Detritus-based patches of high secondary production in the nearshore benthos

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ABSTRACT: Topographical features like depressions and submarine canyons accumulate organic debris that fuel patches of intense secondary production. A submarine canyon system off the coast of La Jolla, California, USA, harbors an assemblage of leptostracan and amphipod crustaceans whose local density and secondary production greatly exceed those of any natural system yet reported. These crustaceans utilize large accumulations of macrophyte detritus as both habitat and food, and are preyed on by numerous species of fishes. Bottom topographies acting as detritus traps are relatively common along many coasts and provide an important mechanism to channel marine macrophyte production into higher trophic levels.

KEY WORDS: Secondary production · Dense assemblage · Leptostracans   Submarine canyon   Detritus · Saprotrophic

INTRODUCTION

Topographical features accumulating organic debris are probable sites of natural organic enrichment. Submarine canyons act as sinks for materials moving along the shore at canyon depths and often provide permanent sources of high food density on the continental shelf and slope (Dill 1964, Shepard & Dill 1966, Griggs et al. 1969, Rowe et al. 1982, Josselyn et al. 1983, McHugh et al. 1992). I studied the potential contribution to the benthos of large quantities of kelp and surfgrass detritus within the La Jolla Bight, which accumulate along the floor of the La Jolla Submarine Canyon in Southern California, USA, forming a persistent mat of organic debris.

A small portion of the canyon's detritus habitat that is shallow enough to study with SCUBA was sampled monthly for 1 yr. The detritus fauna was dominated by leptostracan and amphipod crustaceans whose local density and secondary production exceed all such values found in the literature for natural systems. These abundant crustaceans were consumed by various species of fishes, many of which were ubiquitous over the detritus. If, as seems likely, features which accumulate detritus are relatively common in nearshore regions, they would provide an important but patchy pathway for channeling marine macrophyte production to higher trophic levels through a saprotrophic chain.

The detritus habitat within the La Jolla Submarine Canyon is dominated by amphipod and leptostracan crustaceans, but is also inhabited by a wide variety of animals including crabs, octopuses, juvenile fishes, snails, polychaete worms and isopods. The leptostracans, which include 2 undescribed species of *Nebalia*, and the most abundant amphipods, *Orchomene limodes* and *Aoroides spinosus*, at times achieve a cumulative density of over 3 million individuals m^{-2}, with biomass exceeding 1 kg (dry wt) m^{-2}.

The genus *Nebalia* ranges from the Arctic to the Antarctic and from intertidal to lower continental slope depths. The 2 species of *Nebalia* investigated here are undescribed and inhabit subtidal accumulations of detritus in the La Jolla Canyon, in San Diego Bay, and along the San Diego sewage outfall pipe (Pt. Loma). They have been collected from 5 to 60 m, but may occur much deeper. Length ranges from 1.5 to 17 mm, with an average of 4.5 mm. *Nebalia* spp. brood their young in an external chamber until they are released as juveniles, with no planktonic dispersal stage.

Orchomene limodes, a lysianassid amphipod, was described from Scripps Canyon (Meador & Present 1985) and, like *Nebalia* spp., is a scavenger and detri-

tivore. The average length of these animals is about 2 mm. *Aoroides spinosa*, a corophioid amphipod, is the only member of the mat fauna also present in the sand plain surrounding the canyon. It averages about 3.5 mm in length. *Capitella* sp., a capitellid polychaete, was occasionally abundant in organically enriched sediments on the periphery of the detritus mat. It builds vertical tubes of agglutinated sand grains and ingests the anoxic sediment at the base of the tube (Fauchald & Jumars 1979). This species is commonly used as an indicator of disturbed, polluted or organically enriched sediments. Though at times abundant, *Capitella* sp. was very patchy in space and time. They could recruit and reproduce in less than a month, taking advantage of ephemeral patches of enriched sediments in and around the detritus fields. Their production was likely high relative to that of the surrounding sand community, but still much lower than that of the crustacean populations studied.

MATERIALS AND METHODS

Study site. The La Jolla submarine canyon system, located off the coast of San Diego (32° 52' N, 117°
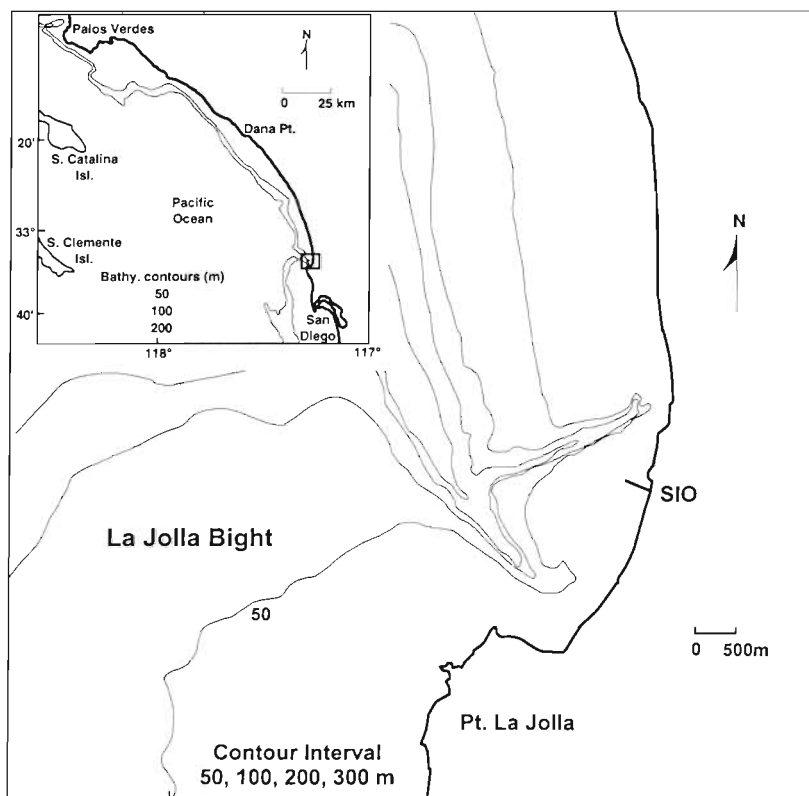

