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A global estimation of mesozooplankton ammonium excretion in the open ocean

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Mesozooplankton ammonium excretion rates in the ocean, based on published data, were studied across all latitudes in order to assess the amount of ammonium excretion by this community. Specific ammonium excretion rates were highest in equatorial waters and decreased rapidly poleward. Global community excretion in the upper 200 m of the oceans, integrated over all latitudes, accounted in general for 1.78 ± 0.60 Gt N·year^{-1}. Excretion rates showed a decrease from tropical (0.65 ± 0.14 Gt N·year^{-1}) to polar waters (0.05 ± 0.02 Gt N·year^{-1}). The substrate metabolized by organisms as indicated by the O/N ratio showed a protein-based metabolism of mesozooplankton with the exception of the temperate and subpolar regions, which showed a more lipid-based metabolism. The largest contribution of ammonium to autotrophs was observed in the tropical and subtropical areas, decreasing to polar areas. On a global basis, nutrient regeneration by mesozooplankton in the oceanic realm was estimated to be in the range of 12–23% of the requirements for phytoplankton and bacterial production.

INTRODUCTION

Phytoplankton production in the ocean is fuelled by nitrogenous forms which are the main limiting nutrients. Nitrate present in the euphotic layer and ammonium excreted by organisms are the principal nutrients used by autotrophs. Nitrate vertically transported to the euphotic zone and nitrogen fixation gives rise to the so-called new production. The ammonium excreted by heterotrophs (bacteria, micro- and mesozooplankton) promotes the regenerated production (Dugdale and Goering, 1967). This production is driven not only by ammonium but also due to the fraction of nitrate which is generated by nitrification in the upper layers of the ocean (Dore and Karl, 1996; Yool *et al.*, 2007, among others).

Ammonium sustains a rather high percentage (up to 100%) of the requirements for primary production (Verity, 1985; Knauer *et al.*, 1990). Average values in the euphotic zone range from about 50% in coastal waters to >90% in the oligotrophic ocean, with a global average of around 80% (Harrison, 1992). However, bacteria in the ocean can be competing for (Kirchman and Wheeler, 1998) or regenerating ammonium (Kirchman, 2000) or both (Zehr and Ward, 2002). Therefore, the knowledge of ammonium release by pelagic organisms is of interest not only to know their metabolic nitrogen budget, but also because they drive phytoplankton and bacterial production as well as the potential for nitrification in shallow waters. This is rather important in the large areas of the tropical and subtropical ocean, as most of the nitrogen used by phytoplankton and bacteria is regenerated because of the intense stratification in these waters.

Ammonium is also important in the metabolism of phytoplankton because it is a reduced form of nitrogen which, in terms of energy, is less costly for uptake. Nitrate assimilation requires more energy expenditure and in some areas of the ocean this nutrient is not fully used in spite of its high concentrations (e.g. the Southern Ocean). Algae growing in a nitrogen-limited environment can assimilate both nitrate and ammonium simultaneously (Bienfang, 1975). However,

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Table I: Literature review of the percentage of primary production accounted for by mesozooplankton ammonium excretion rates in different areas of the ocean

Area	%	Reference
Long Island Sound	43–66	Harris (1959)
Sargasso Sea	10	Dugdale and Goering (1967)
Costa Rica Dome	2–8	Whitledge and Packard (1971)
Oligotrophic waters off NW USA	36	Jawed (1973)
North Pacific central gyre	40–50	Eppley *et al.* (1973)
Upwelling NW Africa	12–36	Smith and Whitledge (1977)
Canadian shelf (Nova Scotia)	2–50	Fournier *et al.* (1977)
Gulf of Guinea	17–57	Le Borgne, 1977a)
Kuroshio Sea	11–44	Ikeda and Motoda (1978)
Perú	25	Smith (1978)
Upwelling NW Africa	1.5–51	Fernández (1981)
Gulf of Mexico	17	Bidigare *et al.* (1982)
Mid Atlantic Bay	30	Harrison *et al.* (1983)
Canary Islands	11–36	Hernández-León (1986)
Great South Bay, New York	5–74	Park *et al.* (1986)
Southeastern Sea of Korea	3–15	Park (1986)
Gulf of Maine	5–31	King *et al.* (1987)
NW Mediterranean	43	Alcaraz *et al.* (1994)
Central tropical Pacific	<7	Dam *et al.* (1995)
Central tropical Pacific	3–17	Zhang *et al.* (1995)
Antarctic Peninsula	10	Alcaraz *et al.* (1998)
Canary Islands	8–19	Hernández-León *et al.* (1998)
Tropical Atlantic (21°N)	3–7	Hernández-León *et al.* (1999a, b)
Antarctic Peninsula	<0.5	Hernández-León *et al.* (1999a, b)
South Georgia (Southern Ocean)	15–82	Atkinson and Whitehouse (2000, 2001)
Equatorial Pacific	31–36	Gaudy *et al.* (2003)
NW Iberian Peninsula	4–30	Isla *et al.* (2004a)
Atlantic Ocean (50°N-30°S)	31–100	Isla *et al.* (2004b)

inhibition of nitrate uptake in the presence of ammonium has been shown in laboratory and field experiments (MacIsaac and Dugdale, 1969, 1972). This difference seems to be related to the internal pool of nitrogen in the cell (Conway *et al.*, 1976). Moreover, it is known that nitrogen limitation increases the sensitivity of photosynthesis to inhibition by ultraviolet radiation in the water column, by decreasing cell size and the photoprotective mycosporine-like aminoacids (Litchman *et al.*, 2002).

