

**Benthic Production and Processes off Baja California,
Northwest Africa and Peru: A classification of
benthic subsystems in upwelling ecosystems**

G. T. ROWE

Oceanographic Sciences Division, Department of Applied Science,
Brookhaven National Laboratory, Upton, New York 11973

**SIMPOSIO INTERNACIONAL SOBRE LAS AREAS DE AFLORAMIENTO
MAS IMPORTANTES DEL OESTE AFRICANO
(CABO BLANCO Y BENGUELA)**

**INSTITUTO DE INVESTIGACIONES PESQUERAS
BARCELONA, 1985**

Benthic Production and Processes off Baja California, Northwest Africa and Peru: A classification of benthic subsystems in upwelling ecosystems *

G. T. ROWE

Oceanographic Sciences Division, Department of Applied Science.
Brookhaven National Laboratory, Upton, New York 11973

Palabras clave: Bentos, áreas de afloramiento, biomasa, producción, metabolismo.

Key words: Benthos, upwelling areas, biomass, production, metabolism.

SUMMARY: Estimates of the standing stocks, secondary production and metabolism of the benthos have been compared in the coastal upwelling ecosystems off northwest Africa, Baja California, and southern Peru. Northwest Africa is characterized by shelf break upwelling and as a result standing stocks, macrobenthic production and sediment organic matter are highest out at the shelf-slope boundary. Sediment microbial activity and biomass on the other hand are highest nearshore in the dynamic zone where aeolian silt and sand are being blown into the sea from the Sahara Desert. Baja California is dominated by the red crab, *Pleuroncodes planipes*, having high rates of growth and metabolic utilization of organic matter, both on bottom and in the water. Peru benthos and metabolism are very different from the above areas because of the low oxygen concentrations in the bottom water. Organic matter is far higher in the sediment and heterotrophic metabolism is principally anaerobic rather than aerobic. A normal offshore benthic fauna is replaced by a mat of sulfur bacteria with unknown production and metabolic rates.

Benthic subsystems in upwelling ecosystems can be placed in two categories: those overloaded with organic matter, depleted of oxygen and dominated by sulfate reduction and those that are not overloaded and remain aerobic. Peru and southwest Africa typify overloaded systems whereas NW Africa and Baja California are examples of aerobic systems. Although benthic metabolism and inorganic nutrient regeneration are high in both types of subsystems, all upwelling ecosystems, with their dynamic open boundaries, export organic particulate matter and import inorganic nutrients at rates that are far in excess of that consumed or produced by benthic metabolism.

RESUMEN: PRODUCCIÓN Y PROCESOS BENTÓNICOS EN BAJA CALIFORNIA, NO DE ÁFRICA Y PERÚ: UNA CLASIFICACIÓN DE SUBSISTEMAS BENTÓNICOS EN ECOSISTEMAS DE AFLORAMIENTO. — Se han comparado estimaciones de la biomasa presente, producción secundaria y metabolismo bentónico en los ecosistemas de afloramiento costero de NO de África, Baja California y Perú meridional. El NO de África se

* This research was performed under the auspices of the United States Department of Energy under Contract No. DE-AC02-76CH00016.
By acceptance of this article, the publisher and/or recipient acknowledges the U.S. Government's right to retain a nonexclusive, royalty-free license in and to any copyright covering this paper.

caracteriza por un afloramiento de borde de la plataforma y, como resultado, la biomasa presente, la producción macrobentónica y la materia orgánica en el sedimento alcanzan los valores más elevados en la frontera entre plataforma y talud. Por otra parte, la actividad microbiana y la biomasa del sedimento tienen sus máximos cerca de la costa, en la zona dinámica en que el cieno y la arena de origen eólico son arrastrados al mar desde el desierto del Sahara. Baja California se caracteriza por el predominio del cangrejo rojo, *Pleuroncodes planipes*, que tiene unas tasas elevadas de crecimiento y de utilización metabólica de la materia orgánica, tanto del fondo como del agua. El bentos y el metabolismo del Perú son muy distintos de los de las áreas anteriores, a causa de las bajas concentraciones de oxígeno en el agua del fondo. Los valores de materia orgánica en el sedimento son mucho más elevados y el metabolismo heterotrófico es principalmente anaeróbico más que aeróbico. La fauna bentónica normal de alta mar está reemplazada por una alfombra de bacterias sulfurosas de producción y tasas metabólicas desconocidas.

Los subsistemas bentónicos en los ecosistemas de afloramiento pueden situarse en dos categorías: los sobrecargados de materia orgánica, agotados en oxígeno y dominados por la sulfatorreducción, y los que no se encuentran sobrecargados y permanecen aeróbicos. Perú y el SO de África tipifican sistemas sobrecargados, mientras que el NO de África y Baja California son ejemplos de sistemas aeróbicos. Aunque el metabolismo bentónico y la regeneración de nutrientes inorgánicos son elevados en ambos tipos de subsistemas, todos los ecosistemas de afloramiento, con sus fronteras abiertas dinámicas, exportan materia orgánica particulada e importan nutrientes inorgánicos a tasas que están muy por encima de lo consumido o producido por el metabolismo bentónico.

INTRODUCTION

In most coastal ecosystems the biota living on the bottom, or total benthos, has greater biomass than all the organisms in the water above it. It is reasonable to suspect, therefore, that the benthos is important in the functioning of the ecosystem as well as in its structure. It should receive a large fraction of the organic matter produced, use it as energy or convert it to biomass and finally release large but poorly quantified amounts of inorganic compounds, some of which are important plant nutrients, back into the water column (Fig. 1). The purpose of my work in upwelling systems has been to quantify these exchanges, to compare their relative importance in different regions and to draw conclusions about the significance of the bottom in general in system function.

As a member of the Coastal Upwelling Ecosystem Analysis Program (CUEA), I have made a series of continually evolving measurements with a number of different collaborators in three different upwelling areas: Baja California (Fig. 2), Northwest Africa (Fig. 3), and the coast of Peru (Fig. 4). The following paper will be a review of our approaches and findings in each area. Most of the work has been or is in the process of being published in individual papers and so this present paper, as a review, will in general not take up the details of methods and techniques used. It will, on the other

Air-Sea
Interface

Rege

Sediment-
Interface

hand, be a
success or f
goal of con
graphic loca

PISCO, PERU,
THE BENTHO

The R/V
has since b
quantitative
macrofauna
and inverse
matter was
no correlat
was to mea
monstrated
off Peru an

NEAR-SHORE ECOSYSTEM

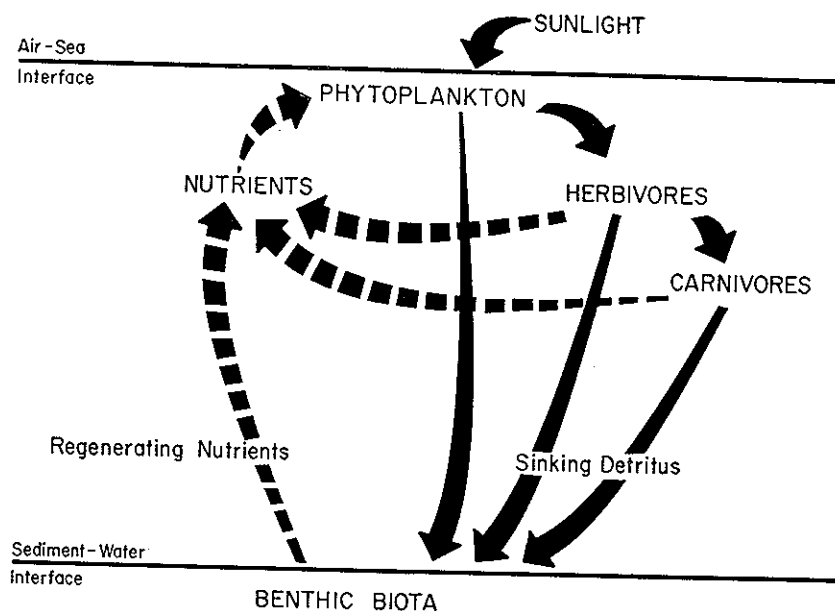


FIG. 1. — Simplified Coastal Ecosystem.

hand, be a chronological trip from one area to another noting the general success or failure of the studies we tried and how close we came to our final goal of constructing a carbon mass balance for the sediment of each geographic locale.