Fig. 1. The coast of Southern California, USA. Area of detail shows the nearshore portion of La Jolla Canyon. Scripps Canyon is seen approaching the coast north of the Scripps Institution of Oceanography (SIO) pier

15' W) is composed of 2 canyons: Scripps Canyon, which originates at a depth of 18 m, 150 m from shore, 900 m north of the Scripps Institution of Oceanography (SIO) pier, and La Jolla Canyon, which originates at a depth of 22 m, 200 m from shore, and 1200 m south of the SIO pier (Fig. 1). The 2 canyons merge 1800 m from shore at a depth of 300 m. Beyond that point, the canyon descends to the northwest to a depth of about 500 m, below which it becomes known as the La Jolla Fan Valley, terminating at the floor of the San Diego Trough at a depth of 1100 m (Shepard & Dill 1966).

Surfgrass and algal detritus are present in the canyon year-round. Large accumulations have been observed as shallow as 10 m and on the deepest submersible dives into the La Jolla Canyon (300 m: Inman et al. 1976; 686 m: Shepard & Dill 1966), and the San Diego Trough (1200 m; R. Dill & R. Vetter pers. comm.). In addition to covering the floor of the canyon, the detritus extends shoreward over the nearshore sand plain where the tributaries of the canyons originate. Most work was conducted on portions of the detritus mat that lie shoreward of Scripps Canyon, because their shallower depth (15 to 28 m) afforded both greater safety and diving time. Samples were taken as deep as 60 m in Scripps Canyon and at various depths in La Jolla Canyon to establish that the same processes studied in the shallow reaches of Scripps Canyon were operating there. Data reported here were collected from March 1992 to March 1993.

Detritus field measurements. One of the larger tributaries of Scripps Canyon, South Branch, was the primary detritus study site. The detritus field that enters South Branch was measured monthly or more frequently if changes in size were observed. A transect line was extended from the origin of South Branch shoreward to the shallow edge of the detritus mat. The width and thickness of the detritus was measured every 3.05 m along the transect. Thickness was measured with a pointed, calibrated rod, which was pushed in until resistance from underlying sediment was encountered. Detritus was often present much deeper than recorded, but further down it was mixed or inter-layered with sand and uninhabited by the macrofaunal invertebrates under study. Such measurements revealed the extent of the detritus habitat, not the overall volume of material. Both

the area and inhabitable volume were calculated in 3.05 m increments and summed to give the total value.

Quantitative sampling. Both the sediments surrounding the detritus and the detritus habitat itself were quantitatively sampled. The detritus mat was sampled at least monthly, weather permitting. The long, tough strands of surfgrass and kelp made sampling this habitat problematic. Cores were ineffective; even metal corers with sharpened edges cut the material with difficulty and allowed many animals to escape. The only method that took reliable samples used a large steel cylinder (0.185 m^2) which was used to isolate a portion of the mat. Hedge trimmers were employed to cut the detritus along the inner wall of the cylinder and then a vacuum lift was used to remove the material in the cylinder. The vacuum lift consisted of an acrylic tube, 182 cm long, 8 cm diameter, with a 500 µm mesh plankton net attached to the upper end and air injection ports on the lower end. Air was injected from a scuba tank with the tube held vertically so that the rising air would expand and displace water out of the upper end, causing a powerful suction at the lower opening. Vacuuming would often need to be interrupted several times to cut more material with the shears. The weight of the cylinder compressed the underlying detritus, preventing animals from entering or exiting beneath it. When the detritus mat was thick (>80 cm) a complete sample (down to sand) could not be obtained. At such times sampling resulted in a cone-shaped excavation beneath the cylinder, but even then, few animals escaped the vacuum because most were distributed in the upper 20 cm of the detritus and were captured in the initial suctioning.

From March through September 1992 only 1 sample was taken per sampling date. Thereafter, based on accumulated experience, we were able to collect and process 2 samples per collection date. More replicates would have been desirable; however, the difficulty involved in working with this material made that unfeasible. The lack of additional replicates is somewhat compensated for by the large size of the sampler (0.185 m^2) and is made less troublesome by the low temporal and spatial variability of the samples (Vetter 1995). When only 1 sample was taken, its location was selected haphazardly; when 2 were taken, the first was selected haphazardly in a central region of the mat, and the second about 1 m from the periphery of the mat. There was no trend detected in abundance or biomass from the center to the periphery of the mat (Vetter 1995). The volume of the samples ranged from 20 to 75 l of detritus.

The animals were separated from the detritus by flotation in a 76 l tub. About 35 l of water was poured onto a handful of detritus from a height of 1.2 m so the detritus would be well mixed and bubbles would be produced to carry the macrofaunal crustaceans to the surface where their hydrophobic exoskeletons would trap them in the surface film. The animals were skimmed off, the remaining water was poured through a 500 µm sieve and the process was repeated. The first wash used fresh water to shock the amphipods into releasing their hold on the detritus. The second used seawater and brought almost all of the remaining animals to the surface. Additional washes were often performed but they usually collected only a few animals. The process was continued, 1 handful of detritus at a time, until the entire sample had been extracted. This method was not 100% effective in recovering the mat fauna, but occasional careful inspection of the washed detritus turned up very few missed amphipods and leptostracans. Animals with a high specific gravity or without hydrophobic cuticles such as gastropods, many isopods, crabs, polychaete worms, and others were not well sampled with this method.

