

ESTIMATED ZOOPLANKTON PRODUCTION AND THEIR AMMONIA EXCRETION IN THE KUROSHIO AND ADJACENT SEAS

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ABSTRACT

Production and ammonia excretion of zooplankton in the Kuroshio and adjacent seas were estimated from field data of biomass, size distribution, and habitat temperature of zooplankton, and from experimental data of respiration and ammonia excretion rates as functions of body size and temperature. Winberg's basic balanced equations were applied to calculate production from respiration data. Further, mortality related to the lifespan and the ratio of herbivores to carnivores in the zooplankton community were estimated from theoretical assumptions.

In this study, 18-72% of primary production was grazed by herbivorous zooplankton, and production of herbivorous zooplankton (= secondary production) was 10-60 mg C/m² per day. The ecological efficiency between primary and secondary production was 5-22%. Ammonia-nitrogen excreted by zooplankton was 4-24 mg N/m² per day, which can support 11-44% of the nitrogen requirements of primary production.

In marine ecosystems solar energy photosynthetically fixed as organic matter by phytoplankton is channelled through zooplankton to nektonic fishes and crustaceans at higher trophic levels. Important features of the roles of zooplankton in this scheme are their extremely high conversion efficiency of phytoplankton organic matter (in contrast with terrestrial ecosystems, see Wiegert and Owen 1971; Steele 1974) and the simultaneous regeneration of nutrients through their excretory activities. The latter role is considered an important mechanism in maintaining constant primary production levels in the seas, especially in oligotrophic areas (Ketchum 1962; Corner and Davies 1971).

These dynamic functions of zooplankton have seldom been quantitatively evaluated in the field. One difficulty lies in the fact that the zooplankton community includes animals belonging to a variety of phyla and a number of species which differ geographically. Information from detailed studies on one or a few species is not adequate for this purpose, and collection of all necessary data on each component species in the community is not practical. Therefore, the development of some alternative approach is needed to overcome this problem.

METHODS

In this study, we treat the zooplankton community as an assemblage of different sizes of animals and use body size-related constant functions for respiration and ammonia excretion from laboratory experiments to estimate feeding, production, and ammonia regeneration in the Kuroshio and adjacent seas. A systematic survey of the study area had been carried out by Japanese participants in the CSK (Co-operative Study of the Kuroshio and adjacent region) organized by UNESCO during 1965-67 (Motoda et al. 1970; Irie and Yamazi 1972).

Biomass, Habitat Temperature, and Size (= Weight) Distribution of Zooplankton

Zooplankton were sampled vertically from 150 m with a NORPAC standard net (mesh aperture, 0.35 mm) in summer (June-October 1965 and 1966) (Figure 1A) and winter seasons (December-April 1965, 1966, and 1967) (Figure 2A). From the average biomass of zooplankton summarized by Yamazi (1971) for 0-150 m, the present study area was divided into four density classes (<10, 10-50, 50-100, and >100 mg wet weight/m³). The isopleth for 100 mg wet weight/m³ shifted northward in the cold season and southward in the warm season, especially in the east China Sea (Motoda et al. 1970; Irie and Yamazi 1972). Seasonal difference in the composition of

