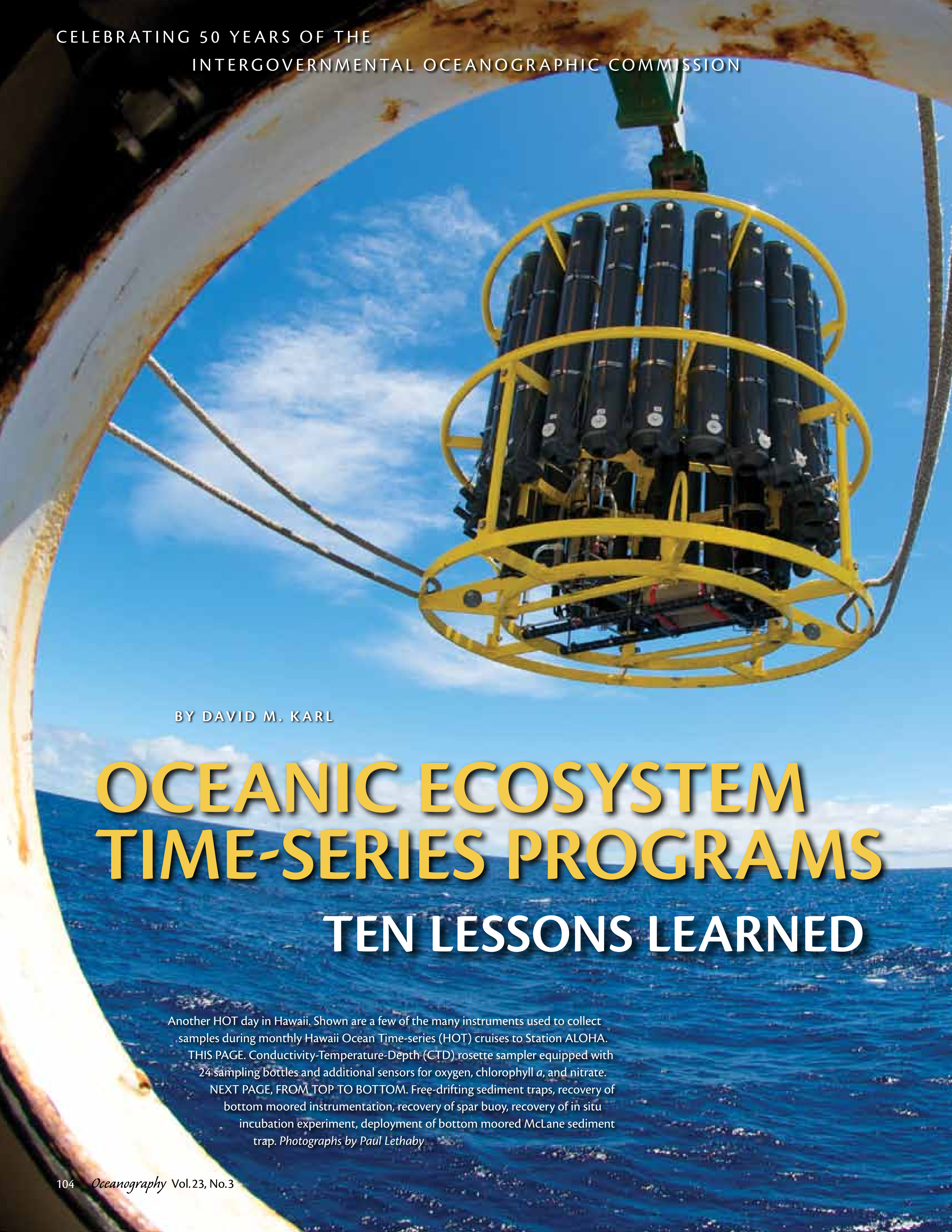

BY DAVID M. KARL

OCEANIC ECOSYSTEM TIME-SERIES PROGRAMS

TEN LESSONS LEARNED

Another HOT day in Hawaii. Shown are a few of the many instruments used to collect samples during monthly Hawaii Ocean Time-series (HOT) cruises to Station ALOHA. THIS PAGE. Conductivity-Temperature-Depth (CTD) rosette sampler equipped with 24 sampling bottles and additional sensors for oxygen, chlorophyll *a*, and nitrate. NEXT PAGE, FROM TOP TO BOTTOM. Free-drifting sediment traps, recovery of bottom moored instrumentation, recovery of spar buoy, recovery of in situ incubation experiment, deployment of bottom moored McLane sediment trap. *Photographs by Paul Lethaby*

INTRODUCTION

Since its creation within UNESCO a half-century ago, the Intergovernmental Oceanographic Commission (IOC) has been at the vanguard of ocean observation, serving to promote international cooperation, coordinate ocean research, and facilitate capacity development. Beginning with the International Indian Ocean Expedition in the early 1960s, and through meaningful partnerships with the Scientific Committee of Ocean Research (SCOR), the International Geosphere-Biosphere Program (IGBP), the Partnership for Observation of the Global Ocean (POGO), and related organizations, IOC has provided invaluable leadership needed to help justify and promote large-scale ocean observation programs. A recent international meeting, co-sponsored by IOC, OceanObs'09: Ocean Information for Society – Sustaining the Benefits, Realizing the Potentials, was held in Venice, Italy, in September 2009. The conference was attended by more than 600 participants from 36 nations to present and discuss ongoing and planned global ocean observation activities. These field efforts represented a diverse spectrum of time-series programs, including the use of satellite remote sensing, moored buoys, autonomous gliders, repeat hydrographic surveys, volunteer ships of opportunity, profiling floats, cabled seafloor observatories, and ship-supported time-series programs, to name a few examples. Each observation program is designed to address a specific set of scientific goals, and each has its own set of challenges to sustain and optimize data return. This article focuses on ecosystem-based, time-series programs that presently rely on ships to make observations, collect samples, and conduct experiments. These ecosystem investigations are an important subset of the much larger portfolio of research-based, ocean time-series programs that derive, in large part, from sustained IOC leadership (Valdés et al., 2010).

THE ARROW OF TIME

The accretion and subduction of oceanic plates, the rise and fall of sea level, the evolution and extinction of species, El Niño-La Niña climate oscillations, the vernal blooming of phytoplankton, and diel vertical migrations of meso-zooplankton all share the common element of time, albeit on very different scales. Time is so fundamental to our understanding of Earth system processes that we sometimes take this important variable for granted, or worse, ignore it, in the development of conceptual models of how ocean habitats are structured and how they function. One undeniable fact of oceanic ecosystems is that they are complex, time variable, nonsteady state, nonlinear features, and need to be studied as such. However, chronic undersampling is a fact of life in oceanography (Platt et al., 1989) and still constrains the interpretation of available field data. Indeed, there are many examples in the scientific literature where interpretations from short-term ecological studies are at odds with similar data sets collected over much longer time scales (Strayer et al., 1986). It is difficult to observe slow or abrupt environmental changes directly, much less to understand the fundamental cause-and-effect relationships of these changes. As data accumulate in a long-term ecological study, new phenomena become apparent and new understanding is achieved.

Much of the temporal change that has occurred in oceanic ecosystems over the 4.5-billion-year history of Earth can be characterized as directional change—for example, the formation of the ocean basins, the transition from a reducing to an oxidizing environment, and the rise of multicellular life. Superimposed on these long-term changes are higher-frequency variations, including epochs, regime shifts, cycles, stochastic habitat variability, and, in recent times, human-induced climate change.

David M. Karl *(dkarl@hawaii.edu) is Professor, Department of Oceanography, University of Hawaii, Honolulu, HI, USA.*

1

Lesson 1: Site selection, sampling design, and frequency, as well as spatial scale of observations (single station vs. survey grid) are all relevant criteria in planning and implementing an oceanic ecosystem time-series program. Although it is impossible to know for sure whether a preselected site is representative of the larger region of interest, it is prudent to use any and all environmental data available at the time, as well as judgment concerning program logistics and costs. Although it is possible to relocate a time-series station that has later been shown to be inappropriately sited, it does mean that the initial time series will end and a new one will begin.

Based on results from the few long-term ecosystem studies that do exist, there is ample evidence that the ocean varies on a number of time scales, including multidecadal cycles as well as secular change. Long-term records are required to sort out the various signals from the noise (Overland et al., 2006) and the relevant time scales of interest will vary depending upon the process under investigation. For example, habitat and ecosystem variability on time scales ranging from decades to millennia, or longer, can be obtained from natural archives, including deep-sea sediments, ice cores, and molecular biomarkers such as genes and genomes, to name a few resources. Instrument records of habitat variability are also invaluable for developing a comprehensive understanding, but cover a much shorter time period, at most a few centuries but more commonly years to a few decades.

