

## Reproductive patterns in meiobenthic Harpacticoida (Crustacea, Copepoda) of the California continental shelf (Santa Maria Basin)

DONALD G. WEBB\*† and PAUL A. MONTAGNA\*

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**Abstract**—The abundance, life-history characteristics (developmental stage and body size) and reproductive parameters (clutch volume and egg diameter) of three dominant meiobenthic harpacticoid copepod species (*Cletodes tuberculatus*, *C. macrura* and *Zosime pacifica*) in the Santa Maria Basin (California continental shelf) were examined. Comparisons were made temporally (eight quarterly sampling dates in 2 years), and spatially on both local (0–10 km) and regional (20–40 km) scales. *Cletodes tuberculatus* attained its highest densities in January 1987 and February 1988, while *C. macrura* were most abundant in May 1987, with no similar maximum in 1988. *Zosime pacifica* densities were highest between October and April in all years. All three species were most abundant at depths <169 m. High proportions of juvenile copepodites and high sex ratios (female:male >1) were observed for all three species, indicating adequate conditions for population growth. However, gravid females were confined to shallow (<169 m) depths. Reproductive parameters exhibited weak relationships to female body size, suggesting a strong environmental influence on reproduction. The three copepod species had different temporal and spatial patterns in reproductive parameters. Reproductive parameters of *C. macrura* did not vary temporally or spatially. There were small differences in reproductive parameters for *Z. pacifica*, but with no detectable pattern. Variations in reproductive parameters of *C. tuberculatus* were related to sediment organic carbon content. Larger clutch volumes and egg diameters of *C. tuberculatus* were found in the northern portion of the basin, where sediment organic carbon content was highest.

### INTRODUCTION

THE meiobenthos, defined as benthic animals that pass through a 0.5 mm sieve but are retained on a 0.063 mm sieve (COULL and BELL, 1979) are considered to be good organisms for monitoring environmental degradation, because of their high abundance, small size, fast growth rate and sensitivity (see WARWICK, 1988 for review). Of all the meiobenthos, harpacticoid copepods are ideal candidates for studies on the effect of environmental influences on reproduction because eggs are externally brooded, and thus easily measured and counted.

On the North American Pacific continental shelf, where hydrocarbon exploration is

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\*Marine Science Institute, University of Texas at Austin, P.O. Box 1267, Port Aransas, TX 78373-1267, U.S.A.

†Present Address: Department of Oceanography, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1.

underway, the benthic fauna may be exposed to environmental changes resulting from drilling activity. Harpacticoid copepods can be sensitive to hydrocarbons (FRICKE *et al.*, 1981; BODIN and BOUCHER, 1983; HENNIG *et al.*, 1983; FRITHSEN *et al.*, 1985) and barite, a common constituent of drilling muds (CANTELMO *et al.*, 1979). Because they disperse at fast rates, harpacticoids are among the first colonizers of disturbed environments (SHERMAN and COULL, 1980). For example, harpacticoid populations recovered within 1 week during a colonization experiment using oiled sediments, whereas nematode populations took up to 90 days to recover fully (ALONGI *et al.*, 1983). In California natural oil seep sediments, harpacticoid copepods colonized azoic sediment faster than nematodes (PALMER *et al.*, 1988).

The Santa Maria Basin on the California continental shelf is currently pristine, but hydrocarbon development is expected within this decade. A baseline study on harpacticoid copepod reproductive patterns is necessary to assess future impacts of development. The three harpacticoid species that were chosen for analysis include one pair of sympatric species (*Cletodes tuberculatus* Fiers and *C. macrura* Fiers, Family Cletodidae) and a third species (*Zosime pacifica* Fiers, Family Tisbidae) with a very different body form. These three species are endemic to the study area (FIERS, 1991) and are three of the four most abundant harpacticoid species in the basin (HYLAND *et al.*, 1990). In harpacticoid copepods, differences in body shape and degree of leg development (e.g. number of segments) are indicative of their lifestyle (MONTAGNA, 1982). Members of the Cletodidae have a streamlined body with reduced leg development, an adaptation for burrowing into sediments. The Tisbidae are more robust, with highly developed legs, and are composed primarily of epiphytic and epibenthic species (HICKS and COULL, 1983). The burrowing (Cletodidae) and epibenthic (Tisbidae) represent the two dominant harpacticoid lifestyles.

This study is based on benthic samples collected as part of the California OCS Phase II Monitoring Program (CAMP; HYLAND *et al.*, 1990), in the Santa Maria Basin of the California continental shelf. The purpose of this monitoring program was to measure long- and short-term changes in the benthic system around drilling platforms and determine whether these changes are related to drilling or are natural phenomena. The goal of this study was to provide a baseline, pre-production description of the life history and reproductive patterns of three dominant harpacticoid copepod species. An analysis of the dynamics of the whole meiobenthic community can be found in MONTAGNA (1991). For each of the chosen species, abundance was estimated. Body lengths were measured and, for gravid females, clutch size (volume), and individual egg diameters were measured. The data were analysed to determine relationships of life-history and reproductive parameters of each harpacticoid species with respect to cruise date, spatial position and water depth.

## METHODS

Samples were collected at both regional stations (R-prefix, Fig. 1) and at a site-specific array of 15 stations within 10 km around the proposed Platform Julius site (PJ-prefix, where PJ-1 is at the proposed platform site, Fig. 1—Site Specific Sampling) in the Santa Maria Basin, during eight cruises from November 1986 to October 1988. Details on site selection, general sampling methodology, meiofauna sample sorting and abundance estimation are described in HYLAND *et al.* (1990) and MONTAGNA (1991). Specific detailed information on sampling the site-specific array can be found in HYLAND *et al.* (1990, Fig. 2).

