Some Development Patterns of Plankton Communities in the Upwelling Areas of the Pacific Ocean

M.E. Vinogradov and E.A. Shushkina

Shirshov Institute of Oceanology, Academy of Sciences USSR; Moscow, USSR

Abstract

The principal trophic levels, each subdivided into groups of organismic elements, are distinguished in the planktonic communities of the Eastern Equatorial and the Peruvian upwellings. Production intensity or metabolism have been determined experimentally for all elements. A scheme is suggested for computing production from data on metabolism for all the elements of a community, as well as for computing net and real production and other functional characteristics for definite trophic levels and the community as a whole. Based on the quantitative estimation of the efficiency of primary production and other functional characteristics, the development of communities is divided into production and destruction periods; they are, in turn, subdivided into steps associated with a certain degree of water trophicity. The balance of net production of the communities in the Peruvian upwelling indicates that the excess production of a community above the shelf is utilized completely in the narrow (100 to 150 sea miles) band of off-shore water. This paper describes an attempt to trace the changes taking place in the functional characteristics of plankton communities and to compare them with the changes observed in the communities of the Peruvian and East-Equatorial upwellings.

Introduction

In modern bio-oceanology, increasing attention is being paid to the study of the patterns of functioning of marine communities and ecosystems. Biological processes in the ocean are most intensive in areas of tropical upwellings. Here, the earliest stages of development and patterns of matter and energy transformation in the communities may be traced in their "purest" form. That is why the study of the communities of these regions is of particular interest.

Several specific cruises were organized by the Plankton Laboratory of the Institute of Oceanology of the USSR Academy of Sciences on the R.V. "Vitiyaz" (Cruises 44, 50, 52) and the R.V. "Akademik Kurchatov" (Cruise 17) for the study of the pelagic communities of tropical regions and their zones of most intensive upwelling. The major results of investigations carried out in the areas of the Equatorial and Peruvian upwellings have been set out in "Ecosystems of the pelagic zone of the Pacific Ocean" (Vinogradov, 1975) and in articles by Vinogradov (1974, 1978), Vinogradov et al. (1976, 1977), Mikheev (1977), Sorokin (1977, 1978), Shushkina et al. (1978), Sukhanova et al. (1978) and others.

Materials and Methods

Field material was collected during Cruise 17 of R.V. "Akademik Kurchatov" at the equator between 97° and 155°W (14 January-7 February, 1974), and along a 130-mile section from the coast of Peru (Cape Pacasmaio, 7°30'S) into the ocean (27 February-4 March, 1974), in the 0 to 150-200 m layer (Fig. 1). A detailed characterization of the area investigated, as well as sampling technique and treatment of collected material has been presented by Vinogradov (1974, 1975), Fedorov et al. (1975a, b), and Sorokin (1978).

The taxonomic composition of microplankton (organisms smaller than 1-2 mm) as well as its concentration and vertical distribution were estimated from samples taken with a 140 1 Plexiglas water bottle. Sampling depths were deter-
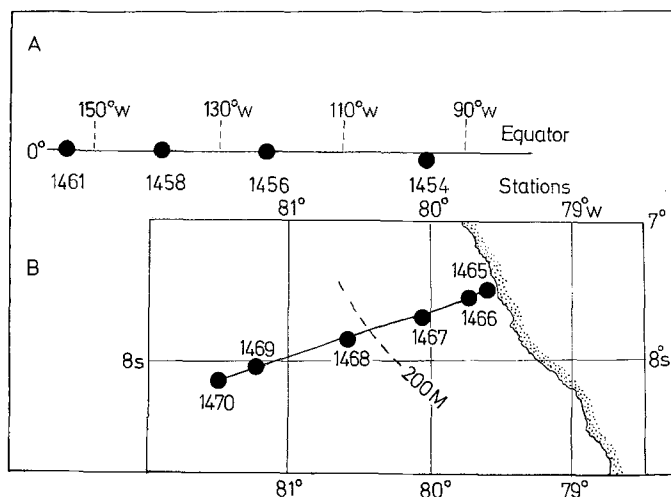
Fig. 1. Location of R.V. "Akademik Kurchatov" stations in areas of East-Pacific upwellings: (A) Stations at Equator; (B) stations on Peruvian coast

mined by preliminary measurements (continuous recordings) of the vertical distribution of temperature, salinity, density, turbidity, chlorophyll luminescence and field of bioluminescence. The samples were collected at the extreme points of these curves or at the depths of maximum gradients. Most of the microplankton elements could be examined using a single sample, a procedure that permitted minimum bias arising from differences in time of collecting outboard samples. The phytoplankton and bacterioplankton from these samples were examined and production, bacterial destruction using the ^{14}C method and the value $K_2 = 0.25$ for bacterioplankton were determined by Sorokin et al. (1975a, b) and Sukhanova et al. (1978). Zooflagellates and infusorians have been dealt with by Tumantseva and Sorokin (1975), and other zooplankton by Vinogradov et al. (1976) and Mikheev (1977).

