

# Secondary production of a Southern California *Nebalia* (Crustacea: Leptostraca)

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**ABSTRACT:** *Nebalia daytoni* is an abundant leptostracan crustacean from the infauna between 10 and 30 m on the sand plain off the coast of San Diego, California, USA. Secondary production of *N. daytoni* was estimated to be 0.930 g dry weight m<sup>-2</sup> yr<sup>-1</sup> between June 1991 and June 1992, and 0.660 g dry weight m<sup>-2</sup> yr<sup>-1</sup> between June 1992 and June 1993. The corresponding ratios between production and biomass were, respectively, 2.92 and 3.17, less than those reported for other leptostracan species living in organically richer environments. Throughout this 2 yr study, adults accounted for most of the secondary production within the population. Few data exist for leptostracan secondary production so reports of amphipod secondary production are used for comparative purposes. Amphipods, in general, also appear to conform to the pattern of both greater productivity in vegetated habitats, or habitats with large inputs of macrophyte detritus, and the pattern of adult production.

**KEY WORDS:** *Nebalia* · Amphipod · Secondary production · Detritus

## INTRODUCTION

Increases in community production are usually linked to increased food availability, and are reflected by higher biomass (Banse & Mosher 1980) or, more controversially, by higher production-to-biomass (P:B) ratios of populations within the community. Because plants are limited by light in most of the ocean, and by the unstable substratum in shallow coastal sediments, most benthic and demersal food webs (and pelagic webs below the photic zone) are based on plant and animal detritus rather than on viable plants (Roman 1984, Mann 1988). The standing stock of detritus can be estimated simply by determining the organic carbon content of the sediment; such measures, however, cannot be used as indices of food available to benthic populations because much detritus is likely to be refractive and unavailable to detritivores (Levinton & Stewart 1988). Furthermore, such static readings give no insight on the rate of supply of detritus that can be assimilated by metazoans. Sediment traps measure the flux of organic matter to the benthos from the water

column, but do not sample the particulate carbon that enters, or passes through, patches of the seafloor horizontally in the bedload and nepheloid layer. Secondary production by benthic detritivores, which accounts for both the quantity and quality of the organic matter available for higher trophic levels, is thus a crucial element in determining community composition and overall productivity of the benthos (Tenore 1988, Gage & Tyler 1991). This paper examines the secondary production of *Nebalia daytoni*, a deposit-feeding detritivore living in a subtidal sand plain off the coast of Southern California, USA, over a 2 yr period. Results from this study, and published reports of *Nebalia* spp. and amphipod production, were used to evaluate the hypothesis that infaunal invertebrates become more productive per unit of biomass as the availability of organic matter increases.

The Leptostraca is a widely distributed, yet poorly studied, order of crustaceans. Of the 7 leptostracan genera, *Nebalia* is the largest, with 16 described species. The habitat of *N. daytoni* surrounds and marginally overlaps that of another member of the genus. That species, *Nebalia hessleri*, occurs at extremely high densities within extensive mats of kelp and surf-grass detritus found in and around the La Jolla Sub-

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marine Canyon (Vetter 1995a). The secondary production of *N. hessleri* within the shallow reaches of the canyon was found to be among the highest reported for benthic macroinvertebrates (Vetter 1995b). Unlike *N. hessleri* and nearly all other members of the genus, *N. daytoni* lives in an organically impoverished environment, and is not attracted to patches enriched with organic matter (Vetter 1996a in this issue). Because of the great difference in density and biomass ( $m^{-2}$ ) between the 2 species, it was obvious that annual production ( $m^{-2}$ ) of *N. daytoni* would be much lower than that of its local congener. Less obvious was how production per unit of biomass (P:B) would differ between the two, although it was predicted that the P:B ratio of *N. hessleri* would be greater because of the abundance of food in the detritus habitat (Vetter 1995a). The P:B ratio of *N. hessleri* inhabiting mats of macrophyte detritus was previously found to be 7.5 (Vetter 1994); the only other report of secondary production for the genus is for *Nebalia* sp. inhabiting seagrass meadows in Western Australia (P:B 22.5; Rainer & Unsworth 1991).

