ON THE RATIO OF NITROGEN TO PHOSPHORUS IN THE SEA

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Harvey (1927) realized that the proportion of nitrate-nitrogen to phosphate-phosphorus is similar both in the depths of the Atlantic and in the water of the English Channel in midwinter. He considered that not only does the decay of plankton organisms give rise to these products in that proportion but also that the requirements of the phytoplankton during life are in the same proportion, since both are almost completely used up by the phytoplankton in the upper layers of the sea during summer. Later Redfield (1934) gathered together data from the Western North Atlantic, the Barents Sea (Kreps & Verjbinskaya, 1932) and the Antarctic (Ruud, 1930), and so was able to show conclusively that the order of the ratio of nitrate-N to phosphate-P is remarkably uniform in the sea and remains so when the store of these salts has been somewhat depleted by plant growth. The ratio lies close to N : P : : 20 : 1 when the salts are expressed as milligram-atoms of the elements concerned or nine times as much nitrate-nitrogen as phosphorus when expressed by weight. Redfield examined the nitrogen and phosphorus content of a number of plankton samples, both plant and animal, and found a mean ratio of 18·2. A number of analyses are also available on samples taken from the English Channel near Plymouth (Table I). The mean ratio is 16·3, similar to Redfield's, and the

Table I. Ratio of Nitrogen to Phosphorus (in gram-atoms) in Plankton Organisms taken in the English Channel at L 4 or two miles east of Eddystone

Date	Sample	mg.-atom N/m.³	N/P
9. iii. 34	Mixed Plankton	0·29	17·2
20. iii. 34	,,	0·32	19·8
26. iii. 34	,,	0·29	16·3
10. v. 34	,,	0·73	17·2
15. v. 34	,,	0·51	16·6
	Diatoms:		
3. iv. 34	Tow-net haul filtered through medium silk, almost entirely diatoms	—	21·6
15. v. 34	Rich in diatoms, particularly *Rhizosolenia*	—	17·0
24. v. 34	*Rhizosolenia*	—	15·5
	Zooplankton:		
5. vi. 36	*Sagitta elegans* mature	—	20·7
5. vi. 36	*Pleurobrachia pileus*	—	12·8
5. vi. 36	Portunid megalopas	—	12·2
5. vi. 36	Portunid zoeas and Crangonid larvae	—	13·7
5. vi. 36	*Callionymus lyra* post larvae	—	11·4

range is from 11·4 to 21·6. Although this ratio of nitrogen to phosphorus varies too much from 20 : 1 for us to speak of it as constant, it is sufficiently remarkable that in the sea as a whole and in plankton organisms, it so seldom shows greater variation.

Considerable deviations in sea water have however been found not only at stations in enclosed seas but also at oceanic stations. These do not necessitate the rejection of the principle but rather do they provide us with a new quantity likely to be of value as an index to the origin of bodies of water and of help in following stages in the nitrogen cycle such as are discussed in the following paper.

In the English Channel at Station E 1 in the winter of 1925–26 according to the results of Atkins & Harvey (cf. Cooper, 1933, Table VII) the ratio of nitrate to phosphate (in milligram-atoms) was about nine. By the following year the ratio had risen to thirteen and by 1930–31 to seventeen. At Station L 4 only surface and bottom results are available and, since high phosphate figures are often found in the surface layer and do not represent the phosphate content of the water immediately beneath, only a rough estimate of the phosphate content of the whole column can be formed. Bearing this in mind, it is still suggestive that the nitrate-phosphate ratio increased from twelve in the winter 1925–26 to fourteen a year later and further to about twenty-two in 1930–31. Thus we see that change in the nature of the water off Plymouth was attended by an increase in the nitrate-phosphate ratio up to 1930–31. That other changes in the nature of the water have taken place within the last fourteen years is shown by the decrease in the winter phosphate maximum after 1930, the related decrease in young fish and plankton generally and by the displacement of *Sagitta elegans* by *S. setosa* after 1931 (Russell, 1936). It should be pointed out that in this paper phosphate results are all uncorrected for error due to presence of salts or of copper* and have been determined by the Denigès-Atkins method. If the ratio of nitrate to phosphate be assumed ideally to approach a value of twenty when both are expressed in milligram-atoms, then deviations from this ratio must be due to definite causes and must clearly be of interest. It is suggested that the amount by which the ratio found differs from twenty be called "the anomaly of the nitrate-phosphate ratio". To illustrate the anomaly, determinations by Helge Thomsen (1931) on board the *Dana* and by the Discovery Committee's ships (1932) repay examination. Table II shows the ratio for three stations in the *Dana*'s Area I (Straits of Gibraltar and Alboran Sea) and the ratio for the mean nitrate and phosphate values in this area and in six other areas extending the length of the Mediterranean as far as the Aegean Sea. In some cases phosphate was completely absent so that the small amounts of nitrate present yield an infinite

* The existence of an error in phosphate determinations in sea water is well established. It does not exceed 25 % but it is still uncertain whether the error is due to the presence of salts, of copper or of both together. Measurements of the error by different workers differ considerably and unpublished work by the writer shows that the issue is far from clear. All data used here are on a comparable basis but are uncorrected.