A total of 4 to 8 l of tightly packed amphipods and leptostracans was collected per sample. Animals were fixed in 4% formalin in seawater for 48 h and transferred to 70% EtOH. A Folsom plankton splitter (Omori & Ikeda 1984) was used to reduce the sample to a manageable size (between $\frac{1}{256}$ and $\frac{1}{1024}$ of the original sample). The preserved animals were sorted to species and counted. Carapace length of the leptostracans was measured using a dissecting microscope equipped with an ocular micrometer (magnification: $\times 12$, $\times 25$ or $\times 50$). Biomass of individual *Nebalia* sp. was calculated by regressing carapace length on dry weight [dry weight (g) = 0.00006(carapace length, mm)$^{2.577}$, r^2 = 0.97]. Dry weight of the amphipods was measured on a Sartorius analytical balance after 2 to 3 d in a drying oven at 52°C.

Density and production data are given in m^2. The animals are concentrated in the upper portion of the mat, rarely being found deeper than 30 cm into the detritus, so all values in m^{-2} are equivalent to values per 0.3 m^3.

Secondary production. Estimates of secondary production were calculated for the *Nebalia* sp. using the average cohort method (Hynes & Coleman 1968, Hamilton 1969, Benke 1979). This involves the calculation of the average cohort, which is simply the average size-frequency distribution of the population based upon samples taken throughout the year. The calculation of production involves quantifying the loss of biomass between successive size intervals. Hamilton's modification of the basic production equation of Hynes & Coleman (1968) is used here:

$$P = i \sum_{j=1}^{i} (\bar{N}_j - \bar{N}_{j+1}) \times \sqrt{W_j W_{j+1}} \qquad (1)$$

where P is estimated production, i is the number of times the loss occurs (this is equivalent to the number of size classes used, the multiplication accounts for the limited time spent in each size class), N_j is the mean number of individuals in size class j, and W_j is the dry weight of individuals belonging to size class j. Here P is calculated as the product of: (1) i, multiplied by the product of (2) the number of animals lost in step j, and (3) the geometric mean of the weight of the animals in step j, summed for each time loss occurs (between size classes). The calculation often results in apparent gain (negative loss) of biomass between size increments. This happens whenever there is an increase in average density between size groups (moving down the table). Of course negative loss is not occurring; these values represent an error and must be included in the summation to balance positive error. If a curve is fitted to the histogram of the average cohort, and the equation for that curve is used to regenerate the average cohort, the resulting production table will not include any negative values and the calculated production will closely match that of the original data.

Results obtained were multiplied by $^{365}/_{CPI}$ (cohort production interval), to account for multiple broods. The CPI is defined as the time in days from hatching to attainment of largest size class. In the laboratory *Nebalia* sp. reproduce at 80 d and attain maximum size by 120 d. Individual female *Nebalia* sp. from the mat produced as many as 3 broods within an 80 d period in the lab. Physical disturbance and predation pressure may lower the number of broods a typical female produces in a year, and therefore results are estimated using a range of possible CPIs.

Calculating secondary production for populations in the detritus mat is complicated by the variable size of the habitat within seasons. When the mat shrinks the animals become concentrated in the habitat remaining and when it expands they disperse (Vetter 1995). For this reason the calculations were conducted using both the m² density and estimates of the population size within the South Branch detritus mat. Those estimates were made by multiplying the density by the mat size at the time of sampling. The value produced using the estimated population size was normalized to the m² value by dividing the estimate of population secondary production by the average size of the mat.

Amphipod production was calculated by multiplying their average dry weight by a production-to-biomass ratio ($P:B$) of 4.0. This value is lower than all the estimates for the leptostracans (see Table 1), but is at the upper end of what is typically reported for benthic amphipods of similar size (2 to 5: Birklund

1977; 3.9: Banse & Mosher 1980; 1.3 to 3.1: Wildish 1984). Given the abundant resources in this habitat, however, a $P:B$ ratio of 4.0 is probably conservative.

RESULTS

The detritus mat

The detritus mat is a dynamic habitat that expands during summer periods of calm and contracts when surge, generated by winter storm waves, moves some or all of the material deeper down into the canyon (Fig. 2). The mat is composed primarily of surfgrass *Phyllospadix* spp. and kelp (*Macrocystis pyrifera Egregia menziesii, Laminaria* spp., *Pterygophora californica*), though other algae including *Sargassum* spp., *Ulva* sp., *Pelvetia fastigiata* and a variety of small red algae are sometimes common. The mat also accumulates animal detritus such as crustacean molts (*Emerita analoga* and *Blepharipoda occidentalis*), carrion (cephalopods, fishes, seabirds, pinnipeds), and living animals from the surrounding sand plain. Large numbers of moribund sand dollars *Dendraster excentricus*, sea pansies *Renilla kollikeri*, mussels *Mytilus californianus* and several species of hydroids, bryozoans, sponges and ascidians were frequently seen in the detritus. Material of terrestrial origin such as wood, leaves, golf balls, Frisbees and snorkeling gear were also found in the mat.

