

Enrichment experiments and infaunal population cycles on a Southern California sand plain: response of the leptostracan *Nebalia daytoni* and other infauna

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ABSTRACT: Field studies on the effects of pulsed enrichments were carried out on macrofaunal invertebrates inhabiting the sandy bottom at a depth of about 20 m off the coast of Southern California, USA. Contrary to expectation, no members of the community studied responded positively to patches artificially enriched with organic material (kelp, fertilizer, or parcels of fish flesh). Although other members of the leptostracan genus *Nebalia* respond favorably to carrion and heavily enriched conditions, *N. daytoni*, one of the most common animals at the study site, showed no response to the enrichments. All other members of the infaunal community declined in abundance in enriched plots, although the opportunistic polychaete *Capitella* sp. recruited heavily into them. In the unenriched habitat, seasonal cycles of abundance were evident for most groups of macrofaunal invertebrates, but were especially strong for amphipods and *N. daytoni*.

KEY WORDS: *Nebalia* · *Capitella* · Organic enrichment · Seasonal cycles

INTRODUCTION

Organic enrichment has long been seen as a crucial structuring agent for the soft sediment benthos, as disturbances (Tarazona et al. 1988, Ritz et al. 1989), a source of heterogeneity (Snelgrove et al. 1992, Grassle & Grassle 1994), or as periodic events necessary for normal community function (Smith 1986, Tsutsumi 1990) depending on the scale, intensity, and location of the enrichment. The immediate source of enrichment may be anthropogenic or natural. Where organic enrichment is massive (e.g. at some sewage outfalls) one commonly observes decreased mean body size, biomass and diversity; restriction of macrofauna to near-surface sediments; and changes in dominance (Pearson & Rosenberg 1978, Swartz et al. 1986, Weston 1990). However, where the volume of effluent or physical conditions result in only moderate enrichment around outfalls, less predictable effects including in-

creased diversity and biomass (Dauer & Conner 1980) or instability of benthic communities (Zmarzly et al. 1994) are possible. Exceptionally, where organic enrichment from outfalls is great, it may result in increases in biomass, diversity and abundance if it occurs in regions which are already disturbed and are naturally high in organic matter (Ansari et al. 1986). Substrate enrichment is also an important part of deep-sea biology, either as a local, massive food fall (e.g. a whale carcass) or as a much less intense, but very widespread rain of detritus (Dayton & Hessler 1972, Thiel 1978, Smith 1985, Levin & Thomas 1989, Smith et al. 1989, Priede et al. 1991, Snelgrove et al. 1992, Bennett et al. 1994, Levin et al. 1994, Rice & Lamshead 1994). Enrichment has also been studied in shallow protected waters, especially in mud flats and estuaries. Although such environments are typically high in organic matter, many studies have shown that further enrichment is important for the persistence of some species (Thrush 1986, Tsutsumi 1990, Sardá et al. 1992) and enhances the reproduction of others (Levin 1986, Bridges et al. 1994, Levin et al. 1994).

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Most research on benthic enrichment has been conducted in regions where hydrodynamic conditions are likely to allow organic matter to accumulate and decompose in place. In one of few studies on small-scale enrichments to sandy sediments exposed to strong wave-generated surge, VanBlaricom (1982) found that pits created by foraging rays accumulated organic matter which attracted some members of the infaunal community and repelled others. The leptostracan crustacean *Nebalia daytoni*, the sixth most abundant animal during VanBlaricom's study, was apparently unaffected by the small-scale, low-intensity enrichments provided by detrital material in the ray pits. This is surprising considering that essentially all natural history information on the genus *Nebalia* refers to these animals as living in habitats rich in organic matter (Menzies & Mohr 1952, Citarella 1965, Ricketts et al. 1985, Kazmi & Tirmizi 1989, Rainer & Unsworth 1991, Vetter 1994) or as scavengers and/or carrion feeders (Nishimura & Hamabe 1964, Wägele 1983, Snelgrove 1993). Furthermore the genus is generally considered to specialize in low oxygen environments (Schram 1986, Brusca & Brusca 1990).

The presence of large numbers of *Nebalia daytoni* in the sediments studied by VanBlaricom (1982) suggests either that enrichment was not limited to ray pits, or that important aspects of the natural history of this leptostracan deviate strongly from all other known members of the genus. The present study examined the community response to small-scale, high-intensity pulses of enrichment on the same sand plain investigated by VanBlaricom (1982). The seemingly incongruous use of this habitat by a leptostracan suggested that this community may be, to some degree, adapted to such disturbances. Three types of particulate enriching material were used. Kelp was the initial choice for enriching media, sodium alginate was also used to control for the possibility of unpalatable or repellent substances potentially present in kelp, and fertilizer served as a high nitrogen enrichment. Fish carcasses were used as a fourth enrichment. It was predicted that *Nebalia daytoni*, and perhaps some other species attracted to ray pits (the amphipods *Acuminodeutopus heteruopus* and *Synchelidium shoemakeri* and the tanaid *Leptochelia dubia*), would increase in density in enriched plots (VanBlaricom 1982).

MATERIALS AND METHODS

Field work was conducted using SCUBA from depths of 19 to 21 m, 0.7 km off the coast of San Diego (California, USA, 32° 52' N, 117° 15.5' W) from June 1991 to September 1994. The study area is exposed to oceanic swell and is subject to strong storm-generated

surge during winter and early spring. Bottom water temperature ranged from 6 to 22° C.

