*J. exp. mar. Biol. Ecol.*, 1978, Vol. 31, pp. 253–265


# AMMONIUM FORMATION IN CAPE TIMIRIS (MAURITANIA) UPWELLING

ROBERT P. LE BORGNE
*Centre de Recherches Océanographiques – O.R.S.T.O.M., Abidjan, Ivory Coast*

**Abstract:** Ammonium formation was studied in two consecutive years by following a newly upwelled ammonium-free 'parcel' of water with a drogue. High concentrations (>2 μg-at. $NH_4$-N $l^{-1}$) were found at the end of each study. The relative importance of WP-2 net mesozooplankton excretion on the ammonium values is greater before the phytoplanktonic bloom (35–48%) than during it (10–16%). From carbon grazing estimates, it is shown that other herbivore excretion does not take the place of WP-2 mesozooplankton and because of synchronous variations of chlorophyll with dissolved organic nitrogen, and bacterial activity with ammonium, it is suggested that much of the ammonium is produced from phytoplankton decay or nitrogen excretion during the bloom.

## INTRODUCTION

Twice, in March 1972 and 1973, *R.V. Capricorne* followed the evolution of a 'parcel' of newly upwelled waters, south of Cape Timiris, by setting a drogue at the point of upwelling and sampling two or three times per day. As pointed out by Herbland, Le Borgne & Voituriez (1974) the situation encountered was particularly easy to study since this upwelling is protected by Cape Timiris and therefore little mixing with northern waters occurs and it is concentrated in space because of a submarine canyon at 20–30 m depth (Fig. 1) which seems to act as a channel for upwelled waters (Gostan & Guibout, 1974). Primary production and nutrient uptake were previously studied by Herbland, Le Borgne & Voituriez (1973) and Herbland & Voituriez (1974). A summary of their conclusions may be found in Herbland *et al.* (1974). The present paper is an attempt to explain the formation of high concentrations of ammonium (>2 μg-at. $NH_4^+$-N $l^{-1}$) that was found twice in the same area at the end of both drogue studies where new upwelled waters were almost ammonium-free at the beginning. Such high concentrations have also been recorded in the Canary Current system by Coste & Slawyk (1974) in upwellings situated further north (Cape Blanc and Cape Corveiro).

## MATERIALS AND METHODS

Only a short description need be given here since the methods have been described in detail by Herbland *et al.* (1973) and Herbland & Voituriez (1974). Drogues were

immersed at a 3–5 m depth and according to salinity measurements followed the same water masses for 6 days each year. Because of time limitations in 1973 the study had to be stopped, whereas in 1972 we met a convergence; upwelling waters were covered by warm surface ones after Station 32.

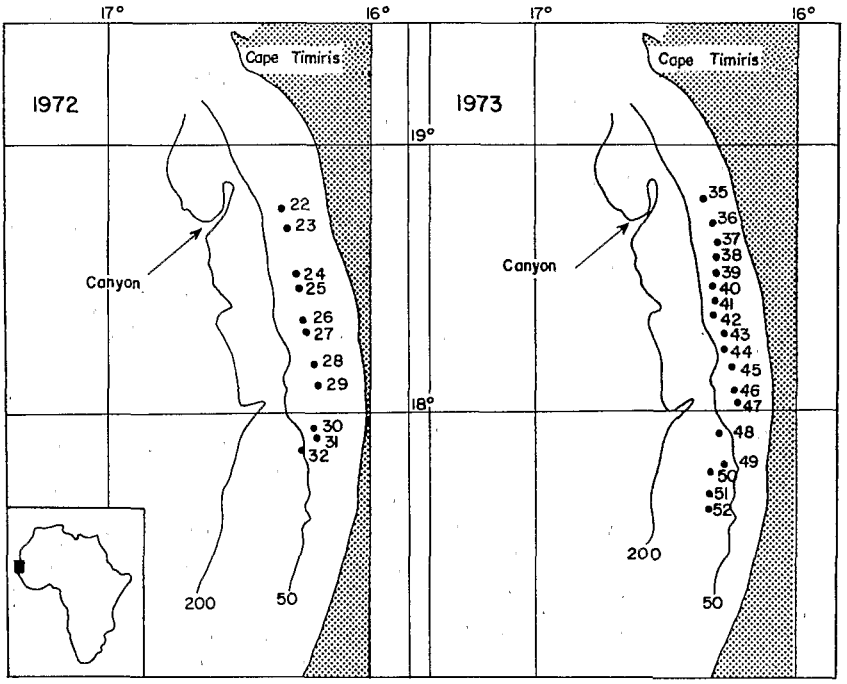


Fig. 1. Station positions during 1972 and 1973 *R.V. Capricorne* drogue studies.

