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Benthic invertebrate communities in Golfo Dulce, Costa Rica, an anoxic basin*

by

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Abstract: Numerical abundance, biomass, and species diversity were determined for the benthic invertebrate communities of Golfo Dulce, an anoxic basin on the west coast of Costa Rica. Both abundance and biomass were less than that expected in a tropical environment. The polychaete *Paraonis lyra* dominated the community within the basin. It is suggested that a life history which includes pelagic larvae allows this species to dominate the benthic assemblage in regions of variable oxygen concentrations.

The term community has been applied to any assemblage of organisms living in a prescribed area or physical habitat (**Odum,** 1959). **Mills** (1969) defined a community as a group of organisms occurring in a particular environment, presumably interacting with each other in the environment and separable, by means of an ecological survey, from other groups. Parameters such as diversity, numerical abundance, and biomass of individuals are used to describe community structure. The structure of benthic communities is dependent upon such biological factors as competition, predation, commensalism, and parasitism as well as physical parameters of light, substrate, temperature and salinity. The purpose of this study was to explore the effect of low oxygen content in bottom water on the benthos community structure.

Gallardo (1963) found that low standing crops of macrofauna corresponded with oxygen concentrations less than 0.5 ml/l off the north coast of Chile. In the oxygen minimum region off Peru the benthos has low species diversity (**Frankenberg** and **Menzies,** 1968). They suggested that the proliferation of those species which tolerated low oxygen concentration was due to the abundance of food in the sediments. **Nichols-Driscoll** (in press) reported that when low-oxygen conditions were stable a diverse benthic community developed.

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Golfo Dulce is an anoxic basin that intermittently receives oxygen enriching water. As such it provides an opportunity to study invertebrate community relationships in a region of intermittent low-oxygen stress. The gulf lies between 8°27' and 8°45'N latitude on the western coast of Costa Rica (Fig. 1). It is approximately 20 km in length, has a sill depth of 64 meters, and a maximum depth of 200 m. **Richards, Anderson** and **Cline** (1971) have recorded hydrogen sulphide concentrations of 5 μg atoms/liter in the bottom water of the basin. They reported that the basin receives boluses of new water at intermittent intervals and postulated that internal wave activity and coastal upwelling combine to introduce, at the sill, water denser than that at intermediate depths. The water flows north towards the head of the gulf, sinking as it progresses and enriching the oxygen content of the bottom water.

METHODS

All samples were obtained during cruise number 76 of R/V *T. G. Thompson.* Two bottom grab samples were obtained with a 0.1 m^2 van Veen grab at each station. On board ship the samples were sieved through a 0.42 mm mesh screen and fixed with 10% formalin in seawater buffered with borax. Upon return to the laboratory the samples were again sieved through 0.42 mm mesh screen and sorted with a dissecting microscope. After sorting, the animals were stored in 80% alcohol. Animals were identified to species; fragments of polychaetes were identified to family. Nematodes and oligochaetes were not included in diversity calculations since they were not identified to species. Wet weights of the preserved animals were obtained by blotting each animal on a paper towel for three minutes before weighing on a Mettler microbalance. Organic carbon and nitrogen content of the sediments was determined with a Perkin Elmer Elemental Analyzer, after acid removal of carbonate. Oxygen content of bottom water was determined by Winkler titration.

Species diversity was determined with the Shannon-Wiener Information Function (**Shannon** and **Weaver,** 1963):

$$H(s) = -\Sigma p_r \ln p_r,$$

where s = total number of species and p_r = observed proportion of individuals that belong to the r^{th} species (r = 1,2 , ... , s).

RESULTS

Oxygen content of sill bottom water was 1.65 ml/1; at stations below sill depth, 64 m, where the benthos was sampled, bottom water oxygen content was less than 1.0 ml/1. In the deepest section of the basin the bottom water oxygen decreased from 0.07 ml/1 at station 3 to undetectable at station 1. Outside the basin (station 12) bottom water contained 0.63 ml O_2/1 (Fig. 1).