In addition to temporal change, ecologists and oceanographers also need to measure and understand the spatial structure of the habitat and its inhabitants (Swanson and Sparks, 1990). Contemporary spatial variability is probably more easily documented, studied, and understood than temporal variability. Indeed, the differences are akin to viewing a snapshot versus a full-length motion picture. However, spatial and temporal variability are inextricably coupled (Stommel, 1963; Figure 1), even though often viewed as independent characteristics. The relevant scales for understanding ecosystem processes range from meters to hundreds of kilometers in space, and from hours to centuries in time. Ocean surveys provide comprehensive, nearly synoptic maps of the distributions of properties and organisms, but are unable to reveal temporal changes unless they are repeated time and again. On the other hand, observations made at geostationary ocean stations can resolve temporal variability over local scales, but cannot easily be extrapolated to regional or biome scales. Recently, it has been reported that the global extent of low-productivity oceanic regions is expanding (Polovina et al., 2008), so spatial scaling of marine ecosystems may also have a key temporal component. The design of the time-series program including both spatial coverage and

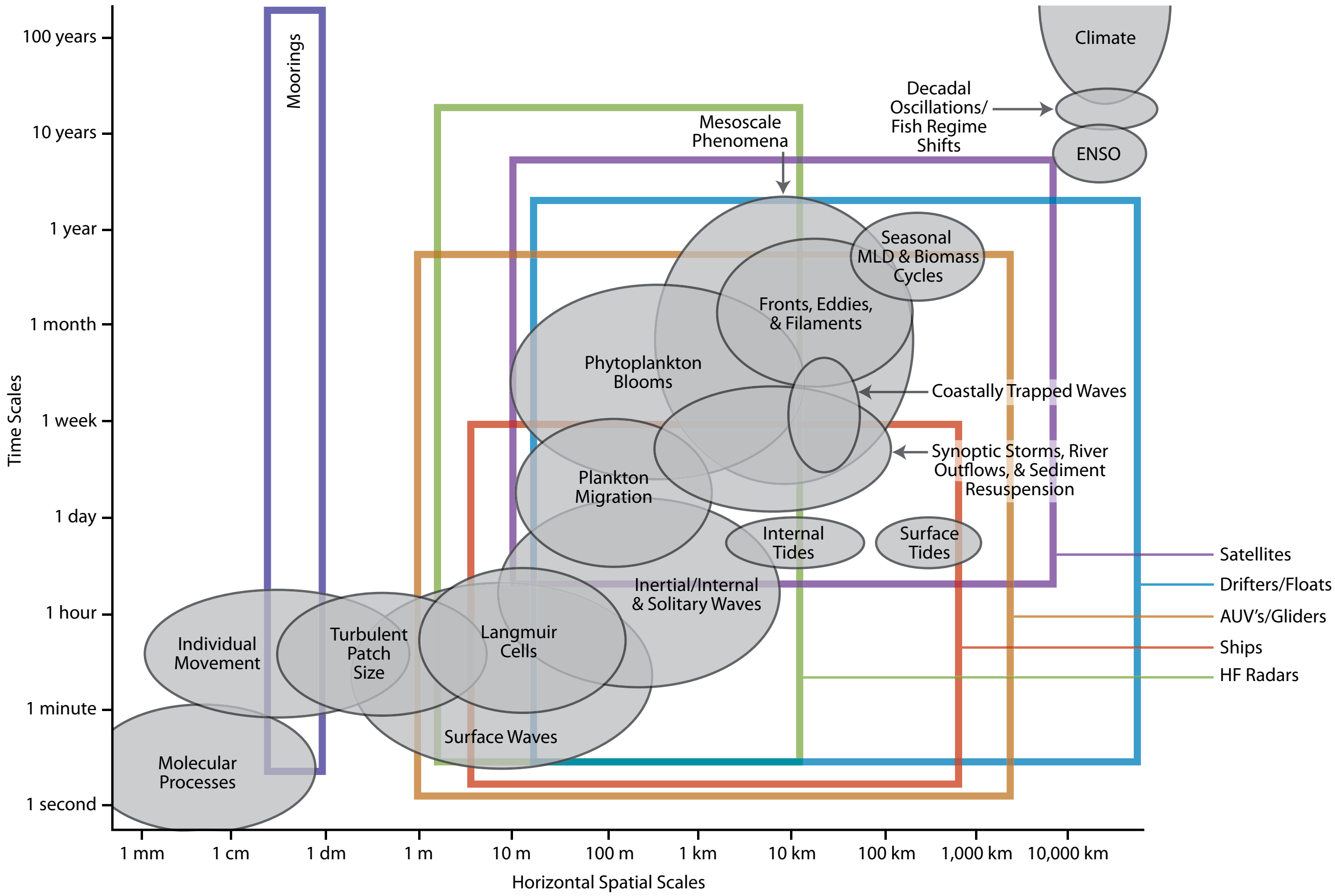

Figure 1. Schematic representation of the relevant temporal and spatial scales for key physical and ecological processes in the sea. The arrows and shaded regions define the approximate boundaries of at-sea time-series observations using current technologies. *Courtesy of Tommy Dickey, University of California, Santa Barbara*

sampling frequency will ultimately define, and sometimes restrict, the scope of the particular ecosystem study.

A BRIEF HISTORY OF OCEAN TIME-SERIES PROGRAMS: WEATHER AND FISH

Time-series measurement programs are a tradition in oceanography, even if we do not always recognize them as such. Scientific interest in ocean time-series observations had at least two independent origins, both rooted in government and societal needs: (1) weather prediction for safe and efficient transoceanic aviation, and (2) commercial fisheries assessment and management.

According to an authoritative account by Robertson Dinsmore, a network of ocean weather ships was established in the North Atlantic Ocean to aid transoceanic aviation and defense activities during World War II. The International Ocean Weather Ship surveillance program soon expanded to the North Pacific Ocean; at its peak, there were 22 Atlantic and 24 Pacific stations. Following the war, 13 permanent ocean weather stations were established by the United Nations Civil Aviation Organization (Dinsmore, 1996). Typically, the ships made frequent reports (many times per day) on surface meteorology, balloon-derived data to 15,000-m elevations, and collected oceanographic data (mostly temperature and salinity). Although many ships were retired as weather satellites and ocean buoys were brought on line to accomplish similar tasks, several of the ocean stations continued to collect important time-series data and, over time, changed their missions from support of aviation to support of oceanography, including both climate and ecosystem research. For example, Ocean Weather Ship Mike (M) in the Norwegian Sea (66°N, 2°E) was strategically positioned for climate studies due to its proximity to the site of bottom water formation and its role in sustaining global thermohaline circulation (Østerhus et al., 2009). Initially, only temperature and salinity data were collected, but later dissolved oxygen, nutrients, and chlorophyll *a* (chl *a*) concentrations were added as core parameters. In 1974, the World Meteorological Organization (WMO) took responsibility for the science mission, with leadership provided by scientists from the Norwegian Meteorological Institute and the Geophysical Institute in Bergen, Norway. Incredibly and regrettably, after more than 60 years of continuous service and immeasurable value to the ocean science community, funding to operate Ocean Weather Ship M was withdrawn at the end of 2009. A new ocean research organization, EuroSITES, has recently taken on the responsibility of sustaining Station M as part of the European Ocean Observatory Network. Plans are underway to design, test, and eventually deploy a subsurface mooring (http://www.eurosites.info/stationm), but this will only be a partial replacement for the manned, long time-series program at Station M, which has now been relegated to history.

The initiation of any long-term, time-series program should be undertaken with a commitment of support for the "long term," and perhaps indefinitely. However, most twentieth-century time-series programs have already been terminated; few survived more than a few decades (Duarte et al., 1992). There may be adequate justification on a case-by-case basis, but in general there is no scientifically defensible reason to terminate any functioning program because the main value of an oceanic ecosystem time-series program is the longevity of the data sets.

Another Ocean Weather Ship program that has left an enduring legacy is Station Peter ("P," later dubbed "PAPA") in the North Pacific Ocean (50°N, 145°W; 4220 m). Station P measurements date back to 1949; systematic operations began in 1956. The hydrographic program at Station P was operated by the Canadian government and employed a variety of Navy and Coast Guard vessels until termination of operations in 1981. Fortunately, the science community continued to collect data at that site via several hypothesis-driven programs, most notably the Subarctic Pacific Ecosystem Research (SUPER) program (1984–1988) and the Canadian Joint Global Flux Study (JGOFS) program (1992–1997). Following the end of JGOFS, the Department of Fisheries and Oceans (DFO), Canada, continued to provide leadership and funding to sustain three to four cruises per annum along "Line P" (a transect of stations from the coast to the open sea) and at Station PAPA. This Line P/PAPA time-series program has attracted numerous international partners, and has grown into a rich multidisciplinary enterprise.

