Reflections About Chance in My Career, and on the Top-Down Regulated World

Karl Banse

School of Oceanography, University of Washington, Seattle, Washington 98195-7940;
email: banse@uw.edu

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Abstract

Paraphrasing Pasteur, in scientific work Fortuna favors only the prepared mind. This is illustrated by my career after an incidental escape from the former German East Prussia just ahead of the Red Army, my switch in Kiel from zoology to oceanography, and my learning of a vacancy in Seattle. Treated here are the accidental discovery of upwelling during the southwest monsoon along India's west coast, studies of benthic polychaetous annelids in the Oregonian zoogeographic province, the discovery of phytoplankton blooms and an absence of upwelling during the northeast monsoon in the northern Arabian Sea, and an ocean-wide description of the seasonality of satellite-derived chlorophyll. My admonition is that grazing rather than cell division rate regulates the abundance and size composition of phytoplankton and affects the dynamics of the understudied zooplankton. I end with a pessimistic view about predicting the vertical flux of particulate organic matter from the euphotic layer with an accuracy useful for deep-sea carbon budgets.

INTRODUCTION

When asked to write an introductory article for the *Annual Review of Marine Science*, I felt really good and a little proud, and accepted the challenge. Then the reality of writing something worthwhile set in. First, I considered that I did not build a "school" of which an account would remain of historical interest. One reason for this "failure" was my broad and, over the years, repeatedly changing interests, so that I did not become the "go-to" person in any particular field. The changes in research emphasis were, and still are, accompanied by a lack of missionary zeal to attend every scientific meeting and promulgate the message. Therefore, I am now mostly known among colleagues who are already retired or approaching that age. Only these relatively few, I thought, might be interested in a personal tale.

Then I toyed with the idea of discussing the current (false) emphasis on the "bottom-up" approach (the resources) especially prevalent among phytoplankton workers, including those using satellites to estimate chlorophyll in the sea, and the biogeochemically inclined oceanographers. The fallacy is to neglect the "top-down" processes (mortality from grazing or predation and, of late, viruses). I did not want to pursue this subject either, even when restricting the discussion to the plankton and nekton and omitting the sea bottom and terrestrial ecological insights.

To me, the only general lesson from my professional life is the great role of chance through serendipity. Major turns were not decided on by rational choices between alternatives. Besides hard work and perseverance, a great deal of luck was involved, be it through an accidental conversation at lunch, an almost-missed phone call, attendance at a somewhat strange seminar, or logistic flukes. After having also been cool about that subject, since it would involve personal remarks, I withdrew my acceptance of the challenge of writing a prefatory article.

But then the journal's editorial committee persuaded me to do just that—to sketch the role of chance in my scientific development and discuss some of my views, e.g., about the top-down mechanisms. So I accepted the invitation. After all, paraphrasing Pasteur, in scientific work the goddess Fortuna favors only the prepared mind.

SKETCH OF MY LIFE HISTORY

I was born in 1929 in Königsberg in the former German East Prussia, a city of 340,000 inhabitants founded in 1255. In 1938 I came to belong to the approximately one-tenth of a year-class selected at age ten (in my case, nine) to proceed to higher education; formal education ended for the other nine-tenths after four more years in elementary school. In 1939 Germany started World War II, which in Europe ended in May 1945. By a fortuitous circumstance, in late January 1945, one day before the Soviet tanks reached Königsberg's outskirts, I was able to join an evacuation transport of women's antiaircraft auxiliaries and escape via the Baltic, instead of being drawn into the two and a half months of siege of the city. While inland in winter and spring of that year the Russians struggled toward Berlin, the German navy and merchant mariners carried 500,000 soldiers, most of them wounded, and more than 1.6 million civilians fleeing the Red Army for 400–650 km to safe western harbors of the Baltic (Kriegsmarine: The Forgotten Service 2011). Apparently only 30,000–40,000 people were lost on ships sunk by bombs, torpedoes, or mines.

Entering university in 1947, I wanted to become a gymnasium civil service teacher in biology. Until the late 1950s, in western Germany only approximately one-twentieth of each year-class went to the tuition-free universities (all state-run; there were no two- or four-year colleges). As also described by Goldschmidt (1956, chap. 1) and Wyrtki (1990), utter personal freedom prevailed. In the humanities and sciences, nobody checked whether one skipped the classes to instead listen to fine art lectures, or disappeared for one or two months into the library to prepare a 45-minute

seminar, or just did not do anything academically. No exams were given until the very end, aside from lab tests in, e.g., quantitative chemistry. Changing to another university was common, so I spent four semesters in Heidelberg and then moved to Kiel, mostly because of its prestige in zoology. The second reason was the threat of the introduction at Heidelberg of an obligatory exam in biology after four semesters, which I considered an entirely inappropriate encroachment upon academic freedom. As described in an earlier article (Banse 1998), by chance during the first year in Kiel I veered into oceanography, thus frivolously also forgoing the secure schoolteacher career.

The Institute of Marine Sciences in Kiel was small by today's standards, with one full and three associate professors and one instructor, who covered all disciplines including fisheries. It was large when compared with, say, the usual zoology departments in Germany, which had one full and one associate professor and one or two instructors. Being situated in the southwest corner of the Baltic, the institute could have provided an excellent training in coastal oceanography or marine biology. However, G. Wüst, the head and physical oceanographer, and J. Krey, the chemist and planktologist (my teacher), addressed the open ocean much of the time and made us think about the system as a whole. My doctoral degree in oceanography was granted in 1955, followed by three wonderful postdoctoral years in Kiel, which in turn were succeeded by two less wonderful years on the southwest coast of India, where I applied my training.

In the German university system—which is also emulated in, e.g., Russia and Japan—the first doctorate (Dr. phil., etc.) does not open the career toward becoming a university professor. Until the first decade of this century, a second degree was required based on truly original research and a much thicker thesis. In the humanities an entire book was preferred. At the end, the so-called habilitation (Dr. habil.) brought permission to announce lectures in the university catalog and offer them. While working toward this second degree, for many years one was still subordinate to a professor. The candidate could not formally supervise a diploma or doctoral thesis, although he or she could write research proposals that did not include a salary. Advancement in rank was possible only when a position opened, and normally it meant moving to another university. Now the system is in flux and the habilitation is no longer a must, but certainly some years of postdoctoral research are required before being invited to fill a professorship.

