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13

PECULIARITIES OF REPRODUCTION AND GENERATIVE PRODUCTION OF TROPICAL COPEPODS

PARTICULARITES DE LA REPRODUCTION ET DE LA PRODUCTION DES COPEPODES TROPICAUX

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Rational use of biological resources in open ocean areas is feasible on condition that regularities occurring in all sections ot the ecosystem are studied. Significance of planktonic copepods in the pelagic zone is great, but lack of evidence on reproduction results in underestimation of productive generative characteristics.

The aim of the present investigation consisted in revealing the regular natural changes of fecundity in mass pelagic copepods of the World ocean tropical zone. Particular emphasis was placed on determination of the clutch size, duration of development, rate of generative production formation at both organism and population levels, and connection of these processes with environmental conditions. The major difficulty lay in the fact that most mass species of tropical copepods are laying eggs immediately into water thus complicating the determination of quantitative characteristics of reproduction.

Though all the findings were obtained in laboratories of expedition vessels, these can characterize the natural fecundity of copepods, since the number of eggs matured under natural conditions and laid by females right after catching was taken as an initial value.

MATERIAL AND METHODS

The investigations involved 9 expeditions of research vessels covering the tropical zone of three oceans ; 1863 fertility determinations included 61 species. Of these, 3 species appear common for the three oceans: 18 for the Atlantic and the Indian, 1 for the Pacific and the Atlantic, and 2 for the Pacific and the Indian oceans.

The material was collected at drifting stations using Juday nets (oceanic model) and a hyponeustonic trawl of the MNT type. Catching was carried out within vertical layers of 0-100 and 0-150 m, or in surface layers with thickness from several centimeters to 10-15 m. Mature females were kept singly in cups of 150-200 ml filled with infiltered sea water taken from the layer containing maximum concentration of suspension and plankton, or taken just from the ocean surface.

Mass of females and eggs was estimated according to the body volume (Petipa, 1957). Reproductive characteristics were determined by the following

categories: *absolute clutch size* (E_n, E_m), i.e. average egg number or average egg mass^{-1} laid by a female per one laying, eggs.female^{-1} .clutch^{-1}, mg.female^{-1}. clutch^{-1}; *relative clutch size* (E%), i.e. egg mass failling within a female's unit of mass in per cent; *reproduction rate or fecundity* (B9, i.e. number of eggs laid by a female per unit of time, eggs.female^{-1}.day^{-1}; *absolute daily generative increment* (P_g), i.e. mass of eggs laid by a female per day, mg.female^{-1}.day^{-1}; specific daily generative increment (Cg), i.e. mass of eggs laid daily versus female's body weight, per cent. Besides, estimations included finding the number of fertile females in populations and the number of species showing reproduction at the time of investigation.

FECONDITY

Reproduction of copepods is associated with temperature, size of females, and food (Marshall and Orr, 1955; McLaren, 1978; Durbin et al., 1983). In our study, we have registered an intensive reproduction of copepods in the neighbourhood of deep water rise zones in the African and Peruvian shelves. These were the neritic and farneritic phytophagans ans euryphagans which were laying eggs into water in large quantities at one go (from 50 to 80-130 eggs.female^{-1}.clutch^{-1}). Such clutch sizes have been obtained in the region where Brazilian and Falkland currents meet in the Atlantic, and in the open regions of the Indian Ocean limited by the local dynamically active waters (Zazhina, 1980, 1982, 1985). Reproduction of predators and interzonal euryphagans was observed over the entire aquatorium unter study. Most of these species bear their eggs-sacs with small number of large (20-25) or great number of small eggs (50-150 eggs.female^{-1}.clutch^{-1}). With the departure from dynamically active productive zones, predators were showing insignificant reduction in clutch sizes (by 1.3-1.5 times).

Correlation of clutch sizes with temperature, length, and mass of females, and also with primary production of the 100 m layer and mesozooplankton biomass of the same layer has revealed a relative linear direct relation between phytophagans, euryphagans and primary production, as well as between predators and mesozooplankton biomass (Table 1). Laying rate is of greater dependence on temperature that clutch sizes (Runge, 1984) with females exhibiting better fecundity when provided with better nutritional conditions (Bernard, 1970).

The number of fertile females in populations varied with 30- 70 per cent, being maximum in dynamically active productive waters, and decreasing with the departure from them. Average female reproduction in phytophagous populations was higher (25 per cent) as compared with predators (18 per cent). Up to 20-30 per cent of copepods, out of all species available, were reproduced in dynamically active productive and coastal zones, while 10 per cent pertained to oligotrophic zones.

Due to high temperature of surface waters (25-30° C), duration of clutch development was rather short. The species laying eggs into water exhibited the least duration (0.5-2 days). Development of eggs in eggs-sacs was much more lasting (3-6 days).