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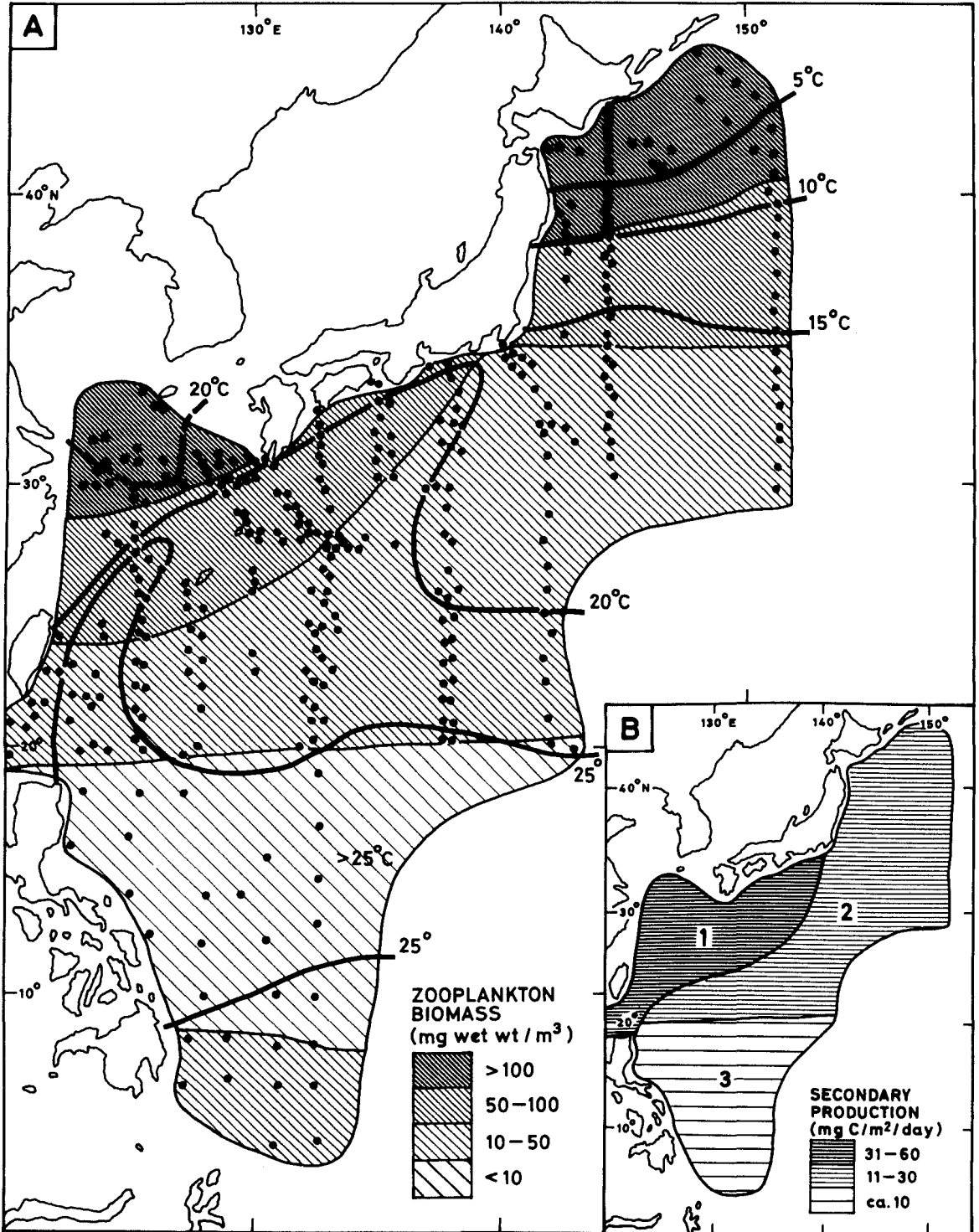


FIGURE 1.—A. Sampling stations, zooplankton biomass, and isotherms (100-m depth, continuous lines; 50-m depth, broken lines) during the warm season (June-October) in the Kuroshio and adjacent seas. B. Distribution of estimated secondary production.