UPWELLING ALONG THE SOUTHWEST COAST OF INDIA

Having decided to aim at a university career, for the habilitation I wished to study an annual time series of plankton in a typical tropical ocean—in those years we all thought there was such a thing. The intent was to see whether seasonality was absent, as was inferred but not established at the time. The recently introduced ^{14}C method for measuring algal photosynthesis was to be compared with the biomass converted to carbon through microscopic counts in order to estimate the turnover rate or generation length of the phytoplankton. A water immersion objective for naked flagellates down to approximately 3–5 μm in size and an inverted microscope were to be used for the phyto- and microzooplankton (as it turned out, for 310 samples; the mesozooplankton dry weight was determined from vertical tows on each station).

In looking for a suitable site, the lack of marine institutes in South America and Africa at that time and the higher living costs in the United States and Bermuda made me apply in 1956 to an Indo-German exchange program. It offered a two-year stipend, which would also provide temporal leeway for a seasonal overlap of the planned time series. A German grant supplemented the stipend and covered the initial expense for equipment and glassware. In part with loaned instruments, I filled four crates, expecting to need only running water, electricity, furniture, and, fairly regularly, a ship.

In view of the river-caused low salinity of the Bay of Bengal, the choice of study region had narrowed to the Arabian Sea. Further, off Bombay (now Mumbai, 19°N), the very broad shelf made it unlikely that oceanic deep water could be accessed regularly. Therefore, I opted for the southwest coast of India. The only year-round open harbor was in Cochin (now Kochi, 10°N), where, moreover, a research vessel was run by the Indo-Norwegian Project (see below). I associated with the substation of the Central Marine Fisheries Research Institute (CMFRI)—India's oceanographic research agency at the time—in Cochin, where I was generously welcomed.

To make sure that the equipment could be brought into India, I had traveled to the Indian embassy in Bonn, where I was provided with an import license, declared as a customs clearance certificate. In early February 1958 I arrived by boat in Bombay, within three days of the luggage brought by a freighter. There it turned out that the embassy was ill informed and that a customs duty of about six times my monthly Indian stipend would be due. I refused to pay. After about seven weeks the Ministry of Education in New Delhi, my official host, granted the money to the Ministry of Finance, which reached customs in Bombay after another five weeks. Thereupon it turned out that demurrage fees (storage in the custom shed) of three times my stipend had accrued, which resulted in another seven weeks of delayed release with additional storage costs. Five months after landing in India I was able to unpack my equipment.

During the waiting time I familiarized myself with the literature about the eastern Arabian and Laccadive Seas off the Indian west coast. Most of it was published in local journals, and in the late 1950s, in the absence of bibliographies, it would have been difficult to find outside of India. The most extensive set of data had been compiled by the CMFRI substation at Calicut (now Kozhikode, around 11°N) with indigenous boats, e.g., a five-year series of at least monthly nutrients and net-collected, enumerated phytoplankton. Eleven principally single-authored, not-integrated papers presented almost entirely surface collections nearshore off Calicut and Cochin for 16 partly overlapping years. Regular large phytoplankton blooms during the southwest (summer) monsoon were associated with somewhat lowered temperature, high phosphate and zooplankton numbers, and huge catches of principally pelagic fishes. No explanations were forthcoming, and I likewise was at a loss. Being without field or laboratory work, I accepted the government's invitation to spend the hottest premonsoon month in a foreign student camp in Kashmir. On the way to and from the mountains I fell in love with the imperial Mogul architecture of forts, mosques, and tombs of the sixteenth and seventeenth centuries in Delhi, Agra, and Fatehpur-Sikri.

Returned to Cochin, I found the running water in the laboratory not yet installed. The previous chemical work (and, as it was to turn out, all of my own) was based on water collected in a large vat filled during the early-morning hours when the city's water pressure reached the former kitchen tap on the outside of the building. Because there was no sink, the residual water was poured out of the windows. Owing to inherent and locally amplified bureaucratic delays, 2 cm of connection between the city and our new indoor plumbing was still lacking when I departed for Europe in January 1960. Fairly high-quality distilled water in carboys, though, was purchased from a lady on the other side of town.

Finally, the needed ship also left much to be desired. Norway had, by about 1952, paid back the loans received from the United States under the Marshall Plan. The country then decided to pay its moral debt by aiding developing countries. Starting in mid-1953, the Indo-Norwegian Project (Sandven 1959) helped two fishing communities on the southwest coast of India near 9°N by, e.g., constructing a running-water supply, a health station, and an ice plant for the fish. The original plan was to mechanize the local beach-launched boats. When it was realized how little was known of the living resources beyond the reach of the indigenous crafts—approximately 10 km from the beaches—the Indo-Norwegian Project added exploratory trawling and offshore oceanographic research out of the Cochin harbor. Three 50–75-foot-long schooners were purchased and arrived

early in 1955. They had been built in Norway of soft wood; two of the vessels were new, while the third, of the same material and launched in the late 1910s, had for more than 40 years transported salted stockfish from Lofoten to southern Norway. The two new ships had to be decommissioned in late 1957 and early 1958, respectively, after about two years of active service because of damage from termites and dry rot. Hence the old boat, renamed *Kalava*, became the oceanographic research vessel. However, likewise suffering from dry rot, it was often under repair—for example, on and off for 7 1/2 months during the first 11 months of 1959, my principal research year—and so I had to find three other vessels during the year.

The resident CMFRI physical oceanographer, A.A. Rama Sastry, had mentioned casually that in the previous fall (1957) off the southwest coast near Quilon (9°N), he had noticed upwelling when running temperature and salinity sections (Rama Sastry & Myrland 1959). He advised to take a bathythermograph along on my first exploratory cruise with an idle steel trawler. In mid-July 1958, armed with a meter wheel, a loop of 150 m of hydrographic wire, the bathythermograph, and a Secchi disk, I found a thermocline at approximately 10 m instead of 80–100 m depth offshore. The next cross-shelf section, performed in late August with the finally repaired *Kalava* using Nansen reversing bottles, yielded <10% of O_2 saturation at 10 m depth. The water came from the upper part of the permanent tropical pycnocline, where the O_2 is quite low to begin with. During the following two months, two along-shelf sections and the study of climatological atlases revealed that upwelling is a regular feature lasting for about five months during the southwest monsoon season and extending from 8°N to at least 15°N (Banse 1959).

The climatology based on the surface observations by merchant mariners, e.g., Schott (1935, table 22, reproduced in Sverdrup et al. 1942, chart 3), clearly showed cool water during the northern summer off the southwest coast. Had I done my homework and looked at these atlases in 1957 before leaving for India, I would not have chosen Cochin as a site for studying the absence or presence of seasonality in a typical tropical ocean.