Organisms ranging in size from 1 to 20-30 mm were recorded from vertical stratified hauls taken with a 80/113 JOM net (mouth opening 1 m^2) and filtering cone made of sieve No. 38 (180 μm) (Flint, 1975; Timonin and Voronina, 1975; Mikheev, 1977).

Analysis of the collected material revealed the following basic trophic groups of plankton communities: phytoplankton (p), bacteria (b), heterotrophic flagellates (a_1), infusorians (a_2), non-predatory zooplankton — small (m) and large (f), and zooplankton with predominantly carnivorous food habits — small (s) and large (v). Each trophic level was, in

turn, divided into smaller trophic groups of organismic elements according to size composition and type of feeding (Table 1).

The experimental material obtained during Cruises 44, 50 and 52 of the R.V. "Vitiyaz" and Cruise 17 of the R.V. "Akademik Kurchatov" allowed quantitative determination of the basic ecological-physiological characteristics of the elements recognized in the communities; however, as the estimates of mean dial rations of the various animals (Pavlova et al., 1971; Petipa et al., 1971, 1975; Arashkevich, 1975) varied widely depending on the effect of a number of factors not lending themselves to recording, these could not be used as a basis for calculations.

More reliable results were obtained from determinations of the rates of metabolism and oxygen consumption, the micromanometric method being used for microplankton (Klekovski et al., 1975), and the polarometric method or the Winkler technique for larger plankters (Shushkina and Pavlova, 1973; Musaeva and Vitek, 1975; Musaeva and Shushkina, 1978, and others). Oxygen consumption was measured at the in situ temperatures of the communities investigated. As the value R (respiration) differed but little in closely related animals living at 20°C in areas of intensive upwelling and at 30°C in oligotrophic waters (Musaeva and Shushkina, 1978), the metabolism-weight relationship $R = f$ (W) was used without introducing corrections for temperature. The caloricity of the various organismic elements (Shushkina, 1977) and the intensity of production of some of them (Shushkina and Pavlova, 1973; Shushkina and Kislyakov, 1975) were determined.

A scheme of energy flow through the community, based on field and experimental data, was constructed for each station (Fig. 2).

The production and food consumption values of the elements were calculated from experimental determinations of metabolic rate, using the maximum value of expenditure for growth (K_2^{max}) accepted from numerous data from the literature and personal experimental data.[1] A K_2^{max} = 0.6 was assumed for different-aged populations, which comprised most of the elements of the communities investigated; and a K_2^{max} = 0.7 for the two elements (meroplankton and juvenile euphausiids) which consisted mostly of larval forms.

The functional characteristics were calculated in accordance with the follow-

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[1] Phyto- and bacterioplankton production was determined experimentally using the ^{14}C method.

Table 1. Characteristics of elements of plankton communities in Pacific upwellings