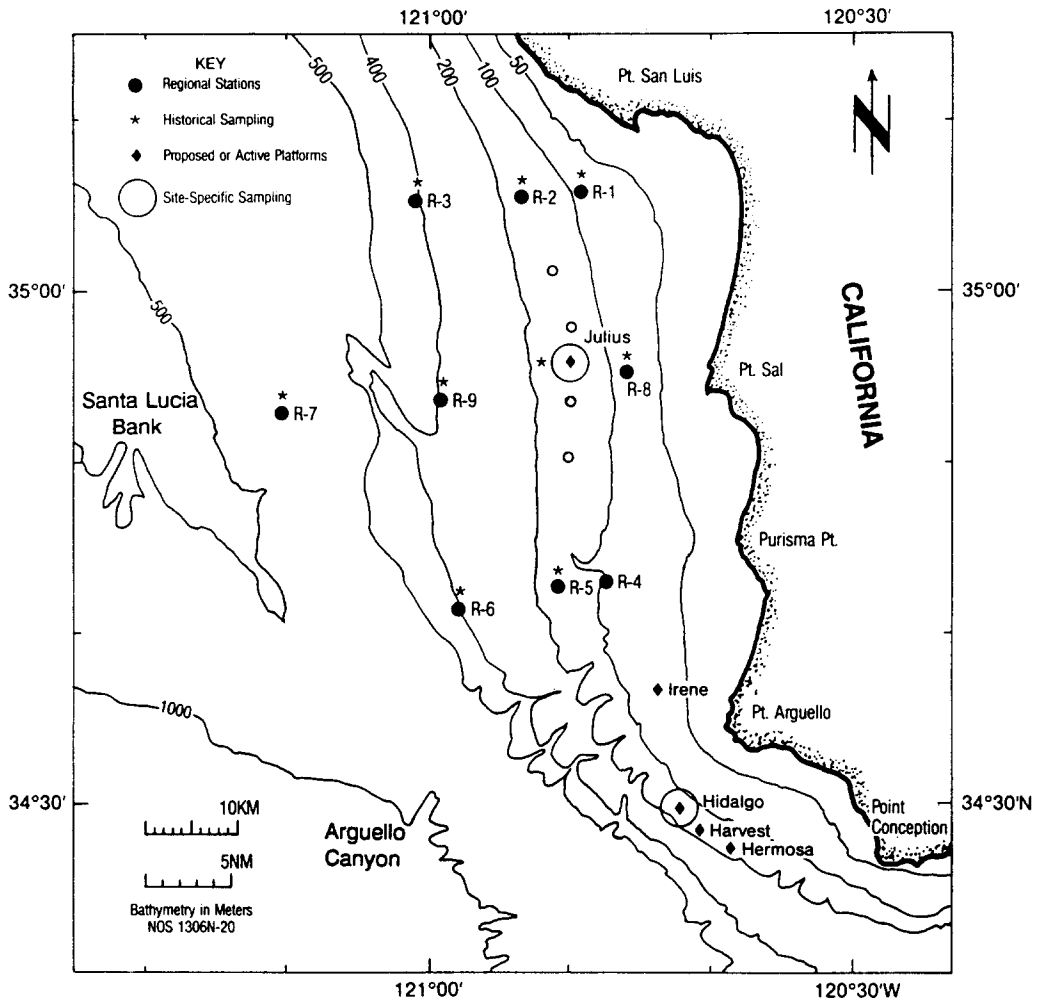


Fig. 1. Study area and sampling locations in the Santa Maria Basin, California. The center of the study area is where Platform Julius (PJ-1) will be located. Regional stations (R-) are denoted with solid circles. Site-specific stations are denoted with open circles. The large open circle contains 14 stations plus PJ-1. Location of the North (R-1, -2, -3), Central (R-8, PJ-1, R-9, -7) and South (R-4, -5, -6) transects are also shown.

In each sample, individuals of *C. tuberculatus*, *C. macrura*, and *Z. pacifica* were isolated and the following parameters determined: copepodite stage, body length and egg diameters of gravid females. Copepodite stage (C1–C6, where C6 is the adult) was determined by counting body segments using a Wild M5 dissecting microscope fitted with an objective doubler at 50 $\times$  magnification. Gender could be identified at the C5 and C6 stages. After staging, the body length of each individual was measured from the base of the rostrum to the end of the anal segment (LANG, 1965), using a calibrated ocular micrometer with a resolution of 5  $\mu$ m. The gravid females in each sample were placed in a drop of glycerin on a depression slide and oriented so that the eggsac was visible. The diameter of

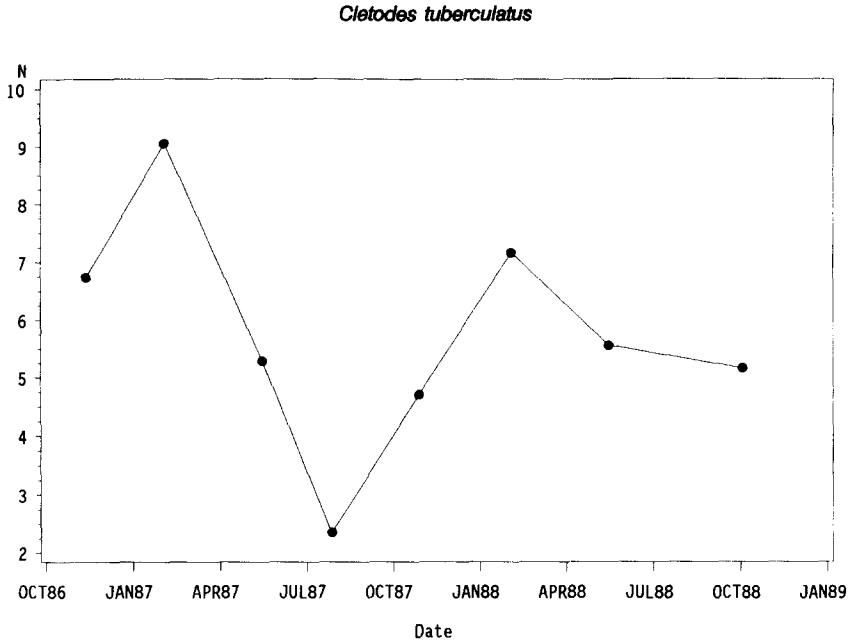


Fig. 2. Temporal change of *C. tuberculatus* abundance ( $N = 10^3$  individuals per  $m^2$ ) from the top 4 cm of sediment for all regional stations.

each egg was measured using a ocular micrometer on a Zeiss phase-contrast compound microscope at  $400\times$  magnification with a resolution of  $1\ \mu m$ . Clutch volume was estimated from individual egg diameters by assuming eggs were spherical, calculating individual egg volumes, and summing the volume of all the eggs in a clutch.

For each harpacticoid species, patterns in adult female body length, clutch volume and egg diameter were compared among cruise dates using 1-way ANOVA by combining data from all stations. Only adult females were used for body length analyses since body size at this stage should reflect environmental influences throughout their entire developmental period. A 2-way ANOVA was used to determine differences in adult female body length, clutch volume and egg diameter among the regional transects [North (R-1, R-2, R-3), Central (R-8, PJ-1, R-9, R-7) and South (R-4, R-5, R-6)] and station depth (90–92 m, 123–169 m and 409–410 m) by combining data from all cruises. At the Platform Julius stations, we used a 1-way ANOVA to test for meso-scale spatial differences in adult female body length, clutch volume and egg diameter by combining data from all cruises. Four distances from PJ-1 were contrasted: (1) within 400 m of, and including, PJ-1; (2) 1 km from PJ-1; (3) 2 km from PJ-1; and (4) 4–10 km from PJ-1. Clutch volume and egg diameter were regressed against female body length for all gravid females. Data were combined either by stations or cruises in the analyses to alleviate statistical problems caused by unbalanced designs due to non-occurrence of these species at some stations during each cruise.

In all cases, statistical analyses were performed on untransformed data since residuals from the linear models did not significantly depart from normality. All statistical analyses were performed on an IBM PC/AT using PC/SAS software (SAS, 1985). The *a posteriori*

Tukey–Kramer multiple comparison test (for unequal sample sizes) was used to test for differences among means at  $\alpha = 0.05$ .

