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Gastropods and Intertidal Soft-Sediments: The Case of *Chilina ovalis* Sowerby (Pulmonata: Basommatophora) in South-Central Chile

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Abstract. Field experiments (exclusion and inclusion of gastropods) were carried out in the intertidal of the Lingue River estuary (south-central Chile) during the summers of 1991 and 1992. Cages were used to analyze the effects of the snail *Chilina ovalis* Sowerby on the macroinfaunal community structure and the sedimentological properties of the top (1.5 cm) layer of the substrate. The experiments lasted 30 (1991) and 90 days (1992). We also studied the quality of sediment in snail trails versus sediment without trails, and the abundance and size structure of *C. ovalis* over a period of 15 months. In both field experiments, *C. ovalis* affected neither the macroinfaunal structure nor the sediment quality. Significant differences were detected for chlorophyll *a* content (phytobenthic biomass) when disturbed (trails sediment) versus undisturbed sediment were compared. The highest abundance of *C. ovalis* (up to 792 ind/m^{-2}) occurred during summer months when the experiments were carried out. It is concluded that the disturbance of intertidal sediment by *C. ovalis* is quite local and of short duration, a situation which is discussed in connection with physical and biological factors involved in sediment stability and community organization of macroinfaunal assemblages.

INTRODUCTION

Epibenthic organisms such as decapod crustaceans and gastropod mollusks can play key roles in structuring the sediment and the macroinfauna of soft bottom substrates (Dayton, 1984; Wilson, 1990; Hall et al., 1993). Biological disturbance can alter the fabric and stability of the sediment (Brenchley, 1981; Posey, 1987) and affect the food availability by depletion of phytobenthic biomass (Connor et al., 1982). Epibenthos can also ingest macroinfaunal larvae or adults (Möller, 1986; Hines et al., 1990), bury and kill post-settlement infauna, or induce escape behavior (Ambrose, 1984; DeWitt & Levinton, 1985; Jensen & Jensen, 1985).

Manipulative experiments carried out with prosobranch gastropods have shown effects of these organisms on various components of the benthos (see Lopez & Levinton, 1987). Levinton & Stewart (1982) documented negative effects of *Ilyanassa obsoleta* Say and *Hydrobia totteni* Morrison on the population growth of the oligochaete *Paranais litoralis* Müller. The same gastropod species affected biomass and metabolism of benthic diatoms (Levinton & Bianchi, 1981; Connor et al., 1982), and the standing stock of bacteria adhering to the sediment (Bianchi & Levinton, 1981). In salt marsh areas of eastern England, Frid & James (1988) found an increase in the abundance of oligochaetes and the polychaete *Capitella capitata* Fauvel, resulting from removal of the epibenthic gastropod *Littorina littorea* (L.). In muddy salt marsh areas of Georgia (USA), Pace et al. (1979) found that the effects of *I. obsoleta* were related more to the ingestion of microorganisms than mechanical changes produced in the substrate. This snail species significantly affected the abundance of recently settled and juvenile meiofauna and macroinfauna in tidal flats of North Carolina, USA (Hunt et al., 1987). Similar results were reported by Wiltse (1980) who studied the effects of the snail *Polinices duplicatus* (Say) on the tidal flats of Barnstable Harbor, USA.

Knowledge of the ecology of epibenthic gastropods on other coasts is rather scarce. In estuarine areas of south central Chile (ca. 38–40° S), the endemic pulmonate gastropod *Chilina ovalis* Sowerby, 1842, resembles *Ilyanassa obsoleta,* in spite of geographical and phylogenetic differences (Brown & Pullan, 1987; Castellanos & Miquel, 1991). *Chilina ovalis* gathers in muddy areas with high nutrient content, i.e., organic matter, and its movement and surface deposit-feeding habits produce noticeable changes in the substrate (trails). Deposit feeding in *C. ovalis* could be a secondary feeding mode, considering that other species of the genus have been described as periphyton consumers above hard sustrates (Miquel, 1986; Bosnia et al., 1990).

In the Queule and Lingue River estuaries, *C. ovalis* coexists with polychaetes and amphipods (Richter, 1985; Bertrán, 1989; Quijón & Jaramillo, 1993; Quijón et al., 1996). Seasonal studies carried out on the subtidal populations of such taxa show that their main periods of recruitment occur during the spring-summer months (Bravo, 1989; Quijón et al., 1996). Our unpublished data show similar trends for intertidal populations. Feeding trails of *C. ovalis* alter the surface layer of the sediment to an approximate depth of 0.5 cm where the highest abundance of adults and recruits of the macroinfauna are