Chlorophyll was measured by *in vivo* fluorescence (Lorenzen, 1966), ammonium according to Koroleff (1969), bacterial activity as by Herbland & Bois (1974) using labelled $^{14}C$ glucose in 1972 and a mixture of amino acids in 1973 (absolute values are, therefore, different from one year to the other and should rather be considered as an index of heterotrophic activity). Dissolved organic nitrogen (DON) and phosphorus (DOP) were measured on filtered sea water after photo-oxidation (Armstrong & Tibbits, 1968). No DON was measured in 1973 and data were approximated from DOP using a DON : DOP ratio of 15.9 found in 1972 for the 0–20 m layer under similar conditions. Mesozooplankton excretion was measured on WP-2 net (UNESCO, 1968), the zooplankton being left in 2 l flasks for 20–24 h (Le Borgne, 1973). Zooplankton dry weights were measured on bottom to surface vertical hauls for the 200 $\mu$m mesh WP-2 net.

## RESULTS

### AMMONIUM FORMATION ALONG THE DROGUE TRACK

Two stages may be seen in the evolution of chlorophyll, DON, heterotrophic activity and ammonium integrated values along the drogue course (Fig. 2); first, a three-day stationary phase when chlorophyll is slowly increasing with the other parameters and secondly a phytoplankton exponential growth period with a high DON production. Ammonium and bacterial activity follow with a 12 to 24 h time-lag. Since no decline in phytoplankton was observed in either of the two years, there is no evidence that its maximum was reached.

Ammonium formation may also be seen in vertical profiles (Figs 3, 4). At the beginning, ammonium was present near the bottom ($\approx 0.3$ $\mu$g-at. $NH_4^+$-N $l^{-1}$) with the smallest concentrations in the shallower water ($< 0.1$ $\mu$g-at. $NH_4^+$-N $l^{-1}$). As upwelled waters moved southward, undergoing primary production, the isolines go up towards the surface but the maximum values never reach it, remaining near or under the 1% light level. The only surface maximum is found at Station 51 (Fig. 4), where there was the largest zooplankton biomass and is probably due to a large animal excretion during the night, together with a high grazing pressure responsible for the observed chlorophyll decline (Fig. 2). Eight hours later, at Station 52 in the afternoon, the maximum ammonium concentrations moved back to the 1% light level.

The increasingly higher integrated ammonium values from the beginning to the end of the track indicate a progressive accumulation. If there were no loss, one might assess the total ammonium production from the beginning to any station as the difference between the integrated value for the first station and that of any other since the time and space 'coincide': according to current measurements the drogues followed the water masses, and the vertical current profiles showed a rather uniform speed along the whole water column. Because, however, of possible losses such as oxidation to nitrite or uptake by phytoplankton, this mode of calculation gives only a minimum estimate of total ammonium production. Since nitrite concentrations were constant throughout the drogue studies, we assume that no oxidation of ammonium took place in such a short period. Yet its uptake by phytoplankton in the euphotic layer is apparent, at least between Stations 51 and 52 in 1973 (Fig. 4). If a part of the produced ammonium is taken up, one would expect higher concentrations below the euphotic layer and higher integrated values for morning than for the afternoon ones since uptake is more rapid with photosynthesis. Higher concentrations are, indeed, observed below the 1% light level (Figs 3,4) and if ammonium were evenly regenerated in the euphotic layer, one might assess its total amount by integrating the maximum concentration from its level up to the surface: however, we have no data showing a uniform regeneration in the euphotic layer and the observed gradient could also be the result of a greater production in the deep levels