Between February 1992 and March 1993, the density of leptostracans plus amphipod crustaceans (hereafter referred to as the mat fauna) varied from 6.40×10^5 to 3.24×10^6 ind. m^{-2} with a mean of 1.47×10^6 ind. m^{-2}. Mean density of the leptostracans was 6.9×10^5 m^{-2} (SD: 4.4×10^5; SD of 2.4×10^5 without the 29 February
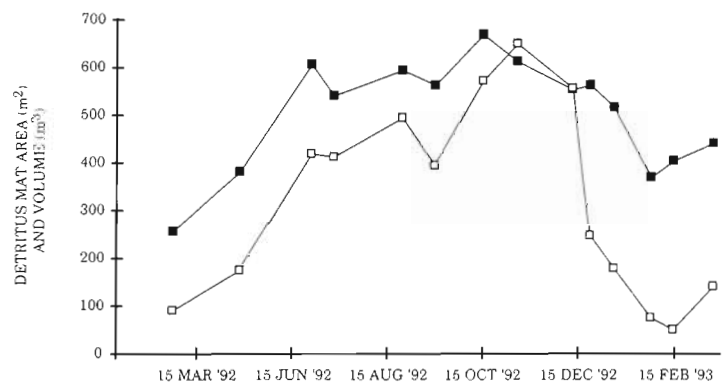

Fig. 2. Area (■) and volume (□) of the South Branch detritus mat from March 1992 to March 1993. Scale is the same for both measures. Mat length averaged 60 m, width 7.5 m. The South Branch detritus mat is usually isolated from the rest of the La Jolla Canyon detritus habitat and probably represents less than 1% of the total habitat
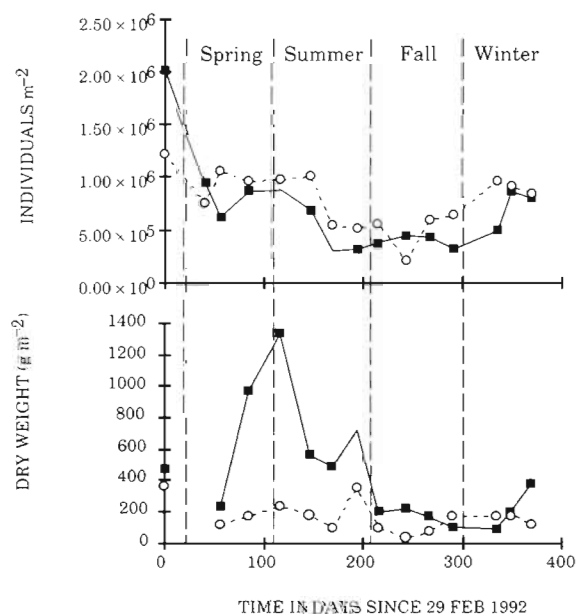
Fig. 3. Density and biomass of leptostracans, Nebalia spp. (■) and amphipods Orchomene limodes and Aoroides spinosus (○) within the detritus mat

1992 value) and that of the amphipods was 7.8×10^5 m^{-2} (SD: 2.7×10^5). Densities were lowest during the summer and fall (Fig. 3a); however, biomass peaked during the early summer due to the large mean size of the animals at that time (Fig. 3b).

Secondary production of the mat fauna

The final step in estimating secondary production by the average cohort method is multiplication of the value obtained from the calculation table by the CPI. Laboratory-reared animals had a minimum potential CPI of 3, but at the canyon, the near elimination of larger size classes following severe physical disturbances should lead to a reduction in the realized CPI. Because of this uncertainty results were determined by using a possible range of CPIs. Tables 1 & 2 contain the basic calculation tables for Nebalia secondary production from March 1992 to March 1993 based on mat density (Table 1), and total mat abundance (Table 2). Both tables yield similar results, rounding down to 2400 g dry wt m^{-2} yr^{-1}. Table 3 contains the range of production estimates obtained using both calculation methods and CPIs ranging from 1 to 3.

The mean dry biomass of the amphipod assemblage during the study was 168 g m^{-2}. Using a P:B ratio of 4.0, the amphipod annual production is estimated as 672 g dry wt m^{-2} yr^{-1}. Amphipod biomass is based on samples that had been preserved in ethanol. Subse-

quent analysis has shown that these animals typically lose about 50% of their dry mass when stored this way, biasing their production estimate downward.

DISCUSSION

Traditionally the seafloor has been thought to receive organic matter as a slow 'rain of detritus' (Agassiz 1888), composed primarily of fecal pellets, crustacean molts and other fine particulate material (Rowe & Staresinic 1979). The recent discovery of large quantities of phytodetritus on the deep sea floor (Lampitt 1985, Thiel et al. 1988/1989) has called into question long-held views on the rate of delivery of food to the benthos and its degree of food limitation. Such material may contribute relatively little to sediments on narrow continental shelves however, because high current velocities reduce deposition, and much of the fine suspended matter incorporated in the sediments first passes through the guts of suspension-feeding animals, which lower its organic content. The frequency and importance of large food falls, such as macrophytes (wood, algae, seagrass) fish, seabird and marine mammal carcasses to the deep-sea and nearshore benthos has also received recent attention (Stockton & DeLaca 1982, Smith 1985, Grassle & Morse-Porteous 1987, Priede et al. 1991). Phytodetritus and carcasses provide a rich resource which is patchy in space and time; because of their more refractory nature, macrophyte falls result in longer lasting, if lower intensity enrichments where they come to rest. The large size and persistence of the enriched area described here results from benthic topography which traps and retains the locally abundant bedload detritus. Most of the more permanent food patches studied are anthropogenic enrichments such as those associated with municipal and industrial sewage outfalls (Pearson & Rosenberg 1978), fish farming (Ritz et al. 1989), or oil contamination (Suchanek 1993).