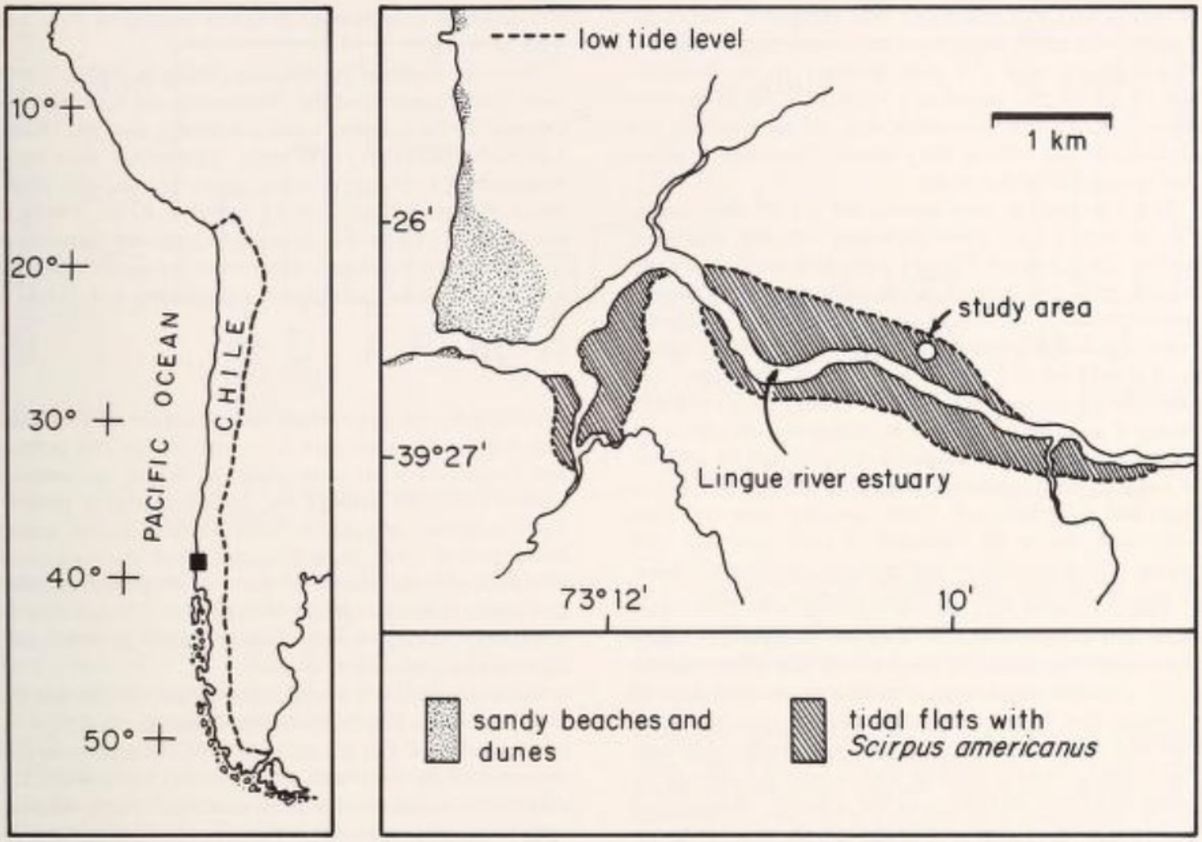

Figure 1

Study area in the Lingue River estuary, south-central Chile.

concentrated (unpublished data). We hypothesize that *C. ovalis* affects the sediment and community structure of the macroinfauna on the intertidal estuarine sediment of southern Chile. In order to test this hypothesis, the abundance of *C. ovalis* was experimentally manipulated in the intertidal zone of the Lingue River estuary during the summers of 1991 and 1992. In addition, analyses of sediment with and without trails of gastropods, as well as gastropod population analyses, were carried out.

MATERIALS AND METHODS

Study site: Figure 1 shows the middle section of the Lingue River estuary, in south-central Chile (39°41′S, 73°13′W). Upper shore levels of tidal flats are occupied by sedges *Scirpus americanus* Pers; close to them, the largest aggregations of *C. ovalis* have been observed. Sedges occur in association with muddy-sand substrates rich in organic content (ca. 20% of dry weight); their stems are used by the snails to deposit their egg masses (cf. Miquel, 1984).

Abundance and population size structure of *C. ovalis*: The abundance of *C. ovalis* and the body size structure of the population were characterized by using 25 cm × 25 cm quadrats on a monthly sampling schedule. The samples (six replicates) were collected in sediments with a representative range of *S. americanus* canopy. The abundance and overall shell length, i.e., body size of the individuals were used to estimate the size structure of the population. The Battacharya's method (Gayanilo et al., 1989) was used for identification of modes, i.e., cohorts in the size-class distribution of *C. ovalis.* "Modal Progress Analysis" (MPA); a section of the "ELEFAN" program was used for the analysis of temporal variability of modes (Gayanilo et al., 1989).

Field experiments: The experimental design consisted of the following treatments: inclusion (natural densities) and exclusion cages of snails, undisturbed sediments (control), and partial walls as a control for possible artifact effects produced by the cages (Reise, 1985; Hall et al., 1990). To detect eventual cage artifact effects, sediments of control and wall treatments were compared. The inclusion and exclusion cages were made with circular meshes of galvanized steel of 1 mm aperture, 30 cm diameter, and 10 cm height, buried to a depth of 3 cm in the substrate. Partial cages were made with similar materials and dimensions, but 50% of the perimeter was open to allow free movement of the snails.

The experiments were carried out for 30 days during the summer of 1991 (four replicates for each treatment, starting date: January 5) and for 90 days during the summer of 1992 (six replicates for each treatment, starting date: November 4, 1991). All the treatments (replicated cages and unmanipulated sites) were located on areas of the flat adjacent to *S. americanus* fronds. The cages, i.e., replicates in the sense of Hurlbert (1984) were randomly placed at an average distance of 40 m from low tide level. Independent sediment samples were collected for analysis of texture, water, organic matter, and chlorophyll *a* contents and macroinfauna. Three samples were collected from each one of the replicates of each treatment with plastic cylinders 1 cm in diameter. Samples were collected during the low tides of days indicated in Figures 3–6.

Sediment comparisons: A sediment comparative study was conducted during a spring low tide of November 1993. Sediment from freshly produced feeding trails of *C. ovalis* and from adjacent undisturbed areas was sampled and compared. Twenty "sets" of samples with similar volumes were collected with a metallic spatula inserted to a depth of 0.5 cm in the substrate. Independent sediment samples were used for analyses of texture, water, organic matter, and chlorophyll *a* contents.

Samples and data analysis: Sedimentological analyses were carried out as follows: sand and biogenic aggregates, i.e., animal feces, tubes (both in the range 63–2000 μm) were separated from the mud fraction (particles < 63 μm) by wet sieving through a 62.5 μ sieve (Anderson et al., 1981). Later, sand and aggregates were separated by wet sieving through a 62.5 μ sieve after disaggregation through sonification for 30 min. The water and organic matter contents of independent sediment samples were determined as the loss in weight of wet samples after drying (80°C, 72 h) and after combustion (550°C, 4 h). Sediment samples for chlorophyll *a* content analysis (used here as an estimate of phytobenthic biomass) were kept in 90% acetone for 24 h to extract pigments; then they were centrifuged at 3500 rpm for 15 min. The absorbance of the supernatant was measured at 750 and 665 nm with and without acidification by HCl 0.1 N (Strickland & Parsons, 1972). The samples for the faunistic analyses were sieved with a 0.25 mm mesh and the residue was preserved in formaldehyde 10% until sorting.