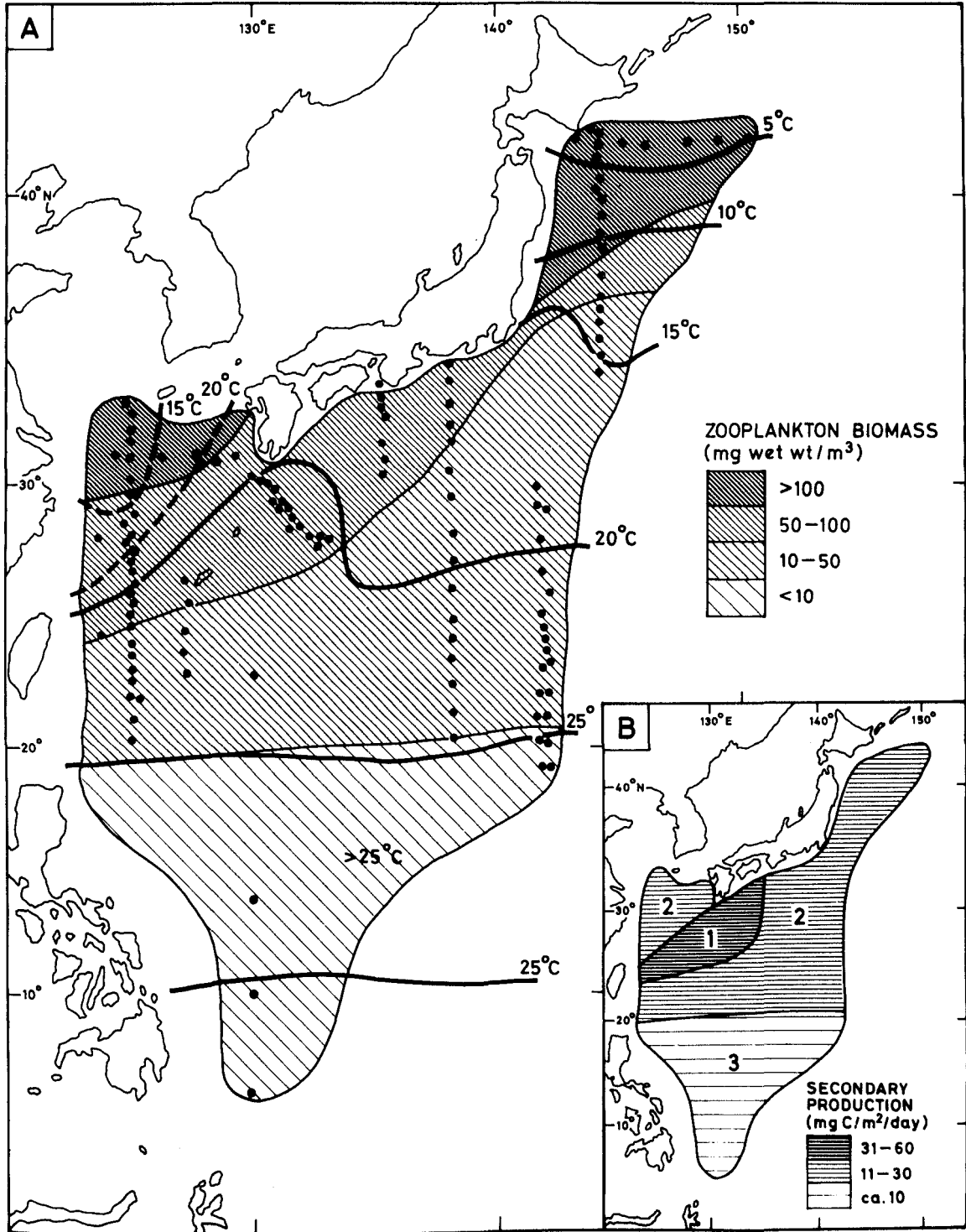


FIGURE 2.—A. Sampling stations, zooplankton biomass, and isotherms (100-m depth, continuous lines; 50-m depth, broken lines) during the cold season (December-April) in the Kuroshio and adjacent seas. B. Distribution of estimated secondary production.

zooplankton taxonomic groups among stations was less pronounced, with copepods dominant (56-65% of total individual number), followed by *Noctiluca* (8-15%), appendicularians (6-7%), and chaetognaths (4-5%) (Yamazi et al. 1972). Biomass expressed per cubic meter was converted to per square meter by multiplying by depth of sampling.

The habitat temperature of zooplankton from 0-150 m was represented by that at 100 m (Japanese Oceanographic Data Center 1967, 1969). In the east China Sea, which is shallower than 150 m, the temperature at 50 m was taken as the habitat temperature (Figures 1A, 2A).

From data summarized by Yamazi (1971), the biomass of zooplankton per haul was divided by total number of individuals per haul to obtain average body weight. Values thus obtained at all sampling stations were grouped into warm or cold season, and assumed as a general size distribution in each season (Figure 3). The highest frequency was observed in the range 0.1-0.2 mg wet weight/animal in both seasons. Faunal differences south

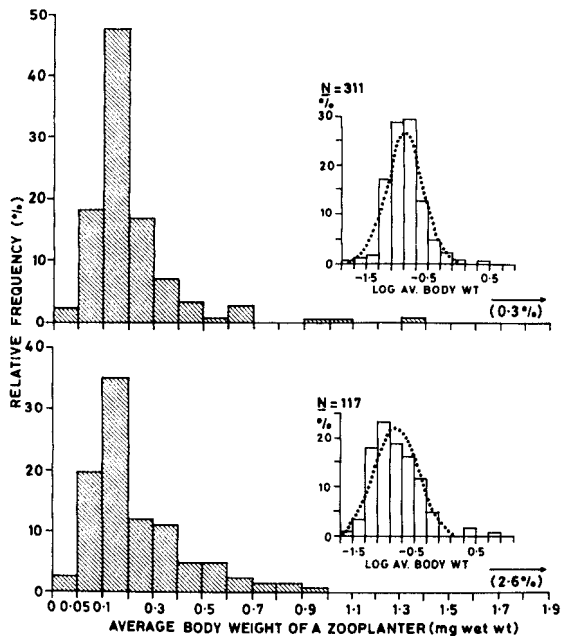


FIGURE 3.—Relative frequency of average size of zooplankton (biomass/number of zooplankton at each sampling station) in warm (June-October) (upper figure) and cold (December-April) (lower figure) seasons in the Kuroshio and adjacent seas. A normalized frequency distribution fitted by logarithmic transformation of body weights is superimposed on the right side of each figure. N is number of sampling stations.