The key to the discovery of this large upwelling region sustaining large fisheries was subsurface sampling with O_2 determinations on the open shelf during the windy southwest monsoon. I was invited to publish in the first issue of the first volume of an Indian marine biology journal, which was unlikely to be seen quickly by physical oceanographers abroad. Further study of the literature and observations in data centers extended the conclusions about upsloping during the southwest monsoon onto the shelf off northwest India and Pakistan, as well as the absence of coastal upwelling during the northeast monsoon (Banse 1968). To this day, the feature remains largely unknown outside the workers studying the North Indian Ocean.

SEATTLE: TAXONOMY OF BENTHIC POLYCHAETOUS ANNELIDS

In an earlier note (Banse 1998), I described the incident that brought me to Seattle in 1960, thus avoiding the long passage to the German habilitation and being able to assume responsibility and teach right away. Briefly, at a lunch during the first International Oceanographic Congress, held in New York in 1959, my former advisor J. Krey happened to sit across from M. Rattray of the University of Washington, who mentioned a vacancy at his Department of Oceanography. For the next 35 years I learned there continuously through classroom instruction, by mutual education with graduate students, from colleagues, and in scientific meetings and on committees. Since my retirement from teaching and administration in 1995, the learning by research has continued.

In my first year in Seattle, during one of the daily morning coffee-cum-faculty meetings I remarked casually that our teaching emphasized the water column of the open sea as if there were no bottom, while certainly the biologically oriented graduates would largely be employed in

studies on the shelf. Our five or six faculty members suggested that I also teach and work on the benthos—the bottom fauna—and so I did.

From my doctoral dissertation on the transport of planktonic larvae from the Kattegat into Kiel Bight, and partially during my postdoctorate years in Kiel, I had become somewhat familiar with polychaetes. About every second animal one picks from bottom samples that have been washed through the conventional 0.5- or 1-mm screens is apt to be such a worm. So, when establishing a level-bottom fauna program with U. Lie in Seattle in the early 1960s, I thought of assisting by identifying and counting the polychaetes. We would use the identification keys for British Columbia, adjoining to the north, which had just over 300 species (Berkeley & Berkeley 1948, 1952). A few additional forms from Washington waters might have been added. Before committing time to Lie's effort, I tried to be on the safe side and avoid having to stare into a nearly bottomless pit full of undescribed species. In 1961 and 1962 at the university's marine station at Friday Harbor, I had looked at a few sand and mud samples. Only two new records for the North American west coast and a new subspecies were found. So, facing a seemingly well-known worm fauna, together with K.D. Hobson and F.H. Nichols I identified the polychaetes from 129 replicate samples collected at eight stations during two seasons of 1963 with a 0.1-m² grab sampler, washed through a 1-mm screen (see Lie 1968).

Alas, the Friday Harbor test results of 1961–1962 turned out to be false. Thirteen years after starting in earnest, we had written 24 papers that covered a new family, two new subfamilies, generic revisions, new species, and two small monographs (Banse & Hobson 1974, Hobson & Banse 1981). The two monographs identified 468 benthic polychaete species from the shelves of British Columbia and Washington instead of a few more than 300. While the tools for ecological studies had certainly been sharpened, no oceanographic principles were elucidated. In contrast, the efforts by R.C. Dugdale of our department in the upwellings off Peru, the US west coast, and northwest Africa fell within the same period, as did active work at sea by other colleagues in which I could not participate because of my commitment to the worms. Also, later I never worked at sea off our coast.

By the late 1970s the novelty of studying worms had worn off. Polychaetes are an old and diverse group, which before the arrival of molecular methods did not easily lend themselves to phylogenetic research with results that could enter textbooks. Also, my late wife became quite tired of answering the question at parties "And what does your husband do?" with "He studies worms," which the interlocutor tended to associate with intestinal parasites. She urged me repeatedly, "Can you not get famous, instead?"—not realizing or appreciating that for quite a while I was number three or so among the polychaetologists on the continent.

NORTHERN ARABIAN SEA

While focusing for about 15 years on the polychaetes, besides keeping my upper-division under-graduate and graduate lectures current, I also worked on, e.g., the methodology of plankton field research; contributed the physiology to the modeling of the phytoplankton dynamics in Puget Sound by Winter et al. (1975) and of the phytoplankton seasonal cycle on the Washington shelf by Jamart et al. (1977); taught twice in Turkey (again drawn in by an accident); and published on the dependence of respiration, growth rates, and production on the cell or body size of phyto-plankton and animals (e.g., Banse 1982a, Banse & Mosher 1980). By chance, in the early 1980s I returned to the Arabian Sea.

Anticipating the Convention on the Law of the Sea, in 1981 the government of Pakistan established the National Institute of Oceanography in Karachi to initiate research in their essen-tially unexplored exclusive economic zone. A workshop of scientists from the United States and

Pakistan in Karachi in November 1982 reviewed the knowledge of the marine sciences in general and especially the northern Arabian Sea. The hope was that it would lead to joint work. Presumably because of my earlier review (Banse 1968) but in spite of my stated definite lack of interest in that region, S.I. Ahmed—an originally Pakistani colleague in our department—arranged for an invitation for me to attend. I turned down a first letter from Pakistan, but "No" was not a sufficient answer and a second inquiry followed. I was prepared to react as before, but then a short new paragraph caught my eye stating that it would be much appreciated if the foreign expert were to also offer a lecture at an institution outside of Karachi. As mentioned, during my forced 1958 summer vacation I had fallen in love with the imperial Mogul architecture in northern India. I knew that the Moguls had invaded from Afghanistan, but I had not done my homework, and so I thought that early development of the style would be found in the former Mogul capital of Lahore, now in Pakistan and relatively close to the gates of entry. Sure enough, there was a university in the city, and I accepted the invitation to the workshop. (However, I saw during that visit that the emperors had built in Lahore with the same superior attainment of style as in the other cities mentioned. I greatly enjoyed the lesson.)

The review of many isolated papers in Seattle for the Karachi workshop yielded new oceanographic insights, in contrast to the initial literature research in Cochin, which only later had led to the discovery of the upwelling off the southwest coast of India. At 20°–24°N, the deepened mixed layer (e.g., Banse 1984, figure 1; Wyrtki 1971, plate 328) from convection due to the cooling of high-salinity surface water should lead to nutrient injection analogous to the winter blooms at 32°N in the North Atlantic near Bermuda. The plotting of scant in situ chlorophyll data from expeditions indeed discovered two bloom periods in the open northern Arabian Sea: a winter bloom due to the northeast monsoon and the usual bloom during the southwest monsoon (Banse 1987). I inferred that the different pattern of phytoplankton seasonality should affect that of the zooplankton.