Fecundity, the resultant of absolute clutch sizes and duration of the egg development, appeared to be higher in phytophagans and euryphagans then in predators. Maximum values were obtained in the Peruvian shelf: 138 eggs.female^{-1} .day^{-1} in *Temora discaudata*, 130 in *Centropages brachiatus*, and 110 in *Calanus australis*. In the African shelf, the maximum fecundity reached 108 eggs.female^{-1}.day^{-1} in *T. discaudata*. The latter species showed the same values in the region of the southern subequatorial divergence of the Indian ocean. Copepods of larger

sizes, e.g. *Undinula darwinii* had maximum values in these water amounting to 94 and 78 eggs.female^{-1}.day^{-1}. Fecundity of *Euchaeta marina*, a predator breeding in all the three oceans, varied from 1.8 to 4.5 eggs.female^{-1}.day^{-1}.

Relative clutch size reflects reproductive capacity of copepods and ensures carrying out a comparative analysis of quantitative consumptions of matter and energy required for formation of generative production in different ecological groups. Maximum values belong to phyto- and euryphagans (50 per cent), thus exceeding considerably those belonging to predators (10 per cent).

GENERATIVE PRODUCTION

Average daily absolute generative increments varied from 1 to 70 μg.female^{-1}.day^{-1} amounting to 0.5-32 per cent of a female's mass. Predators were characterized by least values.

Distribution of generative production over the aquatorium under study was considered while polygons laid out in the Indian ocean were taken as an example. The characteristics were estimated with regard for individual generative increases, number of females in the 0-150 m layer, and percentage ratio of reproducing and non-reproducing females. Figure 1 shows generative production distribution over the polygon aquatorium in two mass copepod species, i.e. phytophagan *U. darwinii* and predator *E. marina*. Maximum values belonged to the phytophagans inhabiting the zones adjacent to currents with different directions (935 μg.m^{-3}). Maximum values found in the predator were attributed to stable, low dynamic oligotrophic waters (99 μg.m^{-3}). Composition of reproducing species may serve as an indicator of the hydrodynamic and, as a whole, productive characteristic of water masses: generative production of phytophagans dominates in divergent productive zones, that of predators dominates in less-dynamic oligotrophic zones.

Generative production of the copepods' cohort is given in figure 2. Maximum values are distinguished in the zone of hydrofront (0.94 mg.m^{-3}) and cyclonic (0.58 mg.m^{-3}) circulations. Minimum values are characteristic to anticyclonic circulations (0.05 mg.m^{-3}) and oligotrophic stable zones (0.04 mg.m^{-3}).

CONCLUSION

Reproductive characteristics of pelagic copepods indicate the state of the ecosystem. In large-scale and local dynamically active systems with high productivity (upwellings, hydrofronts, cyclonic circulations) generative production is much higher than in stable low-active and not very productive systems (Tabl.2).

The major role in the increase of generative production is played by neritic and hyperneritic phytophagans and euryphagans characterized by high reproductive capacities. Laying eggs into water, characteristic to species of this complex, is directed to the strategy of the population survival due to higher fertility under favourable, though sometimes short-term, alimentary conditions occurring in frontal and divergent zones. In low-dynamic zones, generative production is created by hyperneritic and oceanic predators with low reproductive capacities. Bearing eggs in sacs, typical of these species who are in active search for food over vast aquatorium, is obviously a strategy of the population survival at the expense of the progeny better adapted to exist after hatching. It is facilitated by longer terms of eggs development, and endogenous feeding of nauplii. Therefore, reproduction of predators in not limited by productive, often narrow-local, zones which occur over the entire water area ensuring totally generative contribution to production in oligotrophic waters.

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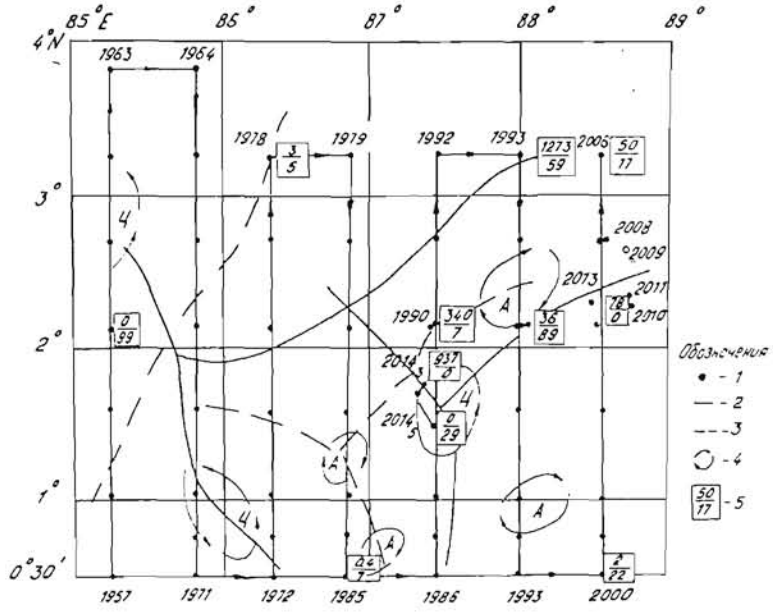

Figure 1 - Generative production distribution of phytophagan *U. darwinii* predator *E. marina* ($\mu g.m^{-3}$) in the 0-150 m layer. References : 1-polygon station ; 2-divergences ; 3-convergences ; 4-circulations ; 5-generative production, *U. darwinii* over *E. marina*.