The sedimentological and faunistic (abundance and species-richness) characteristics were used for statistical comparisons among treatments in the field experiments. In addition, sedimentological characteristics were used for statistical comparisons between sediments with and without trails.

One-way analyses of variance (Sokal & Rohlf, 1969) were used except when the values were not normally distributed. In these cases, a non-parametric analysis (Kruskall-Wallis ANOVA) was used. Percentage data were transformed by the expression arcsin (n) and the abundance values by $\log_{10}(n + 1)$ (Sokal & Rohlf, 1969). If the analyses of variance indicated significant differences ($p < 0.05$) among means, these were compared using the a posteriori Tukey's multiple comparison test (Day & Quinn, 1989).

RESULTS

Abundance and population size structure of *C. ovalis*: The highest abundance of *C. ovalis* (up to 792 ind/m^2) and number of trails were observed during the summer months (after the start of the snail recruitment period). The population abundance declined to 0 ind/m^2 during the winter of 1992 (July–August). Then the population increased after September of that year (Figure 2; no samples were collected during November). Comparison of abundance during December and January of both years indicated interannual variations.

Table 1 shows the average size of the cohorts and the monthly increase in these averages (months with N < 50 were not included in the analyses). The largest mean size increases of the 1990 and 1991 cohorts (1.335 and 2.251 mm/month, respectively) were observed during summer months (February–March 1992).

Field experiments: Most of the statistical comparisons (one way ANOVA) carried out with the data of the field experiments showed no significant differences ($p > 0.05$) among treatments (Tables 2, 3 and Figures 3–6).

The results of analyses with sedimentological characteristics (Table 4) showed F values between 0.05 and 2.58 during the experiment carried out in 1991, and between 0.02 and 5.58 during 1992. The *P* values fluctuated between 0.101 and 0.984 in 1991, and between 0.006 and 0.996 in 1992. Thus, only during the second experimental period were significant differences among the treatments detected (Figure 4): the sand content of the control treatment was significantly higher than those estimated for inclusion and exclusion sediments (day 8, $P = 0.006$); and the sand content of the control sediments was higher than that estimated for inclusión treatment (day 90, $P = 0.037$).

When the abundance and species-richness of the macroinfauna were used for statistical comparisons (Table 3), the F values fluctuated between 0.03 and 2.29 (1991) and between 0.06 and 5.21 (1992). The *P* values fluctuated between 0.130 and 0.994 during 1991, and between 0.008 and 0.980 during 1992. Thus, as in the case of the sedimentological characteristics, only during the second experimental period (1992) did the P values indicate sig-

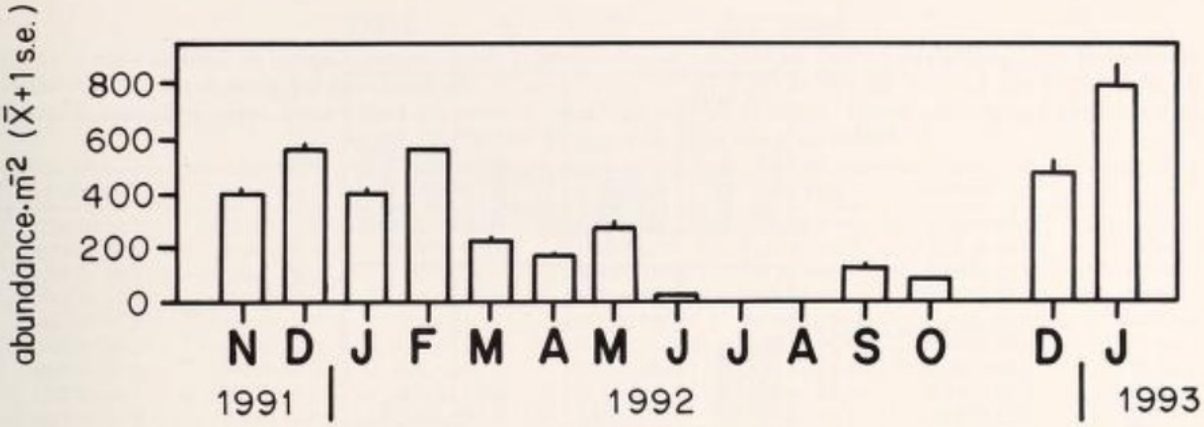

Figure 2

Temporal variability of the population abundance of *C. ovalis* in the sediments of the study area. No samples were collected in November 1992.

nificant difference between the treatments (Figure 6): the abundance of *C. capitata* in control and wall sediments was significantly higher than that calculated in the exclusion sediments ($P = 0.008$, day 60); the abundance of the *Littoridina* species was significantly different when inclusion and exclusion sediments were compared ($P = 0.023$).

The macroinfaunal analyses rendered a total of six species, the most abundant taxa being the ostracod *Cyprideis beaconensis* Leroy (2–122 ind/4 cm^2), the polychaete *Capitella capitata* Fauvel (1–34 ind/4 cm^2), and a species of *Littoridina* (0–4 ind/4 cm^2) (Figures 5, 6). Other species were occasionally recorded: the polychaetes *Perinereis gualpensis* Jeldes, *Prionospio* (*Minuspio*) *patagonica* Augener, and the amphipod *Paracorophium hartmannorum* Andrés. No species composition difference was detected when the treatments were compared.

The total abundance of the macroinfauna (up to 137 ind/4 cm^2) decreased toward the end of the summer of 1991, following the trends of *C. beaconensis* and *C. capitata* abundance (Figures 5, 6). Species richness (two to four species) did not show temporal variability.

Sediment comparisons: In the comparison of sediments with snail trails versus undisturbed sediment, sand, aggregates, mud, water, organic matter, and chlorophyll *a* contents showed some differences in magnitude (Figure 7). However, only the chlorophyll *a* content was significantly lower ($P = 0.001$) in disturbed (87.2 ug/g) versus undisturbed sediment (101.1 ug/g).