## RESULTS

The abundance of *C. tuberculatus* was maximal in January 1987 and February 1988 (Fig. 2). This species was most abundant at station R-1 in January 1987 and at PJ-1 in February 1988 (Fig. 3). *Cletodes tuberculatus* was uncommon at stations deeper than 169 m (Fig. 3). *Cletodes macrura* attained its highest abundance in the study area in May 1987 and another maximum was not observed in 1988 (Fig. 4). This species was most common at stations R-4, PJ-1 and R-1 and was also uncommon below 169 m (Fig. 5). The abundance of *Z. pacifica* was high between October and April in both 1986 and 1987 and was maximal in October 1988 (Fig. 6). This species became relatively more abundant at station PJ-1 after July 1987 and was also generally uncommon below 169 m depth (Fig. 7).

For all three copepod species, juvenile copepodites always composed >25% of total numbers (Fig. 8). Both *C. macrura* and *Z. pacifica* had a greater proportion of the total population as juvenile copepodites than *C. tuberculatus*. Highest levels of percentages of females of *C. tuberculatus* occurred in November 1986 and October 1987. Highest levels of percentages of gravid females were seen in May 1987 and 1988 [Fig. 8(a)]. Highest levels of

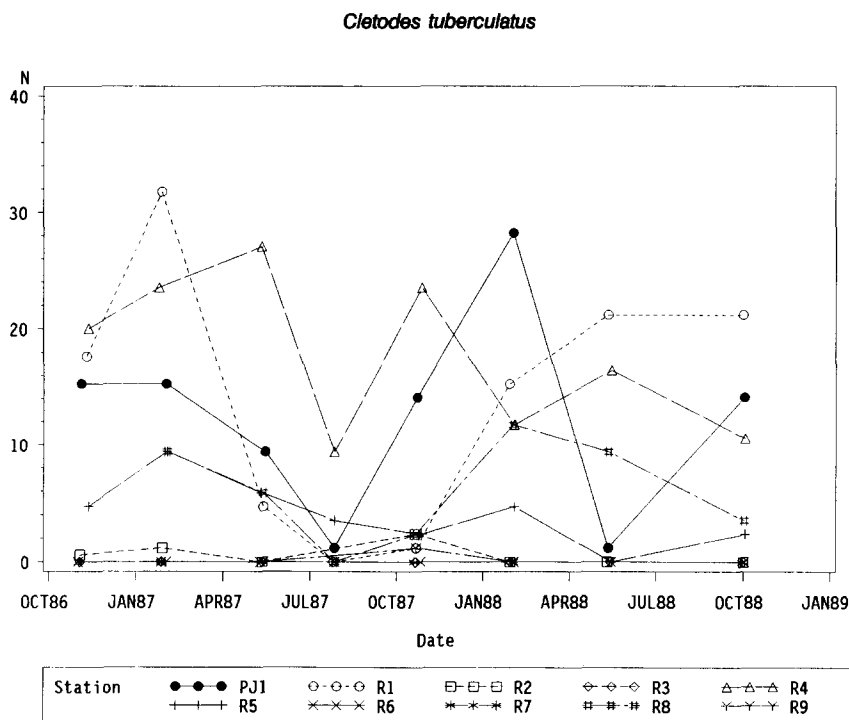


Fig. 3. Spatial and temporal differences of *C. tuberculatus* abundance ( $N = 10^3$  individuals per  $m^2$ ) in top 4 cm of sediment at each of the regional stations.

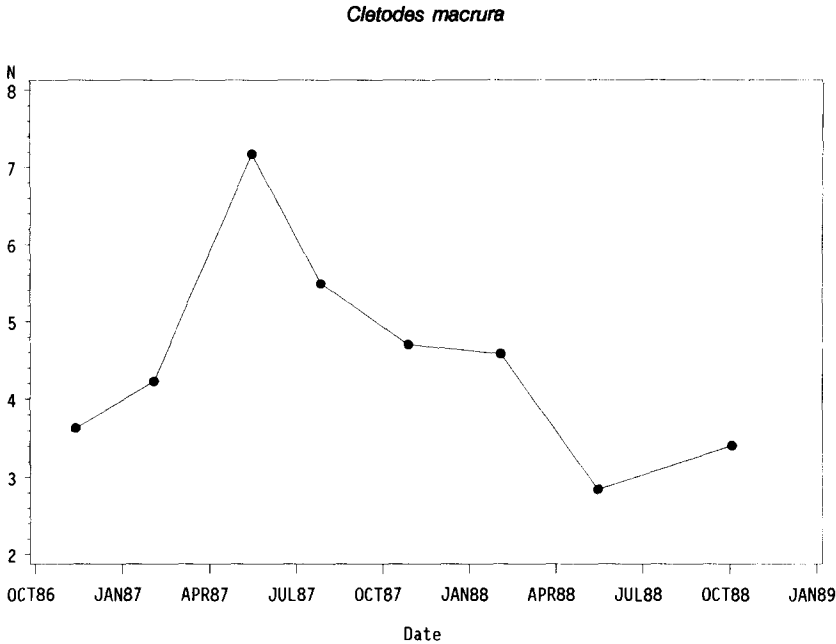


Fig. 4. Temporal change of *C. macrura* abundance ( $N = 10^3$  individuals per  $m^2$ ) from the top 4 cm of sediment for all regional stations.

percentages of females of *C. macrura* were seen in November 1986 and May 1988 [Fig. 8(b)], while the proportional abundance of *Z. marina* females was highest in July 1987 and May 1988 [Fig. 8(c)]. Percentages of gravid females were highest in July 1987 for *C. macrura* and May 1987 for *Z. pacifica*. Sex ratios (female:male) for each species were greater than 1 on each sampling date, except for *C. macrura* in October 1988 [Fig. 8(b)].

#### *Temporal patterns in reproductive parameters*

Adult female body length varied significantly with cruise date for *C. tuberculatus* and *Z. pacifica*, but not for *C. macrura* (Table 1). *Cletodes tuberculatus* females sampled in October 1988 were significantly larger than those at all times except July 1987 (Tukey–Kramer test,  $P \leq 0.05$ ). Females of this species collected in May and October 1987, and February 1988 were significantly larger than those in January 1987 (Tukey–Kramer test,  $P \leq 0.05$ ). Females in May 1987 were also significantly larger than those collected in November 1986 (Tukey–Kramer test,  $P \leq 0.05$ ). *Zosime pacifica* female body lengths were significantly larger in samples from October 1988 than in samples from November 1986, and January and October 1987 (Tukey–Kramer test,  $P \leq 0.05$ ).

Clutch volume varied significantly with cruise date only for *C. tuberculatus* (Table 1). Clutch volumes on October 1988 were significantly larger than those from all cruises except July 1987 and May 1988 (Tukey–Kramer test,  $P \leq 0.05$ ). In addition, clutch volumes from May 1988 were significantly larger than those from November 1986 (Tukey–Kramer test,  $P \leq 0.05$ ).