The second major root of oceanic ecosystem time-series programs was the need to understand and manage commercial fisheries. In the United States, Spencer F. Baird helped convince Congress to establish the US Commission of Fish and Fisheries in 1871. He was later appointed the inaugural Commissioner and established a laboratory in Woods Hole, MA. The 72-m, steel-built steamer, *Albatross*, became the first US government oceanographic research vessel. In 1903, the organization became part of the Department of Commerce, and after the National Oceanic and Atmospheric Administration (NOAA) was created in the early 1970s, it was renamed the National Marine Fisheries Service (NMFS). As part of the federal government, this organization conducts research on life histories, physiology, breeding, and ecology of many commercially important fish and shellfish, including stock assessments.

2

Lesson 2: Serious consideration must be given before a long-term measurement program is either initiated or terminated. A new time-series program requires both careful planning and an explicit commitment for long-term support. Termination of an ongoing effort is final because one can never resample the past to provide the "gap-filling" data sets even if the measurement program is later restarted. Ideally, time-series observatories should have multiple sponsors and patrons who are all interested in its data and committed to its continuity.

3

Lesson 3: Due to the existence of historical, long-term data and the independent collections of contemporary "background" hydrographical and biogeochemical data, there is a logical and meaningful attraction to these special time-series sites of scientific importance. In essence, if you build them, they will come, and PAPA is an excellent example.

The concept of the marine food chain—wherein small phytoplankton cells capture solar energy and use nutrients like phosphorus and nitrogen to build new biomass that is subsequently consumed in a stepwise series of transfers to larger and larger animals—was developed more than a century ago. Its origins can be traced to commercial fisheries, and their assessment and management. The population dynamics of most fish species vary considerably over both short (seasonally) and long time scales. Even in the absence of fishing pressure by humans, we now know that there have been natural population cycles that most likely track changes in climate. This research was, and still is, inextricably linked to time-series analyses of variations in ocean habitat, including climate changes, and to nutrient and phytoplankton dynamics. Interest in and time-series analysis of key commercial fisheries was not restricted to the United States; other federal research programs co-emerged in Canada, Russia, and Europe about this same time (see *The Russell Cycle: Western English Channel* section).

Several contemporary oceanic ecosystem time-series programs had their origins as commercial fishery investigations. The California Cooperative Oceanic Fisheries Investigation (CalCOFI) is an exemplar. CalCOFI was initiated in 1949 to investigate the collapse of the sardine fishery off California and Mexico. The initial scientific motivation was to study, understand, and ultimately predict the approximately 50- to 70-year cycle of appearance/disappearance of sardines (Chavez et al., 2003). A comprehensive oceanographic time series was established and managed by a consortium that included US federal and State of California agencies, as well as scientists from Scripps Institution of Oceanography.

Although the CalCOFI program is still in operation today, the frequency of the ship-based sampling and the geographic extent of the survey area have both changed over time. For example, from 1950–1960, monthly cruises were conducted over the study grid with few interruptions. But in 1961, the monthly sampling frequency was reduced to approximately quarterly. This design was maintained until 1968 when it was realized that this reduced frequency of sampling was insufficient for the intended scientific objectives. Because funding was limited, the program leadership decided, in 1969, to revert back to monthly cruises, but to sample only every third year (1969, 1972, 1975, 1978, 1981). Unfortunately, and tragically, this sampling design imposed serious limitation on data analysis and on the detection of climate-related impacts on ecosystem dynamics (Chelton et al., 1982). For example, the 1976–1977 phase shift in the Pacific Decadal Oscillation (PDO) and the major 1982–1983 El Niño event—both impacting ecosystem productivity and fisheries—were missed by the revised triennial sampling design. In 1984, the survey station grid was significantly reduced to include the California coastal region from San Francisco to San Diego out to approximately 124°W longitude (300–600 km offshore depending on latitude; http://www.calcofi.org) in order to accommodate a new quarterly cruise schedule.

In 2004, the CalCOFI program was greatly enhanced when scientists from Scripps Institution of Oceanography landed a major NSF grant to establish the California Current Ecosystem (CCE) as a new component of the US Long-Term Ecological Research (LTER) network of terrestrial and marine sites (Franklin et al., 1990). The new funding and prestige derived from membership in the LTER network would augment core CalCOFI measurements, promote new intellectual partnerships, and ultimately lead to an improved understanding of the complex linkages between marine ecosystem processes and climate variability.

4

Lesson 4: The CalCOFI program serves to illustrate that science objectives alone are not always sufficient to justify the logistics and expense of sustaining a long-term ocean time-series program. However, if the sampling design is altered to fit within shrinking budgets, it is imperative to protect the primary science mission.

LOOK-AND-SEE VS. SEE-AND-DO

Some have argued that time-series science is akin to routine monitoring (i.e., "look-and-see") and has no place in the portfolio of scholarly academic activities. Even the pioneering, and now invaluable, efforts of Charles D. Keeling's atmospheric CO_2 measurement program at the Mauna Loa Observatory, Hawaii, were criticized by the science funding agencies early on as routine monitoring that "strayed from basic science" (Keeling, 1998). I strongly disagree with this assessment; the legacy and scientific value of Keeling's time series and related programs has already been clearly demonstrated.

There is, however, a fundamental, but perhaps subtle, difference between monitoring and observing. Both imply serial measurement; however, the latter is designed—at least in science—to lead to hypothesis generation, prediction, and experimentation (i.e., "see-and-do"). Whereas both types of time-series programs capture environmental variability and change, only the latter has a required mission for new scientific understanding.

The use of time-series data to generate testable hypotheses demands that the measurement program be properly designed and that the observations are analytically consistent, accurate, and relevant. A hallmark of most oceanic ecosystem time-series programs is a rigorous hypothesis-testing component, either built in from the start or added later as the novel data sets are made available. In this way, time-series programs contribute greatly to the scientific method of creating new knowledge and lead to better understanding and prediction.

The unique value of a time-series observation program is the ability to detect change (stochastic disturbance, cyclic behavior, long-term trends) in one or more of the measured parameters. The main mission is then to interpret that change in the context of existing models of how we believe ocean ecosystems are structured and how they function (or to improve them), including model predictions of how ecosystems might change in the future. To succeed in this mission, the measured parameters must be carefully selected and well calibrated, using consistent methodology and instrumentation. Those individuals who are committed to time-series observations are constantly challenged with external criticisms regarding the sometimes limited scope of core measurements, the reluctance of the lead investigators to change sampling or measurement protocols in spite of new advances in technology, and an intellectual struggle between a desire to chart the course of oceanic variability and an equally strong desire to understand the underlying cause of the observed temporal change.

The struggle between observation and understanding has recently been highlighted with the marine genomics revolution (DeLong and Karl, 2005), which has led to a re-evaluation of some of the most basic principles of ecology and evolution. Because this new information is rapidly changing the way we view the most fundamental processes of solar energy capture and dissipation, the probable impacts of climate-induced changes to the oceanic carbon cycle, and the very nature of life in the sea, it is leading to paradigm shifts in marine ecology and biogeochemistry such that existing ocean observation programs may not be well positioned to observe these novel and arguably important properties. In many ways, the microbial genomics revolution is one of the most exciting aspects of contemporary oceanography—but, at the same time, the worst nightmare for ocean time-series managers and those who use these key data sets for global ocean modeling and prediction (see *Role of Oceanic Ecosystem Modeling* section).

5

Lesson 5: There is an enormous need for standard reference materials (SRM) that can be used for analytical comparability among otherwise independent time-series measurement programs. The advent of reference materials for dissolved inorganic (Dickson et al., 2003) and organic (Hansell, 2005) carbon has already had a major influence on oceanic ecosystem time-series research.

OCEANIC ECOSYSTEM TIME-SERIES PROGRAMS: TWO CASE STUDIES

To gain a better understanding of the intellectual motivation behind the establishment of ocean observation programs with an emphasis on biogeochemistry and ecology, I present two case studies: (1) Western English Channel (1923–present), and (2) North Pacific Subtropical Gyre (1968–present). Each of these long-term ecosystem observation programs had a modest beginning, but each has evolved into a comprehensive, multidisciplinary, hypothesis-driven program that was justified on the successes and relevance of the initial efforts.

The Russell Cycle: Western English Channel

Sir Frederick Russell, the discoverer of the so-called "Russell Cycle," was already a well-established fisheries oceanographer when he joined the Marine Biological Laboratory at Plymouth, UK, in 1924; he would later go on to serve as the Director of the Laboratory for two decades (1945–1965), and in 1965 he was knighted for his career scientific contributions. The Russell Cycle describes a set of interrelated physical, chemical, and biological features that led to a significant and fairly rapid change in both the species and abundance of fish stocks off Plymouth during the 1930s. The declining trend reversed between 1966 and 1972, and the entire ecosystem structure and its function reverted back to the state that had been observed in the late 1920s. These fundamental ecosystem changes were linked to variations in climate, specifically a general warming of the Northern Hemisphere (post-1930) followed by a period of general cooling (post-1966). Without a comprehensive time-series measurement program in place during this time, it is doubtful whether this relationship would have been discovered.

