above was followed, an analytical balance (0.0001mg), was employed.

Biometrical relationships: Two ostracod species were used to calculate biometrical relationships. Three hundred animals were measured with respect to length of body and height of carapace. The relationship between height

TABLE 1
Sampling program at Rincón Bay and Punta Estrella, Golfo Dulce, Pacific coast of Costa Rica, during 1995

| Date | Time | O ₂ content, Salinity and Temperature | Nutrients (NO ₂ ⁻ , NO ₃ ⁻ , PO ₄ ⁻ , SiO ₄) | Tide condition | Zooplankton samples |
|----------|-------|--|--|----------------|---------------------|
| May, 2 | 10:45 | Rincón Bay | - | Low | X |
| May, 2 | 15:45 | - | - | High | X |
| May, 2 | 22:35 | - | - | Low | X |
| May, 3 | 05:15 | - | - | High | X |
| May, 3 | 10:35 | Rincón Bay | - | Low | X |
| May, 3 | 17:20 | Pta Estrella | Pta Estrella | High | X |
| Sept., 6 | 09:20 | Rincón Bay | - | Low | X |
| Sept., 6 | 15:35 | Rincón Bay | - | High | X |
| Sept., 6 | 21:10 | - | - | Low | X |
| Sept., 7 | 03:20 | - | - | High | X |
| Sept., 7 | 08:50 | Pta Estrella | Pta Estrella | Low | X |
| Sept., 7 | 13:45 | - | - | High | X |

and length can change through ontogenesis and will be expressed by the allometric formula:

$$H: b \cdot \text{length } a,$$

where a is all dependent growth factors, while b represents all independent growth factors. For the investigations regarding body size, two procedures were applied: A. Diagram growth factors, where values will be given as $N+1$ against the general (in percent) growth radius, so it will allow examination of whether growth stages remain constant, and B. By Hiatt diagram growth (Hiatt 1948), will be given as length against length $N+1$. The data points have been adjusted to the higher correlation coefficient. Body size was measured from rostrum tip to the end of caudal rami and from rostrum tip to the end of the posteriordorsal caudal rami. Measurements were made by means of a stereoscope (100x, and 60x). Differences between classes size-development stages were tested with ANOVA.

RESULTS

Physical parameters: In general, for both months two very well-identified water layers were found in the 100m depth water column: a non-homogeneous layer from 0 to 50m depth, where temperature and salinity gradients were often observed, and a second homogeneous layer from 50 to 100m depth. Surface temperature had an average of 30°C, while in the deep layer the average was 19°C. A thermocline was observed between 20 and 50m depth for both months (Fig. 2). Oxygen content shows a behavior similar to that of temperature (Fig. 2), but a strong oxycline was observed within the first 20m depth in May and 40m depth in September, while in May values of $0.7\text{mgO}_2\cdot\text{L}^{-1}$ found at 20m, a rise in the oxygen concentration is shown at 30m depth ($1.3\text{mgO}_2\cdot\text{L}^{-1}$). On the other hand, salinity shows a fluctuation between 28 and 32PSU in the first 10m in May, compared to 28-33PSU in September (Fig. 2). Below 50m, salinity was very constant for both months (34-35PSU).

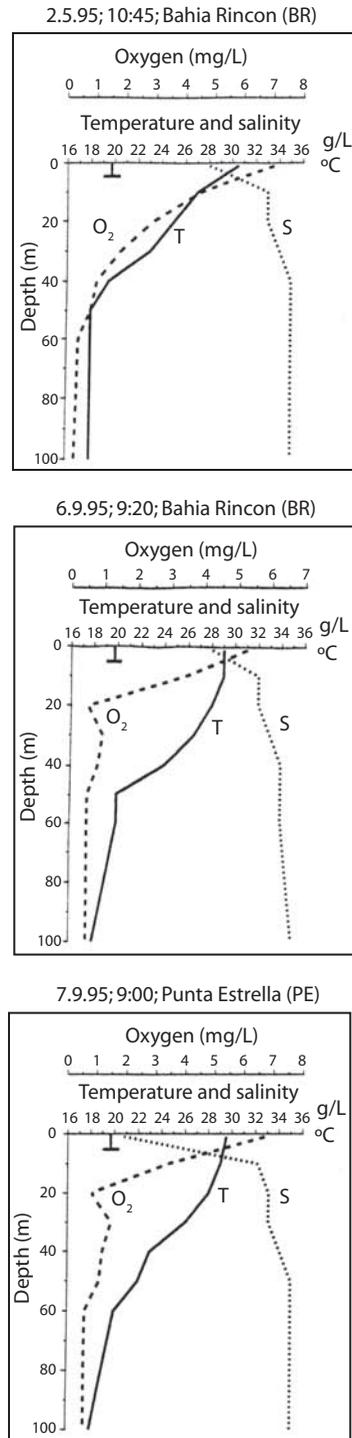


Fig. 2. Profiles of temperature ($^{\circ}\text{C}$), salinity (UPS) and oxygen concentration ($\text{mgO}_2\cdot\text{L}^{-1}$) at the sampling stations, Golfo Dulce, Costa Rica.

Lastly, Secchi disc depth had an average of about 4.2m.

Biometric relationships: Four ostracod species were found: *Cypridina americana* Müller 1890, *Euconchoecia chierchiae* Müller 1890, *Porroecia spinostris* Claus 1874, and *Porroecia* sp. Only results for the two former species are presented, because they are the dominant species. Both *P. spinostris* and *Porroecia* sp. were very scarce, also all data of abundance and biomass are related to the former species. Body length and body height have been measured for all five juvenile stages of *C. americana* (described by Jakob 1996) and all six juvenile stages for *E. chierchiae*, for both males and females. According to Heitkamp (1978), Myodocopida species of ostracods have five or six developmental stages, although Angel (1996) has established six developmental stages for Myodocopida, and Ikeda (1992) seven for *Conchaecia pseudodiscophora*. ANOVA tests have given significant differences between all stages of the two species, both in average length and year season ($p < 5.10^{-7}$).

Three older stages of *Cypridina americana* showed seasonal differences in length, height, and dry weight, while *Euconchoecia chierchiae* did not show any seasonal difference in size and weight. On average, the body length and height in May for *C. americana* was 0.36 and 0.50mm for the smallest stage, 1.07 and 1.76mm for males and 0.99 and 1.53mm for females (Fig. 3). Adults showed marked sexual dimorphisms, which are reflected in the long antennas of the males. In September, there was a decrease in the body size of *C. americana*, especially for the three older stages. On average adults measured 1.02 and 1.62mm for males and 0.92-1.38 for females. Significant seasonal differences for stage V males and females (Fig. 3) were found (ANOVA, $p < 0.0007$). For *E. chierchiae* growth in length dominated over growth in height throughout the complete period of development for individuals (Fig. 3B). Females have on average a body size of 1.10mm while for males the average is only 0.97mm, with

strongly marked sexual dimorphisms as in *C. americana*.

The increase in length and height were, for both species, not constant (Fig. 4, growth factor diagram). Values fluctuated between 113 and 135% for *C. americana* in May and 118 and 133% in September; while for *E. chierchiae* these values fluctuated between 109 and 128% in September (Fig. 4). The length curves of *E. chierchiae* run parallel to the height curves, which indicate a constant development in both growth parameters. The curves for *C. americana* are practically the same for both months, except for the development in males in September. Differences can be observed from the growth factors of juvenile stages in September. Both species during both seasons show lower growth factors for stages II to III than from I to II or from III to IV. A decrease can be observed for stages V to VI by *Euconchoecia chierchiae* (Fig. 3). *C. americana* shows minimal values for the molting of females compared with those observed for *E. chierchiae* males (Fig. 3B).

Results of the Hiatt-growth diagram are presented in Fig. 5, where the best regression for length is when N is adjusted to N+1. Males of *C. americana* exhibited a linear regression, while body size increase for females can be described by a second degree polynomial. This is applicable for both sexes of *E. chierchiae*, although it had negative allometric growth where $a=0.752$ (Fig. 6). While juvenile stages data show little scattering, sexual dimorphisms of adults cause greater scattering. The development in males was characterized by a height increase against a low increase in length. On the other hand, females show precisely the opposite tendency. *C. americana* females show linear growth (isometric growth) where $a=0.97$.

Biomass and abundance: For *C. americana* seasonal differences have been found for dry weight depending on developmental stages (Fig. 7, M=Males, F=Females, FE=Females with eggs). The weight difference was on average 32%, because ovigerous

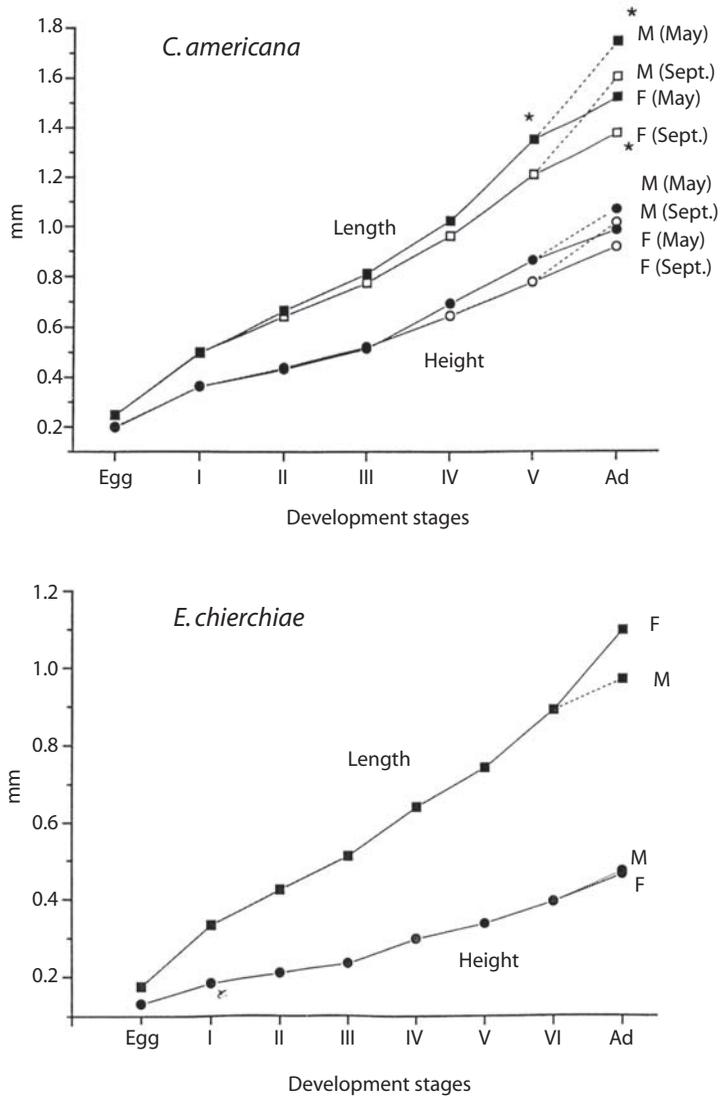


Fig. 3. Biometrical relationships for both ostracods species, development stages, and season, Golfo Dulce, Costa Rica, 1995. (M= Males, F= Females, Ad= Adults).