DISCUSSION

Most of the results of the field experiments suggest that *C. ovalis* does not affect the structure of the intertidal

Table 1

Mean sizes in mm of the cohorts of *C. ovalis*, detected by "Modal Progress Analysis" (MPA). Mean monthly growth rates are also presented.

Date	Cohort 1990		Cohort 1991		Cohort 1992	
	Size	Growth	Size	Growth	Size	Growth
November 1991	15.764	—	5.224	—	—	—
December	16.665	0.901	5.448	0.224	—	—
January 1992	16.884	0.219	6.902	1.545	—	—
February	17.020	0.136	7.852	0.950	—	—
March	18.355	1.335	10.103	2.251	—	—
April	—	—	11.908	1.805	—	—
May	—	—	12.973	1.065	—	—
September	—	—	16.273	0.825	—	—
October	—	—	16.500	0.227	—	—
December	—	—	16.712	0.106	5.423	—
January 1993	—	—	17.593	0.881	7.545	2.122

Table 2

Summary of variance analysis carried out with the sedimentological characteristics. Degrees of freedom were 3–12 for the period 1991 and 3–20 for the period 1992. The values of F and P (in parentheses) are given in the columns below each sedimentological characteristic. Asterisks indicate significant difference in sand content among sediments of control versus inclusion treatments (days 8 and 90) (cf. Figure 4).

	Sand	Aggregates	Mud	Water	Org. matter	Chlorophyll *a*
1991–start	0.59 (0.633)	1.19 (0.362)	1.19 (0.362)	0.74 (0.550)	1.30 (0.325)	2.58 (0.102)
day 6	0.43 (0.737)	0.05 (0.984)	0.15 (0.928)	0.69 (0.579)	0.19 (0.900)	0.26 (0.853)
day 11	0.24 (0.863)	0.62 (0.616)	0.18 (0.905)	1.57 (0.249)	0.09 (0.965)	2.59 (0.101)
day 30	1.32 (0.313)	0.39 (0.762)	0.46 (0.714)	1.23 (0.346)	0.53 (0.672)	1.71 (0.217)
1992–start	0.40 (0.755)	0.59 (0.629)	0.82 (0.500)	0.06 (0.979)	0.62 (0.608)	0.36 (0.783)
day 3	0.47 (0.708)	0.20 (0.894)	0.17 (0.919)	1.32 (0.297)	0.19 (0.901)	2.38 (0.100)
day 8	5.58 (0.006)*	1.62 (0.217)	0.68 (0.576)	1.44 (0.260)	0.02 (0.996)	0.49 (0.700)
day 30	0.49 (0.693)	0.21 (0.888)	0.11 (0.953)	0.71 (0.560)	0.61 (0.620)	1.60 (0.222)
day 60	0.28 (0.840)	1.03 (0.400)	1.02 (0.406)	1.18 (0.341)	0.33 (0.802)	0.17 (0.913)
day 90	3.55 (0.037)*	2.95 (0.062)	2.06 (0.144)	0.31 (0.821)	0.79 (0.513)	0.45 (0.720)

sediment and macroinfauna in the Lingue River estuary. The experiments were set up intuitively expecting the dramatic changes that occur with the manipulation of some species (Paine, 1980). However, these changes did not occur or were trivial, leading to rejection of the hypothesis. In addition, the experiments did not detect the existence of confounding effects such as artifacts; i.e., no differences were found between the sediment of the control and wall treatments on any occasion (cf. Hall et al., 1990).

The results of the comparisons of sediment with and without feeding trails indicate that *C. ovalis* indeed affects the phytobenthic biomass on a time scale of minutes or hours. However, these effects do not persist longer than one tidal cycle. These results differ from those described by Pace et al. (1979), who detected effects of *Ilyanassa obsoleta* on the phytobenthos only after the third day and lasting until at least 10 days after the start of their experiments. Laboratory studies have detected a negative effect on the phytobenthos by a high abundance of *I. obsoleta*, but a positive effect when abundance of the gastropod was lower (Connor et al., 1982). A similar relationship characterized the interaction between *Hydrobia totteni* and the phytobenthic standing-stock in tidal flats of Long Island, New York (Levinton & Bianchi, 1981).

Our experiments were carried out during summer periods characterized by the presence of greater abundance, higher growth rates of gastropods, and more trails on the sediment surface (personal observation). Later in the year because the snails are present in minor abundance , we can expect similar or smaller effects than those detected with these experiments (cf. Hunt et al., 1987; Cammen, 1989; Peterson & Black, 1993).

Possible explanations for the absence of effects of C.

Table 3

Summary of variance analysis carried out with faunal characteristics. Degrees of freedom were 3–12 for the period 1991 and 3–20 for the period 1992. The values of F and P (in parentheses) are given in the columns below each faunal characteristic. Asterisks indicate significant difference in faunal abundance. Among *C. capitata* in sediments of the wall and exclusion treatments versus that in control sediments (day 60); and between the abundance of *Littoridina* sp. in sediments of the exclusion versus that in inclusion sediments (day 90) (cf. Figure 6).

	C. beaconensis	*C. capitata*	*Littoridina* sp.	Total abundance	Spp. richness
1991–start	0.79 (0.523)	0.35 (0.788)	0.22 (0.879)	0.51 (0.685)	0.49 (0.699)
day 6	0.44 (0.734)	0.23 (0.870)	0.38 (0.773)	0.31 (0.816)	0.19 (0.896)
day 20	0.70 (0.570)	0.03 (0.994)	0.47 (0.706)	0.46 (0.717)	0.36 (0.781)
day 30	0.36 (0.787)	2.29 (0.130)	0.41 (0.746)	0.45 (0.724)	0.48 (0.705)
1992–start	0.39 (0.761)	0.93 (0.444)	1.01 (0.412)	0.46 (0.712)	0.48 (0.703)
day 3	1.78 (0.184)	0.47 (0.704)	1.97 (0.151)	1.01 (0.408)	0.06 (0.980)
day 8	0.37 (0.775)	0.08 (0.972)	3.08 (0.051)	0.22 (0.885)	2.75 (0.070)
day 15	0.76 (0.531)	0.37 (0.777)	0.51 (0.679)	0.55 (0.654)	1.43 (0.264)
day 30	0.79 (0.515)	0.60 (0.622)	0.34 (0.795)	0.76 (0.533)	0.68 (0.578)
day 60	2.14 (0.127)	5.21 (0.008)*	1.11 (0.368)	2.88 (0.061)	1.57 (0.228)
day 90	0.60 (0.621)	1.03 (0.401)	3.97 (0.023)*	0.99 (0.416)	0.79 (0.512)

