Protist, Vol. 157, 345—358, July 2006
http://www.elsevier.de/protis
Published online date 25 July 2006

Protist

TRIBUTE

The 'Droop Equation' — Michael Droop and the Legacy of the 'Cell-Quota Model' of Phytoplankton Growth

Introduction

The *Droop* Equation, or the *Cell-Quota Model* as it is alternatively known (Droop 1968), is the summation of a lifetime's research carried out on the growth and utilization of nutrients, particularly organic nutrients, by algal cells. However, to summarize a lifetime's work in a single equation is manifestly unfair, for Michael Droop (Fig. 1), the author of the model, achieved many other things as well. Nevertheless, the Cell-Quota Model is specifically Michael Droop's legacy to science and it stands alongside the famous earlier Monod expression relating microbial growth rate to ambient substrate concentration (Monod 1942) Droop's contribution was to relate growth rate to the internal nutrient content of a cell (the cell quota) rather than to the nutrient concentration in the surrounding medium. The story of how and why Michael Droop came to achieve this legacy requires an understanding of his life and the times in which he lived.

Michael Droop: Biographical Details

Michael Richmond Droop, who is still very much alive and enjoying retirement near Oban, in Argyllshire, was born in London on November 3 1918. The name Droop is of German origin and is pronounced to rhyme with 'soap'; the name Richmond comes from his great grandmother's side of the family. Michael had two sisters, one older and one younger than himself. His father, John Percival Droop (1882—1963), was a Cambridge-educated archaeologist, who spent the early part of his career working in association with the British School at Athens. His speciality was the study of Greek pottery and a type of Laconian cup was named in his honour (the Droop cup). During the First World War, J.P. Droop was attached to the Admiralty (1914—1921). Subsequently he was elected to the Charles W. Jones chair of Classical Archaeology at the University of Liverpool. Most of Michael's youth was spent in Liverpool and he remembers at the age of three being taken for walks in Sefton Park. At the age of 10 he was sent to a preparatory school near Folkestone in Kent, which was followed, at the age of 14, by 5 years (1932—1937) at Marlborough College, a leading public school in Wiltshire. A tradition spanning many generations had been established within the Droop family for its boys to attend Marlborough College, a school originally founded in 1843 for the sons of Anglican clergy. As Michael says, "Marlborough taught me how to survive the rigours of communal life".

During his time at Marlborough College, Michael developed interests in biology and painting. His enthusiasm for biology dated back to his youth in Liverpool, where he took an interest in pond life, an activity that was fostered by his contact with Dr Margery Knight, a phycologist and lecturer in the Botany Department of Liverpool University and friend of the Droop family. At Marlborough College he was taught biology by the 'legendary' Ashley Gordon (Tubby) Lowndes (Wyatt 2005). Boarding school offered Michael plenty of time and opportunity to pursue his interest in aquatic organisms and it was with Tubby Lowndes that Michael first visited the Marine Station at Millport on the Isle of Cumbrae. Michael joined a lineage of Old Malburnians, including J.Z. Young, Sir Peter Medawar and John Cloudsley-Thompson, who subsequently became eminent biologists. Michael was also a keen painter, an activity he pursued mostly in his spare time, and in one year won all the school prizes awarded for art.

This combination of interests in biology and art to some extent determined the final stages of his

doi:10.1016/j.protis.2006.05.009

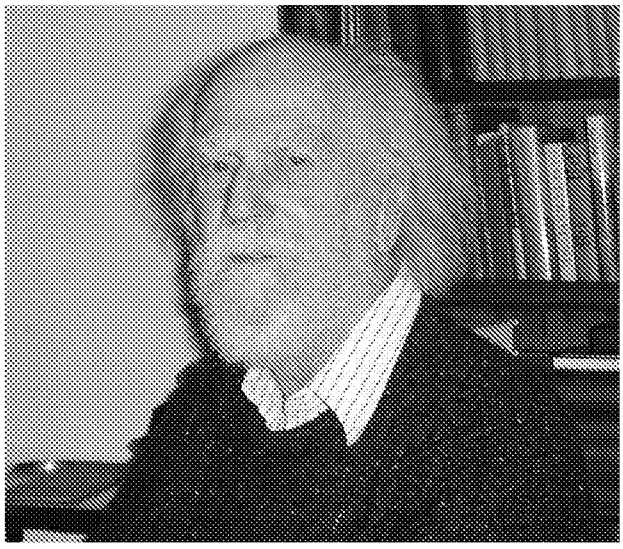

Figure 1. Michael Droop (2006).

time at Marlborough and his subsequent student career at Cambridge. On entering the sixth form he first enrolled on the 'modern' side but changed in his final year at school to the 'science' side. This enabled him to sit the 1st MB examination as well as the School Certificate examination. Both of these he passed sufficiently well to allow him to proceed to Trinity College, Cambridge to study medicine. On arriving at Trinity College in 1937, Michael found that he was able to combine the study of medicine with a course in botany and in this way he was able to maintain his wider interests in biology. However, this was not sufficient to resolve the conflict between his interests in science and the arts and so, for his second year (1938), he chose to study English literature. When it came to Part 1 of the Tripos Examinations in 1939, Michael decided that a visit to the opera to see *The Marriage of Figaro* was more to his liking than sitting an examination. As a result of his failure to take, let alone pass, his examinations he was sent down from Cambridge. His tutor, the historian George Kitson Clark, whose sister was an archaeologist and had worked with Michael's father, made Michael telephone his father to explain where the responsibility for this disaster lay.

The abrupt ending of Michael's student career at Cambridge in 1939 coincided with the much larger catastrophe that was about to engulf the European powers. Michael, now aged 21, was immediately called up to serve in the army and was eventually sent to the Royal Military College, Sandhurst, which housed the Infantry Officer Cadet Training Unit. Within 3 months the Sandhurst authorities decided that Michael was not 'officer material'. Michael puts this down to his artistic inclinations and holds no ill feeling about the decision since it probably saved his life. However, his artistic interests led to him being sent to the Royal Engineers Army Camouflage Unit at Aldershot where his first task was to calculate, using a set of five-figure trig and log tables, the shadow length of a 10-foot pole at hourly intervals for every day of the year. During the London Blitz (winter 1940), Michael was transferred to the Royal Engineers Bomb Disposal Company in South London. Two years later he volunteered for a radiolocation course, which involved the study of electronics and radar. This was followed by a period in the Newcastle area where he worked on radar associated with the gun sights of anti-aircraft weaponry. His final military posting, which lasted 18 months, was to Nigeria and brought together his respective expertise in radar and botany. The task before him was to devise methods of protecting radar installations from the action of fungal moulds, a major problem in tropical countries, especially since most of the electrical wiring used in conjunction with radar was insulated with an acetate-based plastic. This was a prescient task, for some years later he was to work on the utilization of organic substrates by algal cells.