The importance of ammonium excretion by mesozooplankton has been measured in many areas of the ocean and, in general, different studies agree that the contribution of this excretion to primary production lies within a very wide range (from <0.5 to 100%, Table I), mainly depending on the productivity of the area. However, weight-specific ammonium excretion varies with temperature, animal size (Ikeda, 1985) and the nutritional status of the organisms (Ikeda and Dixon, 1984), and total community excretion rates also vary with mesozooplankton biomass. Because of this, it is of interest to study the latitudinal variability of the specific and community rates, and the contribution of ammonium excretion to primary and bacterial production, as has been done in the recent assessments of biomass and respiration rates at the global scale by Hernández-León and Ikeda (Hernández-León and Ikeda, 2005a). Such an estimation of ammonium excretion by mesozooplankton and its importance to nutrient regeneration in the ocean has not yet been attempted at the global scale.

METHOD

We found 775 values of specific ammonium excretion for the epipelagic zone (<200 m deep) in the literature of which 79.4% were expressed on a dry weight basis, 7.5% per individual, 6.1% on a wet weight basis and 7.0% on a carbon basis. Mixed zooplankton was used in 39.9% of the experiments, whereas 60.1% were performed using different crustacean mesozooplankton. The latter experiments were performed with copepods (78.1% of experiments), euphausiids (13.5%), other crustaceans (0.9%) and mixed crustaceans (7.5%). In this study, ammonium excretion rates were standardized as the fraction of the body nitrogen excreted daily, assuming a carbon to nitrogen ratio of 4 (Båmstedt, 1986) and also assuming that nitrogen is 10% of the dry weight (Båmstedt, 1986). In order to compare with previous assessments of metabolism at the global scale (Hernández-León and Ikeda, 2005a), we used the same biomass data set based on weight measurements, excluding displacement volume and wet weight data. The latter measurements were not used in order to avoid large variability of conversion factors as much as possible. All the biomass data were expressed in carbon units but converted here to nitrogen. Details of the conversion factors used to estimate biomass are given by Hernández-León and Ikeda (Hernández-León and Ikeda, 2005a). As was the case for biomass and respiration values (Hernández-León and Ikeda, 2005a), ammonium excretion data were scarce in waters between 20–40°S and 60–80°N.

Total ammonium excretion and nutrient regeneration of mesozooplankton by latitude was calculated using the areas and values of primary production given by Longhurst *et al.* (Longhurst *et al.*, 1995) and converted to nitrogen requirements using the N/C ratio of 0.16 (Goldman and McCarthy, 1978). The values of autotrophic production of each biogeochemical province were assigned to the mid-point of their latitudinal range. Coastal provinces were not included in order to obtain a general assessment for the oceanic realm, and in order to compare with the results obtained in the previous study of the metabolism of this community at a global scale (Hernández-León and Ikeda, 2005a). Bacterial production in oceanic areas over different latitudes was taken from Ducklow (Ducklow, 1999). Values given for the different latitudinal ranges were used to build a polar to tropical range of values, which were used for the northern and southern hemisphere.

RESULTS

Specific ammonium excretion rates, as expected, increased in relation to temperature (Fig. 1). The magnitude of the variability was rather high with a Q_{10} of 3.60, higher than the 2.03 obtained for specific respiration rates in a similar set of data (Hernández-León and Ikeda, 2005b). This higher Q_{10} value can be explained by the latitudinal changes in specific ammonium excretion rates of zooplankton (Fig. 2). As observed, polar and temperate values (mainly in the northern hemisphere where data coverage is high) are similar to that hypothesized previously (Fig. 2; Ikeda, 1985). Tropical data reviewed, however, were slightly higher which supported the higher Q_{10} value observed in Fig. 1. This difference between Q_{10} values for respiration and excretion was also observed by Le Borgne (1986).

Latitudinal variability in total mesozooplankton ammonium excretion can be calculated as the product of specific ammonium excretion rates of the organisms and their biomass (Fig. 3). Because we found no differences in the northern hemisphere between the results of Ikeda (Ikeda, 1985) and the present review, we used the equation given by the latter author in order to estimate the community excretion rate on a latitudinal basis. The results show a higher ammonium excretion in tropical

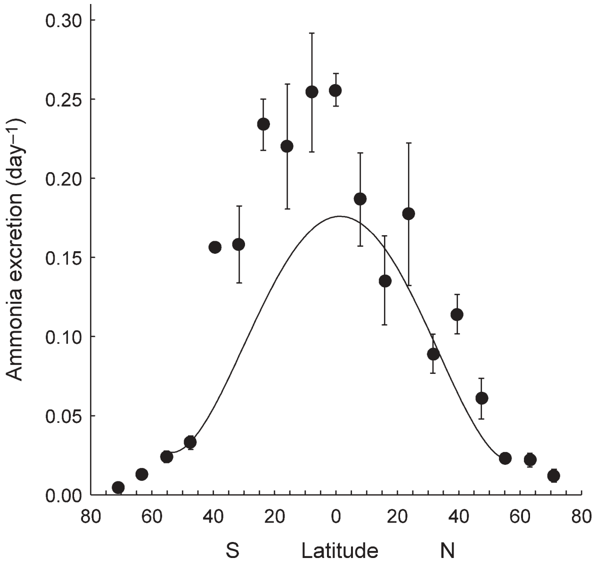

Fig. 2. Average values (±SE) of literature data on specific ammonium excretion rates of epipelagic mesozooplankton by latitude ranges. The continuous line is the specific ammonium excretion rates given in Ikeda (Ikeda, 1985).