females weighed twice as much in May as in September ($0.0617 \pm 0.0029 \text{mgDW}$ against $0.036 \pm 0.0057 \text{mgDW}$). A higher proportion of the female's weight in September was due to a higher proportion of eggs. Weight ratios between *Cypridina americana* and *Euconchoecia chierchiai* were 3.2:1 for juvenile stages and 6:1 for adults (only May). Seston concentration

(>100 μm) was higher for both seasons (Fig. 8) at the first 50m of depth. Below 50m, zooplankton samples contained mainly detritus, excavates, and small copepods in both months. In May, on average $51 \text{mg DW} \cdot \text{m}^{-3}$ were found in the first 20m, $21 \text{mgDW} \cdot \text{m}^{-3}$ between 20 and 50m depth, and only $1 \text{mgDW} \cdot \text{m}^{-3}$ at the deepest sampled layer (50-100m). In September

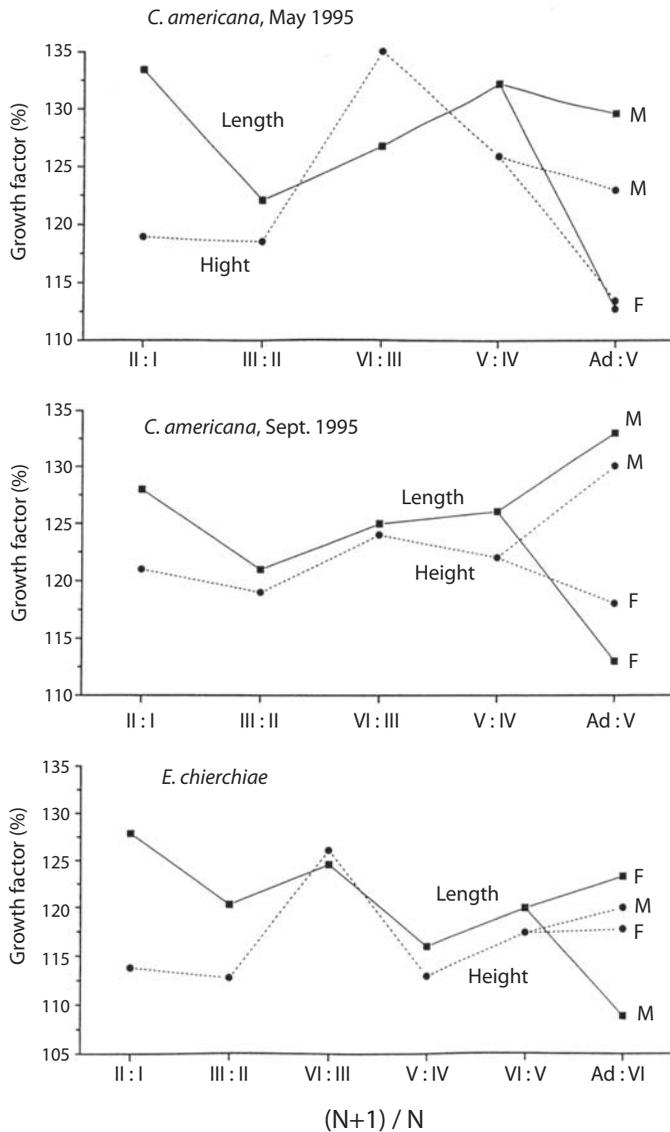


Fig. 4. Growth factor diagram to relate the increase in length and height of *E. chierchiai* and *C. americana* in Golfo Dulce, Costa Rica. (M= Males, F= Females, Ad= Adults).

110mg DW·m⁻³ were recorded in the first 20m depth. In the other two layers seston concentration was negligible (except the sample at 21:10h, 0-20m depth), where the major part consisted of detritus (Fig. 8). Seston dry weight density was 30-50% greater in September than in May. The contribution of ostracods to

seston (>100µm) fluctuated seasonally between 10-20% in May and 20-40% in September. *C. americana* was the species responsible for this in the majority of cases at the 20-50m depth layer; especially in September. On the other hand, the biomass dominance between both species changed in May, where at 17:20h

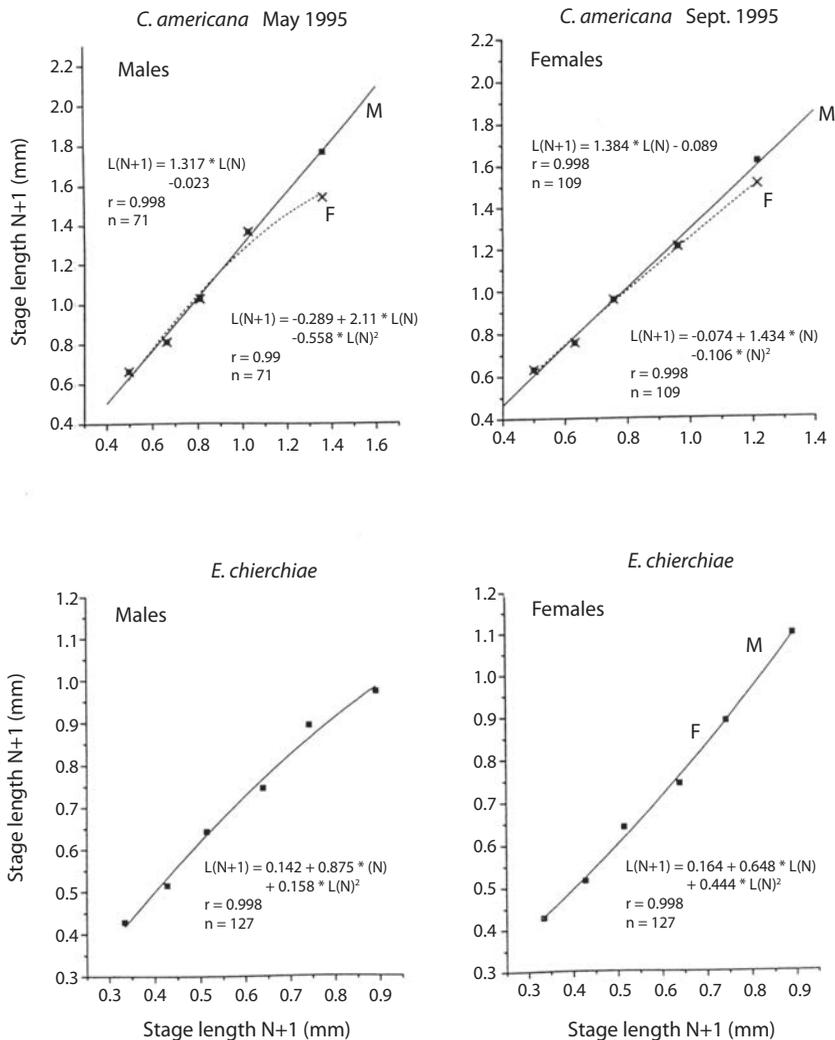


Fig. 5. Hiatt-growth diagram for both ostracods species in Golfo Dulce, Costa Rica, during 1995.

practically only individuals from *E. chierchiai* were found. Ostracod biomass averaged 7.6 in May and only 3.1mgDW·m⁻³ in September.

In May in the Rincon Bay station, *E. chierchiai* decreased in abundance compared to September (Fig. 9). Both days in May, *E. chierchiai* clearly dominated over *C. americana* by up to ten times more individuals·m⁻³ (Fig. 9), but in September the *C. americana* population increased while *E. chierchiai* was completely

absent. In general, ostracod abundance remained constant (700 and 880 organisms·m⁻³ in May and September, respectively). The period of greater ostracod abundance shows a higher proportion of juvenile stages (Table 2), with a ratio of males to females of 1:18 for *C. americana*. Although density was low in May, the number of females carrying many eggs was double in May what it was in September (Table 2). *E. chierchiai* showed a similar trend of low