The Marine Biological Laboratory at Plymouth, UK, opened in 1888, the same year that the Marine Biological Laboratory at Woods Hole was founded in the United States. Both facilities provided new opportunities for shore- and sea-based marine research, including time-series research. One of the primary missions of the Plymouth laboratory was to develop a comprehensive understanding of life in the sea, including, but not limited to, commercial fisheries (Allen and Harvey, 1928). In 1894, E.J. Allen was appointed the director of the laboratory, and shortly thereafter—in 1896—an 18.5-m vessel was purchased and outfitted to support local fieldwork (Southward and Roberts, 1987). In addition to his leadership of the laboratory, Allen also conducted research on marine phytoplankton. Among other achievements, Allen and his colleagues were able to establish laboratory cultures of selected phytoplankton that provided an opportunity to study their growth requirements, growth rates, and related functions.

The merger of laboratory research on algal growth and fieldwork in the English Channel off Plymouth can be traced to the pioneering measurements of dissolved phosphorus by D.J. Matthews. His improved method for the measurement of low concentrations of dissolved inorganic phosphorus (DIP) in seawater used a pre-concentration step that involved co-precipitation with iron hydroxide (Matthews, 1916, 1917), a predecessor of the modern "MAGIC" method (Karl and Tien, 1992) that was introduced to oceanography 75 years later.

6

Lesson 6: It is important to periodically review overall progress toward the stated goals, to reassess the design of the field sampling program in light of new knowledge, and to disseminate comprehensive, integrated interpretations to the scientific community for their evaluation and comment. Time-series programs should themselves be subject to change, whenever it is necessary to do so.

In a series of publications on "phosphates in water at Knap Buoy, Plymouth Sound," Matthews presented the first ever ocean time series of plant nutrients, showing a large, nearly tenfold seasonal variation with relatively high DIP concentrations (reported as 0.05–0.06 mg P_2O_5 per liter, which equates to 0.70–0.85 µmol P L^{-1}) in winter and relatively low DIP concentrations (reported as 0.005–0.006 mg P_2O_5 per liter, which equates to 0.072–0.085 µmol P L^{-1}) in late spring. Following the late spring minimum, DIP remained low throughout the summer until concentrations increased again in late fall. In addition to these pioneering field measurements of DIP, Matthews (1916, 1917) also presented the first ever estimates of dissolved organic phosphorus (DOP) in seawater; the highest DOP concentrations were observed in summer when DIP was at a minimum. The initial location of his time series, just one-half mile outside the breakwater at Plymouth, was set by "Admiralty regulations" due to perceived and real dangers associated with the hostilities during World War I. This 16-month time series laid the foundation for subsequent post-war ecosystem research in the western English Channel by contemporaries and future scientists from the Plymouth laboratory, and elsewhere.

Following World War I, and with expansion of laboratory staff, the western English Channel ecosystem time-series program was resumed under the leadership of W.R.G. Atkins (appointed head of the Department of General Physiology), H.W. Harvey (who replaced Matthews as staff hydrographer), and F.S. Russell (specializing in zooplankton and fish), working in close collaboration with chemist L.H.H. Cooper and biologist M. Lebour. This team at Plymouth, led initially by Atkins, developed new analytical and experimental approaches to study many variables related to the fertility of the sea, including the lability of dissolved organic matter (Atkins, 1923), the importance of thermal stratification and mixing for phytoplankton growth (Atkins, 1924a,b), and the proton balance in relation to net photosynthesis (Atkins, 1922a,b). The research at Plymouth was built on the pioneering work of Victor Hansen and his team, especially Karl Brandt and Hans Lohmann, at Kiel who developed most of our modern concepts regarding plankton production in the sea (Mills, 1989). Coincident with the re-establishment of the time-series program, Atkins prepared a two-part synthesis of what was known at that time about the controls of phytoplankton growth in the sea, including both physical (Atkins, 1926a) and chemical (Atkins, 1926b) factors. This body of extant knowledge served as a blueprint to focus the new phase of time-series research in the western English Channel.

As they began this second phase of fieldwork, the team also established a survey line of stations from Plymouth to Ushant. These sites were periodically occupied, but eventually the team concentrated their sampling efforts at the International Council for the Exploration of the Sea (ICES) Hydrographic Station England number 1 (E1), located 22 nautical miles southwest of Plymouth at a water depth of 72 m (50°0.2'N and 4°22'W).

Station E1 soon became the proving ground for many new analytical techniques, and once confidence was established, these parameters were added to the list of core measurements to track seasonal and interannual ecosystem variability. A series of very influential papers appeared during the period 1925–1935, including a confirmation of the seasonal variation in DIP that had been observed previously by Matthews (Atkins, 1926c, 1930; Figure 2), the first ever time series of nitrate using a novel colorimetric method that had been perfected for seawater analysis (Harvey, 1926, 1928), observations on the penetration of sunlight into seawater using a new photoelectric instrument (Poole and Atkins, 1937), and use of a novel silk net sampler to concentrate and quantify the amount of phytoplankton in the water column (Harvey, 1934). These time-series data, combined with the routine measurements of water temperature and salinity, provided a foundation for understanding plankton production and its control. This new knowledge, now part of the enduring legacy of biological oceanography, was reported in an article by the same title, "Plankton Production and Its Control" (Harvey et al., 1935), and later in key review articles (Harvey, 1942, 1950) and in an influential monograph (Harvey, 1955). It is fun to imagine how thrilled this team of scientists must have been when they assembled the annual data sets from their recent field efforts and compared them to previous years. As is true for all time-series scientists, one is always torn between trying to interpret the data in hand and waiting "another year" for confirmation of a developing trend. One of the early papers from the time-series sampling at Station E1 entitled "Seasonal Variations in the Phosphate and Silicate Content of Sea-water in Relation to the Phytoplankton Crop. Part V. November 1927 to April 1929, Compared with Earlier Years from 1923" (Atkins, 1930)

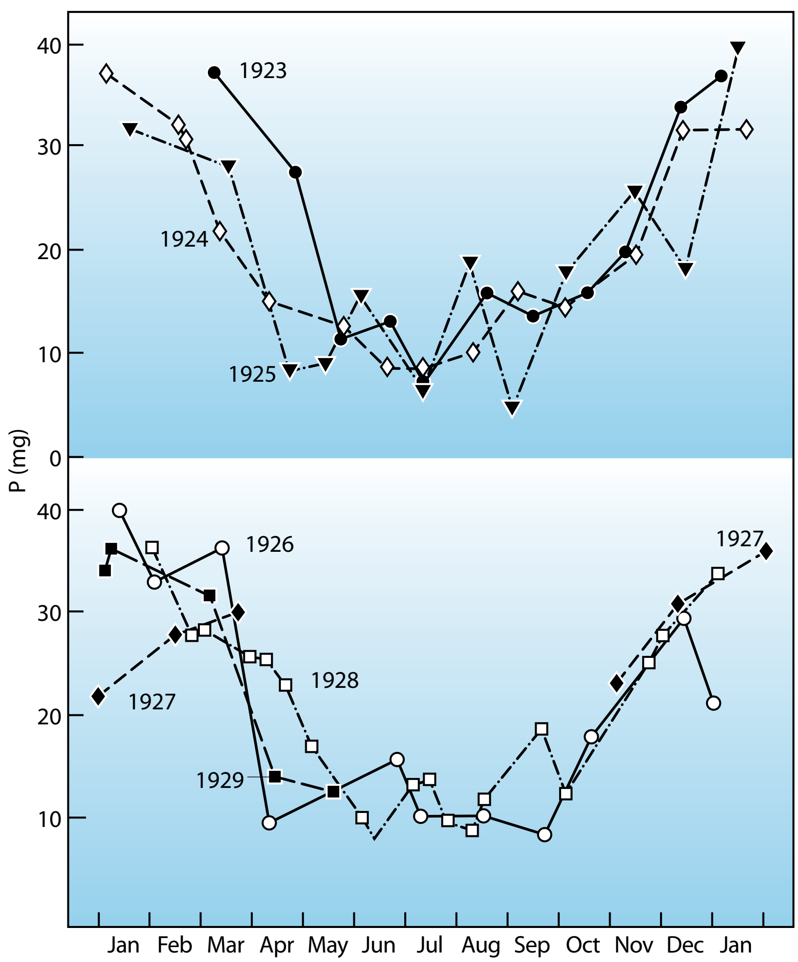

Figure 2. Seasonal and interannual variations in mean water column phosphate (expressed as mg P_2O_5 per m^3) at Station E1 in the western English Channel for the period 1923–1929. *From Atkins (1930) reproduced with permission from Cambridge University Press.*

pretty much sums it up.