| Trophic levels and groups	Size (length), L	Predominant weight, w (mcal)	Cal mg wet weight^{-1}	Metabolism $R = aw^b$		Assimilability U^{-1}
				a	b	
Phytoplankton, p						
Nanno	4–7 μm		1.0			
Small, p_1	8–20 μm		0.7			
Medium, p_2	21–100 μm		0.4			
Large, p_3	>100 μm		0.2			
Bacteria, b	1–5 μm		1.0			1.0
Unicellular heterotrophs, a						
Flagellates, a_1	3–5 μm	4×10^{-5}	0.8			0.6
Ciliates, a_2	10–100 μm	5×10^{-3}	0.8	0.26	0.76	0.6
Non-carnivorous metazoan plankton						
Fine filterers, m						
Meroplankton, m_1	0,1–3,5 mm	2–30	0.7	0.59	0.76	0.6
Appendicularians, m_1	0,1–2,5 mm	1–10	0.1	5.27	0.66	0.6
Doliolids, m_1	1–2,5 mm	4–10	0.01	5.27	0.66	0.6
Small calanoids, m_2	<1 mm	1–5	0.7	0.80	0.73	0.6
Coarse filterers, f						
Medium-sized calanoids, f_1	>1 mm	30–100	0.7	0.80	0.73	0.6
Juvenile euphausiids, f_2	<10 mm	120–2000	0.7	0.42	0.90	0.6
Predatory zooplankton						
Cyclopoids, s_1	0,2–1,5 mm	3–6	0.7	0.44	0.60	0.7
Calanoids, s_2	1,0–4 mm	500–2000	0.7	0.80	0.73	0.7
Small tomopterids, s_2	<3 mm	30–80	0.7	0.59	0.76	0.7
Small coelenterates, s_2	<5 mm	10–30	0.03	6.38	0.58	0.7
Chaetognaths, v	<20 mm	500–1200	0.7	5.30	0.52	0.7
Polychaetes, v	>3 mm	1300–8400	0.7	0.59	0.76	0.7
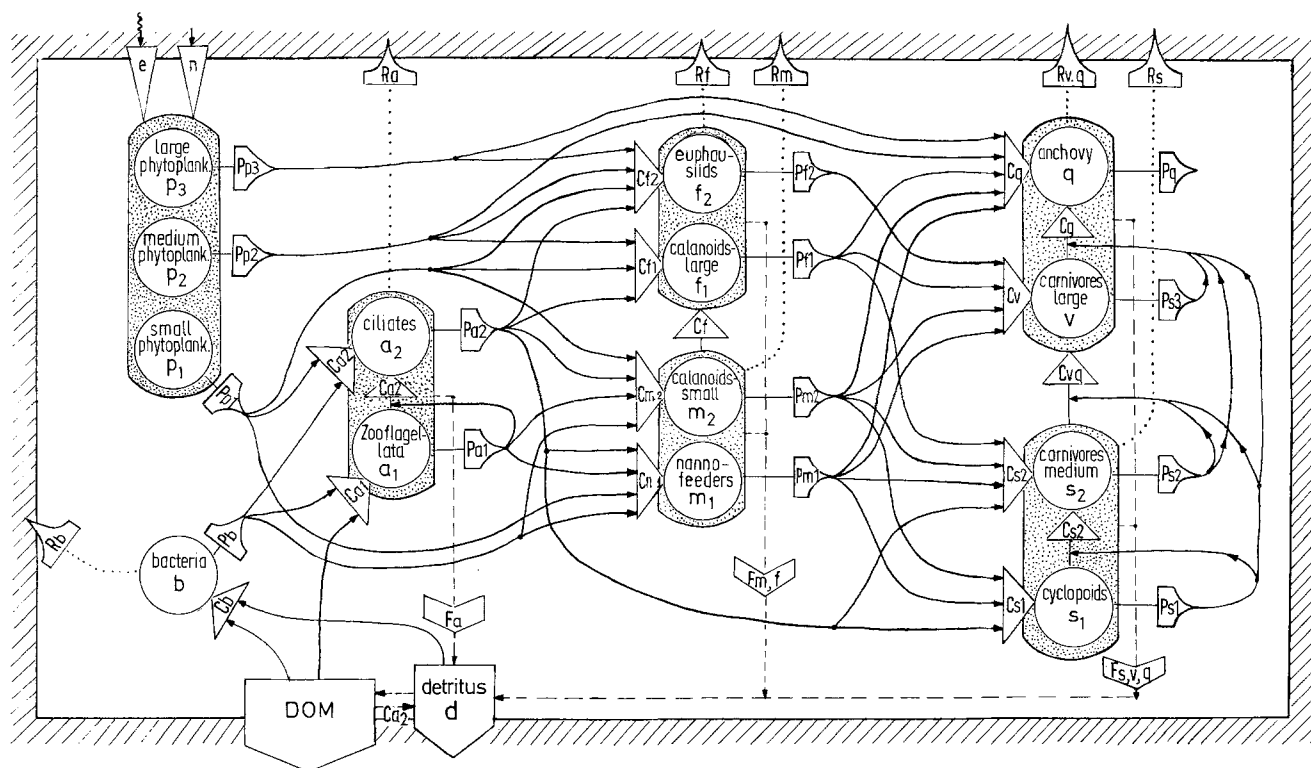
Fig. 2. Scheme of energy transfer through a plankton community in the zone of upwelling. e: solar radiation; n: nutrients. For explanation of other terms, please refer to Table 1 and text equations (1) to (3)

ing scheme, developed by E.A. Shushkina (Vinogradov *et al.*, 1976): The value of the maximum food consumption, c^{max}, assuring maximum growth of the populations, p^{max}, of each zooplankton element of the community was determined from the known relationship

$$c^{max} = (p^{max} + R) \times U, \qquad (1)$$

where R is metabolic rate and U^{-1} is food assimilability.