Michael returned from the tropics, via the Caribbean and Freetown, to a Britain at the end of 1945 enveloped in icy temperatures and austerity. Without a job and unsure of what he wanted to do next, he joined the Wilson Barrett repertory company in Edinburgh as a scenic artist earning £5 per week. At the same time he showed a portfolio of his paintings to Professor Randolph Schwabe at the Slade School of Fine Art, London. He was accepted as a student but, again, indecision about the direction of his future career caused him to turn down the offer. Instead, Michael decided to return to academia, this time in Liverpool, to read science. Thus in autumn 1946 he enrolled onto a Zoology and Botany degree course at the University of Liverpool. He renewed his acquaintance with Dr Margery Knight, who had already been an influence earlier in his life, and at last felt comfortable about the direction of his career. After 3 years of study he gained a first class pass in his examinations. This was followed by a fourth year during which he specialized in botany finally graduating with a first class honours degree. During his 4 years as a student in Liverpool he accompanied Dr Margery Knight at

least four times on field courses to Port Erin, Isle of Man and so gained acquaintance at first-hand of working with marine algae. On one summer vacation he was sent to Kew by the then professor of botany, John McLean Thompson, and set to work on a thirty year old collection of myrtaceous plants from Malaya. The outcome of this experience was that he would "have no further truck with dead plants". Living plants were to be the object of his study for the rest of his life. The link between the Liverpool Botany Department and his future study of living plants (algae) was to be a slender volume entitled *Pure Cultures of Algae* written by Ernst Georg Pringsheim (1946), at that time working in Cambridge. As a result of reading this book, Michael wrote to Pringsheim and secured a studentship funded by Liverpool University to study in Cambridge under his tutelage. This had the joint effect of allowing Michael to work on living plants and also of returning to Cambridge, where he renewed his connection with Trinity College.

Professor Ernst Georg Pringsheim (1881—1970), who was to become Michael's PhD supervisor, was born in Silesia and studied first in Munich and then Leipzig under the great plant physiologist Wilhelm Pfeffer. After a period at Breslau he obtained a lectureship at the Halle University in 1909. The interruption of the First World War provided him with experience in practical bacteriology. After the war he worked in Berlin and in 1923 was appointed to the Chair of Plant Physiology at the German University of Prague. It was here that he laid the foundations of his algal culture collection and carried out pioneering work on the nutrition of heterotrophic flagellates. Pringsheim remained in Prague until 1938 when the political situation forced him to flee Czechoslovakia with his family and culture collection and take up residence as guests of Professor F.E. Fritsch at Queen Mary College, London. From 1939—1945 the staff and students of Queen Mary College were evacuated to Cambridge and both Fritsch and Pringsheim moved to the Cambridge Botany School. Pringsheim and his wife Olga, remained in Cambridge until his retirement in 1952 after which he returned in 1953 to Germany and continued to work in the Pflanzenphysiologisches Institut, Göttingen (Droop 1971a; Mollenhauer 2003). When Michael moved to Cambridge in 1950, he joined a group of four comprising Pringsheim, his wife Olga, a technician and Eric George, who was later to become Curator of the 'Cambridge Culture Collection'. Richard Starr, who ultimately founded and assembled the UTEX Culture Collection in the USA, spent a sabbatical year (1950—1951) in the Pringsheim laboratory on a Fulbright Scholarship.

Research Studentship at Cambridge

At the time of Michael's arrival in Cambridge in October 1950, Pringsheim had just returned from a collecting trip to the Tvärminne archipelago in Finland and brought back with him a box full of mud samples collected from coastal rock pools, which he passed on to Michael "to make what he could of them". Use of the Pringsheim 'micropipette' method of single cell isolation, removal of bacteria by repeated washing in sterile medium, and axenic cultivation of flagellates in precisely constructed media, permitted Michael to make painstaking observations on a wide range of rock-pool flagellates, in particular of cells attributable to the genus *Haematococcus* Agardh. As part of his study Michael visited the Tvärminne archipelago in July 1951. The immediate results of this visit were published in his first major paper (Droop 1953a). This is of particular interest because it includes not only a combination of ecological and taxonomic information but also physiological data clearly demonstrating a desire by the author to move beyond straightforward descriptive ecology into experimental areas. A total of 147 rock pools were sampled, including those defined as brackish, rain and peat pools. Fifty-two flagellate species were identified including three new descriptions: *Monochrysis lutheri* Droop (= *Pavlova lutheri* (Droop) Green); *Nephromonas hyalina* Droop; *Pedinomonas upsilon* Droop. The two most common flagellates to be found were *Oxyrrhis marina* Dujardin and *Brachiomonas submarina* Bohlin (Volvocida). Axenic cultures of some of these species now available in culture collections around the world date back to Michael's 1951 Tvärminne visit.

Professor Fritsch, after he retired from Queen Mary College, London, retained a room in the Cambridge Botany School where Michael would often meet him for a discussion on Saturday mornings. During one such meeting in 1952, Fritsch mentioned that a job was available at the Marine Station in Millport on the Isle of Cumbrae. Michael, having originally visited the Millport Station with his biology teacher in the 1930s, duly applied for the position and was interviewed by Professor Maurice Yonge, who at the time was Regius Professor of Zoology at Glasgow University and President of the Scottish Marine Biological

Association (SMBA). Michael was offered the job with almost complete freedom to develop his research interests as he wished. This was a considerable act of faith, for at the time Michael had only just completed his second year of a postgraduate studentship and was still 3 years away from submitting his PhD thesis. Nevertheless, the job offered him the time and opportunity to pursue his interest in rock pool flagellates using the techniques he had learnt at Cambridge with Pringsheim, and to combine it with the possibility of developing more sophisticated methods of culture. His wish to achieve the latter came about as a result of reading Jacques Monod's (1942) book entitled *Recherches sur la Croissance des Cultures Bactériennes.*

The Marine Laboratory, Millport: Rock Pool Flagellates and Auxotrophy

The Marine Station at Millport had its origins in a small flat-bottomed barge known as the *Ark*, which was moored on a flooded quarry at Granton, near Edinburgh (Marshall 1987). The barge was converted into a floating laboratory, which was commissioned for work in 1883, making it the oldest marine laboratory in the British Isles. In 1885 the *Ark* was transferred to Port Foy, near Millport on the Isle of Cumbrae. In 1897 the barge was replaced by an onshore building which became the Millport Marine Station. In 1901 The Marine Biological Association of the West of Scotland was formed and membership was open to the public. This was subsequently 1 renamed the Scottish Marine Biological Association (SMBA). Funding for the laboratory came from the membership of the SMBA, from donations, bequests and from money paid directly by the Government to the laboratory in the form of a grant-in-aid from the Development Commission.

Michael's research priority was now to complete the work for his PhD thesis, the main theme of which was a study of the Family Sphaerellaceae (= Stephanosphaeraceae Korshikov, 1938; Haematococcaceae G.M. Smith, 1950), in particular *Haematococcus pluvialis* Flotow and its allies. This work required further isolation and cultivation of flagellates from the supra-littoral rock pools in the vicinity of Millport. Interestingly, many of the species found in pools on the exposed Devonian rocks of Cumbrae were equivalent to those that had previously been found in pools on the glaciated granite of the Baltic. Michael's thesis, entitled 'On the Biology of *Haematococcus pluvialis* Flotow', was awarded a Cambridge PhD in 1956; Dr John Lund of the FBA Windermere Laboratory was the external examiner. The contents of the thesis were subsequently published in six papers which dealt with the complex nomenclature and taxonomy of *Haematococcus pluvialis* and its allies, as well as the factors that affected encystment and governed the production of the bright red carotenoid pigment, astaxanthin (Droop 1952, 1954b, c, 1955c, 1956a, b, see also 1961b, 1971b).