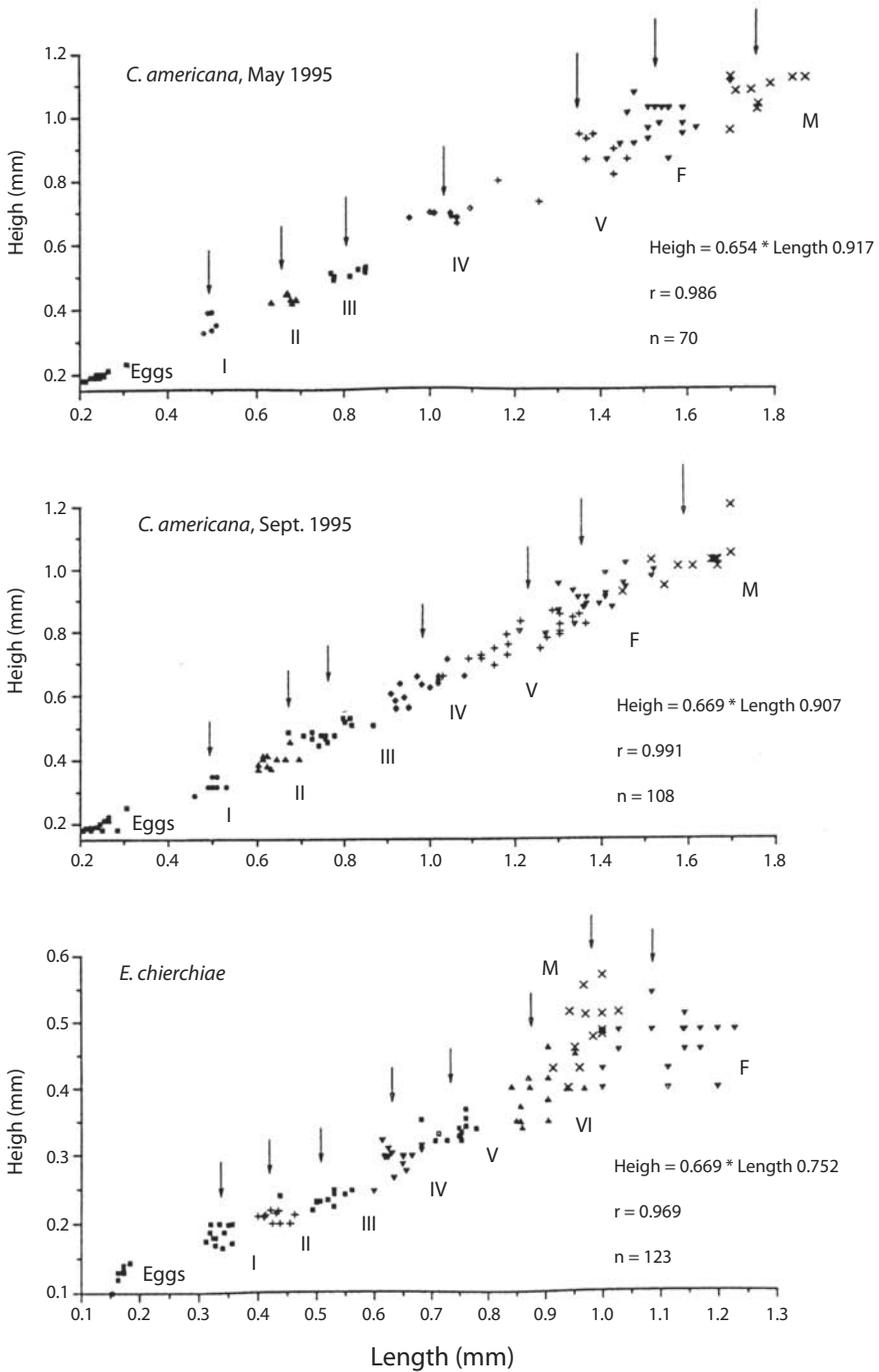


Fig. 6. Lineal regressions for the development stages and adults of *C. americana* and *E. chierchiai* in Golfo Dulce, Costa Rica.

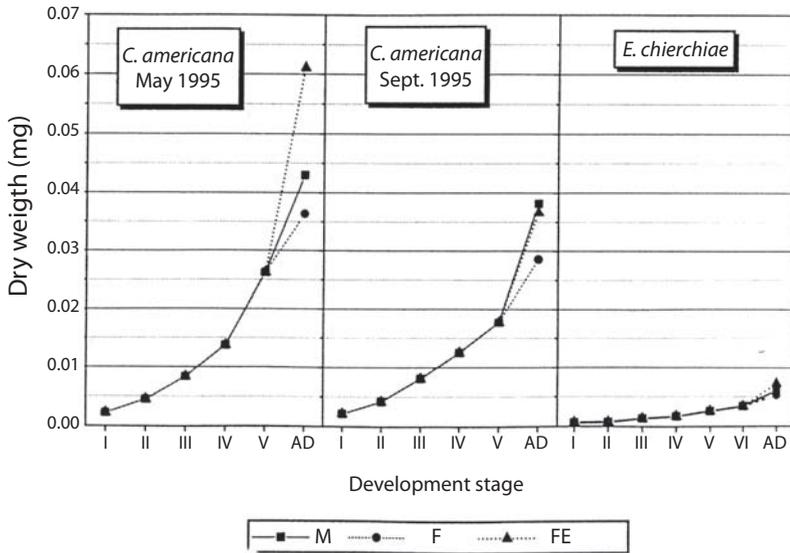


Fig. 7. Dry weight values depending of the development stages of *C. americana* and *E. chierchiaie* in Golfo Dulce, Costa Rica.

numbers of males when the number of females carrying eggs was higher, but its ratio was lower (1:4, Table 2).

Vertical distribution: In May, populations of both species were primarily found in the uppermost 20m, with the exception of *C. americana* at 22:35h and 17:20h, (Fig. 10). Below 50m, abundance was only between 2 and 0.4% for *C. americana* and *E. chierchiaie*, respectively. Ratios of abundance in the first and second water layers were 244:115 for *C. americana* and 2 543:360 organisms·m⁻³ for *E. chierchiaie*. With respect to sample

distributions, both species had similar behavior at 10:45 and 15:45 to May 2nd and 17:20. In the 0-20m strata, over 95% of the population of *E. chierchiaie* and 85% of *C. americana* was found at night (May 2nd) until 10:35 in the morning the next day. In the morning and afternoon of May 2nd, one third of the population was found in the middle water layer. Here *C. americana* shows a higher abundance at 22:35 and 17:20 of the following day (129 and 198 organisms·m⁻³ respectively). In September, *C. americana* more than 97.5% of the population was in the upper layer; its concentration averaged 4 650 organisms·m⁻³. On the second day

TABLE 2

Sex ratio(M:F), percent (%) developmental stages of the population as well as female with eggs to female without eggs ratio (FEW: FOE) and number of eggs per female for C. americana and E. chierchiaie between 2th-3th May and 6th-7th September 1995, Rincón Bay Station, Golfo Dulce

| <i>C. americana</i> | | | | |
|-----------------------|------------------|-----------|---------|------------|
| Date | Young stages (%) | M:F ratio | FWE:FOE | # eggs/FWE |
| May, Rincón Station | 70% | 1: 3.5 | 1.5 : 1 | 13.5 |
| Sep. Rincón Station | 92 | 1: 18 | 1 : 1.5 | 6.2 |
| <i>E. chierchiaie</i> | | | | |
| May, Rincón Station | 89 | 1 : 4 | 1.5 : 1 | 3 |

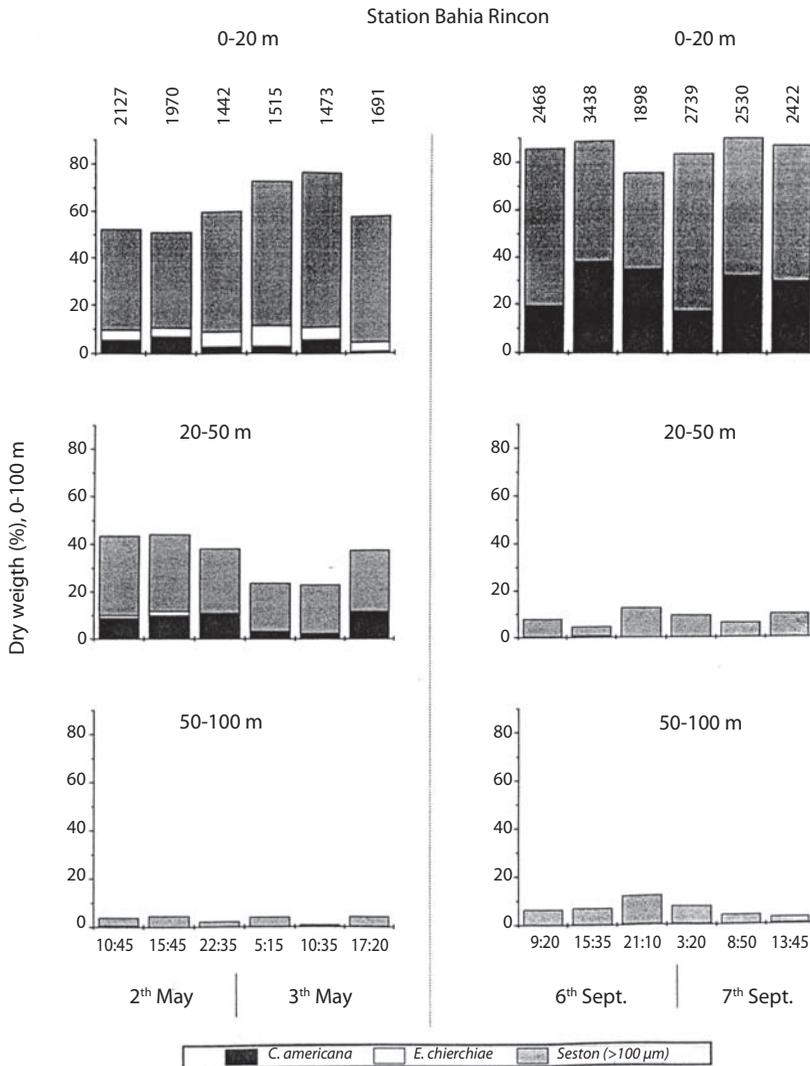


Fig. 8. Percent dry weight for both ostracod species relative to seston, Rincón Bay, Golfo Dulce, Costa Rica.

at 3:20 and 13:40h only 1.5% of individuals were found in the deeper layers (Fig. 10). To compare biomass and ostracod abundance with hydrographical features, positive correlations with temperature and oxygen contents were identified, whereas a negative correlation with salinity was exhibited. In September, data was best correlated with oxygen content. Oxygen deficiency below 20m resulted in remnants of *C. americana* in the upper layers, while

individuals of *E. chierchiae* were apparently absent. Developmental stages of *C. americana* in May show no clear trend related to day/night rhythms, except for stage I, which always has been found in the first 20m (Fig. 11A). Stages I-IV mainly remained in the upper layer. Stages II and IV show a different behavior at 17:20h on May 3rd, when they preferred the strata at 20-50m, as did stage IV at 22:35h. Stage V showed the highest abundance in this layer at