This study was undertaken to examine the production of a numerically dominant member of the local sand-plain infauna. Of more general interest, however, is the discussion of how organic enrichment affects the P:B ratios of macrofaunal crustaceans. A comparison of the results from this study with those for other leptostracans and amphipods suggests that increased availability of detritus results in greater P:B. Amphipods were chosen for comparative purposes because they have been well studied, are similar in size, and share many life-history characteristics with leptostracans. The size and/or age classes of populations that are responsible for most secondary production are also discussed.

## 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.

Sediments were sampled monthly (from 19 to 20 m, as part of a larger study) using nine 7.6 cm diameter clear butyrate tube-corers, 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. Several non-quantitative samples were taken on each collection date to increase the number of *Nebalia daytoni* sampled for this study

(nearly tripling the area sampled). Over the 2 yr of the study 2377 individuals were sampled for production estimates (on average 97.9 ind.  $mo^{-1}$  in Year 1 and 100.2 ind.  $mo^{-1}$  in Year 2). Sediments were live-sieved with a 500  $\mu m$  mesh screen within 2 hr 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 to separate the *N. daytoni* for carapace measurement. Measurements were made from the anteriormost point (just below the eye) to the posteriormost point of the carapace using a Wild M5A dissecting microscope with ocular micrometer.

Several non-quantitative collections were made to capture enough leptostracans to determine the relationship between carapace length and dry weight. Live animals were narcotized with dilute ethanol, measured using a dissecting microscope with an ocular micrometer, dried to constant weight at 62° C, and weighed with a Sartorius analytical balance. Curve fits were carried out using the Macintosh statistical program DeltaGraph Pro® (version 3.5).

Secondary production of *Nebalia daytoni* was estimated using the average-cohort method (Hynes & Coleman 1968, Hamilton 1969, Benke 1979). This method involves calculation of the average cohort, the average size-frequency distribution of the population obtained from samples taken throughout the year. The calculation of production involves quantifying the loss of biomass between successive size intervals. Hamilton's (1969) modification of the basic-production equation of Hynes & Coleman (1968) is used here:

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

where  $P$  is estimated production,  $i$  is the number of times the loss occurs (equivalent to the number of size classes used; the multiplication accounts for the limited time spent in each size class),  $\bar{N}_j$  is the mean number of individuals in size class  $j$  (averaged over the entire year), and  $\bar{W}_j$  is the mean dry weight of individuals belonging to size class  $j$ . Here  $P$  is calculated as: (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 geometric mean is used because it always gives a value lower than the arithmetic mean and more accurately reflects logarithmic growth patterns (Krueger & Martin 1980). The size class interval used was 0.2 mm. Instars could not be reliably identified so were unavailable for use as a grouping device. This species survived poorly in the laboratory, though 2 other species of *Nebalia* that had been laboratory reared molted frequently with little change in size (*Nebalia* sp., Dahl 1985; *N. hessleri*, Vetter unpubl.).

Even though well over 2000 animals were collected for this study, the presumably small change in size between instars made separating them impossible.

The secondary production calculation used here often results in apparent gain (negative loss) of biomass between size increments. This happens whenever there is an increase in average abundance between successively larger size groups or when there is non-uniformity of growth rates between size classes. Of course negative loss is not occurring; these values represent a sampling error and must be included in the summation to balance positive error. A curve was fitted to the histogram of the average cohort, and the equation for that curve was used to recreate the average cohort. The resulting production table did not include any negative values and the calculated production closely matched that of the original data.

The average-cohort method requires multiplying the results by 365/CPI (cohort production interval = time in days from hatching to attainment of largest size class) to account for multiple broods (Benke 1979); however, *Nebalia daytoni* breed only once (Vetter 1995a), so values obtained from the calculation tables were not modified.