REMOTE SENSING OF PHYTOPLANKTON CHLOROPHYLL

While plotting those ship-collected pigment data, I grew pessimistic about the utility of further expeditions along transects where spatial and temporal changes cannot be separated easily, if at all. Then chance intervened again. During a lunch at a meeting in the mid-1980s, J.K.B. Bishop asked whether I had thought of satellites.

Well, I had not, in spite of having listened during those years to many raving talks about them. The Coastal Zone Color Scanner (CZCS), contrary to its name, had recorded phytoplankton pigment in the open sea since late 1978. Its repeated, successive mapping of large areas would circumvent the confounding of place and time.

Thus, in 1985 I set out to compare satellite-derived pigment and sea surface temperature in the northern Arabian Sea. The CZCS carried only 30 minutes of tape time before data had to be transmitted, so observation time was at a premium. About 6 minutes was needed to cross the Arabian Sea. Luckily, however, NASA's committee charged with selecting target areas for the satellite mission had for extraneous reasons prioritized the Arabian Sea (see Banse & English 2000, p. 1667). Therefore, the temporal coverage during the northeast monsoon, with its few clouds, was excellent, and Banse & McClain (1986) described the winter blooms in the northern Arabian Sea. After the data were recalculated with new algorithms, the homology with the mentioned seasonal sequence of vertical mixing, inferred nutrient supply, and phytoplankton development off Bermuda, including the expected difference in pigment between the springs of 1979 and 1980, was confirmed (Banse & English 1993).

Subsequently, Banse & English (1994) described the ocean-wide seasonal chlorophyll distribution for 48 offshore sites with eight or more months of CZCS pigment means. Similarly to Yoder

et al. (1993), we found quite a small range of monthly medians over much of the tropical and subtropical seas. Where it could be determined, the ratio of the maximal to minimal medians was <2.5 (Banse & English 1994, figure 6, explanation on p. 7326). Further, Longhurst (1998, p. 44) demonstrated for the trade wind zones that the *monthly* changes of CZCS pigment correspond to about half a *day* of primary production (^{14}C uptake). The average concentrations of phytoplankton are equivalent to one-half to three days of production. So, the day-to-day changes of pigment in large areas are small relative to the daily rates of cell division. The difference is due to removal by sinking as well as mixing, and especially mortality by grazing, as shown below.

Among other regional papers of mine concerning parts of oceans or basins and using the CZCS as the tool were Banse & English (1999, 2000). After studying the seasonal open-sea patterns with the CZCS, however, I did not follow the upswing of satellite studies when the next generation of color instruments appeared [in the United States, especially, the Sea-Viewing Wide Field-of-View Sensor (SeaWiFS)].

Last but not least, and again fortuitously, in 1988 my 18-year-old daughter applied for admission to Pomona College and on her own entitled the required brief essay something like "What If Mermaids Were Still Around?" During a Hawaiian vacation I fleshed out the image's skeleton, and when back in Seattle I clothed her with a quilt of citations (Banse 1990). I trust that the paper will provide good reading decades hence.

PHYTOPLANKTON CELL DIVISION VERSUS GRAZING LOSSES

In the following admonitions I wish to treat my long-standing concerns about the broad neglect of top-down mechanisms acting in the lower levels of pelagic food webs. Chance is not involved except in unplanned encounters with recent papers.

Phytoplankton physiology and, hence, cell division are driven by the so-called bottom-up mechanisms (principally light, nutrients, and temperature, besides idiosyncrasies of the species). The grazing upon the algae and the predation upon the grazers constitute the so-called top-down effect. The digestion and recycling of nutrients concurrent with the grazing, which feeds back to the phytoplankton, show that it is unwise to focus on only one of the two pathways. This was noted many decades ago, e.g., by Cushing (1959), who entitled a modeling paper "The Seasonal Variation in Plankton Production as a Problem in Population Dynamics," carrying an implied ". . . but Not Exclusively of Phytoplankton Physiology." The bottom-up view of the waxing and the neglect of the waning of phytoplankton populations, however, appear to be ingrained to this day, as seen from five comprehensive treatments of phytoplankton processes of the past three decades, comprising two free-standing books and three edited international symposium collections: Falkowski & Raven (2007), Falkowski & Woodhead (1992), Platt & Li (1986), Reynolds (1984), and Williams et al. (2002). Aside from mentions of nutrient recycling, two do not present grazing, mortality, etc.; the two earliest works treat them in subsections of chapters; and only one contains an entire chapter, which, however, was added to the agenda only as an afterthought.

Any observed time change of phytoplankton concentration may be due to the difference between two small or two large numbers (e.g., rates of cell division and mortality). As shown below, measured rates of phytoplankton increases leading to blooms following enhanced nutrients or underwater irradiance turn out to be smaller, often greatly so, than the increases of division rates, because grazers always accompany the phytoplankton even in milliliters of water, and physical mixing never ceases. For the same reasons, the drawdown of CO_2 in the euphotic zone is significantly smaller than would be expected from the measured uptake of $^{14}CO_2$ (for the sake of argument, the concurrent sea-air exchange of the gas is neglected). Consequences of the feedback from the zooplankton metabolism to the phytoplankton were reviewed in Banse (1995).

How large are the rates of gains and losses in the field? Until two to three decades ago, marine phytoplankton instantaneous division rates (k herein, usually μ in the physiological literature) were thought to be low (≤ 0.1 day^{-1}) in view of the low nutrient concentrations observed, particularly in the wide expanses of the nutrient-depleted ocean regions. (For three decades, new analytical methods have broadly demonstrated values of inorganic nitrogen that are lower than those found previously by one to two orders of magnitude, but the following argument is not altered.) Also, for about three decades, using the dilution method we could measure the actual cell division rates in the presence of the grazers, which at the same time provides the grazing mortality (Banse 1995, figure 2; Landry & Hassett 1982; Landry et al. 1995; Selph et al. 2011). Often the bulk phytoplankton division rates are near 0.7 day^{-1}, i.e., approximately one cell division and hence one doubling of mass per day; rates may often be ≥ 1 day^{-1} (Laws 2013). The high division rates at low nutrient concentrations are due to the continuous nutrient supply from phytoplankton mortality through the feeding and digestion by the concurrent zooplankton. These recycled nutrients are immediately taken up again. Yet in spite of the high division rates, the phytoplankton abundance averaged over 24-h periods changes little, if at all. The production process appears to be balanced.