PISCO, PERU, 1969,

THE BENTHOS IN THE 15° S UPWELLING ECOSYSTEM

The R/V GOSNOLD and the R/V THOMPSON journeyed to Peru in 1969 for what has since been called the PISCO expedition. Using an anchor dredge (semi-quantitative) and a van Veen grab, we determined that standing stock of the macrofauna (>0.42 mm sieve mesh) varied directly with oxygen concentration and inversely with depth (Fig. 5, from ROWE, 1971 a). As sediment organic matter was highest where oxygen was lowest (<5 % saturation), there was no correlation between sediment % C and standing stock. Our intention was to measure how primary production affected bottom life and it was demonstrated that if the variables of oxygen and depth are eliminated, stocks off Peru are far higher than areas where production is much less (ROWE,

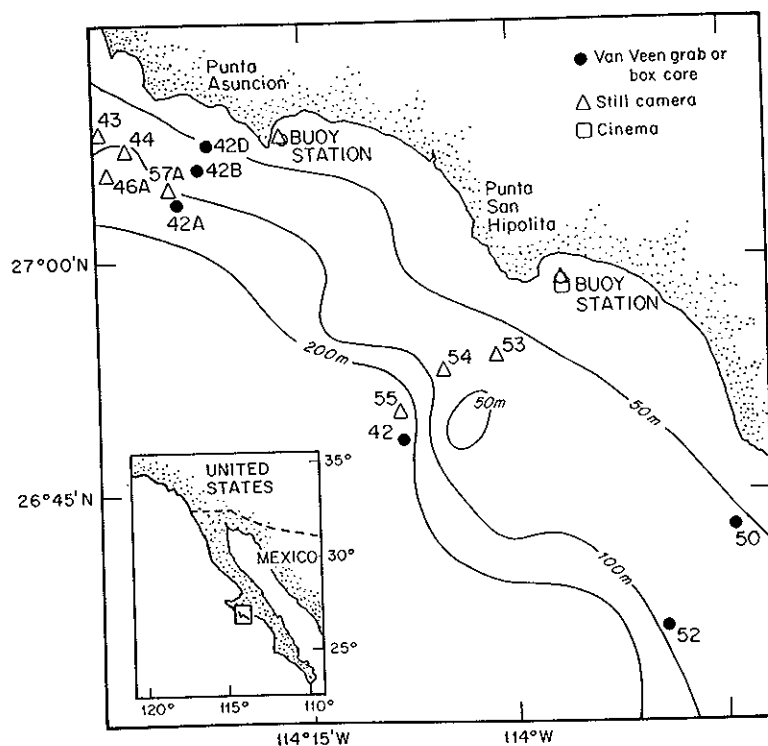


FIG. 2. — Baja California sampling area.

1971 b). For example, in both the Gulf of Mexico and off Peru the biomass and abundance decreased exponentially with depth, but there was two orders of magnitude less in the Gulf of Mexico than off Peru at slope depths and there is about that big a difference or greater in the rates of primary production ($25 \text{ g C m}^{-2} \text{ y}^{-1}$, from CORWIN, 1969, in the Gulf, versus 300 to $1500 \text{ g C m}^{-2} \text{ y}^{-1}$, from RYTHER, 1963, off Peru).

These stocks were more or less in agreement with other studies off the west coast of South America (FRANKENBERG and MENZIES, 1968; GALLARDO, 1963). More recent work has defined the relationship of benthos to low oxygen more critically (ROSENBERG *et al.*, 1983).

In the process of taking sediment samples to measure the concentration of organic matter, we also found the opportunity to measure the concentration of phosphorite. At some depths just on the edge of the oxygen minimum we discovered that CaCO_3 benthic foram tests are changing gradually to phosphorite pellets (MANHEIM, ROWE and JIPA, 1975). That the forams are recent in age suggests that the phosphorite was not a fossil deposit but was

precipitation
concentration
 PO_4 being
interface.

These
primary
matter, but
With the
oriented r

BAJA CALI
THE MESC
A SYSTEM

Use of
tunity to
Scuba div
and few
equipped
that an a
et al., 197
enriched

precipitating out or replacing the CaCO_3 in the tests presently from high concentrations of PO_4 in the anoxic pore water, with escape of dissolved free PO_4 being blocked by a somewhat less reducing layer at the sediment-water interface.

These early studies off Peru demonstrated the expected effects of high primary productivity on concentrations of benthos, oxygen, and organic matter, but these parameters tell us little of the cycling of carbon and energy. With the formal organization of CUEA in 1972, we began a study that was oriented more to the rates of cycling of carbon than its stocks.

BAJA CALIFORNIA, MEXICO,
THE MESCAL II EXPEDITION IN 1972:

A SYSTEM DOMINATED BY RED CRAB *Pleuroncodes planipes*

Use of the R/V THOMPSON on the MESCAL II expedition provided an opportunity to study rates of processes in the benthos of an upwelling ecosystem. Scuba divers put down bell jar-like enclosures covering a small area of bottom and few liters of bottom water at depths of 20-30 m. The bell jars were equipped with polarographic oxygen electrodes, and the conclusion was made that an average of $36.3 \text{ ml O}_2 \text{ m}^{-2} \text{ h}^{-1}$ was consumed by the bottom (SMITH *et al.*, 1974). This ranged from $39.1 (\pm 1.8)$ in the area presumed to be most enriched or closer to the upwelling plume, as determined by temperature

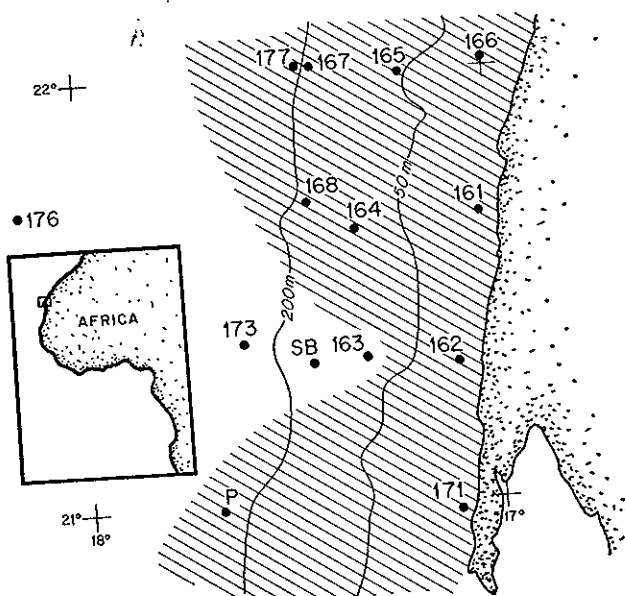


FIG. 3. — NW Africa sampling area. (From NICHOLS and ROWE, 1977.)

and chlorophyll, to $28.9 (\pm 1.2) \text{ ml O}_2 \text{ m}^{-2} \text{ h}^{-1}$, in an area apparently away from the plume (SMITH *et al.*, 1974).

The oxygen utilization can be used to make an estimate of organic matter oxidation or conversion to CO_2 . Using an RQ (respiratory quotient) of 0.85, meaning 0.85 moles of CO_2 are formed for each mole of O_2 consumed, one can assume that about 0.45 mg organic carbon is consumed per ml O_2 consumed, a calculation we will make at each locale. This would mean that about $16 \text{ mg of organic carbon m}^{-2} \text{ h}^{-1}$ or $0.38 \text{ g C m}^{-2} \text{ d}^{-1}$ is consumed by the benthos in this system close to shore.