and north of the subarctic boundary (ca. lat. 40°N) reported by Motoda and Marumo (1965) were ignored here, because no systematic difference was found in average body size of zooplankton between these areas. The skewed size distribution was converted to a normal distribution curve by logarithmic transformation (base 10). Fitness to the curve was tested primarily by the normal probability paper (Harding 1949) and finally confirmed by chi-square test (warm season: $\chi^2 = 17.85$, $df = 6$, $P < 0.01$; cold season: $\chi^2 = 7.24$, $df = 6$, $0.25 < P < 0.5$). The normal distribution curves of log body size thus obtained were $\mu = -0.8033$ (SD = 0.2856) for the warm season and $\mu = -0.7350$ (SD = 0.3705) for the cold season.

Respiration and Ammonia Excretion

From measurements of respiration and ammonia excretion rates on various zooplankton species from tropical to boreal seas, Ikeda (1974) found that the body weight and habitat temperature are most important factors which affect rates. As a result of stepwise regression analyses, the relationship among these parameters was expressed as:

$$R \text{ or } E = aW^b \quad (1)$$

$$\text{or } \log_{10} R \text{ or } \log_{10} E = \log_{10} a + b \log_{10} W \quad (2)$$

where R is respiration rate ($\mu\text{l O}_2/\text{animal per h}$); E , ammonia excretion rate ($\mu\text{g N}/\text{animal per h}$); and W , body dry weight (mg/animal). Constants, a and b , are given as a function of habitat temperature ($^{\circ}\text{C}$) (Ikeda 1974 amended the bias introduced by logarithmic transformation),

$$\text{for } R: b = -0.01089T + 0.8918$$

$$\log_{10} a = 0.02538T - 0.1259$$

$$\text{for } E: b = -0.00941T + 0.8338$$

$$\log_{10} a = 0.02865T - 1.2802.$$

Combining the normalized body size distribution of zooplankton obtained above and the values in Table 1, total respiration and ammonia excretion rates were estimated from the sum of the rates of six classes of the normal distribution curve equally divided by the SD, i.e., -3 to -2 , -2 to -1 , -1 to 0 , 0 to 1 , 1 to 2 , and 2 to 3 , which covers over 99% of the total area under the curve. In each class, body size of zooplankton was represented by the median value, i.e., SD = -2.5 , -1.5 , -0.5 , 0.5 ,

TABLE 1.—Analysis of body size distribution of zooplankton in the Kuroshio and adjacent seas from a normalized catch distribution curve. Warm season (June-October): $\mu = -0.8033$, $SD = 0.2856$; cold season (December-April): $\mu = -0.7350$, $SD = 0.3705$. The interval of $\mu \pm 3 SD$ of the normal curve was equally divided by the SD class intervals (1-6), and median value in each class interval was taken as the representative body size ($W_1 - W_6$) for that class interval.

No.	Class interval	Median body size		Median body size equivalent (mg wet wt/animal)		Theoretical frequency (%)
		W_i	SD	Warm	Cold	
1	-3 to -2	W_1	-2.5	0.030	0.020	2.15
2	-2 to -1	W_2	-1.5	0.058	0.051	13.59
3	-1 to 0	W_3	-0.5	0.113	0.120	34.13
4	0 to 1	W_4	0.5	0.218	0.282	34.13
5	1 to 2	W_5	1.5	0.422	0.662	13.59
6	2 to 3	W_6	2.5	0.815	1.553	2.15
				$\Sigma Wf = 19.63$	26.79	$\Sigma f = 99.74$

1.5, and 2.5. Then, total respiration (R_{tot}) and total ammonia excretion rates (E_{tot}) became

$$R_{tot} = R_1 f_1 + R_2 f_2 + \dots + R_6 f_6 \quad (3)$$

$$E_{tot} = E_1 f_1 + E_2 f_2 + \dots + E_6 f_6 \quad (4)$$

where R_1, R_2, \dots, R_6 and E_1, E_2, \dots, E_6 are the respiration rates and ammonia excretion rates of zooplankton with body weight W_1, W_2, \dots, W_6 , respectively, and f_1, f_2, \dots, f_6 are respective theoretical frequencies (= individual number) in each weight category. A wet weight:dry weight conversion factor of 10 was assumed (Wiebe et al. 1975). Frequency f_1, f_2, \dots, f_6 of a given zooplankton biomass (ΣW) was calculated by multiplying $f/\Sigma Wf$. To facilitate calculation, respiration and ammonia excretion rates per unit biomass of zooplankton characterized by the size distribution curve in warm and cold seasons were computed as functions of habitat temperature (Table 2). Respiration was expressed as carbon units assuming $RQ = 0.8$ (protein metabolism).