The value p^{max} was determined from the relationship

$$p^{max} = R \cdot \frac{K_2^{max}}{1 - K_2^{max}} = R \times K_3^{max}. \qquad (2)$$

The maximum particular ration, r_{ij}^{max} of each ith element was determined from the relationship:

$$r_{ij}^{max} = C_i^{max} \times \frac{B_j \times I_{ij}}{\sum\limits_{k=1}^{n} I_{ik} \times B_k} = C_i^{max} \times G_{ij} \qquad (3)$$

where I_{ij} is the coefficient of feeding selectivity, which value has been discussed previously (Vinogradov *et al.*, 1976).

The real particular ration r_{ij} may be determined by using Ivlev's equation (Ivlev, 1955):

$$r_{ij} = C_i^{max} \times G_{ij} \left(1 - e^{-\frac{\xi_i I_{ij} \cdot B_j}{\sum\limits_i r_{ij}^{max}}} \right), (4)$$

where ξ = the coefficient close to unity (Menshutkin, 1971).

The real total ration of the ith group, C_i, was calculated as the sum of particular rations:

$$C_i = \sum_{j=1}^{n} r_{ij}, \qquad (5)$$

and the total consumption of the jth group was calculated as:

$$E_j = \sum_i r_{ij} . \qquad (6)$$

The production of the ith element was determined from the equation:

$$P_i = C_i U^{-1} - R_i . \qquad (7)$$

The production efficiency of any element, trophic group or trophic level of the system was evaluated by

$$K_3 = P/R , \qquad (8)$$

a value widely used in hydrobiological investigations of production.

A more convenient characteristic is, in our opinion, the ratio of assimilated food $A = P + R$ to the metabolic expenditure R, which we name efficiency of food assimilation:

$$H = \frac{A}{R} = \frac{P + R}{R} . \qquad (9)$$

A rise of H at R = constant signifies a greater expenditure for growth of the energy from assimilated food. At $P = 0$ the value H = 1. A minimum value, H ≈ 0, signifies that metabolism is assured only by the biomass present, and that there is no external supply of energy to this trophic level.

The value H is convenient for characterization of the production process in waters with different trophic conditions. If the metabolic rate is assumed to be constant under changing feeding conditions, then a reduction in efficiency of food assimilation will signify a decrease in the trophicity of the water.

Besides these indices, the following functional characteristics were used:

degree of satisfaction of food requirements (Menshutkin, 1971)

$$\delta = \frac{C}{C^{max}} , \qquad (10)$$

degree of approximation of observed production to maximum possible production

$$\beta = P/P^{max} , \qquad (11)$$

balance of production and consumption (Vinogradov *et al.*, 1976)

$$\varepsilon_j = \frac{P_j}{\sum\limits_i^n r_{ij}} = \frac{P_j}{E_j} . \qquad (12)$$

The maximum and minimum values of the above characteristics and their relationship with other functional indices are given in Table 2.

The data obtained made it possible to calculate the basic production characteristics not merely for the individual elements but also for the basic trophic levels and the entire community.

Most representative are:

(1) Real zooplankton production P_r, i.e., the production that may be utilized by higher trophic levels not accounted for in the calculations (carnivorous fishes, squids), or by any other form of exploitation (Shushkina, 1966):

$$P_r = \sum_{i=a}^{s} P_i - \sum_{i=f}^{s} C_i . \qquad (13)$$

Similar relationships were used for calculations of the production of protozoans (P_a) and non-predatory (P_f) and predatory (P_s) zooplankton, i.e., for groups in which cannibalism occurs.

Table 2. Estimates of some structural/functional characteristics

Structural/functional characteristics	Determination	Relationship with other characteristics	Minimum value at		Maximum value at		Characteristic value at	
Efficiency of food assimilation	$H = \frac{P+R}{R}$	$H = K_3 + 1$ $H^{max} = (1-K_2^{max})^{-1}$	0	$R = -P$	2.5 4.0	$K_2^{max} = 0.6$ $K_2^{max} = 0.75$	>1 <1 =1	$P > 0$ $P < 0$ $P = 0$
Degree of approximation to maximum production	$\beta = \frac{P}{P^{max}}$	$\beta = \frac{K_3}{K_3^{max} i}$	0	$R = 0$	1	$P = P^{max}$	0.67 0.43	$P = R \; K_2^{max} = 0.6$ $P = R \; K_2^{max} = 0.7$
Degree of satisfaction of food requirements	$\delta = \frac{C}{C^{max}}$	$\delta = H(1-K_2^{max})$, if U^{-1} = constant	0	$C = 0$	1	$C = C^{max}$	0.4 0.3	$P = R \; K_2^{max} = 0.6$ $P = R \; K_2^{max} = 0.7$