Egg diameter varied significantly with cruise date for *C. tuberculatus* and *Z. pacifica*, but

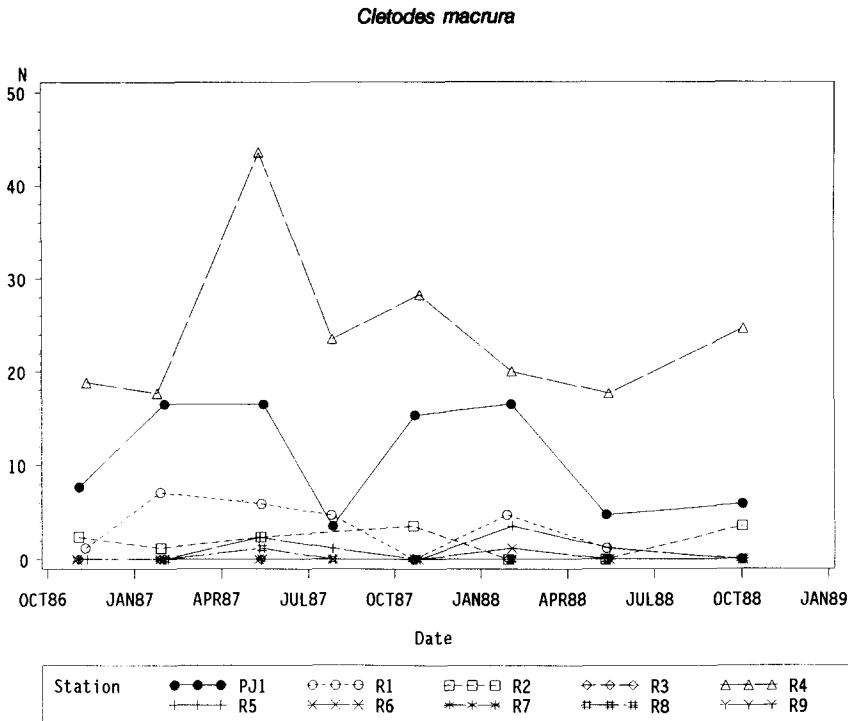


Fig. 5. Spatial and temporal differences of *C. macrura* abundance ( $N = 10^3$  individuals per  $m^2$ ) in top 4 cm of sediment at each of the regional stations.

not for *C. macrura* (Table 1). For *C. tuberculatus*, egg diameters in October 1988 were significantly larger than those from all cruises except January and July 1987, and May 1988 (Tukey–Kramer test,  $P \leq 0.05$ ). Egg diameters from May 1988 were significantly larger than those from all cruises except July 1987 and October 1988 (Tukey–Kramer test,  $P \leq 0.05$ ). Also, egg diameters from January, May and July 1987 were all significantly larger than those from November 1986 (Tukey–Kramer test,  $P \leq 0.05$ ). For *Z. pacifica*, egg diameters from November 1986 were significantly larger than those from October 1987 (Tukey–Kramer test,  $P \leq 0.05$ ).

#### *Spatial patterns in reproductive parameters—Platform Julius stations*

*Cletodes tuberculatus* and *C. macrura* exhibited no significant difference in adult female body length, clutch volume or egg diameter at the site-specific stations around Platform Julius (Table 2). The only significant difference observed among the four locations for these parameters was that egg diameters of *Z. pacifica* were significantly larger at stations within 400 m of, and including, PJ-1, than at stations 4–10 km from PJ-1 (Tukey–Kramer test,  $P \leq 0.05$ ; Table 2).

#### *Spatial patterns in reproductive parameters—regional stations*

Variations in adult female body length with depth were observed for *C. tuberculatus* and *Z. pacifica*, but not for *C. macrura* [Fig. 9(a)]. *Cletodes tuberculatus* female body lengths

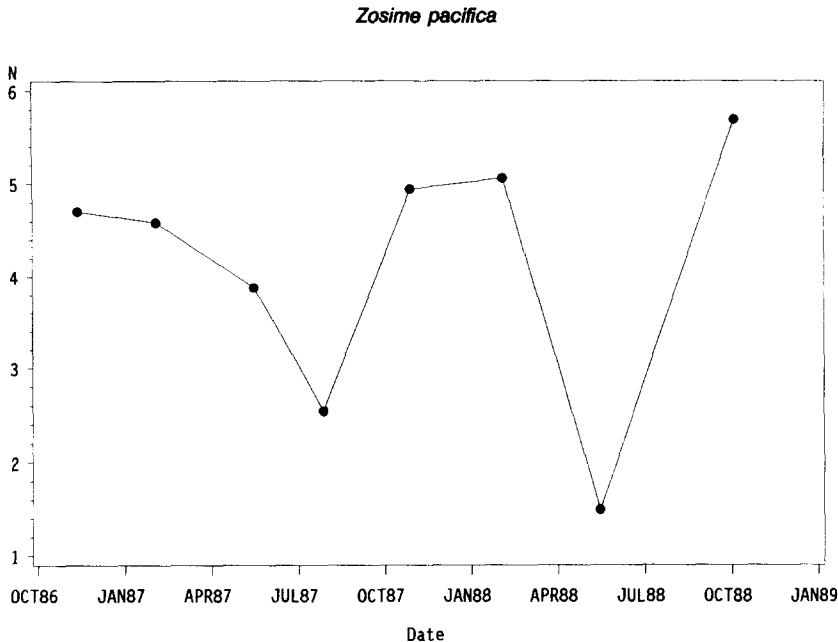


Fig. 6. Temporal change of *Z. pacifica* abundance ( $N = 10^3$  individuals per  $m^2$ ) from the top 4 cm of sediment for all regional stations.

were significantly larger at 90–92 m than at 123–169 m (Tukey–Kramer test,  $P \leq 0.05$ ). *Zosime pacifica* females were significantly larger at 409–410 m than those at 123–169 m (Tukey–Kramer test,  $P \leq 0.05$ ), but were not significantly larger than females at 90–92 m. Female body length of this species was not significantly different between 90–92 m and 123–169 m. No significant effect of transect location on female body length was observed for any species [Fig. 9(b)].

Depth had no effect on clutch volume for any of the three harpacticoid species [Fig. 10(a)]. A significant effect of transect location on clutch volume was observed for *C. tuberculatus* only [Fig. 10(b)]. Clutch volumes of this species were significantly larger on the North transect compared to the Central or South transect (Tukey–Kramer test,  $P \leq 0.05$ ). Clutch volumes were not significantly different between the Central and South transects.

Transect location or depth had no significant effect on egg diameter for *C. macrura* or *Z. pacifica* [Fig. 11(a) and (b)]. For *C. tuberculatus*, however, egg diameters were significantly larger on the North transect compared to the Central and South transects [Tukey–Kramer test,  $P \leq 0.05$ ; Fig. 11(a) and (b)]. Egg diameters were not significantly different between the Central and South transects. Egg diameters were significantly larger at 90–92 m depth compared to 123–169 m (Tukey–Kramer test,  $P \leq 0.05$ ).