Total oxygen consumption by the bottom is a very difficult but important measurement. It was once believed that *total* consumption, or respiration

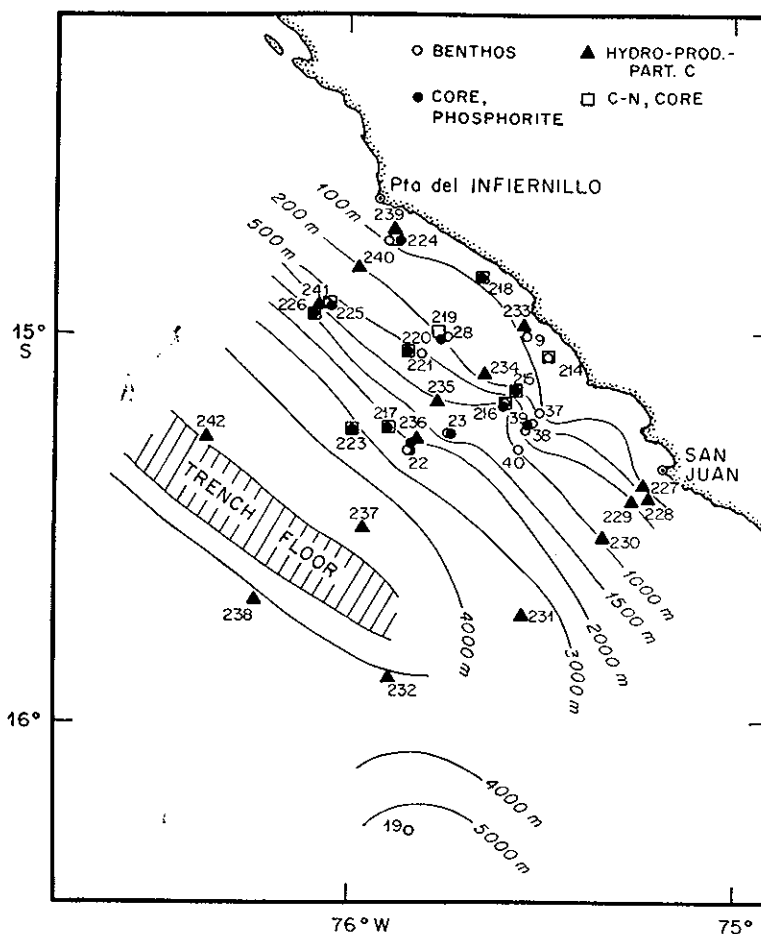


FIG. 4. — Peru, PISCO (1969) expedition sampling area. (From ROWE, 1971 a.)

by aerobes plus oxygen uptake by reduced ions such as sulfide, was a measure of total anaerobic respiration, but this is not always the case. Reduced products of anaerobic respiration (sulfides and elemental sulfur, mostly) may not oxidize fast enough after diffusion into the chamber to affect oxygen levels, and therefore would not accurately reflect the production of the end products. (The sulfides can poison the electrodes as well.) Other approaches to measuring anaerobic processes were necessary (see sections on Africa and Peru).

Biomass of the invertebrate macrofauna based on van Veen grabs and hand-held box corers (Fig. 2, Table 1) averaged 38.8 g m^{-2} with an average of 3347 animals m^{-2} . The most prominent organism in the system is the swimming galatheid crab *Pleuroncodes planipes*, whose abundance on bottom near-

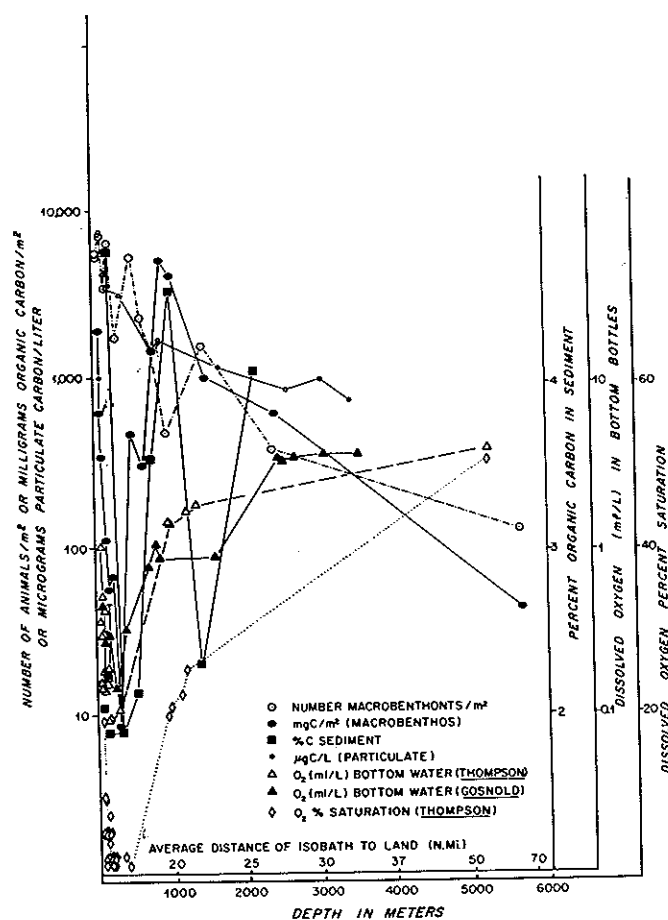


FIG. 5.—Summary relationship of biomass, O_2 , organic carbon with depth at 15° S off Peru, in 1969. (From Rowe, 1971 a).

TABLE 1

Benthic biomass and abundance, excluding *Pleuroncodes planipes*, sampled during THOMPSON Cruise 78, off Baja California (Fig. 2)

Station	Depth (m)	Abundance (\sim/m^2)	(wet weight gm/m ²) Biomass
Pta Asunción	23	3360 \pm 310*	9,1 \pm 2,7*
Pta St. Hipolito	23	6408 \pm 1571*	13,8 \pm 0,2*
39**	33	960	14,7
50	56	730	56,5
42D	65	3660	22,0
42B	70	5870	30,8
52	96	4420	158,0
42B	104	1380	21,0
42	240	259	78,5

* (n = 2, from SMITH *et al.*, 1974)

** 30°55.5'N \times 116°19.1'W, off chart, hand-held box core sample.

shore averaged 246 animals m⁻². Offshore it averaged 41 m⁻². Both estimates were made using photographic surveys (Fig. 6, Table 2). Using average biomass per crab values, we made estimates of 1373 g m⁻² nearshore and 229 g m⁻² offshore.

Few ecosystems are so overwhelmingly dominated by a single organism that can be both pelagic and benthic. As such a dominant species would have significant influence on the dynamics of the ecosystem, it is necessary to measure individual crab respiration (SMITH *et al.*, 1975). Average rates were 404 to 728 μ l O₂ g⁻¹ h⁻¹ (as free dry weight) or overall average of 566 μ l O₂ g⁻¹ h⁻¹. If we assume ash-free dry weight is 9 % of the wet weight (SMITH *et al.*, 1975), the rate would be 566 μ l O₂ per 11.1 g (wet weight)⁻¹ h⁻¹ or 51 μ l O₂ g (wet weight)⁻¹ h⁻¹. Applying this rate to our abundance estimates gives 70 ml O₂ m⁻² h⁻¹ nearshore and 12 ml O₂ m⁻² h⁻¹ offshore, for *P. planipes* alone. Again using an RQ of 0.85, we can estimate that the crab used 0.8 g C m⁻² d⁻¹ near the beach and 0.1 g C m⁻² d⁻¹ out on the outer half of the continental shelf. SMITH *et al.* (1975) made similar estimates with caloric equivalents, but related them to a density of 0.33 crabs m⁻² in the water column.

A rough estimate of secondary production by the macrofauna would be 38.8 g m⁻² y⁻¹, assuming a production to biomass (P/B) ratio of 1. The larger itinerant benthos, *P. planipes*, lives about 3 years, and using an average weight of 5.58 g indiv.⁻¹, one could estimate production to be 1.86 g indiv.⁻¹ y⁻¹. On a square meter basis that is equivalent to about 76 g m⁻² y⁻¹ production by

TABLE 2
Camera stations off Baja California Thompson cruise. Locations in Figure 2.