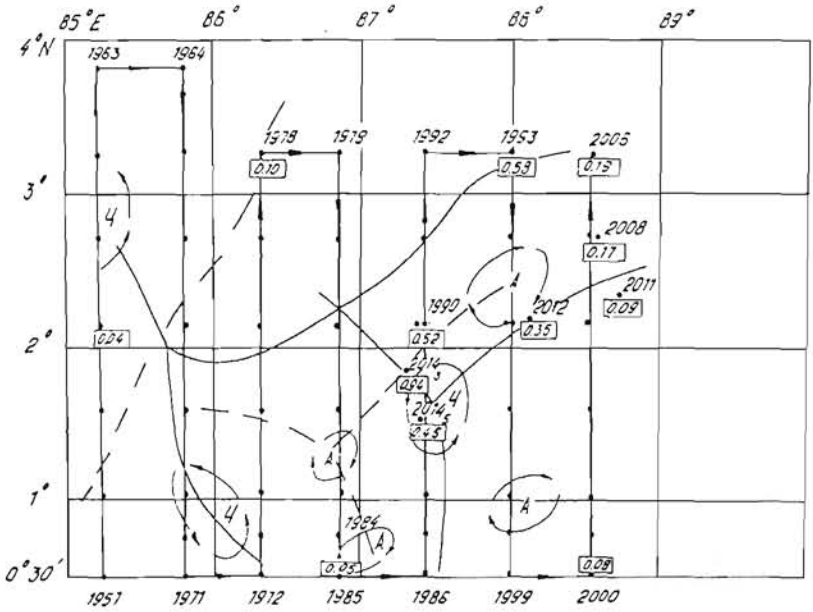

Figure 2 - Copepod generative production in the 0-150 m layer ($mg.m^{-3}$). References are similar to those of figure 1. Generative production is given for the entire cohort of copepods.

Region	Species	Number of observations	Range of values		Dependence	r
			E_n	P_g, $mgC.m^{-3}$		
Atlantic Ocean	Nannocalanus minor	6	25-57	118.2-1477.2	$E_n=25.88+0.018P_g$	0.96
	Clausocalanus furcatus	5	13-41	11.9-191.1	$E_n=15.17+0.125P_g$	0.86
	Pleuromamma borealis	12	10-23	84.9-249.2	$E_n= 8.52+0.072P_g$	0.77
	Pleuromamma gracilis	8	4-28	11.9-84.9	$E_n= 5.99+0.232P_g$	0.89
Indian Ocean	Undinula darwinii	14	13-84	22-134	$E_n= 42.2+3.7P_g$	0.65
	Clausocalamus furcatus	10	7-43	25-400	$E_n= 26.0+0.24P_g$	0.72
	Pleuromamma piseki	17	11-40	57-147	$E_n= 20.4+3.2P_g$	0.68
			E_n	B, $mg.m^{-3}$		
	Euchaeta marina	30	8.15	74.9-142.0	$E_n= 17.3-0.008$	0.42

TABLE I - RELATION BETWEEN ABSOLUTE CLUTCH SIZE (En) AND PRIMARY PRODUCTION OF THE 100 M LAYER (P_g) AS WELL AS MESOZOOPLANKTON BIOMASS (B)

Region	Primary production in 0-100 m layer, $mgC.m^{-2}.day$	Mesozoo-plankton biomass in 0-100 m layer, $mg.m^{-3}$	Type of food	Genus	Type of laying	Generative production in 0-100 layer, $\mu g.m^{-3}$
Eutrophic	>500	>100-500	phyto- and eury-phagans	Neocalanus, Nannocalanus, Undinula, Acrocalanus, Paracalanus, Clausocalanus, Temora, Centropages, Acartia	water	100-1000
			predators	Candacia, Scolecithrix	water	50
			predators	Euchaeta, Oncaea, Oithona	eggsac	20-100
Mesotrophic	<500>100	<100>50	phyto- and eury-phagans	Neocalanus, Nannocalanus, Undinula, Acrocalanus, Paracalanus, Clausocalanus, Temora, Centropages, Acartia	water	100
			predators	Candacia, Scolecithrix	water	20-50
			predators	Euchaeta, Oithona, Oncaea, Corycaeus, Sapphirina	eggsac	10-20
Oligotrophic	<100	<50	eury-phagans	Pleuromamma, Eucalanus	water	20
			predators	Euchaeta, Oncaea, Corycaeus, Sapphirina, Miracia	eggsac	10

TABLE II - GENERATIVE PRODUCTION OF TROPICAL COPEPODS IN DIFFERENT TROPHIC REGIONS OF THE OCEAN