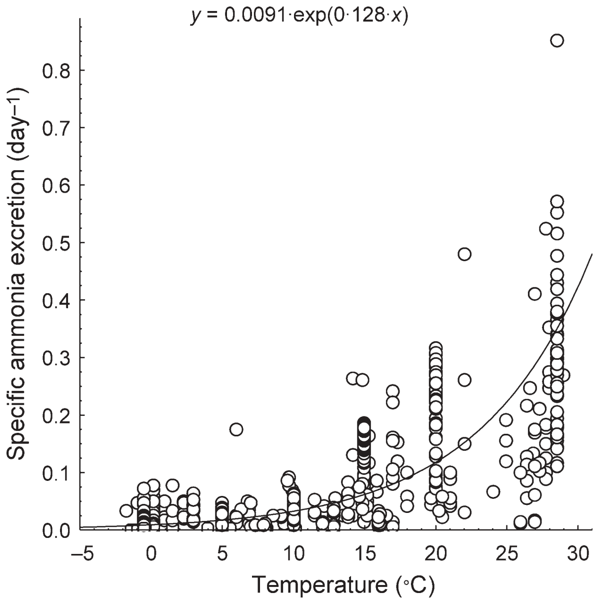

Fig. 1. Review of published values of specific ammonium excretion rates of epipelagic mesozooplankton in relation to temperature.

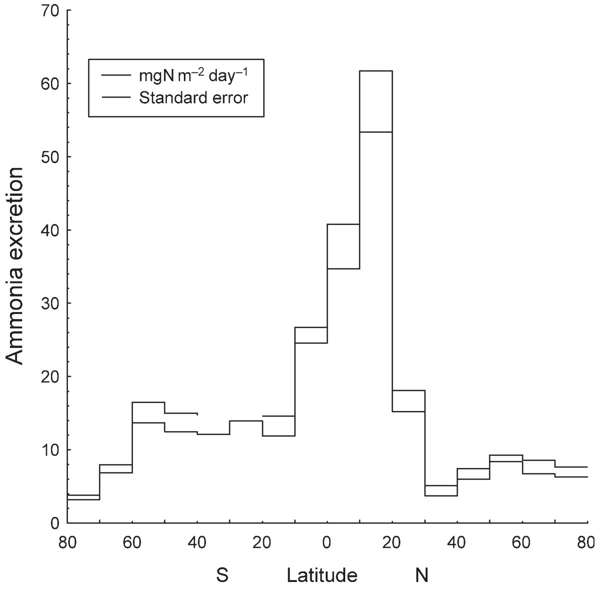

Fig. 3. Average values (±SE) of community ammonium excretion rates of epipelagic mesozooplankton by latitude ranges. Error (dashed line) was calculated using the propagation of error values through multiplication of biomass and specific rates by latitude.

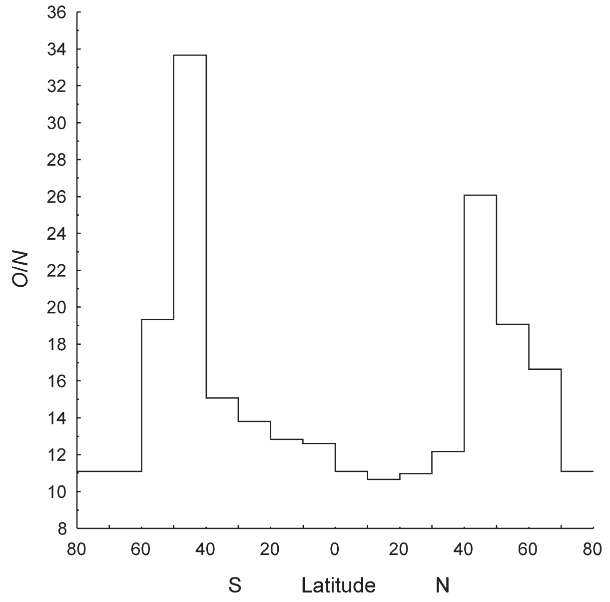

Fig. 4. Respiration to ammonium excretion ratio by atoms of epipelagic mesozooplankton by latitude ranges.

waters due to the high biomass (Hernández-León and Ikeda, 2005a), and high specific rates (Fig. 2) resulting from the higher temperature and the smaller size of mesozooplankton.

The substrate metabolized by mesozooplankton was estimated by comparing the respiration rates obtained in a previous study (Hernández-León and Ikeda, 2005a) and the present ammonium excretion rates. The ratio of oxygen consumed to ammonium excreted (O/N) was calculated (Fig. 4). As expected, the latitudinal distribution showed higher values in the polar and subpolar waters (O/N ratio >16), whereas the lowest values were observed in tropical and subtropical areas (O/N ratio between 10 and 16). The highest values (O/N > 24) were observed in the same latitudinal bands in both hemispheres (40–50°N and 40–50°S).

The contribution of mesozooplankton community ammonium excretion to primary production in the epipelagic zone was calculated using the mean daily values for the period 1978–86 given by Longhurst *et al.* (Longhurst *et al.*, 1995). As expected, primary production was higher in both polar areas (Fig. 5A). However, bacterial production showed higher values in the tropical area (Fig. 5A). The largest contribution of ammonium to autotrophs and bacteria was observed in the tropical and subtropical areas, decreasing to polar areas (Fig. 5B). Total ammonium excretion by mesozooplankton at the global scale is also related to the area of the different oceans. Taking into account the areas of the oceans at the different latitudinal bands, mesozooplankton community excretion rates and their contribution to primary production also showed a decrease from the tropical (0.65 ± 0.14 Gt N·year^{-1}) to the polar waters (0.05–0.12 Gt N·year^{-1}; Table II). Total excretion rates accounted for a general 1.78 ± 0.60 Gt N·year^{-1}.