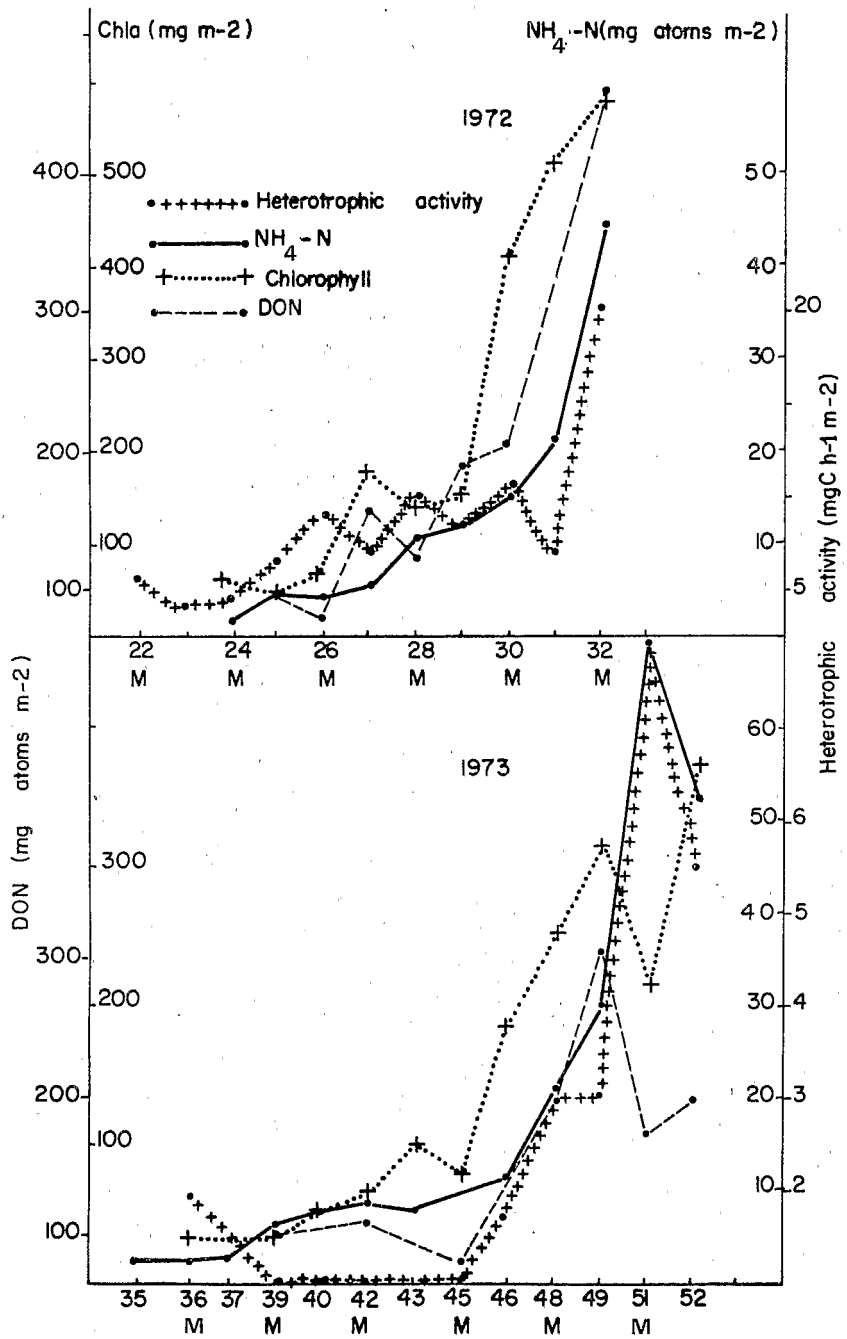


Fig. 2. Changes in integrated values of chlorophyll, DON, amonium, and heterotrophic activity along the drogue track in 1972 and 1973: M, morning stations.

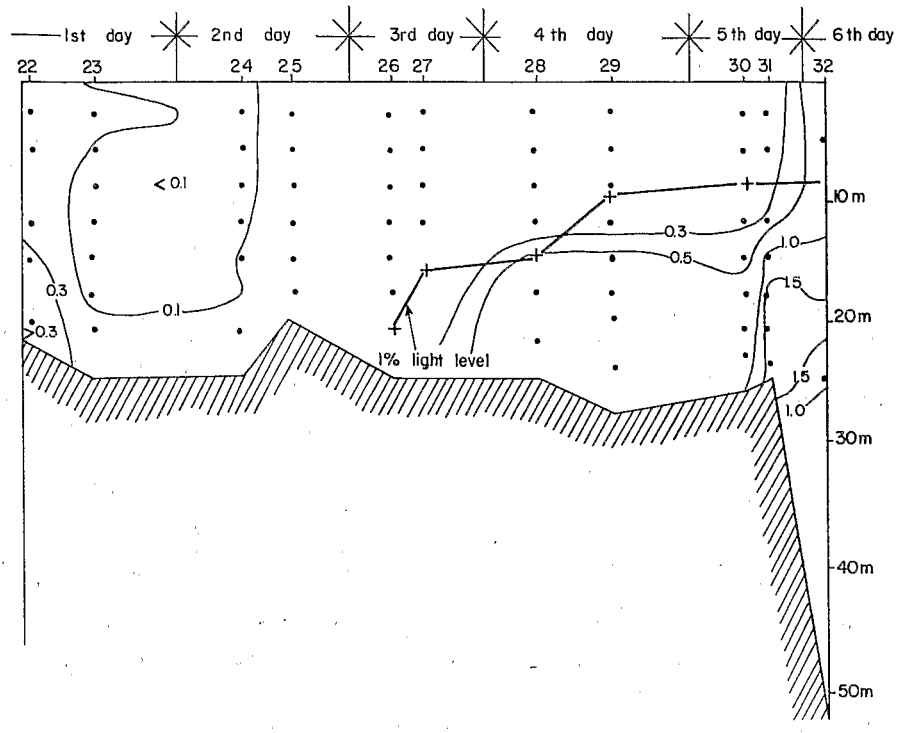


Fig. 3. Vertical distribution of ammonium along the drogue course in 1972: concentrations in μg-at. $NH_4^+$-N $l^{-1}$).