Table 1 lists the percent organic content of the surface sediments. Carbon content was around 2% by weight throughout the basin. Carbon/nitrogen ratio was highest (9) at the sill; both carbon and nitrogen contents were lower (0.36 and 0.04 percent, respectively) than at any other station in the gulf. The low C/N ratios indicate that there had been little reworking of sediments by the benthos. However, there was no correlation between animal distribution and organic content of the surface sediments.

TABLE 1

Percent organic content of surface sediment by weight

Station No.	%N	%C	C/N
1	0.28	1.80	6.49
2	0.22	2.14	5.18
3	0.27	2.17	8.03
7	0.40	2.05	5.12
11	0.04	0.36	9.00
89	0.18	1.58	8.33

Bottom photographs show the sill to have well developed ripple marks and scouring around rocks. Urchins appear in sill photos along with several light-colored vermiform organisms. Photographs taken at station 6 show large leaves and coconuts on a smooth mud bottom with no evidence of animal life. At station 89 the bottom water was murky; however, a smooth, probably azoic bottom, was discernible.

Live animals were found in grab samples at all stations within the basin shallower than 100 m (a species list is contained in the Appendix). At depths greater than 100 m the samples were either azoic or contained one or two individuals of the amphipod genus *Erichthonius* (Table 2). Samples from station 7 (70 m) contained a total of twenty-seven polychaete species. *Paraonis lyra* was the numerically dominant species in both samples. The decapods, *Beteaus* sp. and Carcinoplacinid *Pilumnoplax americana* composed the dominant portion of the total biomass at the station. At station 11, located on the sill, samples contained specimens representing eleven orders. A caprellid amphipod, (cf.) *Petrotripus brevis* was the numerically dominant species in both samples. Vertebrates and hemichordates were represented by single individuals of *Conger congrus* and *Phoronis* sp. Polychaetes were represented by twenty-five species, amphipods by six species, pelecypods by two and nemerteans and nematodes each had one representative. At the same depth within the embayment, station 95, there were seven polychaete, two pelecypod, two amphipod and one cumacea species represented. The numerically dominant species in sample A was the polychaete *Paraonis lyra.* In sample B numerical dominance was shared by three species of polychaetes, a spionid, the pilargid *Sigambra tentaculata,* and lumbrinereid *Ninoe* sp. Amphipods were represented by single individuals of the species *Corophium bonelli* and *Erichthonius* sp. *Nucula schencki* and *Adrana* sp. were also represented by single specimens. The cumacean *Eudorella* sp. was represented by two individuals. There were eight species outside the basin at station 12 (200 m). Nematodes, represented by four individuals, were numerically dominant. The polychaete *Pareulepis* sp. contributed the largest amount of biomass with a single individual of 12.2 mg. The amphipod *Ericthonius* sp. was again represented by one individual as was the cumacean *Eudorella* sp.

Table 2 contains diversity (H [s]) values for all samples containing more than one species. Biomass diversity values include polychaete fragments identified to family. The inclusion of fragments caused little variation in the calculated values.

Diversity values within the basin fell into the narrow range of 1.3 to 1.8. These values are low based on what would be expected from published data on marine benthos (**Sanders,** 1968), as are the values from the one station outside the basin. Values of 2.877 and 2.401 for the sill station are low for a nonstressed tropical environment.

TABLE 2

Number of species, individuals, and total biomass for each grab sample. Diversity (H [s]) based on numbers of species and biomass of species for all samples containing more than one species

Sample No.	Depth (m)	No. of species	No. of Individuals	Total Biomass (mg)	H (s) Numbers	H (s) Biomass
1 a & b	192	0	0	0.0		
2 a & b	182	0	0	0.0		
3 a	190	1	2	5.9		
3 b	190	1	1	1.3		
4 a & b	201	0	0	0.0		
5 a	189	1	2	11.3		
5 b	189	0	0	0.0		
6 a & b	143	0	0	0.0		
7 a	70	24	924	789.5	1.599	1.033
7 b	70	15	348	1,707.2	1.624	1.067
11 a	64	29	140	4,638.4	2.877	0.352
11 b	64	18	65	113.8	2.401	2.178
12 a	254	7	13	31.2	1.778	1.494
12 b	254	2	2	2.4	0.693	1.677
89 a	134	0	0	0.0		
89 b	134	1	1	0.1		
93 a & b	134	0	0	0.1		
94 a	105	0	0	0.0		
94 b	105	1	1	0.4		
95 a	64	8	32	137.4	1.377	1.035
95 b	64	7	15	111.3	1.807	1.156