Linear regressions of clutch volume or egg diameter on female body length were significant ( $P \leq 0.05$ ) only for *C. tuberculatus*. This species exhibited a significant relationship between clutch volume and body length (slope  $\pm$  SE =  $354.7 \pm 168.5$ ,  $n = 69$ ,  $r^2 = 0.06$ ) and egg diameter and body length (slope  $\pm$  SE =  $0.027 \pm 0.013$ ,  $n = 225$ ,  $r^2 = 0.02$ ). However, the coefficients of determination were extremely small signifying



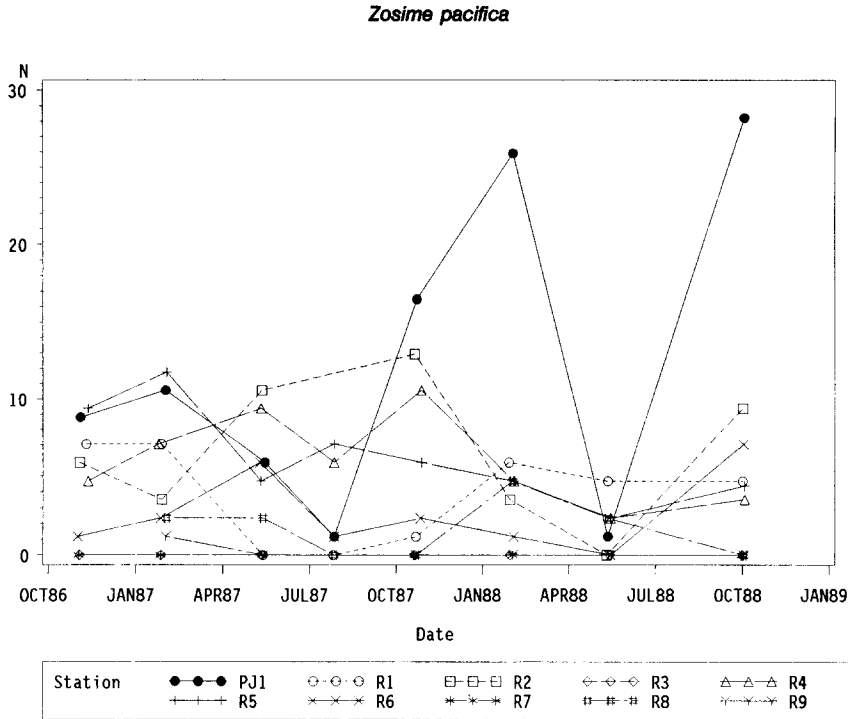


Fig. 7. Spatial and temporal differences of *Z. pacifica* abundance ( $N = 10^3$  individuals per  $m^2$ ) in top 4 cm of sediment at each of the regional stations.

that very little of the variance (at most 6%) in either clutch volume or egg diameter were accounted for by changes in body length.

### DISCUSSION

While the existence of spatio-temporal variations in harpacticoid copepod abundance are well known from a variety of habitats (see HICKS and COULL, 1983, for review), little research has been performed on spatio-temporal patterns in life history characteristics and reproductive parameters. PALMER (1980) found that clutch size (number of eggs per gravid female) in *Microarthridion littorale* was larger subtidally than intertidally in a South Carolina salt marsh. KERN and BELL (1984a) observed small-scale (meters) spatial patterns in size-structure and proportions of adults of *Zausodes arenicolus* inhabiting a subtidal sandflat in Tampa Bay. Short-term temporal variations in sex ratio and number of gravid females were also observed for *Zausodes arenicolus* and *Paradactylopodia brevicornis* in the same area during recolonization of disturbed sediment (KERN and BELL, 1984b). Recently, FLEEGER and SHIRLEY (1990) observed striking patterns in sex ratio and population structure of a number of harpacticoid species at 27–50 m depth during the spring in Alaska. In this continental shelf habitat, variations in abundance, life history characteristics and reproductive parameters occurred for *C. tuberculatus*, *C. macrura* and *Z. pacifica* over combinations of time and/or space. However, patterns differed markedly

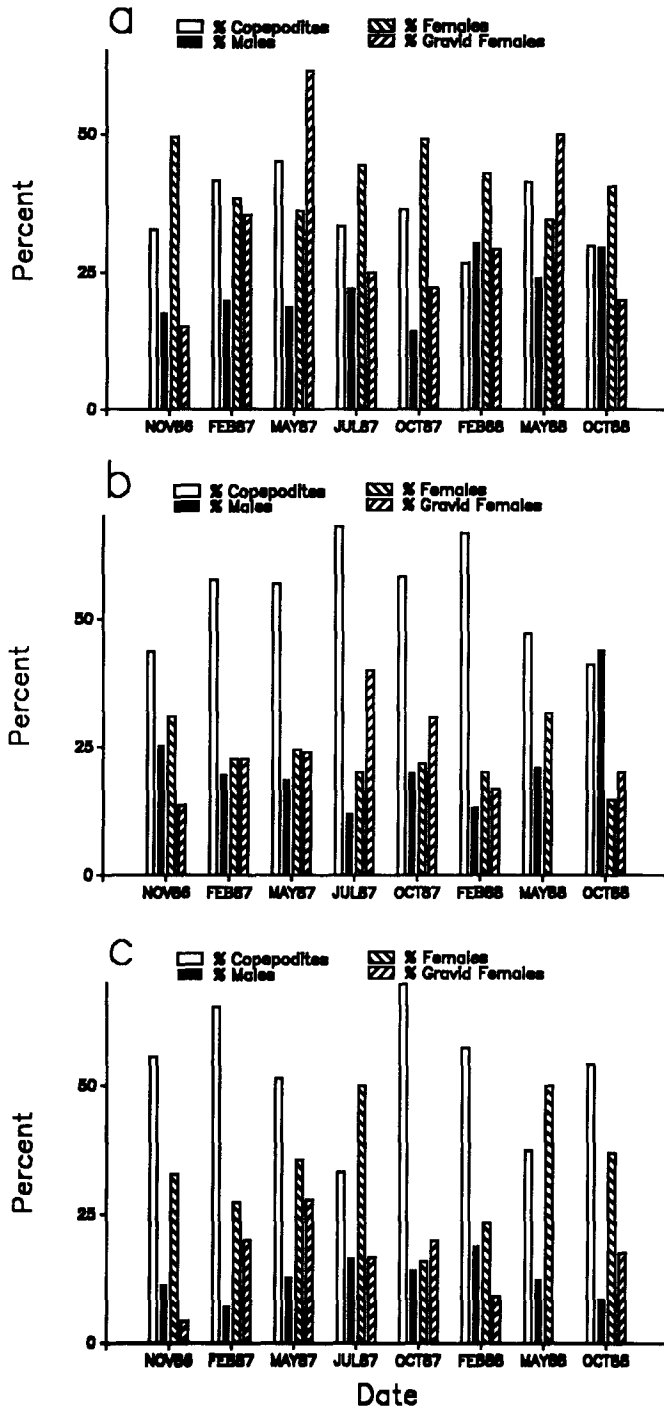


Fig. 8. Population structure of the three harpacticoid species. Percentage of individuals as juvenile copepodites, males, females and gravid females (females carrying external egg sac) for all stations (regional and site-specific array) on each cruise. (a) *C. tuberculatus*, (b) *C. macrura*, (c) *Z. pacifica*.