The supra-littoral rock pools of Cumbrae were not only productive in terms of providing cultureable flagellates for experimentation but also in initiating Michael's long-term research career in algal growth and nutrient uptake kinetics (Droop 1955b). Following in Pringsheim's footsteps, Michael pursued his interest in the composition of culture media and, in particular, in the non-mineral (organic) components required for cell growth. Having achieved bacteria-free, clonal cultures (Droop 1954a) it was then possible to ascertain the minimum growth requirements of individual species. Whilst some algae, for example *Phaeodactylum tricornutum* Bohlin, were able to grow on inorganic salts alone, others had an obligate requirement for specific organic supplements (auxotrophy). One of the first species that Michael studied in this context was *Oxyrrhis marina*, the phagotrophic colourless dinoflagellate (Droop 1953b). He had already obtained this species in monoxenic, bacteria-free cultures with the food organism, a pure culture of *Brachiomonas,* at Cambridge. Now, during the course of the next 10 years in Millport, he was to achieve *Oxyrrhis* in a completely defined medium without solid prey (see below). The next three species he tested were *Pavlova (Monochrysis) lutheri, Prymnesium parvum* Carter *and Syracosphaera elongata* Droop where, under normal circumstances, axenic cultures were grown in natural seawater supplemented with soil or preferably liver extract. Droop (1954d, 1955a) was able to replace the seawater by a synthetic metal-buffered medium containing guanine and glycine (cf. Provasoli and Pintner 1953) and the soil and liver extracts by a combination of cobalamin (vitamin B_{12}) and thiamine (vitamin B_1). The requirement for cobalamin was absolute and quantitative whereas thiamine appeared to be a 'stimulating' substance (Droop 1954d).

Michael's culturing work during the first half of the 1950s coincided with a general upsurge of interest in vitamins as nutritional supplements for algae and protozoa. Whilst thiamine (vitamin B_1)

had been isolated in its pure form in 1926 and its structure was fully elucidated and the vitamin synthesized in 1936, it was not until 1948 that cobalamin (vitamin B_{12}) was produced in its pure form and at this time the structure of the molecule had not been fully described. Seymour Hutner (1911–2003), working at the Haskins Laboratories in New York, discovered that axenic cultures of *Euglena gracilis* inoculated into a defined medium were incapable of growth without the addition of an extract of animal proteins (Hutner 1936). In particular, liver concentrates devised to combat pernicious anaemia were highly stimulatory to the growth of this alga. Eventually, Hutner et al. (1949) demonstrated that the active ingredient in these various extracts was vitamin B_{12} and based on this finding he was able to devise an assay involving *Euglena* for the determination of vitamins in human tissues. In this rather curious manner, progress in understanding the metabolism of vitamin B_{12} in animals became linked to studies on algae and protozoa.

The Eighth International Botanical Congress in Paris (1954) provided Michael with an opportunity to meet Luigi Provasoli, who at that time was working with Seymour Hutner at the Haskins Laboratories in New York. It quickly became apparent that they shared many common research interests and so Luigi extended an invitation to Michael to visit New York for 3 months in 1955. This visit was seminal for Michael's future work not only for the expertise that he gained but also for the many contacts he made both in the world of algal culturing and phytoplankton ecology.

During the second half of the 1950s, much effort was put into determining the vitamin requirements of different algae and certain patterns emerged (Droop 1955b, 1957a, b, 1958b, 1962b). About 60% of species tested had an obligate exogenous vitamin requirement (auxotrophs), the remainder being self-sufficient in this respect (autotrophs). Commonly three vitamins were utilized: biotin (B_7), thiamine (B_1) and cobalamin (B_{12}). However, of the three, use of B_{12} was the most widespread with about 80% of auxotrophic species demonstrating a B_{12} requirement. There are three groups of B_{12} analogues utilized by flagellates with individual species having a particular requirement for one or more of these forms (Droop 1962b). Thiamine (B_1), required by about 50% of auxotrophs, comprises a thiazole and pyrimidine moiety. Again some species had an absolute requirement for one or other of these moieties and some species for both (Droop 1958b; Droop et al 1959).

During the period 1958–1962 two interesting diversions interrupted the general thread of Michael's vitamin work on photoautotrophic flagellates. Both had their origin in organisms isolated from supralittoral rock pools; one, a study of the nutritional requirements of *Oxyrrhis marina*, related back to the Tvärminne collecting trip of 1951 (Droop 1959a, b); the other, involving *Heteramoeba globosa* Droop, was quite different in that it involved the discovery of a sexual phase in the life-cycle of an amoeba (Droop 1961a, 1962c). The work on *Oxyrrhis* is particularly interesting since this phagotroph, which normally requires a particulate prey, can be grown axenically without a prey but with complex organic supplements, such as soya meal, *corpus luteum* extract, cream and beef extract, thus probably satisfying a fat requirement (Droop 1959a, b). Success in growing *Oxyrrhis* in this way was first achieved by John McLaughlin at the Haskins Laboratories but not brought to a conclusion by him. Michael took on this work and using his Tvärminne culture of *Oxyrrhis* found that he could maintain a monoxenic, bacteria-free culture by the addition of sterile neutralized, strained but unfiltered lemon juice. A carbon tetrachloride extract of lemon rind and extracts of grass clippings were also capable of supplying the critical growth factor. At a later stage Michael, with the assistance of Doyle from Millport and subsequently Pennock from Liverpool, was able to demonstrate that the active ingredient in the extracts of lemons and grass cuttings was ubiquinone (Droop and Doyle 1966; Droop and Pennock 1971). From this combination of studies Michael was able to conclude that *Oxyrrhis* conformed to being an 'acetate flagellate' with respect to its carbon nutrition since it used acetic acid and ethanol for growth, but not glucose nor the carbon of amino acids (Droop 1959b). With respect to sources of nitrogen for growth, these must be in the form of ammonia or any one of a number of simple organic compounds provided they can be made to yield an amino group. The requirement for ubiquinone highlighted the fact that, at the very minimum, the prey particles phagocytosed must supply this component for growth to occur.

Vitamin B_{12}, *Monochrysis* (= *Pavlova*) *lutheri* and Chemostat Experiments

Throughout the 1960s, in addition to full-time research work, Michael was regularly involved in writing review articles. These included detailed

appreciations of synthetic media for marine algae (Droop 1961d, e); organic micronutrients (Droop 1962b); algae and invertebrates in symbiosis (Droop 1963a). However, the major theme of his work during the 1960s centred on the vitamin B_{12} requirement of *Pavlova* (*Monochrysis*) *lutheri* (Droop) Green (Droop 1957b, 1961c, 1966b, 1968). *Monochrysis lutheri* (Chrysophyceae) was one of the flagellates Michael had named from the Tvärminne collections he made in 1951. As a result of a detailed ultrastructural study (Green 1975), this species was later re-allocated to *Pavlova* Butcher (Prymnesiophyceae). However, the name *Monochrysis lutheri* will continue to be used here for the sake of consistency since it is mentioned in all the Droop publications of this period and is still used world-wide in the oyster-rearing industry. In 1954 Michael had demonstrated that *Monochrysis* had an absolute requirement for vitamin B_{12} (Droop 1954d). Since so many flagellates have subsequently been shown to have an obligate requirement for this vitamin the possibility has arisen that vitamin B_{12} might exert a controlling influence on the growth and limitation of phytoplankton populations and productivity in natural water masses (Droop 1962b). To investigate this possibility Michael carried out an experiment in which he determined the response of *Monochrysis* to various 'dosages' (initial concentrations) of vitamin B_{12} (as the limiting nutrient) in batch culture (Droop 1957b). The relationship between yield and dosage he obtained was linear between 0.1 and 10 pg vitamin $B_{12}\,cm^{-3}$. Within this range each pg of vitamin B_{12} supported approximately 8×10^5 cells, that is about 540 molecules vitamin B_{12} per cell, or reckoning on $200\,\mu m^{-3}$ as the mean volume of a *Monochrysis* cell, 3 molecules μm^{-3} of living alga. Concentrations of vitamin B_{12} in the open sea (northern North Sea) vary from 0.5 to 1.0 pg cm^{-3}. Based on the *Monochrysis* requirement for vitamin B_{12}, natural concentrations of this vitamin would be sufficient, without limitation, to support the known population densities of phytoplankton that generally occur in the North Sea. Only in the case of 'red tides' would the availability of vitamin B_{12} be likely to become limiting (see also Droop 1961c).