Figure 1, originally drawn two decades ago, applies the principle of the pigment balance to an upper layer at quasi-steady state. This temporal stability is shown by satellites to prevail for many months in the open sea of the tropics and subtropics, during the summer in the temperature zones in oceans and large lakes, and in the marine high-nitrate–low-chlorophyll iron-depleted regions. In the latter areas, "grazer-controlled phytoplankton populations" of small cells live "in an iron-limited environment" (Price et al. 1994, p. 520; cf. Banse 1996 for the subantarctic water ring, which occupies approximately 10% of the oceans' area, and Landry et al. 1997 for the equatorial Pacific). **Figure 1b** lists the measured k and the inferred average g values. At the time, grazing was thought to be the principal biological source of loss (hence g in the figure), while now viruses also need to be kept in mind (see Breitbart 2012, Miki & Jacquet 2008), making mortality the more accurate term. Note that the units of k and g are the same. For g, a value of 0.693 (=ln 2) means that the suspension feeders clear 1 liter of phytoplankton per day. The horizontal terms are negligible because the near-absent observed gradients make the terms small relative to the other variables.

The figure shows that for the low-latitude offshore regions and the other mentioned seas where pigment is in a quasi-steady state for many months, the cell division rates can only be balanced by grazing (including viral mortality, if any), which insures the recycling of nutrients within the euphotic zone. The observed near-perfect balance between rates of cell division and mortality at periods of ≥ 24 h is astonishing. Because of the daily compounding of interest in exponential growth, a positive difference of 0.1 day^{-1} would double a population in seven days! With the two large, dominating biological numbers of k and g, errors or variability in the other terms in **Figure 1b** rarely matter in the lower latitudes. (For increased nocturnal mixing rates, see Wiggert et al. 2000.) Only in the high latitudes is vertical mixing a substantial loss term for periods of ≥ 24 h. While **Figure 1** describes the quasi-steady state of the larger part of the oceans, the huge losses of phytoplankton also hold for blooms (see next section).

Apparently the broadly low abundance of phytoplankton in the temporally stable regions is due to the grazers and has little to do with cell division rates or the near-constant (on a 24-h basis) nutrient regime [see the early review by Frost (1980)]. It is still unclear why the average levels are not one-third or three times the observed values. Obviously the grazers cannot reduce their food, the phytoplankton, to zero, because without further food their ongoing metabolism and the need for cell division or growth would make the population vanish from grazing, mixing, etc. (see Strom et al. 2000). Therefore, a feeding threshold or another mechanism like carnivory (top-down control of grazers) leading to the reduction of grazing pressure must exist in the field.
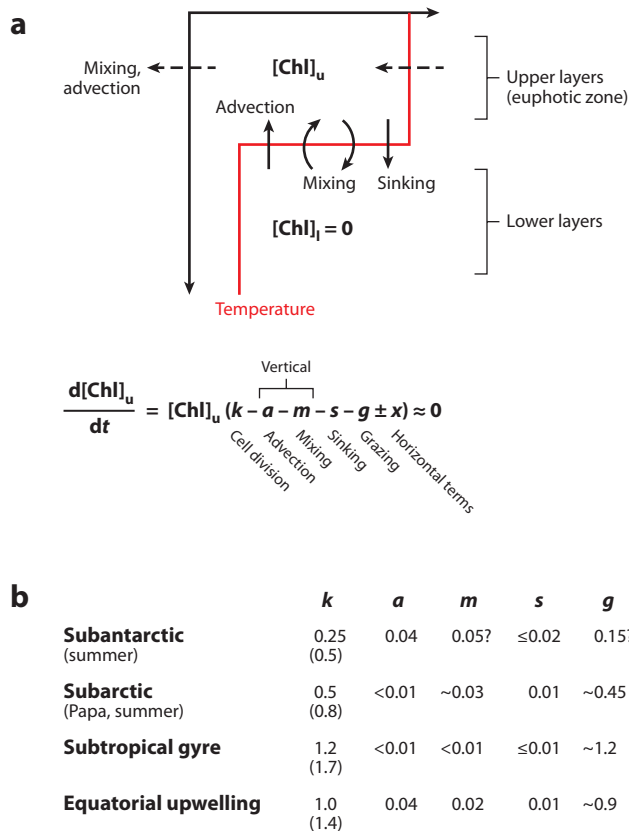
Figure 1

The maintenance of the grazing balance of a quasi-steady state concentration of phytoplankton chlorophyll. (*a*) Model for deriving the balance; Chl_u and Chl_l are the chlorophyll in the upper and lower layers, respectively. (*b*) Numerical values for four open-sea domains: average cell division and inferred grazing as instantaneous rates (day^{-1}) and advection, mixing, and sinking as fractions of Chl_u added or removed (mass m^{-2} day^{-1}). In parentheses below the measured k are maximal 24-h values estimated from Eppley (1972), considering day length and average temperature. Papa refers to the location of the former weather ship P at 50°N, 145°W. Adapted with expanded caption from Banse (1992, p. 413, figure 2) with kind permission from Springer+Business Media B.V.

In models, an actual threshold can be replaced by a sigmoidal function. An elaborate treatment of such models, which include multiple food sources and switching as well as models of food uptake, was provided by Gentleman et al. (2003).

PHYTOPLANKTON MORTALITY FROM GRAZERS

In support of the grazing rates deduced in **Figure 1**, the average dilution-determined daily mortalities indeed range between 3/5 and 3/4 of the newly produced phytoplankton in oceanic and coastal, tropical, temperate, and subpolar regions, as reviewed by Landry & Calbet (2004). The principal grazers studied by the approach are very small and mostly unicellular (the so-called microzooplankton, at sizes of <0.2 mm but generally <0.1 mm). In three well-documented situations during the later stage of the open temperate North Atlantic spring phytoplankton bloom, microzooplankton even removed the entire daily primary production (Burkill et al. 1993, Verity

et al. 1993). The losses from microplankton are accompanied by the grazing of larger zooplankton as usually collected by nets (the mesozooplankton, at sizes of 0.2–1 mm). Their grazing rates are measured by adding specimens to bottles with the natural plankton assembly (cf. Frost 1980) and usually amount to 1/10–2/10 of the newly produced cells. Most of the particles settling as feces out of the euphotic zone are due to these larger animals. As a cautionary note regarding those averages, the ratio between the mortalities due to the two fractions in particular situations ranged between almost 0 to almost 0.8 on five stations along a section in the Arabian Sea (Landry 2009, figure 6), and elsewhere the mesozooplankton cropped more than the small fraction did, as off southern California (Landry et al. 2009, figure 4).