A standard protocol was followed when taking all cores. Sediments were cored with 9 clear butyrate tubes (7.6 cm diameter) pushed 20 cm into the sediment. Sampling was haphazard, with cores taken in 3 groups of 3 cores each. Cores within each group were all taken within 1 m of each other, and groups of cores were separated by 4 to 8 m. Sediments were live-sieved with a 500 µm mesh screen within 2 h of collection. Samples were fixed in 4% formalin in sea water and stained with rose Bengal for 48 h, after which they were transferred to 70% ethanol and sorted under a dissecting microscope. On 7 dates, a single core (7.6 cm diameter, 50 cm into the sediment) was taken to estimate the vertical distribution of the sand plain infauna. Immediately after the core was taken, it was returned to the boat, sectioned into 5 cm layers and fixed for later sieving and sorting.

Habitat manipulations. Areas of bottom were isolated by enclosing them within cylindrical corrals (diameter 70 cm, height 30 cm) constructed of 1 cm plastic mesh (vexar®) tied onto a steel frame, which was anchored with 4 evenly spaced rods driven 60 cm into the sand. Nine corrals were laid out in a 3 × 3 grid with a 5 m separation. In the first enrichment experiment, treatments consisted of enrichment, habitat addition and control corrals. Kelp mud, a product which is created when the kelp *Macrocystis pyrifera* is processed to extract sodium alginate, was used as the enriching medium. Kelp mud consists of roughly equal proportions of ash (perlite) and kelp (minus most of the sodium alginate), and was chosen for its fine grain size (less than the local sand), and because its organic base (kelp) is a locally available food resource. At the start of the experiment 2500 g of kelp mud were worked into the sediment of the 3 enrichment corrals by hand to a depth of 10 cm.

The habitat-addition treatment was composed of several hundred 30 cm long ribbons of nylon fabric anchored in the corrals, designed to simulate surfgrass, while providing no additional organic matter. The remaining (3) corrals served as (cage) controls. The sand in all corrals was turned over to a depth of approximately 10 cm to control for the disturbance caused by mixing the kelp mud into the enrichment corrals.

For sampling, three 7.6 cm cores were bored in each corral and 9 control cores were bored 5 to 15 m away from the cages (as described above). Data from the 3 cores from each corral were averaged to give 1 value per corral. Coring was infrequent to reduce the effect of this disturbance on the animals within the corrals. Corals were sampled 48 and 95 d after the treatments were introduced (28 June 1991).

Two additional sediment enriching media were used to control for the possibility of unpalatable or otherwise repellent substances potentially present in kelp. The second enrichment experiment was comprised of 2 control corrals, 2 corrals enriched with 500 g of kelp mud, and 2 corrals enriched with 2500 g of sodium alginate (derived from kelp). Sodium alginate was chosen because it is a kelp product, but contains no tannins or phenolic compounds which are present at various concentrations in kelps, and are unpalatable to some animals (Hay & Fenical 1988 and references therein). Corrals were sampled 18, 25, 32, and 46 d after the treatments were introduced (13 September 1991). With this higher frequency sampling protocol, there was a risk that sampling disturbance could affect later samples. However, this was necessary to evaluate the effects of the enrichment at a finer time scale.

The last enrichment experiment used nine 1 m² plots without corrals, the corners of which were marked with steel rods. Three plots served as undisturbed controls; in 3 others 1800 g of the turf fertilizer milorganite® (6% N, 2% P₂O₅; activated sewage sludge) were worked into the sand; and 3 adjacent control plots were similarly disturbed without enrichment. This material differed from the other two by contributing relatively more nitrogen than carbon. These 9 plots were sampled 4, 13, 20, 28, and 48 d after the start of the experiment (20 September 1991).

Sediments from enriched plots were analyzed for organic carbon and nitrogen content 18 and 36 d after the enriching material was added. Control samples from unmanipulated sediments were also taken. Sediments were dried for 2 d at 50°C, homogenized by grinding, and acidified with HCl to remove carbonates before being analyzed for carbon and nitrogen on a Perkin-Elmer 2400 CHN elemental analyzer. Statistical significance of treatment effects independent of time were evaluated with a repeated measures analysis of variance (ANOVA) using the Macintosh statistical package SYSTAT® (version 5.2).

Response to carrion. Three parcels of carrion (kelp bass *Paralabrax clathratus*) were staked out 3 m apart at a depth of 20 m. The fish were placed in unrolled tuffy® scrubbers, which provided a tube of interwoven plastic mesh (1 mm wide plastic ribbons). Each end of the tube was tied to a steel rod which was hammered into the sand. The tubes allowed easy access to the invertebrate macrofauna but interfered with feeding by fish, and to a lesser degree, asteroids and crabs. The experiment was sampled 24 and 72 h following deployment of the bait. Three 7.6 cm cores were taken directly adjacent to each of the carrion tubes (partially under the fish) and 9 control cores were taken at least 3 m away from the bait. Statistical significance was tested using a nested ANOVA (SYSTAT®, as above).

Sediment grain size distribution was measured for sand collected at 18 and 21 m depth in March 1995. Three cores were collected from each depth, the sediments were dried for 72 h at 60°C, and shaken for 20 min each through an array of 12 geological sieves using a Ro-tap machine.