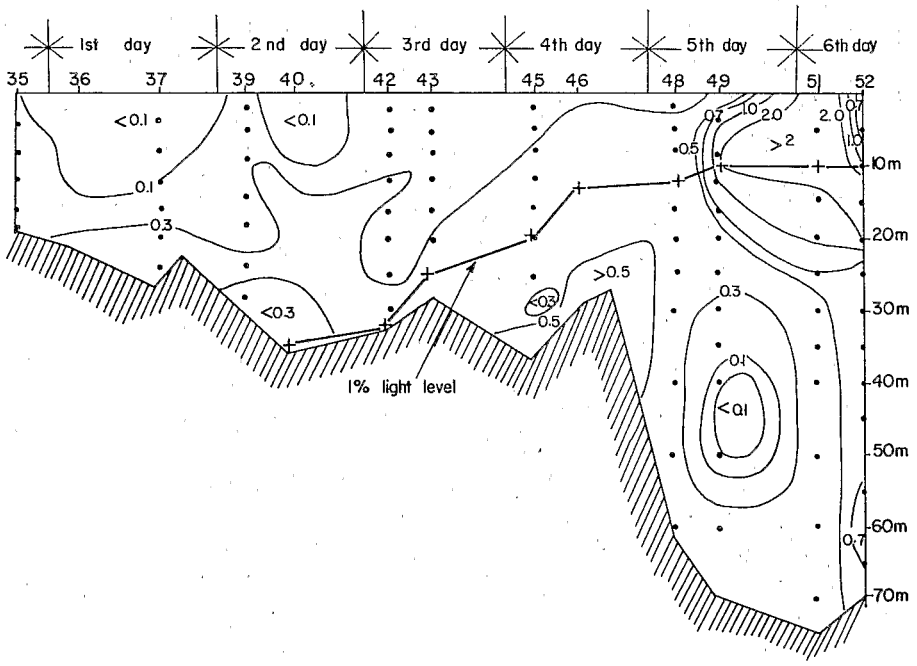


Fig. 4. Vertical distribution of ammonium along the drogue course in 1973: concentrations in μg-at. $NH_4^+$-N $l^{-1}$).

as a result of phytoplankton decay or excretion by benthic and pelagic animals. Furthermore, afternoon integrated values are not lower than morning ones (except for Stations 51 and 52), so that ammonium production in the whole water column is equal to, or greater, than its consumption in the upper levels during the daytime.

The difference of integrated ammonium values gives, then, a minimum estimate of the total ammonium production. For six days, between Stations 22 and 32 in 1972 and Stations 35 and 52 in 1973, it is 53 and 50 mg-at. $NH_4^+$-N $m^{-2}$, respectively. It represents 22% of nitrate uptake in 1972 and 28% in 1973 according to uptake estimates of Herbland *et al.* (1973) and Herbland & Voituriez (1974). These were obtained by following the nitrate decrease in the euphotic zone and a corresponding increase of chlorophyll, primary production ($^{14}C$ method), particulate nitrogen, and carbon along the drogue course.

## PATHWAYS OF AMMONIUM PRODUCTION

In coastal upwelling off desert countries, with little river outflow and precipitation from the atmosphere, ammonium in sea water has an almost entirely biological origin. The main sources are excretion by benthic and pelagic animals and heterotrophic activity on dissolved or particulate organic nitrogen.

### *Mesozooplankton excretion*

Only the data for 1973 will be considered because in 1972 the zooplankton hauls were contaminated with large amounts of algae from Station 28 to the end, and so gave doubtful values for the zooplankton biomasses. Extrapolating the situation encountered in 1973 to that of 1972 would be misleading since the zooplanktonic populations were different: larvacea and cirripede larvae dominated in the first year but gastropod and lamellibranch veligers in 1973.

We may consider that the planktonic populations caught by bottom to surface vertical WP-2 hauls followed the same parcel of water because there was no real trend of diel periodicity for the biomass, the morning values (08.00 h) not being systematically greater or smaller than afternoon ones (18.00 h). These two times are 1 h after sunrise and 1 h after sunset when animals are known to be at lower levels. We may, therefore, have missed animals living on or near the bottom and undertaking vertical migrations at different times; however, they probably do not follow the same parcel of water all the time. As we noted before, we can make time and space coincide and assess the ammonium excretion from Station *m* to Station *n*, 24 h later, as the product of their mean biomass divided by their mean excretion rate. Biomass and metabolic rate variations are thus considered to be constant during a 24-h period. Excretion rates were masured at a single temperature, because this was the same from bottom to surface (the diference increased slightly at the end of the observations but remained $<2°C$). As the drogue is drifting southwards, total zooplankton excretion is the sum of the previous stations. To show how the

values in Table I were obtained, let us take Station 43. The ammonium excreted between Stations 40 and 43 ($E_{NH_4}$) is equal to:

$$E_{NH_4} = \frac{(1734 + 1061)}{2} \cdot \frac{(0.423 + 0.530)}{2} = 670 \ \mu\text{g-at. m}^{-2}$$

The cumulated excretion ($\Sigma E_{NH_4}$) from the beginning to Station 43, is the sum of $E_{NH_4}$ between Stations 35 and 37, 37 and 40, 40 and 43, *i.e.*,

$$\Sigma E_{NH_4} = 1.06 + 0.95 + 0.67 = 2.68 \text{ mg-at. m}^{-2}$$

TABLE I

WP-2 zooplankton dry weights (mg m$^{-2}$), WP-2 ammonium excretion rates ($\mu$g-at. $NH_4^+$-N (mg dry wt)$^{-1}$ day$^{-1}$), and WP-2 cumulated excretion and integrated ammonium (mg.-at. $NH_4^+$-N m$^{-2}$): percentage importance of WP-2 plankton excretion in observed integrated ammonium (see text for method of calculation):* morning stations.