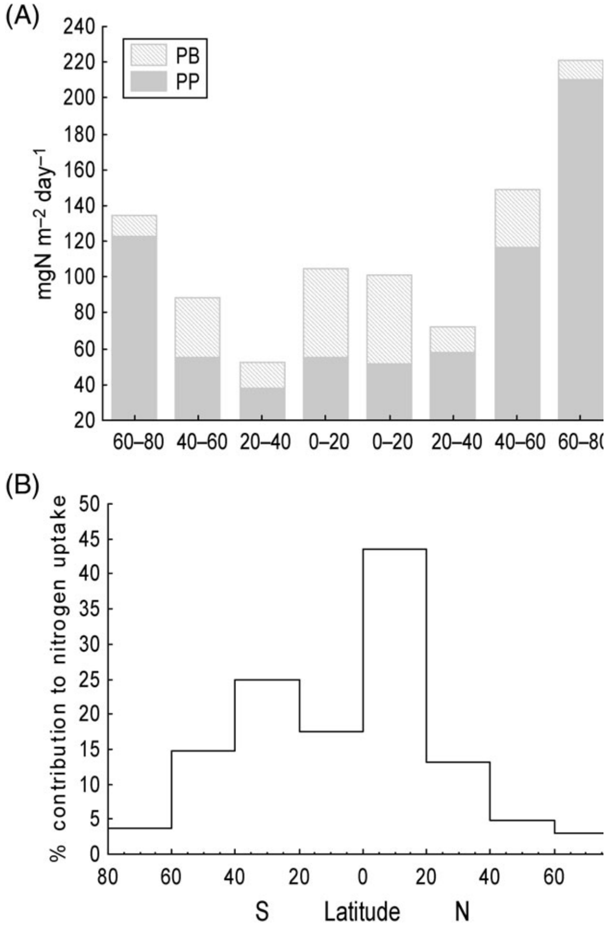

Fig. 5. Latitudinal range of (**A**) primary and bacterial production obtained from the values published by Longhurst *et al.* (Longhurst *et al.*, 1995) and Ducklow (Ducklow, 1999), and (**B**) the contribution of mesozooplankton ammonium excretion rates to total nitrogen uptake (primary plus bacterial production).

DISCUSSION

Latitudinal distribution of specific ammonium excretion showed higher values than expected from the equations of Ikeda (Ikeda, 1985) in tropical areas, also supporting a higher than expected Q_{10} value (Fig. 1). This could result from the seasonal variability in the oceanographic conditions of these areas of the ocean. Differences in temperature and the presence or absence of upwelling give rise to quite different metabolic and feeding scenarios (Le Borgne, 1977a, 1977b). In any case, this

Table II: Epipelagic mesozooplankton ammonium excretion rates (mean ± SE) obtained for each latitude range using the biomass and specific ammonium excretion rates reviewed in the present work

Latitude range	Area (10^6 km^2)	Biomass (mg N m^{-2})	Ammonium excretion (mg N m^{-2} day^{-1})	Global excretion (Gt N year^{-1})	PP (Gt N year^{-1})	Nitrogen Uptake	PP (%)	NU (%)
50–80°N	19.58	361.4 ± 61.4	7.14 ± 2.48	0.05 ± 0.02	1.28	1.36	3.9	3.7
10–50°N	68.14	166.2 ± 45.8	19.58 ± 9.09	0.49 ± 0.23	1.73	2.54	28.4	19.3
10–10°S	60.20	176.8 ± 25.1	29.63 ± 6.48	0.65 ± 0.14	1.39	2.40	46.8	27.0
10–50°S	101.64	166.4 ± 75.0	12.60 ± 4.43	0.47 ± 0.16	1.72	2.94	27.3	16.0
50–80°S	41.05	377.3 ± 99.1	7.93 ± 3.05	0.12 ± 0.05	1.49	1.66	8.0	7.2
Total	290.61			1.78 ± 0.60	7.61	10.90	23.4	16.3

PP stands for primary production and NU for total nitrogen uptake (primary plus bacterial production), respectively.

seasonal variability was also accounted for in the whole northern hemisphere (Fig. 2), showing a good match between the present set of data and the results of the equation of Ikeda (Ikeda, 1985). Therefore, in order to be conservative we used the latter equation to estimate the total excretion on a global basis. Despite this, the tropical values were more than double those for excretion in other latitudes (Fig. 3).

The O/N ratio is normally used as an index of the substrate metabolized. A low ratio is normally observed in organisms processing proteins, whereas a high ratio is an indication of the use of lipid storage products. Ikeda (Ikeda, 1974) suggested that an O/N ratio of 24 is indicative of the utilization of lipid and proteins in equal proportions. Therefore, our assessment suggests a protein-based metabolism for mesozooplankton with the exception, as expected, of the polar and subpolar areas (Fig. 4). In these areas, the importance of lipid storage is known because of the high seasonality of primary production and the overwintering strategy of the organisms. The values obtained in the present study are higher than the O/N ratio of 24 only at 40–50°N and 40–50°S. These areas are characterized by the seasonal variability of primary production giving rise to the so-called spring bloom. This bloom progresses to the polar areas, ending in summer. However, a decrease in the O/N ratio was also observed in both polar areas (>60°S and 70–80°N), reflecting perhaps a protein-based metabolism in these areas because of the rather short pulse of primary production during the seasonal cycle and/or, perhaps, the lack of ammonium excretion experiments during winter. The low values observed in the tropical areas agree with measurements made during different seasons (Le Borgne, 1977a) and with recent observations (Gaudy *et al*., 2003). In general, mesozooplankton showed a protein-based metabolism, which supports the omnivory of these organisms. Hernández-León and Ikeda (Hernández-León and Ikeda, 2005a), comparing their results with those of Calbet (Calbet, 2001), found that only 21% of the ingestion by mesozooplankton was phytoplankton. Therefore, our finding of a rather low O/N ratio across latitudes agrees with the now widely accepted feeding pressure of these organisms on microzooplankton.