Feeding and Production Estimates From Respiration

Winberg (1956) proposed the following basic balanced equations for fishes:

$$0.8F = P + R \quad (5)$$

$$K_1 = P/F \cdot 100 \quad (6)$$

$$K_2 = P/(0.8F) \cdot 100 \quad (7)$$

where F is feeding; P , growth (= production); R , respiration; K_1 , gross growth efficiency; K_2 , net

TABLE 2.—Respiration and ammonia excretion rates per unit biomass of zooplankton in warm (June-October) and cold (December-April) seasons as derived from calculations in the text.

Habitat temp (°C)	Respiration rate ($\mu g C/mg$ dry wt per h)		Ammonia excretion rate ($\mu g N/mg$ dry wt per h)	
	Warm	Cold	Warm	Cold
5	0.790	0.735	0.162	0.148
10	1.300	1.183	0.270	0.242
15	2.144	1.911	0.450	0.396
20	3.538	3.091	0.750	0.648
25	5.849	5.011	1.252	1.065

growth efficiency; and 0.8, digestion efficiency for fishes. From these equations F and P are derived by knowing R and K_1 ,

$$F = 100R/[0.8(100 - K_2)] = 100R/(80 - K_1) \quad (8)$$

$$P = K_2 R/(100 - K_2) = K_1 R/(80 - K_1) \quad (9)$$

Apparently both digestion efficiency and gross growth efficiency (K_1) of marine zooplankton differ to a great degree, not only among zooplankton species but also within a single species (Table 3). Marshall and Orr (1955a) observed that the digestion efficiency of *Calanus finmarchicus* changed with a variety of food phytoplankton species offered. Apparently K_1 can be affected by developmental stages (Mullin and Brooks 1970b; Paffenhöfer 1976; Harris and Paffenhöfer 1976), feeding rate (Mullin and Brooks 1970b; Harris and Paffenhöfer 1976), kinds of food (Paffenhöfer 1976), and method of estimation (Butler et al. 1969, 1970). Moreover, both quality and quantity of foods used in these experiments are not necessarily the same as those that zooplankton will meet in the field. Although we have little information about the exact nature of foods of zooplankton in the field, their digestion efficiency is assumed to be quite high, because zooplankton have an ability to select suitable foods (Lasker 1966; Marshall 1973). The value of K_1 has a tendency to increase with a decrease in food concentration (Mullin and Brooks 1970a; Harris and Paffenhöfer 1976). In the field, food concentration is much lower than in laboratory experiments so that a higher K_1 value would be expected.

For these reasons we finally chose values of 70% for digestion and 30% for K_1 as realistic values of zooplankton in the field, regardless of species and food habit. Then, Equations (8) and (9) for fishes were rewritten for zooplankton, as

$$F = 100R/(70 - 30) = 2.5R \quad (10)$$

TABLE 3.—Digestion efficiency and gross growth efficiency (K_1) of marine zooplankton species obtained from laboratory experiments. Methods of estimation are with radioactive isotopes (^{14}C , ^{32}P , and ^{35}S), elemental analyses (C, N, and P), calories, weight, and ratio method of Conover (1966a). (Means in parentheses.)