Station Bahía Rincon

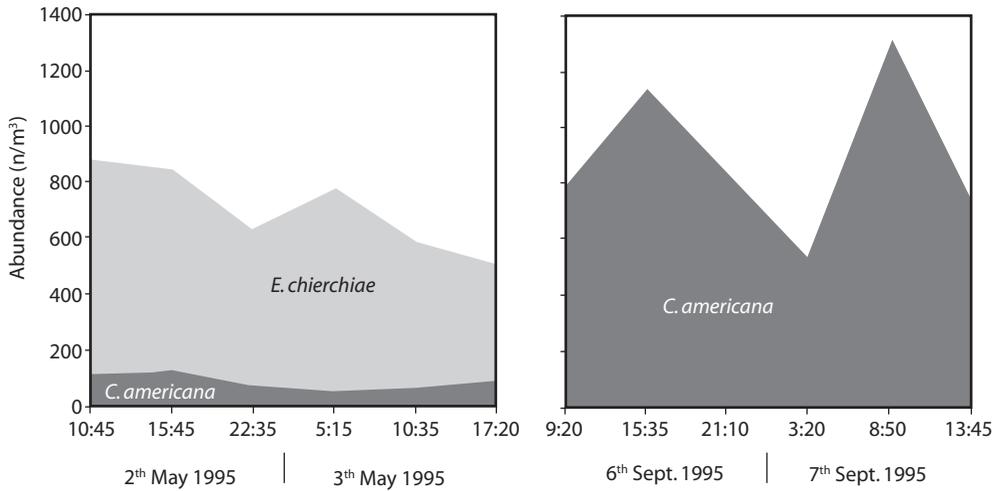


Fig. 9. Abundances de *E.chierchiaie* and *C. Americana* at Rincón Bay during the study period, Golfo Dulce, Costa Rica.

22:35h and at twilight the next day. All males and females were found in these depth strata as well. In September all stages of *C. americana* were found in the surface layer (Fig. 11B). For *E. chierchiaie* in May (Fig 12), all developmental stages remained at the first sampled layer, except for stage I. During the day, stage I remained at 20-50m (exception at 10:35 from May 3rd), and stages I-V were found as well at 15:45h on May 2nd. Females of *Euconchoecia chierchiaie* carrying eggs were found usually in the upper water layer (0-20m).

DISCUSSION

Hydrography: Hydrographical results are similar to those found in other studies for Golfo Dulce (Richards *et al.* 1971, Brenes & León 1988, Wolff & Vargas 1994). Gradients in the physical parameters in the first 50m and homogeneous layer below 50m demonstrate the low water circulation in this gulf. Normally a thermocline has been found between 20 and 6m, while during this study the thermocline began at 10m. Low oxygen content below 20m is probably a consequence of the entry of run-off

organic matter, as well as a high sediment flow. The great amount of detritus in September is further evidence for the contribution of rivers, especially the Rincon River (Fig. 1). This leads to a strong decomposition through microbial activity. Another explanation could be the introduction of oceanic water mass. Richards *et al.* (1971) observed a rise in the oxygen isopleths until 10m with a marked north-south gradient, with higher oxygen concentrations in the direction toward the open ocean (south). Although it was not observed for the rainy season, the thermocline showed a rise in the northern direction at this time (Jacob 1996). Mixed processes through tide currents produced the differences found. Surface salinity was on average lower than that reported previously (>31 PSU, Richard *et al.* 1971, Brenes & León 1988), a direct consequence of the heavy rains in the second half of the year. Recently, Quesada-Alpízar & Morales-Ramírez (2004) detected biannual events in the basin of the Golfo in the influx of cold, high salinity, and oxygen rich oceanic water masses, which might be related to the same forces driving the coastal upwelling system in the Gulf of Panamá.

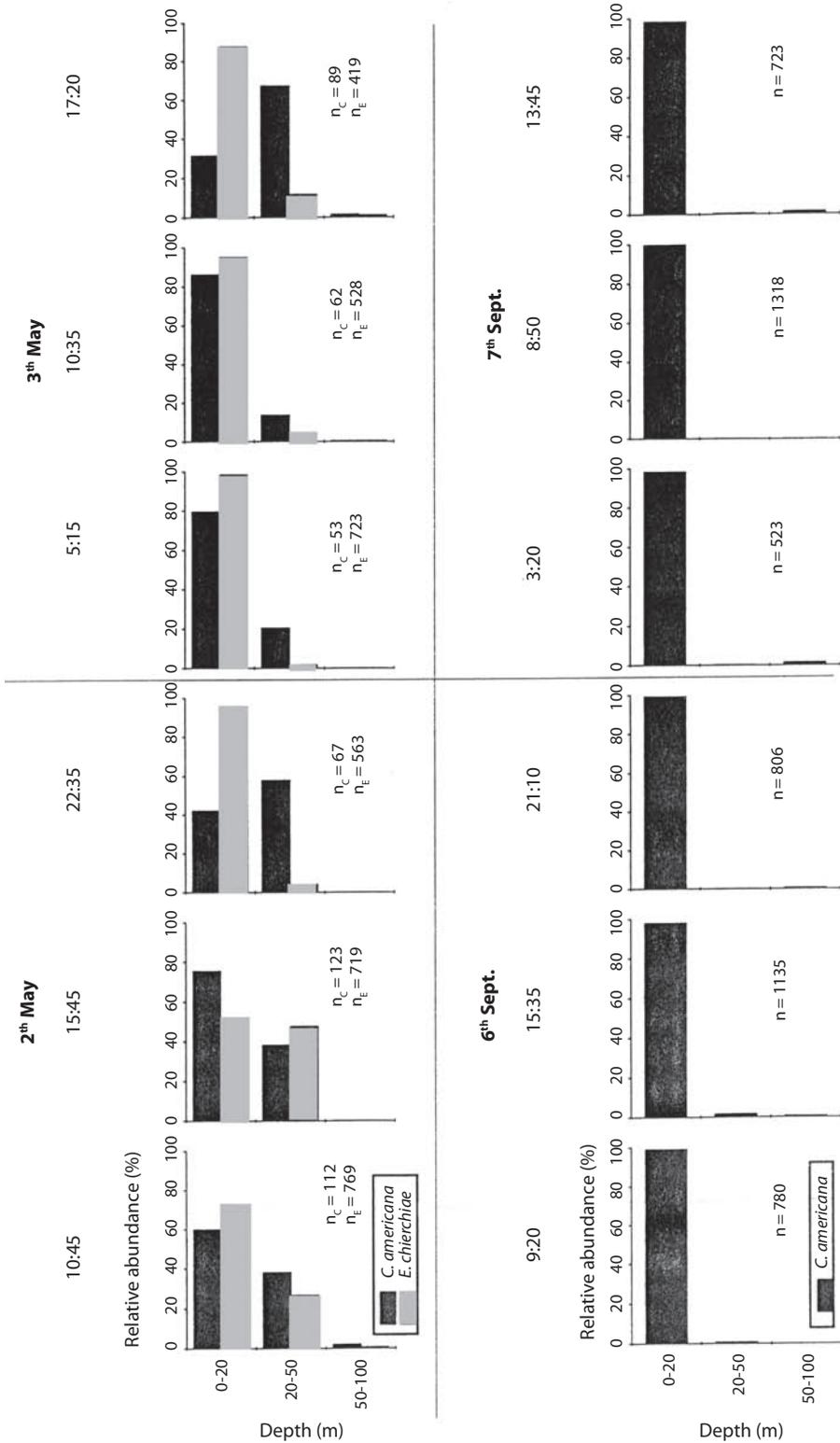


Fig. 10. Vertical distribution of the relative abundance of *C. americana* and *E. chierchiai* over the 100m depth in Rincon Bay in May and September 1995, Golfo Dulce, Costa Rica.