Another parameter that describes a community is the distribution of biomass. At all stations within the basin (with more than one species present) and the sill station, the average individual biomass of the numerically dominant species was within the range 0.12-0.17 mg/ind. At station 12, outside the basin, a polychaete *Glycinde armigera,* was the numerically dominant species and had an average individual biomass of 1.3 mg. A few individuals representing larger species occurred at all stations. However, at stations where the bottom-water oxygen content was less than 1.0 ml/1 dominant individuals were motile species such as the amphipod *Ericthonius* and the shrimp *Beteaus* sp. Only the sill and station 95 (62 m) samples contained sedentary organisms, such as bivalves.

DISCUSSION

The small number of individuals contained within each sample does not allow definitive conclusions concerning diversity of the benthic community in Golfo

Dulce. However, a tendency toward decreased diversity of the benthic assemblages within the basin is indicated. Decreased diversity associated with decreased oxygen concentration is not surprising. Of interest is the organisms, living and dead, found at station 7. Large numbers (4 liters in volume) of empty mollusc shells, both gastropods and pelecypods, and living shrimps and carcinoplacinid crabs were found in both samples. The slope of the bottom is not steep in the region of this particular station, so it is unlikely that the shells were transported down slope from another area. A more plausible explanation is that the mollusc shells and decapods are remains of a previous community that existed when the oxygen concentration was higher. As the oxygen supply decreased various components of the community migrated or died until a few species, capable of reproducing in the stressed environment, dominated the existing community.

When the physical environment fluctuates severely with time, one theory suggests that significant biological interactions do not develop and community structure is dictated by physical factors (Sanders, 1968). Animals living in a physically controlled community tend to have high reproductive rates and rapid development. Pianka (1971) has suggested an r-K continuum. The r-end is a physically controlled community where no competition for energy sources exists and the optimal strategy is to use available energy to maintain a high reproductive rate. This is done by maintenance of small bodies, early reproduction and short life span.

The small number of species per sample makes definite conclusions difficult, but it appears that the postulated intermittent flushing occuring in Golfo Dulce probably causes a fluctuating oxygen concentration that is the primary physical factor controlling the benthos community structure. The result is a community dominated by r-regulated species. The numerically dominant species *Paraonis lyra* is a small (average 0.1 mg/ind.) polychaete. Its distribution is widespread even though its small size causes it to be easily missed during sieving and sorting. Paraonidae are known to produce pelagic larvae (Pettibone, 1963) but the life history of *P. lyra* is not known. Due to its small size *P. lyra* is probably capable of efficient cutaneous respiration as well as respiring through gills. Such respiratory mechanisms would allow a minimal expenditure of energy for the exchange of oxygen in a region of low-oxygen concentration. These characteristics of small size and efficient energy utilization locate it more towards the r-end of Pianka's continuum than species found outside of the basin.

In response to a variable oxygen supply in the bottom water the benthic community structure of Golfo Dulce is composed of very small-bodied organisms and heavily dominated by *Paraonis lyra.* Apparently, a life history which allows repeated recolonization has enabled this polychaete species to survive in regions of unpredictable and low oxygen concentrations.

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RESUMEN

Se determinó la cantidad, la biomasa y la diversidad de especies de las comunidades bénticas de invertebrados del Golfo Dulce, un estuario tropical de fondo anóxico en la costa sudoeste de Costa Rica. Tanto la cantidad como la biomasa fueron menores de lo que se puede esperar en un ambiente tropical. El poliqueto *Paraonis lyra* fue el organismo dominante dentro del golfo. Se cree que por poseer la especie una etapa larval pelágica, le permite dominar las comunidades bénticas en regiones de concentraciones variables de oxígeno.