Table 1. Adult female body length ( $\mu\text{m}$ ), clutch volume ( $/10^5 \mu\text{m}^3$ ) and egg diameter ( $\mu\text{m}$ ) for *Cletodes tuberculatus*, *Cletodes macrura* and *Zosime pacifica* for each cruise. Values are the mean  $\pm$  1 standard error. Numbers in brackets are the sample sizes for each mean and error term. Dashed lines indicate no gravid females present

Cruise	Body length	Clutch volume	Egg diameter
<i>Cletodes tuberculatus</i>			
Nov 86	377.4 $\pm$ 3.37 (53)	0.881 $\pm$ 0.12 (7)	35.1 $\pm$ 1.3 (25)
Jan 87	369.5 $\pm$ 5.29 (48)	1.24 $\pm$ 0.076 (16)	41.4 $\pm$ 0.71 (51)
May 87	396.6 $\pm$ 5.05 (44)	1.08 $\pm$ 0.080 (26)	40.1 $\pm$ 0.69 (78)
Jul 87	401.2 $\pm$ 5.91 (4)	1.61 (1)	46.8 $\pm$ 0.79 (3)
Oct 87	397.2 $\pm$ 6.04 (27)	1.08 $\pm$ 0.11 (6)	39.0 $\pm$ 1.1 (20)
Feb 88	394.2 $\pm$ 5.32 (24)	1.25 $\pm$ 0.11 (6)	39.5 $\pm$ 1.2 (22)
May 88	381.0 $\pm$ 5.21 (10)	1.56 $\pm$ 0.23 (5)	46.8 $\pm$ 1.6 (14)
Oct 88	436.7 $\pm$ 6.11 (15)	2.32 $\pm$ 0.32 (3)	46.0 $\pm$ 1.7 (13)
<i>Cletodes macrura</i>			
Nov 86	403.9 $\pm$ 5.88 (22)	1.30 $\pm$ 0.21 (3)	37.7 $\pm$ 1.7 (13)
Jan 87	395.5 $\pm$ 6.52 (22)	1.31 $\pm$ 0.17 (5)	41.2 $\pm$ 1.4 (17)
May 87	408.8 $\pm$ 12.0 (25)	1.29 $\pm$ 0.22 (6)	41.8 $\pm$ 1.5 (19)
Jul 87	423.0 $\pm$ 8.00 (5)	1.66 $\pm$ 0.24 (2)	41.6 $\pm$ 2.9 (8)
Oct 87	410.4 $\pm$ 4.06 (13)	1.51 $\pm$ 0.22 (4)	41.6 $\pm$ 1.7 (15)
Feb 88	412.5 $\pm$ 7.93 (6)	1.97 (1)	50.0 $\pm$ 1.4 (3)
May 88	413.3 $\pm$ 13.3 (6)	—	—
Oct 88	417.0 $\pm$ 38.2 (5)	1.29 (1)	42.8 $\pm$ 3.6 (3)
<i>Zosime pacifica</i>			
Nov 86	404.1 $\pm$ 7.89 (23)	3.42 (1)	54.1 $\pm$ 3.1 (4)
Jan 87	411.2 $\pm$ 9.35 (30)	2.01 $\pm$ 0.41 (6)	43.6 $\pm$ 1.4 (26)
May 87	440.4 $\pm$ 9.78 (36)	1.79 $\pm$ 0.20 (10)	42.7 $\pm$ 1.2 (40)
Jul 87	446.7 $\pm$ 14.5 (6)	4.25 (1)	47.9 $\pm$ 2.6 (7)
Oct 87	408.5 $\pm$ 5.87 (10)	2.60 $\pm$ 0.47 (2)	47.1 $\pm$ 2.2 (9)
Feb 88	455.9 $\pm$ 12.4 (11)	0.720 (1)	39.3 $\pm$ 8.3 (2)
May 88	410.0 $\pm$ 24.7 (4)	—	—
Oct 88	470.6 $\pm$ 7.99 (17)	1.96 $\pm$ 0.63 (3)	48.1 $\pm$ 1.1 (10)

among species, possibly indicating spatio-temporal habitat partitioning, or differential tolerance to environmental conditions.

Over time, the abundance and population structure of *C. tuberculatus*, *C. macrura* and *Z. pacifica* varied. Seasonality in the abundance of continental shelf meiofauna has been previously established (e.g. RUDNICK *et al.*, 1985). Density of *C. tuberculatus* was highest in January or February, while *C. macrura* reached high abundance in May. *Zosime pacifica* was most abundant during the winter (October–April). The lack of similarity in abundance maxima suggests there may be temporal habitat partitioning of these three species, as found by COULL and FLEEGER (1977), or a differential response in abundance to environmental conditions. However, the percentages of gravid females in the populations indicate that each species has their major period of reproductive activity between May and July, although gravid females can usually be found throughout the year. Therefore, conditions for reproduction appear to affect each species similarly. All three harpacticoid species had a large proportion (>25%) of their total numbers as juvenile copepodites on

Table 2. Adult female body length ( $\mu\text{m}$ ), clutch volume ( $/10^5 \mu\text{m}^3$ ) and egg diameter ( $\mu\text{m}$ ) for *Cletodes tuberculatus*, *Cletodes macrura*, and *Zosime pacifica* in the site-specific stations around proposed Platform Julius site over all cruises. Values are the mean  $\pm 1$  standard error. Numbers in brackets are the sample sizes for each mean and error term. 400 m = stations 400 m from, and including, PJ-1; 1 km = stations 1 km from PJ-1; 2 km = stations 2 km from PJ-1; 4–10 km = stations 4–10 km from PJ-1

