Journal of Coastal Research	11	3	849–857	Fort Lauderdale, Florida	Summer 1995

Scaling Population Density to Body Size: Tests in Two Soft-Sediment Intertidal Communities

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ABSTRACT

DUGAN, J.E.; HUBBARD, D.M., and PAGE, H.M., 1995. Scaling population density to body size: Tests in two soft-sediment intertidal communities. *Journal of Coastal Research,* 11(3), 849–857. Fort Lauderdale (Flordia), ISSN 0749-0208.

An inverse relationship between population density and body size has been reported for a number of natural communities and taxonomic assemblages in terrestrial and aquatic systems. Such relationships have not been widely examined in marine communities. No evidence of an inverse relationship between population density and body size was found in samples of macrofauna from marine intertidal communities with soft sediments, exposed sand beaches and salt marsh tidal channels over a range of up to four orders of magnitude in population density and five orders of magnitude in body size. Relationships between population density and body size in those communities were generally not significant. For all but one of the samples, the slope of a linear regression between population density and body size was positive. We propose that the role of physical processes and disturbance in community structure, the nature of food and space resources, and the survival value conferred by size and hard exoskeletons contribute to that result for marine intertidal macrofauna communities in soft sediments.

ADDITIONAL INDEX WORDS: *Macrofauna, sand beach, salt marsh tidal channel.*

INTRODUCTION

Body size is believed to underlie many ecological patterns in population and community dynamics (PETERS, 1983). One such pattern, an inverse relationship between body size and population density, has been reported in a variety of terrestrial animal assemblages and communities (DAMUTH, 1981, 1987; PETERS and WASSENBERG, 1983; BROWN and MAURER, 1986; GASTON and LAWTON, 1988; NEE *et al.,* 1991) and in an aquatic animal assemblage (DAMUTH, 1987). That pattern has been proposed as a general rule which allows much of the variation in animal population abundance to be explained by body size (PETERS, 1983; DAMUTH, 1987). Although an inverse relationship between abundance and size appears to occur consistently on a global scale for regional and ecological densities of organisms (DAMUTH, 1991), its slope, form and applicability to individual natural communities, smaller spatial scales, guilds and taxonomic assemblages are the subject of considerable debate (PETERS and RAELSON, 1984; JUANES, 1986; BROWN and MAURER, 1986, 1987, 1989; LABARBERA, 1989; LAWTON, 1989, 1990, 1991; BLACKBURN *et al.,* 1990, 1993a; STRATHMAN, 1990; DAMUTH, 1991; PAGEL *et al.,* 1991; PERRY and ARTHUR, 1991; COTGREAVE, 1993).

Similar patterns of scaling of population density and body size may occur in marine organisms and communities, but relatively few tests have been made. For fish assemblages, nonsignificant negative relationships between population density and body size were reported in reviews by BROWN and MAURER (1986) and PAGEL *et al.* (1991). The only study to directly address the question of body size and density scaling in a marine community reported a significant negative relationship between density and body size for Chilean rocky intertidal macrofauna (MARQUET *et al.,* 1990). The slope of that relationship did not vary between locations subjected to different harvest regimes and was comparable to slopes reported for terrestrial organisms (*e.g.,* DAMUTH, 1987).

Relationships between population density and

93126 received 8 November 1993; accepted in Revision 7 June 1994.