Station	Depth (m)	Time	Date of photos	Number	Area covered	Total crabs	\bar{X}/photo	V	\bar{X}/m^2	Biomass (g/m ²)	Compass orienta- tion	Comments (sediments, currents, etc.)
Pta Asuncion	23	1300	4/16/73	6(22)	0.15	226	37.7	67.6	251	1400	face south	Crabs randomly dispersed, water turbid, crabs face south, away from current
Pta San Hipolito	23	1200	4/15	17	1.8	7200	423	—	240	1339	—	Crabs in dense patches ca. 0.5-1 m diameter, rippled sand between areas of coral
43	88	1400	4/13	20	1.8	106	5.3	—	7.6	42	face south	All crabs in single clump in one photo, bottom of rippled silt
44	98	2130	4/14	21	0.7	680	64.8	109.0	92	516	+	Water slightly more turbid
46A	108	0945	4/14	21	0.7	0	0	—	0	0	—	Gorgonians on coral rubble, interspersed with silt patches, water clear
53	72	0915	4/17	17	0.7	0	0	—	0	0	—	Coarse silt, rippled, many fusiform gastropod shells, water clear
54	92	1030	4/17	14	0.7	0	0	—	0	0	—	Smooth Silt, water clear
55	342	1200	4/17	16	0.7	0	0	—	0	0	—	Smooth silt, fusiform gastropods school of herring-like fishes in one photograph
57A	103	2130	4/18	19	0.5	234	12.3	10.4	24.6	137	+	Urchins, cancer crabs, gastropods, flounder, coarse silt, smooth
San Hipolito	28	0800	4/19	Super 8 movie 20 feet exposed								Crabs in clumps, rippled sand, water clear



FIG. 6.—*Pleuroncodes planipes* at 25 m off Baja California, during Mescal II, 1972.

the crab offshore, based on benthic densities (41 m^{-2}) and benthic average sizes ($5.58 \text{ g indiv.}^{-1}$), not pelagic estimates (3 indiv. m^{-3} and 3 g indiv.^{-1}).

Based on the measurements above, it appeared that the crabs had an importance in total respiration, biomass, and production that was as great as or greater than that of the other benthic macrofauna. For this system we did not investigate organisms smaller than the macrofauna ($<0.42 \text{ mm}$ sieve). The weakness in our analysis was in our uncertainty in the estimates of overall crab density based on the photographs. The next stage of the work tried to include some of these omissions for a more complete budget.

NORTHWEST AFRICA, THE JOINT I EXPEDITION:

A SYSTEM DOMINATED BY AEOLIAN SAND AND SILT DEPOSITION

The barren flat sands of the Sahara, devoid of plant life, are being blown by strong, prevailing long-shore winds to the south and west into the ocean, off Cap Blanc (Fig. 3). Some of this reaches great distances as dust-sized particles at altitudes of 1 to 4 km in the western North Atlantic (PROSPERO and CARLSON, 1972), at rates of 25 to 37×10^6 tons per year through the

longitude of the Barbados. Tremendous quantities of sand move south, off the desert into the sea where eventually the sand moves via submarine canyons to the deep-sea (SARNTHEIN and WALGER, 1974; SENIN, 1974; BEIN and FÜTTERER, 1977; KOOPMAN *et al.*, 1978). On the outer shelf and continental slope where biogenic material, especially carbonates, are predominant there is little evidence in the water column or in the sediments of sediment transport (MILLIMAN, 1977). Nearshore it is a different story. We added small sediment trap moorings to our sampling scheme and made the conservative estimate that an average total sediment vertical flux rate was about 4 cm/yr (NICHOLS and ROWE, 1977). This is *not* a net accumulation necessarily, because once in the benthic boundary layer it is subject to resuspension and continued transport along and offshore (DIESTER-HAASS, 1978).

The addition of sediment traps was not necessarily to measure terrigenous rates, but rather as an aid in balancing the carbon budget. Unfortunately, we do not believe the data contribute to a knowledge of the sinking of phytoplankton to the bottom because the arrays captured too much resuspended material (Table 3). The organic carbon flux rate for example at 3 m off bottom would be about $8 \text{ g C m}^{-2} \text{ d}^{-1}$, *far above the primary production rate*, and so a large fraction of the nearshore material must be resuspended over and over.

Many of the same measurements made off Baja on stocks and concentrations were also made in the JOINT I area or elsewhere off NW Africa (BOUCHER and GLÉMAREC, 1974; THIEL, 1982, BRAVO DE LAGUNA, 1982; DOMAIN, 1982). Macrofaunal biomass was surveyed and found to average 34.7 g m^{-2}

TABLE 3
Sediment Trap Data from Northwest Africa

	Water depth	Trap distance off bottom	Total ($\text{gm m}^{-2} \text{ h}^{-1}$)	Organic N ($\text{gm N m}^{-2} \text{ h}^{-1}$)	Organic C ($\text{gm C m}^{-2} \text{ h}^{-1}$)
Sta 171					
28 April 1974	25 m	1 m	216	0.34	6.70
		2 m	22	0.026	0.51
Sta 162					
3 May 1974	25 m	1 m	15	0.023	0.21
		2 m	13	0.022	0.30
		3 m	8	0.010	0.10
6 May 1974	25 m	2 m	62	0.077	1.70
		3 m	32	0.039	0.57
\bar{x} of 2 m.o.b.* traps			32	0.042	0.84
\bar{x} of 3 m.o.b.* traps			20	0.024	0.34

* m.o.b. is meters off bottom

(NICHOLS and ROWE, 1977), while megabenthos, including fishes and squid, weighed 4.2 g m^{-2} (HAEDRICH, BLACKBURN and BRULHET, 1976). Using a P/B ratio of 2 to 3.5, NICHOLS and ROWE (1977) estimated that coastal secondary production of the macrobenthos might be about $40 \text{ g m}^{-2} \text{ y}^{-1}$, whereas on the outer shelf it might be about $60 \text{ g m}^{-2} \text{ y}^{-1}$. Species closely related to those found in the region have somewhat lower P/B ratios (0.8-0.9) in the literature, and so it is probably reasonable, they implied, to lower those estimates about 50 %. In either case, the offshore macrobenthos appeared more productive than that nearshore, including the megafauna (HAEDRICH *et al.*, 1976). Such a pattern conforms to the patterns found in primary production, zooplankton and nekton biomass and organic matter in the sediments. Biomass of the meiofauna was not measured, but abundances on a transect off Cap Blanc were greatest ($10^3 \times 10^4 \text{ indiv./10 cm}^2$) between 500 and 1000 m depth (THIEL, 1978). Organic matter in the sediments displayed like patterns, whether measured as carbon (DIESTER-HAAS, 1978; NICHOLS and ROWE, 1977), nitrogen (MILLIMAN, 1977) or chloroplastic pigments (THIEL, 1978): maximum concentrations were at intermediate (continental slope or outer shelf) depths, and not in the carbonate sands of the intermediate shelf (ROWE *et al.*, 1976).

Microbial and bacterial stocks and total infaunal metabolic activity were measured in several different ways in the sediments in the JOINT I area. WATSON (1978) used the adenosine triphosphate (ATP) technique and his own lipopolysaccharide (LSP) technique to investigate total biomass and bacterial biomass in both the water and sediments during JOINT I (Table 4). CRISTENSEN and PACKARD (1977) estimated the respiration of the small infauna and microbes, or what Watson measured as total biomass, at a number of the same locations, using an assay for the activity of the respiratory electron transport system. As indicated (Table 5), oxygen utilization, as with microbial biomass,

TABLE 4
Sediment biomass of bacteria and other small infauna,
JOINT I area, modified from WATSON (1978).

Area	Stations (Fig. 2)	Total biomass (gC m^{-2})	Bacterial biomass (gC m^{-2})
Shelf	161, 171, 162 (30-39 cm)	19 (8-37)	8 (0.8-4.8)
Slope	173, 169, 176 (469-1800 m)	2.5 (0.4-7.0)	3.5 (1.8-3.3)

* See WATSON 1978 for explanations of why bacterial biomass is higher than the total biomass.

TABLE 5

Respiration (ETS), carbon utilization and biomass estimates in sediments in the JOINT I area, Northwest Africa (from CHRISTENSEN and PACKARD, 1977).

	<i>Nearshore zone</i> (27-30 m)	<i>Outer shelf</i> (65-190 m)	<i>Slope</i> (480 to 1820 m)
Oxygen utilization (ml O ₂ m ⁻² h ⁻¹)	29	10,6	1,25
Organic carbon utilization (g C m ⁻² d ⁻¹)	0,30	0,16	0,013
Biomass (g C m ⁻²)	53	22	2,4

was greatest nearshore and decreased over 20 times on the average offshore. Biomass estimates (CRISTENSEN and PACKARD, 1977; and WATSON, 1978) were not very different for each depth and the ETS pattern agreed with the ship-board experimental substrate utilization patterns Watson observed. Most activity in sediments was nearshore and it decreased offshore.

Pore water dissolved inorganic nutrients which are the products of heterotrophic metabolism were also measured to get an indirect estimate of total benthic metabolism (ROWE, CLIFFORD and SMITH, 1977). Ammonium displayed steep gradients into the sediments, but such within-sediment gradients decreased offshore, following the same offshore decline as ETS and "microbial" biomass.