RESULTS

Habitat manipulations were carried out to test whether *Nebalia daytoni* and other members of the infaunal assemblage would be attracted to organically enriched sediments or regions with increased structural complexity which could provide increased living space and/or protection from predation. The first experiment using corrals containing increased organic matter (particulate *Macrocystis pyrifera*), or imitation surfgrass resulted in significant treatment effects for all taxa (Table 1). *N. daytoni* was depressed or absent in all corrals relative to controls (Fig. 1A), while amphipods were depressed in enrichment corrals (Fig. 1B). In contrast, polychaetes underwent a dramatic but temporary increase in enrichment corrals (Fig. 1C) due exclusively to *Capitella* sp. Of several thousand polychaetes in these cores, only 23 belonged to species other than *Capitella* sp. Most of the non-capitellids were spionids. The most abundant amphipods in control cores were *Rhepoxynius abronius*, *Acuminodeutopus heteruropus*, *Amphideutopus oculatus*, and *Ampelisca compressa*. *R. abronius* was never present in the enrichment plots (all experiments); all others were occasionally present at reduced density.

In the second set of habitat manipulations, the quantity of kelp mud was reduced and alginate was used as an alternative enrichment; there were no fake surfgrass corrals. Here, there were significant treatment effects only for the amphipods and polychaetes (Table 2). *Nebalia daytoni* was unaffected by the cages or

Table 1. Corral Expt 1 Summary of repeated measures ANOVA results. Treatments are control, corral control, fake seagrass, and enrichment (kelp mud)

Source of variation	df	MS	F	p
<i>Nebalia daytoni</i> :				
Treatment	3	1.51 × 10 ¹	7.54	0.0031
Error	14	2.00		
Amphipods:				
Treatment	3	5.92 × 10 ²	9.06	0.0014
Error	14	6.54 × 10 ¹		
Polychaetes:				
Treatment	3	1.87 × 10 ⁶	165.68	<0.0001
Error	14	1.12 × 10 ³		

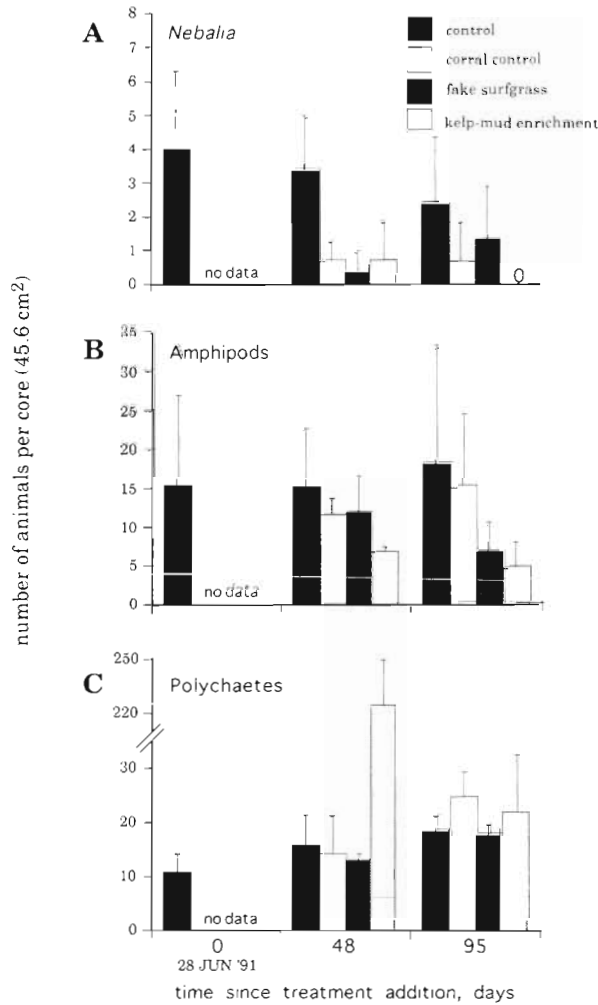


Fig. 1. Corral Expt 1. Numbers of *Nebalia daytoni*, amphipods, and polychaetes in unmanipulated sediments and within control corral, and corral enriched with kelp mud or provided with fake seagrass. Note change in scale in (C): over 99% of polychaetes in the kelp mud enrichment on Day 48 were *Capitella* sp. Only unmanipulated sediments were sampled on the start date (28 June 1991). Error bars are 1 SD

Table 2. Corral Expt 2. Summary of repeated measures ANOVA. Treatments are control, corral control, alginate enrichment, and kelp mud enrichment

Source of variation	df	MS	F	p
<i>Nebalia daytoni</i> :				
Treatment	3	12.26	2.31	0.1530
Error	8	5.31		
Amphipods:				
Treatment	3	2.20 × 10 ³	13.82	0.0015
Error	8	1.59 × 10 ²		
Polychaetes:				
Treatment	3	1.18 × 10 ⁵	153.76	<0.0001
Error	8	7.70 × 10 ²		

treatments (Fig. 2A); however, the amphipods' numbers were reduced by both cage and enrichment effects (Fig. 2B). The polychaetes (specifically, *Capitella* sp.) greatly increased in density in response to the alginate enrichment (Fig. 2C). *Capitella* sp. brood tubes were present in the alginate enrichments on Days 17, 24 and 38. Reproductive maturity of *Capitella* sp. is easily observed by the presence of eggs which line the walls of the animals' brood tubes. The animals that recruited here deposited on the order of 1000 eggs