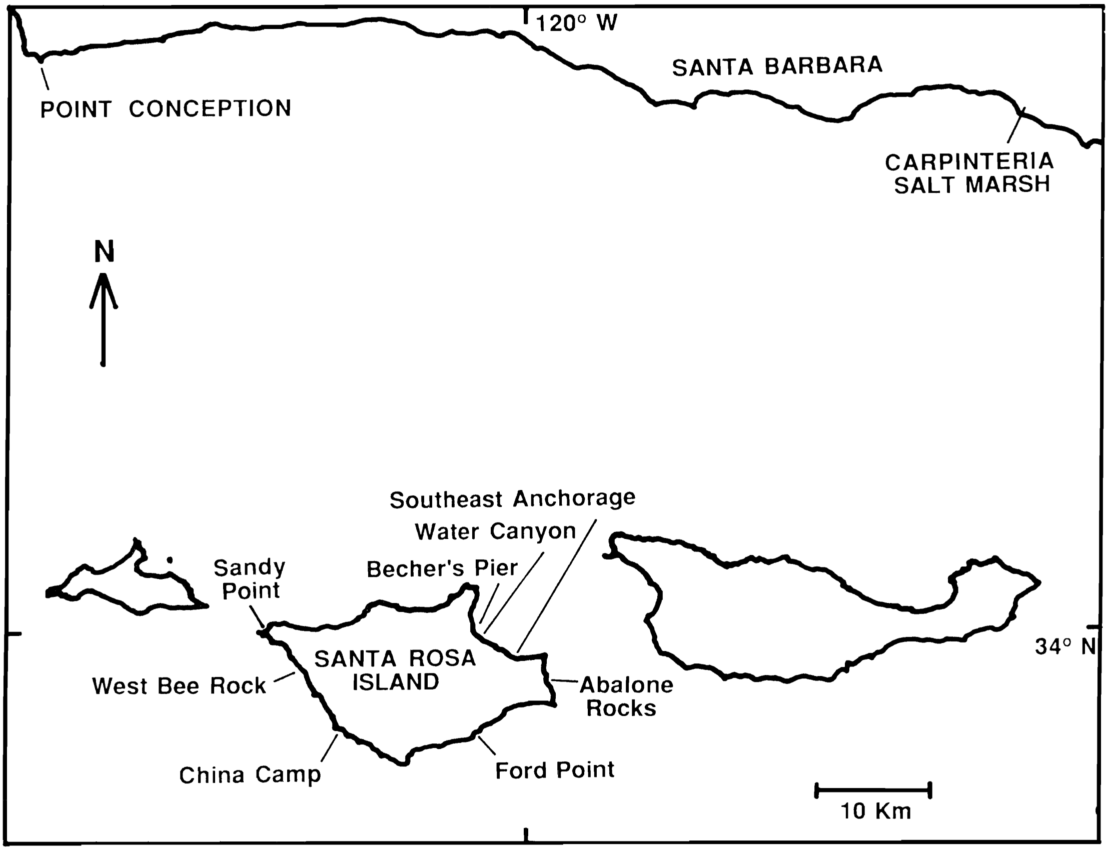

Figure 1. Geographic location of sampling sites for sand beach communities on Santa Rosa Island and for salt marsh tidal channel communities in Carpinteria Salt Marsh.

body size have not been directly examined in soft-sediment intertidal marine communities. Exposed sand beaches and salt marsh tidal channels of temperate regions are characterized by a lack of attached plants, shifting sediments, harsh physical conditions, frequent environmental disturbance and a macrofauna that is often dominated by large suspension-feeding invertebrates with indeterminate growth, such as crabs and bivalves. We hypothesize that the physically stressful conditions and unstable sediments characteristic of those habitats could influence the scaling of population density and body size of the macrofauna relative to other intertidal communities. Our preliminary observations suggested that, for macrofauna, population density would not scale inversely with body size in sand beach and salt marsh tidal channel communities. We test that prediction by examining the relationships between population density and body size of macrofauna in samples from exposed sand beaches and from coastal salt marsh tidal channels.

METHODS

Study Locations

Samples of sand beach communities were collected on Santa Rosa Island, located 42 kilometers off the California mainland coast (Figure 1). The island is owned by the National Park Service and has extensive sand beaches with minimal human disturbance. We sampled eight sand beaches representing different orientations to prevailing currents, winds and swell as shown in Figure 1. In terms of wave energy regime, all beaches sampled were intermediate with respect to morphodynamic type with Dean's parameter values between 1.8 and 4.1 (*sensu* McLachlan, 1990). Sand beach sampling was conducted primarily in the spring and early summer (May–July) of 1988 and 1989. Two beaches were sampled in October of 1988 (Abalone Rocks and Sandy Point).

Samples of salt marsh tidal channel communities were collected in Carpinteria Salt Marsh, a University of California Natural Reserve with limited public access (Figure 1). Salt marsh tidal channels were sampled in February and October of 1991 at two locations.