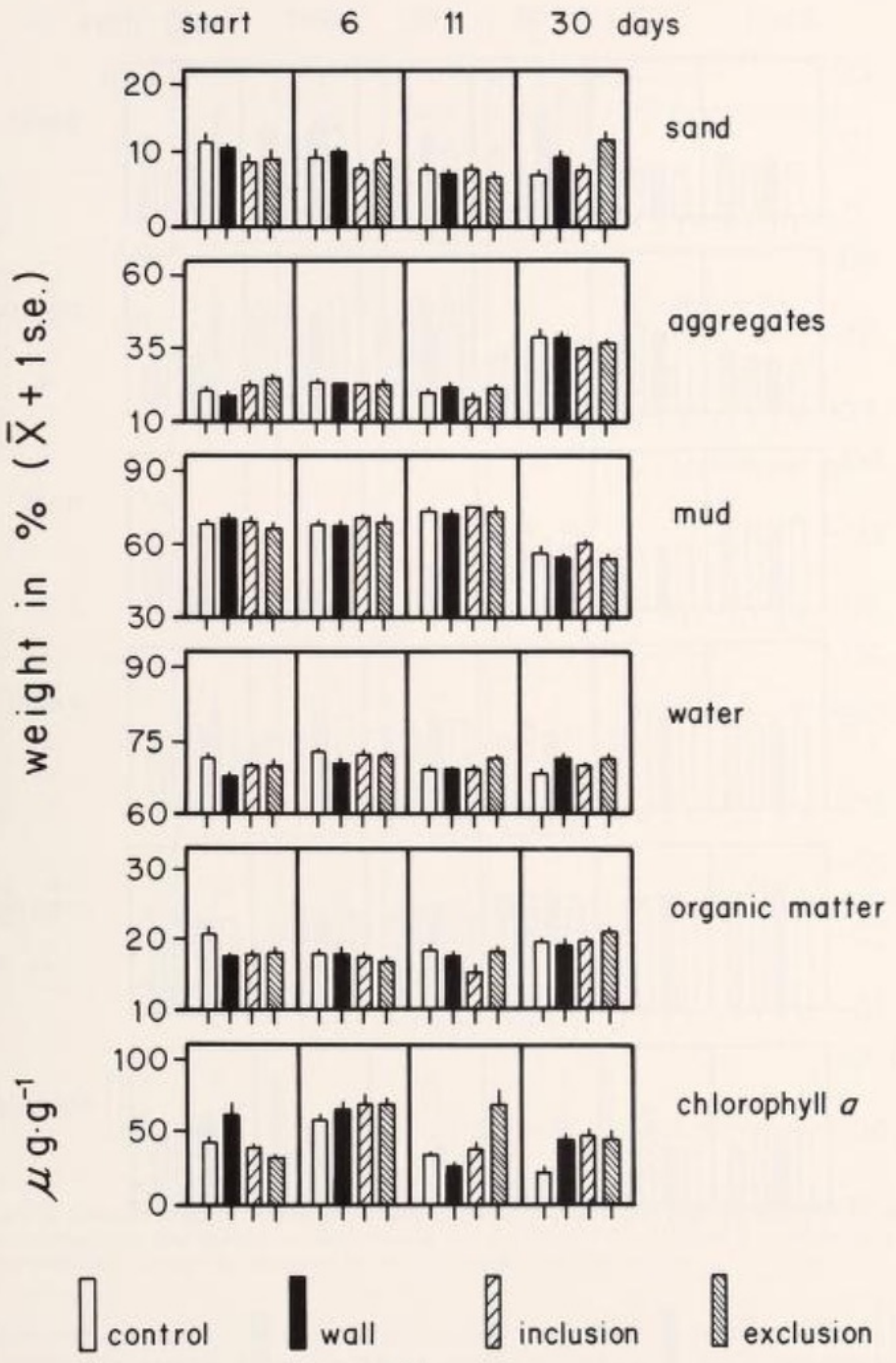

Figure 3

Sedimentological characteristics resulting from field experiments carried out in the summer of 1991. Asterisks indicate the days when significant differences among the treatments ($p < 0.05$) were detected (see Table 2).