## RESULTS

From June 1991 to June 1993, the density of *Nebalia daytoni* averaged 950 ind. m<sup>-2</sup> (SD 300), with maxi-

imum density in late spring-early summer, and minimum density in late summer-early fall.

Secondary production for the *Nebalia daytoni* was calculated for 2 yr, June 1991 through June 1993. Biomass was estimated using a regression equation for carapace length (CL) and dry weight (dry wt) from fresh animals [dry wt = (8.90 × 10<sup>-5</sup>) × (CL)<sup>2.16</sup>]. Production in the first year (Table 1) was estimated at 0.93 g dry wt m<sup>-2</sup> yr<sup>-1</sup>. Estimated P:B was 2.92 and average density was 1087 ind. m<sup>-2</sup>. In the second year (Table 2), the estimated P:B ratio increased to 3.17 but estimated production fell to 0.66 g dry wt m<sup>-2</sup> yr<sup>-1</sup> because of decreased density (814 ind. m<sup>-2</sup>) and smaller average size (Vetter 1995a).

Averaged over 2 yr, 22% of individuals sampled were sexually mature (>2 mm CL; Vetter 1995a). Mature animals amounted to 53% of the population's biomass over the 2 yr study (Fig. 1), and were responsible for 76% of production in the first year and 63% in the second year (Tables 1 & 2).

## DISCUSSION

Secondary production can be estimated using published production to biomass ratios or algorithms based on life span (in years) (Robertson 1979), adult body mass (Banse & Mosher 1980) or a combination of mean annual biomass, mean individual biomass, annual mean temperature, and depth (Tumbiolo & Downing

Table 1. *Nebalia daytoni*. Calculation of standing biomass and secondary production from June 1991 to June 1992 using the average cohort method (Eq. 1). Size class: carapace length;  $\bar{N}_j$ : average number of individuals of class  $j$ ;  $\bar{N}_j - \bar{N}_{j+1}$ : number of individuals lost from one size class to the next;  $\bar{W}_j$ : dry weight of individuals belonging to size class  $j$ ;  $\bar{N}_j \bar{W}_j$ : biomass (dry) of size class  $j$ ;  $\bar{W}_{gm}$ : geometric mean of dry weight of 2 successive size classes; biomass lost =  $\bar{N}_j - \bar{N}_{j+1} \times \bar{W}_{gm}$ ;  $P_j$ : production = biomass lost × number of times loss occurred

Size class (mm)	$\bar{N}$	$\bar{N}_j - \bar{N}_{j+1}$	$\bar{W}_j$ (g)	$\bar{N}_j \bar{W}_j$ (g)	$\bar{W}_{gm}$ (g)	Biomass lost (g)	$P_j$ (g)
0.9	129		0.00007	0.00913			
1.1	168	-38.90	0.00011	0.01834	0.00009	-0.00343	-0.03768
1.3	131	36.95	0.00016	0.02052	0.00013	0.00484	0.05323
1.5	123	8.00	0.00021	0.02624	0.00018	0.00146	0.01611
1.7	109	13.71	0.00028	0.03055	0.00024	0.00335	0.03689
1.9	71	38.38	0.00036	0.02518	0.00032	0.01212	0.13331
2.1	66	4.35	0.00044	0.02933	0.00040	0.00173	0.01898
2.3	108	-41.51	0.00054	0.05803	0.00049	-0.02024	-0.22263
2.5	94	13.97	0.00064	0.06048	0.00059	0.00822	0.09045
2.7	76	17.57	0.00076	0.05805	0.00070	0.01230	0.13530
2.9	12	64.07	0.00089	0.01087	0.00082	0.05264	0.57907
3.1		12.25	0.00103	0.00000	0.00095	0.01169	0.12854
	Density (m <sup>-2</sup> )		Biomass (g dry wt m <sup>-2</sup> )		Production (g dry wt m <sup>-2</sup> yr <sup>-1</sup> )		P:B
	1087		0.32		0.93		2.92