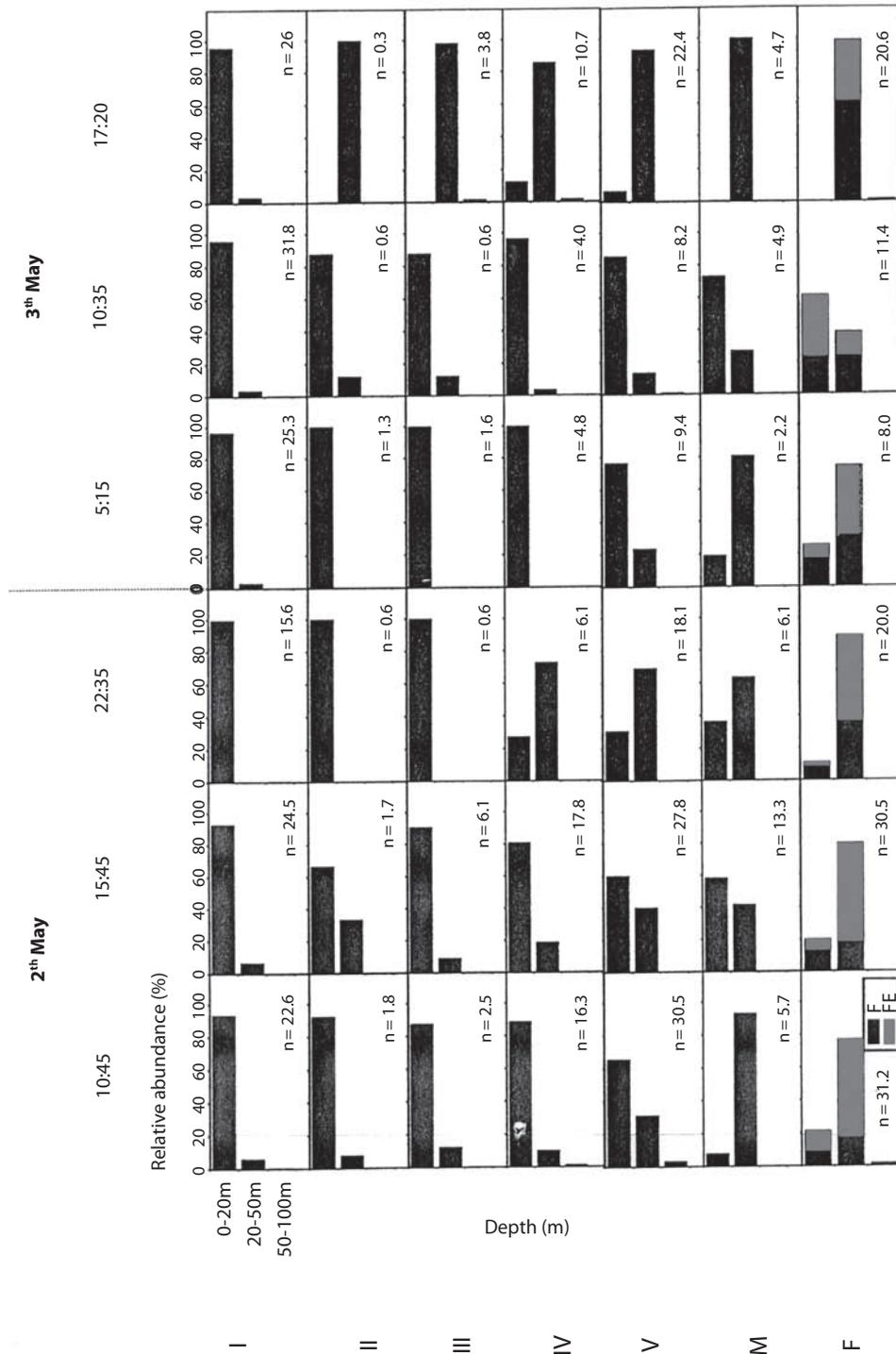


Fig. 11. Vertical distribution of the relative abundance of the development stages I-V and adults of *C. americana* in Rincon Bay, Golfo Dulce, Costa Rica. A. May 1995. n = average number·m⁻³ in the first 100m depth.

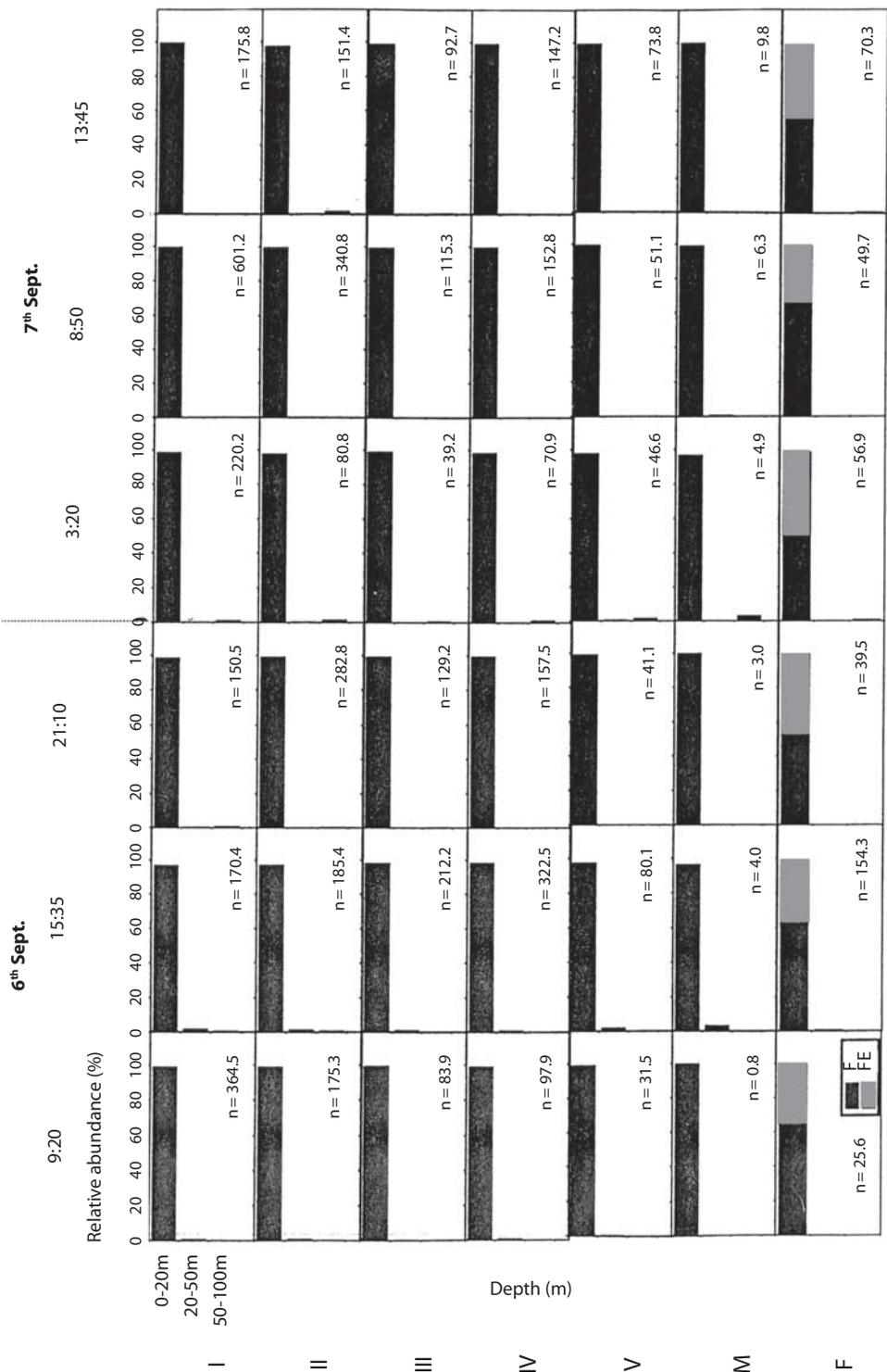


Fig. 11. *Continued.* Vertical distribution of the relative abundance of the development stages I-V and adults of *C. americana* in Rincon Bay, Golfo Dulce. **B.** September 1995. n = average number·m⁻³ in the first 100m depth.

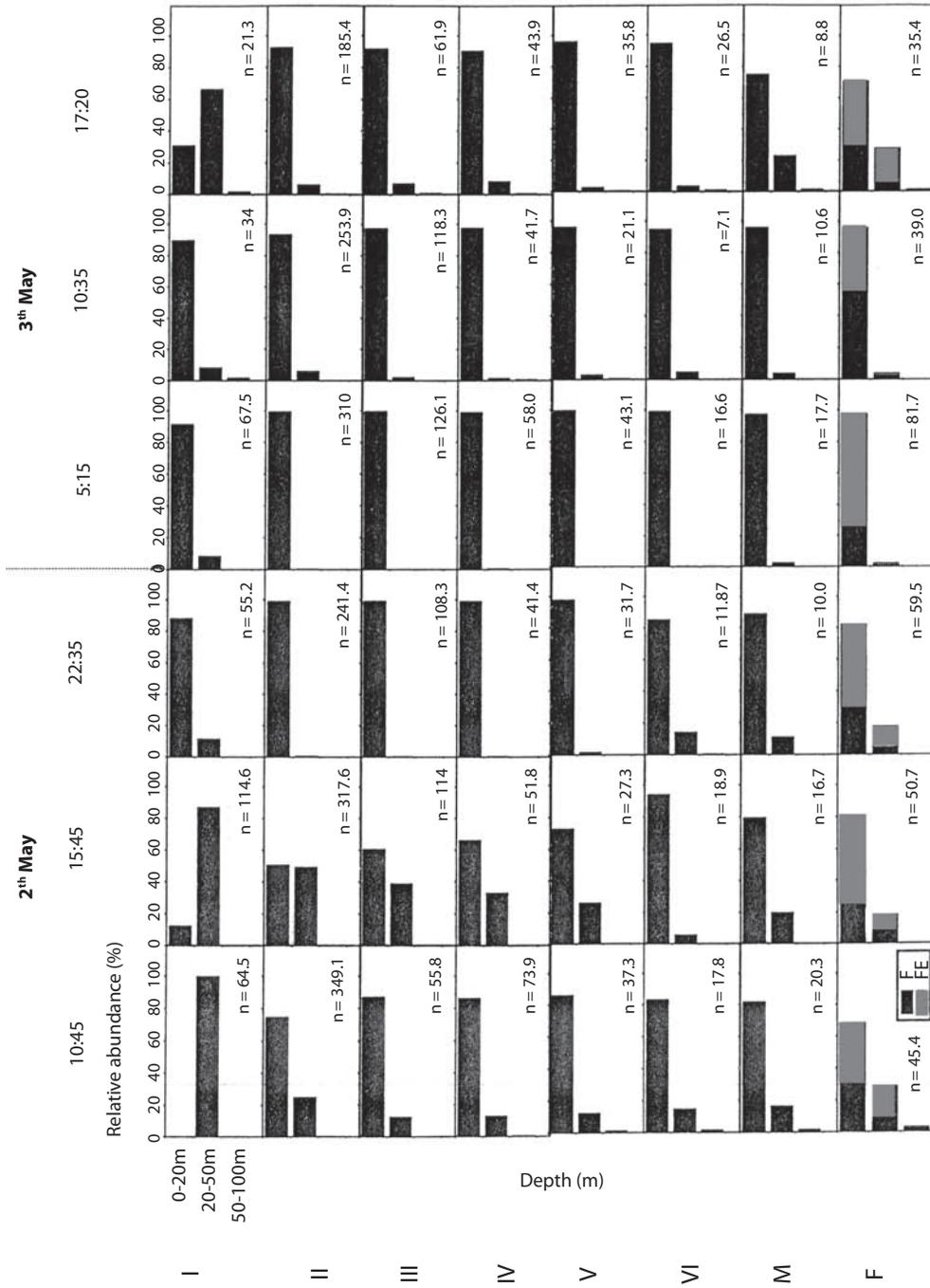


Fig. 12. Vertical distribution of the relative abundance of the development stages I-VI and adults of *E. chierchiae* in Rincon Bay, Golfo Dulce, during May 1995. n = average number.m⁻³ in the first 100m depth.