Table 3. Production-destruction characteristics of plankton of Pacific upwellings (kcal m^{-2} 24 h^{-1})

Area investigated and station no.	Depth layer (m)	Community biomass, B	Phytoplankton production, P_p	Destruction of heterotrophs, $R_{b-s} = D$	$K_{3p} = P_p/D$	Net production, P_0 of community
Peruvian upwelling						
1465	0-10	58.1	23.1	19.0	1.22	4.1
1466	0-25	75.9	55.9	33.5	1.67	22.4
1467	0-70	142.7	89.7	42.0	2.14	47.7
1468	0-125	134.8	30.2	38.1	0.80	-7.9
1469	0-150	72.3	12.6	23.2	0.54	-10.6
1470	0-150	43.1	13.2	17.4	0.75	-4.1
Equator						
1454	0-150	45.0	18.0	15.3	1.18	2.7
1456	0-150	10.1	5.0	10.1	0.5	-5.1
1458	0-150	12.0	3.2	8.6	0.37	-5.4
1461	0-150	10.7	4.2	13.1	0.32	-8.9

(2) Net production of the whole plankton community P_0, which according to Winberg (1934, 1960) is equal to

$$P_0 = P_p - \sum_{i=b}^{s} R_i, \qquad (14)$$

where P_p is primary production. The value P_0 can also be calculated in another way (Zaika, 1972; Shushkina, 1977):

$$P_0 = \sum_{i=p}^{s} P_i - \sum_{i=b}^{s} C_i \cdot U^{-1}. \qquad (14a)$$

(3) Intensity of total plankton production (specific production):

$$c = \frac{P_0}{B}, \qquad (15)$$

where $B = \sum_{i=p}^{s} B_i$.

(4) The ratio of net primary production to total destruction (Winberg,

1960) or efficiency of primary organic matter production, K_{3p}:

$$K_{3p} = \frac{P_p}{\sum\limits_{i=b}^{s} R_i} = \frac{P_p}{D}. \qquad (16)$$

At $K_{3p} > 1$, $P_0 > 0$, which signifies that the formation of primary organic matter exceeds total destruction thereof and that conditions correspond to the production period of the succession. At $K_{3p} < 1$, the $P_0 < 0$, which is characteristic of the destruction period of the succession.

The functional characteristics listed above were calculated in accordance with the described scheme for each of the 10 points of observations (Table 3) on the computer HP-3000, using the programmes prepared by L.P. Lebedeva to whom the authors wish to express their sincere gratitude.

Results and Discussion

All characteristics studied were found to vary in Pacific upwellings from area to area (Table 3). This implies, that the communities in question are at different stages of succession. Evidence for this is provided first of all by the regular change in the efficiency of primary production (K_{3p}). This value is somewhat greater than unity during the earliest stages of community development in the centre of the patch of ascending water in intensive coastal upwellings (Station 1465), when a bloom of phytoplankton has not as yet developed in the newly upwelled water and zooplankton also is very scarce. Closer to the periphery of the local patch of upwelling, where primary production reaches its maximum, the value K_{3p} rises to 2.1, falling again with the development of zooplankton populations. The drop is most abrupt in the frontal zone between the local shelf upwelling and offshore general background upwelling, where huge aggregations of herbivorous euphausiids (*Euphausia mucronata*) are formed, attaining up to 27 g of wet weight per m³.

According to observations in marine and freshwater basins, the value K_{3p} usually varies from 1.0 to 2.0 during the production period of succession. In lakes and fish ponds with highest productivity, maximum values of K_{3p} are close to 5 with a seasonal average of about 2 to 3 (Winberg, 1934, 1960).

With distance from the area of most intensive upwelling, both at the Peru coast and at the equator, K_{3p} drops below 1.0. Destruction processes prevail over the formation of organic matter. In the early stage of the destruction period K_{3p} is fairly high, varying between 1.0 and 0.5 off the shelf in the background of the Peruvian upwelling (Stations 1469 and 1470); it falls to 0.5-0.3 in the more adult communities at the equator between 120° and 155°W, with a concomitant decrease of upwelling intensity and trophicity of the water. In oligotrophic waters, the value apparently drops below 0.2.