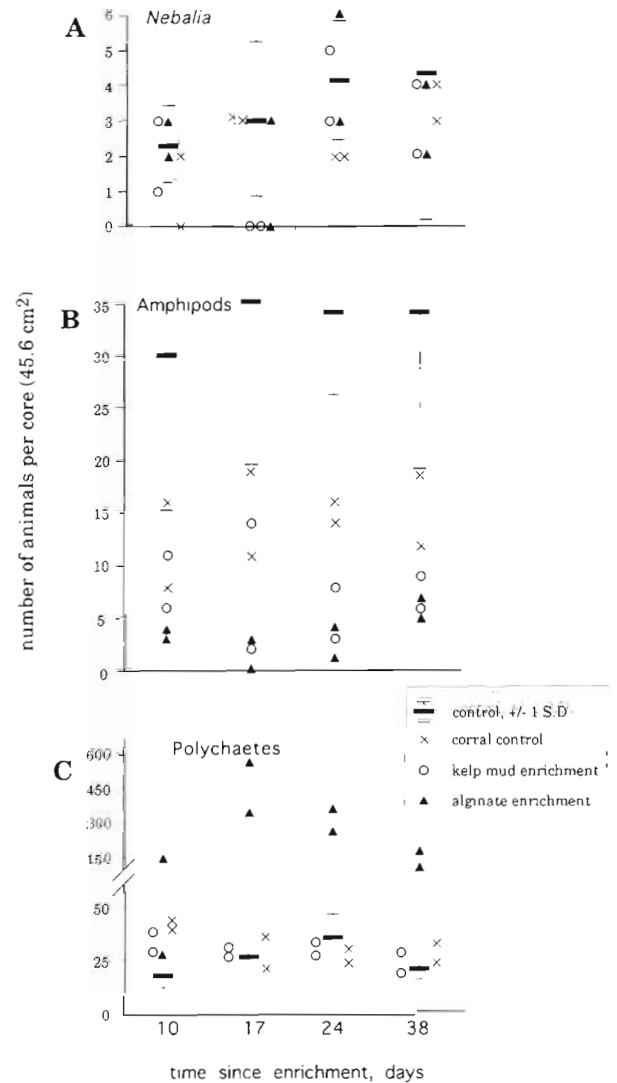


Fig. 2. Corral Expt 2. Numbers of *Nebalia daytoni*, amphipods, and polychaetes in unmanipulated sediments and within control corral and corral enriched with kelp mud or alginate. Note change in scale in (C): *Capitella* sp. amounted to over 95% of polychaetes in all cores from the alginate enrichment except on Day 10, when they made up 0 and 91% of all polychaetes. There were only 2 corral per treatment so data from each corral are provided. The mean of 9 cores is provided for the non-corral control (unmanipulated sediments). Error bars are 1 SD

with a diameter of about 80 μm , suggesting that this species produces planktotrophic larvae (Grassle & Grassle 1976, Pearson & Pearson 1991). Reducing the kelp mud enrichment to 20% of that used in the first experiment eliminated or at least greatly reduced the effects of that manipulation relative to the previous experiment for polychaetes and the leptostracan. Amphipod density was strongly reduced by the alginate enrichment, and less so by the kelp mud enrichment (Fig. 2B).

The final enrichment experiment using fertilizer (milorganite) on un-corralled plots had similar results (Table 3). There were no significant treatment effects for *Nebalia daytoni*, while the amphipods were depressed and a dense population of *Capitella* sp. developed in the enriched plots (Fig. 3). The recruitment and growth of the *Capitella* sp. was extremely rapid in the enriched plots; a large number of the worms were found with brooding eggs on the first post-enrichment sampling date (Day 9). All other species except for a few (0 to 4 per core) spionids had disappeared from the enrichment plots on Days 9, 16 and 24 (Fig. 3C). By Day 44, only 5 *Capitella* sp. remained (in 3 cores). The worms that replaced them were common in the control cores and, because of their large size, probably migrated into the plots as adults. In all enrichment experiments in which particulate material was worked into the sediments, except for the low dose kelp mud enrichment in Expt 2, the sediments darkened and smelled of hydrogen sulfide, suggesting hypoxic and anoxic conditions.

Organic carbon and nitrogen in the sediments at the study site were very low; the percentage of organic carbon in control samples was 0.12% (SD 0.013) and nitrogen was 0.02% (SD 0.005). The carbon to nitrogen ratio (6.37) was surprisingly low, falling within the expected range for phytoplankton (Parsons et al. 1984). After 18 d, the low dose kelp mud enrichment did not differ from controls. However, the other enriched plots contained 6 to 8 times the organic content of controls. Except for the milorganite enrichment (C/N of 3.5), the C/N ratios within the enrichments were similar to controls. Organic carbon levels were only slightly elevated 36 d after enrichment, and nitrogen content was not different from controls (C/N was thus elevated with respect to controls).

The density of *Nebalia daytoni* was not consistently affected by the presence of carrion (dead fish) 1 or 3 d following deployment of the bait (Fig. 4, Table 4), although the fish flesh was approximately 75 to 90% consumed by Day 3. Other taxa were not evaluated. On 2 occasions ray carcasses were found in the vicinity of the study site. One of those was in a late stage of decomposition, with darkened sediment underlying and surrounding the carcass suggesting that it had

Table 3. Milorganite enrichment. Summary of repeated measures ANOVA results. Treatments are control, disturbance control, and milorganite enrichment

Source of variation	df	MS	F	p
<i>Nebalia daytoni</i> :				
Treatment	2	11.35	1.60	0.2902
Error	5	7.09		
Amphipods:				
Treatment	2	2.15×10^3	36.04	<0.0011
Error	5	5.97×10^1		
Polychaetes:				
Treatment	2	3.00×10^5	51.00	0.0005
Error	5	5.87×10^3		