APPENDIX

Species List: Animals were identified with the aid of published keys and species descriptions. As the intent of this study was to determine the different types of species occurring in an area, letter designations were used to denote different species when the author could not be confident of specific identifications from the information available. Even when species names were given, no zoogeographic interpretations were intended and none should be assumed. The samples are preserved in alcohol and are available to those wishing to pursue zoogeographic studies.

Species data are presented in the following format:

Station No.	1	1
Grab	A	B
Species		X
name		Y
Species		
name		

X = number of individuals present in 0.1 m^2 sample

Y = biomass (wet weight, mg) of individuals present in van Veen grab sample

Blocks with biomass values and no numbers are fragments of the family found in the sample.

Station No.	1	1	2	2	3	3	4	4	5	5	6	6	7	7	11	11	12	12	89	89	93	93	94	94	95	95
Grab letter	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Coelenterata Anemone															2 4.6											
Nematoda													12		2	1	4									
Nemertea Nemertean														2	2 19.8											
Oligochaeta													4													
Sipunculida														2 0.2												
Pareulepidae *Pareulepis* sp.																	1 12. 2									
Phyllodocidae *Eteone* sp.													4 0.4													
Pilangidae *Sigambra* *tentaculata*															4 1.0											3 0.9
Syllidae *Exogone* sp.													4 0.4													
Nereidae *Ceratonereis* sp.																1 11.7										

Station	1	1	2	2	3	3	4	4	5	5	6	6	7	7	11	11	12	12	89	89	93	93	94	94	95	95
Grab letter	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Nereidae *Nereis* sp.													12 17.6	1.2	2 1.0		1 7.6									
Nephtyidae *Nephtys* sp.																									2 304	2 9.3
Goniadidae *Glyeinde* *armigera*															6 7.6	8 13.2	3 4.0	1 1.4								
Onuphidae *Onuphis* sp.													8 1.2	29.0		2 5.5										
Eunicidae *Eunice* *shemacephala*													5.0	6 13.0												
Lumbrineridae *Angeneria* sp.													4 76.4													
Lumbrineris *acuta*																4 1.5										
Lumbrineris *inflata*													64 14.0		8 3.2	1 0.4										
Lumbrineris *latreilli*																5 14.9										
Lumbrineris *moorei*															8 0.6											

Station No.	1	1	2	2	3	3	4	4	5	5	6	6	7	7	11	11	12	12	89	89	93	93	94	94	95	95
Grab Letter	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Lumbrineris zonata														44 10.6												
Ninoe fusca															2 0.2											
Ninoe gemma																1 0.4										
Ninoe sp. a													4 0.4													
Ninoe sp. b													4 0.4													
Lumbrineridae fragments												92.4	1.2	0.2		3.3										
Arabellidae *Arabellida* sp.													2.4	0.2											2 8 7	
Arabellidae c.f. *Notocirrus californiensis*																	2 0.1									
Dorvilleidae													4 0.4													
Questidae													4													
Paraonidae *Paraonis lyra*												544 64.4	190 24.6		4 0.2										20 2.5	

Station No.	1	1	2	2	3	3	4	4	5	5	6	6	7	7	11	11	12	12	89	89	93	93	94	94	95	95
Grab letter	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Paraonidae *Paraonis* sp. a													4													
Paraonidae *Paraonis* sp. b													20 0.5													
Cirratulidae *Acrocirrus* sp.															2 1.2											
Cirratulidae *Chaetozone* sp.															2 0.2											
Cirratulidae c.f. *Tharyx* *epitoca*															4 2.8											
Cossuridae													12 2.4		4 0.6											
Flabelligeriidae *Pherusa* sp.														6 62.6	2 1.0		5.4									
Capitellidae *Meidomastus* sp.															4 16.2											
Maldanidae fragments													6.4			10.5										
Ampharetidae fragments															35.0											