In response to the 1957 paper (Droop 1957b) several criticisms were made (Daisley 1957, Ford 1958) including: (i) that the concentrations of vitamin B_{12} in natural seawater might be an overestimate because some of the vitamin measured might in reality be bound and therefore unavailable to algal cells, (ii) that the calculated magnitude of vitamin B_{12} required by each *Monochrysis* cell (3 molecules μm^{-3} of alga) might be an underestimate and (iii) in nature, competition between phytoplankton species might be more affected by the dosage/growth rate relationship rather than the dosage/yield ratio as measured by Droop (1957b). In response to these criticisms Michael performed a further series of batch culture experiments in which, at three temperatures, he measured growth of *Monochrysis* in medium with vitamin B_{12} dosage increasing geometrically from 0.1 to 100 pg cm^{-3} (Droop 1961c). The outcome of these experiments was that, irrespective of vitamin B_{12} dosage or temperature, all cultures grew at a rate of approximately 1.1 divisions day^{-1}. Then as the vitamin B_{12} content of the medium became exhausted the growth curve flattened so that, for the range of vitamin dosages used in each experiment, the final cell numbers gave the familiar linear dosage/yield relationship. In these experiments each pg of vitamin B_{12} supported 5.5×10^5 cells, a similar ratio to that obtained in the earlier experiment (Droop 1957b). Michael came to the conclusion that limitation of the division rate must occur at vitamin B_{12} dosages below 0.1 pg cm^{-3} and that to achieve measurable limitation of growth rate in batch cultures was probably impossible. Thus use of a continuous culture system would be required to obtain the parameters of the vitamin B_{12} requirement of *Monochrysis* (Y (yield constant) and K_s (saturation constant)).

One of Michael's tasks at the Millport Laboratory was to assist zoologists with the cultivation of oyster larvae by producing suitable cultures of algal flagellates as food organisms. In 1959 he designed and built two continuous culture systems for the routine supply of unicellular algae (*Phaeodactylum* and *Monochrysis*) for oysters (Marshall 1987). The experience he gained with these chemostats was to be good training for the more exacting vitamin B_{12} work that he was about to undertake (Fig. 2). His initial aim in this context was to measure the parameters of vitamin B_{12} requirement (Y and K_s) in *Monochrysis*. However, the results obtained during the first series of chemostat experiments (Droop 1966b) produced discrepant results when compared with the values that had been gained from earlier batch culture experiments (Droop 1957b, 1961c). The yield constant (2.5×10^5 cells. pg vitamin $B_{12}{}^{-1}$) was about one third that obtained from earlier batch culture experiments and the saturation constant (2—6 pg vitamin $B_{12}\,cm^{-3}$) was at least 20 times the maximum value suggested in the earlier work.

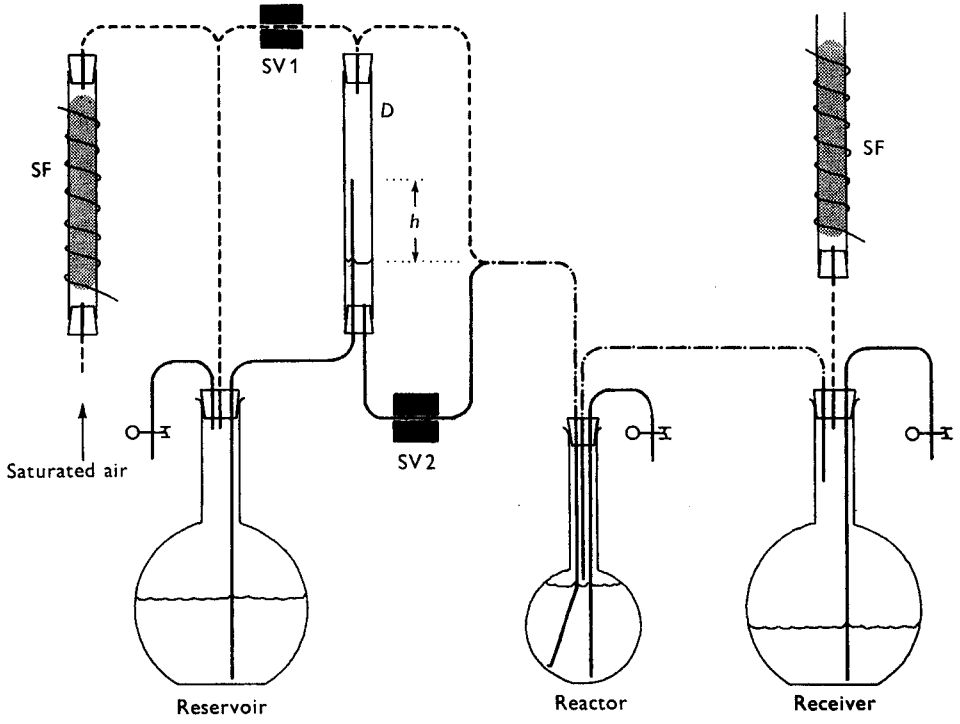

Figure 2. Schematic diagram of the chemostat used for vitamin B_{12} experiments with *Monochrysis lutheri* (not to scale). The air pump, air saturator, inoculating port on the reactor and thermostat water bath are not shown. —— culture medium; – – – – air; — • — • air and medium. The clipped ends of the sampling ports are kept in 70% ethanol. SF = sterile filter; SV = solenoid valve; D = dosage system; h = measure of culture medium dosage. Reproduced from Droop 1966b with permission of the Journal of the Marine Biological Association UK.

The only explanation that could account for the anomalies encountered was that there had been a release of protein-bound vitamin into the medium (Droop 1966b).

Michael now embarked on his most ambitious and comprehensive experiment to date (Droop 1968). In terms of concept, technical difficulty and mathematical analysis, it was to surpass by far all that had gone before. The basis of the experiment was to use ^{57}Co-labelled vitamin B_{12} to study the kinetics of vitamin B_{12} limitation in *Monochrysis lutheri* in continuous and exponentially growing batch cultures and in washed cell suspensions (see Fig. 2). The overall aim of the chemostat experiments was to relate specific growth rate to substrate (vitamin B_{12}) concentration and, in particular, to determine whether a protein-bound interfering factor was released into the medium as a result of growth (Droop 1966b). In practical terms the experiment involved the measurement of dilution rate, cell number, substrate concentration in the input, in the culture vessel, both as free- and protein-bound vitamin, and in the cells for numerous steady-states of the chemostat between zero dilution rate and the washout point. Batch cultures were used to supplement these results by supplying information on maximum exponential growth rates in high nutrient conditions.