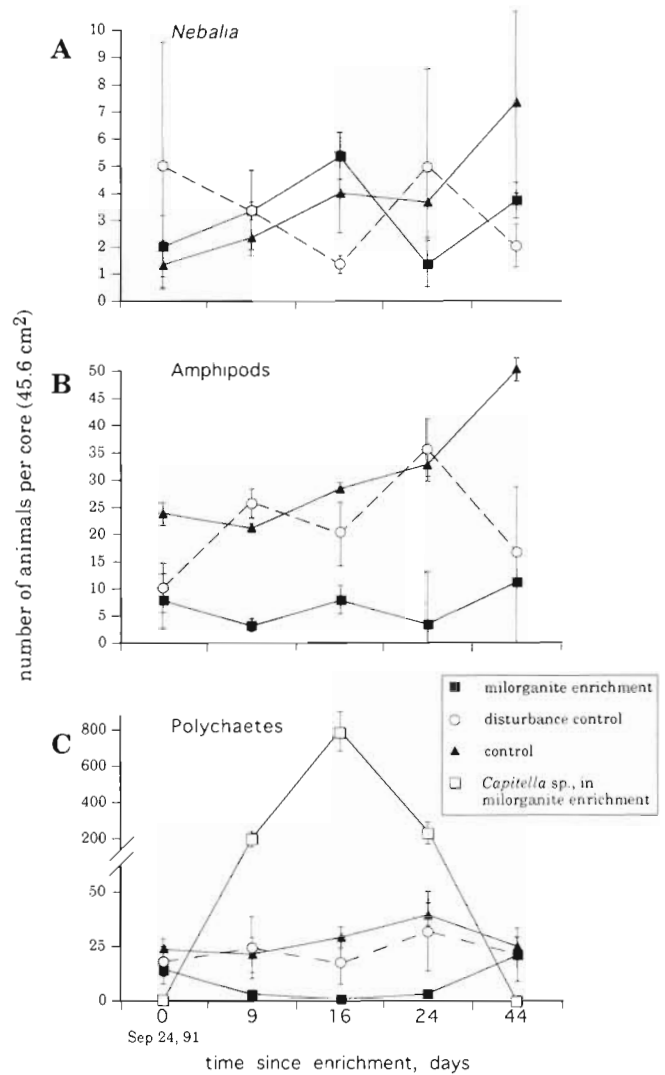


Fig. 3. Milorganite® enrichment. Numbers of *Nebalia daytoni*, amphipods, and polychaetes in unmanipulated plots and within plots enriched with fertilizer and plots manipulated to simulate the disturbance caused by mixing fertilizer into the sand. Note the change in scale in (C). Error bars are 1 SD

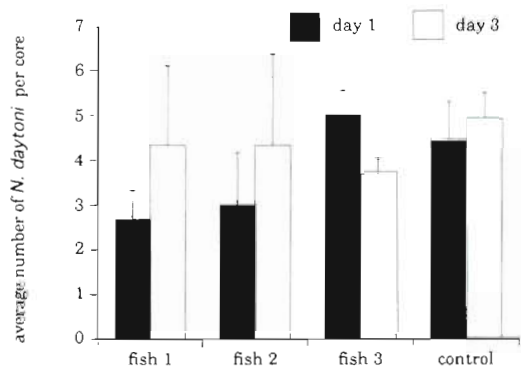


Fig. 4. *Nebalia daytoni*. Density adjacent to each of 3 parcels of carrion (kelp bass), 1 and 3 d after deployment. Error bars are 1 SE

Table 4. *Nebalia daytoni*. Response to bait 1 and 3 d following placement of carrion. Summary of nested ANOVA results with treatment type (near carrion or away from carrion (= control)) as the independent variable and density of *N. daytoni* (per core) as the dependent variable. Treatment type was nested in Plot. There were 6 plots, 3 with each treatment type. Three cores were taken in each plot

Source of variation	df	MS	F	p
Day 1:				
<i>Nebalia daytoni</i> :				
Treatment	1	3.56	0.74	0.408
Plot (Treatment)	4	3.11	0.64	0.642
Residual	12	4.83		
Day 3:				
<i>N. daytoni</i> :				
Treatment	1	2.72	0.49	0.499
Plot (Treatment)	4	0.611	0.11	0.977
Residual	12	5.611		

probably been lying in the same place for at least several days. Several *Capitella* sp. were present in a non-quantitative sediment sample taken near that carcass.

Field collections and annual cycles of abundance

Average sediment grain sizes at 18 and 21 m in March 1995 were 3.03 and 2.97 ϕ , respectively. In all 7 cores taken for quantifying of vertical distribution (all on different dates), the *Nebalia daytoni* was found only in the top 5 cm of the sand (Fig. 5). Most of the polychaetes were in the top 10 cm, but some were present as deep as 31 to 35 cm. Amphipods were most abundant from the surface to 10 cm into the sediment, though a few were found deeper. All other taxa (clams, nemertean, cumaceans, ostracods, platyhelminthes, gastropods, ophiuroids) were only present in the upper 5 cm.