Similar relationships between primary production and destruction with decreasing trophicity of the water were traced in other marine bodies of water and in freshwater lakes and reservoirs. Maximum values of K_{3p}, calculated for the vegetation period from data cited by Winberg (1976), reached 1.5 in eutrophic lakes, were close to unity or somewhat lower in mesotrophic lakes, and fell to 0.8-0.4 in oligotrophic lakes.

The changes in K_{3p} accompanying the maturing of communities permit the iden-

tification of well defined production and destruction periods. The production period was found to be confined to hypertrophic waters with a primary production of more than 25 kcal m⁻³ per 24 h (kcal up to 50 and even 90 kcal m⁻³), while the destruction process develops in eutrophic (P_p = 10 to 25 kcal m⁻³ 24 h⁻¹), mesotrophic (P_p = 2.5 to 10 kcal m⁻³ 24 h⁻¹) and oligotrophic (P_p <2.5 kcal m⁻³ 24 h⁻¹) waters.

The classification of water types by the values of primary production for oceanic hypertrophic, eutrophic and mesotrophic waters given in Table 4[2] coincides with the classification of Winberg (1960) for freshwater basins, and differs from the classification of Steemann Nielsen and Jensen (1957) and Koblentz-Mishke (1965) in that it includes in addition the hypertrophic waters of intensive upwellings.

The restriction of the productive period in the development of communities to hypertrophic waters only is probably a feature characteristic of the most highly productive tropical regions of the ocean, i.e., of upwelling areas. In communities formed in poorer areas, productive phases of succession may occur in less trophic waters; however, in such cases, the values of net production will be lower. In this case too, the waters in which the communities pass through productive and destructive phases of development differ with regard to trophicity. The problem is of great interest and requires further detailed research.

The maturity-dependent changes in K_{3p}, in conjunction with changes in other structural/functional characteristics such as biomass, species and trophic diversity, production of trophic groups etc. (Shushkina *et al.*, 1978), make possible a further subdivision of the production and destruction periods into stages or "steps" of community development. Such a subdivision is naturally rather conditional, but it allows, for instance, the communities of the Peru and Equatorial upwellings to be ranked

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[2] Station 1454, at the equator (Latitude 97°W), is not included in Table 4. At this station, the waters of the Cromwell Countercurrent which carry from the west a more mature community with many predators, rise to the very surface, thus creating conditions favourable for the formation of a young upwelling community. The resulting mixed community is characterized by features inherent in both very young and fully mature communities, and its functional singularities require special investigation. At Station 1468, macroplankton euphausiids >10 mm were not recorded.

Table 4. Accepted development stages of community using parameter $K_{3p} = P_p/D$ and water trophicity of Pacific upwellings. nd: no data

Range of K_{3p}	Devel-opment stage	Station No.	K_{3p}	Type of water	Period of succes-sion
1.0-1.5	1	1465	1.22		
1.5-2.0	2	1466	1.67	Hyper-trophic	Produc-tive
>2.0	3	1467	2.17		
2.0-1.5	4	nd	nd		
1.5-1.0	5	nd	nd		
1.0-0.8	6	1468	0.8		
0.8-0.7	7	1470	0.75	Eu-trophic	
0.7-0.6	8	nd	nd		
0.6-0.5	9	1469	0.54		Destruc-tive
0.5-0.4	10	1456	0.5	Meso-trophic	
0.4-0.3	11	1458	0.37		
0.3-0.2	12	1461	0.32		

Fig. 3. Changes in (1) efficiency of primary production (K_{3p}) and (2) specific production (C) of the communities in waters of the Peruvian and Equatorial upwellings

according to their K_{3p} value, which reflects their degree of maturity (Table 4; Fig. 3).

Let us consider, step by step, the maturity-dependent changes in some other functional characteristics.

Fig. 4 illustrates such a change in the food assimilation efficiency of some trophic groups. With decreasing trophicity and progressing development, this value decreases substantially, the drop being most marked in mesotrophic waters.

There is also a decrease in the efficiency of production (K_{3p}), the degree of satisfaction of food requirements (δ), and in the efficiency of food assimilation (H) for the basic trophic levels of the communities investigated (Table 5). For predatory zooplankton all these characteristics reach their maximum values not at the early, but at the more mature stages of community development. This is accounted for by the slower development of predatory zooplankton compared with herbivores, and by the conditions most favourable for the development of carnivores setting in at a later period than for phytophages (Vinogradov et al., 1973).