Biometrical relationships: The investigated ostracod species are small pelagic species (<2mm). Poulsen (1977) found that out of 92 species, the smallest species (1.5mm) preferred the upper water, while species of greater body size (3-4mm) preferred deeper water. Similar results were found by Angel & Fashman (1975) for the Northeast Atlantic. Both *Cypridina americana* and *E. chierchiaie* have transparent shells that signify an adaptation for pelagic life. Furthermore, small body size is characteristic for tropical microcrustaceans (e.g. Raymont 1983) and it has been found for the Atlantic, Pacific, and Indo-Indonesian oceans that ostracods from higher latitudes are longer than those of equatorial ranges (Poulsen 1977). Percentages for *C. americana* in length-height vs. developmental stages are similar to those found for freshwater ostracods (Heitkamp 1978), between 110-140%. On the other hand, the large growth per stage for *E. chierchiaie* was similar to those found by Gilland (1977) for *Cypridopsis parvoide*, 106-128%. However, in numerous research projects very different growth factors have been reported for more marine and freshwater ostracods, between species as well as among maturity stages (Gilland 1977, Angel 1977, Heitkamp 1978).

The parallel running of the growth curves is an indication that both exo- and endogenous factors even affect the length and height development in ostracods. But which of these factors, genetic regulation or environmental influence, is more important? As will be discussed below, depending on age individuals of *C. americana* remained at different depth strata, in which were found different temperatures. Also seasonal differences in the growth curves are expected, but were not observed. Temperature has an ability to modify the height, but it does not seem to do so in the curves. Both species of ostracods show low growth rates from stage II to stage III. This may perhaps be a consequence of the external growth. Kornicker (1974) found for *Cypridina spina* and *C. spinula* a strong building of the first thoracopods in the development from stage II to III. Gilland (1977) and Heitkamp (1978) found similar results. The

first author, for example, found a minimum growth value for height, length, and width from stage VI to VII in *Cypridopsis parvoide*, while the second author found a minimal specific growth in freshwater cyprinids. The low body increase from stage IV to V in *E. chierchiaie* is perhaps related to the development of sexual organs, as has been proposed for *Candona neglecta* (Heitkamp 1978). The low growth of sub-adults to females relative to males is due to the large energy investment in eggs. This investment may be greater in *C. americana* than in *E. chierchiaie* since sexual dimorphism in the former species is showier. In contrast to *C. americana*, higher length growth factors for development in females, as compared to males, have been found for halocyprid species in the Northeast Atlantic (Angel 1977), which commonly appears to be the case (Poulsen 1977). An opposite trend, like that found for *C. americana* is, in the best sense of the word, an exception. Additional controversial evidence related to growth in length in ostracods is given by the Hiatt growth diagram (Fig. 5), where the growth of *C. americana* males remained constant and was described through a linear regression, while for *E. chierchiaie* there is evidence of greatest relative growth in the young stages. Sexual growth of *C. americana* could be described mainly as a linear or polynomial regression. Early investigations in malacostracan crustaceans suggest that the relative growth in length from one stage to the next decreases (Mauchline 1976). On the other hand, Hiatt (1948) proposed a polygonal regression for growth of juvenile and adults of *Pychygrapsus crassipes*, while other recent studies proposed linear regressions as the best fit for crustacean growth (Somerton 1980, Wolff & Soto 1992). Also, the decrease of the relative growth in both ostracod species suggests that the growth in ostracods follows other laws, as has been proposed (Mauchline 1976).

The early displacement of the relative growth of the three older developmental stages of *C. americana*, which was low in both average length and dry weight, is not easy to explain. High temperatures in September

restricted animals to the first 20m and may be a possible explanation as to why earlier stages remain in shallower strata while older stages remain between 20 and 50m depth, which was the case during May at those depths. Heitkamp (1978) found for two species of freshwater ostracods, lower length during May/June-July as results of higher temperatures, because optimal temperature is less 20°C. Another possibility may be the influence of salinity on the growth regulation for ostracods, but there is neither field nor experimental evidence to demonstrate potential effects. In September low salinity in the first 10m could have an influence on the growth of *C. americana* and *E. chierchiae*. More research must be carried out to gain evidence for this point.

Biomass and abundance: Ostracod abundance showed no marked differences during either season (700-880 organisms·m⁻³), however the biomass was higher in September (mean 8mgDW·m⁻³) than in May (mean 3mgDW·m⁻³), probably due to the contribution of *C. americana*. Another cause could be the contribution of organic matter during the rainy season. The high biomass values of ostracods, especially *C. americana* in September, are in concordance with results of zooplankton abundance, especially ostracods, in El Caño Island, southwest of Costa Rica. High species' numbers and high biomass were found in the dry season and rainy season (Guzmán & Obando 1988). In the last case, after copepods, ostracods were the predominant group. This is due to reproductive strategies coupled with high food availability in the form of polychaetes, small copepods, and organic matter, resulting in high abundance in the dry season. A similar pattern was observed for ostracods in Culebra Bay, Gulf of Papagayo in the North Pacific of Costa Rica, although the ostracod abundance was higher (mean over 1 500 in dry season and nearly 1 000 ind·m⁻³ in rainy season) (Bednarski & Morales-Ramírez 2004). In December 1993, ostracods show very low biomass values for Rincon Bay (only 0.35mgDW·m⁻³, van Wangelin & Wolff 1996), while the dry season was characterized by high

ostracod biomass values (12.32mgDW·m⁻³, van Wangelin & Wolff 1996). Ostracod abundance in Golfo Dulce (700-880 organisms·m⁻³), in comparison with the oceanic environment, is extraordinarily high. Some oceanic regions report abundance by 19 organisms·m⁻³ (Sargasso Sea, Deevey 1968), 6 organisms·m⁻³ (Northeast and Northwest Atlantic, Angel 1979), 5 organisms·m⁻³ in Northeast Atlantic (Morales-Ramírez 1993), 700 organisms·m⁻³ (Northwest Pacific, Chavtur 1976), and a mean abundance <100 organisms·m⁻³ from 16 ostracod species of the Humboldt Current in the upper 0-50m off of the Peru coast during 1998 and 2001 (Castillo *et al.* 2007). Even biomass values are higher: 0.26mgDW·m⁻³, Gulf of Mexico (Hopkins 1982), 0.40-4mgDW·m⁻³ for the first 800m depth in Northwest Pacific (Chavtur 1976), in spite of the oceanic features of Golfo Dulce (Wolff *et al.* 1996).

How physical parameters affect the occurrence, biomass, and abundance of ostracods in Golfo Dulce is an important question to answer. Oxygen content was lower than 0.3mgO₂·L⁻¹ in May and 0.6mgO₂·L⁻¹ during September. Poulsen (1977) found low ostracod abundance in low-oxygen regions in the equatorial Atlantic (1-2mgO₂·L⁻¹, 10 organisms·haul) in comparison with 300 organisms·haul in oxygen-rich neighboring areas, and concluded that ostracods are poorly adapted to living in waters with oxygen content less than 2-3mgO₂·L⁻¹. Similar behavior has been reported for copepods in the Arabic Sea (Vinogradov & Voronina 1962). Also, the absence of ostracods in the central region of the Humboldt Current with a reduction of the diversity and abundance was related to an Oxygen Minimum Zone (OMZ) (Castillo *et al.* 2007). On the other hand, Roman & Guazens (1993) found high copepod abundance in the Chesapeake Bay with an oxygen concentration of 1 mgO₂·L⁻¹ during a circulation period. During oxygen deficiency in summer, they found minimal abundance of copepods and their nauplii. In addition, Sameoto (1986) found a correlation between the vertical distribution of mesozooplankton and oxygen content and temperature. Copepods

remained within the thermocline (0-100m), but the biomass distribution of mesozooplankton beneath the thermocline is positively correlated with the oxygen curve. A correlation between high zooplankton abundance and temperature was also found by Longhurst (1976) in a tropical region of the east Pacific. The salinity in September for the first 10m could be an ecological barrier for stenohaline species (20-28PSU). The absence of *E. chierchiae* in Rincon Bay in September could be a result of the low salinity, because this species has an optimal range between 35.37 and 36.75PSU (Moguilevsky & Angel 1975), although this species may tolerate salinities around 32PSU (Poulsen 1969). On September 20th 1995 in another station (Golfito Station) the population of *E. chierchiae* (>81%) was found at depths greater than 10m (Jacob 1996), when salinity toward the surface was lower (16 PSU). Salinity concentrations lower than 30PSU could represent a physiological stress factor where marine animals react to higher oxygen consumption (Pearse & Gunter 1966), something that could have occurred during September in Golfo Dulce. The combination of both factors can represent physical conditions unfavorable to the tolerance of *E. chierchiae* in Rincon Bay during the rainy season. This had, apparently, a stronger effect on its population than for *Cypridina americana*.

Vertical distribution: The vertical distribution and signal of diel vertical migration of both species must be considered with some precautions, because we have only a few hauls. We suggest that in September migration in Rincon Bay could be carried out between 0 and 20m, with *C. americana* showing a positive phototactic vertical migration, in that a great part of the population migrated during the night at greater depths. Stages IV-V and males contributed up to 40% of the population. Angel & Fasham (1975) demonstrated the existence of diel inverse vertical migration for pelagic ostracods in the North Atlantic. The youngest developmental stages (I-II-III) of *C. americana* remained in the first 20m, especially stage I,

with over 95% of its population in this stratum. Females, especially carrying eggs, stayed mostly in the median stratum. This may be to avoid visual predators, as has been demonstrated for other ostracod species of females carrying eggs (Angel 1979), who remain exclusively in the first 100m. This pattern corresponds to an ontogenetic vertical migration-the youngest stages stay in shallow water while older stages and females stay in deeper waters, a commonly described phenomenon for copepods (Ambler & Miller 1989, Uye *et al.* 1990), chaetognaths (Kehayias *et al.* 1994), and ostracod species (Angel 1979), that implies a potential ecological niche separation and creates the possibility of significant intra-inter specific competition decreasing (Williams 1991).