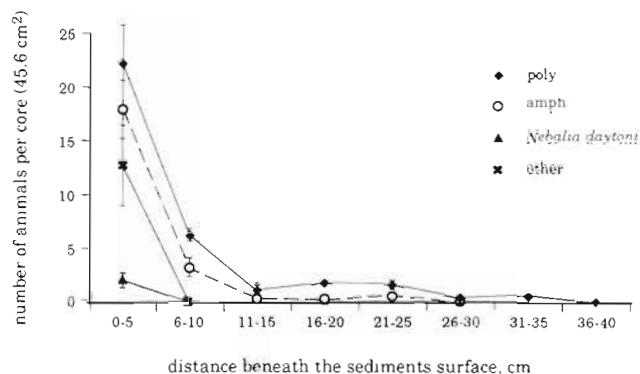


Fig. 5. Depth distribution of polychaetes, amphipods, *Nebalia daytoni*, and all other taxa within the sand near the depth of maximum abundance of *N. daytoni* (20 m). Error bars are 1 SD

Nebalia daytoni and the amphipod assemblage as a whole both underwent distinct annual cycles of abundance, although they were out of phase with one another. From June 1991 to June 1993, the density of *N. daytoni* averaged 950 ind. m⁻² (SD 300), with maximum abundance in late spring-early summer, and minimum in late summer-early fall (Fig. 6A). Amphipod density also had a seasonal pattern, but with peak abundance in late fall and early winter, and low values in spring and summer (Fig. 6B). Average amphipod density was 4800 ind. m⁻² (SD 2300). The annual pattern of amphipod abundance (Fig. 6B) dominated that of all other infauna. Average polychaete density was 4200 ind. m⁻² (SD 1060), with lowest abundance in spring (Fig. 6C). All other taxa were grouped together. The only pattern among the 'other' taxa was a sharp increase from September to December 1991, followed by a rapid decline (Fig. 7A). No single taxon dominated this increase; bivalves, ostracods, nemertean, ophiuroids and gastropods all figured prominently. The average density of all infauna over the period of study was about 15000 ind. m⁻² (Fig. 7B); approximately the same density was found by VanBlaricom (1978) 15 yr earlier.

There was a large decrease in non-polychaete macrofaunal abundance following June 1992. In the first 12 mo of the record, the density of all non-polychaete macrofauna averaged 13800 ind. m⁻²; in the subsequent 12 mo they averaged 10500 ind. m⁻² (ANOVA: p = 0.019). This decrease was driven largely by lower numbers of amphipods and leptostracans rather than the 'other' category.

DISCUSSION

Studies of naturally or anthropogenically enriched sedimentary habitats have consistently demonstrated

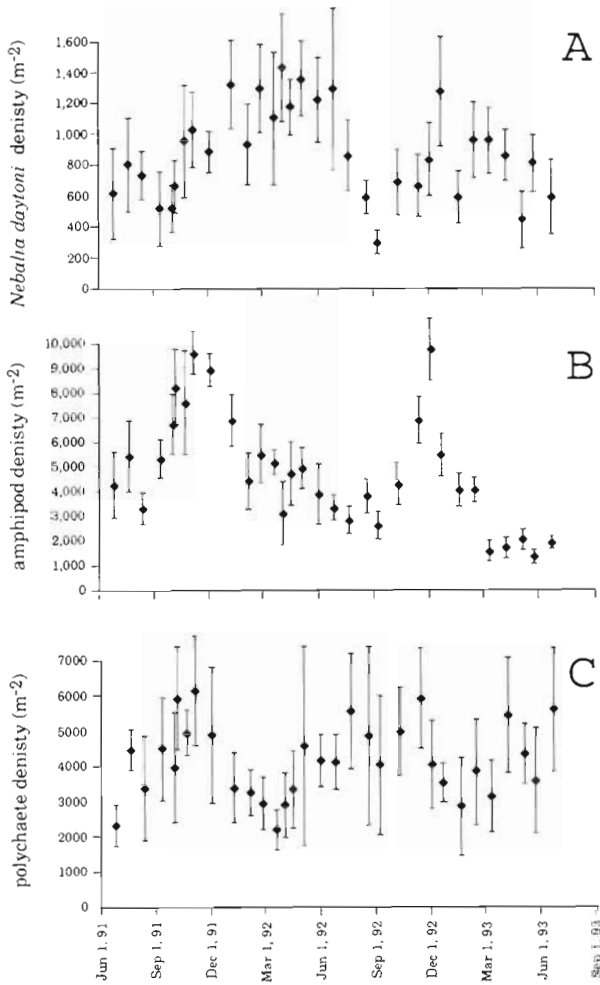


Fig. 6. Density (no. m⁻²) of (A) *Nebalia daytoni*, (B) amphipods, and (C) polychaetes at 20 m. N ≥ 9 cores; error bars are 1 SD

negative effects on the fauna normally present in undisturbed conditions. The trajectory of the community response to enrichment generally involves a continual decrease in diversity, and replacement of the pre-disturbance community with a depauperate disturbance assemblage dominated by a few opportunists (Pearson & Rosenberg 1978, Conlan & Ellis 1979, Thrush 1986, Gray 1989, Weston 1990). The effects in the present study essentially conformed to that pattern, and did not vary with the enriching material, but, predictably, depended on the level of enrichment. The initial prediction that this community was in some measure adapted to periodic enrichments was based upon the presence of large numbers of leptostracan crustaceans (*Nebalia daytoni*). Most of the literature on the genus *Nebalia* is taxonomic, and the few papers that deal with natural history focus on species that inhabit intertidal mud-flats rich in organic matter (Menzies & Mohr 1952, Ricketts et al. 1985), vegetated

or detritus habitats (Kazmi & Tirmizi 1989, Rainer & Unsworth 1991, Vetter 1994), or polluted waters (Citarella 1965); an additional study concerns *Nebalia* sp. scavenging on carrion (Nishimura & Hamabe 1964). Snelgrove (1993) found that a continental slope (depth 900 m) species of *Nebalia*, presumably living in generally non-enriched conditions such as those in this study, achieved very high densities in experimental trays enriched with either *Sargassum* sp. or *Thalassiosira* sp. Judging by the habitats and behavior of its morphologically very similar congeners, it seemed reasonable to expect *N. daytoni* to respond favorably to enrichment.