The results of this experiment had far-reaching consequences. The specific growth rate (μ) of *Monochrysis* in the chemostats was found not to depend directly on medium substrate concentration, as would be expected in the classical Monod manner. However, as Michael puts it, the one relationship that did stand out "in all its pristine beauty" was that growth depended on the intracellular concentration of vitamin B_{12} (cell quota Q) (Fig. 3).

The relationship between specific growth rate (μ) and cell quota (Q) took the form of a rectangular hyperbola (Fig. 3) summarized by Eq. (1) below, with one intercept (k_q) on the abscissa and the asymptote being μ'_m:

$$\mu = \mu'_m\left(1 - \frac{k_q}{Q}\right). \qquad (1)$$

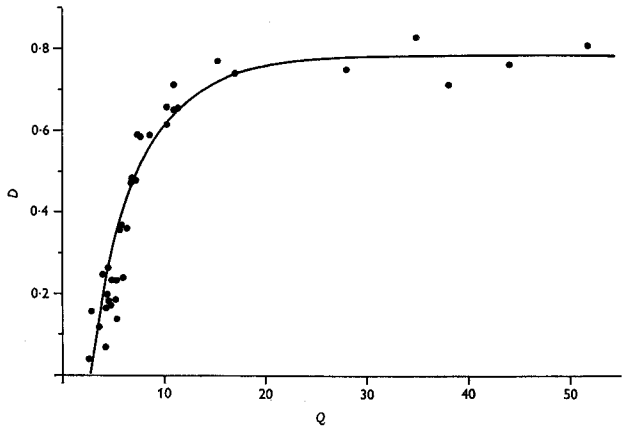

Figure 3. Chemostat steady states. Relation between dilution rate (*D*) and cell quota (*Q*). Reproduced from Droop 1968 with permission of the Journal of the Marine Biological Association UK.

The parameter k_q, the value of the intercept, is interpreted as the minimum quota necessary for life (the *subsistence quota*) and represents the value of *Q* at zero growth rate. μ'_m is the growth rate at infinite internal nutrient content (maximum specific growth rate when $1/Q = 0$) and is an abstraction (Droop 1968, 1983; Tett and Droop 1988). This must not be confused with μ_{max}, the maximum growth rate of the Monod equation, which is always less than μ'_m. The overall specific rate of vitamin B_{12} uptake by exponentially growing cells in dilute batch cultures obeyed the conventional Langmuir isotherm in relation to medium concentration. Since, under steady-state conditions, the cell quota is the quotient of the specific rates of uptake and growth, the saturation constant for growth could be obtained and had the value of 0.142 pg vitamin B_{12} cm^{-3}. This value accords well with that estimated from earlier batch culture work (Droop 1961c).

This experiment also gave insights into the mechanism of vitamin B_{12} uptake by *Monochrysis*. When vitamin-starved cells were presented with a replenishment of vitamin, adsorption on to the cell surface was rapid, more rapid than the steady-state rate of uptake, but the cell surface capacity was small compared with the maximum steady-state cell quota. Thus it was possible to distinguish the rates of adsorption and transport. Adsorption was more-or-less irreversible. Vitamin B_{12} concentrations in the chemostats failed to reach the very low values predicted by classical equations. This was due to excretion of a non-dialysable, heat-labile inhibitor at an apparently constant relative rate that combined with soluble vitamin rendering it unavailable (Droop 1968).

This publication of the 1968 'milestone' paper (Droop 1968) coincided with major administrative changes at the Millport Marine Station. By 1966 the Development Commission, which, since 1921, had provided financial support for the grant-aided marine laboratories, handed over responsibility to a newly constituted larger body, the Natural Environmental Research Council (NERC). This body gave its approval to plans for a new mainland laboratory for west of Scotland and authorized the spending of the first instalment of the grant in 1966—1967 on a building at Dunstaffnage, just north of Oban. The original plan had been that some research work, particularly on shellfish, would remain in Millport, whilst the remainder would move to the new laboratory. However, in 1968 NERC decided to withdraw funding from Millport and so the relationship between the SMBA and Millport, which started with the establishment of this laboratory, was finally brought to a conclusion (Marshall 1987). Michael moved, together with his chemostats and culture collection, to Dunstaffnage in 1969.

The 1968 paper introducing the *Cell-Quota Nutrient Model* was to have far reaching consequences for phytoplankton physiology and ecology. The earlier Monod (1942) equation for substrate-limited growth of microorganisms had been widely accepted by microbiologists, particularly for studies of bacterial growth limited by the supply of an organic substrate. The Monod model explicitly stated that the rate of utilization of a limiting nutrient by a microorganism was in constant proportion to its rate of growth. Whilst this generality usually applies to osmotrophic protista in steady-state conditions, in fluctuating substrate conditions nutrient uptake and cell growth are usually no longer closely linked and attention focuses on the nutrient content within the cell (*Q*) (Droop 1973b). Whereas the Monod model can be visualized as comprising one compartment, the cell biomass, which is linked by the specific growth rate to the external substrate, the Cell-Quota model comprises two compartments: (1) the cell quota, which is linked by the specific nutrient uptake rate to the external substrate. (2) the biomass of the cell, which is linked to the cell quota by the specific growth rate (Droop 1983). There are several advantages of the Cell-Quota model over the Monod model, in particular: (i) the Cell-Quota model makes allowances for transient situations characteristic of natural environments, (ii) the Cell-Quota model

has the advantage of being easier to apply than the Monod model because rate-limiting external substrate concentrations are frequently below the limits of chemical analysis whereas the cell quota (Q) and subsistence quota (k_q) are usually easily measured, (iii) the prediction of potential biomass in an isolated water body is likely to be considerably higher according to the Cell-Quota model because the Monod equation only takes account of the ambient nutrient whereas the Cell-Quota model takes account of the level of nutrient already in the cells, which is usually greater than the ambient nutrient concentration because of luxury consumption.

The Cell-Quota model did not come about in isolation. 'Luxury consumption' of nutrients, particularly phosphorus, was already a well-known phenomenon. Ketchum (1939) and Kuenzler and Ketchum (1962) showed that the diatom *Phaeodactylum tricornutum*, when inoculated into fresh medium, completely depleted the medium of phosphorus within the first few hours of culture. Subsequent algal growth was therefore independent of the phosphorus content of the medium and control of growth had to be viewed in terms of the internal concentration. Phosphorus is not unique in this manner for much evidence has now accumulated that luxury consumption of a nutrient is the rule under such circumstances. Almost contemporaneously with Michael's work, Caperon (1968), working with *Isochrysis galbana* Parke in chemostat experiments in which nitrate was a limiting nutrient, appreciated that the concentration of internal nitrogen controls growth rate when nitrogen supply in the medium is limiting. He too obtained a hyperbolic relationship relating growth rate to the inferred internal nitrogen concentration. However, it was Michael who produced and championed the Cell-Quota equation that is now in common use.

The *Cell-Quota Model* and Phytoplankton Ecology

To some extent Michael's research work can be considered in decades. The 1950s focussed on determining the precise nutritional requirements of flagellates; the 1960s were dominated by the vitamin B_{12} work. Now, during the 1970s, Michael's major interest centred on the applicability of the Cell-Quota model to other nutrients essential to phytoplankton growth, particularly phosphorus and nitrogen, and the relevance of the model in all its ramifications to phytoplankton populations in the natural environment. Michael's output of publications during the 1970s became more expansive and mathematical. He was able to develop his ideas through a combination of original research papers and review articles (Droop 1973a, 1974a, 1975a, b, 1977).