Mesozooplankton ammonium excretion supports a rather variable percentage of phytoplankton production in the ocean (Table I). However, our results show that mesozooplankton nutrient regeneration is more important in tropical and subtropical areas than in temperate or polar areas. Except for the polar and subpolar areas where this percentage is rather low (4–8%), nutrient regeneration by mesozooplankton ranges between 27 and 47% of the requirements of primary production and between 7 and 27% for the total ammonium uptake (including bacteria uptake) between 50°N and 50°S, with a global value of about 23% for primary production and 16% for the total uptake (Table II). Taking into account the range of global gross primary production given by del Giorgio and Duarte (del Giorgio and Duarte, 2002) of 41–77 Gt C·year^{-1}, we estimated a range of 15–27% for the nutrient contribution of mesozooplankton to primary production. Assuming bacterial production as 20% of primary production (Ducklow, 1999), estimated nutrient regeneration of mesozooplankton in the oceanic realm on a global basis is in the range of 12–23%.

Our assessment of the importance of mesozooplankton in recycling nitrogen in the epipelagic zone depends first on the values of biomass. As discussed in a previous study (Hernández-León and Ikeda, 2005a), the estimation of biomass on a global basis is a difficult task because (i) most of the values in the literature are given as wet weight or displacement volume (as a strategy to not destroy the samples) and their conversion to carbon units is still a challenge and (ii) daily and seasonal variability, as well as patchiness, also results in a high variability in a given area. Secondly, specific ammonium excretion rates also vary with temperature and body mass but also show daily and seasonal variability, not only due to temperature but also because of the seasonal production cycles in each area. The values of specific ammonium excretion rates found in the tropical areas in the present study seem to be above the rates predicted using the equation of Ikeda (Ikeda, 1985) as observed from the Q_{10} values and their latitudinal distribution (Fig. 2). However, the rather good match between the results of the latter equation and the values of our review in the northern hemisphere (Fig. 2), where we obtained the largest amount of data, suggests that the use of this equation is the most appropriate to assess the importance of ammonium excretion on a global basis. Thirdly, feeding condition of the organisms is another source of variability, poorly known at present. For example, Ikeda and Dixon (Ikeda and Dixon, 1984) observed that specific ammonium excretion by krill (*Euphaussia superba*) was 4.5 times higher in well-fed than in starving organisms. This is a rather large difference, taking into account that experiments to determine ammonium excretion rates are performed in filtered seawater over long periods (12–24 h), and most of the determinations made during the last decades were done with methods not sensitive enough (e.g. the phenol-hypoclorite method) to measure rates in shorter (<2 h) experiments. Ikeda and Skjoldal (Ikeda and Skjoldal, 1980) found that the rapid decrease of excretion rates at the start of the experiments was not due to capture stress but to food shortage. Therefore, it is reasonable to consider the values used in this review as conservative estimates of excretion rate.

In addition to ammonium, mesozooplankton excrete other organic nitrogenous compounds such as urea and amines. Utilization of urea by phytoplankton is well documented (McCarthy, 1971, 1972; Carpenter *et al.*, 1972a, 1972b; Fan *et al.*, 2003) and, for example, McCarthy (McCarthy, 1972) found that the primary production accounted for by urea averaged 28%. The proportion of total nitrogen excreted by mesozooplankton in relation to ammonium excretion is quite variable (Le Borgne, 1973, 1977a; Corner *et al.*, 1976). Eppley *et al.* (Eppley *et al.*, 1973) found that roughly half of the nitrogen excreted by mesozooplankotn was in the form of urea. Le Borgne (Le Borgne, 1977a) found that ammonium accounted for 60% of total nitrogen excreted by mesozooplankton, and Steinberg *et al.* (Steinberg *et al.*, 2002) found, on average, that 32% of dissolved nitrogen excretion was organic. Miller and Glibert (Miller and Glibert, 1998) observed similar proportions in the excretion rates of the three compounds (ammonium, urea and amines). Thus, our conservative estimates of ammonium excretion rates and their impact on autotrophs should be enlarged by at least 30% in order to assess the impact of mesozooplankton nitrogen regeneration on phytoplankton and bacterial growth. Ammonium excretion rates and regeneration of nutrients by microzooplankton and bacteria is even more important (Verity, 1985; Miller *et al.*, 1995; Maguer *et al.*, 1999) and, in fact, nutrient regeneration by mesozooplankton has been considered as a minor contribution to regenerated production (Harrison, 1992). Therefore, except for the case of polar and subpolar areas, nitrogenous compounds regenerated in the ocean seem to be enough to maintain steady-state levels of primary production in absence of competition with bacteria. Finally, reliable assessment of biomass in shelf areas will still increase our estimation of nitrogen regenerated by mesozooplankton.

In polar areas, however, the regenerated production supported by mesozooplankton is rather low and although other organic nitrogen compounds increase the contribution of mesozooplankton regeneration, it is still a low number. Moreover, Cohhlan and Bronk (Cohhlan and Bronk, 2001) observed higher phytoplankton uptake rates for nitrate and ammonium than for urea. Nutrient regeneration in polar areas is quite variable and the *f*-ratio (proportion of nitrate uptake in relation to total inorganic nutrient uptake by autotrophs) varies greatly. In the Southern Ocean, this ratio is rather low (from about 8 to 61%, Savoye *et al.*, 2004), despite the very high concentrations of nitrate there, an order of magnitude higher than ammonium. This low utilization of nitrate could be due to light limitation, the fact that ammonium uptake is less costly in terms of energy (Dugdale, 1976), the low affinity of phytoplankton for nitrate due to the low temperature in polar environments (Reay *et al.*, 1999), and/or the effect of iron limitation (Martin and Fitzwater, 1988). In contrast, ammonium uptake did not appear to be affected by the low temperature and it is a more important substrate for autotrophs than nitrate, explaining at least in part, the low utilization of the latter substrate. Ammonium content in the ice is of importance to the bloom produced during melting, but ammonium excretion by micro- and mesozooplankton should be of importance in the regulation of primary productivity in cold environments during the rest of the productive season. In this sense, the excretion by krill and zooplankton should also be of importance as previously observed (up to 82% of the requirements of primary production, Atkinson and Whitehouse, 2000). Moreover, large swarms of krill could have, locally, an important role as they could fulfil the requirements of phytoplankton as these swarms move large distances daily. Thus, it is of interest to point out the importance of ammonium regeneration in driving primary production in polar waters despite the very high concentrations of nitrate.