The amphipod and leptostracan densities measured here are an order of magnitude greater than any natural macrofaunal assemblage previously reported in the literature (Vetter 1994). The maximum density for both taxa occurred on 29 February 1992 when the leptostracan density was estimated as 2.02×10^6 m^{-2} and amphipod density as 1.22×10^6 m^{-2}. Studies on substrates other than detrital mats have rarely reported macrofaunal densities that exceed 10^5 m^{-2}. The sand plain surrounding this habitat has much lower macrofaunal densities, ranging from 4.0×10^3 to 2.0×10^4 m^{-2}, with a mean of 9.0×10^3 m^{-2}. Of the 4 abundant crustaceans in the detritus, only Aoroides spinosus lives in the surrounding sediments where it may achieve densities of 200 to 300 m^{-2}. Another un-

Table 1. *Nebalia* sp. Calculation of standing biomass and secondary production (g dry wt m^{-2} yr^{-1}) using the average cohort method (Eq. 1). Data based on density in the South Branch detritus mat. Size class: carapace length; $\overline{N}$: average number of individuals of class *j*; $\overline{N}_j - \overline{N}_{j+1}$: number of individuals lost from one size class to the next. W_j: mean dry weight of individuals belonging to size class *j*; $\overline{N}_j \overline{W}_j$: biomass (dry) of size class *j*; W_{gm}: geometric mean of mean dry weight of 2 successive size classes; Biomass lost = $(N_j - N_{j+1}) \times W_{gm}$; P_j: production = Biomass lost × number of times loss occurred

Size class (mm)	$\overline{N}$ (ind. m^{-2})	$\overline{N}_j - \overline{N}_{j+1}$ (ind. m^{-2})	W_j (g)	$\overline{N}_j \overline{W}_j$ (g m^{-2})	W_{gm} (g)	Biomass lost (g m^{-2})	P_j (g m^{-2})
0.8	134 858	–	0.00003	4.553	–	–	–
1	119 889	14 969	0.00006	7.193	0.00005	0.674	21
1.2	72 080	47 809	0.00010	6.919	0.00008	3.628	112
1.4	81 614	–9 534	0.00014	11.654	0.00012	–1.116	–35
1.6	78 610	3 005	0.00020	15.836	0.00017	0.510	16
1.8	56 872	21 737	0.00027	15.520	0.00023	5.097	158
2	42 546	14 327	0.00036	15.232	0.00031	4.478	139
2.2	27 895	14 651	0.00046	12.767	0.00040	5.931	184
2.4	24 030	3 866	0.00057	13.763	0.00051	1.979	61
2.6	19 985	4 044	0.00070	14.069	0.00063	2.568	80
2.8	20 779	–794	0.00085	17.705	0.00077	–0.615	–19
3	17 441	3 338	0.00102	17.753	0.00093	3.109	96
3.2	17 354	87	0.00120	20.861	0.00111	0.096	3
3.4	16 501	854	0.00141	23.189	0.00130	1.109	34
3.6	11 172	5 329	0.00163	18.191	0.00151	8.061	250
3.8	9 189	1 983	0.00187	17.200	0.00175	3.461	107
4	10 470	–1 281	0.00214	22.367	0.00200	–2.561	–79
4.2	3 832	6 638	0.00242	9.284	0.00227	15.100	468
4.4	4 288	–456	0.00273	11.711	0.00257	–1.173	–36
4.6	3 199	1 090	0.00306	9.796	0.00289	3.151	98
4.8	1 254	1 945	0.00342	4.285	0.00324	6.292	195
5	3 753	–2 499	0.00380	14.247	0.00360	–9.000	–279
5.2	2 219	1 533	0.00420	9.322	0.00399	6.123	190
5.4	2 228	–9	0.00463	10.314	0.00441	–0.037	–1
5.6	2 117	111	0.00508	10.764	0.00485	0.537	17
5.8	2 778	–660	0.00557	15.458	0.00532	–3.513	–109
6	4 014	–1 236	0.00607	24.378	0.00581	–7.188	–223
6.2	3 629	385	0.00661	23.983	0.00634	2.439	76
6.4	4 742	–1 113	0.00717	34.009	0.00689	–7.662	–238
6.6	1 553	3 188	0.00776	12.061	0.00746	23.793	738
6.8	912	641	0.00839	7.651	0.00807	5.172	160
7	0	912	–	–	0.00839	7.655	237
Total:	801 802			452			2 421

described species of *Nebalia* inhabits the surrounding sediments at densities as high as 1.0×10^3 m^{-2}. Few previous studies have reported macrofaunal densities above 1.0×10^5 m^{-2}; the highest found was 7.5×10^5 m^{-2}, for capitellid polychaetes (*Mediomastus ambiseta*) inhabiting sediments contaminated by oil (Grassle & Grassle 1974). No other reports of densities exceeding 2.5×10^5 m^{-2} were found.

The great densities achieved by the detritus-mat fauna may partially result from the relatively large 3-dimensional extent of their habitat. The surface portion of the mat is composed of unconsolidated macrophyte detritus typically overlying a layer of mixed sand and detritus that is usually devoid of macrofauna. The detritus layer itself is often more than 1 m thick. However, oxygen levels fall off rapidly, being 3- to 4-fold lower 20 cm into the detritus mat than at the mat

surface (Vetter 1995) and the animals are typically distributed only within the top 20 to 30 cm. The highest density of these animals found in enriched sediments surrounding the detrital accumulations was 6.2×10^5 m^{-2} (all juvenile leptostracans and amphipods). *Capitella* sp., frequently abundant in a halo of enriched sediments around the mat, had a maximum density of 1.01×10^5 m^{-2}.