In the few instances when both grazing rates were measured in the same water, the sums were close to the measured phytoplankton production in the quasi-steady-state high-nitrate–low-chlorophyll region of the equatorial Pacific (e.g., Landry et al. 2011). Similarly, the observed variable phytoplankton abundance changes during eight three-to-five-day runs near a buoy drifting in a coastal upwelling system matched fairly well with those predicted from concurrent grazing experiments (Landry et al. 2009, Stukel et al. 2011).

The ratios of mortality by the small and large fractions on a particular day or at a specific site depend both on the compositions of the phytoplankton and on the grazer communities, because of the size-selective grazing (see below). Also, in nonequilibrium settings (see Goericke 2002 for the Arabian Sea) the phytoplankton-grazer interactions appear to govern the phytoplankton abundance as well as its composition in species and cell sizes, rather than, e.g., the nutrients, with the exception of silicon and in places iron (for lakes, see Porter 1977; Reynolds 1984, chap. 7). These views are quite different from strictly bottom-up scenarios, e.g., in models of self-assembling phytoplankton communities where resource competition is posited as playing a large role at long timescales, at least in the temporally stable oligotrophic regions (Barton et al. 2010); the underlying global three-dimensional model by Follows et al. (2007) does incorporate grazing, but it is treated as a minor issue (likewise in Follows & Dutkiewicz 2011). The further development of the model by Prowe et al. (2012), who added variable grazing pressure and allowed switching of ingestion among phytoplankton types, resulted in profound differences of phytoplankton community structure, seasonal succession, and net production, as well as better agreement with observations.

Excepting these studies by Follows and his successors, note that most citations and conclusions herein refer to and are based on one-shot expeditions collecting at sites often affected by horizontal advection, which bring snapshots of abundance and community composition that are interpreted post hoc. In contrast, limnologists study a few lakes year after year (see below, toward the end of this section). Yet even they face unpredictable variability in abundance and specific phytoplankton assemblies between seasons and across years. The variability, however, can be explained qualitatively post hoc [e.g., figure 8.2 by Reynolds (2002), who is leaning toward bottom-up mechanisms]. In the sea we cannot yet anticipate the occurrence and succession of particular phyto- or zooplankton species, except post hoc from size-selective grazing or, for a few mesozooplankton species, from advection of seed stock.

Mortality is an emergent property of populations. Measuring it requires revisiting, which is easy, for example, for intertidal benthos. For phytoplankton in open water, however, three-dimensional advection and mixing (eddy diffusion) have to be accounted for in addition to cell division and mortality. This has been achieved by labeling a few square kilometers with an inert gas [previously SF_6, now, instead, SF_5CF_3 (Ho et al. 2008)]. The patch is followed in its movement, so that advection is eliminated. The physical dilution from mixing and the loss by sea-air exchange can be estimated from the decline of the gas concentration. **Figure 2** shows a result of such a true field experiment in 1995. By the time the patch had drifted by >800 km and the peak of the phytoplankton bloom was reached, 3/4 of the measured cumulative carbon uptake had vanished,
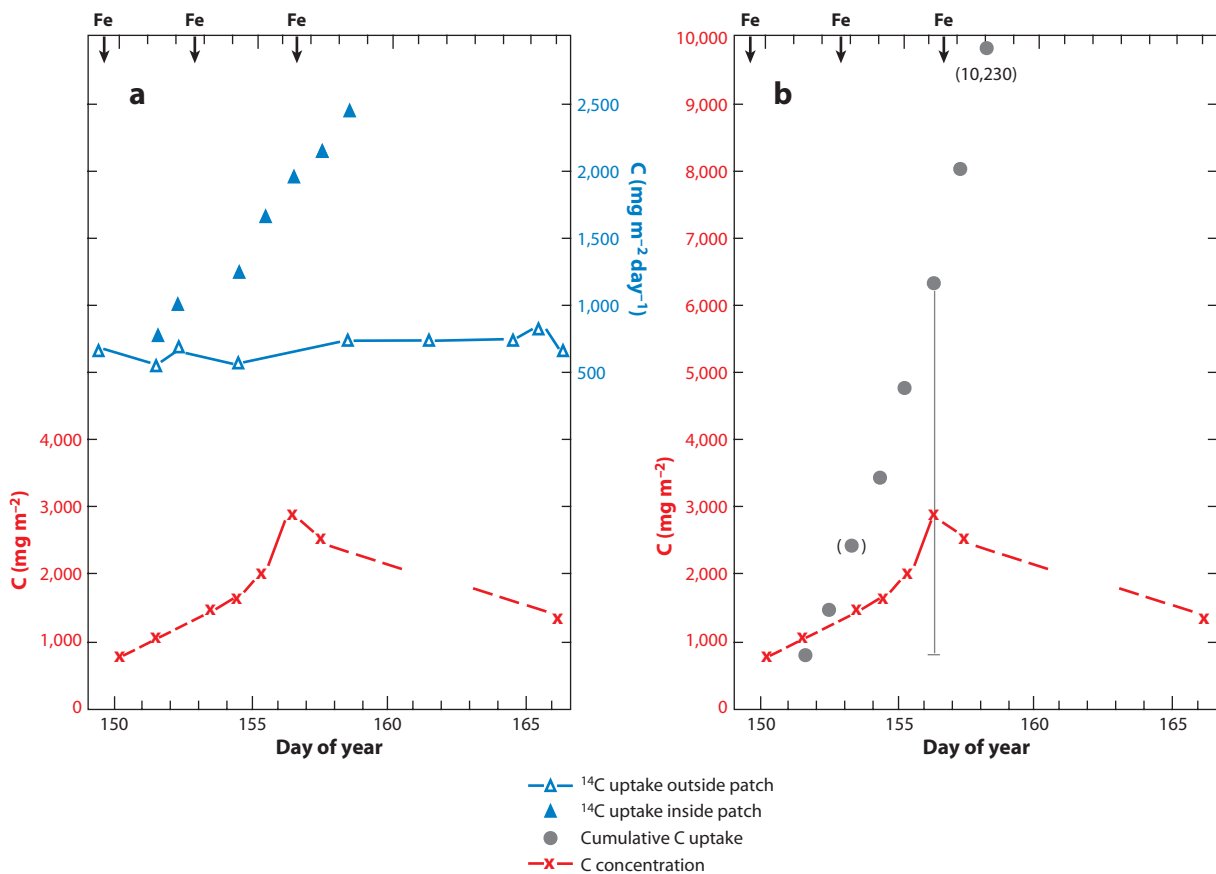
Figure 2