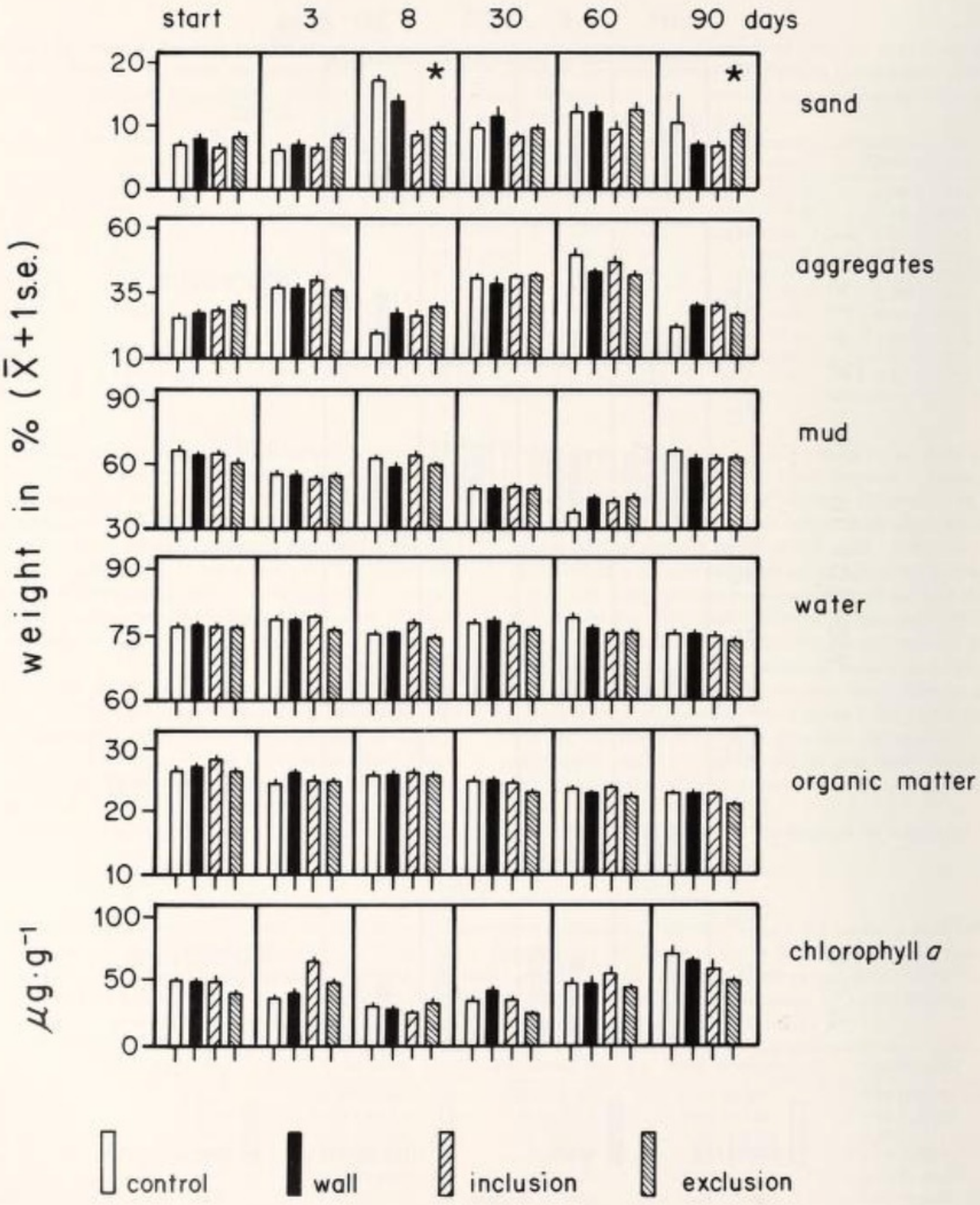

Figure 4

Sedimentological characteristics resulting from field experiments carried out in the summer of 1992. Asterisks indicate the days when significant differences between the treatments ($p < 0.05$) were detected (see Table 2).

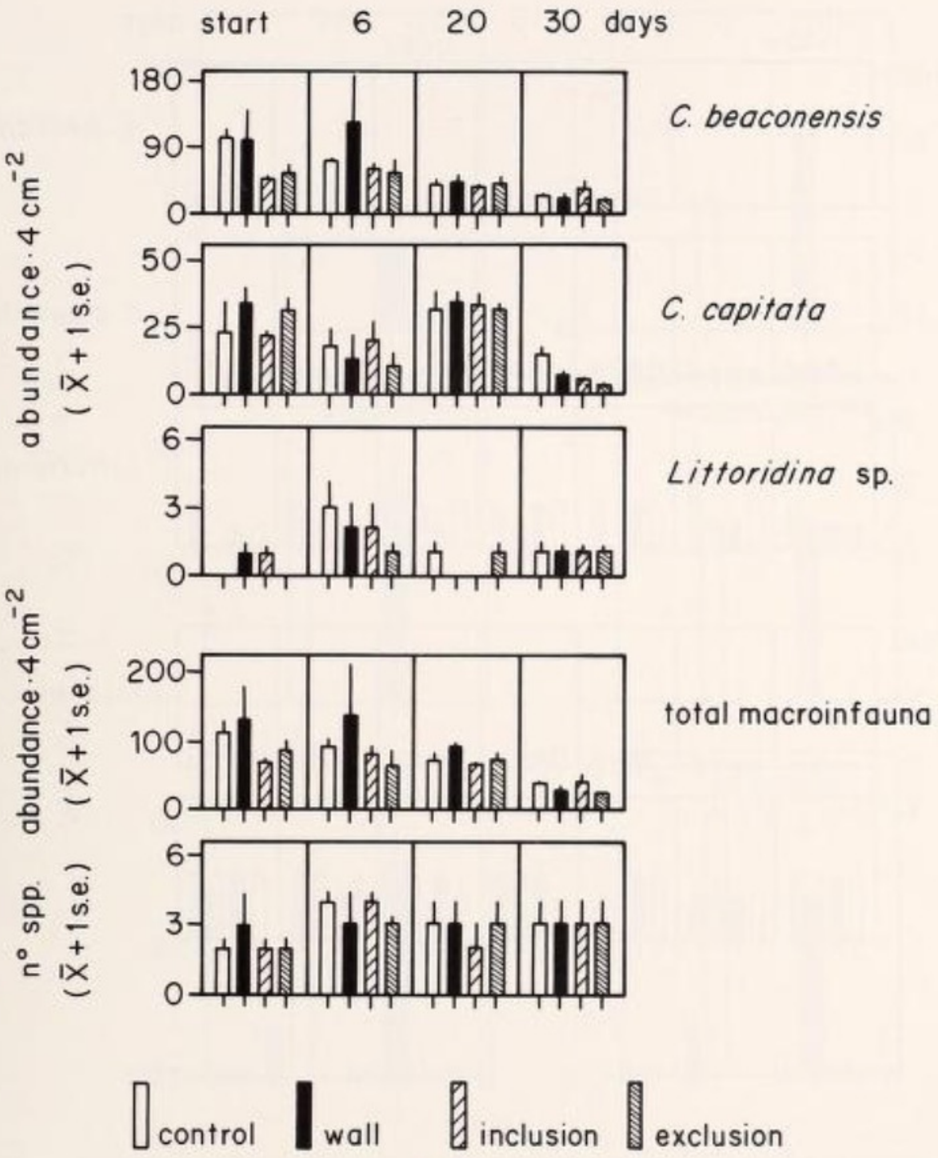

Figure 5

Abundance of *C. beaconensis*, *C. capitata*, the species of *Littoridina* genus, and total macroinfauna and species-richness resulting from field experiment, carried out in the summer of 1991. Asterisks indicate the days when significant differences between the treatments ($p < 0.05$) were detected (see Table 3).