Table II. Nitrate-Phosphate Ratio (Milligram-Atoms)

Station	Position	Date	Depth in metres 50	75	100	150	200	300	400	500	600	800	1000	1200	1500	2000	2500	3000	3500	4000	Mean for all depths
Mediterranean (*Dana*):																					
4025	Straits of Gibraltar and Alboran Sea	9. iv. 30	27	33	25	38	30	29	35	19	26	32	—	—	—	—	—	—	—	—	30
4027		11. iv. 30	(75)	35	29	32	24	27	47	37	26	25	—	—	—	—	—	—	—	—	31
4140		9. vi. 30	(60)	33	33	28	35	27	—	24	44	—	—	—	—	—	—	—	—	—	32
Area I			(45)	34	29	33	28	28	41	26	32	28	—	—	—	—	—	—	—	—	30
Area II	Balearic Sea, south	11. iv. 30 to 7. vi. 30	(55)	(150)	(106)	(57)	40	41	42	39	34	42	34	40	43	37	50	—	—	—	40
Area III	Sardinia-Tunis	23–25. iv. 30	∞	∞	∞	∞	(350)	(110)	(140)	(96)	—	—	—	—	—	—	—	—	—	—	(high)
Area IV	Tyrrhenian Sea, south	May, 30	o/o	o/o	∞	(93)	25	32	35	31	34	29	23	27	25	28	30	—	30	—	29
Area V	Straits of Messina	5–6. v. 30	∞	∞	∞	∞	∞	∞	∞	∞	∞	∞	∞	—	—	—	—	—	—	—	∞
Area VI	Ionian Sea	May, 30	∞	∞	∞	∞	(190)	(125)	(90)	(75)	(64)	54	36	47	42	50	55	43	57	54	49
Area VII	Aegean Sea	17–18. v. 30	o/o	o/o	∞	∞	∞	∞	∞	∞	∞	∞	—	—	—	—	—	—	—	—	∞
Atlantic (*Dana*):																					
3978	30° 24′ S, 13° 27′ E	13. ii. 30	8	17	14	18	20	21	19	25	20	19	19	19	22	24	—	—	—	—	19
4000	0° 45′ S, 11° 01′ W	4. iii. 30	9	18	17	15	18	—	20	17	18	19	20	18	15	14	—	—	—	—	16
4009	24° 26′ N, 17° 35′ W	18. iii. 30	o	(3)	(3)	20	16	19	18	18	17	17	17	19	18	16	—	—	—	—	18
4019	33° 08′ N, 10° 22′ W	30. iii. 30	∞	∞	(25)	16	19	20	—	19	24	24	25	24	20	21	20	20	20	20	21
Atlantic off Iberian Peninsula (*Dana*):																					
4141	36° 11′ N, 6° 57′ W	9. vi. 30	o	o	(20)	24	44	28	27	28	22	27	—	—	—	—	—	—	—	—	29
4142	36° 01′ N, 7° 29′ W	10. vi. 30	o/o	o/o	∞	21	30	28	25	25	33	27	**27**	—	—	—	—	—	—	—	27
4147	36° 39′ N, 8° 06′ W	10. vi. 30	o	(15)	23	17	23	21	25	25	28	**22**	—	—	—	—	—	—	—	—	23
4148	37° 02′ N, 9° 17′ W	11. vi. 30	∞	(61)	20	25	21	25	27	23	29	**29**	33	28	23	—	—	—	—	—	26
4149	38° 19′ N, 9° 26′ W	11. vi. 30	o/o	∞	(10)	24	27	28	25	25	—	**33**	38	26	25	—	—	—	—	—	28
4156	42° 41′ N, 9° 49′ W	16. vi. 30	∞	∞	33	25	18	25	20	25	23	**28**	23	25	22	25	—	—	—	—	24
Bay of Biscay (*Dana*):																					
4158	46° 28′ N, 8° 01′ W	17. vi. 30	12	19	19	17	15	22	19	18	19	21	20	19	16	16	15	15	15	15	17
4159	47° 20′ N, 6° 28′ W	19. vi. 30	(34)	22	19	21	19	18	28	25	25	23	23	—	—	—	—	—	—	—	22
Atlantic (Atkins & Harvey, 1925):																					
—	37° 44′ N, 13° 21′ W	12. x. 25	∞	(6)	(35)	(33)	23	19	—	20	—	—	18	—	—	17	—	16	—	—	19

o/o Both salts had zero concentration.
o Nitrate zero; phosphate positive.
∞ Nitrate positive; phosphate zero.
( ) Parentheses indicate that either nitrate or phosphate was too low to give a trustworthy ratio.
At 0, 10 and 25 metres at all stations one or both of the salts were absent.
Heavy type denotes water showing a temperature maximum indicating a Mediterranean origin. This water and that immediately above or below shows a high nitrate-phosphate ratio similar to that found inside the Mediterranean.

ratio. Where finite figures emerge, in nearly every case the ratio is much in excess of twenty, implying a large positive anomaly. Thomsen's results showed clearly that the Mediterranean is an impoverished sea, but the present comparison shows further that it is more impoverished in phosphate than in nitrate. In the Straits of Gibraltar the boundary between the incoming surface Atlantic Water and the outgoing deeper Mediterranean water oscillates around 150–200 metres (Murray & Hjort, 1912) so that, judged from the *Dana* stations 4025 and 4140, it appears that both the incoming and outgoing waters in early summer have a large positive anomaly of the nitrate-phosphate ratio. If this state of affairs is usual we have an explanation of the large positive anomaly found in the Mediterranean as a whole.