Zooplankton species	Digestion efficiency and method of estimation		K_1 and method of estimation		Sources
<i>Calanus finmarchicus</i>	26-99	^{32}P			Marshall and Orr (1955a)
<i>Calanus finmarchicus</i>	53-78	^{14}C			Marshall and Orr (1955b)
<i>Euphausia pacifica</i>			11-74(32)	^{14}C	Lasker (1960)
<i>Calanus helgolandicus</i>	74-91	dry wt			Corner (1961)
<i>Temora longicornis</i>	52-98	^{32}P			Berner (1962)
<i>Calanus hyperboreus</i>	44-65 (55)	ratio method	4-36(21) 5-50(30)	weight calories	Conover (1964)
<i>Calanus finmarchicus</i> and <i>C. helgolandicus</i>			36	N	Corner et al. (1965)
<i>Calanus hyperboreus</i>	39-86(69)	ratio method			Conover (1966a)
Mixed zooplankton	18-92(63)	ratio method			Conover (1966a)
<i>Calanus hyperboreus</i>	40-87	ratio method			Conover (1966b)
<i>Euphausia pacifica</i>	46-95(84)	^{14}C	6-46(26)	^{14}C	Lasker (1966)
<i>Calanus finmarchicus</i> and <i>C. helgolandicus</i>	54-68(62)	N	14-34	N	Corner et al. (1967)
<i>Metridia longa</i>	54-57	ratio method			Haq (1967)
<i>Metridia lucens</i>	35-94(70)	ratio method			Haq (1967)
<i>Calanus finmarchicus</i> and <i>C. helgolandicus</i>			21-38	N	Butler et al. (1969)
<i>Calanus finmarchicus</i> and <i>C. helgolandicus</i>	77	P	19-35	P	
<i>Calanus finmarchicus</i> and <i>C. helgolandicus</i>	62	N	17	P	Butler et al. (1970)
<i>Calanus helgolandicus</i>			27	N	
<i>Rhincalanus nasutus</i>			34-35	C	Mullin and Brooks (1970a)
<i>Sagitta hispida</i>			30-45	C	Mullin and Brooks (1970a)
<i>Lucifer chasei</i>	8-22	^{35}S	36	N	Reeve (1970)
<i>Chiridius armatus</i>	81-97	ratio method	7-14	calories	Zimmerman (1973)
<i>Calanus helgolandicus</i>			3.7-35	C	Alvarez and Matthews (1975)
<i>Pseudocalanus elongata</i>			14-18	C	Paffenhöfer (1976)
<i>Temora longicornis</i>			17-27	C	Harris and Paffenhöfer (1976)

$$P = 30R/(70 - 30) = 0.75R. \quad (11)$$

Mortality Loss During Production

Production calculated as in Equation (11) assumes zero mortality. But production is always accompanied by mortality, caused mainly through predation by other animals and natural physiological mortality. We considered only mortality from the latter source.³

Assuming that 1 ml of oxygen is required to combust about 1 mg of organic matter (Jørgensen 1962), the instantaneous growth rate of zooplankton is expressed as follows from Equations (1) and (11),

$$dW/dt = (0.75/1,000)\alpha W^b \quad (12)$$

where W is body dry weight (milligrams) and t , time (hours). The time required to grow from egg (W_0 in milligrams) to adult (W in milligrams) is

³In addition to natural physiological mortality, molting loss by copepods, the most dominant group in zooplankton community, was included in the original calculations of Ikeda and Motoda (1975). Here we ignore the molting loss because neither molting intervals nor body size at molting were known. Therefore, present production estimate (10-60 mg C/m² per day) is slightly higher than original one (9-57 mg C/m² per day; Ikeda and Motoda 1975).

derived from the integrated form of Equation (12),

$$t = 1,000 (W^{1-b} - W_0^{1-b}) / (0.75(1 - b)). \quad (13)$$

Chiba (1956) measured egg size in 55 species of copepods. From his data and the body length-weight relation of copepods developed by Krylov (1968) the $W_0:W$ ratio was calculated as 0.0001:1 to 0.01:1. A similar range of the ratios is also found in the data of euphausiids, reviewed by Mauchline and Fisher (1969). The lifespan of zooplankters was defined arbitrarily as $1.5t$ (duration of adult stage is one-half that of the preadult). Daily mortality (M) caused by the length of life span becomes

$$M = 24/(1.5t). \quad (14)$$

Total mortality (M_{tot}) of the zooplankton community in terms of percent of biomass is given in the following equation:

$$M_{tot} = 100(M_1 f_1 W_1 + M_2 f_2 W_2 + \dots + M_6 f_6 W_6) \\ \div (f_1 W_1 + f_2 W_2 + \dots + f_6 W_6) \quad (15)$$

where M_1, M_2, \dots, M_6 are daily mortalities of zooplankters with body weight W_1, W_2, \dots, W_6 ,

TABLE 4.—Daily mortality related to the lifespan of zooplankton in warm (June-October) and cold (December-April) seasons as derived in the text.

Habitat temp (°C)	Season	Weight ratio of egg to adult			Average (% of biomass)
		0.01:1	0.001:1	0.0001:1	
5	Warm	0.68	0.53	0.46	0.51
	Cold	0.63	0.49	0.43	
10	Warm	1.24	1.01	0.91	0.96
	Cold	1.13	0.92	0.83	
15	Warm	2.27	1.92	1.77	1.81
	Cold	2.03	1.71	1.58	
20	Warm	4.14	3.60	3.39	3.37
	Cold	3.63	3.15	2.96	
25	Warm	7.51	6.69	6.40	6.21
	Cold	6.45	5.74	5.49	

respectively. For M_{tot} as a function of habitat temperature and $W_0:W$ ratio (0.0001:1, 0.001:1, and 0.01:1) see Table 4.