Benthic chambers were again used nearshore (Sta 162 and 171 again) to measure oxygen demand, but additionally nutrient flux out of the sediment was estimated by measuring concentrations at the beginning and end of each incubation. Total nitrogen flux, in the form of either HN₄⁺ or NO₃, averaged of 420 μ mole m⁻² h⁻¹ (141 mg N m⁻² d⁻¹). Oxygen uptake averaged 19 milliliters O₂ m⁻² h⁻¹, equivalent to about 8.6 mg organic carbon oxidation. Assuming a 5 to 1 C to N ratio, this would equal to 1.7 mg N m⁻² h⁻¹ or 40 mg N m⁻² d⁻¹. This 40 mg N predicted from the O₂ uptake was 3.5 times less than the 141 mg N m⁻² d⁻¹ estimated above from the benthic chamber incubation.

JOINT II, PERU, 1976-1978

Off Northwest Africa several important aspects of a carbon budget were not measured. These included vertical flux of particulate matter in deep water, anaerobic metabolism, secondary production and variations in both biological and chemical variables over ecological (days to years) time scales. Designing our work off Peru with these deficiencies in mind, we added middle

TABLE 6
Sediment Trap Data, JOINT II, Peru

Station	Water depth	Trap distance off bottom	Total ($\text{g m}^{-2} \text{h}^{-1}$)	Organic N ($\text{mg N m}^{-2} \text{h}^{-1}$)	Organic C ($\text{mg C m}^{-2} \text{h}^{-1}$)	Comments
C-1 14 June 1976	60 m	2 m 4 8	1.56 0.66 0.41	3.9 2.0 1.2	30.9 13.8 10.9	Resuspension
B-1 14°58.5S × 75°31.5W 17 June 1976	60 m	2 4 8	134.8 6.9 4.4	363.9 11.0 7.9	2736.2 89.0 55.5	Intense Resuspension
C-1 20 June 1976	60 m	2 8 24	1.75 0.42 0.15	6.7 2.3 2.0	50.2 16.7 16.0	Resuspension
C-3 22 June 1976	120 m	8 16 24	0.02 0.09 0.15	0.2 0.9 1.2	1.4 6.8 9.4	
Rio Pisco, 13°40.4S × 76°17.3W 9 October 1976	23 m	3 7 10	1.45 0.94 0.35	4.1 2.5 2.5	27.1 19.1 14.0	Resuspension
C-3 10 October 1976	106 m	3 10 30	0.22 0.23 0.23	2.9 2.4 3.5	17.1 19.0 22.9	
C-1 12 October 1976	60 m	3 7 10	1.19 0.92 0.46	9.2 4.8 3.5	44.1 30.1 25.9	Resuspension
Callao, 11°58.5S × 77°11.0W 18 October 1976	30 m	3 7 10	10.15 1.75 0.70	24.4 6.1 3.9	194.9 46.1 28.8	Resuspension
Huarmey 10°04.2S × 78°11.2W 22 October 1976	29 m	3 7 10	3.18 1.76 1.06	11.8 7.7 6.3	79.2 58.1 42.4	Resuspension

Location	Depth	Date	3	7	10	Resuspension
Chicama 7°39.5S × 79°31.9W 22 October 1976	32 m		—	—	—	—
			3	7	10	43.1
C-3 5 April 1977	117 m		3	6	9	20.8 15.9 4.4
			3	6	9	2.5 2.3 0.7
Punta Azua 6 April 1977	75 m		3	6	9	32.3 40.3 22.1
			3	6	9	4.5 4.6 3.2
C-3 8 April 1977	120 m		3	6	9	10.5 13.6 19.2
			3	6	9	1.7 1.6 1.6
C-3 11 April 1977	117 m		3	6	9	5.6 4.6 8.0
			3	6	9	0.7 0.8 1.3
C-1a 2 March 1978 (less than 0.5 n. mi. inshore of C-1)	30 m		3	7	10	35.7 17.6 9.2
			3	7	10	5.2 2.9 1.7
C-2 (between C-1 and C-3, see Fig.) (day) 3 March 1978	80 m		3	7	10	12.6 16.8 17.3
			3	7	10	1.8 2.2 2.6
C-2 (night) 3-4 March 1978	80 m		3	7	10	12.7 7.4 9.1
			3	7	10	1.5 1.0 1.3
\bar{X} at C-1, 8 or 10 m traps, including C-1a and C-2's. (n=6)						2.1 (1.2-3.5)
						14.85 (9.1-25.9)
\bar{X} at C-3, top trap						12.8 (4.4-22.9)
						1.66 (0.7-3.5)
						0.248 or 200 gm cm ⁻² 1000y ⁻¹
						0.325 or 280 gm cm ⁻² 1000y ⁻¹

(60 m, C1), and outer continental shelf (120 m, C3) moored sediment trap (MST's) arrays, floating sediment traps (STARESINIC *et al.*, 1978) (FST's), conducted radiolabelled $^{35}\text{SO}_4^{=}$ experiments to measure one form of anaerobic metabolism, and took macrofaunal and sediment samples at several stations (C1-C5) sequentially over an extended period in an attempt to observe variations over small times scales (Figs. 4 and 7).

Moored sediment traps were deployed at a number of shelf stations between 1976 and 1978 (Table 6). The traps, similar in design to those used by ROWE and GARDNER (1979), were placed at 3 levels above bottom. In some arrays the near-bottom gradient was reversed, possibly due to winnowing by a strong near-bottom current or a higher trap being located in a particle-rich layer. The average fluxes at C1 and C3 where our work concentrated (Fig. 7) were $14.85 \text{ mg C m}^{-2} \text{ h}^{-1}$ or $0.36 \text{ g C m}^{-2} \text{ d}^{-1}$, and $12.8 \text{ mg C m}^{-2} \text{ h}^{-1}$ or $0.31 \text{ g C m}^{-2} \text{ d}^{-1}$, respectively. The rate of the total sediment vertical particulate flux ranged from $280 \text{ g cm}^{-2} 1000 \text{ y}^{-1}$ to $200 \text{ g cm}^{-2} 1000 \text{ y}^{-1}$. Given a porosity of 0.9, and a density of 2.6 g/cm^3 , this would be converted to about 1.0 to 0.8 cm y^{-1} , important numbers presumably in a total carbon or nitrogen

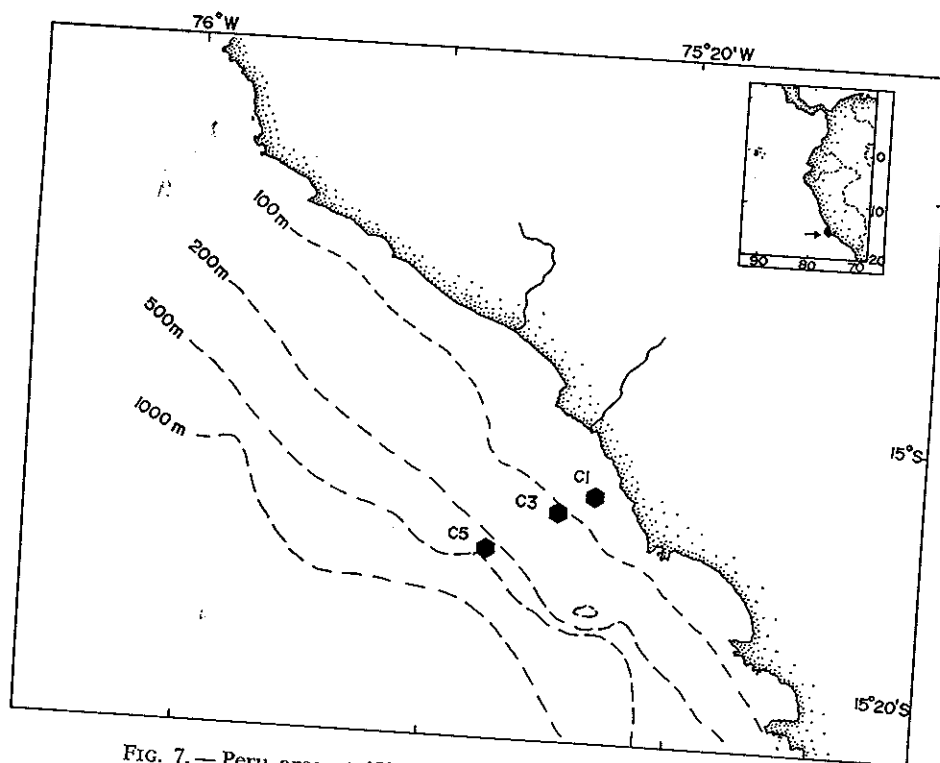


FIG. 7. — Peru area at 15°S showing principal station locations. (From ROWE and HOWARTH, submitted.)

budg
distr
Peru
of 37
F
of 0.
were
flux
was
comp
long
havin
zone
turbu
B
as ex
had
range
oxyge
low
high
mass
regio
static

Stat
C-1
C-3
C-4
C-5
C-6
C-7

budget. Rates of total accumulation, however, based on unsupported Pb-210 distribution have been estimated to be up to 1.2 cm/y in this same area off Peru (HENRICH, 1980). At 6 % organic carbon, this would amount to a burial of 374 g C/m²-y.