Station No.	1	1	2	2	3	3	4	4	5	5	6	6	7	7	11	11	12	12	89	89	93	93	94	94	95	95
Grab letter	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Terebellidae *Polycerine* sp.													4 0.4													
Sabellariidae *Sabellida* sp.													4 0.8	2 119												
Cirratulidae *Cirratulus cirratus*													57.2	2 42.6	24	4.6		0.3							1.6	
Cirratulidae *Cirratulus* sp. a													48 4.0		4 3.4	4 2.1										
Cirratulidae *Cirratulus* sp. b													16 0.8													
Cirratulidae *Cirriforma spirabrancha*													4 0.4													
Cirratulidae *Tharyx marconi*															4 198.2											
Cirratulidae *Tharyx monilaris*																2 1.2										
Cirratulidae *Tharyx multifilis*													116 10.8	56 8.6		1 26.8										
Spionidae *Pygospio* sp.															4 0.2											

Station No.	1	1	2	2	3	3	4	4	5	5	6	6	7	7	11	11	12	12	89	89	93	93	94	94	95	95
Grab letter	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Spionidae													1.2	2 3.2												
Spionidae													4 1.2												2 0.5	4 0.7
Spionidae *Nerinides maculata*																										
Serpulidae c.f. *Vermiliopsis multiannulata*														2 0.2												
Echinodermata Ophiuroid fragment															155.8											
Pelecypoda *Adrana* sp.																									1 3.5	
Pelecypoda *Caspidaria costata*															2 6.8											
Pelecypoda *Glycymeris* sp.															2 1.8											
Pelecypoda *Nucula schencki*																										1 51.0
Stomatopoda *Beteaus* sp.												8 520.4		4 76.8												

Station No.	1	1	2	2	3	3	4	4	5	5	6	6	7	7	11	11	12	12	89	89	93	93	94	94	95	95
Grab letter	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Cumacea Leuconidae *eudorella* sp.																	1 0.1									
Isopoda *Paranthura* *elegans*															2 15. 6	2 2.1										
Amphipoda Corophiidae *Corophium* *bonelli*																		1 0.7								1 4.4
Amphipoda *Erichthonius* sp.					2 2.9	1 1.3			2 11.3					18.6			1 1.8									1 0.5
Amphipoda Lyssianassid															4 1.2											
Amphipoda Calliopiidae																				1 0.1						
Amphipoda .*Cerapus* sp.																								1 0.3		
Amphipoda *Deutella* *californica*															2 1.2											
Amphipoda *Periotripus* *brevis*															28 3.6	20 2.6										

Station No.	1	1	2	2	3	3	4	4	5	5	6	6	7	7	11	11	12	12	89	89	93	93	94	94	95	95
Grab letter	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Amphipoda																										
Amphitoe																1										
sp.																0.1										
Amphipoda																										
Mandibulo-																										
phous																6										
sp.																6.3										
Amphipoda																3										
Talitroidea																5.1										
Decapoda																										
Callianassa															4											
major															28.4											
Decapoda																										
Carcinoplaci-														22		2										
nae														117	76	10.0										
Phoronida																										
Phoronis																1										
sp.																0.5										
Vertebrata																										
Conger															1											
congrus															41	23.5										

LITERATURE CITED

Frankenberg, D., & R. J. Menzies
1968. Some quantitavie analyses of deep-sea benthos off Peru. *Deep-Sea Res.,* 15: 623-626.

Gallardo, Ariel
1963. Notas sobre la densidad de la fauna bentónica en el sublitoral del norte de Chile. *Gayana Zool.,* 10: 3-15.

Mills, Eric. L.
1969. The community concept in marine zoology, with comments on continua and instability in some marine communities; a review. *J. Fish. Res. Bd. Canada,* 26: 1415-1428.

Nichols-Driscoll, J.
1976. The effect of stable dissolved-oxygen stress on marine benthic invertebrate community diversity. *Inter. Rev. der ges. Hydrobiol.,* (in press).