Table 2. *Nebalia daytoni*. Calculation of standing biomass and secondary production from June 1992 to June 1993 using the average cohort method (Eq. 1). Size class: carapace length;  $\bar{N}$ : average number of individuals of class  $j$ ;  $\bar{N}_j - \bar{N}_{j+1}$ : number of individuals lost from one size class to the next;  $\bar{W}_j$ : dry weight of individuals belonging to size class  $j$ ;  $\bar{N}_j \bar{W}_j$ : biomass (dry) of size class  $j$ ;  $\bar{W}_{gm}$ : geometric mean of dry weight of 2 successive size classes; biomass lost =  $\bar{N}_j - \bar{N}_{j+1} \times \bar{W}_{gm}$ ;  $P_j$ : production = biomass lost  $\times$  number of times loss occurred

Size class (mm)	$\bar{N}$	$\bar{N}_j - \bar{N}_{j+1}$	$\bar{W}_j$ (g)	$\bar{N}_j \bar{W}_j$ (g)	$\bar{W}_{gm}$ (g)	Biomass lost (g)	$P_j$ (g)
0.9	95		0.00007	0.00671			
1.1	152	-57.03	0.00011	0.01659	0.00009	-0.00502	-0.055227
1.3	144	7.29	0.00016	0.02265	0.00013	0.00095	0.010498
1.5	106	37.90	0.00021	0.02276	0.00018	0.00694	0.076318
1.7	64	42.02	0.00028	0.01805	0.00024	0.01028	0.113059
1.9	45	19.54	0.00036	0.01600	0.00032	0.00617	0.067859
2.1	38	7.10	0.00044	0.01672	0.00040	0.00282	0.030977
2.3	56	-17.80	0.00054	0.02993	0.00049	-0.00868	-0.095469
2.5	62	-5.95	0.00064	0.03967	0.00059	-0.00350	-0.038545
2.7	44	17.90	0.00076	0.03323	0.00070	0.01253	0.137846
2.9	9	35.15	0.00089	0.00757	0.00082	0.02888	0.317695
3.1		8.53	0.00103	0.00000	0.00095	0.00814	0.089531
	Density (m <sup>-2</sup> )		Biomass (g dry wt m <sup>-2</sup> )		Production (g dry wt m <sup>-2</sup> yr <sup>-1</sup> )		P:B
	814		0.21		0.66		3.17

1994). Estimates based on such calculations may work well in some situations, but the applicability of those techniques is limited because of variations in growth rate as many invertebrates age (Highsmith & Coyle 1991) and increases in P:B ratios for populations of a single species along a gradient of food availability (Möller & Rosenberg 1982). For those reasons, and because so little comparative data are available for leptostracans, production was estimated directly from population abundance and size frequency data.

Few data exist for leptostracan secondary production (Rainer & Unsworth 1991, Vetter 1994), so reports of

amphipod secondary production were used for comparative purposes. Amphipods were chosen because of ecological similarities between the 2 groups, and the relatively large amount of data for amphipods. As with amphipods, all species of *Nebalia* brood, with non-planktonic juveniles exiting the brood chamber ready to take up the adult habitat. Amphipods and leptostracans also overlap considerably in size, habitats and trophic modes (Calman 1909, Schram 1986, Highsmith & Coyle 1991, Vetter 1995a). The effects of food supply on leptostracan and amphipod secondary production appear to be similar (see Table 3, and Möller & Rosenberg 1982).

Prior to the present research, only 2 studies of leptostracan secondary production had been published. Rainer & Unsworth (1991) studied a population of *Nebalia* sp. inhabiting a seagrass meadow in Western Australia and reported an annual production of 5.8 g ash-free dry wt (AFDW) m<sup>-2</sup> and a P:B of 22.5 (Table 3). Vetter (1994) found a population of *N. hessleri* living within subtidal accumulations of macrophyte detritus with an annual production of approximately 3300 g dry wt m<sup>-2</sup> and a P:B of 7.8 (but see Vetter 1995b). Both of these species occur in habitats rich in detritus and both have greater secondary production and P:B ratios than are typically reported for amphipods (Table 3). The annual production for *N. daytoni* reported here (0.66 to 0.93 g dry wt m<sup>-2</sup>) is lower than that of the other leptostracans studied because of the modest density of *N. daytoni* (950 m<sup>-2</sup>) and especially its small size.