In summary, the variability of nutrient regeneration by mesozooplankton is rather large as observed in the literature (Table I) but it is explained by the latitudinal variability in temperature, zooplankton biomass and primary and bacterial production. In general, the largest contribution of nitrogen to autotrophs and bacteria was observed in the tropical region while the lowest was observed in the polar areas, despite the large zooplankton biomass there. However, it is in these areas where ammonium could be a limiting factor to primary and bacterial production. The substrate metabolized by mesozooplankton as observed by the O/N ratio showed a protein-based metabolism with the exception of some temperate regions (40–50°N and 40–50°S). This result supports the widely accepted notion of a microzooplankton-based diet for these organisms. Finally, despite (i) the methodological problems related to the determination of ammonium excretion rates, (ii) the inherent errors associated with the exercise to assess global ammonium excretion and (iii) the fact that our estimates should be considered as conservative because of the lack of estimates of mesozooplankton biomass in shelf and coastal areas in this study, our assessment shows the significance of mesozooplankton in nutrient regeneration in the ocean and its pivotal role in polar environments.

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REFERENCES

Alcaraz, M., Saiz, E. and Estrada, M. (1994) Excretion of ammonium by zooplankton and its potential contribution to nitrogen requirements for primary production in the Catalan Sea (NW Mediterranean). *Mar. Biol.*, **119**, 69–76.

Alcaraz, M., Saiz, E., Fernandez, J. A. *et al.* (1998) Antarctic zooplankton metabolism: carbon requirements and ammonium excretion of salps crustacean zooplankton in the vicinity of the Bransfield Strait during January 1994. *J. Mar. Syst.*, **17**, 347–359.

Atkinson, A. and Whitehouse, M. J. (2000) Ammonium excretion by Antarctic krill *Euphausia superba* at South Georgia. *Limnol. Oceanogr.*, **45**, 55–63.

Atkinson, A. and Whitehouse, M. J. (2001) Ammonium regeneration by Antarctic mesozooplankton: an allometric approach. *Mar. Biol.*, **139**, 301–312.

Båmstedt, U. (1986) Chemical composition and energy content. In Corner, E. D. S. and O'Hara, S. C. M. (eds), *The Biological Chemistry of Marine Copepods*. Clarendon, pp. 1–58.

Bidigare, R. R., King, F. D. and Biggs, D. C. (1982) Glutamate dehydrogenase (GDH) and respiratory electron transport system (ETS) activities in Gulf of Mexico zooplankton. *J. Plankton Res.*, **4**, 895–911.

Bienfang, P. (1975) Steady state analysis of nitrate-ammonium assimilation by phytoplankton. *Limnol. Oceanogr.*, **20**, 405–411.

Calbet, A. (2001) Mesozooplankton grazing effect on primary production: a global comparative analysis in marine ecosystems. *Limnol. Oceanogr.*, **46**, 1824–1830.

Carpenter, E. J., Remsen, C. C. and Watson, S. W. (1972a) Utilization of urea by some marine phytoplankters. *Limnol. Oceanogr.*, **17**, 265–269.

Carpenter, E. J., Remsen, C. C. and Schroeder, B. W. (1972b) Comparison of laboratory and in situ measurements of urea decomposition by a marine diatom. *J. Exp. Mar. Biol. Ecol.*, **8**, 259–264.

Cohhlan, W. P. and Bronk, D. A. (2001) Nitrogen uptake kinetics in the Ross Sea, Antarctica. *Deep-Sea Res. II*, **48**, 4127–4153.

Conway, H. L., Harrison, P. J. and Davis, C. O. (1976) Marine diatoms grown in chemostats under silicate or ammonium limitation. 2. Transient-response of *Skeletonema costatum* to a single addition of limiting nutrient. *Mar. Biol.*, **35**, 187–199.

Corner, E. D. S., Head, R. N., Kilvington, C. C. *et al.* (1976) On the nutrition and metabolism of zooplankton. X. Quantitative aspects of *Calanus helgolandicus* feeding as a carnivore. *J. Mar. Biol. Assoc. UK*, **56**, 345–358.

Dam, H. G., Zhang, X., Butler, M. *et al.* (1995) Mesozooplankton grazing and metabolism at the equator in the Central Pacific: implications for carbon and nitrogen fluxes. *Deep-Sea Res.*, **42**, 735–756.

del Giorgio, P. A. and Duarte, C. M. (2002) Respiration in the open ocean. *Nature*, **420**, 379–384.

Dore, J. E. and Karl, D. M. (1996) Nitrification in the euphotic zone as a source for nitrite, nitrate, and nitrous oxide at Station ALOHA. *Limnol. Oceanogr.*, **41**, 1619–1628.

Ducklow, H. W. (1999) The bacterial component of the oceanic euphotic zone. *FEMS Microbiol. Ecol.*, **30**, 1–10.

Dugdale, R. C. and Goering, J. J. (1967) Uptake of new and regenera forms of nitrogen in primary productivity. *Limnol. Oceanogr.*, **12**, 196–206.

Dugdale, R. C. and Goering, J. J. (1976) Nutrient cycles. In Cushing, D. H. and Walsh, J. J. (eds), The Ecology of the Seas. Saunders, pp. 141–172.