Fieldwork at Station E1 continued to expand in scope until the start of World War II. By the mid 1930s, Russell, Cooper, and others had come to recognize an important connection between the numbers of young fish that spawned in summer and survived through early larval stages, and the winter maximum of DIP in the water column (Cooper, 1938; Harvey, 1942). This observation not only suggested a strong link between nutrient delivery—which was ultimately tied to ocean circulation—and organic matter production at higher trophic levels, but also revealed large year-to-year variations in ecosystem structure and function (Figure 3).

As the length of the record grew and new understanding was gained, the temporal variations in the structure and efficiency of the marine food web leading to fish were explicitly tied to climate change, specifically a general warming. Indeed, this warming trend had initially gone unnoticed in part due to methods used for data and trend analysis. Upon re-analysis, Southward (1960) discovered a significant warming in the period of 1930–1960, especially in near-surface waters.

However, the most fundamental knowledge of the relationships between climate and fish would not emerge until there was a reversal in the general warming trend that began in the 1930s and a reversion of the abundance and type of fish; this change began in the early 1960s (Figure 3). The identification and interpretation of the multidecadal cycle in ecosystem structure that emerged as a result of this important measurement program (Russell et al., 1971; Cushing and Dickson, 1976; Southward, 1974, 1980, 1995) would probably not have been possible without continuous and comprehensive ecosystem surveillance. The emerging data on climate and fish stocks also served as an incentive to look more closely at historical fisheries landing records. An elegant reconstruction of the past 400 years showed a strong coherence in the fluctuation of dominant fish species and temperature—herring during cooler periods and pilchards during warmer periods (Southward et al., 1988).

An independent, but complementary sampling program dubbed the Continuous Plankton Recorder (CPR) survey, initiated in the 1920s as the vision of Sir Alister Hardy, began to systematically collect samples in the western English Channel in the mid 1950s. Space limitation does not permit a detailed account of the importance and value of this most impressive effort; there is a majestic synthesis in Reid et al. (2003). Today, this long-term program, operated since 1990 by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS), has combined its efforts with the sampling at E1 to track coupled coastal and open-ocean ecosystem changes that are linked to climate change. One of the more provocative and potentially important results obtained to date is the suggestion that climate change in the North Sea may have led to a trophic mismatch

7 Lesson 7: The mathematical and statistical methods used for trend analysis need to be constantly reviewed and, if necessary, improved in order to provide the most meaningful and robust results. The training of time-series scientists should include exposure to modern methods in statistics, spectral analysis, cross-variance/correlation, and related topics.

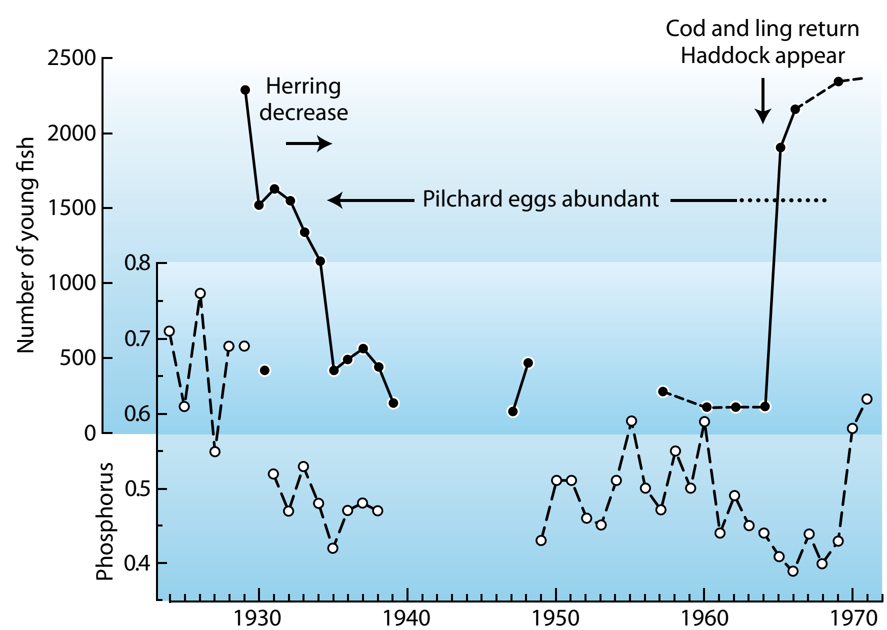

Figure 3. The first report (Russell, 1971) of what would later be dubbed "The Russell Cycle." This graph shows data on: (•) numbers of young fish, and (o) winter maxima in concentration of phosphate. *From Russell et al. (1971) reproduced with permission from Nature Publishing Group*

between phytoplankton and zooplankton in the pelagic ecosystem (Edwards and Richardson, 2004). Using data collected from the CPR survey, the authors hypothesized that climate warming has resulted in variable responses among different trophic levels, and ultimately to a decoupling in the seasonal synchrony of primary and secondary production.

Ecosystem science seeks understanding of the often complex relationships that exist in nature. Along the way, data are collected, hypotheses are generated, tested, refined, and tested again, as new knowledge is achieved. The discovery of the Russell Cycle (Cushing and Dickson, 1976) led to the generation and evaluation of numerous testable hypotheses (Southward, 1980; Southward et al., 1988), including the previously mentioned link between wintertime DIP concentrations and fish production. The connection between DIP and ecosystem function was first made by Russell using the time-series data collected at Station E1. The ecosystem processes that were impacted ranged from zooplankton community structure to fishery yields; this was an excellent example of what is now called "bottom-up" or resource control of community structure and function. Climate variations were shown to be responsible for interdecadal shifts in ecosystem dynamics ultimately as a result of changes in DIP (Russell et al., 1971).

Unfortunately, when the time-series program at E1 began, the method used for DIP analysis was less than optimal compared to contemporary methods of analysis. It took several decades, and several scientific careers, to devise, test, and confirm a more reliable method. The DIP data used by Russell et al. (1971) in their landmark *Nature* paper on climate, phosphate, and fisheries, were actually derived from several different methods. Following a careful re-examination of the DIP data set, including a critical analysis of the validity of a correction factor of 1.5 that had been applied, retroactively, to data collected prior to 1938, Joint et al. (1997) concluded that there was "sufficient uncertainty in the accuracy of the pre-1948 measurements of phosphate concentration to preclude their use in long time-series analysis." They ended their important paper by concluding that the "evidence is weak that variations in winter phosphate concentrations are the cause of the observed Russell Cycle hypothesis" (Joint et al., 1997).

As part of their analysis, Joint et al. (1997) also commented that the "official" Marine Biological Association archive of DIP data is not identical to the data set published previously in support of the Russell Cycle. Unfortunately, the data originators have all since passed on, and there are no water sample archives available for re-analysis. As a consequence, a large portion of the DIP data must be considered questionable despite pioneering analytical contributions of Matthews, Atkins, and Cooper, and the enormous time and effort they invested to obtain these field data. Several alternative hypotheses for the Russell Cycle have been formulated and tested (Southward et al., 1988); the search for a comprehensive understanding marches on.

Like most other oceanic ecosystem time-series programs that exist today, the western English Channel program has evolved and expanded its scope over the years. While many of the basic physical, chemical, and biological parameters remain as core measurements, other more specialized analyses, frequently tied to a single investigator, have been added or have come and gone. One of the more interesting ancillary data sets was the comprehensive analysis of inorganic and organic nutrients during a decade-long study (1969–1977) near Station E1 (Butler et al., 1979). Although earlier research at Knap Buoy by Matthews had already shown an accumulation of DOP in spring and summer as DIP was removed from the water column by phytoplankton, reliable methods for coupled dissolved organic nitrogen (DON) and DOP determinations were not available until the later 1960s (Armstrong and Tibbitts, 1968). The new field results revealed that both DON and DOP accumulate in the surface waters as nitrate and DIP are consumed (Figure 4). Consequently, the total dissolved N and P (TDN and TDP respectively), are much more constant than either the inorganic or organic subcomponents. This observation has significant implications for estimating potential fish production from DIP loss, as was done early in the time-series

8

Lesson 8: Even when a particular assumed cause-and-effect relationship is thought to be correct, it is important to also consider alternative viewpoints and explanations as the time-series data set is lengthened and knowledge of the phenomenon of interest is improved. It is difficult, and dangerous, to claim a comprehensive knowledge of the complex behavior that characterizes natural ecosystems.

study, or for predicting nutrient stress or limitation. It is assumed that DON and DOP are less available to the phytoplankton assemblages—otherwise they too would be consumed in summer when environmental conditions (sufficient light, warmer water temperature, less turbulent mixing) would be optimal for growth—but there are few direct observations on DON or DOP bioavailability. Throughout the year, for the entire decade of observation, the total N:total P ratio was approximately 20:1, suggesting a tightly coupled biochemical balance in this ecosystem (Butler et al., 1979).