Photosynthetic carbon uptake and grazing losses during the iron fertilization experiment IronEx II carried out west of the Galapagos Islands, integrated for the euphotic zone and corrected for physical dilution of the fertilized patch. Dates on the bottom are for 1995; the arrows on top mark the dates of iron additions. (*a*) The upper traces (*blue*) show simulated in situ ^{14}C uptake outside and inside the patch (*open triangles* and *filled triangles*, respectively). The lower trace (*red*) shows carbon concentrations, with concentrations for days 150–54 estimated from 15-m values in Landry et al. (2000). (*b*) Cumulative carbon uptake (*gray circles*), corrected for 13% daily losses from mixing, and carbon concentration (*red crosses*); the vertical bar indicates the uptake since day 151. At 15 m depth, the diatoms showed the same pattern and degree of losses as the total phytoplankton (Banse 2002, figures 3*b*,*c*). The parentheses indicate an uncertain value. Adapted from Banse (2002, p. 24, figure 2A) with kind permission from Springer+Business Media B.V.

apparently not from sinking. Because of the grazing and the recycling of the newly formed organic matter, the drawdown of CO_2 was much below the measured carbon uptake of the phytoplankton.

Similar losses of newly produced phytoplankton in the only two other revisited waters available in 2001, with physical dilution effects considered, were 3/4, mostly from grazing, when the peak concentration of the diatom bloom was reached (Cushing's *Calanus* patch of 1954), and 9/10 during an aborted iron fertilization experiment in 1993 (for both, see Banse 2002). As reviewed by de Baar et al. (2005), six later open-sea studies of these iron-induced blooms yielded a particulate organic carbon increase of 18%–26% (five data sets) and a CO_2 drawdown of 51% ± 26% of primary production. The particulate organic carbon comprises phytoplankton and live and dead nonphytoplankton particulates. The increase of dissolved organic matter was not well studied, and

its modest export to depth "hardly exceed[s] the noise" of the data (de Baar et al. 2005, p. 18). In one of these manipulations in antarctic high-silicate, high-nitrate water, Buesseler et al. (2005, figure 10) studied ^{234}Th deficiency. They derived mean percentages of export of primary production, both integrated to 50 m depth, of 6%, 8%, and 11% for the first three weeks inside the fertilized patch and 12%, 13%, and 19% for the same three weeks on the outside (the control), respectively. In the already-mentioned Lagrangian-type revisiting study off southern California by Landry et al. (2009), the ^{234}Th method yielded ratios of export from the euphotic zone to primary production that ranged between 7% and 14% (four stations) (Stukel et al. 2011). The paper concluded that the zooplankton were the major regulator of vertical export for those quite-different plankton assemblages.

Apparently none of these major experiments studied the time changes of zooplankton, which is easier said than done. As Ohman (2012) stated, zooplankton mortality is regarded by many as inherently unknowable, while I note that much of fisheries science deals with mortality fairly routinely. Fishes, of course, are the best-known animals in the sea, and their ages can be determined, in contrast to zooplankton. Ohman (2012), dealing with stage- but not age-structured plankton populations, pointed toward routes to improvements of the mortality riddle. Remember that without a better understanding of and some predictability in the population dynamics of zooplanktonic suspension feeders ("herbivores") and their predators, a mechanistic prediction of the feces production and hence of a salient part of particulate export from the euphotic zone is hazardous—the percentage of flux is not just a function of the kind and abundance of phytoplankton.

On a few occasions, mass sinking of diatoms has been observed in the open sea upon silicon exhaustion, and a carpet of diatoms has even been recorded from deep-sea depths. Clearly, the resulting change in abundance in the euphotic zone must have been large and for a few days may have surpassed losses from grazing. Also, diatoms and some other phytoplankton have been found in the field and in enclosures (mesocosms; see below) to aggregate and sink. The mechanisms have been modeled. I have not surveyed this literature, thinking that the high algal concentrations preceding such events are rare and, to my knowledge, have not been caught in sediment traps. The potential selective role of sinking on phytoplankton composition, while subject to grazing, is seen from actual loss budgets for 14 species during nine months of weekly or biweekly sampling in two freshwater enclosures approximately 45 m in diameter (so-called Lund tubes, "lakes within lakes" without through flow; Reynolds et al. 1982, figure 8). I do not know of any time series like it from the marine literature.

To stay with grazing experiments by the dilution method or with added mesozooplankton, note that the same bottled water is revisited, and hence mortality can be measured. Also, large enclosures of usually natural water (mesocosms, normally ≥ 1 m^3 in volume under natural light) will permit direct mortality determination. I regret that after Banse (1982b), I have not followed this literature. During the past two to three decades many replicated studies, a week to a few months long and with or without chemical or biological manipulation, have been performed. I sense that too rarely have the mass balances, calculated from the rate measurements inside, been checked by emptying the entire containers.

In conclusion, as previously noted in Banse (1994) and illustrated in **Figure 2**, the bottom-up controlled cell division rates (measured, estimated from remotely sensed chlorophyll, or calculated from environmental data) greatly overestimate the rate of population change during a bloom. Moreover, they cannot even predict the correct sign of the change because of the neglect of mortality. Riley (1946) had already noted this in his model of the seasonal phytoplankton cycle on Georges Bank. The inability to determine phytoplankton mortality—and, beyond that, the inability to "see" the zooplankton remotely—is the fundamental handicap of satellite-based estimates of the dynamics of primary production.

TOP-DOWN EFFECTS, ALSO AMONG THE ZOOPLANKTON

In many respects, the zooplankton are our big black box, shown by the litany of missing knowledge ranging from taxonomy, natural history, and basic physiological rates to seasonal and geographic distributions to fundamental modeling issues (see, e.g., Hofmann 2010, Ohman 2012). Here I introduce only size-selective grazing and predation.

The size range of most phytoplankton cells is approximately 10^2-fold, so the mass range is near 10^6-fold, which is similar to that between voles (small mouse-like mammals) and elephants. The size range for the unicellular zooplankton or protists, which are the smaller but more abundant part of the microzooplankton, may be similar. However, just as there is no net that catches mice together with elephants, so size-selective grazing and predation reign among the one-celled organisms. Certainly larger species within this microbial food web eat small species (e.g., Calbet & Landry 1999). The ranges of size and body mass among the adult zooplanktonic animals (multicellular = metazoans), and above them the fish and squids, are much larger. Individual growth in body mass may well extend over a range of 10^2- or 10^3-fold. Because of this often large change, grazing and predation are not simply "big species eats small species"; figuratively, while any wolf could eat any goat, an adult goat could eat a young wolf. Especially among the metazoans, there is much (in a way unpredictable) opportunistic feeding.