Sampling Methods

At the sand beach sites, randomly selected vertical transects which extended across the intertidal gradient from the lower limit of terrestrial vegetation to −0.5 m tidal height were sampled with cores on spring low tides. At five of the sand beach sites, ten transects were sampled with cores (100 mm diameter, 100 mm depth) taken at uniform intervals of 0.5 to 2 meters depending on the beach width. At three of the sand beach sites, four transects were samped with cores (3 of 100 mm diameter, 135 mm depth) in a modified stratified random design (Straughan, 1982). All core sediments were passed through a sieve of 1.5 mm mesh, a sieve size commonly used in studies of macrofauna on exposed sand beaches (McLachlan, 1977, 1983, 1990), which retained numbers and sizes of macrofauna that were not different from those retained by a 1 mm sieve in preliminary surveys of 3 of the beaches sampled in our study. Macrofauna were enumerated, weighed and identified to species. The three species of talitrid amphipods, *Megalorchestia* spp., present were identified to genus only for this analysis. Animals were blotted to remove excess water and weighed to the nearest 0.0001 g. Densities of macrofauna were calculated as the mean number of individuals per vertical meter strip of beach as suggested for beach macrofauna by Brown and McLachlan (1990). (To convert densities given per meter strip of beach to square meters, divide the per meter density by the intertidal width as follows for each sampling site: Becher's Pier 33 m, Water Canyon 57 m, Southeast Anchorage 45 m, Abalone Rocks 47 m, Ford Point 38 m, China Camp 65 m, West Bee Rock 81 m and Sandy Point 84 m.)

At salt marsh tidal channel sites, five randomly selected transects were sampled with cores (100 mm diameter, 500 mm depth) taken every 0.5 meter of tidal height from the lower edge of marsh vegetation to the bottom of the channel during low tides. All core sediments were passed through a 1.0 mm sieve as suggested by Pacific Estuarine Research Laboratory (1990) for macrofauna studies in California coastal salt marshes. Macrofauna were treated as above. Densities of macrofauna were calculated per square meter of surface area.

Data Analysis

We examined a linear model of body size density scaling by plotting log transformed (base 10) mean population density as a function of log transformed mean wet weight for each species and calculating ordinary least squares regressions (OLS) for each sample. Composite OLS regressions were calculated using the average densities and body weights of each species at the sites where they occurred for each of the communities.

RESULTS

Sand beach macrofauna densities and body sizes ranged over three and five orders of magnitude respectively. A total of 46 species occurred in the sand beach samples (Table 1). The number of species per sample ranged from 5 to 22 for the sand beaches.

Salt marsh tidal channel macrofauna densities and body sizes ranged over two and four orders of magnitude respectively. A total of 16 species occurred in the salt marsh samples (Table 1). The number of species per sample ranged from 9 to 16 for the salt marsh tidal channels.

The sand beach macrofauna samples were dominated by crustaceans (Figure 2a), primarily the suspension-feeding hippid crab, *Emerita analoga*, which occurred at all eight beaches at average densities ranging from 433 to 52,300 crabs m^{-1}. Two other crustaceans occurred on all eight beaches in high abundances, the scavenging isopod, *Excirolana chiltoni* (1,250 to 8,060 individuals m^{-1}) and the kelp-feeding talitrid amphipod *Megalorchestia* spp. (42 to 23,400 individuals m^{-1}).

The salt marsh tidal channel samples were dominated by mollusks (Figure 2b), primarily suspension-feeding bivalves, *Tagelus californianus* (47 to 123 m^{-2}), *Protothaca staminea* (4 to 102 clams m^{-2}) and *Cryptomya californica* (9 to 175 m^{-2}), and the gastropod, *Cerithidea californica* (80 to 276 m^{-2}).