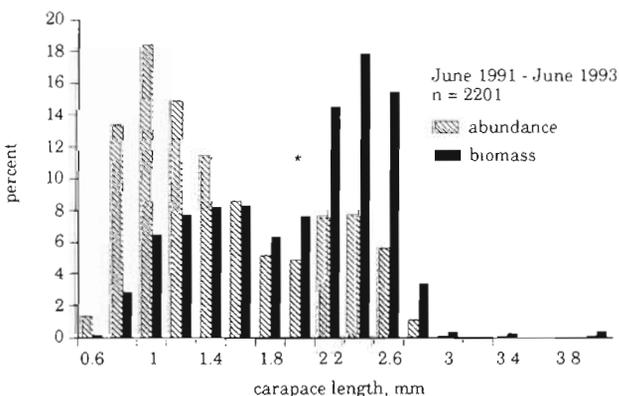


Fig. 1. *Nebalia daytoni*. Abundance (hatched columns) and biomass (solid columns) of animals by size. \*Smallest size class with mature animals

Table 3. Reported production and P:B ratios for *Nebalia* and some amphipods. Where more than one report was found for an individual species, only the first found was included unless the duplicated species was included with the report of a species new to the list

Species	Location	Production (g dry wt m <sup>-2</sup> yr <sup>-1</sup> )	P:B	Source
<b>Amphipods</b>				
<i>Ampelisca abdita</i>	New York, USA, 1–10 m	25–47	3.5–4.2	Franz & Tanacredi (1992)
<i>Pontoporeia affinis</i>	Finland, 21–25 m	7.4 <sup>a</sup>	2.9	Sarvala & Uitto (1991)
<i>A. araucana</i>	Chile, 65 m	8.3	4.4	Carrasco & Arcos (1984)
<i>A. armoricana</i>	English Channel, 17 m	10.4	2.7	Dauvin (1988d)
<i>A. tenuicornis</i>		1.7	3.7	Dauvin (1988a)
<i>A. typica</i>		0.2	4.1–4.4	Dauvin (1988c)
<i>A. brevicornis</i>		0.5	2.2–2.8	Dauvin (1988b)
<i>A. macrocephala</i>	Bering Sea, 35–50 m	39.8	0.9	Highsmith & Coyle (1990)
<i>A. brevicornis</i>	North Sea	0.48	3.48	Klein et al. (1975)
<i>Parhyale basrensis</i>	Iraq, intertidal	5.6	3.1	Ali & Salman (1987)
<i>A. agassizi</i>	Georges Bank, USA, 69–84 m	2.2	1.5	Collie (1985)
<i>Unciola inermis</i>		2.8	2.5	Collie (1985)
<i>Erichthonius fasciatus</i>		2.3	4.4	Collie (1985)
<i>Corophium volutator</i>	Sweden, intertidal	1.6–27	5.1–11.3	Möller & Rosenberg (1982)
<i>Pontoporeia femorata</i>	Nova Scotia, Canada, 4–10 m	2.8–3.5	3.6–4.8	Wildish & Peer (1981)
<i>Gammarus mucronatus</i>	Chesapeake Bay, USA, 1 m	8.3	23.6	Frédette et al. (1990)
<i>Rhepoxynius abronius</i>	Northwestern USA, 5 m	0.6–1.1	1.3–2.1	Kemp et al. (1985)
<i>C. insidiosum</i>	Denmark, 1 m	0.2–8	2–5	Birklund (1977)
<i>C. volutator</i>		2–4	3–4	
<b><i>Nebalia</i></b>				
<i>Nebalia</i> sp.	Australia, 1 m	7 <sup>a</sup>	22.5	Rainer & Unsworth (1991)
<i>N. hessleri</i>	California, USA, 15–25 m	3300	7.2	Vetter (1994)
<i>N. daytoni</i>	California, USA, 20 m	0.7–0.9	2.9–3.2	This study