The changes that take place in the balance of production and consumption of different trophic groups (ε) are highly characteristic. With the maturing of the community and the impoverishment of the water, the balance improves and ε approaches unity. In rich waters where production exceeds consumption, ε rises above 1; in mesotrophic waters it is below 1, which points to over-utilization of prey production. However, it must be kept in mind that the balance tends to change considerably with increasing depth, so that — as has been demonstrated for the Equatorial upwelling (Vinogradov et al., 1977) — at one and the same sta-
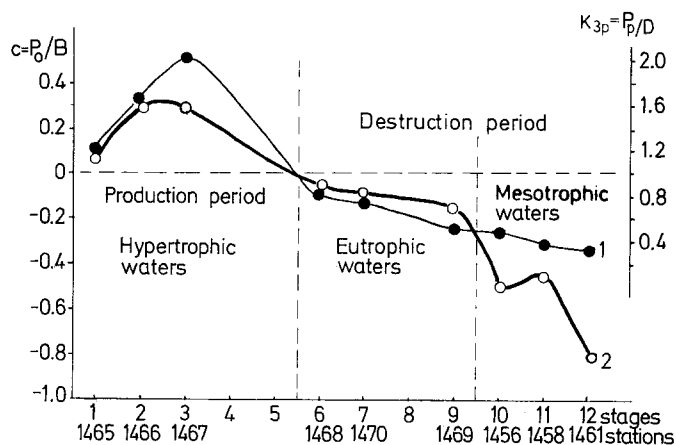

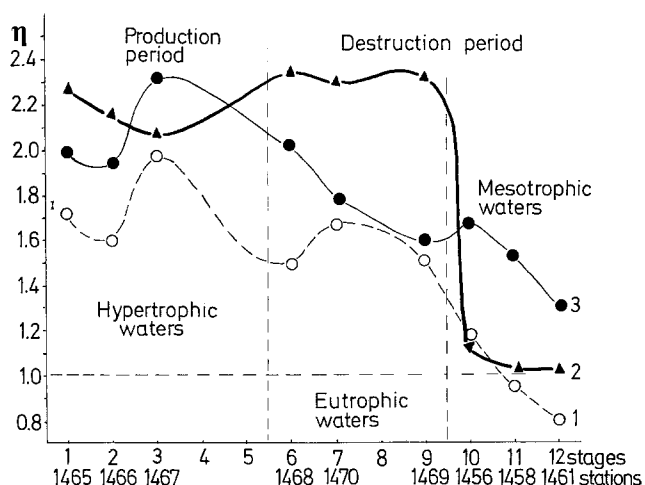Fig. 4. Changes in efficiency of food assimilation (H) in the different trophic groups of the communities of the Peruvian and Equatorial upwellings. 1: Carnivorous zooplankton; 2: non-predatory zooplankton; 3: protozoans

Table 5. Structural/functional characteristics of trophic levels of zooplankton in waters of different trophicity in Pacific upwellings

Trophic groups and water type	$H = \dfrac{P+R}{R}$	$\delta = \dfrac{C}{C^{max}}$	$\varepsilon = \dfrac{P_j}{E_j}$
Protozoans, a			
Hypertrophic	1.76	0.73	1.94
Eutrophic	1.60	0.62	1.50
Mesotrophic	1.05	0.43	0.60
Non-predatory metazoan zoo-plankton, f			
Hypertrophic	2.13	0.80	2.83
Eutrophic	1.70	0.66	1.17
Mesotrophic	1.49	0.50	0.50
Carnivorous metazoan zoo-plankton, s			
Hypertrophic	1.98	0.84	2.48
Eutrophic	2.24	0.89	1.84
Mesotrophic	1.04	0.65	0.50

Table 6. Characteristics of plankton communities in waters of different trophicity in Pacific upwellings. Values are in kcal m^{-2} 24 h^{-1}. (For definition of "protofood" see Footnote 3 in text)

Type of water	Total plankton biomass, $B = \sum_{i=p}^{s} B_i$	Primary production, P_p	P/B of phyto-plankton per 24 h	$K_{3p} = P_p/D$	Contribution of primary production to "protofood" production P_p/P_{p+b}	Contribution to destruction of primary production by		Specific plankton production $c = P_o/B$
						Bacteria R_b/P_p	All hetero-trophs, D/P_p	
Hypertrophic	92	46.7	0.6-1.8	1.5	0.9	0.47	0.67	0.2
Eutrophic	84	18.7	0.3-1.5	0.7	0.8	0.72	1.48	-0.1
Mesotrophic	1o	4.1	1.3-3.5	0.4	0.6	1.58	2.5	-0.6

tion the production of individual trophic groups may be under-utilized in certain depths, and over-utilized in others. Changes in some other functional characteristics of the communities of the Peruvian and Equatorial upwelling have been discussed previously in greater detail (Vinogradov et al., 1976; Mikheev, 1977).