In late 1987, the western English Channel time-series program was terminated due to changes in UK government funding priorities. This was a major loss for ocean science. Fortunately, several visionary individuals from Plymouth and elsewhere continued to collect a limited sample set and fought hard to re-establish the permanent time series. Eventually, they were able to mount a strong enough defense, and monthly sampling at E1 was started again in 2002. During the interim period (1988–2002) several key, short-term time-series studies were conducted. For example, in May 1997, the Plymouth Marine Bio-Optical Databuoy (PlyMBODy) was deployed in the western English Channel to serve as a local, vicarious validation of the NASA SeaWiFS ocean color satellite (Pinkerton et al., 2003). Data from this buoy provided an invaluable time-space assessment of phytoplankton dynamics that improved interpretations of data collected at Station E1. Another specialized study included a 15-month plankton time series (viruses to mesozooplankton) to provide data to inform conceptual trophodynamic models, including the microbial loop component (Rodriguez et al., 2000). Finally, a detailed study of the annual cycle (2001) of photosynthetic quantum efficiency and bio-optical characteristics of the western English Channel provided new insights into the process and controls of phytoplankton production (Aiken et al., 2004).

A long-lasting legacy of this, and all other, oceanic ecosystem time-series programs is the data and any sample archives that result from the intensive field efforts. If properly managed and maintained, they can be readily used by future investigators. An excellent example is the re-analysis of Station E1 nutrient data (Jordan and Joint, 1998). A summary of over 1000 paired nitrate (N) and phosphate (P) measurements for the period 1930–1987 documented seasonally variable N:P ratios with

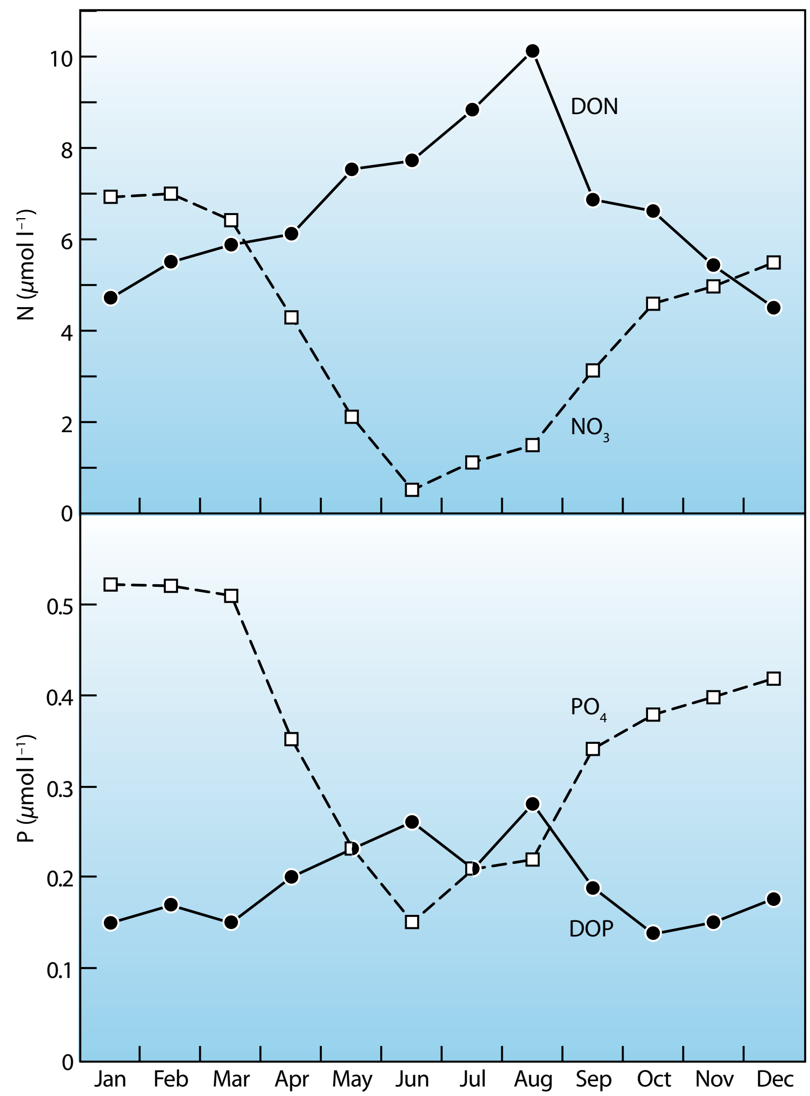

Figure 4. Relationships between dissolved inorganic and organic nutrients in the English Channel. The seasonal climatologies are based on observations made during an 11-year study period (1969–1977). *From Butler et al. (1979) reproduced with permission from Cambridge University Press*

lower values in summer (Figure 5); the overall mean molar N:P ratio was 11.6, lower than the predicted Cooper Ratio of 15:1 or the Redfield Ratio of 16:1 (Jordan and Joint, 1998). The authors also reported evidence for transient increases in P that did not show up as corresponding increases in N, as might be expected from deep-water intrusions or mixing. Similar near-surface enrichments have been reported for the North Pacific Ocean (Haury et al., 1994; Karl and Tien, 1997), but to date have not been explained. Consequently, these living data sets continue to fuel important and fundamental hypothesis-driven research nearly three-quarters of a century after they were first collected. Few science programs can legitimately make that claim.

CLIMAX, HOT, and C-MORE: The North Pacific Subtropical Gyre

The subtropical gyres of the world's ocean are extensive, coherent regions that occupy approximately 40% of Earth's surface. The North Pacific Subtropical Gyre (NPSG), delimited from approximately 15°N to 35°N longitude and 135°E to 135°W latitude, occupies nearly 2 x 10^7 km^2 and is the largest circulation feature on our planet (Sverdrup et al., 1946).