In all enrichment experiments (except the low dose kelp mud treatment), the pre-disturbance polychaete assemblage was replaced by a virtual monoculture of *Capitella* sp., a species not present prior to the enrichments. This population explosion no doubt resulted from settlement of larvae that were probably produced by large populations of the capitellids in sediments naturally enriched with kelp and surfgrass detritus about 600 m from the study site (Vetter 1995). VanBlaricom (1982) also noted that just inshore of the present study site (at 17 m), *Capitella* was absent in the sediment, but recruited heavily to jars of azoic sand. In an enrichment experiment conducted in the Santa Barbara Channel (Southern California, USA) at 16 m, Spies et al. (1988) used an array of containers (8.1 × 8.1 × 6 cm) filled with azoic sand enriched with various amounts of kelp *Macrocystis pyrifera* or oil. As in the

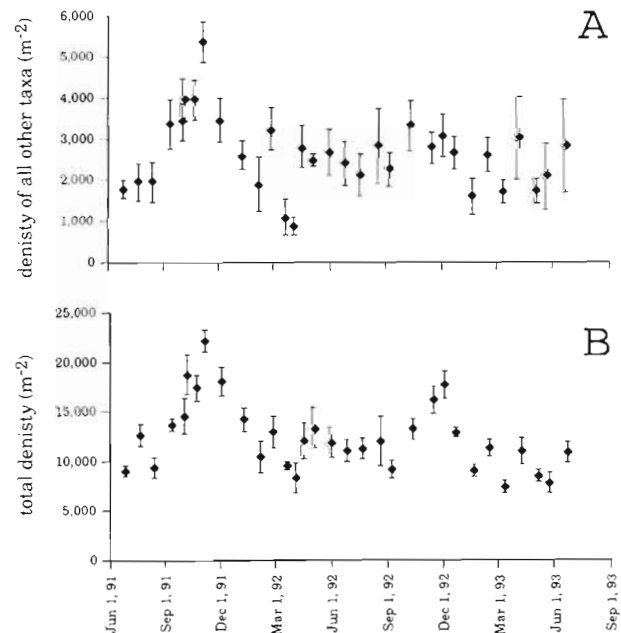


Fig. 7 Density (no. m⁻²) at 20 m of (A) all invertebrates other than *Nebalia daytoni*, amphipods and polychaetes; and (B) all macrofaunal invertebrates. N ≥ 9 cores; error bars are 1 SD

present study, few species other than a single species of *Capitella* with planktotrophic larvae recruited into heavily enriched containers.

Even if larvae were immediately available for recruitment, it is remarkable that the recruits managed to mature and produce eggs within 9 d in plots enriched with fertilizer. The density of *Capitella* sp. was high on Day 10 of corral Expt 2 in one of the alginate enrichment plots, but no eggs were present. Eggs were found in both alginate plots by Day 17 of that experiment. In controlled laboratory experiments, Bridges et al. (1994) found that *Capitella* sp.1 raised in sediments supplemented with milorganite® or blue-green algae grew faster, attained a dramatically larger size, and reproduced sooner than animals raised in untreated marsh mud. In addition to greatly increasing the organic content of the sediment, those enrichments substantially lowered their C/N ratios, thus increasing both the quantity and quality of available food (Tenore 1975, 1983). The kelp mud and alginate enrichments did not affect the C/N ratio of the sediments, but the sediments here have a normally low C/N ratio, and algal detritus is generally readily utilizable by *Capitella* spp. (Tenore 1983). The milorganite enrichments did depress sediment C/N ratios relative to controls, and *Capitella* sp. within those enrichments matured earlier than those in alginate enrichments, suggesting that the lower nitrogen levels in the alginate were less favorable for capitellid growth.

The *Capitella* sp. recruited to the enriched plots in the first 2 to 3 wk after enrichment when the production of hydrogen sulfide, a probable larval settlement cue for these polychaetes (Cuomo 1985), would have presumably been strongest. *Capitella* sp. have a life history as short as 30 d (Reish 1977), so within about a month of the cessation of the production of the sulfide settlement cue (assuming that this was the sole cue available during this study, and that its loss and food loss were concurrent), it would be reasonable to expect the population to begin to recede, as was observed. Rapid decreases of populations of opportunistic species have been frequently witnessed (McCall 1977), and may often be due to a density dependent depletion of food (Grassle & Grassle 1974), although predation may also be an important factor in some population declines (Young & Young 1978). Further, in areas where enrichment is especially great, development of very strong reducing conditions also leads to rapid population reductions (Tsutsumi 1990).

Naturally enriched areas are important for the growth and reproduction of opportunistic species (Tsutsumi et al. 1990) but, away from mud flats and other enriched coastal habitats, natural enrichments are probably ephemeral and patchy. Vertebrate carcasses such as the rays observed during this

study could be an important source of such patchiness. Smith (1985, 1987) concluded that vertebrate carcasses were an important source of food to the deep sea floor (1310 m) within the Southern California Bight; however, he reported that little of the meat was available to the infauna without first passing through the guts of motile scavengers. Many large scavengers are present in the location studied here (especially crabs and asteroids); it may be that carcasses persisting long enough to enrich the sediments are the exception rather than the rule. The most common patches of elevated food found in this study site are detrital accumulations within pits formed by foraging rays. Flocculant organic matter, and pieces of macroalgae and surfgrass, are common in these pits, which have elevated organic carbon, nitrogen and nitrogen-to-carbon ratios relative to undisturbed areas (VanBlaricom 1978). The disturbance that results from the creation of these patches, and the subsequent organic enrichment, did not, however, result in recruitment of *Capitella* sp. (VanBlaricom 1978, author's pers. obs.).