For *E. chierchiae*, an assumed ontogenetic vertical migration between 0-20m and 20-50m was not found, because, with the exception of stage I, all other stages remained between 0-20m. This means that *E. chierchiae* is not a migrating species or that the low depth restricts the population to the first 20m. The first idea can be rejected, because *E. chierchiae* practices vertical migration in the Northwest Atlantic (32°N-57° W, Angel 1979). Probably the lower oxygen content below 50m may be a limitation for this species, as has been demonstrated for some ostracod species from the Humboldt Current off the Peruvian coast (Castillo *et al.* 2007). Both species play an important role in the trophic ecology of Golfo Dulce. *C. americana* is a detritivorous species and facultative predator, while *E. chierchiae* grazes on organic matter (Jacob 1996). This condition can represent a fast remineralization rate of nutrients in the pelagic food web before the organic matter reaches the deep layer. The high abundance of both species in the inner part of Golfo Dulce could be an indicator of the good environmental conditions, despite the low biological productivity typical of this system (Wolff *et al.* 1996). Future studies must evaluate the role of these species as ecological stabilizers of the system Golfo Dulce, as has been proposed for some copepod species in pelagic environments (Paffenhöfer 1993).

ACKNOWLEDGMENTS

We are grateful to J.A. Vargas and E. Ruiz for the help in the field work. The comments of two referees are much appreciated. We thank P. Hansen and A.M. Gavlas for correcting our English.

RESUMEN

La abundancia, biomasa y distribución vertical de ostrácodos, así como algunas relaciones biométricas fueron investigadas durante un ciclo de 24 h, dos días en el mes de Mayo y Septiembre de 1995 en el Golfo Dulce, costa Pacífica de Costa Rica. El programa de muestreo siguió un ciclo de marea, se realizó un perfil de 0-10-20-30-40-50-70-80 and 100m de profundidad para determinar temperatura, salinidad, concentración de oxígeno y profundidad del disco Secchi. Muestras de zooplancton fueron tomadas con una red Nansen con un sistema de cierre-abertura, de 70cm de diámetro y 100 micras de tamaño de poro. Las muestras fueron fijadas con formaldehído al 4%. La abundancia de ostrácodos (adultos y estadios de desarrollo) y la biomasa total como peso seco fueron estimadas de una alícuota obtenida con un separador de plancton Folsom. La biomasa de los ostrácodos fue determinada pesando de 5 a 50 individuos de un estadio particular de desarrollo. Cuatro especies de ostrácodos fueron identificadas: *Cypridina americana* Müller 1890, *Euchonchoecia chierchiae* Müller 1890, *Porroecia spinirostris* Cluas 1879 and *Porroecia* sp. Relaciones biométricas de las primeras dos especies reveló diferencias significativas entre todos los estadios de desarrollo tanto para la longitud corporal como para la estación del año ($p < 5 \cdot 10^{-7}$) y diferencias significativas estacionales en el tamaño entre hembras y machos de ambas especies, con fuerte dimorfismo sexual en los machos. Diferencias estacionales en la biomasa fueron encontradas en *C. americana* dependiendo del estadio de desarrollo debido a que hembras ovígeras pesaron el doble en Mayo que en Septiembre. Abundancia de ostrácodos varióLa dominancia en la abundancia de ostrácodos mostró una alternancia entre *E. chierchiae* y *C. americana*, dependiendo de la estación. Algunas diferencias en el ritmo día/noche fueron detectadas para *C. americana* para todos los estadios de desarrollo en Mayo, excepto para el I estadio, el cual siempre fue encontrado en los primeros 20m, opuesto a *E. chierchiae* donde todos los estadios permanecieron en la primera capa muestreada excepto el estadio I. Diferencias en los patrones verticales de distribución podría ser un comportamiento para evitar predación o potencializar los recursos alimentarios, con un fuerte componente ontogenético, al menos para *C. americana*. La abundancia de ostrácodos en Golfo Dulce es extraordinariamente alta, comparada con los ambientes oceánicos, a pesar de los rasgos oceánicos de este Golfo. Ambas especies juegan un papel importante en la ecología trófica del Golfo Dulce, donde *C. americana*

es una especie detritívora y predatora facultativa, mientras que *E. chierchiae* forrajea sobre materia orgánica. Este es el primer esfuerzo por describir algunos aspectos ecológicos sobre ostrácodos en las aguas costeras costarricenses.

Key words: ostracodos, Golfo Dulce, Pacífico, abundancia, biomasa, distribución, *Cypridina americana*, Costa Rica.

REFERENCES

- Amari, Z.A. & H. Pasulekar. 1993. Distribution, abundance and ecology of the meiofauna in a tropical estuary along the west-coast of India. *Hydrobiologia* 262: 115-126.
- Ambler, J.W. & C.B. Miller. 1987. Vertical habitat-partitioning by copepodites and adults of subtropical oceanic copepods. *Mar. Biol.* 94: 561-577.
- Angel, M. 1968. The thermocline as an ecological boundary. *Sarsia* 34: 299-312.
- Angel, M. 1977. Some speculation on the caparace length in planktonic halocyprid ostracods, p. 45-54. *In* H. Löffler & D. Danielpol (eds). *Aspects of ecology and zoogeography of recent and fossil Ostracoda*. Junk. The Hague, The Netherlands.
- Angel, M. 1979. Studies on Atlantic halocyprid ostracods: their vertical distribution and community structure in the central gyre region along 30° N from off Africa to Bermuda. *Prog. Oceanog.* 8: 3-124.
- Angel, M. 1981. Ostracoda, p. 543-585. *In* D. Boltovskoy (ed.). *Atlas del Zooplancton del Atlántico Sudoccidental y Métodos de Trabajo*. IPN, Buenos Aires, Argentina.
- Angel, M. 1984. The diel migration and distribution within a mesopelagic community in the Northeast Atlantic. III. Planktonic ostracods, a stable component in the community. *Prog. Oceanog.* 13: 319-351.
- Angel, M. 1996. Ostracoda, p. 213-247. *In* R. Gasca & E. Suárez (eds.). *Introducción al estudio del zooplancton marino*. ECOSUR-CONACYT, Mexico DF, Mexico.
- Angel, M. 1999. Ostracoda, p. 815-868. *In* D. Boltovskoy (ed.). *South Atlantic Zooplankton*. Backhuys Publ. Leiden, The Netherlands.
- Angel, M. & M.J.R. Fasham. 1975. Analysis of the vertical and geographical distribution of the abundant species of planktonic ostracods in the North-east Atlantic. *J. Mar. Biol. Assoc. UK* 54: 879-894.
- Bednarski, M. & A. Morales-Ramírez. 2004. Composition, abundance and distribution of macrozooplankton

- in Culebra Bay, Gulf of Papagayo, Pacific coast of Costa Rica and its value as bioindicator of pollution. *Rev. Biol. Trop.* 52 (Suppl. 2): 105-118.
- Brautović, I., N. Bojanić, M. Batistić & M. Carić. 2006. Annual variability of planktonic ostracods (Crustacea) in the South Adriatic Sea. *Mar. Ecol.* 27: 124-132.
- Brenes, C.L. & S. León. 1988. Algunos aspectos físico-químicos del Golfo Dulce. *Ing. Cienc. Quím.* 12: 12-16.
- Castillo, R., T. Antezna & P. Ayon. 2007. The influence of El Niño 1997-98 on pelagic ostracods in the Humboldt Current ecosystem off Peru. *Hydrobiologia* 585: 29-41.
- Chavtur, V.G. 1976. Fauna of pelagic ostracods of the halocyprididae family in the northwestern part of the Pacific Ocean. *Trans. Inst. Mar. Biol. Akad. Sci. USSR Far. East Sci Center* 6: 99-109.
- Cornils, A., S. B. Schnack-Schiel, W. Hagen, M. Dowidar, N. Stambler, O. Plähn & C. Richter. 2005. Spatial and temporal distribution of mesozooplankton in the Gulf of Aqaba and the Northern Red Sea in February/March 1999. *J. Plank. Res.* 27: 505-518.
- Deevey, G.B. 1968. Pelagic Ostracods of the Sargasso Sea off Bermuda. *Peabody Mus. Nat. Hist. Bull.* 26: 1-125.
- Elofson, O. 1941. Zur Kenntnis der marinen ostracoden Schwedens mit besonderer berücksichtigung des skageraks. *Zool. Bidr. Uppsala* 19: 215-534.
- Elorduy-Garay, J.F. & J. Caraveo-Patiño. 1994. Feeding habitats of ocean whitefish *Caulobatilus princeps* Jenys 1842 (Piscis :Branchiostegidae) in La Paz Bay, B.C.S., Mexico. *Cienc. Mar.* 20: 199-218.
- Gilland, L. 1977. Grössenwachstum bei Ostracoden : untersucht an der Larvalentwicklung von *Cypridopsis parvoides* Martens 1977. *Abh. Verh. Naturwiss. Ver. Hamburg* 20: 99-112.
- Guerao, G. 1995. Locomotor-activity patterns and feeding habitats in the prawn *Palaemon xiphias* (Crustacea, Decapoda: Palaemonidae) in Alfar Bay, Ebro Delta (Northwest Mediterranean). *Mar. Biol.* 122: 115-119.
- Guzmán, H. & V. Obando. 1988. Diversidad y abundancia diaria y estacional del zooplankton marino de la Isla del Caño, Costa Rica. *Rev. Biol. Trop.* 36: 139-150.
- Heitkamp, U. 1978. Postembrionales Grössenwachstum limnischer Cyprididae (Crustacea: Ostracoda). *Zool. Anz. Jena* 202: 391-412.
- Hiatt, R.W. 1948. The biology of the lined shore crab *Pachyrapsus crassipes* Randal. *Pacific Sci.* 2: 135-213.
- Hopkins, T.L. 1982. The vertical distribution of zooplankton in the eastern Gulf of Mexico. *Deep Sea Res.* 29: 1069-1083.
- Hopkins, T.L. & R.C. Baird. 1985. Feeding ecology of four hatchet fishes (Sternoptychidae) in the Eastern Gulf of Mexico. *Bull. Mar. Sci.* 36: 260-277.
- Hopkins, T.L., M.E. Flock, J.V. Gartner & J.J. Torres. 1994. Structure and trophic ecology of a low-latitude midwater decapod and mysid assemblage. *Mar. Ecol. Prog. Ser.* 109: 143-156.
- Ikeda, T. 1990. Ecological and biological features of a mesopelagic ostracod, *Conchoecia pseudodiscophora*, in the Japan Sea. *Mar. Biol.* 107: 453-461.
- Ikeda, T. 1991. Laboratory observations on spawning, fecundity and early development of a mesopelagic ostracod, *Conchoecia pseudodiscophora*, from the Japan Sea. *Mar. Biol.* 112: 313-318
- Ikeda, T. 1992. Population structure and life cycles of the mesopelagic ostracod *Conchoecia pseudodiscophora* in Toyoma Bay, southern Japan Sea. *Mar. Biol.* 113: 595-601.
- Hossfeld, B., H. Molina & A. Morales. 1994. Zooplankton, p. 42-53. *In* M. Wolff & J.A. Vargas (eds.). *RV Victor Hensen Costa Rica Expedition 1993-1994. Cruise Report.* Center for Tropical Marine Ecology. Bremen, Germany.
- Jacob, J. 1996. Zur Ökologie und Biometrie pelagischer Ostracoden im Golfo Dulce (Costa Rica). M.Sc. Thesis, University of Berlin, Germany.
- Johnson, J.M. 1995. Diel feeding ecology of three species of aquatic insects. *J. Freshwater Ecology* 10: 183-188.
- Kehayias, G., N. Fragopoulou & J. Lykakis. 1994. Vertical community structure and ontogenetic distribution of chaetognats in upper pelagic waters of the eastern Mediterranean. *Mar. Biol.* 119: 647-653.
- Kesling, R.V. 1952. Doubling in size of ostracod carapaces in each molt stage. *J. Paleont.* 26: 772-780
- Kesling, R.V. 1953. A slide rule for the determination of instar in ostracod species. *Contrib. Mus. Paleont. Univ. Michigan* 11: 97-109.