Secondary production of the leptostracans is estimated at between 2400 and 7200 g dry wt m^{-2} yr^{-1}. The estimated *P*:*B* ratio was between 5.2 and 15.7. Because these animals are capable of producing at least 3 broods in the lab, and grow larger in nature than in the most favorable lab conditions, I consider a CPI of 1.5 to be the lowest plausible value for this population and will use it for comparative purposes. A CPI of 1.5 yields a *P*:*B* of 7.86, the only other reported

Table 2. *Nebalia* sp. Calculation of standing biomass and secondary production (g dry wt m^{-2} yr^{-1}) using the average cohort method (Eq. 1). Data adjusted for estimated population size in the South Branch detritus mat. Size class: carapace length; $\overline{N}$: average number of individuals of class j; $\overline{N}_j - \overline{N}_{j+1}$: number of individuals lost from one size class to the next. W_j: mean dry weight of individuals belonging to size class j; $\overline{N}_j \overline{W}_j$: biomass (dry) of size class j; W_{gm}: geometric mean of mean dry weight of 2 successive size classes; Biomass lost = $(N_j - N_{j+1}) \times W_{gm}$; P_j: production = Biomass lost × number of times loss occurred

Size class (mm)	$\overline{N}$	$\overline{N}_j - \overline{N}_{j+1}$	W_j (g)	$\overline{N}_j \overline{W}_j$ (g)	W_{gm} (g)	Biomass lost (g)	P_j (g)
0.8	49 320 680	–	0.00003	1 665	–	–	–
1	43 612 439	5 708 241	0.00006	2 617	0.00005	257	7 964
1.2	34 882 207	8 730 232	0.00010	3 348	0.00008	663	20 538
1.4	38 944 985	−4 062 778	0.00014	5 561	0.00012	−476	−14 745
1.6	36 805 294	2 139 691	0.00020	7 414	0.00017	363	11 250
1.8	26 871 844	9 933 451	0.00027	7 333	0.00023	2 329	72 201
2	21 654 520	5 217 324	0.00036	7 753	0.00031	1 631	50 554
2.2	14 763 899	6 890 621	0.00046	6 757	0.00040	2 789	86 469
2.4	12 265 386	2 498 514	0.00057	7 025	0.00051	1 279	39 656
2.6	10 127 502	2 137 884	0.00070	7 129	0.00063	1 357	42 082
2.8	10 587 119	−459 618	0.00085	9 021	0.00077	−356	−11 035
3	9 324 941	1 262 178	0.00102	9 492	0.00093	1 175	36 439
3.2	9 434 772	−109 830	0.00120	11 341	0.00111	−121	−3 766
3.4	8 292 767	1 142 004	0.00141	11 654	0.00130	1 484	46 013
3.6	5 880 381	2 412 386	0.00163	9 575	0.00151	3 649	113 127
3.8	5 014 785	865 596	0.00187	9 387	0.00175	1 511	46 846
4	5 623 923	−609 138	0.00214	12 014	0.00200	−1 218	−37 760
4.2	2 033 659	3 590 264	0.00242	4 927	0.00227	8 167	253 192
4.4	2 363 666	−330 007	0.00273	6 455	0.00257	−849	−26 314
4.6	1 587 018	776 648	0.00306	4 860	0.00289	2 246	69 629
4.8	728 952	858 067	0.00342	2 491	0.00324	2 776	86 055
5	1 896 504	−1 167 552	0.00380	7 200	0.00360	−4 206	−130 374
5.2	1 189 494	707 010	0.00420	4 996	0.00399	2 823	87 525
5.4	1 114 492	75 002	0.00463	5 159	0.00441	331	10 253
5.6	1 016 890	97 602	0.00508	5 170	0.00485	474	14 679
5.8	1 293 483	−276 593	0.00557	7 199	0.00532	−1 471	−45 611
6	1 599 667	−306 184	0.00607	9 716	0.00581	−1 780	−55 185
6.2	1 558 701	40 966	0.00661	10 302	0.00634	260	8 046
6.4	2 176 641	−617 940	0.00717	15 612	0.00689	−4 255	−131 892
6.6	840 366	1 336 275	0.00776	6 525	0.00746	9 972	309 139
6.8	407 984	432 383	0.00839	3 421	0.00807	3 489	108 156
7	0	407 984	–	–	0.00839	3 423	106 112
Total mat:	363 214 960			223 121			1 169 243
m^{-2}	747 356			459			2 406

leptostracan $P{:}B$ ratio is 22.5 (Rainer & Unsworth 1991). Because the food source of the animals and their habitat are one and the same, these animals are unlikely to be resource limited and a high $P{:}B$ ratio is not surprising. The minimum annual production of amphipods was calculated to be 672 g dry wt m^{-2} yr^{-1}, a value that should be considered a minimum estimate for 2 reasons: (1) the $P{:}B$ ratio involved (4.0) is likely to be an underestimate because of the abundance of food, and was deliberately chosen to be conservative; and (2) the storage of amphipods in alcohol prior to drying and weighing caused them to lose a considerable amount of their biomass into solution. For the

Table 3. Secondary production (g m^{-2} yr^{-1}) and production-to-biomass ratios of the *Nebalia* sp., from March 1992 to March 1993, from calculation tables based on either estimated population size or measured density, and a range of possible cohort production intervals (CPI)