ovalis include factors that regulate the production of trails and others that inhibit their potential effects. The population size of *C. ovalis* and the consequent feeding pressure which it exerts could be below the level at which food becomes a limiting resource (see Peterson & Black, 1987). The high availability of nutrients in the area should allow an increase in population size and age reached by individuals (cf. Forbes & Lopez, 1986). However, more than two cohorts were never directly observed simultaneously, while individuals reached an age of at least 18 months. By comparison, in the same genus ages of 2 years and two or more reproductive periods have been described for *C. gibbosa* in an Argentine freshwater reserve located at a latitude comparable to the Lingue River estuary (Bosnia et al., 1990).

Other factors can diminish the possible effects of the

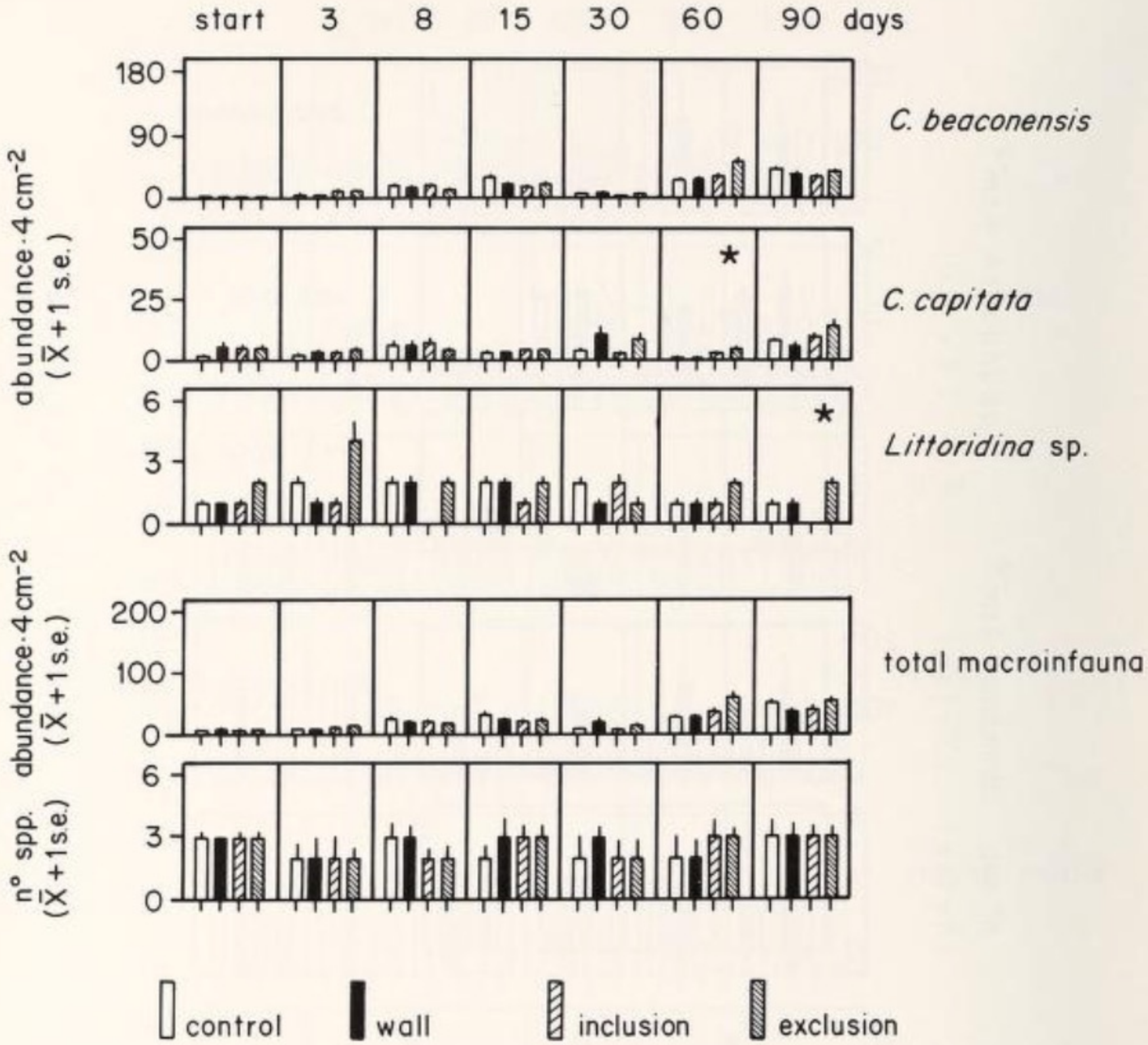

Figure 6

Abundance of *C. beaconensis, C. capitata,* the species of *Littoridina* genus, and total macroinfauna and species-richness resulting from field experiment carried out in the summer of 1992. Asterisks indicate the days when significant differences between the treatments ($p < 0.05$) were detected (see Table 2).

Table 4

Summary of variance analysis carried out with the sedimentological characteristics of sediments in areas with and without trails of *C. ovalis*. Degrees of freedom were 1–38. The values of F and P (in parentheses) are given in the columns below each sedimentological characteristic. Asterisk indicates significant difference in the contents of chlorophyll *a*. (cf. Figure 7).