Michael took his three postulates relating specific growth rate in steady state systems to nutrient status and subjected them to experimental scrutiny (Droop 1973a, b). In particular he was interested to test how the Cell-Quota model would adapt to transient conditions in culture. For instance he investigated the effects of one limiting nutrient on the uptake and quota concentrations of others since the unavailability of one nutrient would not necessarily affect the uptake of other non-limiting nutrients. He also investigated the effects of two nutrients (vitamin B_{12} and phosphorus on *Monochrysis*) where either or both together effected control of growth (Droop 1973a, b, 1974a, 1975b). Two possibilities were hypothesized; either one or other of the limiting nutrients would exert control over growth, the *threshold* hypothesis; or, secondly, the effects of two nutrients would be multiplicative in that they would interact with each other to affect growth. Michael's work showed that the threshold hypothesis was operational and that growth was not affected by non-limiting nutrients (Droop 1974a). From these experiments Michael generated a model that could, with a single set of constants, predict simultaneously biomass, medium and cell phosphorus; and medium and cell vitamin B_{12} at any time subsequent to the lag phase of cultures of *Monochrysis lutheri* (1974a, 1975b). He coined the term 'luxury coefficient' (ρ) for the factor by which an excess of nutrient was enlarged. Later the term was refined to refer to the ratio between the standardized rate of uptake of an excess nutrient compared to that of a limiting nutrient at the same growth rate (Droop 1983).

Michael and his co-workers (Droop et al. 1982) expanded the Cell-Quota model to include the interaction of light on nutrient uptake and growth of *Monochrysis*. Their aim was to treat light limitation and excess in terms compatible with nutrients in the model. Adaptation of the Cell-Quota model to include light involved the concept of a 'cell quota for light' analogous to the nutrient cell quota. This required a study of energy budgets as well as cell quotas under different light and nutrient regimes. In extending the Cell-Quota model to the natural environment, Michael in collaboration with Paul Tett, a Millport and Dunstaffnage colleague of long standing, sought

to apply the Cell-Quota model to nutrient/growth interactions in natural phytoplankton populations. Their conclusion was that, although there remained gaps, the Cell-Quota model provided "a substantially complete, internally consistent, and simple but adequate physiological account of algal growth processes, suitable for incorporation into a range of ecological models of planktonic processes" (Tett and Droop 1988).

Michael officially retired from the Dunstaffnage Laboratory in 1983. However, he continued to work in the laboratory for some time post-retirement and still contributes notes to journals, mainly about comments and criticisms of his Cell-Quota model (Droop 1978, 1979, 2003). In 1983, 15 years after the first publication of his model, Michael published a retrospective appraisal of algal growth kinetics over 25 years in which he was able to review the success of his original model in the context of general algal physiological and ecological studies (Droop 1983). He was able to list 35 publications by other authors in which there was a hyperbolic relationship between specific growth rate and cell quota. However, there have been a few instances when the equation was not applicable, most notably with nitrogen- and ammonium-limited growth in *Monochrysis* and *Dunaliella* (Caperon and Meyer 1972; Laws and Caperon 1976). There have been suggestions that the model applies best to 'minor' cell nutrients and not to the major requirements, such as nitrogen and carbon. However, looking at the list of successful applications of the Cell-Quota model, phosphorus and nitrogen make a frequent appearance. The number of compartments has also been questioned (Davis et al. 1978) with suggestions that there should be three or more. Michael responds to this in two ways, the first being that the model should be kept as simple as possible; the second being that, in some instances, an additional pool (e.g. the soluble silicon compartment within a diatom cell) might be so small as to add complication for a very minor gain. Michael is not dogmatic in defending his model and concludes in the Droop (1983) article by saying that the Cell-Quota model "has the minimum structure necessary both for functioning in transient situations and for handling more than one nutrient or organism simultaneously".

Postlude

As recorded here, Michael's work was an integral part of his life although it was not his only interest in life. His wife Margarete who he met in Cambridge and married in 1951, died in 1996. His three sons, all of who were educated at Marlborough College, and their families remain an important part of his life. He has retained his interest in painting, which is primarily for his own satisfaction although he has exhibited locally and elsewhere (Fig. 4). His research work was what would now be described as 'curiosity-driven' in that at no time did he set out with a 'life plan' but pursued what was interesting at the time. However, this was not as casual as it might appear for he was constantly expanding and refining the questions he was asking. It took Michael some time to decide upon his career. To some extent he had a false start at Cambridge and it was good news for algal physiology and ecology that *The Marriage of Figaro* deflected Michael from his examinations in 1939. His career was interrupted by the war, which meant that he was a mature student by the time he became an undergraduate at Liverpool University. His return to Cambridge to work with Pringsheim was also an opportunity to 'mend fences' with Trinity College and went some way to demonstrating to his father that he was not as feckless as he might have appeared. His transfer to the remoteness of the Marine Laboratory at Millport suited his temperament, for here he was given a free hand to pursue his research career relatively untroubled by the distractions of teaching and administration.

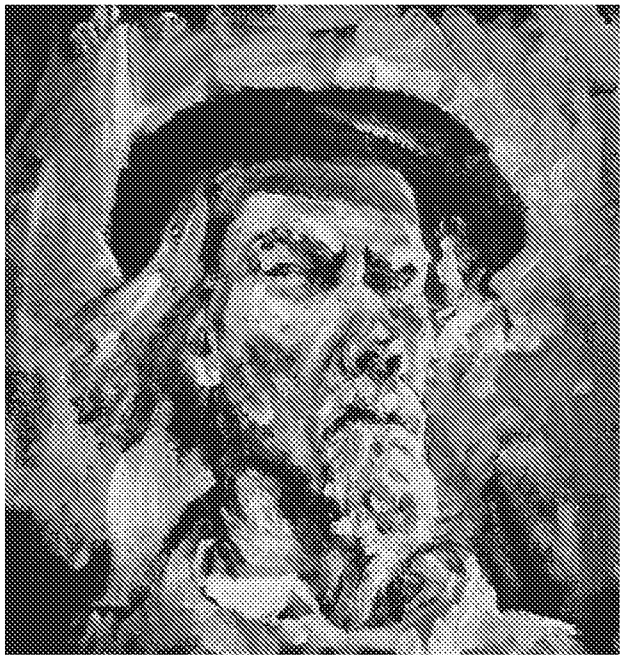

Figure 4. Michael Droop—self-portrait (1984).

Michael was by nature a bench worker preferring to design and carry out experiments himself rather than delegate the tasks. His work bears the hallmarks of a craftsman; the technical skills required for the acquisition of axenic, clonal flagellate cultures are painstaking in the extreme, and they were only the prerequisite to work that was to come. No doubt Pringsheim, with his Germanic fastidiousness for single cell isolations as detailed in his book (Pringsheim 1946), provided good training for Michael's future work. It is noticeable, even in his earliest papers, that Michael was keen to include quantitative and experimental components wherever possible to enhance what could otherwise be called descriptive ecology. As Pringsheim once said to Michael "have you always got to count cells?" His move into continuous culture work, initially to provide algal cultures for oyster larvae, called upon his skills of designing and building apparatus since this period predated the era of commercially available kits. Nevertheless, building equipment from scratch appealed to his work ethic. Perhaps the most striking developments to be noted in his papers, particularly during the 1970s and early 1980s, are the increasing technical complexity of his experiments, including the use of radiolabelled nutrients and the multiplicity of variables measured, and the increasingly complex mathematical methods used to analyse the collected data. Michael makes light of his mathematical ability but essentially in this respect he was self-taught on the basis of extensive reading. He considers that the progression he made from natural history to mathematical modelling has something to do with the artistic side of his make-up and his appreciation of pattern, an attribute he shares with many mathematicians.