The differences in the functional state of communities at different stages of maturity and inhabiting waters with different trophic conditions are presented in Table 6.

With progressive decrease in biomass and primary production (such decreases in the waters investigated are about 1 order of magnutide), the efficiency of primary production (K_{3p}) decreases to the same extent (Table 6). The contribution of primary production to total production of "protofood"[3] (P_p/P_{p+b}) is reduced by almost one-half. Naturally, all these changes tend to increase the destructive potential of bacteria in the community, and bacterial dispersion of the energy of primary production (R_b/P_p). Simultaneously, the dispersion of the energy of the entire heterotrophic part of the community (D/P_p) increases. In eutrophic and mesotrophic waters, the latter value rises substantially above 1 (Table 6). This signifies that the production of the community is negative, and that additional advection of organic nutrients is necessary for the sustenance of the communities inhabiting these regions. This is followed by a change in specific production (c) from positive in hypertrophic waters into negative in eutrophic and mesotrophic waters (Fig. 3).
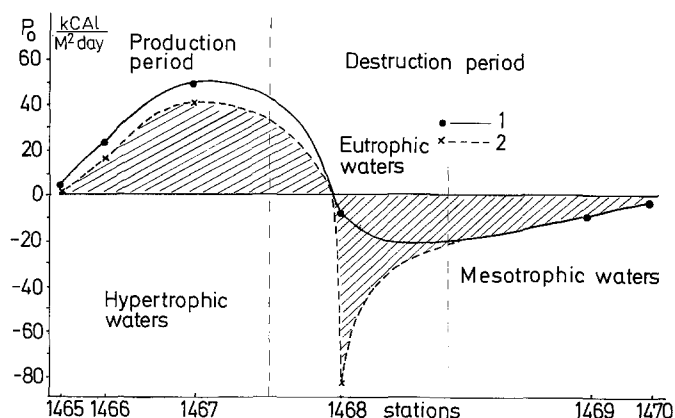

Fig. 5. Changes in value of net production of the plankton community in a 130-mile section from Cape Pakasmaio into the ocean. Figure shows net production of community not taking into account (1) and taking into account (2) anchovies and large euphausiids

An attempt was made to estimate the biotic balance of communities in a section through the zone of the Peruvian upwelling, and to explore how far in the ocean the utilization of surplus production from the rich waters of the shelf upwelling could be traced.

Fig. 5 shows the distribution of community net production (P_O) in a 130-mile section extending from Cape Pacasmaio into the ocean. The communities over the shelf were in the productive phase of development ($P_O \gg 0$) and those off the shelf, in the background zone of the upwelling, were in the destructive phase ($P_O < 0$). In a 1 m-wide band over the shelf, the plankton community was found to under-utilize 3,840 kcal of the energy produced. If grazing by anchovy[4] is taken into account, the value decreases to 2,960 kcal. At the same time, the plankton community off the shelf has a

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[3] Under the term "protofood" Sorokin (1973) combines phyto- and bacterioplankton. According to Sorokin, the bacterioplankton of tropical waters acts as a pseudoproducer, by assimilating substantial amounts of dissolved allochthonous organic matter and thus introducing it into the food chains of the communities.

[4] For method of estimation of anchovy production see Shushkina et al. (1978).

deficit of 1,900 kcal, which increases to 2,870 kcal if the aggregations of large euphausiids in the front zone are taken into account. Thus, the balance of net production in the section is close to zero (2960 - 2870 = 90 kcal). The calculation is very rough and approximate, not allowing for the outflow of organic matter from the system and influence of currents; nevertheless, it shows that in the region investigated the organic matter (energy) produced by pelagic communities is practically fully utilized in the relatively narrow 150-mile coastal zone and, consequently, cannot contribute substantially to the productivity of more remote oceanic regions, at least at the trophic levels investigated.

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Dr. M.E. Vinogradov
Institute of Oceanology
Academy of Sciences of the USSR
23 Krasikova
Moscow 117218
USSR