Sand	Aggregates	Mud	Water	Org. matter	Chlorophyll ^{a}
3.83 (0.058)	1.42 (0.241)	1.80 (0.187)	3.23 (0.080)	0.03 (0.873)	12.40 (0.001)*

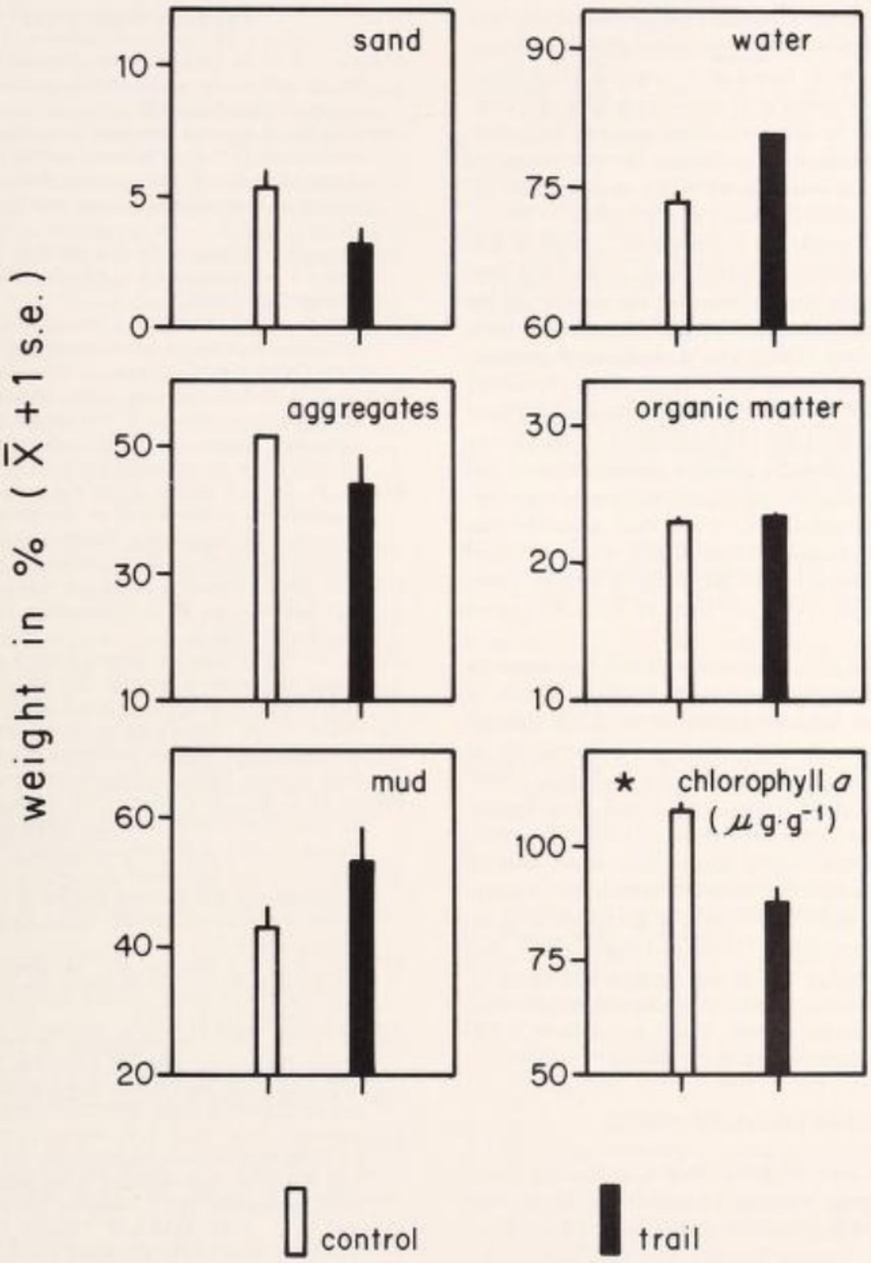

Figure 7

Sedimentological characteristics in areas with and without trails (control sediments) of *C. ovalis.* Asterisk indicates the existence of significant differences ($p < 0.05$).

trails and explain the lack of lasting and cumulative effects of *C. ovalis.* The tides import, resuspend, redistribute, and export sediments (Eisma & Li, 1993), fecal aggregates (Risk & Moffat, 1977; Taghon & Jumars, 1984), phytobenthos (de Jonge & van Beusecom, 1995), and organisms of the macroinfauna (Butman et al., 1988a,b). The tides are also associated with bottom diatom proliferation and recolonization (Admiraal & Peletier, 1987) on recently altered patches of sediment (trails).

The macroinfauna could also be responding to the local disturbance exerted by *C. ovalis.* Capitellid species, for example, can rapidly recolonize recently altered sediment patches, supposedly in response to nutrient availability and the temporary absence of competing species (Tsutsumi et al., 1990). In addition, other species can escape mechanical disturbance of sediment by burrowing to deeper layers in the sediment (refuge), avoiding the effects of the disturbance (Roberts et al., 1989).

Surprisingly, *C. ovalis* did not affect the texture or water content of the sediment, which suggests that this species alters neither the resuspension nor the stability of the substrate (cf. Rhoads & Boyer, 1982). This differs from the findings of Boyer (1980) who demonstrated throughout laboratory experiments that a larger snail (*Polinices duplicatus*) was able to destabilize the sediment of a tidal flat in Massachusetts, USA. The effects of *P. duplicatus* were first observed after 24 hours of experimentation and remained until at least 4 days after the snails were excluded. Thus, it seems that *C. ovalis* does not form part of the biological component that affects water-sediment interaction (see Meadows & Tait, 1989; Paterson, 1989; Paterson & Daborn, 1991), at least in the time period studied.

The role of *C. ovalis* contrasts with what is currently known about gastropods such as *I. obsoleta,* which in terms of size and habitat appears to be a functionally comparable species. *I. obsoleta* affects the structure of macroinfaunal (Hunt et al., 1987; Frid & James, 1988), bacterial (Bianchi & Levinton, 1981), and phytobenthic (Pace et al., 1979; Lopez & Levinton, 1987) communities. These differences could result from factors such as dietary flexibility (Feller, 1984), behavioral aspects (Cranford, 1987), and the existence of intrapopulation interactions (Levinton, 1985; Forbes & Lopez, 1986). The absence of previous work on the natural history of *C. ovalis* remains the main obstacle to identifying the role of this species and the degree of its similarity to *I. obsoleta* and other species around the world.

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