Distance	Body length	Clutch volume	Egg diameter
<i>Cletodes tuberculatus</i>			
400 m	381.1 $\pm$ 6.52 (27)	0.969 $\pm$ 0.11 (10)	37.4 $\pm$ 1.0 (33)
1 km	401.3 $\pm$ 7.58 (15)	1.09 $\pm$ 0.16 (5)	40.7 $\pm$ 1.0 (15)
2 km	378.0 $\pm$ 4.94 (48)	1.15 $\pm$ 0.11 (16)	39.3 $\pm$ 0.94 (53)
4–10 km	388.9 $\pm$ 3.70 (36)	1.16 $\pm$ 0.068 (16)	41.0 $\pm$ 0.77 (49)
<i>Cletodes macrura</i>			
400 m	416.0 $\pm$ 12.1 (20)	1.47 $\pm$ 0.41 (3)	39.8 $\pm$ 2.4 (12)
1 km	433.6 $\pm$ 11.5 (11)	1.79 (1)	40.5 $\pm$ 2.1 (5)
2 km	399.6 $\pm$ 4.87 (25)	1.20 $\pm$ 0.094 (7)	40.9 $\pm$ 1.4 (22)
4–10 km	422.8 $\pm$ 10.6 (9)	1.51 $\pm$ 0.059 (3)	42.5 $\pm$ 1.1 (11)
<i>Zosime pacifica</i>			
400 m	435.8 $\pm$ 10.2 (25)	2.29 $\pm$ 0.45 (5)	49.1 $\pm$ 1.2 (18)
1 km	419.2 $\pm$ 18.5 (6)	1.74 $\pm$ 0.58 (2)	45.2 $\pm$ 1.7 (7)
2 km	416.9 $\pm$ 5.36 (36)	1.62 $\pm$ 0.23 (7)	46.5 $\pm$ 1.7 (20)
4–10 km	431.6 $\pm$ 19.0 (16)	2.72 $\pm$ 0.45 (5)	42.1 $\pm$ 1.5 (31)

each sampling date. Coupled with sex ratios generally  $>1$  on each sampling date, populations of *C. tuberculatus*, *C. macrura* and *Z. pacifica* in the Santa Maria Basin are healthy and actively reproducing.

Over time, reproductive parameters varied for *C. tuberculatus* and *Z. pacifica*, but not for *C. macrura*. Adult female body lengths, clutch volumes and egg diameters of *C. tuberculatus* changed the most between dates. Values for these three variables in this species increased as the CAMP study progressed. Increases in clutch volume and egg diameter for *C. tuberculatus* could be related to increases in female body length, since both clutch volume and egg diameter are positively related to body length in this species. However, the miniscule proportion of the variance in these two variables explained by body length makes this unlikely. The increases in clutch volume and egg diameter suggest conditions for growth of *C. tuberculatus* improved during the course of this study. For *Z. pacifica*, female body length was largest on the last cruise (October 1988) but clutch volume and egg diameter did not show a corresponding change. Although positive relationships between body length and/or clutch volume and egg diameter are common for harpacticoid copepods (WEBB and MARCOTTE, 1984) and other animals (BLUEWEISS *et al.*, 1978), there was no relationship between these variables for *C. macrura* and *Z. pacifica*. The lack of influence of body length on clutch volume or egg diameter for these two species suggests that extrinsic factors (e.g. food supply) are controlling reproductive output independently of somatic growth.

A large amount of naturally occurring meso-scale patchiness (i.e. within a 10 km radius of station PJ-1) in reproductive parameters was not evident for any of the three

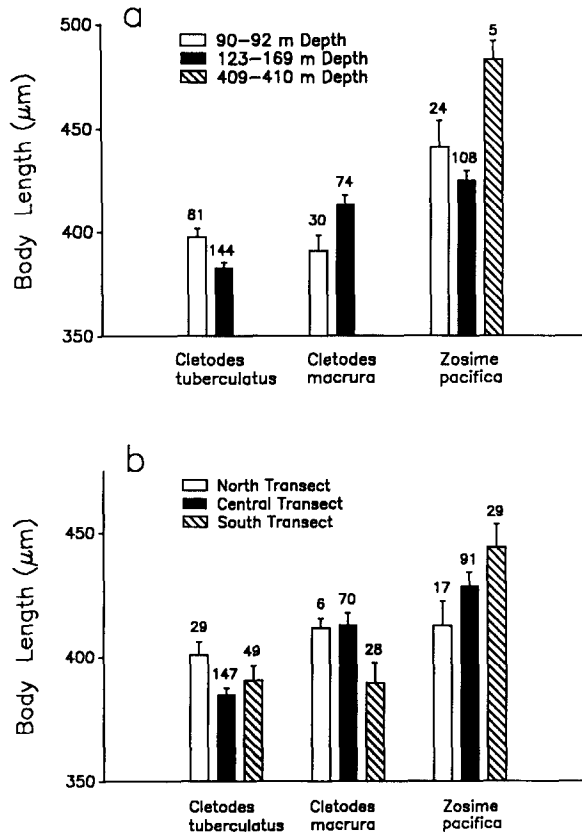


Fig. 9. Adult female body length of *C. tuberculatus*, *C. macrura* and *Z. pacifica* averaged over all cruises compared to (a) water depth, and (b) transect location. Bars are mean body length ( $\mu\text{m}$ )  $\pm 1$  standard error. Number above each bar indicates sample size.

harpacticoid species. Apart from the difference in egg diameters of *Z. pacifica* between two of the site-specific Platform Julius station groupings, no differences were detected for female body length, clutch volume and egg diameter for any species in the region surrounding the Platform Julius site. This suggests that these species are not responding to environmental changes (if any) on this scale.

On a regional scale (20–40 km; i.e. between the regional transects and with water depth), differences in reproductive parameters were detected for *C. tuberculatus* and *Z. pacifica*, but not for *C. macrura*. *Zosime pacifica* had larger females at greater depth. Reasons for this change are not known. For *C. tuberculatus*, female body length and egg diameters were larger at shallower depths. Both clutch volume and egg diameters were larger on the North regional transect compared to the Central and South transects for this species. Intriguingly, there appears to be a strong relationship between the sedimentary environment and the reproductive parameters of *C. tuberculatus* on the regional scale.

If increased sediment organic carbon content translates to increased food resources for harpacticoids, which is likely given that these animals will feed mainly on detritus and its associated bacterial fauna in shelf systems (see HICKS and COULL, 1983), it appears that the reproductive parameters of *C. tuberculatus* are linked to food supply. KINNEY *et al.* (1990)

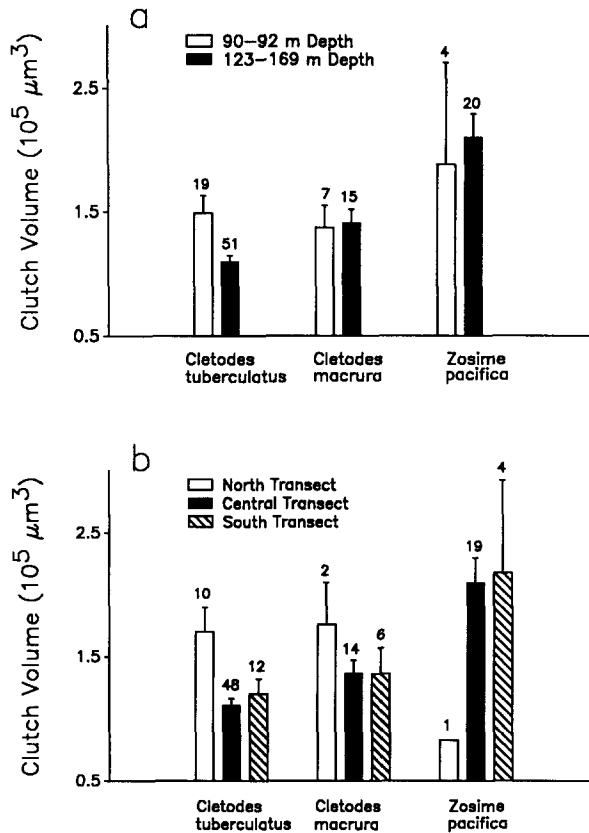


Fig. 10. Gravid female clutch volume of *C. tuberculatus*, *C. macrura* and *Z. pacifica* averaged over all cruises compared to (a) water depth, and (b) transect location. Bars are mean clutch volume (in  $10^5 \mu\text{m}^3$ )  $\pm 1$  standard error. Number above each bar indicates sample size.