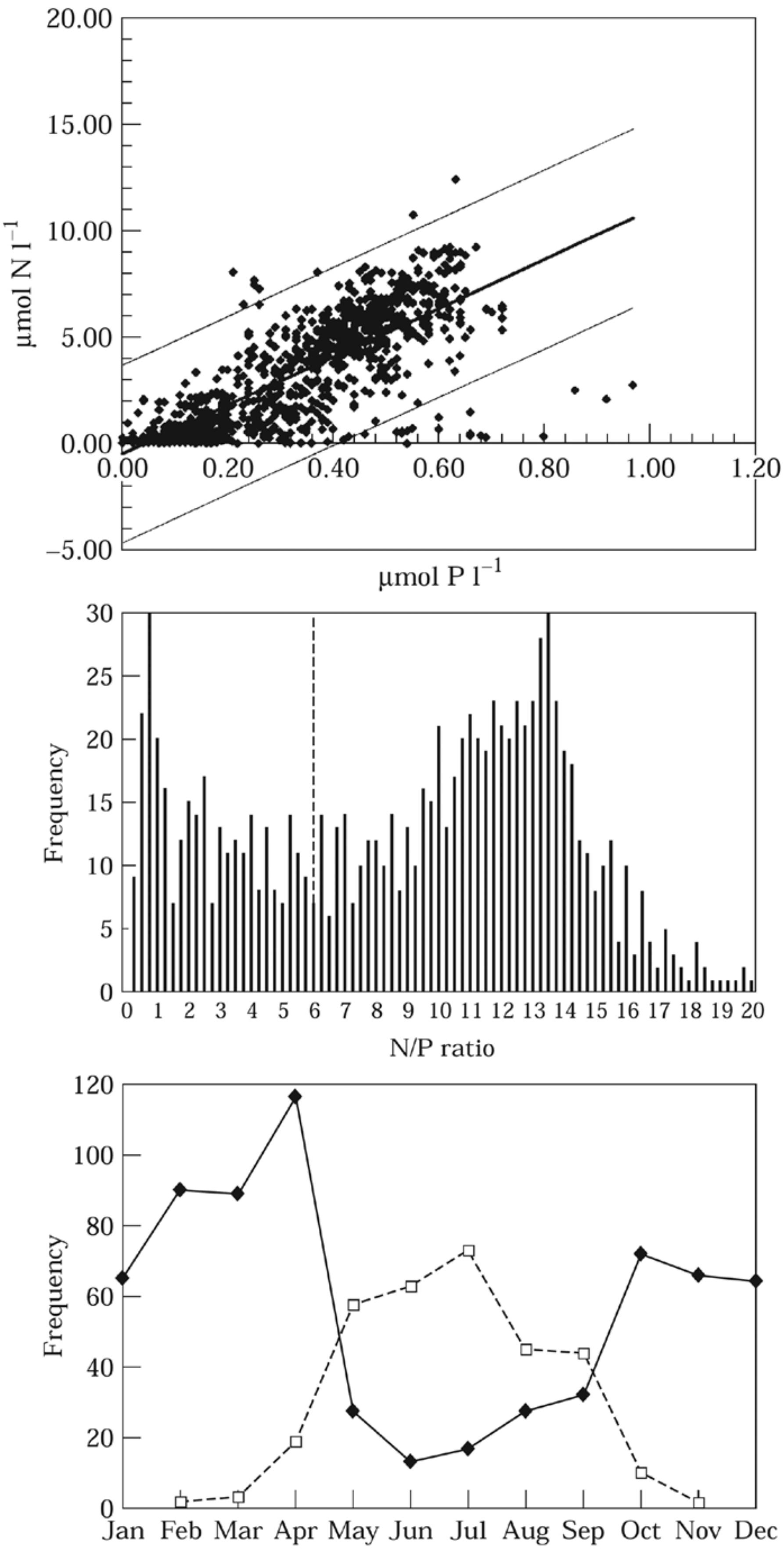

Figure 5. Nitrate-to-phosphate (N:P) ratios measured at Station E1 in the western English Channel during the period 1930–1987. (top) Nitrate vs. phosphate with best fit (NO_3 = 11.62 PO_4 − 0.52) and 99% confidence envelope. (middle) Frequency distribution of number of samples with same N:P ratio. The vertical dashed line is N:P = 6, a value that is at the trough in the bimodal distribution of N:P ratios in the data set. (bottom) Seasonal frequency distribution of all samples with N:P > 6 (solid symbols) and N:P < 6 (open symbols). The low N:P ratio waters are most common in summer. *From Jordan and Joint (1998) reproduced with permission from Elsevier*

The NPSG ecosystem is very old; present boundaries have persisted since the Pliocene (approximately 10^7 years before present), or earlier (McGowan and Walker, 1985). This great age and relative isolation were primary factors leading to the "climax community" hypothesis: an ecosystem in its final stages of succession is time and space invariable. A test of this general hypothesis was the primary motivation behind the establishment of a multiyear observational program centered near 28°N, 155°W in an area dubbed the "CLIMAX region" (Venrick, 1990). However, once thought to be a homogeneous and static habitat, there is now increasing evidence, based largely on high-frequency time-series observations, that the NPSG exhibits substantial physical, chemical, and biological variability on a variety of time scales, from months to decades.

The NPSG ecosystem is characterized by a relatively deep permanent pycnocline (and nutricline) and fairly shallow (≤ 100 m) mixed-layer depths throughout the year. Consequently, the mixed layer is chronically nutrient starved, and the near-zero nutrient concentration gradient routinely observed in the upper 100 m of the water column suggests that continuous vertical nutrient flux cannot be the primary source of dissolved inorganic nutrients (e.g., nitrate and phosphate) to the upper euphotic zone (Hayward, 1991). The observed separation of light in the surface waters from inorganic nutrients beneath the euphotic zone predicts environmental conditions of extreme oligotrophy (low standing stocks of nutrients and biomass), low rates of primary production of organic matter, and low rates of carbon export to the deep sea. Because subtropical ocean gyres are dominant habitats of the world's ocean, accurate estimation of global ocean production and export will require reliable estimation of NPSG ecosystem processes.

Although the NPSG was sampled during the *Challenger* Expedition (1872–1876), and several later "voyages of discovery" (e.g., *Albatross* in 1903, *Carnegie* in 1928), it was not until after World War II that extensive and systematic ship-based observations were initiated. These projects included the NORPAC expedition, which deployed 19 ships from Canada, Japan, and the United States to survey the entire Pacific Ocean north of 20°N during summer 1955, and Weather Ship Station November (30°N, 140°W), which was occupied during 121 cruises between July 1966 and May 1974. In 1968, the CLIMAX I expedition from Scripps Institution of Oceanography occupied a series of stations near 28°N, 155°W during August and September; CLIMAX II reoccupied the site during September the following year. Thus began an important oceanic ecosystem time-series study in the NPSG; an additional 18 major cruises would be conducted between 1971 and 1985 (Hayward, 1987). Despite the fact that this extensive time series was biased with respect to season (70% of the cruises were in summer, June–September, and 35% in August alone) and was discontinuous over the 17-year period of observation (there were no cruises in 1970, 1975, 1978-79, 1981, or 1984), the CLIMAX program observations provided an unprecedented view of ecosystem structure and function.

From January 1969 to June 1970, a deep ocean hydrostation (Gollum) was established by scientists at the University of Hawaii at a location 47 km north of Oahu (22°10'N, 158°00'W; Gordon, 1970). At approximately monthly intervals, 13 research cruises were conducted to observe and interpret variations in particulate organic matter distributions in the water column in addition to other chemical and physical parameters (Gordon, 1970). Unfortunately, this pioneering NPSG time series was terminated due to lack of funding and interest to sustain the intensive field effort.

With the abandonment of the central North Pacific Ocean Weather Ship and time-series programs such as Gollum, there was no location where comprehensive, seasonally resolved measurements of the ecosystem variability of the NPSG were available. IOC and the World Climate Research Programme (WCRP) Committee on Climate Change in the Ocean (CCCO) recognized this deficiency and, in 1981, endorsed the initiation of new ocean observation programs. Reactivation of Gollum was an explicit Committee recommendation.

In response to the growing awareness of the ocean's role in climate and global environmental change, and the need for additional and more comprehensive oceanic time-series measurements, the Board on Ocean Science and Policy of the National Research Council (NRC) sponsored a workshop on "Global Observations and Understanding of the General Circulation of the Oceans" in August 1983. The proceedings of this workshop served as a prospectus for the development of the US component of the World Ocean Circulation Experiment (US-WOCE). Shortly thereafter, in September 1984, NRC's Board on Ocean Science and Policy sponsored a second workshop on "Global Ocean Flux Study," which served as an eventual blueprint for the JGOFS program. In 1986, the International Council of Scientific Unions (ICSU) established IGBP: A Study of Global Change, and the following year, JGOFS was designated as a core project of IGBP. US-JGOFS research efforts centered on the oceanic carbon cycle, its sensitivity to change, and the regulation of the atmosphere-ocean CO_2 balance (Brewer et al., 1986; Sabine et al., 2010).

In 1988, two open-ocean time-series programs were established—one in the North Atlantic near Bermuda and the other in the North Pacific near Hawaii (Karl and Michaels, 1996). The Bermuda Atlantic Time-series Study (BATS) was an extension of the Hydrostation S program started by Henry Stommel and co-workers in 1954 (dubbed Panularis Station after the beloved 19-m research vessel that was initially used to support the approximately biweekly occupations; Michaels and Knap, 1996). During the more than half-century of ocean time-series sampling at Bermuda, pioneering research on several important physical, chemical, and biological processes has been supported mostly through logistical and intellectual support of scientists and staff of the Bermuda Biological Station for Research (now Bermuda Institute of Ocean Sciences). Additional JGOFS-sponsored, IOC-inspired biogeochemical time-series programs were eventually established at key locations in the Ligurian Sea (DYFAMED), near Gran Canaria (ESTOC), southwest of Kerguelen Island (KERFIX), northwest of Hokkaido Island (KNOT), and southwest of Taiwan (SEATS) as part of a coordinated international effort (Karl et al., 2003).

The Hawaii Ocean Time-series (HOT) program's deep ocean station was established in 1988 to address WOCE and JGOFS scientific goals (Karl and Winn, 1991; Karl and Lukas, 1996). The NPSG benchmark location, dubbed Station ALOHA (A Long-term Oligotrophic Habitat Assessment), is located at 22°45'N, 158°W, approximately 100 km north of Oahu, Hawaii, in deep water (4800 m), outside any biogeochemical influence of the Hawaiian Ridge, yet still close enough to facilitate approximately monthly sampling from shore-based facilities (Karl and Lukas, 1996). Now, after 20 years of intensive sampling, the NPSG has become one of the most well-studied open-ocean ecosystems, providing a global reference point for tracking the health of the ocean, including the rate of CO_2 sequestration and ocean acidification (Dore et al., 2009), and an experimental framework for studying seasonal and interannual ecosystem dynamics.

One of the major goals of the NPSG time series (1968–present) is to link oceanic ecosystem changes to climate variability. Just as the CLIMAX study was winding down, and prior to the start of HOT, a significant paper was published that reported a major change in the plankton community—and the presumed productivity—in the NPSG. Venrick et al. (1987) reported that the average euphotic zone (0–200 m) chl *a* concentration in the oligotrophic North Pacific Ocean during summer (May–October) had nearly doubled from 1968 to 1985. The sampling frequency was insufficient to determine whether the chl *a* increase had been continuous over time or whether there had been a "step-function" increase between 1973 and 1980 (Venrick et al., 1987; Figure 6). An abrupt shift in climate, beginning in the mid 1970s, appears to be one example of a recurring pattern of interdecadal climate variability referred to as the PDO (Mantua et al., 1997). Venrick et al. (1987) attributed their field observations to the North Pacific regime shift that caused an enhanced nutrient flux, and resulted in a significant long-term change in the carrying capacity of the NPSG ecosystem. However, no direct measurements of nutrient loading were presented.