<sup>a</sup>Conversion from ash free dry weight (AFDW) (dry wt = 1.25 × AFDW)

Production per unit biomass is less sensitive to differences in density and size and thus is better for comparative purposes. *N. daytoni* differs from the other 2 members of its genus studied in possessing a considerably lower P:B ratio (2.9 to 3.2), and living in much less organically rich conditions (Vetter 1995a).

In general, vegetated habitats should support greater productivity than non-vegetated ones, owing presumably to greater food availability, habitat structure and/or refuge from predation (Virnstein et al. 1983, Vetter 1995a). It has been demonstrated that even though much carbon from macrophyte detritus may remain unavailable for macrofaunal nutrition (Levinton & Stewart 1988), it still enhances the growth of detritivores (Tenore 1975, Tenore et al. 1979, Peterson et al. 1986). Vascular plants like *Spartina* apparently need some microbial processing before consumption by macrofauna (Fenchel 1977, Findlay & Tenore 1982). Thus, in comparison to vascular plants, algae should

supply detritus more immediately useful for growth of deposit feeders (Stephenson et al. 1986).

Increased productivity is usually linked to increasing food availability; this is reflected by higher secondary production of communities and/or higher P:B ratios of populations. Tumbiolo & Downing (1994) found that seagrass beds support, on average, 2.4 times the secondary production of other non-vegetated environments (for a given temperature, depth, biomass per unit area, and body mass). The highest P:B value for amphipods in the literature was found for a population of *Gammarus mucronatus* inhabiting a seagrass bed in Chesapeake Bay, USA (Fredette et al. 1990). At 23.6, its P:B value is equivalent to that of *Nebalia* sp. inhabiting a similar habitat in Australia (Rainer & Unsworth 1991; Table 3). Möller & Rosenberg (1982) estimated the production of the amphipod *Corophium volutator* at 3 locations with different grain sizes (sand, silty sand, and mud) and organic content (1.0, 1.6 and 3.5%,

respectively). They found that both production and P:B ratios were considerably greater in populations inhabiting the more organically rich muds than at the other 2 sites. Amphipods living in deeper, and supposedly less enriched, habitats typically have P:B ratios ranging between 1.0 and 5.0 (Table 3).

An unexpected result was that adults produce more despite faster growth rates of the young. During this study, each percent of the *Nebalia daytoni* population made up by adults contributed 3.2% of the annual production and, taken together, adults amounted to slightly more than half of the biomass (fig. 1). In a 2 yr study of a nearby population of *N. hessleri* inhabiting subtidal mats of decaying macrophyte detritus, adults made up 11% of the population (numerically), 62% of the biomass, and 66% of the production in the first year, and 6% of the population, 30% of the biomass and 43% of production in the subsequent year (Vetter 1995a). For both years, each 1% of the population made up by adults contributed roughly 6% of annual production, and each percent of the population made up by juveniles contributed roughly 0.5% of annual production. Concentration of biomass and production into the larger size classes has been frequently reported in amphipods (Wildish & Peer 1981, Highsmith & Coyle 1991) and, to the extent that *N. daytoni* and *N. hessleri* from the detritus mat are typical, may well be the norm for leptostracans.

Clearly more than 3 data points are necessary to evaluate the relationship between food availability and growth in leptostracans; however, if one judges by the 3 species of *Nebalia* thus far investigated, leptostracans and amphipods become more productive per unit of biomass as the availability of organic material (mostly in the form of detritus) increases. Leptostracans and amphipods are also similar in that the adults account for most of the secondary production.

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