Michael was an innovator; his work and life have all the hallmarks of a pioneer in that he was restlessly inquisitive, ascetic, self-contained, committed and determined to achieve. He was clearly an original thinker and flourished during a period when researchers were given time and freedom to pursue their own ideas. Whether or not his work was fully recognized for the quality of its content is a matter of debate. He was elected a Fellow of the Royal Society of Edinburgh in 1962. Michael was not a politician; he shunned the limelight and did not court friends for his own ends. He was highly regarded by his colleagues and was supportive of the next generation as witnessed by the help he gave Paul Tett and others. The fact that his work and, in particular, the Cell-Quota model still shapes thinking on phytoplankton physiology and ecology today is a measure of the enduring importance of his legacy to science.

Acknowledgements

I wish to thank Professor Paul Tett and Mr Michael Turner, past colleagues of Michael Droop, for discussing aspects of Michael's life and work. I am grateful to Michael for the hospitality he offered me during 2 days of discussions in preparation for writing this article. Not only was this helpful in providing background information but it was also a pleasant and rewarding experience.

References

(by authors other than Michael Droop)

Caperon J (1968) Population growth response of *Isochrysis galbana* to nitrate variation of limiting concentrations. Ecology **49**: 866—872

Caperon J, Meyer J (1972) Nitrogen-limited growth of marine phytoplankton. 1. Changes in population characteristics with steady state growth rate. Deep-Sea Res **19**: 601—618

Daisley KW (1957) Vitamin B_{12} in marine ecology. Nature **180**: 1042

Davis CO, Breitner NF, Harrison PJ (1978) Continuous culture of marine diatoms under silicon limitation, 3: a model of silicon-limited growth. Limnol Oceanogr **23**: 41—52

Ford JE (1958) B_{12}-vitamins and growth of the flagellate *Ochromonas malhamensis*. J Gen Microbiol **19**: 161—172

Green JC (1975) The fine structure and taxonomy of the haptophycean flagellate *Pavlova lutheri* (Droop) comb. nov. (= *Monochrysis lutheri* Droop). J Mar Biol Assoc UK **55**: 785—793

Hutner SH (1936) The nutritional requirements of two species of *Euglena*. Arch Protistenkd **88**: 93—106

Hutner SH, Provasoli L, Stockstad ELR, Hoffmann CE, Belt M, Franklin AL, Jukesm TH (1949) Assay of antipernicious anemia factor with *Euglena*. Proc Soc Exp Biol Med **70**: 118—120

Ketchum BH (1939) The absorption of phosphate and nitrate by illuminated cultures of *Nitzschia closterium*. Am J Bot **26**: 399—407

Kuenzler EJ, Ketchum BH (1962) Rate of phosphorus uptake by *Phaeodactylum tricornutum*. Biol Bull Mar Biol Lab, Woods Hole **123**: 134—145

Laws EA, Caperon J (1976) Carbon and nitrogen metabolism of *Monochrysis lutheri*: measurement of growth dependent respiration rates. Mar Biol **36**: 85—97

Marshall SM (1987) An Account of the Marine Station at Millport. University Marine Biological Station. Isle of Cumbrae. Occasional Publication 4, pp 1—133

Mollenhauer D (2003) The protistologist Ernst Georg Pringsheim and his four lives. Protist **154**: 157—171

Monod J (1942) Recherches sur la Croissance des Cultures Bactériennes. Herman, Paris, pp 1—211

Provasoli L, Pintner IJ (1953) Ecological implications of in vitro nutritional requirements of algal flagellates. Ann NY Acad Sci **56**: 839—851

Pringsheim EG (1946) Pure Cultures of Algae. Hafner Publ Co, London pp 1—119

Wyatt HV (2005) Who was...Dr. AG Lowndes? Biologist **52**

References

(involving Michael Droop as an author; some not mentioned in the text)

Bonin DJ, Droop MR, Maestrini SY (1986) Physiological features of six microalgae to be used as indicators of seawater quality. Cryptogam Algol **7**: 23—83

Droop MR (1952) *Stephanosphaera pluvialis* Cohn. Naturalist **12**: 12

Droop MR (1953a) On the ecology of flagellates from some brackish and fresh water rock pools of Finland. Acta Bot Fenn **51**: 1—52

Droop MR (1953b) Phagotrophy in *Oxyrrhis marina*. Nature Lond **172**: 250

Droop MR (1954a) A note on the isolation of small algae and flagellates for pure cultures. J Mar Biol Assoc UK **33**: 511—514

Droop MR (1954b) Conditions governing haematochrome formation and loss in the alga *Haematococcus pluvialis* Flotow. Arch Mikrobiol **20**: 391—397

Droop MR (1954c) Carotogenesis in Haematococcus pluvialis. Nature Lond **174**: 42

Droop MR (1954d) Cobalamin requirement in Chrysophyceae. Nature Lond **174**: 520

Droop MR (1955a) A pelagic marine diatom requiring cobalamin. J Mar Biol Assoc UK **34**: 229—231

Droop MR (1955b) Some new supra-littoral protista. J Mar Biol Assoc UK **34**: 233—245

Droop MR (1955c) Some factors governing encystment in the alga *Haematococcus pluvialis*. Arch Mikrobiol **21**: 267—272

Droop MR (1955d) A suggested method for the Assay of vitamin B_{12} in sea water. J Mar Biol Assoc UK **34**: 435—440

Droop MR (1956a) *Haematococcus pluvialis* and its allies, I: the Sphaerellaceae. Revue Algol NS **2**: 53—71

Droop MR (1956b) *Haematococcus pluvialis* and its allies, II: nomenclature in *Haematococcus*. Rev Algol **3**: 182—192

Droop MR (1957a) Auxotrophy and organic compounds in the nutrition of marine phytoplankton. J Gen Microbiol **16**: 286—293

Droop MR (1957b) Vitamin B_{12} and marine ecology. Nature Lond **180**: 1041—1042

Droop MR (1958a) Optimum relative and actual ionic concentrations for growth of some euryhaline algae. Verh Int Ver Limnol **13**: 722—730

Droop MR (1958b) Requirement for thiamine among some marine and supralittoral protista. J Mar Biol Assoc UK **37**: 323—329

Droop MR (1959a) A note on some physical conditions for cultivating *Oxyrrhis marina*. J Mar Biol Assoc UK **38**: 599—604

Droop MR (1959b) Water-soluble factors in the nutrition of *Oxyrrhis marina*. J Mar Biol Assoc UK **38**: 605—620

Droop MR (1961a) Evidence for a sexual phase in the life-cycle of an amoeba. Nature **192**: 281

Droop MR (1961b) *Haematococcus pluvialis* and its allies, III: organic nutrition. Rev Algol NS **4**: 247—259

Droop MR (1961c) Vitamin B_{12} and marine ecology: the response of *Monochrysis lutheri*. J Mar Biol Assoc UK **41**: 69—76

Droop MR (1961d) Some chemical considerations in the design of synthetic culture media for marine algae. Bot Mar **2**: 231—246