Floating sediment traps (FST's) measured a flux at 50 m, in the area of C3, of 0.24 g C m⁻² d⁻¹, or about 9 % of primary production. In 1978 the FST's were also put at the 1 % light level, usually about 10-13 m depth, and the flux as 0.53 g C m⁻² d⁻¹ or 17 % of the primary production. At 50 m the rate was halved (STARESINIC, 1978), or about equal to 1977 rates at 50 m. Important components in 1978 were fecal casts from anchovies. Several millimeters long in the water, they were broken in processing into 0.3 mg fragments having sinking rates of up to 850 m d⁻¹. Rates at night across the euphotic zone were 50 % greater than in the day, possibly due to greater wind-induced turbulence in the daytime (STARESINIC, pers. com.).

Biomass on the bottom displayed peculiar patterns because of low oxygen, as explained in the first section. Meiofauna, studied by Dr. Jean Ann Nichols, had a similar correlation with oxygen (Table 7). Abundances and biomass ranged from 23.9 g m⁻² in 1.1×10^6 individuals nearshore (63 m) above the oxygen minimum down to 0.24 g m⁻² in 1.5×10^3 individuals in the heart of low oxygen water (<0.1 ml/L). The biomass nearshore and at 484 m were high for meiofauna, but this would be expected since high macrofaunal biomass was also found at these depths (Rowe, 1971 a, b), compared to other regions. Average wet weight per individual was 1.7×10^{-2} mg ind.⁻¹, for all stations (NICHOLS, unpubl.).

TABLE 7

Biomass of Meiobenthos on C-line, 15°S, off Peru,
(data from JEAN ANN NICHOLS, pers. comm.)

Station	Depth	Biomass (g m ⁻² wet weight)	Abundance (individuals m ⁻²)	Number of samples
C-1	63 m	23.9	1,134,214 ind. m ⁻² (2.1×10^{-2} mg/ind.)	(n = 4)
C-3	110 m	4.22	609,251 (0.7×10^{-2} mg/ind.)	(n = 4)
C-4	191 m	4.38	380,314 (1.2×10^{-2} mg/ind.)	(n = 5)
C-5	251 m	0.52	15,745 (3.3×10^{-2} mg/ind.)	(n = 6)
C-6	319 m	0.24	14,960 (1.6×10^{-2} mg/ind.)	(n = 5)
C-7	484 m	9.7	934,055 (1.0×10^{-2} mg/ind.)	(n = 4)

Calculation of secondary production is difficult because of the peculiar distribution of the bulk of the fauna *only* along the shore and not out on the shelf. At C1, where maximum biomass occurred, we can estimate macrofaunal production at $86 \text{ g C m}^{-2} \text{ y}^{-1}$ ($P/B = 1$) and meiofaunal production at $69 \text{ g C m}^{-2} \text{ y}^{-1}$ ($P/B = 4$, assuming 4 generations per year). (The macrofaunal biomass was derived from ROWE, 1971 a, assuming organic carbon is 6 % of wet weight).

Offshore, at C3 through C7, metazoan biomass was low and anaerobic metabolism must predominate because oxygen concentrations were so low. Biomass of microbial populations was probably high. Although we do not know what this was exactly, extensive areas of the bottom were covered by a mat of sulfur bacteria similar to *Thioploca* spp., a beggiatocean that is possibly chemolithotrophic. It was observed on JOINT II in October 1976, March and April 1977, and April 1978, from C3 (110 m) through C6 at 319 m, consistently. It is most dense in the top 3 cm of sediment, and in April, 1977, it penetrated to 20 cm. If it occupies about 5 % of the sediment volume in the thickest mat, and has a density of 1.2 g/cc of filaments, it would have a wet weight biomass on the order of $1,530 \text{ g/m}^2$ or about 90 g C m^{-2} . GALLARDO (1977) found sulfur bacteria of about $160 \text{ g wet weight m}^{-2}$, after preservation in alcohol, or about 50 g m^{-2} dry weight in the Bay of Concepcion, Chile. This would equal about 25 g C, probably well within the margin of error of our indirect estimates for the Perú sediments. We do not know its source of energy, rates of metabolism or production, although potentially these could all be quite high (KUZNETSOV, 1959).

Because most of the outer shelf and upper slope is exposed to low-oxygen water, experiments were conducted to determine sulfate reduction rates at C1, C3 and C5 (Fig. 7) using newly developed techniques with ^{35}S (JORGENSEN, 1978). The integrated rates were $27 \text{ nm SO}_4^{2-} \text{ reduction m}^{-3} \text{ d}^{-1}$ nearshore and $5.5 \text{ mM m}^{-2} \text{ d}^{-1}$ offshore, assuming 0.8 ml water per cc wet mud. In terms of organic carbon, therefore, the rates would be $0.65 \text{ g C m}^{-2} \text{ d}^{-1}$ nearshore versus $0.13 \text{ g C m}^{-2} \text{ d}^{-1}$ converted to CO_2 . These equate to 240 and $47 \text{ g C m}^{-2} \text{ y}^{-1}$ (ROWE and HOWARTH, in press).

It has been suggested that more organic matter is being deposited off Peru presently than before the *el Niño* of 1972 because the anchovies are not present to consume the primary production (WALSH, 1981; ROWE, 1981). The sediment organic carbon profiles presented in ROWE and HOWARTH (in press), however, suggest that this deposition is not on the shelf. The accumulation referred to above is evidently at continental slope and abyssal trench depths (ROWE, 1979), moved there by mechanisms not dissimilar to those reviewed by THIEL (1982) for NW Africa.

DISCUSSION

A comparison of the benthos and sediments in the three upwelling systems is a useful endeavor (Table 8). Even though upwelling areas have been compared before (DIESTER-HAASS, 1978; THIEL, 1978), a summary of the information brings out the contrasting nature of the systems and allows one to separate them into distinct categories. I would like to propose that the bottoms in upwelling ecosystems be divided on the basis of dominant type of heterotrophic metabolism and the concentration of organic matter in the sediments. Such a distinction allows us to separate southwest Africa (the Benguela current region), Peru, etc., from northwest Africa, Baja California, etc. In this context the organically overloaded system (Peru) sees a more profound "memoire" (MARGALEF, 1978) of water column events, than does the more aerobic system that does not suffer extensive oxygen debt (Cape Blanc region). Most environmental and biological parameters follow the dichotomy. Macrofaunal biomass for example has a bimodal distribution with depth in overloaded systems because the depletion of oxygen in the bottom water.

Peru and the Benguela region are characterized by a mud bottom, severely low oxygen concentrations and biota that is far different from the other two systems; they typify the overloaded benthic system. Macrofauna and for the most part meiofauna disappear offshore where sedimentation of organic particulates are high and oxygen low. The fauna is replaced by a mat of sulfur bacteria with high biomass and unknown productivity. The mat may be composed of chemolithotrophs, but as the sediment is so rich in organic compounds they are probably heterotrophs or perhaps facultative autotrophs. While aerobic respiration dominated off Baja and Northwest Africa, as representatives of aerobic, dispersive systems, sulfate reduction was most important in Peru. Comparison of respiratory utilization of organic matter suggests that it was somewhat greater off Baja, than elsewhere. Macrofaunal production, not counting the area off Peru where low O_2 impairs macrofaunal life, can be greatest in overloaded systems, right next to the Peruvian coast. Meiofaunal biomass was far higher off Peru than off Africa, using a weight per individual conversion factor from the Peru data ($1.7 \text{ mg} \times 10^{-2} \text{ mg ind}^{-1}$). Nutrient flux can be high in both types of systems. While that measured off Africa was very high — higher than predicted from pore water gradients and from O_2 demand — it was also high off Peru. The distinction is that off Peru it was ammonium rather than nitrate.