Eppley, R. W., Renger, E. H., Venrick, E. L. *et al.* (1973) A study of plankton dynamics and nutrient cycling in the Central Gyre of the North Pacific Ocean. *Limnol. Oceanogr.*, **18**, 534–551.

Fan, C., Glibert, P. M., Alexander, J. *et al.* (2003) Characterization of urease activity in three marine phytoplankton species, *Aureococcus anophagefferens*, *Prorocentrum minimum*, and *Thalassiosira weisflogii*. *Mar. Biol.*, **142**, 949–958.

Fernández, F. (1981) Nutrient regeneration and particulate organic matter consumption by crustacean mesozooplankton in the upwelling region of NW Africa, with some notes on the community structure. *J. Exp. Mar. Biol. Ecol.*, **51**, 187–206.

Fournier, R. O., Marra, J., Bohrer, R. *et al.* (1977) Plankton dynamics and nutrient enrichment of the Scotian shelf. *J. Fish. Res. Board Can.*, **34**, 1004–1018.

Gaudy, R., Champalbert, G. and Le Borgne, R. (2003) Feeding and metabolism of mesozooplankton in the equatorial Pacific high-nutrient, low-chlorophyll zone along 180°. *J. Geophys. Res.*, **108**, 8144–8156.

Goldman, J. C. and McCarthy, J. J. (1978) Steady state growth and ammonium uptake of a fast growing marine diatom. *Limnol. Oceanogr.*, **23**, 695–703.

Harris, E. (1959) The nitrogen cycle in Long Island Sound. *Bull. Bingham Oceanogr. Coll.*, **17**, 31–65.

Harrison, W. G., Douglas, D., Falkowski, P. G. *et al.* (1983) Summer nutrient dynamics of the Middle Atlantic Bight: nitrogen uptake and regeneration. *J. Plankton Res.*, **5**, 539–556.

Harrison, W. G. (1992) Regeneration of nutrients. In Falkowski, P. G. and Woodhead, A. D. (eds), *Primary Productivity and Biogeochemical Cycles in the Sea.* Plenum Press, pp. 385–409.

Hernández-León, S. (1986) Nota sobre la regeneración de amonio por el mesozooplancton en aguas de Canarias. *Bol. Inst. Esp. Oceanogr.*, **3**, 75–80.

Hernández-León, S. and Ikeda, T. (2005a) A global assessment of mesozooplankton respiration in the ocean. *J. Plankton Res.*, **27**, 153–158.

Hernández-León, S. and Ikeda, T. (2005b) Zooplankton respiration. In del Giorgio, P. A. and Williams, P. J. L. B. (eds), *Respiration in Aquatic Ecosystems.* Oxford University Press, pp. 57–82.

Hernández-León, S., Arístegui, J., Gómez, M. *et al.* (1998) Mesozooplankton metabolism and its effect on chlorophyll and primary production in slope waters of the Canary Islands. *Ann. Inst. Océanogr. Paris*, **74**, 127–138.

Hernández-León, S., Postel, L., Arístegui, J. *et al.* (1999a) Large-scale and mesoscale distribution of plankton biomass and metabolic activity in the northeastern Central Atlantic. *J. Oceanogr.*, **55**, 471–482.

Hernández-León, S., Torres, S., Gómez, M. *et al.* (1999b) Biomass and metabolism of zooplankton in the Bransfield Strait (Antarctic Peninsula) during austral spring. *Polar Biol.*, **21**, 214–219.

Ikeda, T. (1974) Nutritional ecology of marine zooplankton. *Mem. Fac. Fish. Hokkaido Univ.*, **22**, 1–97.

Ikeda, T. (1985) Metabolic rates of epipelagic zooplankton as a function of body size and temperature. *Mar. Biol.*, **85**, 1–11.

Ikeda, T. and Motoda, S. (1978) Estimated zooplankton production and their ammonium excretion in the Kuroshio and adjacent seas. *Fish. Bull.*, **76**, 357–368.

Ikeda, T. and Skjoldal, H. R. (1980) The effect of laboratory conditions on the extrapolation of experimental measurements to the ecology of marine zooplankton. VI Changes in physiological activities and biochemical components of *Acetes sibogae* and *Acartia australis* after capture. *Mar. Biol.*, **58**, 283–293.

Ikeda, T. and Dixon, P. (1984) The influence of feeding on the metabolic activity of Antarctic Krill (*Euphausia superba* Dana). *Polar. Biol.*, **3**, 1–9.

Isla, J. A., Ceballos, S. and Anadón, R. (2004a) Mesozooplankton metabolism and feeding in the NW Iberian upwelling. *Est. Coast. Shelf Sci.*, **61**, 151–160.

Isla, J. L., Llope, M. and Anadón, R. (2004b) Size-fractionated mesozooplankton biomass, metabolism and grazing along a 50°N-30°S transect of the Atlantic Ocean. *J. Plankton Res.*, **26**, 1301–1313.

Jawed, M. (1973) Ammonium excretion by zooplankton and its significance to primary productivity during summer. *Mar. Biol.*, **23**, 115–120.

King, F. D., Cucci, T. L. and Townsend, D. W. (1987) Microzooplankton and macrozooplankton glutamate dehydrogenase as indices of the relative contribution of these fractions to ammonium regeneration in the Gulf of Maine. *J. Plankton Res.*, **9**, 277–289.

Kirchman, D. L. (2000) Uptake and regeneration of inorganic nutrients by marine heterotrophic bacteria. In Kirchman, D. L. (ed.), *Microbial Ecology of the Oceans.* Wiley-Liss, pp. 261–288.

Kirchman, D. L. and Wheeler, P. A. (1998) Uptake of ammonium and nitrate by heterotrophic bacteria and phytoplankton in the Sub-Arctic Pacific. *Deep-Sea Res. I*, **45**, 347–365.