| Station | Zpkl. dry wt | Excretion rates | Cumulated excretion | Integrated ammonium | Zooplankton importance (%) |
|---|---|---|---|---|---|
| 35 | 2455 | 0.398 | – | 2.20 | – |
| 36* | 3402 | 0.398 | – | 1.90 | – |
| 37 | 2868 | 0.398 | 1.06 | – | – |
| 39* | 2478 | 0.423 | 1.21 | 5.97 | 32.1 |
| 40 | 1734 | 0.423 | 2.01 | 6.78 | 43.9 |
| 42* | 2955 | 0.530 | 2.51 | 8.64 | 39.0 |
| 43 | 1061 | 0.530 | 2.68 | 7.37 | 51.8 |
| 45* | 1886 | 0.536 | 3.58 | 12.44 | 35.0 |
| 46 | 2007 | 0.536 | 3.50 | 11.01 | 39.7 |
| 48* | 2971 | 0.510 | 4.85 | 21.12 | 25.6 |
| 49 | 5157 | 0.510 | 5.38 | 30.18 | 19.2 |
| 51* | 4995 | 0.510 | 6.88 | 68.92 | 10.3 |
| 52 | – | 0.510 | 8.02 | 52.56 | 15.9 |

The importance of zooplankton excretion in ammonium formation is the ratio of the cumulated excretion to the integrated ammonium ratio; there are, however, integrated ammonium data for Stations 35 and 36, but not for ammonium excretion. The importance of mesozooplankton (Fig. 5 and Table I) has, therefore, been calculated taking into account at each station, integrated values minus the first station: *e.g.*, at Station 43, the percentage importance of zooplankton is, $(2.68 \times 100)/(7.37 - 2.20) = 51.8\%$. The zooplankton importance is over-estimated because integrated ammonium is a minimum estimation of the total ammonium production. This over-estimation is evident when considering afternoon values which are higher than morning ones (Table I, Fig. 5). Zooplankton biomass and excretion rates are not different but ammonium is under-estimated for the afternoon stations, because of its quicker uptake during daytime. For this reason, morning and afternoon values are considered separately.

The importance of WP-2 zooplankton excretion to the total ammonium formation is greater before phytoplankton growth (Station 46). During the bloom, its value falls from 35 to 10% (Station 51) for morning values and from 48 to 16% (Station 52) for afternoon ones (Fig. 5).

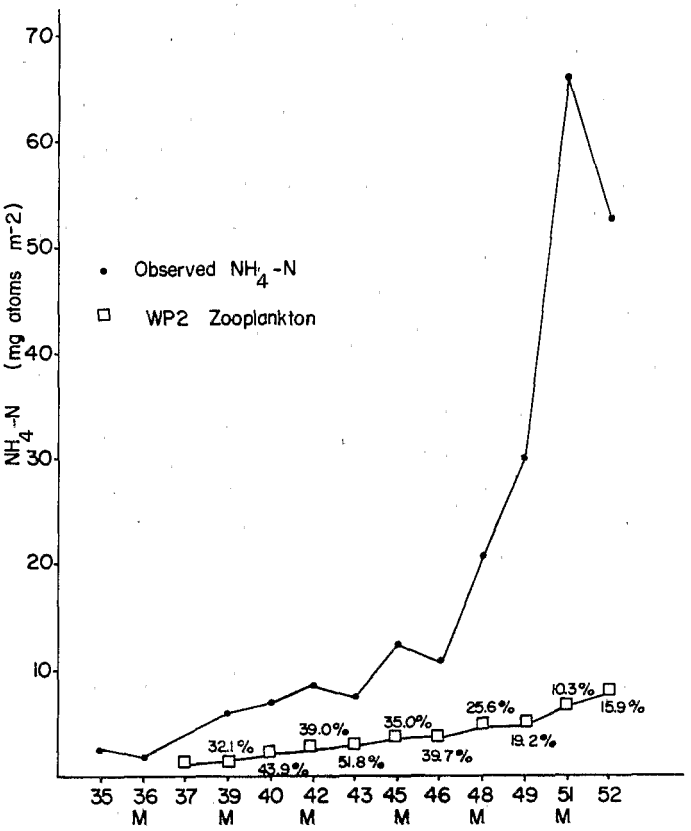


Fig. 5. Integrated ammonium and its excretion by WP-2 mesozooplankton along the drogue track in 1973: percentage importance of zooplankton excretion in total ammonium: M, morning stations.

*Ammonium of other origin*

Benthos, nekton, and microzooplankton excretion was not measured but could represent most of the remaining production when phytoplankton biomasses are still low. Their excretion would then account for 52 or 65% of the minimum ammonium formation for afternoon or morning WP-2 values, respectively; however, during the bloom, mesozooplankton excretion goes down to 10-16% of the integrated ammonium values and some other means of production must take place. It may be from animal origin, but it seems unlikely that ammonium is excreted by other

herbivores for two reasons since the phytoplankton (taken by a 5 l Niskin bottle and counted by the Utermöhl method) was almost entirely composed of rather large diatoms (*Chaetoceros* sp.) that apparently could not be used by microzooplankton, and the importance of WP-2 animal ingestion in total carbon grazing, does not decrease during the bloom.