- Kinsey, S.T. & T.L. Hopkins. 1994. Trophic strategies of euphausiids in low-latitudes ecosystem. *Mar. Biol.* 118: 650-661.
- Kock, R. 1992. Ostracoden im epipelagial von der Antarktischen halbinsel-ein Beitrag zur Systematik sowie zur Verbreitung und Populationsstruktur unter Berücksichtigung der Saisonalität. *Berichte Polarforsch.* 106: 1-209.
- Kornicker, L.S. 1967. The myodocopid ostracods: families Philomedidae and Pseudophilomedidae (new family). *Proc.U.S.A. Nat. Mus.* 12: 1-35.
- Kornicker, L.S. 1968. Bathyal myodocopid Ostracoda from the Northeastern Gulf of Mexico. *Proc. Biol. Soc. Washington* 81: 439-472.
- Kornicker, L.S. 1970a. Ostracoda (Myodocopina) from the Peru-Chile Trench and the Antarctic Ocean. *Smithsonian Contrib. Zool.* 32: 1-42.
- Kornicker, L.S. 1970b. Myocopid Ostracoda (Cypridinacea) from Philippine Islands. *Smithsonian Contrib. Zool.* 39: 1-32.
- Kornicker, L.S. 1974. Revision of the Cypridinacea of the Gulf of Naples (Ostracoda). *Smithsonian Contrib. Zool.* 178: 1-64.
- Kornicker, L.S. 1975. Antarctic ostracoda (Myodocopina), parts I and II. *Smithsonian Contrib. Zool.* 163: 1-720.
- Kornicker, L.S. 1983. The ostracod family Cypridinidae and the genus *Pterocypridina*. *Smithsonian Contrib. Zool.* 32: 1-42.
- Kornicker, L.S. 1987. Supplementary description of *Cypridina americana* (Müller 1890), a bioluminescent myodocopid ostracod from the east Pacific. *Proc. Biol. Soc. Washington* 100: 173-181.
- Kornicker, L.S. 1991. Myocopid Ostracoda of Enewetak and Bikini Atolls. *Smithsonian Contrib. Zool.* 505: 1-139.
- Kornicker, L.S., S. Wirsing & M. MacManus. 1976. Biological studies of the Bermuda Ocean Area: planktonic ostracods. *Smithsonian Contrib. Zool.* 233: 1-34.
- Lancroft, T.M., T.L. Hopkins & J.J. Torres 1988. Aspects of the ecology of the mesopelagic *Ganostoma elongatum* (Ganostomatidae, Stomiiformes) in the Eastern Gulf of Mexico. *Mar. Ecol. Prog. Ser.* 49: 27-40.
- Longhurst, A.R. 1976. Interaction between zooplankton and phytoplankton profiles in the Eastern tropical Pacific Ocean. *Deep Sea Res.* 23: 729-754.
- Mauchline, J. 1976. The Hiatt growth diagram for Crustacea. *Mar. Biol.* 35: 79-84.
- Moguilevsky, A. & M. Angel. 1975. Halocyprid ostracods in Atlantic neuston. *Mar. Biol.* 32: 295-302.
- Morales-Ramirez, A. 1993. Vertikale und regionale Verteilung des Mesozooplanktons in Nordostatlantik unter des besonderen Berücksichtigung von Copepoden. *Berichte aus dem Institut für Meereskunde an der Universität Kiel, Germany.* 229 p.
- Olafson, E. & R. Elmgren. 1997. Seasonal dynamics of sublittoral meiobenthos in relation to phytoplankton sedimentation in the Baltic Sea. *Est. Coast. And Shelf Sci.* 45: 149-164.
- Paffenhöfer, G.A. 1993. On the ecology of marine cyclopoid copepods (Crustacea, Copepoda). *J. Plankton Res.* 15: 37-55.
- Pearse, A.S. & G. Gunter. 1966. Salinity. *In* J.W. Hedgepeth (ed.). *Treatise on Marine Ecology and Paleontology.* Vol. I. *Geol. Soc. Amer. Mem.* 67.
- Poulsen, E.M. 1977. Zoogeographical remarks on marine pelagic Ostracoda. *Dana-Report N°87:* 1-34.
- Quesada-Alpizar, M.A. & A. Morales-Ramirez. 2004. Comportamiento de las masas de agua en el Golfo Dulce, Costa Rica durante el Niño (1997-1998). *Rev. Biol. Trop.* 52 (Suppl. 2): 95-103.
- Raymont, J.E.G. 1983. *Plankton and productivity in the Ocean.* Vol. II. Zooplankton. Pergamon. New Jersey, USA.
- Richards, F.A., J.J. Anderson & J.D. Cline. 1971. Chemical and physical observations in Golfo Dulce, an anoxic basin in the Pacific coast of Costa Rica. *Limnol. Oceanog.* 16: 43-50.
- Roman, M.R. & A.L. Gauzens. 1993. Effects of low oxygen waters on Chesapeake Bay zooplankton. *Limnol. Oceanog.* 38: 1603-1614.
- Ruiz, F., M. Abad, A.M. Bodergat, P. Carbonel, J. Rodríguez-Lázaro & M. Yasuhara. 2005. Marine and brackish-water ostracods as sentinels of antropogenic impact. *Earth Sci. Rev.* 72: 89-11
- Sameoto, D.D. 1986. Influence of the biological and physical environment on the vertical distribution of mesozooplankton and micronekton in the Eastern tropical Pacific. *Mar. Biol.* 93: 263-279.
- Sazar, P.M. & G.J. Glova. 1998. Diel feeding and prey selection of three size classes of short finned eel (*Anguilla australis*) in New Zeland. *New Zeal J. Mar Freshwat Res.* 49: 421-428.

- Segura, L., R.M. Hernández & L. Mosones. 1992. Distribución y abundancia de los quetognatos (Chaetognatha) en la región del Domo de Costa Rica. *Rev. Biol. Trop.* 40: 35-42.
- Shimomura, O. 2006. The ostracod *Cypridina* (*Vargula*) and others luminous crustaceans. p. 47-86. In O. Shimomura (ed.) *Bioluminescence: chemical principles and methods*. World Scientific Pub. Co. Inc. London. UK.
- Somerton, D.A. 1981. Fitting striglm lines to Hiatt growth diagrams: a re-evaluation. *J. Cons. Int. Explor. Mer* 39 : 15-19.
- Uye, S., C. Huang & T. Onbe. 1990. Ontogenic diel migration of the planktonic copepod *Calanus sinicus* in the inland Sea of Japan. *Mar. Biol.* 104: 389-396.
- van Wangelin, M. & M. Wolff. 1996. Comparative biomass spectra and species composition of the zooplankton communities in Golfo Dulce and Golfo de Nicoya, Pacific coast of Costa Rica. *Rev. Biol. Trop.* 44 (Suppl. 3): 135-156.
- Vijayalakshmi R., N & M. Madhupratap. 1984. Latitudinal range of epiplanktonic chaetognatha and ostracoda in the western tropical Indian Ocean. *Hydrobiologia* 112: 209-216.
- Vinogradov, M.E. & N.M. Voronina. 1962. The influence of oxygen deficit upon the plankton distribution in the Arabian Sea. *Deep Sea Res.* 9: 523-530.
- Williams, R. 1991. Spatial heterogeneity and niche differentiation in oceanic zooplankton. *Hydrobiology* 167/168: 151-160.
- Wolff, M. & M. Soto. 1992. Population dynamics of *Cancer polyodon* in La Herradura Bay, Northern Chile. *Mar. Ecol. Prog. Ser.* 85: 89-101.
- Wolff, M. & J.A. Vargas. 1994. RV Victor Hensen Costa Rica Expedition 1993-1994. Cruise Report. ZMT (Tropical Marine Ecology Center), University of Bremen, Bremen, Germany.
- Wolff, M., H.J. Hartmann & V. Koch. 1996. A pilot trophic model for Golfo Dulce, a fjord-like embayment, Costa Rica. *Rev. Biol. Trop.* 44 (Suppl. 3): 215-231.