Ratio of Herbivores to Carnivores in Zooplankton Community

Although zooplankton include both herbivores and carnivores, this distinction of food habits is probably of little importance regarding ammonia excretion by zooplankton. However, the difference is essential when production is considered, especially secondary production.

We assumed that the zooplankton community at any trophic level is represented by a similar size distribution, same digestion efficiency (70%) and same K_1 value (30%). Assuming that the daily production of herbivores ($0.75\alpha \sum W_i^b (b_i/B_0)B_0$) equals the daily consumption by the primary carnivores ($2.5\alpha \sum W_i^b (b_i/B_1)B_1$) (derived from Equations (1), (3), (10), and (11)) the relation can be simplified to

$$B_1 = (0.75/2.5)B_0 \quad (16)$$

where B_0 and B_1 are the total number of herbivores and primary carnivores, respectively, in a community, and b_i is the number of zooplankters of a given body size. Assuming that the daily production of carnivores in the lower trophic level is equal to the daily feeding of carnivores at the next trophic level, the number of carnivores at trophic level n becomes

$$B_n = (0.75/2.5)^n B_0 \quad (17)$$

The total number of zooplankters from the primary carnivore level to the carnivore trophic level n becomes

$$\begin{aligned} B_1 + B_2 + \dots + B_n &= B_0((0.75/2.5) + (0.75/2.5)^2 + \dots + (0.75/2.5)^n) \\ &= B_0((0.75/2.5)(1 - (0.75/2.5)^n)/(1 - 0.75/2.5). \end{aligned}$$

If the number of trophic levels of carnivores is simply taken as 2, then the number of primary and secondary carnivores can be calculated to be

$$B_1 + B_2 = 0.39B_0.$$

This value does not differ greatly from the value obtained when an infinite number of carnivorous trophic levels are considered

$$B_1 + B_2 + \dots + B_\infty = 0.43B_0.$$

Therefore, the value 0.4:1 seems appropriate for the ratio of numbers of carnivorous zooplankton to all herbivorous zooplankton.

RESULTS AND DISCUSSION

Distribution of estimated production of herbivorous zooplankton (i.e., secondary production) is summarized for warm and cold seasons in Figures 1B and 2B. Table 5 summarizes our estimates for grazing, production, and natural physiological mortality of herbivorous zooplankton and ammonia-nitrogen excretion of zooplankton (herbivores plus carnivores).

Production

The present use of Winberg's balanced equations to estimate productivity (growth) from data on respiration is not new. Shushkina (1968) estimated the production of the copepod, *Haloptilus longicornis*, in the Fiji Sea from an indirectly calculated respiration rate for this species and K_2 values from the literature including zooplankton species. In order to determine whether zooplankton in the field were supplied adequate food, we used a set of values for digestion efficiency, and gross growth efficiency (K_1), instead of a single value of net growth efficiency (K_2), to obtain feeding requirements and production simultaneously (which is not possible when K_2 is used, see Equation (8)). When the feeding requirements of zooplankton exceed food availability (i.e., food shortage), any estimate of production from Winberg's equation is unrealistic. However, our data indicate that feeding requirements of herbivorous zooplankton was 18-72% of primary production (Table 5).

TABLE 5.—Estimates of grazing, production (corrected for natural physiological mortality), and ammonia nitrogen excretion of zooplankton collected from 0 to 150-m depth with NORPAC net (0.35-mm mesh) in the Kuroshio and adjacent seas, together with primary production values from the literature (Anonymous 1967, 1968, 1969; Saijo et al. 1972). For designation of subareas, see Figures 1B and 2B.

Item	Subarea			Range
	1	2	3	
Zooplankton:				
a. Herbivorous zooplankton grazing (mg C/m ² per day)	107-214	36-107	ca. 36	36-214
b. Herbivorous zooplankton production (mg C/m ² per day)	31-60	11-30	ca. 10	10-60
c. Herbivorous zooplankton natural physiological mortality (mg C/m ² per day)	1-4	0-2	ca. 1	0-4
d. Zooplankton excretion (mg N/m ² per day)	12-24	4-12	ca. 4	4-24
Phytoplankton:				
e. Primary production (mg C/m ² per day)	200-500	50-500	50-200	50-500
f. Phytoplankton nitrogen requirement (mg N/m ² per day)	35-88	9-88	9-35	9-88
Phytoplankton:zooplankton relation:				
g. Ratio of herbivorous zooplankton grazing to primary production (a/e) (%)	43-54	21-72	18-72	18-72
h. Ecological efficiency from primary production to secondary production (b/e) (%)	12-16	6-22	5-20	5-22
i. Ratio of zooplankton nitrogen excretion to phytoplankton nitrogen requirement (d/f) (%)	27-34	14-44	11-44	11-44