In order to get an estimation of their importance in total grazing, ingested carbon was assessed from WP-2 excreted ammonium. Following Corner & Davies (1971), herbivorous nitrogen production ($W_N$) and excretion ($T_N$) are linked to ingestion ($I_N$) by gross growth efficiency ($K_{1,N}$) and percentage assimilation ($D_N$) as follows:

$$K_{1,N} = W_N/I_N \text{ and } D_N = (W_N + T_N)/I_N$$

From these equations, we get: $I_N = T_N/(D_N + K_{1,N})$, which links excretion and ingestion. According to Corner & Davies (*op. cit.*), there is no overgrazing under natural conditions and $D_N$ is constant. It was found to be 0.6 for nitrogen by Corner, Cowey & Marshall (1967) and Butler, Corner & Marshall (1969, 1970). $K_{1,N}$ may be taken as 0.2 in rich waters, where it would be lower than in oligotrophic ones (Conover, 1964); this gives, $I_N = T_N/0.4$. Since, according to Le Borgne (1973), ammonium excretion represents 50% of the total nitrogen excretion in the Cape Timiris upwelling, $T_N$ is twice as much as the ammonium excretion. Ingested nitrogen $I_N$, may be converted into carbon using a C : N atomic ratio of 7.2 found by Herbland & Voituriez (1974) for particles in 1973. The total grazing was obtained from the difference between observed particulate carbon and that expected from primary production data of Herbland & Voituriez (*op. cit.*). Calculation begins at Station 39 since there were no $^{14}C$ measurements at Station 37 (Table II). The importance of the WP-2 plankton is indicated by the WP-2 grazing : total grazing ratio. It is 0.532 (1042 : 1920) before the bloom and 0.758 (1953 : 2576) during the bloom (Table II). Even if this mode of calculation gives only a rough estimate, it

TABLE II

Assessment of total phytoplankton carbon grazing and WP-2 zooplankton carbon ingestion, before and during the bloom in 1973.

| | Before the bloom | | During the bloom | |
|---|---|---|---|---|
| | Stations | mgC $m^{-2}$ | Stations | mgC $m^{-2}$ |
| Particulate carbon | 39 | 2880 | 46 | 6660 |
| $^{14}C$ production | 39–40 | 860 | 46–48 | 810 |
| | 40–42 | 800 | 48–49 | 2190 |
| | 42–43 | 940 | 49–51 | 1000 |
| | 43–45 | 670 | 51–52 | 1720 |
| Total particul. carbon | 45 | 6150 | 52 | 12380 |
| Observed particul. carbon | 45 | 4230 | 52 | 9804 |
| Total grazing | 39–45 | 1920 | 46–52 | 2576 |
| WP-2 carbon ingestion | 39–45 | 1024 | 46–52 | 1953 |

shows WP-2 grazing does not decrease (and even increases) during the bloom and that the grazing of phytoplankton is rather low compared with its biomass. In this calculation, we suppose that all ingested carbon is of vegetal origin, which is true if all WP-2 zooplankton is herbivorous and if most of particulate carbon is made of autrophic cells (Hobson, Menzel & Barber, 1973, showed phytoplankton represents 70–90% of particulate carbon in upwelling situations). An alternative hypothesis would be that losses due to sinking are negligible which is probably correct since we used integrated carbon and chlorophyll data and very low values were found in deeper layers.

If WP-2 plankton importance in total grazing is not lower during the bloom, other herbivores are not responsible for the high ammonium values observed, and these could come either from carnivores such as nekton, or from phytoplankton as a result of bacterial activity. Thus, as mentioned before, synchronous variations of both chlorophyll and DON on the one hand and heterotrophic activity with ammonium on the other suggest that DON is produced by phytoplankton, organic compounds induce an heterotrophic activity the variation of which occurs with a 12–24 h time lag after those of chlorophyll and DON and that ammonium production closely related to heterotrophic activity (Fig. 2), would be its direct or indirect consequence.

## Discussion

Ammonium of vegetal origin, which is also suspected in Cape Blanc upwelling (Collos, Coste, Minas & Slawyk, pers. comm.), proceeds through DON released by phytoplankton excretion or by the degenerating of dead cells. The release of dissolved organic matter by phytoplankton has been known for a decade (see Berman & Holm-Hansen, 1974 and Smith, Barber & Huntsman, 1977, for reviews). Another DON production process is zooplankton excretion, the organic fraction being half of the total excreted nitrogen given by Le Borgne (1973); but this excretion is negligible compared with phytoplankton DON release in our case. Thus, if we calculate the minimum DON production from the difference between the beginning and the end of the drogue course (whereby, uptake by bacteria and phytoplankton is not taken into account), the zooplankton excretion only represents 6.3% of total DON production in 1973. If we convert the direct phytoplankton organic charbon excretion values of Herbland & Voituriez (1974) into DON with their C : N atomic ratio of 7.2, it accounts for 70.2% of total DON yield (their uptake and constitution ratios are close and we suppose the excretion ratio to be of the same order of magnitude). The importance of phytoplanktonic origin is greater since the fraction of DON coming from the lysis of dead cells is not measured.