Table 1. *OLS regressions of log body size on log population density of intertidal macrofauna samples from sand beaches on Santa Rosa Island and salt marsh tidal channels in Carpinteria Salt Marsh. (* $p < 0.05$, ** $p < 0.01$).*

Location	Date	Slope	Std. Error	Intercept	Correlation Coefficient	Number of species
Sand beach						
Becher's Pier	5/7/88	0.52	0.17	3.06	0.60**	18
Water Canyon	5/24/89	0.34	0.63	2.41	0.20	9
Southeast Anchorage	5/8/88	0.21	0.15	2.37	0.30	22
Abalone Rocks	10/26/88	0.15	0.15	1.96	0.22	22
Ford Point	5/6/88	0.36	1.24	2.45	0.17	5
China Camp	5/23/89	0.04	0.29	2.31	0.05	9
West Bee Rock	7/19/89	0.27	0.18	2.73	0..35	17
Sandy Point	10/25/88	0.20	0.25	2.96	0.19	19
Composite of beaches		0.09	0.10	2.20	0.14	46
Salt marsh tidal channel						
Main channel	2/6/91	0.26	0.28	1.44	0.33	9
	10/18/91	0.21	0.11	1.36	0.46	16
Composite	Feb/Oct.	0.18	0.09	1.25	0.44	17
Apple Street Creek	2/6/91	0.19	0.37	1.34	0.19	9

Rare macrofauna species occurred at all body sizes in both community types. The largest species were not the rarest species. The largest species in the sand beach samples was the spiny sand crab, *Blepharipoda occidentalis*, weighing an average of 18.4 g and occurring in average densities ranging from 12 to 307 crabs m ^{1}. The smallest species in the beach samples were the beetle, *Neochthebius vandykei*, and the amphipod, *Mandibulophoxus gilesi*, both weighing 0.0002 g and occur-

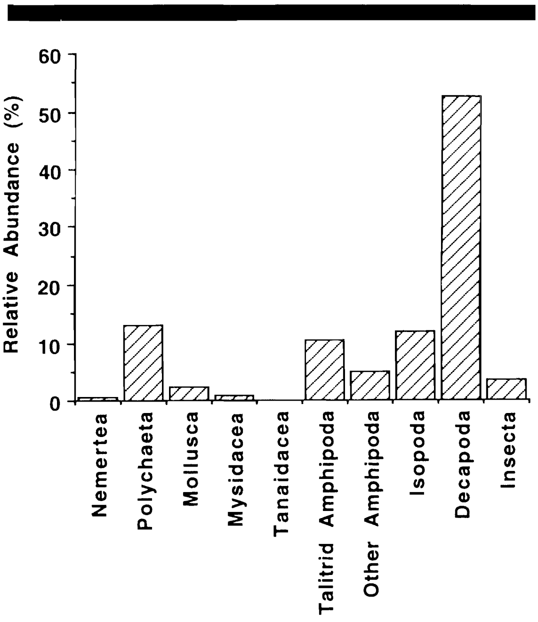

Figure 2a. Relative abundances of macrofauna taxa in sand beach samples.

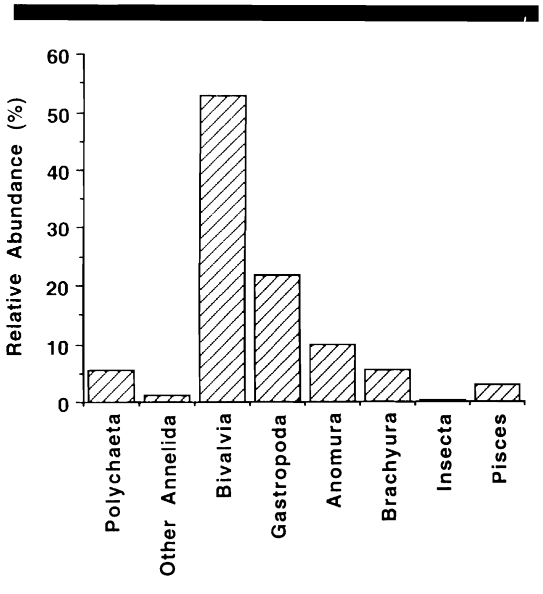

Figure 2b. Relative abundances of macrofauna taxa in salt marsh tidal channel samples.