Engelmann (1969) summarized annual production (P_a) and respiration (R_a) of animal populations (mostly terrestrial invertebrates and vertebrates) and found that $\log_{10} P_a$ was proportional to $\log_{10} R_a$. His findings were further confirmed with a large amount of data by McNeill and Lawton (1970). For comparatively short-lived poikilotherms (generation time <2 yr) the relation is expressed in the following equation (McNeill and Lawton 1970),

$$\log_{10} P_a = 0.8262 \log_{10} R_a - 0.0948$$

or
$$P_a = 0.804 R_a^{0.8262}$$

This empirical equation resembles $P = 0.75 R$ (Equation (11)) that we derived from Winberg's equations for marine zooplankton in this study.

Mullin (1969) reviewed production estimates for marine zooplankton and gave 5-224 mg C/m² per day as a summary value for zooplankton production at various sea areas, exclusive of values on a single species. Our estimate of secondary production (10-60 mg C/m² per day) falls in these ranges. It is noted, however, that some data cited by Mullin (1969) are on mixed zooplankton (herbivores plus carnivores) so that these are not comparable to our results which referred only to herbivorous zooplankton. For the same reason, the ecological efficiency between primary production and secondary production obtained in our study (5-22%) is not necessarily comparable to the ratio of zooplankton production to primary production (9-58%) in Mullin (1969).

Ammonia Excretion

The Kuroshio and its adjacent region in the

Pacific Ocean (south of the subarctic boundary at ca. lat. 40°N) are oligotrophic (Reid 1962). Taniguchi (1972) studied geographical variation of primary production in the western Pacific Ocean and suggested that nutrients are the most important factor limiting the primary production level in the Kuroshio region. In situ primary production reported in this area is in the range of 50-500 mg C/m² per day (Anonymous 1967, 1968, 1969; Saijo et al. 1972) which is equivalent to 9-88 mg N/m² per day from a C:N ratio of 5.7:1 on phytoplankton (Redfield et al. 1963). Our estimate of ammonia-nitrogen regeneration through zooplankton excretion which can support 11-44% of the nitrogen requirement for primary production was 4-24 mg N/m² per day. Eppley et al. (1973) estimated that 40-50% of nitrogen demand for primary production was supplied by zooplankton excretion in the nutrient depleted subtropical gyre of the northern Pacific Ocean. A significant contribution of zooplankton excretion (up to 77-90% of the nitrogen requirement for primary production) was reported in Long Island Sound (Harris 1959) and offshore waters off the Washington and Oregon coasts in summer (Jawed 1973). The importance of ammonia as a nitrogen source for phytoplankton is further substantiated by its preferential utilization by phytoplankton (cf. Dugdale 1976).

Future Aspects

The production and ammonia regeneration models presented here are advantageous for understanding the marine zooplankton community which includes diversified species and widely divergent body sizes, like those inhabiting subtropical and tropical seas. Models require basically

three parameters: zooplankton biomass, size distribution, and habitat temperature. Although we obtained size distribution indirectly it should be obtainable directly. The fitting of zooplankton size distribution data to the normal distribution curve may not be necessary in some instances but this will facilitate calculations. To estimate production from respiration data, constant values of digestion efficiency and K_1 were used in this study, but these can be used as variables. From morphological characteristics of feeding organs, Timonin (1971) reported that 50-80% of zooplankton biomass in the Indian Ocean were carnivores and Motoda and Minoda (1972) reported that 20-27% of zooplankton numbers in the Kuroshio region were herbivores. These values are below the herbivore:carnivore ratios we calculated.

Since only zooplankton data were collected with 0.35-mm mesh nets and smaller zooplankters pass through this mesh size, we probably underestimated zooplankton biomass. According to Beers and Stewart (1971) biomass of microzooplankton including copepod nauplii, ciliates, foraminiferans, and radiolarians was 12-71% (24% on average) of total zooplankton collected in 202- μ m nets in the eastern tropical Pacific Ocean. The important role of microzooplankton as a secondary producer and nutrient regenerator in pelagic marine ecosystems is anticipated but suitable data are yet unavailable for modeling.

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