Organic matter excreted by phytoplankton induces bacterial activity the maximum of which was attained in two days during laboratory experiments (Waksman *et al.*,

1938; Herbland, 1975). Under natural conditions Herbland (1974) noticed that bacterial blooms were associated with high concentrations of dissolved organic matter – the result of high phytoplankton biomasses. Castellvi & Ballester (1974) in several northwest African upwelling situations also found bacterial blooms at the limits of phytoplankton ones. The last stage is the mineralization by bacteria. 60 to 80% of the dissolved organic carbon taken up is mineralized by bacteria, the remainder being assimilated (Herbland, 1975) and it could also be true for nitrogen and phosphorus. The rôle of bacteria in ammonification was shown by Waksman & Renn (1936), von Brand, Rakestraw & Renn (1937) and Waksman *et al.* (1938), but it is a rather slow process; 8–20 days are necessary to mineralize 65–70% of organic carbon (Herbland, 1975) and 5 days for 50–75% of amino acids (Waksman & Renn, 1936). We may, therefore, have only observed the beginning of ammonium formation by heterotrophic activity after 12–24 h (this appears on Fig. 2 where DON is 2–10 times as great as $NH_4^+$-N in 1972 and 1973). Another hypothesis proposed by Johannes (1968) could explain this quick mineralization, namely, that bacteria are ingested by protozoans excreting ammonium, thus leading to a more rapid regeneration.

The part played by the mineralization of organic matter in total ammonium yield may be roughly assessed if we suppose the ratio of mesozooplankton to other animal excretion is the same before and during the phytoplankton bloom. This is probably true as far as herbivores are concerned as we previously noted. When considering WP-2 values the excretion of which accounts, on an average, for 35.4% of the ammonium formation at morning stations before phytoplankton growth, other excretion represents 64.6%. Using the same ratio (35.4 : 64.6 = 0.546) at Station 51 where the importance of WP-2 excretion is 10.3%, would give 18.9% for other animal excretion(10.3 : 18.9 = 0.546). Ammonium originating from phytoplankton and bacteria at Station 51 would then account for 70.8% (100–10.3–18.9). A similar calculation may be used for the afternoon stations to give a value of 66.8% from vegetal origin at Station 52. This important mineralization from phytoplankton seems to be an example of 'wasted' primary production, probably because of a low grazing pressure by herbivores as we noted before (Table II). Since the work of Harris (1959) zooplankton have usually been considered important in the regeneration of nitrogen and phosphorus. Johannes (1968) writes "marine ecosystems are generally dominated by grazing food-chains": vegetal organic matter should then be entirely grazed by herbivores, which in turn would be ingested by carnivores, mineralization being through animal excretion. Grazing was thought to be responsible for phytoplankton decline by Ryther *et al.* (1971) during their drogue study in the Peru upwelling. In Cape Timiris, at least in 1973, it appears that primary and secondary productions were not well synchronized. Although zooplankton biomass increased 24 h after the beginning of phytoplankton growth in 1972 and 1973, the increment is not enough to indicate phytoplankton decline by grazing. Unfortunately we could not watch the evolution any longer to know whether this

zooplankton growth would continue and so take a greater part in ammonium formation. In the Peru upwelling, for the trophic conditions met by Ryther *et al.* (*op. cit.*) it appears that herbivorous fish (anchovies) can rapidly use phytoplankton outbursts which hence quickly decline and with the production of one-third of ammonium observed values (Whitledge & Packard, 1971). Such excretion is ten times as great as that of zooplankton, which is 18–420 $\mu$g-at. $NH_4^+$-N $m^{-2}$ $day^{-1}$ instead of 670–2460 in Mauritania, *i.e.*, 6 times greater for the maximum values with the same net. This difference may be explained by a higher zooplankton biomass in Mauritania, either because of a lack of competition with other grazers (fish) or weak predation. But these higher biomass values are still too low to use the very large phytoplankton stocks which are partly wasted, at least at this stage of the upwelling evolution.

## References


ARMSTRONG, F. A. J. & S. TIBBITTS, 1968. Photochemical combustion of organic matter in seawater for nitrogen, phosphorus and carbon determination. *J. mar. biol. Ass. U.K.*, Vol. 48, pp. 143–152.

BERMAN, T. & O. HOLM-HANSEN, 1974. Release of photoassimilated carbon as dissolved organic matter by phytoplankton. *Mar. Biol.*, Vol. 28, pp. 305–310.

BRAND, T. VON, N. W. RAKESTRAW & C. E. RENN, 1937. The experimental decomposition and regeneration of nitrogenous organic matter in sea-water. *Biol. Bull. mar. biol. Lab., Woods Hole*, Vol. 72, pp. 165–175.

BUTLER, E. I., E. D. S. CORNER & S. M. MARSHALL, 1969. On the nutrition and metabolism of zooplankton. VI. Feeding efficiency of *Calanus* in terms of nitrogen and phosphorus. *J. mar. biol. Ass. U.K.*, Vol. 49, pp. 977–1001.

BUTLER, E. I, E. D. S. CORNER & S. M. MARSHALL, 1970. On the nutrition and metabolism of zooplankton. VII. Seasonal survey of nitrogen and phosphorus excretion by *Calanus* in the Clyde Sea-Area. *J. mar. biol. Ass. U.K.*, Vol. 50, pp. 525–560.