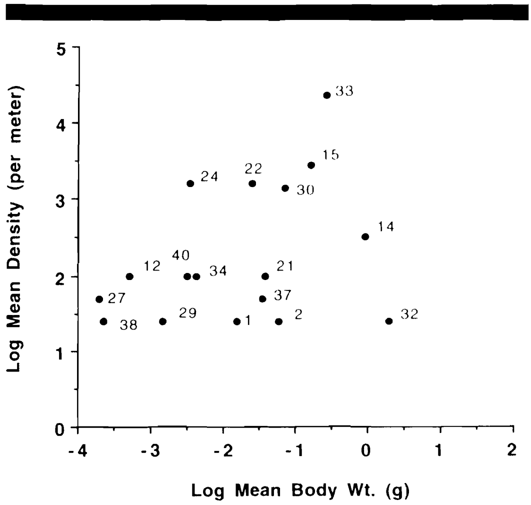

Figure 3. Plot of log transformed population density on log transformed body size for sandy intertidal macrofauna from the West Bee Rock sample. Points represent the average density per meter and body size for each species. Numbers next to points correspond to the species list given in the legend for Figure 5.

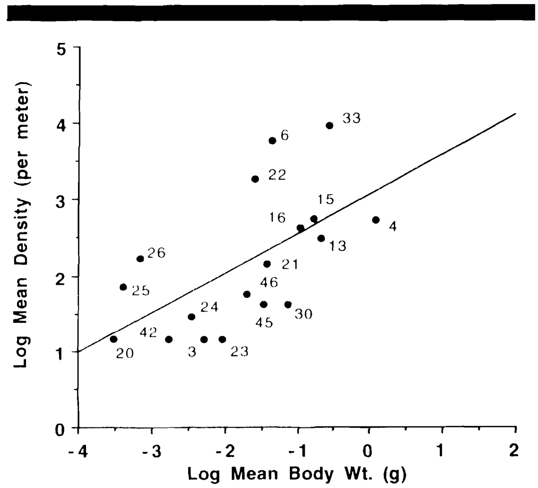

Figure 4. Plot of log transformed population density on log transformed body size for sandy intertidal macrofauna from the Becher's Pier sample with ordinary least squares regression fitted to points. Points represent the average density per meter and body size for each species. Numbers next to points correspond to the species list given in the legend for Figure 5.

ring at average densities of 25, and 25 to 500 individuals m^{-1} respectively. In the salt marsh samples, the largest species was the California jackknife clam, *Tagelus californianus* weighing an average of 12.9 g (densities above). The smallest salt marsh species was a spionid polychaete weighing an average of 0.002 g that occurred at an average density of 15 individuals m^{-2}.

We found no evidence of inverse relationships between mean population density and mean body size in our samples from sand beach and salt marsh tidal channel macrofauna communities. For the individual beach samples, the slopes of the relationships between body size and population density were generally not significant and positive (Table 1; Figures 3 and 4). A significant positive relationship between population density and body size occurred in one sample, Becher's Pier (Table 1, Figure 4). The only sample with a negative relationship (not significant) was Ford Point, a depauperate south-facing beach where only five species occurred in the sample (Table 1). When data for all eight beaches were averaged and combined, there was a nonsignificant positive relationship between population density and body size (Table 1, Figure 5). The salt marsh tidal channel samples yielded similar patterns (Table 1, Figure 6); all relationships were nonsignificant and positive.

Using the eight beach samples in Table 1, we examined the probability of finding generally positive slopes between population density and body size in soft sediments with a binomial test. For any one sample from a random distribution, the probability of finding a positive slope by chance is 0.5. For the beach samples, 7 out of 8 samples had a positive slope (one-tailed test, $p = 0.0352$).