An attempt to compare the sources and sinks of organic carbon is an interesting exercise for the two types of ecosystem. Off Peru a simplified budget for the outer shelf/upper slope environment is markedly out of balance. Burial rate ($\sim 370 \text{ g C m}^{-2} \text{ y}^{-1}$) assumes a total deposition of 1.2 cm y^{-1}

TABLA 8

	MESCAL II Baja California	JOINT I Northwest Africa	PISCO and JOINT II Peru
Primary Production	3.9 g C m ⁻² d ⁻¹	1-3 g C m ⁻² d ⁻¹ (Huntsman and Barber, 1974)	5.7 g C m ⁻² d ⁻¹ (Walsh et al., 1974)
Sediment Particle Flux	—	Extensive resuspension	0.30-0.53 g C m ⁻² d ⁻¹ (MST's and FST's) Nearshore resuspension
Sediment Accumulation Rate	—	—	~ 1 cm y ⁻¹ or 300 g C m ⁻² y ⁻¹
Sediment % C and % N	0.1 - 2 % C and 0.02 - 0.05 % N, <i>nearshore</i>	< 1 % to > 2 % C	2 to > 10 % C
Macrofaunal Biomass ¹	38.8 g m ⁻²	34.7 ^s	0.128-86 g m ⁻² (0.008-5.4 g C m ⁻²)
Meiofaunal Biomass ¹	—	0.17-17 g m ⁻² (wet wt.) (based on Peru wt./ind.) (0.01-1.02 g C m ⁻²)	0.24-23.9 g m ⁻² (0.01-1.4 g C m ⁻²)
Microbial Biomass	—	2.6-19 g C m ⁻² based on Watson's ATP or 2.4-53 g C m ⁻² based on ETS	<i>Thioploca</i> spp. ³ 1530 g m ⁻² (90 g C m ⁻²) ⁶
Megafaunal Biomass ¹	228 g m ⁻² (14 g C m ⁻²)	4.2 g m ⁻² (2.1 fishes + 0.8 squill) (0.25 g C m ⁻²)	—
Total Bottom O ₂ Demand	36.3 ml m ⁻² h ⁻¹ ¹⁰ (142 g C m ⁻² y ⁻¹)	19.0 (75 g C m ⁻² y ⁻¹)	—
Rate Sulfate Reduction	—	—	0.65-0.13 g C/m ⁻² d
Megafaunal Respiration	12 to 70 ml m ⁻² h ⁻¹ (47-276 g C m ⁻² y ⁻¹)	—	—
Infaunal and Microbial Respiration (ETS)	—	1.25 to 29 ml m ⁻² h ⁻¹	—
Porewater Nutrient Concentrations (gradient)	100 μm cm ⁻¹ <i>nearshore</i>	100 μm cm ⁻¹ (NH ₄) (to 10 m cm ⁻¹ offshore)	400 μm cm ⁻¹ (NH ₄)
Secondary Production of Macrofauna	38.8 g m ⁻² y ⁻¹ (2.3 g C m ⁻² y ⁻¹)	40 to 60 g m ⁻² y ⁻¹ (2.4-3.6 g C m ⁻² y ⁻¹)	86 g m ⁻² y ⁻¹ (5.2 g C m ⁻² y ⁻¹)

TABLE 8 (Cont.)

	MESCAL II Baja California	JOINT I Northwest Africa	PISCO and JOINT II Peru
Secondary Production of Megafauna	76 g m ⁻² y ⁻¹ (4.6 g C m ⁻² y ⁻¹)	4.2 g m ⁻² y ⁻¹ (0.2 g C m ⁻² y ⁻¹)	
Secondary Production of Meiofauna	—	68 g m ⁻² y ⁻¹ (4 g C m ⁻² y ⁻¹) (using P/B = 4)	96 g m ⁻² y ⁻¹ (5.8 g C m ⁻² y ⁻¹) (using P/B = 4)
Nutrient Flux	18 μm m ⁻² h ⁻¹ (NH ₄ ⁺ , using K _{diff} = 0.5 × 10 ⁵ cm ² /sec or 77 mg N m ⁻² d ⁻¹ (based on O ₂ demand)	420 μm m ⁻² h ⁻¹ (NH ₄ ⁺ + NO ₃) (based on belljar incubations)	360 μm m ⁻² h ⁻¹ or 120 mg N m ⁻² d ⁻¹ using K _{diff} = 0.5 × 10 ⁻⁵ cm ² /sec

¹ All biomass values are wet weight preserved in formalin. Numbers in parentheses are carbon units, assuming C is 6 % of wet weight. See text for sources of data.

² See WATSON (1978) and CHRISTENSEN and PACKARD (1977) for alternative methods for carbon biomass estimates.

³ Biomass estimated from volume displacement, see text.

and a concentration of 6 % organic carbon. The vertical flux to the bottom ($\sim 100\text{--}200 \text{ g C m}^{-2} \text{ y}^{-1}$) is an average organic carbon flux in the top moored trap at C-3 (120 m) and the average in the 50 m FST, which would not include bedload transport. The loss to metabolism ($44 \text{ g C m}^{-2} \text{ y}^{-1}$ offshore) is based only on estimated SO_4^{2-} reduction stoichiometry. Some emphasis should be put on possible sources of error. First, the system may not be in a steady state and therefore it would be unrealistic to expect input to equal the sinks exactly. Burial was based on a concentration of 6 % organic carbon. If that were somewhat higher, as suggested by much of our data (ROWE, 1979), burial would be proportionately greater. Anaerobic sulfate reduction may underestimate total metabolism. Considerable denitrification and some aerobic metabolism could also be occurring. If both loss terms are underestimates, then the balance between input and sinks is not even as good as was calculated. One possible explanation is that anaerobic metabolism, with its reduced end products, retains considerable energy within the system, and this is used by chemolithotrophs (nitrifiers and some sulfur bacteria) to synthesize "new" organic matter. This "feedback" of organic carbon could account for having more organic matter than would be predicted. The extremely high biomass of sulfur bacteria certainly implies that this may be an important process,

but such processes, although common in anaerobic-aerobic boundaries, remain to be measured in these sediments.

A final goal of this discussion might be similar figures of the sources and fates of organic matter in each area. Unfortunately, that is not possible. Too many important aspects of each remain unknown. For example, the production (growth) and respiration of the microbiota for each area cannot be compared. The production of the macrofauna was based on presumed P/B ratios which may be very inaccurate. Nutrient fluxes need to be measured and not based on poorly known (even though widely accepted) diffusion coefficients. Sediment redistribution (erosion) and shelf export are unknown for all three regions. When these parameters are better understood we will be better able to compare the systems.

In summary, several conclusions can be made concerning the classification of benthic subsystems within upwelling ecosystems. Bottom metabolism is high in all upwelling systems, even in those that are overloaded with organic matter and go anoxic. While inorganic nutrient regeneration too is high, it is of less significance as a percentage of the total nutrient demand in the whole system. In stratified systems the within-system regeneration is proportionately more important than in ecosystems that import nutrients (ROWE, 1981). In stratified, coastal ecosystems the benthic biomass mimics primary production, but in upwelling systems the biomass parallels advective movement of produced organic matter, such as export offshore in the NW Africa area (THIEL, 1978; NICHOLS and ROWE, 1977), or is bimodal (Fig. 5) due to oxygen impoverishment at slope depths (ROWE, 1971 a; ROSENBERG *et al.*, 1983).