Droop MR (1961e) Recent development in the culturing of algae: chemical and ecological considerations in the design of synthetic culture media for marine algae. Recent Adv Bot 243—247

Droop MR (1962a) On cultivating *Skeletonema costatum:* some problems. Ber Deutsch Bot Ges NF **1**: 77—82

Droop MR (1962b) Organic Micronutrients. In Lewin RA (ed) Physiology and Biochemistry of Algae. Academic Press, London and New York, pp 141—159

Droop MR (1962c) *Heteramoeba clara* n. gen, n. sp., a sexual biphasic amoeba. Arch Mikrobiol **42**: 254—266

Droop MR (1963a) Algae and invertebrates in symbiosis. Symposia of the Society for General Microbiology, XIII: Symbiotic Associations, pp 171—199

Droop MR (1963b) A feeding experiment. Br Phycol Bull **2**: 278

Droop MR (1965) Growth dynamics of a marine photosynthetic flagellate under continuous flow conditions in limiting vitamin B_{12} concentration. J Gen Microbiol 41: pp XXI

Droop MR (1966a) The Role of Algae in the Nutrition of *Heteramoeba clara* Droop, with Notes on *Oxyrrhis marina* Dujardin and *Philodina roseola* Ehrenberg. In Barnes H (ed) Some Contemporary Studies in Marine Science. Allen and Unwin Ltd., London, pp 269—282

Droop MR (1966b) Vitamin B_{12} and marine ecology: III, an experiment with a chemostat. J Mar Biol Assoc UK **46**: 659—671

Droop MR (1966c) Organic acids and bases and the lag phase in *Nannochloris oculata*. J Mar Biol Assoc UK **46**: 673—678

Droop MR (1967a) A procedure for routine purification of algal cultures with antibiotics. Br Phycol Bull **3**: 295—297

Droop MR (1967b) Variable levels of nutrient requirement in a marine chrysophyte. Rep. Challenger Soc **3**: 19

Droop MR (1968) Vitamin B_{12} and marine ecology, IV: the kinetics of uptake, growth and inhibition in *Monochrysis lutheri*. J Mar Biol Assoc UK **48**: 689—733

Droop MR (1969a) Algae. In: Norris, J.R., Ribbons, D.R., (eds.), Methods in Microbiology, Vol. 3B. Academic Press, London and New York, pp 269-313

Droop MR (1969b) New thoughts on nutrient limitation in microalgae. Proc Challenger Soc **4**: 17—18

Droop MR (1970a) Nutritional investigation of phagotrophic Protozoa under axenic conditions. Helgoländer Wiss Meersunters **20**: 272—277

Droop MR (1970b) Vitamin B_{12} and marine ecology, V: continuous culture as an approach to nutritional kinetics. Helgoländer Wiss Meeresunters **20**: 629—636

Droop MR (1971a) Obituary. Professor Dr Dr h.c. Ernst G. Pringsheim: 1881—1970. Br Phycol J **6**: 109—110

Droop MR (1971b) Conditions governing haematochrome formation and the loss in the alga *Haematococcus pluvialis* Flotow. Arch Mikrobiol **20**: 391—397

Droop MR (1973a) Some thoughts on nutrient limitation in algae. J Phycol **9**: 264—272

Droop MR (1973b) Nutrient limitation in osmotrophic protista. Am Zool **13**: 209—214

Droop MR (1974a) The nutrient status of algal cells in continuous culture. J Mar Biol Assoc UK **54**: 825—855

Droop MR (1974b) Heterotrophy of Carbon. In Stewart WDP (ed) Algal Physiology and Biochemistry. Blackwell Scientific Publications, Oxford, pp 550—559

Droop MR (1975a) Towards a model for phytoplankton growth. Rep. Challenger Soc

Droop MR (1975b) The nutrient status of algal cells in batch culture. J Mar Biol Assoc UK **55**: 541—555

Droop MR (1976) The chemostat in mariculture. Proc 10th Eur Symp Mar Biol **1**: 71—93

Droop MR (1977) An approach to quantitative nutrition of phytoplankton. J Protozool **24**: 528—532

Droop MR (1978) Comments on the Davis/Breitner/Harrison model for silicon uptake and utilisation in diatoms. Limnol Oceanogr **23**: 383—385

Droop MR (1979) On the definition of x and of Q in the Cell Quota model. J Exp Mar Biol Ecol **39**: 203

Droop MR (1980) Aspects of the Cell Quota Concept. In Sikyta B, Fencl Z, Poláček (eds.), Continuous Culture of Microorganisms, Prague, pp 279—290

Droop MR (1983) Twenty-five years of algal growth kinetics, a personal view. Bot Mar **26**: 99—112

Droop MR (1985) Fluorescence and light/nutrient interaction in *Monochrysis*. J Mar Biol Assoc UK **65**: 221—237

Droop MR (2003) In defence of the Cell Quota model of micro-algal growth. J Plankton Res **25**: 103—107

Droop MR, Doyle J (1966) Ubiquinone as a protozoan growth factor. Nature **212**: 1474—1475

Droop MR, Elson KGR (1966) Are pelagic diatoms free from bacteria? Nature **211**: 1096—1097

Droop MR, McGill S (1966) The carbon nutrition of some algae: the inability to utilize glycolic acid for growth. J Mar Biol Assoc UK **46**: 679—684

Droop MR, Pennock JF (1971) Terpenoid quinones and steroids in the nutrition of *Oxyrrhis marina*. J Mar Biol Assoc UK **51**: 455—470

Droop MR, Scott JM (1978) Steady-state energetics of a planktonic herbivore. J Mar Biol Assoc UK **58**: 749—772

Droop MR, Scott JM (1982) A steady-state approach to some microplankton problems. Ann Inst Océanogr NS **58**: 47—54

Droop MR, McLaughlin JJA, Pintner LJ, Provasoli L (1959) Specificity of Some Protophytes toward Vitamin B_{12} like Compounds. In Sears M (ed) Preprints of Abstracts of Papers: International Oceanographic Congress, New York 1959. American Association for the Advancement of Science, Washington, DC, pp 916—918

Droop MR, Mickelson MJ, Scott JM, Turner MF (1982) Light and nutrient status of algal cells. J Mar Biol Assoc UK **62**: 403—434

Maestrini SY, Bonin DJ, Droop MR (1984) Phytoplankton as Indicators of Sea Water Quality: Bio Assay Approaches and Protocols. In Shubert LE (ed) Algae as Ecological Indicators. Academic Press, London, pp 71—132

Maestrini SY, Droop MR, Bonin DJ (1984) Test Algae as Indicators of Sea Water Quality: Prospects. In Shubert LE (ed) Algae as Ecological Indicators. Academic Press, London, pp 133—188

Provasoli L, McLaughlin JJA, Droop MR (1957) The development of artificial media for marine algae. Arch Mikrobiol **25**: 392—428

Tett P, Droop M.R (1988). Cell Quota Models and Planktonic Primary Production. In Wimpenny JWT (ed) Handbook of Laboratory Model Systems for Microbial Ecosystems, Vol. 2. CRC Press, Florida, pp 177—233

Tett P, Heaney SL, Droop MR (1985) The Redfield ratio and phytoplankton growth rate. J Mar Biol Assoc UK **65**: 487—504

Barry S.C. Leadbeater
School of Biosciences, University of Birmingham, Birmingham B15 2TT, UK

fax 44 121 414 5925
e-mail b.s.c.Leadbeater@bham.ac.uk