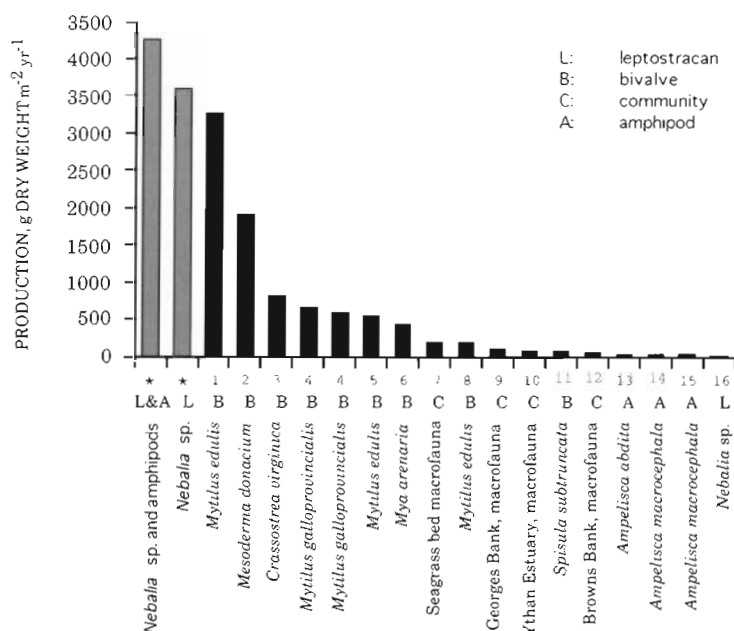| CPI	Population		Density	
	P	$P{:}B$	P	$P{:}B$
1	2406	5.24	2421	5.27
1.5	3609	7.86	3632	7.91
2	4812	10.48	4842	10.55
2.5	6015	13.10	6053	13.19
3	7218	15.73	7263	15.82

Fig. 4. Secondary production (shell-free dry weight for bivalves) of the detritus mat fauna compared with reports of high secondary production, and highest reports of amphipod and leptostracan production from the literature (numbers indicate citation listed in Table 4; *data from this study). The first column combines leptostracan and amphipod production, the second shows only leptostracan production

purposes of this study it matters little whether their secondary production is 500 or 1500 g dry wt m⁻² yr⁻¹; in either case it is an enormous value.

I have found only 2 reports of secondary production in the literature with values even approaching those estimated in the present study (Fig. 4, Table 4). These were production by a *Mytilus edulis* bed composed of 0, 1, and 2 year class mussels, all of which recruited in great number (3260 g shell-free dry wt m⁻² yr⁻¹; Dare 1976), and by another intertidal bivalve, *Mesoderma donacium* (1996 g shell-free dry wt m⁻² yr⁻¹; Arntz et al. 1987). The next 3 highest production reports are from an oyster bed and from mature *Mytilus* spp. beds, and are at least 4-fold lower. The highest secondary production found for an amphipod is 2 orders of magnitude lower (Franz & Tanacredi 1992) than the values reported here.

Detritus mats are probably common in other areas. They have been reported from the Monterey Canyon (Central California) with infaunal densities as high as 5.0 × 10⁵ (Okey 1993). A sample collected by the City of San Diego ocean monitoring program 30 m

to the south at a depth of 65 m contained the same species of *Nebalia* found at the La Jolla Canyon, and detritus was recovered with the sample. Surveys in San Diego Bay have turned up leptostracan densities as high as 10000 m⁻² in small (1 to 2 m²) detritus patches throughout the bay. Other regions accumulating large detrital mats surely exist along the west coast of North America, since all that seems to be required is a source of detritus, a topographic sink, and a favorable current regime. Shepard & Dill (1966) reported detritus mats in several California canyons, and others are likely to be present in most West Coast canyons. The lack of extensive documentation more likely reflects under-reporting than nonexistence.

Until very recently there have been few published references to localized patches of organic material in the subtidal ocean. Rowe & Staresinic (1979) reported that in over 200 otter trawls, 50 dives by the submersible ALVIN, and more than 50000 photographs of the deep sea floor, no evidence of large carcasses had ever been observed. However, Smith (1985, 1987) found several fish carcasses and 1 whale carcass, and estimated that nekton falls accounted for about 11% of the benthic community respiration in the Santa Catalina Basin (Southern California Bight). There have been numerous recent reports of seagrasses, macroalgae, and other plant debris in the deep sea (Menzies et al. 1967, Wolff 1976, George & Higgins 1979, Rowe & Staresinic 1979, Josselyn et al. 1983, Suchanek et al. 1985, Bach et al. 1986, Alongi 1990), although I have found no reports of regions with a persistent cover of such material. This may be attributable in part to diffi-

Table 4. Citations and taxa for data used in Fig. 4

1	Mussel	*Mytilus edulis*	Dare (1976)
2	Clam	*Mesoderma donacium*	Arntz et al. (1987)
3	Oyster	*Crassostrea virginica*	Dame (1976)
4	Mussel	*Mytilus galloprovincialis*	Ceccherelli & Rossi (1984)
5	Mussel	*Mytilus edulis*	Asmus (1987)
6	Clam	*Mya arenaria*	Möller & Rosenberg (1983)
7	Community	Seagrass bed macrofauna	Fredette et al. (1990)
8	Mussel	*Mytilus edulis*	Craeymeersch et al. (1986)
9	Community	Georges Bank, macrofauna	Steimle (1987)
10	Community	Ythan Estuary, macrofauna	Baird & Milne (1981)
11	Clam	*Spisula subtruncata*	Ambrogi & Ambrogi (1987)
12	Community	Browns Bank, macrofauna	Wildish et al. (1989)
13	Amphipod	*Ampelisca abdita*	Franz & Tanacredi (1992)
14	Amphipod	*Ampelisca macrocephala*	Highsmith & Coyle (1990)
15	Amphipod	*Ampelisca macrocephala*	Highsmith & Coyle (1991)
16	Leptostracan	*Nebalia* sp.	Unsworth (1987)

culties associated with making repeated visits to sites on the deep sea floor.