Knauer, G. A., Redalje, D. G., Harrison, W. G. *et al.* (1990) New production at the VERTEX time-series site. *Deep-Sea Res.*, **37**, 1121–1134.

Le Borgne, R. (1973) Etude de la respiration et de l'excrétion d'azote et de phosphore des populations zooplanctoniques de l'upwelling mauritanien (mars-avril 1972). *Mar. Biol.*, **19**, 249–257.

Le Borgne, R. (1977a) Etude de la production pélagique de la zone équatoriale de l'Atlantique à 4° W. III. Respiration et excrétion d'azote et de phosphore du zooplancton. *Cah. ORSTOM Ser. Oceanogr.*, **15**, 349–362.

Le Borgne, R. (1977b) Etude de la production pélagique de la zone équatoriale de l'Atlantique à 4° W. IV. Production et rôle du zooplancton dans le réseau trophique. *Cah. ORSTOM Ser. Oceanogr.*, **15**, 363–374.

Le Borgne, R. (1986) The release of soluble end products of metabolism. In Corner, E. D. S. and O'Hara, S. C. M. (eds), *The Biological Chemistry of Marine Copepods.* Clarendon, pp. 109–164.

Litchman, E., Neale, P. J. and Banaszak, A. T. (2002) Increased sensitivity to ultraviolet radiation in nitrogen-limited dinoflagellates: photoprotection and repair. *Limnol. Oceanogr.*, **47**, 86–94.

Longhurst, A. R., Sathyendranath, S., Platt, T. *et al.* (1995) An estimate of global primary production in the ocean from satellite radiometer data. *J. Plankton Res.*, **17**, 1245–1271.

MacIsaac, J. J. and Dugdale, R. C. (1969) The kinetics of nitrate and ammonium uptake by natural populations of marine phytoplankton. *Deep-Sea Res.*, **16**, 415–422.

MacIsaac, J. J. and Dugdale, R. C. (1972) Interactions of light and inorganic nitrogen in controlling nitrogen uptake in the sea. *Deep-Sea Res.*, **19**, 209–232.

Maguer, J. F., ĹHelguen, S., Madec, C. *et al.* (1999) Seasonal patterns of ammonium regeneration from size-fractionated microheterotrophs. *Cont. Shelf Res.*, **19**, 1755–1770.

Martin, J. H. and Fitzwater, S. E. (1988) Iron deficiency limits phytoplankton growth in the north-east Pacific subarctic. *Nature*, **331**, 341–343.

McCarthy, J. (1971) The role of urea in marine phytoplankton ecology. PhD Thesis. University of California, San Diego.

McCarthy, J. (1972) The uptake of urea by natural populations of marine phytoplankton. *Limnol. Oceanogr.*, **17**, 738–748.

Miller, C. and Glibert, P. (1998) Nitrogen excretion by the calanoid copepod *Acartia tonsa*: results of mesocosm experiments. *J. Plankton Res.*, **20**, 1767–1780.

Miller, C. A., Penry, D. L. and Glibert, P. M. (1995) The impact of trophic interactions on rates of nitrogen regeneration and grazing in Chesapeake Bay. *Limnol. Oceanogr.*, **40**, 1005–1011.

Park, Y. H. (1986) Water characteristics and movements of the Yellow Sea Warm Current in Summer. *Prog. Oceanogr.*, **17**, 243–254.

Park, Y. C., Carpenter, E. J. and Falkowski, P. G. (1986) Ammonium excretion and Glutamate dehydrogenase activity of zooplankton in Great South Bay, New York. *J. Plankton Res.*, **8**, 489–503.

Reay, D. S., Nedwell, D. B., Priddle, J. *et al.* (1999) Temperature dependence of inorganic nitrogen uptake: reduced affinity for nitrate at suboptimal temperatures in both algae and bacteria. *App. Environ. Microbiol.*, **65**, 2577–2584.

Savoye, N., Dehairs, F., Elskens, M. *et al.* (2004) Regional variation of spring N-uptake and new production in the Southern Ocean. *Geophys. Res. Lett.*, **31**, 1–4.

Smith, S. L. (1978) Nutrient regeneration by zooplankton during a red tide off Peru, with notes on biomass and species composition of zooplankton. *Mar. Biol.*, **49**, 125–132.

Smith, S. L. and Whitledge, T. E. (1977) The role of zooplankton in the regeneration of nitrogen in a coastal upwelling system off northwest Africa. *Deep-Sea Res.*, **24**, 49–56.

Steinberg, D. K., Goldthwait, S. A. and Hansell, D. A. (2002) Zooplankton vertical migration and the active transport of dissolved organic and inorganic nitrogen in the Sargasso Sea. *Deep-Sea Res. I*, **49**, 1445–1461.

Verity, P. G. (1985) Grazing, respiration, excretion, and growth rates of tintinnids. *Limnol. Oceanogr.*, **30**, 1268–1282.

Whitledge, T. E. and Packard, T. T. (1971) Nutrient excretion by anchovies and zooplankton in Pacific upwelling regions. *Invest. Pesq.*, **35**, 243–250.

Yool, A., Adrian, A. P., Fernández, C. *et al.* (2007) The significance of nitrification for oceanic new production. *Nature*, **447**, 999–1002.

Zehr, J. P. and Ward, B. B. (2002) Nitrogen cycling in the ocean: new perspectives on processes and paradigms. *Appl. Environ. Microbiol.*, **68**, 1015–1024.

Zhang, X., Dam, H. G., White, J. R. *et al.* (1995) Latitudinal variations in mesozooplankton grazing and metabolism in the central tropical Pacific during the U.S. JGOFS EqPac study. *Deep-Sea Res. II*, **42**, 695–714.