Odum, E. P.
1959. *Fundamentals of Ecology.* 2d ed. W. B Saunders Company. Philadelphia. p. 145.

Pettibone, M.
1963. *Marine Polychaete worms of the New England Region.* Smithsonian Institution Bull. 227, part 1. 354 pp.

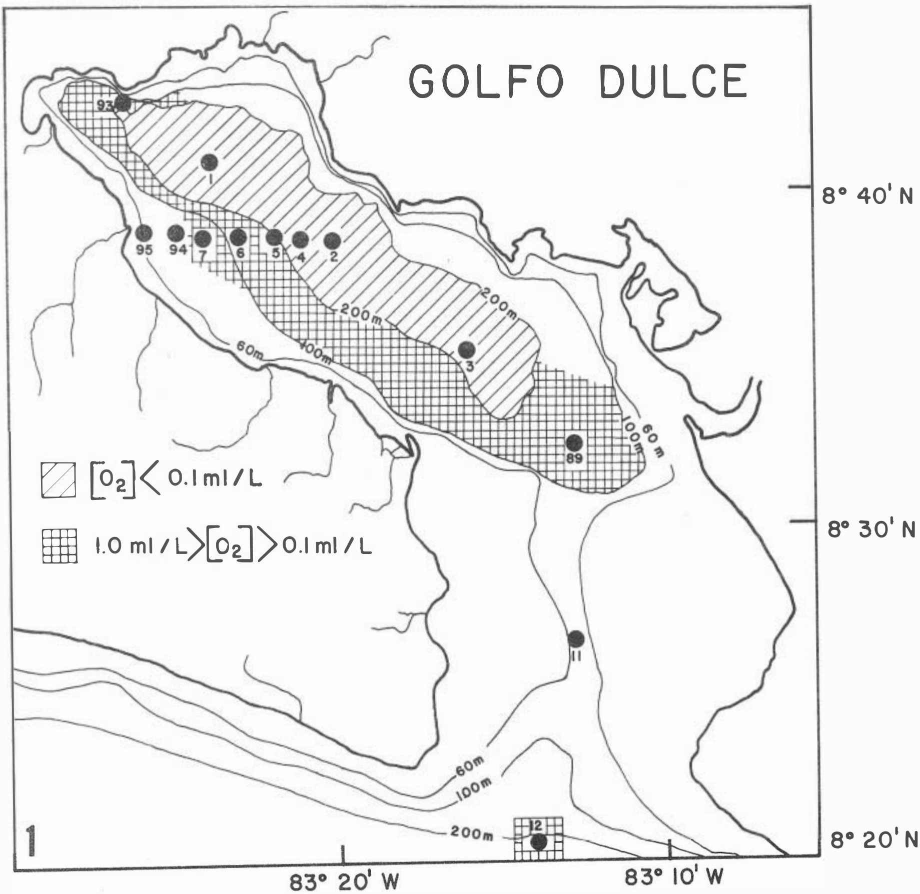
Pianka, Eric R.
1971. On r- and K-selection. *Amer. Nat.,* 104: 592-597.

Richards, F. A., J. J. Anderson, & J. D. Cline
1971. Chemical and physical observations in Golfo Dulce, an anoxic basin on the Pacific coast of Costa Rica. *Limnol. Oceanogr.,* 16: 43-50.

Sanders, H. L.
1968. Marine benthic diversity: a comparative study. *Amer. Nat.,* 102: 243-282.

Shannon, C. E., & W. Weaver
1963. *The Mathematical Theory of Communication.* Urbana, Univ. of Ill. Press. 125 pp.

Fig.1. Golfo Dulce, Costa Rica. Approximate bathymetry, station locations, and bottom water oxygen concentration. From H.O. 21562.


GOLFO DULCE
8° 40' N
8° 30' N
8° 20' N
83° 20' W
83° 10' W
[O2] < 0.1 ml / L
1.0 ml / L > [O2] > 0.1 ml / L
93
1
95
94
7
6
5
4
2
3
89
11
12
60m
100m
200m
1