DISCUSSION

A broadly applicable ecological pattern of inverse scaling between population density and body size in marine communities is not supported by our results from soft-sediment intertidal macrofauna communities. We found no evidence of an inverse relationship between population density and body size for a range of up to three orders of magnitude in population density and five orders of magnitude in body size for macrofauna communities from sand beaches with a variety of exposures and wave energy regimes and from salt marsh tidal channels at different seasons and locations. Our results indicated a generally positive relationship between population density and body size of macrofauna in soft-sediment intertidal

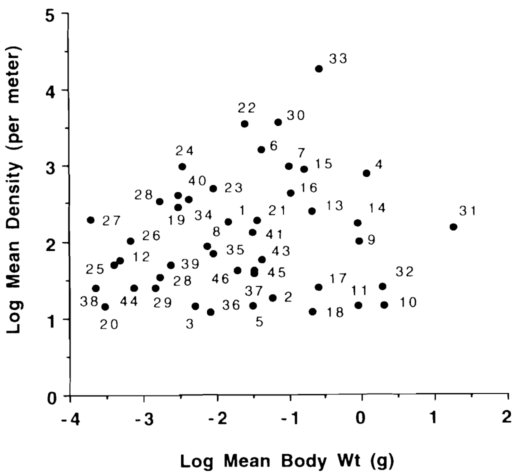

Figure 5. Composite plot of log transformed population density on log transformed body size for sandy intertidal macrofauna. Points represent the average density per meter and body size for each species, for pooled data from the eight beach samples. Numbers next to points correspond to the following species list. The number of samples in which a species occurred is given by the number in parentheses following the species name. 1. *Carinoma mutabilis* (3). 2. *Paranemertes californica* (5). 3. *Caecum crebicinctum* (2). 4. *Olivella biplicata* (3). 5. *Mysella pedroana* (1). 6. *Scololepis squamata* (4). 7. *Scoloplos nr. armiger* (1). 8. *Dispio uncinata* (1). 9. *Cirriformia spirabrancha* (1). 10. *Sthenelais berkeleyi* (1). 11. *Naineris dendritica* (1). 12. *Paraonella platybranchia* (2). 13. *Lumbrinereis zonata* (5). 14. *Nephtys californiensis* (6). 15. *Euzonus mucronata* (5). 16. *Euzonus dillonensis* (1). 17. *Polychaeta* species A (1). 18. *Polychaeta* species B (1). 19. *Archeomysis grebnitzkii* (3). 20. *Zeuxo paranormani* (1). 21. *Alloniscus perconvexus* (5). 22. *Excirolana chiltoni* (8). 23. *Exosphaeroma inornata* (2). 24. *Eohaustorius washingtonianus* (4). 25. *Hyale frequens* (2). 26. *Synchelidium shoemakeri* (4). 27. *Mandibulophoxus gilesi* (3). 28. *Paraphoxus milleri* (1). 29. *Rhepoxynius abronius* (1). 30. *Megalorchestia* spp. (8). 31. *Blepharipoda occidentalis* (3). 32. *Lepidopa californica* (1). 33. *Emerita analoga* (8). 34. *Coelopa vanduzei* (3). 35. *Dyschirius marinus* (1). 36. *Phalaria rotundata* (1). 37. *Neopachylopus sulcifrons* (1). 38. *Neochthobius vandykei* (1). 39. *Cercyon luniger* (1). 40. *Bledius fenyesi* (2). 41. *Cafius canscens* (2). 42. *Pontomalota opaca* (3). 43. *Thinopinus pictus* (2). 44. *Carpelimus* sp. (1). 45. *Emplenota arenaria* (1). 46. *Emphyastes fucicola* (2).