CASTELLVI, J. & A. BALLESTER, 1974. Activité hétérotrophique bactérienne en rapport avec les conditions hydrologiques des systèmes marins. *Téthys*, Vol. 6, pp. 189–202.

CONOVER, R. J., 1964. Food relations and nutrition of zooplankton. *Occ. Publs Narragansett Mar. Lab.*, No. 2, pp. 81–91.

CORNER, E. D. S., C. B. COWEY & S. M. MARSHALL, 1967. On the nutrition and metabolism of zooplankton V. Feeding efficiency of *Calanus finmarchicus*. *J. mar. biol. Ass. U.K.*, Vol. 47, pp. 259–270.

CORNER, E. D. S. & A. G. DAVIES, 1971. Plankton as a factor in the nitrogen and phosphorus cycles in the sea. *Adv. Mar. Biol.*, Vol. 9, pp. 101–204.

COSTE, B. & G. SLAWYK, 1974. Structure de répartitions superficielles des sels nutritifs dans une zone d'upwelling (Cap Corveiro, Sahara espagnol). *Téthys*, Vol. 6, pp. 123–132.

GOSTAN, J. & P. GUIBOUT, 1974. Sur quelques mesures de courant effectuées dans la zone d'upwelling de Mauritanie au voisinage et à l'intérieur d'un canon. *Téthys*, Vol. 6, pp. 349–362.

HARRIS, E., 1959. The nitrogen cycle in Long Island Sound. *Bull. Bingham oceanogr. Coll.*, Vol. 17, pp. 31–65.

HERBLAND, A., 1974. Activité bactérienne dans l'upwelling mauritanien. Relation avec l'oxygène et la matière organique. *Téthys*, Vol. 6, pp. 203–212.

HERBLAND, A., 1975. Utilisation par la flore hétérotrophe de la matière organique naturelle dans l'eau de mer. *J. exp. mar. Biol. Ecol.*, Vol. 19, pp. 19–31.

HERBLAND, A. & J. F. BOIS, 1974. Assimilation et minéralisation de la matière organique dissoute dans la mer. Méthode par scintillation liquide. *Mar. Biol.*, Vol. 24, pp. 203–212.

HERBLAND, A., R. LE BORGNE & B. VOITURIEZ, 1973. Production primaire et secondaire et régénération

des sels nutritifs dans l'upwelling de Mauritanie. *Doc. Scient. Centre Rech. Océanogr. Abidjan*, T. 4, No. 1, 75 pp.

HERBLAND, A., R. LE BORGNE & B. VOITURIEZ, 1974. Main physical and biological features of the Cape Timiris area (Northwest Africa). *CUEA Newsletter*, Vol. 3, No. 5, pp. 10–13.

HERBLAND, A. & B. VOITURIEZ, 1974. La production dans l'upwelling mauritanien en mars 1973. *Cah. ORSTOM, sér. Océanogr.*, T. 12, No. 2, pp. 187–201.

HOBSON, L. A., D. W. MENZEL & R. T. BARBER, 1973. Primary productivity and sizes of pools of organic carbon in the mixed layer of the ocean. *Mar. Biol.*, Vol. 19, pp. 298–306.

JOHANNES, R. E., 1968. Nutrient regeneration in lakes and oceans. *Adv. Microbiol. Sea*, Vol. 1, pp. 208–213.

KOROLEFF, F., 1969. Direct determination of ammonia in natural waters as indophenol blue. *Cons. Int. Explor. Mer*, CM 1969/C, No. 9.

LE BORGNE, R. P., 1973. Étude de la respiration et de l'excrétion d'azote et de phosphore des populations zooplanctoniques de l'upwelling mauritanien (mars–avril 1972). *Mar. Biol.*, Vol. 19, pp. 249–257.

LORENZEN, C. J., 1966. A method for continuous measurement of *in vivo* chlorophyll concentration. *Deep-Sea Res.*, Vol. 13, pp. 223–227.

RYTHER, J. H., D. W. MENZEL, E. M. HULBURT, C. J. LORENZEN & N. CORWIN, 1971. The production and utilization of organic matter in Peru coastal current. *Investigacion pesq.*, T 35, pp. 43–59.

SMITH, W. E., R. T. BARBER & S. A. HUNTSMAN, 1977. Primary production off the coast of Northwest Africa: excretion of dissolved organic matter and its heterotrophic uptake. *Deep-Sea Res.*, Vol. 24, pp. 35–47.

UNESCO, 1968. Zooplankton sampling. *Monogr. Oceanogr.*, Vol. 2, 174 pp.

WAKSMAN, S. A. & C. E. RENN, 1936. Decomposition of organic matter in seawater by bacteria. III. Factors influencing the rate of decomposition. *Biol. Bull. mar. biol. Lab., Woods Hole*, Vol. 70, pp. 472–483.

WAKSMAN, S. A., M. HOTCHKISS, C. L. CAREY & Y. HARDMAN, 1938. Decomposition of nitrogenous substances in seawater by bacteria. *J. Bact.*, Vol. 35, pp. 477–486.

WHITLEDGE, T. E. & T. T. PACKARD, 1971. Nutrient regeneration by anchovies and zooplankton in Pacific upwelling regions. *Investigacion pesq.*, T. 35, pp. 243–250.