REFERENCES

- BEIN, A., and D. FÜTTERER. — 1977. Texture and composition of continental shelf to rise sediments off the northwestern coast of Africa: An indication of downslope transportation. *«Meteor» Forsch.-Ergebn. C*, 27: 46-74.
- BOUCHER, D. and M. GLEMAREC. — 1974. Données préliminaires sur le benthos de la côte sud de l'Atlantique Marocain. *Tethys*, 6: 29-32.
- BRAVO DE LAGUNA, J. — 1982. Distribution and abundance of demersal resources of the CINECA region. *Rapp. P-V. Réun. Cons. Int. Explor. Mer*, 180: 432-446.
- CHRISTENSEN, J. P., and T. T. PACKARD. — 1977. Sediment metabolism from the northwest African upwelling system. *Deep-Sea Res.*, 24: 331-343.
- CORWIN, N. — 1969. Reduced data reports for *Atlantis II*, 31, 42, 48. *WHOI Tech. Rept.*, Ref. No. 69-20.
- DIESTER-HAASS, L. — 1978. Sediments as indicators of upwelling, pp. 261-281. In: R. BOJE and M. TOMCZAK (eds.), *Upwelling Ecosystems*, Springer, Berlin.
- DOMAIN, F. — 1982. Repartition de la biomasse globale du benthos sur le plateau continental ouest-africain de 17° N, a 12° N: densités comparées liées aux différents types de fond. *Rapp. P-N. Réun. Cons. Inst. Explor. Mer*, 180: 335-336.
- FRANKENBERG, D., and R. J. MENZIES. — 1968. Some quantitative analyses of deep-sea benthos off Peru. *Deep-Sea Res.*, 15: 623-626.
- GALLARDO, A. — 1963. Notas sobre la densidad de la fauna bentónica en el sublitoral del norte de Chile. *Gayana Zoo.*, 8: 3-15.
- GALLARDO, V. — 1977. Large benthic microbial communities in sulphide biota under Peru-Chile Subsurface Countercurrent. *Nature*, 268: 331-332.
- HAEDRICH, R. L., M. BLACKBURN, and J. BRULHET. — 1976. Distribution and biomass of trawl-caught animals off Spanish Sahara, West Africa. *Matsya*, 2: 38-46, 1976.
- HENRICH, S. — 1980. *Biogeochemistry of dissolved free aminoacids in marine sediments*. Ph. D. Thesis, Woods Hole Oceanogr. Inst. and Mass. Inst. Tech., 253 pp.
- HUNTSMAN, S. A., and R. T. BARBER. — 1977. Primary production off northwest Africa: the relationship to wind and nutrient conditions. *Deep-Sea Res.*, 24: 25-33.
- JORGENSEN, B. B. — 1978. A comparison of methods for the quantification of bacterial sulfate reduction in coastal marine sediments. I. Measurement with radiotracer techniques. *Geomicrobiology Journal*, 1: 11-27.
- KOOPMANN, D., M. SARNTHEIN, and H.-J. SCHRADER. — 1978. Sedimentation influenced by upwelling in the subtropical Baie du Levrier (West Africa), pp. 282-288. In: R. BOJE and M. TOMCZAK (eds.), *Upwelling Ecosystems*, Springer, Berlin.
- KUZNETSOV, S. I. — 1959. *Die Rolle der Mikroorganismen in Stoffkreislauf der Seen*, Deutscher Verlag der Wissenschaften, Berlin, 301 p.
- MANHEIM, F., G. ROWE and D. JIPA. — 1975. Marine phosphorite formation off Peru. *J. Sedimentary Petrology*, 45: 243-251.
- MARGALEF, R. — 1978. What is an upwelling ecosystem? In: R. BOJE and M. TOMCZAK (eds.), *Upwelling Ecosystems*, Springer-Verlag, New York.
- MILLIMAN, J. D. — 1977. Effects of arid climate and upwelling upon the sedimentary regime off southern Spanish Sahara. *Deep-Sea Res.*, 24: 95-103.
- NICHOLS, J. A., and G. T. ROWE. — 1977. Infaunal macrobenthos off Cap Blanc, Spanish Sahara. *J. Mar. Res.*, 35: 525-536.
- PROSPERO, J. M., and T. N. CARLSON. — 1972. Vertical and areal distribution of Saharan dust over the western equatorial North Atlantic Ocean. *J. Geophys. Res.*, 77: 5255-5265.
- ROSENBERG, R., W. ARNTZ, E. CHUMAN DE FLORES, L. FLORES, G. CARBAJAL, I. FINGER, and J. TARRAZPNA. — 1983. Benthos biomass and oxygen deficiency in the upwelling system off Peru. *J. Mar. Res.*, 41: 263-279.

- ROWE, G. T. — 1971a. Benthic biomass in the Pisco, Peru upwelling. *Inv. Pesq.*, 35: 127-135.
- 1971b. Benthic biomass and surface productivity, pp. 441-454. In: J. D. COSTLOW, Jr. (ed.), *Fertility of the Sea*, Vol. II, Gordon and Breach, New York.
- 1979. Sediment data from short cores during JOINT II off Peru. *CUEA data report* 65. 57 pp.
- 1981. The benthic processes of coastal upwelling ecosystems, pp. 464-471. In: RICHARDS, F. A. (ed.), *Coastal Upwelling*. Coastal and Estuarine Sciences 1, Amer. Geophys. Union, Washington, 529 pp.
- ROWE, G. T., C. H. CLIFFORD, and K. L. SMITH, JR. — 1977. Nutrient regeneration in sediments off Cap Blanc, Spanish Sahara. *Deep-Sea Res.*, 24: 57-63.
- ROWE, G., and W. GARDNER. — 1979. Sedimentation rates in the slope water of the north-west Atlantic Ocean measured directly with sediment traps. *J. Mar. Res.*, 37: 581-600.
- ROWE, G. and HOWARTH. — Diagenesis of organic matter in sediments off the coast of Peru. *Deep-Sea Res.* (in press).
- ROWE, G., A. A. WESTHAGEN, C. CLIFFORD, J. NICHOLS-DRISCOLL, and J. MILLIMAN. — 1976. JOINT I - Benthos and sediment station data - R/V *Atlantis II* cruise 82. *IDOE/CUEA data rept.* 31. 26 pp.
- RYTHER, J. H. — 1963. Geographic variations in productivity, pp. 347-380. In: HILL, M. N. (ed.), *The Sea*, Vol. II, Wiley-Interscience, New York.
- SARNTHEIN, M. and E. WALGER. — 1974. Der oolische sandstrom aus der W-Sahara zur Atlantikküste. *Geologische Rundschau*, 63: 1065-1087.
- SENIN, YU. M. — 1974. The climatic zonality of the recent sedimentation on the west Africa shelf. *Oceanology*, 14: 102-110.
- SMITH, K. L., JR., G. R. HARBISON, G. T. ROWE, and C. H. CLIFFORD. — 1975. Respiration and chemical composition of *Pleuroncodes planipes* (Decapoda: Galatheididae): Energetic significance in an Upwelling System. *Journal of the Fisheries Research Board of Canada*, 32: 1607-1612.
- SMITH, K. L., JR., G. T. ROWE, and C. H. CLIFFORD. — 1974. Sediment oxygen demand in an outwelling and upwelling area. *Tethys*, 6: 223-229.
- STARESINIC, N. — 1978. The vertical flux of particulate organic matter in the Peru coastal upwelling as measured with a free-drifting sediment trap. *Ph. D. Thesis*. Woods Hole Oceanographic Institution and Mass. Inst. Tech., 255 pp.
- STARESINIC, N., G. T. ROWE, D. SHAUGHNESSEY and A. J. WILLIAMS, III. — 1978. Measurement of the vertical flux of particulate organic matter with a free-drifting sediment trap. *Limnol. Oceanogr.*, 23: 559-563.
- THIEL, H. — 1979. Benthos in upwelling regions, pp. 124-138. In: R. BOJE and M. TOMCZAK (eds.), *Upwelling Ecosystems*, Springer, Berlin.
- 1982. Zoobenthos of the CINECA area and other upwelling regions. *Rapp. P.-V. Reun. Cons. int. Explor. Mer*, 180: 323-334.
- WALSH, J. J. — 1981. A carbon budget for overfishing off Peru. *Nature*, 290: 300-304.
- WALSH, J. J., J. C. KELLEY, T. WHITLEY, J. J. MACISAAC, and S. HUNTSMAN. — 1974. Spin-up of the Baja California upwelling ecosystem. *Limnology and Oceanography*, 19: 553-572.
- WATSON, E. — 1978. Role of bacteria in an upwelling ecosystem, pp. 139-154. In: R. BOJE and M. TOMCZAK (eds.), *Upwelling Ecosystems*, Springer, Berlin.