found that the northern regional stations of the Santa Maria Basin have a finer grain size with higher clay content than the stations on the South cross-shelf transect. Average grain size also decreases with depth. The organic carbon content of sediments in the study area increases with decreasing grain size. Larger clutch volumes and egg diameters of *C. tuberculatus* were found on the North transect, where organic carbon content was highest. Food availability has been shown to influence clutch size for other harpacticoid copepods (WEBB and MARCOTTE, 1984). The fact that grain sizes in the 10 km around the Platform Julius site were uniform and no differences in clutch volume or egg diameters of *C. tuberculatus* were seen in this area, is consistent with this argument. In addition, as previously stated, clutch volume and egg diameters of *C. tuberculatus* tended to increase through time during the CAMP program. KINNEY *et al.* (1990) found a tendency towards smaller grain sizes in later surveys, thus suggesting a similar response of reproductive activity to organic carbon content with time. Meiofaunal density (including harpacticoid copepods) has been found to be directly correlated with increases in sediment organic carbon content (e.g. TIETJEN *et al.*, 1989), but, to our knowledge, this is the first time a response in the reproductive status of the meiofauna to sediment organic carbon has been noted. Surprisingly, MONTAGNA (1991) found an inverse relationship between total

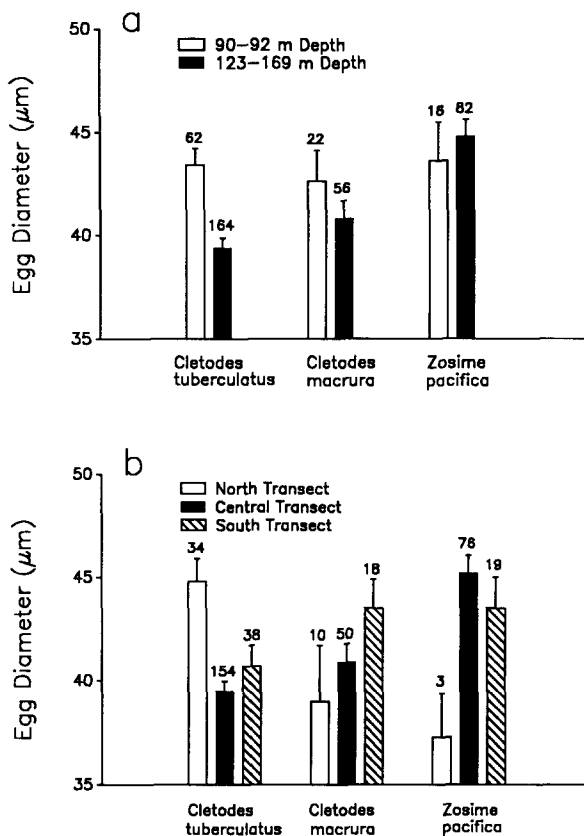


Fig. 11. Gravid female egg diameters of *C. tuberculatus*, *C. macrura* and *Z. pacifica* averaged over all cruises compared to (a) water depth, and (b) transect location. Bars are mean egg diameter ( $\mu\text{m}$ )  $\pm 1$  standard error. Number above each bar indicates sample size.

meiofauna density and sediment organic carbon in the Santa Maria Basin, especially in relation to water depth. He suggested that the low meiofauna density and high organic carbon levels at deeper depths are functions of low dissolved  $\text{O}_2$  levels. No gravid females of these three dominant harpacticoids were found below 169 m depth. This suggests that despite an enhanced food supply, low  $\text{O}_2$  levels at increasing depth limits reproductive activity. Overall, however, it appears that the reproductive parameters of *C. tuberculatus* may be linked to sediment organic carbon content.

Conventional life-history theory contends that trade-offs between number and size of eggs are responses to environmental adversity (STEARNS, 1976). *Cletodes tuberculatus* females were larger and had bigger individual eggs (with no change in clutch volume) at depths less than 100 m, suggesting a reproductive trade-off with production of fewer, larger eggs at shallower depths. Larger size at hatching may confer a competitive advantage to the newborn (STEARNS, 1976). Production of fewer, larger eggs at shallower stations by this species may be in response to food limitation or increased competition from other animals (STEARNS, 1976).

The largest differences in sensitivity of reproductive parameters to environmental

conditions were observed between the two congeneric *Cletodes* species. Both species are burrowers and differed only in aspects of swimming-leg setation (FIERS, 1991). Given their similarity of lifestyle and morphology, these differences are surprising but suggest that these two species are different in reproductive response. At a time when benthic ecologists are attempting to define faunal communities on the basis of "functional groups" (i.e. species that "act" the same) while sacrificing taxonomic resolution (see POSEY, 1990), analysis confined to the genus level or above would not have provided the information presented here. Therefore, while meiofaunal analyses are relatively straightforward in sampling and sorting considerations, the observed differences in these closely related species suggests that final analysis of reproductive patterns may have to be performed at the species level.

In conclusion, there were differences in patterns of some life history characteristics and reproductive parameters among *C. tuberculatus*, *C. macrura* and *Z. pacifica* in space and time. The high proportions of juveniles and sex ratios greater than unity indicated all three species had healthy, actively reproducing populations in the Santa Maria Basin. All three species exhibited little relationship between female body size and clutch volume or egg diameter, suggesting environmental factors which affect body size (e.g. temperature) do not control reproductive output. Female body length, clutch volume and egg diameter of *C. macrura* did not vary temporally or spatially. The stability of reproductive activity of this species may not allow detection of any impacts of drilling activity in the area. However, it may be a good marker species for the detection of extremely large scale (i.e. ocean basin) environmental changes. *Z. pacifica* exhibited minor differences in reproductive patterns through time and space, with no easily detectable pattern. *Cletodes tuberculatus* would appear to be the species of choice for monitoring the environmental impact of drilling activity since it seems to be sensitive to changes in grain size and/or organic carbon content of the sediment. *Cletodes tuberculatus* was also the most abundant of the three species in terms of number of gravid females obtained in the samples. We suggest that analysis of the reproductive parameters of *C. tuberculatus* alone can provide enough information to detect possible environmental impacts of drilling activity in the Santa Maria Basin.

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