The 2 *Nebalia* spp. and *Orchomene limodes* of the detrital mat are known only from this habitat, but presumably are found where similar conditions exist along the North American west coast. The success of the mat fauna may be due to a suite of several common natural-history traits. All the animals are scavengers, capable of feeding on algal and seagrass detritus and carrion. The leptostracans can grow and reproduce in the laboratory with only organically rich sediments. *Nebalia* spp. are capable of surviving at very low oxygen tension, although the amphipods are somewhat less tolerant and tend to be found closer to the surface of the mat. All reproduce throughout the year, and at least the *Nebalia* sp. are iteroparous, capable of producing 2 broods in a 3 mo period. Finally, all of these animals release juveniles ready to exploit the adult habitat, so few, if any, young are exported from the population. It is possible for portions of the habitat to be eliminated by physical disturbance, such as sediment slumps which could bury large portions of the habitat, or storms that could wash it away, exposing uninhabited sediments or rock. Once the detritus builds up again such areas are quickly recolonized by the residual mat fauna from patches that survive disturbances in this topographically complex system.

How important are such localized food hot-spots to fish populations in general? At first glance they seem a modest contribution in relation to the general shelf habitat, but the oceanographic literature suggests that hot-spots may be of crucial importance to some species. In the pelagic realm the importance of food patches to the growth and survival of fishes has long been recognized (Lasker 1975). A long-standing problem has been the apparent insufficiency of the average concentrations of prey to sustain predators (Mullin 1993). On a scale of hundreds of kilometers, Hakanson (1987) found that the nutritional state of zooplankton could be predicted by mesoscale phytoplankton concentration; however, on a population scale it has often been found that over 50 % of zooplankton apparently do not have enough prey immediately available to sustain growth (Mullin & Brooks 1976, Cox et al. 1983). The problem has been that plankton nets yield an average standing stock of potential prey over an area larger than the scale of dense food patches. As a result, even if the sampling net goes through a food-rich patch, measured concentrations are typically much lower than needed to sustain predators. Many of the pelagic fishes and zooplankton that survive and reproduce have somehow been able to locate and exploit food-rich patches. The same may well be true for some benthic and demersal fishes.

Submarine canyons can facilitate the formation of high-density food patches of vertically migrating animals. Using a dual-beam bioacoustic technique, Greene et. al (1988) found high density demersal layers of krill in submarine canyons off Georges Bank, NW Atlatnic. These layers may result from a funneling effect that concentrates the krill into the canyons as they migrate down during the day. However it comes about, those canyons host a highly concentrated food source on a daily basis. Greene et al. (1988) suggest that squid and demersal fish stocks on Georges Bank are subsidized by exploiting this resource. This is an example of submarine canyons temporarily accumulating food-rich patches through the behavior of the potential prey. In the La Jolla Canyon, food for benthic detritivores is accumulated (and persists) in the canyon through physical processes. The end result is the same, greater production of predators than would be possible in the absence of the rich supply of prey.

The fishes exploiting the detritus-dwelling crustaceans in the La Jolla Canyon include not only species that are resident in the canyon (*Oxyjulis californica, Chromis punctipinnis, Scorpaena guttata, Semicossyphus pulcher, Chilera taylori, Paralabrax clathratus*), but also others which are frequent visitors (*Anisotremis davidsonii, Damalichthys vacra, Embiotoca jacksoni, Phanerodon furcatus*). All of the above species are known to prey heavily on the mat fauna (Vetter 1995), and several other species are suspected of doing so. Many of these fish do not typically take small benthic invertebrates (Quast 1971, Allen 1982). However, the high abundance of macrofaunal crustaceans may have led all of these fish to become benthic browsers in this habitat.

The areal extent of the detritus habitat within the La Jolla Canyon system is unknown but probably exceeds 10 ha. The huge secondary production here is made more significant by the taxa that are responsible for it. These macrofaunal crustaceans are easily taken by fishes and thus provide a direct conduit for marine macrophyte production into higher trophic levels. The mat habitat greatly fuels production of local fishes and presumably can subsidize nomadic or long-ranging fishes. Hot-spots of benthic secondary production are likely to be common, but few may be as 'hot' as the habitat described here. Any patch of the seafloor that receives a greater supply of food than its surroundings is hot in the sense that it should have higher than background production. In the calm conditions of the deep sea, such patches can occur on very small scales such as in and around mounds, pits and other biogenic structures in the sediment (Rice & Lambshead 1994). Grassle & Grassle (1994, and references therein) assert that such small-scale spatial and temporal variability in food supply is an important factor in maintaining the

high diversity found in the deep-sea benthos. This patchiness of resources leads to patchy production by species that might not be present if the deep ocean floor were homogeneous with regard to structure and available food (Snelgrove et al. 1992). Hydrothermal vents support the most dramatic examples of benthic hyperproductivity. Lutz et. al (1994) report that vestimentiferan worms at a hydrothermal vent on the East Pacific Rise attained tube length of 85 cm within 1 yr. These worms occur in highly discrete patches of densely packed individuals and their annual production in some instances may well exceed the values reported here.

The general importance of patchiness in natural systems involving everything from disturbance to recruitment to resources is becoming increasingly apparent. Physical features that result in localized enhanced production from ray-pits (VanBlaricom 1982) to seamounts (Rogers 1994) are common. These and other patches of benthic hyperproductivity are important ecologically and could well enhance commercial and sport fisheries over very wide areas.

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