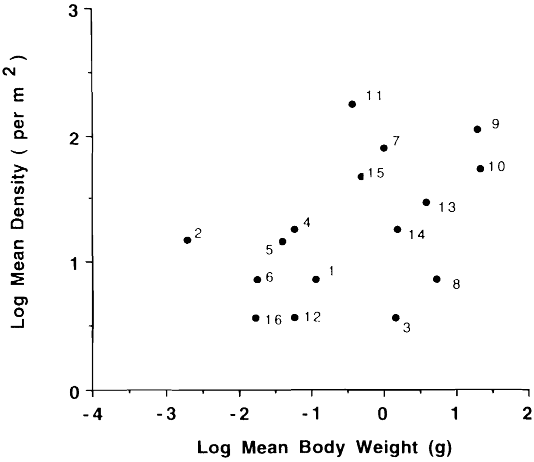

Figure 6. Plot of log transformed population density on log transformed body size for salt marsh tidal channel macrofauna sample at the main channel site in October. Points represent the average density per square meter and body size for each species. Numbers next to points correspond to the following species list: 1. Platyhelminthes sp. 2. Spionidae sp. A. 3. *Nephtys californianus*. 4. *Glycera americana*. 5. *Capitella capitata*. 6. Oligochaeta species A. 7. *Cerithidea californica*. 8. *Macoma nasuta*. 9. *Tagelus californianus*. 10. *Protothaca staminea*. 11. *Cryptomya californica*. 12. *Ione* sp. 13. *Upogebia pugettensis*. 14. *Callianassa californiensis*. 15. *Hemigrapsus oregonensis*. 16. Diptera sp.

communities and are in contrast to those of MARQUET *et al.* (1990) who reported an inverse relationship for marine rocky intertidal macrofauna communities over similar body size ranges. Our results also contrast with those reported in terrestrial communities and local ecological assemblages where weak negative relationships between body size and population abundance are considered typical (*e.g.*, BLACKBURN *et al.*, 1993a). Differences between our results and those of other workers may be related to a number of factors associated with soft-sediment intertidal marine habitats and macrofauna community structure.

Biotic interactions, such as competition for limiting resources, including space and food, and predation are believed to have a dominant role in structuring many terrestrial and marine communities, including the rocky intertidal (*e.g.*, CONNELL, 1961; PAINE, 1974). Those biotic interactions, in particular interspecific competition for limiting resources, have been proposed as potential causes of the inverse scaling of population density with body size in some assemblages, guilds and natural communities by a number of workers (DAMUTH, 1981, 1987, 1991; PETERS and WASSENBERG, 1983; MARQUET *et al.*, 1990; LAWTON, 1991; COTGREAVE, 1993). That pattern and the postulated biotic interactions underlying it have been attributed to the scaling of metabolic rates with body mass (DAMUTH, 1987). However, the effects of biotic interactions and metabolic constraints on relationships between population density and body size have not been clearly demonstrated in natural communities (see MARQUET *et al.*, 1990) or other ecological or taxonomic assemblages (BLACKBURN *et al.*, 1993b).

In soft-sediment intertidal and other physically controlled communities, physical processes may play a relatively more important role than biotic interactions in community structure; such communities may be structured more by individual species responding to the physical environment rather than to each other (SANDERS, 1968; NOY-MEIR, 1979; BROWN and MCLACHLAN, 1990; MCLACHLAN, 1990). The degree to which sand beach and salt marsh tidal channel communities are structured by physical factors could thus contribute to the differences between our results and those of other workers with respect to the scaling of population density and body size. In support of that idea, MCLACHLAN (1990) found that, in general for sand beach macrofauna communities, species diversity decreases, abundance decreases and overall biomass increases with increasing wave energy and the associated changes in physical parameters such as beach morphology and sediment grain size. Similarly, in salt marsh infaunal communities, exclusion of predators did not result in competitive exclusion by dominant species or declines in species diversity (PETERSON, 1979), and relatively weak interspecific interactions may prevail (WILSON, 1991).

Sand beach and salt marsh tidal channel community structure may reflect disturbance regimes more than biotic interactions. Intertidal sand beach and salt marsh tidal channel habitats are subject to relatively frequent and extreme disturbances in the form of heavy surf or storm runoff events. In two southern California marshes, significant changes in benthic species assemblages were related to disturbances, such as siltation, reduction of tidal flushing, and increased fresh and wastewater input (NORDBY and ZEDLER, 1991). Disturbance may maintain macrofauna populations at densities below the carrying capacity of the soft-sediment habitats we examined, contributing to a reduced intensity of competitive interactions and to the lack of an inverse relationship between density and body size.