It is generally recognized that Mediterranean water of high temperature and salinity flows out into the Atlantic around 800 metres and at that depth spreads westwards and northwards. The *Dana* stations 4141 to 4156 lay off the Atlantic Coast of the Iberian peninsula and there Thomsen found temperatures at 800 or 1000 metres higher than in the water above or below. The nitrate-phosphate ratios in these waters of maximum temperature are shown by heavy type in Table II whence it will be seen that these strata or those immediately adjacent have positive anomalies of eight or more; that is, the high anomaly characteristic of Mediterranean water persists after it has flowed out into the Atlantic.

In the Atlantic at Station 661 of *Discovery II* (Table III), at the Discovery Station examined by Atkins & Harvey (1925) and at Stations 3978, 4000, 4009, 4019 and 4158 of the *Dana* (Table II), the ratio conforms closely to

Table III. NITRATE-PHOSPHORUS RATIO IN SOUTH ATLANTIC

(*Discovery II*, 1932)

Station	661		668		673	
Lat.	57° 36′ S		46° 43′ S		38° 37′ S	
Long.	29° 45′ W		30° 22′ W		29° 59′ W	
Date	April 2 1931		April 19 1931		April 24–25 1931	
Depth metres	N/P (mg.-atoms)	Anomaly of N/P ratio	N/P (mg.-atoms)	Anomaly of N/P ratio	N/P (mg.-atoms)	Anomaly of N/P ratio
0	24·5	+4·5	13·4	−6·6	(33·8)	(+13·8)
20	23·2	+3·2	13·4	−6·6	15·2	−4·8
40	23·3	+3·3	13·3	−6·7	17·7	−2·3
60	20·3	+0·3	14·4	−5·6	12·6	−7·4
80	20·0	0·0	13·6	−6·4	17·7	−2·3
100	20·6	+0·6	13·5	−6·5	18·1	−1·9
150	19·0	−1·0	15·4	−4·6	17·0	−3·0
200	18·5	−1·5	17·5	−2·5	22·1	+2·1
400	19·0	−1·0	19·9	−0·1	17·3	−2·7
800	19·1	−0·9	17·6	−2·4	16·8	−3·2
1500	19·0	−1·0	17·0	−3·0	12·4	−7·6
2500	18·4	−1·6	17·2	−2·8	12·6	−7·4
3200	17·6	−2·4	—	—	—	—
3500	—	—	17·3	−2·7	11·5	−8·5
4500	—	—	16·1	−3·9	—	—
Mean	20·2	+0·2	16·6	−3·4	15·9	−4·1

twenty at all depths and the anomaly is small. Other Discovery stations (Tables III and IV) show a large negative anomaly and at Stations 668, 673 and 681 there are obvious variations as different water strata are traversed. An explanation of these results, presumably dependent upon the hydrography of the regions investigated, is beyond the scope of this paper.

Table IV

Discovery II: Station 681; 21° 13′ S, 29° 55¼′ W; May 1 1931; mg.-atoms per cubic metre

Depth metres	N	P	N/P	Anomaly of N/P ratio
0–200	0·0–0·5	0·0–0·14	—	—
400	7·15	0·75	9·6	−10·4
800	17·15	1·54	11·2	− 8·8
1500	12·15	1·30	10·7	− 9·3
2500	12·85	1·00	12·9	− 7·1
3500	12·15	0·97	12·5	− 7·5
4900	20·0	1·65	12·1	− 7·9
Mean	—	—	11·5	− 8·5

Summary

Data are presented confirming the belief of Harvey and of Redfield that, in broad outline, the ratio of nitrate-nitrogen and of phosphate-phosphorus in the sea and of nitrogen and phosphorus in marine plankton lies within fairly narrow limits. The ratio approaches twenty to one when expressed in terms of milligram-atoms or nine to one by weight. There are however deviations from this broad generalization, but they do not provide a reason for discarding the concept but rather suggest close examination of the causes of the variations.

The amount by which the N-P ratio in sea water differs from twenty is provisionally termed the "anomaly of the nitrate-phosphate ratio".

It is shown that Mediterranean water possesses a high positive anomaly and that this appears to persist when Mediterranean deep water intrudes into the Atlantic.

The N-P ratio in the English Channel increased between 1926 and 1931.

Attention is drawn to a negative anomaly in certain waters in the South Atlantic.

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