Looking finally at top predators, two early examples of the drastic top-down effects of one added planktivorous fish species each on food webs are two freshwater studies, which may serve as warning signs for the next several decades. Brooks & Dodson (1965) evaluated an accidental invasion of fish in a pond where the zooplankton had been well studied previously. The second case concerned the experimental, replicated effects on phyto- and zooplankton and benthos of added fish under three nutrient regimes (Hall et al. 1970, figures 33 and 34). The large changes in both studies of the species and size composition of zooplankton could certainly not be predicted even by an improved contemporary nutrient-phytoplankton-zooplankton-detritus model. As noted by Hofmann (2010), emergent behavior in food webs is not well modeled. Once again, the zooplankton are the enigmatic link in relating primary production to fish by the so-called end-to-end models (cf. Mitra & Davis 2010, Steele & Gifford 2010), and as outlined in the present article, they remain so.

Verity et al. (2002) urged thinking about a new conceptual framework and considering predation as a major agent in organizing the functioning of pelagic ecosystems. I have observed that the same top-down regulation as in the pelagic zone holds for coral reefs, the intertidal zone, and terrestrial plants and predators (e.g., review in Banse 2007; cf. Pimm 2008).

ON THE FLUX OF PARTICULATE ORGANIC MATTER TO DEPTH

The implication of the previous section is a pessimistic view of accurate predictability within the euphotic zone of the numbers or biomass and kinds of zooplankton as the intermediary between primary production and the sinking flux of live or dead particles. My skepticism applies even to in situ observations from research vessels, let alone remote predictions, of grazing mortality and the resulting vertical flux from environmental variables. The point here is the issue of attaining a *useful* accuracy in the particulate flux into the mesopelagic (twilight) zone. The zone extends from 150 or 200 m to approximately 1,000 m depth. Much of the sinking particulate matter will be degraded and recycled there. The fraction that is not will remove CO_2 from the euphotic zone, and hence the atmosphere, toward at least partial sequestering in the deep ocean, or actually the seabed below. Recent reviews and syntheses for the mesopelagic zone and associated questions were contributed by Boyd & Trull (2007), Buesseler & Boyd (2009), Burd et al. (2010), Guidi

et al. (2009), Henson et al. (2011), Koppelmann & Frost (2008), and Robinson et al. (2010). I note only that the zooplankton-mediated processes in the twilight zone are even less well studied than those for the epipelagic zone, and more difficult to investigate. In addition, we must not forget the bacterial and archaeal respiration and growth with their carbon demand, which in the meso- and bathypelagic zones is generally thought to greatly outrank that by eukaryotes, including the animals (i.e., Burd et al. 2010).

With the increase into the hundreds of measured flux (export) estimates from sediment traps, at first glance the standard errors of correlations with some near-surface parameter and the R^2 values look better and better every half-decade. However, using figure 1 in Henson et al. (2011) just as an example, the variability around the mean below 25°C, below the upper layers, is unacceptably large. What level of precision, though, is needed in budgets for the mesopelagic and abyssal zones? A prediction for organic flux of, say, "80%–90% of phytoplankton net production is remineralized in the epipelagic layer" would for the mesopelagic denizens mean 20% or 10% of net production being made available. This is a twofold range of supply of organic matter! A range of 85%–95% would translate into a threefold range. I fear that neither of the two predictions with such narrow confidence limits is presently attainable except perhaps for single, well-investigated stations. How are the students of the twilight zone and the deep sea at large to live with that degree of uncertainty?

AFTERTHOUGHTS

For about four decades I have been on the side of the few colleagues, like D.H. Cushing, B.W. Frost, J.H. Steele, and E. Steemann Nielsen, who showed early and repeatedly the importance of grazing losses. We all stressed that phytoplankton dynamics cannot be understood by considering only the abiotic environment and algal physiology (bottom-up approach). Neither can the admittedly more difficult dynamics of the animal plankton be fully tackled just by learning all about reproduction and growth (see Banse 1982b, pp. 16 and 18). From reading proposals for fieldwork and many papers of the first decade of this century, it appears to me that the message has not fully sunk in. How does one change a paradigm, the false bottom-up-only view? Is it only through much more of the "missionary zeal" mentioned in the introduction? Or does the saying reign that old soldiers never die but just fade away?

Happily, I note that recent limnology textbooks do present the role of grazing in phytoplankton composition and abundance, mention the feedback via nutrient regeneration, and treat top-down predation by fish (Horne & Goldman 1994, Kalff 2002, Lampert & Sommer 2007, Wetzel 1983). These insights are not yet broadly shared among marine science colleagues, as indicated. Regarding the possible reasons, I wonder whether food web features are conceptually easily accessible to limnologists, whose roots tend to be in zoology or biology departments. In contrast, biogeochemically thinking oceanographers may have entered from laboratories of algal cell physiology or be converts from chemistry or physics in the broad sense, and model the forests in spite of the trees. Why are there so few textbooks in biological oceanography from which the "bottom-up addicts" could benefit?

My last comment will address a scientific scene like that prevailing, e.g., in North America but less so in countries where networking, connections, and even nepotism greatly matter for personal advance. Very young colleagues in the former setting may wonder now whether a successful career, besides requiring perseverance and persistence, is largely a matter of pure chance, of being in the right place at the right time. I suggest that this is not entirely so, but certainly an open and prepared mind is needed. "Where observation is concerned, chance favors only the prepared mind" (Tulloch 1992, p. 509, citing Pasteur from 1854). I admit that a few decades ago it was easier to acquire and maintain an open mind by thumbing weekly through the new journals in the library rather than

relying, as is the case now, on electronic searches in subjects one already broadly knows. Certainly there were far fewer scientists around, and hence a smaller body of literature to cope with, and there were only hard-copy journals, easy to peruse. If, however, one never sees papers on topics other than one's own, is one not missing the chance to make important links that happen only through serendipity? This message is meant not to discourage the young readers of this article, but perhaps to motivate them to peruse a favorite journal from front to back, rather than just selecting the one paper of immediate interest.

DISCLOSURE STATEMENT

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Errata

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