Amphipods are highly sensitive to organic enrichment and other environmental disturbances (Thomas 1993 and references therein), so it is not surprising that there were few or no amphipods in enrichment plots; however *Acuminodeutopus heteruropus* and *Synchelidium shoemakeri* were considered to be likely candidates to respond positively to the enriched plots because of their affinity for the detritus rich conditions in newly formed ray pits (VanBlaricom 1982). Contrary to expectation, *Nebalia daytoni* did not increase in abundance in enrichment plots. Its abundance was lower in the first corral experiment. However, that appeared to be due to cage effects rather than the enrichment (Fig 1). In both subsequent experiments, there was no significant difference in *N. daytoni* density between enrichment and control plots. This, along with the observation that the leptostracans did not respond to carrion, demonstrates that not all members of this genus are trophically similar.

Another *Nebalia* sp. in Southern California was found to have a refuge from predation in nearby mats of kelp and surfgrass detritus (Vetter 1995). The fake surfgrass treatments were designed to give similar protection from predation by fishes without altering food supply. Rather than increasing in abundance in these plots, *N. daytoni* abundance was lower (Day 48) or similar to (Day 95) controls. None of the habitat manipulations led to an increase in *N. daytoni*, and when their abundance was reduced, a cage effect was indicated.

The seasonal cycle in abundance is less dramatic for *Nebalia daytoni* than for the amphipods, possibly due to a longer hatching period in the leptostracans. *N. daytoni* is an annual, semelparous species, with maxi-

mal abundance of adults during summer and few if any present during winter months (Vetter 1996). The strong seasonal cycle of abundance of amphipods suggests that they also largely complete their life cycles within a year, with high adult mortality following release of the young from the marsupium in autumn. Alternatively, the rapid decline in amphipod density during winter could be due to high juvenile mortality. Support for the assertion that the amphipod assemblage is dominated by annuals is found in latitudinal trends in amphipod life histories. Morino (1978), Highsmith & Coyle (1991), and Sainte-Marie (1991) reported that temperate amphipods generally have annual life histories, in contrast to 2 to 5 yr cycles in higher latitude amphipods and 4 to 6 mo cycles in lower latitude ones. Further, according to Wildish (1982), amphipods with annual life histories may be either semelparous or iteroparous (with some variation between populations within a species); so the rapid rise in amphipod abundance from September to December (Fig. 6B) is likely due to most of the amphipods releasing their broods at that time, and the subsequent decline in abundance may be attributed to senescence in annual species. Annual cycles of abundance of several amphipod species were also observed by VanBlaricom (1978), though periods of maximum abundance tended to occur slightly earlier in the year.

All taxa, with the exception of polychaetes, were more abundant from June 1991 to June 1992 than in the subsequent 12 mo period. Density reduction began 4 to 5 mo following the onset of El Niño conditions within the California Current. Environmental changes at this study site included positive sea surface temperature anomalies and a thicker mixed layer (Hayward 1993, Hayward et al. 1994). It is intriguing to speculate that such environmental change may have directly affected faunal abundances in this study, although no other data exist to test this idea.

Experimental studies by VanBlaricom (1978, 1982) demonstrated that community dynamics in this habitat were largely driven by localized disturbances resulting from ray foraging. Pits created by rays accumulated organic debris which was attractive to some infaunal species and repellent to at least one, the amphipod *Rhepoxynius abronius*. From 1974 to 1977, VanBlaricom found that on average about 25% of the bottom was in some stage of recovery from disturbance, and during peak foraging periods of the rays, that value approached 100%. That pattern has since changed, with ray disturbance being much less frequent. During the period of this study, it was unusual to find more than 5% of the bottom recovering from ray disturbance (author's pers. obs.), and rays were infrequently seen. Other changes since the mid 1970s include increased average grain size of the sediment from about 3.26 to

3.03 ϕ at 18 m and from about 3.20 to 2.97 ϕ at 21 m (1970s data from VanBlaricom 1978) and shifts in the depth distribution of some infaunal invertebrates. For example, the seaward edge of the zone dominated by crustaceans shifted from 18 m to beyond 22 m, and the depth of maximum abundance for *Nebalia daytoni* shifted from about 18 m to 21 m. Density of *N. daytoni* has also increased from 400 ind. m^{-2} in 1977 to over 900 ind. m^{-2} in 1993. The increased grain size of the sediment, decreased density of ray pits, faunal shift seaward, and changes in the abundance of some taxa represent an interdecadal change in biological and physical parameters at this site.

The present study highlights the hazards involved with generalizing life history traits across taxonomic levels as low as the genus. The failure of *Nebalia daytoni* to respond to organic enrichment demonstrates a tolerance to eutrophic conditions, but unlike their congeners thus far studied, there was apparently no exploitation of the increased availability of resources under such conditions. The inability of any members of the native community to take advantage of the pulsed enrichments suggests that such events are not common on the sand flat studied. The rapid exploitation of the artificial enrichments by *Capitella* sp. was likely facilitated by a nearby source of larvae from populations living in the naturally enriched conditions of the La Jolla Submarine Canyon, California (Vetter 1995). Had the present study been conducted in a region more distant from a natural *Capitella* habitat, different macrofauna, or perhaps primarily meiofauna and/or microbes would have been the chief beneficiaries of the enrichments.

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