The nature of limiting resources differs between soft-sediment and rocky intertidal habitats and may influence relationships between density and body size. Space may not be an important limiting resource in intertidal soft sediments where the usable space for infaunal macrofauna is three-dimensional in nature and may not be saturated (PETERSON, 1979; BROWN and MCLACHLAN, 1990). In addition, soft-sediment macrofauna may have little influence on food resources which may be primarily delivered by wave wash or tidal flux from largely allocthonous sources. Relatively large suspension-feeding species, such as hippid crabs and bivalves, were the most abundant macrofauna forms in the soft-sediment communities we examined. Suspension-feeding species of all sizes occur in rocky intertidal habitats; however, in that habitat, space is an important limiting resource for sessile macrofauna communities (DAYTON, 1971). Although the range of macrofauna densities in our study overlapped those found by MARQUET *et al.* (1990) in the rocky intertidal, sand beach and salt marsh tidal channel macrofauna may occur in densities lower than those in which space and food are limiting. This combination of the lack of space and community influence on sources of primary production may reduce the intensity of competitive interactions for resources, allow species of larger sizes to attain relatively higher densities, and influence community structure and body size scaling in the soft-sediment habitats we examined.

Large body size may confer relatively greater survival value in sedimentary intertidal habitats than in the rocky intertidal and alter the relative abundances of larger animals in soft-sediment communities. Small sessile animals were prevalent in the rocky intertidal study (MARQUET *et al.*, 1990). In that habitat, large size may be relatively less advantageous because of the effects of wave-generated hydrodynamic forces on sessile forms (DENNY *et al.*, 1985). In conditons of shifting soft sediments, erosion and wave impact, large size may allow burrowing infaunal animals such as clams and crabs to better maintain position in the intertidal. Greater mobility of active forms is related to larger size which may be advantageous in avoiding predation (BROWN and MAURER, 1986) and in burrowing. In shifting sediments, particularly in coarser sands, larger macrofauna species may have enhanced burrowing ability relative to smaller species or those of a size close to the sediment pore size (SCHWINGHAMER, 1983, 1985). MCLACHLAN'S (1990) results of increasing average individual size with increasingly reflective wave energy regime and increasing sediment grain size in sand beach macrofauna communities indicates that average size may vary predictably, relative to the energy regime and sediment characteristics of a soft-sediment habitat and supports the concept of an advantage in larger size for animals inhabiting disturbed soft sediments.

In soft-sediment intertidal habitats, characteristics associated with particular taxa may confer greater survival value and alter the relative abundances of those forms. The dominant taxa in our study were forms with rigid exoskeletons such as highly mobile crustaceans on sand beaches and heavy-shelled bivalve and gastropod mollusks in the salt marsh tidal channels. Such forms may survive disturbance events and resist abrasion in unstable sediments more successfully than soft-bodied forms. In support of this idea, crustaceans are generally more abundant than mollusks or polychaetes on exposed sand beaches with higher wave energy and are relatively less abundant on more protected beaches (McLachlan, 1983).

CONCLUSIONS

Given the results of the present study and others (see Cotgreave, 1993), the search for an "ecological scaling rule" of population density and body size in marine and terrestrial communities is not over. In intertidal marine macrofauna communities in soft sediments, a combination of factors including the dominant role of physical processes and disturbance events in structuring communities, the nature of limiting resources and the survival advantage conferred by large size and hard exoskeletons may contribute to the lack of inverse relationships between population density and body size found in our study. Our results from sand beach and salt marsh macrofauna communities do not lead us to reject hypotheses that community level biotic processes could cause the inverse relationships between population density and body size reported for some natural communities and on larger geographic scales. Our work implies, however, that different types of natural communities may be structured in varied and potentially predictable ways with respect to population density and body size scaling. Tests of such predictions in other marine and terrestrial communities could lead to a greater understanding of the relative influence of ongoing ecological and physical processes, as well as those occurring on evolutionary time scales, upon population density and body size scaling in natural communities.

ACKNOWLEDGEMENTS

We gratefully acknowledge the laboratory and field assistance of C. Soiseth, D. Forcucci, M. Hewell, K. Lafferty, and W. James. We thank J. Damuth, K. Lafferty, and A. Wenner and two anonymous reviewers for comments on the project and R. Kropp, S. Williams, R. Orth, and L. Bousfield for assistance with species identifications. This study was supported in part by Channel Island National Park (Santa Rosa Island sand beaches) and the University of California Natural Reserve System (Carpinteria Salt Marsh).

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