A subsequent study, which also included a decade of HOT observations, confirmed the high chl *a* concentrations and provided evidence for decreases in silicate and phosphate; primary production was also much higher than in the period prior to approximately 1980 (Karl et al., 2001). This observation period coincided with improvements in the measurement of in situ primary production, especially the use of trace-metal-free incubation techniques, so it is difficult to separate methodological changes from habitat differences. However, the observed increases in chl *a* are independent of the primary

9

Lesson 9: Time-series measurement programs should use consistent methods for sample analysis until it can be shown that any "new and improved" methodology provides similar, if not identical, results. Any deviations in protocol, instrumentation, standardization, or data analysis need to be carefully documented and made available to data users. If possible or practical, a sample archive should be established.

production measurements, so at the very least one can conclude that there have been changes in phytoplankton biomass, efficiency of photosynthesis, or both. Karl et al. (2001) hypothesized that there had been a "domain shift" in the photoautotrophic communities from a eukaryote-dominated ecosystem to one dominated by *Prochlorococcus*. This fundamental change would have significant ecological implications, including altered food web structure and changes in new, export, and fish production (Karl, 1999; Karl et al., 2001).

Both Venrick et al. (1987) and, later, Polovina et al. (1994) suggested that ecosystem changes in the subtropical North Pacific following the 1976 climate step were a result of increased mixed-layer depths and a higher frequency of deep mixing events due especially to an intensification of the Aleutian low-pressure system in late winter. This vigorous mixing might be expected to enhance nutrient input to the euphotic zone and stimulate ecosystem productivity. However, it is important to emphasize that the Aleutian low-pressure system returned to its normal, pre-1976, condition in 1988 just at the start of the HOT program. The concentrations of chl *a* and primary production, on the other hand, have remained at the elevated "regime-shift" values (Figure 6). Given the rapid doubling times of microorganisms in the NPSG (one to a few days) and the relatively rapid turnover of particulate organic matter pools (10–20 days), it is unlikely that the oceanic biogeochemical response to climate forcing or relaxation would have a two-decade-long time lag. It is conceivable, even possible, that the NPSG has alternative or multiple stable states and once a new state is established it is resilient to change until some new environmental threshold is achieved (Ives and Carpenter, 2007).

Like all other complex processes in nature, a single climate indicator such as PDO, or any other one, may not be adequate to characterize climate variability (Bond et al., 2003). Corno et al. (2007) and Saba et al. (2010) reported significant two-decade-long changes in NPSG ecosystem processes, including an approximately 30–50% increase in primary production, and variations in mixed-layer depth, nutrient fluxes, microbial abundances, and pigment inventories. These variations were attributed to the magnitude, duration, and synchrony of the El Niño/Southern Oscillation (ENSO) and PDO (Corno et al., 2007). Because these two climate variables are independent and have different frequencies, phase shifts or temporal alignment can lead to fundamentally different ecological and biogeochemical consequences. More recently, Bidigare et al. (2009) used both HOT observations and model simulations to reveal a cascade of interacting physical, chemical, and biological shifts that might result from rapid climate changes.

One of the unexpected and potentially significant ecological trends observed at Station ALOHA is the long-term "disappearance" of DIP and particulate

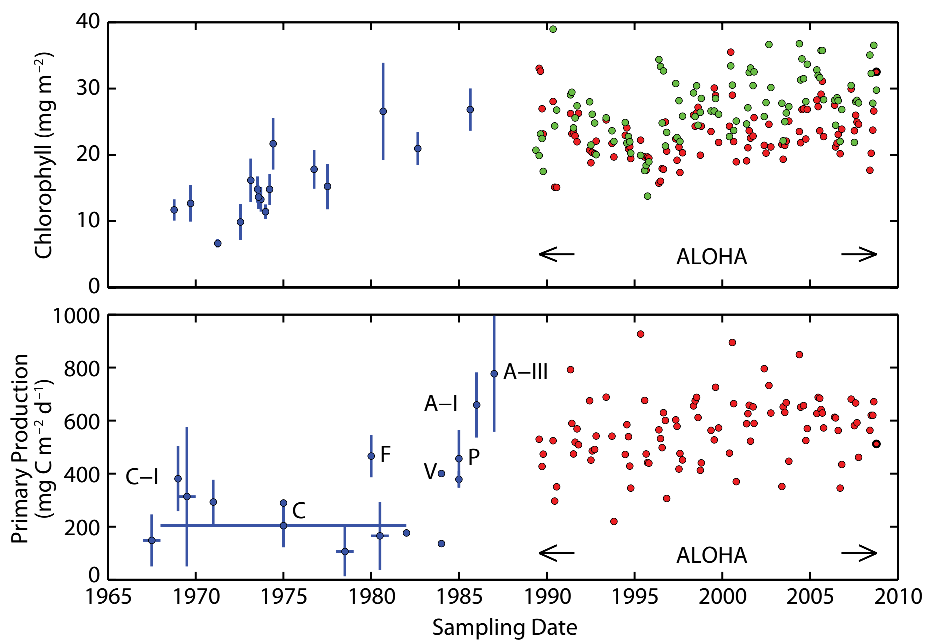

Figure 6. Composite time-series analysis of phytoplankton community abundance, measured as total euphotic zone integrated chlorophyll *a* (chl) concentration (mg m^{-2}), and productivity, measured using the ^{14}C-radiotracer technique. The green symbols in the upper plot are chl *a* derived from HPLC analyses and the red symbols are based on fluorometric analyses. The letters in the lower panel represent individual research expeditions or programs: C-I = Climax I, G = Gollum, C = Climax time-series, F = Fiona, V = VERTEX, P = PRPOOS, A-I = ADIOS I, A-III = ADIOS III, ALOHA–Hawaii Ocean Time-series. The data-relevant metadata and data source credits are available from the author. The pre-1988 data were collected in the CLIMAX region (see text) and the post-1988 data were collected at Station ALOHA. *Redrawn and updated from Karl et al. (2001)*

phosphorus, and its relationship to the coupled cycles of carbon, nitrogen, and, possibly, iron (Karl et al., 2001, 2003; Karl, 2002, 2007b). At the start of the HOT program (October 1988), the near-surface (0–60 m) inventory of DIP was approximately 6–7 mmol P m^{-2}, which was considered, at that time, to be a very low concentration. Twenty years later, the 0–60 m DIP inventory has decreased by 80% to approximately 1–2 mmol P m^{-2}. Clearly, the balance over years to decades between P delivery and P export that maintains many marine ecosystems in a long-term steady state has been perturbed at Station ALOHA. It has been hypothesized that the two-decade-long drawdown of DIP at Station ALOHA is a manifestation of enhanced N_2 fixation (Karl, 1999, 2002). If true, this situation could eventually lead to a 20- to 30-year cycle of N vs. P limitation of productivity (Karl, 2002), and a shift in microbial community structure and ecosystem services.

Stochastic events of major ecological significance may be short lived and are undoubtedly undersampled by present ship-based observation programs. Despite chronic nutrient limitation, oceanic subtropical gyres can support blooms of phytoplankton generally during summer months when the water column is well stratified and most depleted of essential inorganic nutrients like nitrate and phosphate (Dore et al., 2008). These aperiodic and enigmatic phytoplankton blooms consume CO_2 and recharge the upper water column with dissolved organic matter and oxygen that support post-bloom heterotrophic metabolism. More importantly, blooms contribute to the seascape mosaic that is essential for maintaining genetic diversity in these expansive habitats. Specifically, mesoscale physical forcing may be an important control on the abundance, diversity, and activity of N_2-fixing microorganisms and, hence, on the nutrification of the gyre (Church et al., 2009). Even the approximately monthly sampling schedule adopted in the HOT program may be too infrequent to resolve these and related, intermittent physical processes that may impact nutrient budgets in the NPSG (Johnson et al., 2010).

In the past few years, the scale and scope of ocean observation at Station ALOHA has been enhanced by several new programs, including: (1) an ocean mooring for meteorological and physical oceanographic observations (WHOTS), (2) deployment of a fleet of APEX profiling floats equipped with sensors to measure oxygen and nitrate concentrations (Riser and Johnson, 2008; Johnson et al., 2010), (3) deployment of a fleet of Seagliders equipped with sensors to detect a variety of environmental variables, including chl, colored dissolved organic matter, and particle scattering, and (4) placement of a commercial fiber-optic telecommunications cable at Station ALOHA. The latter project, dubbed the ALOHA Cabled Observatory (ACO), provides an "extension cord" from shore into the deep sea for interactive instrumentation, delivery of power, and high-speed/optical transmission of data, video, and related information. The ongoing 22-year-long HOT study is changing the way we view the NPSG. Numerous unexpected discoveries, some serendipitous, have already been made including new microbes, new metabolic processes, and new paradigms, and several emerging climate-ecosystem connections have been revealed (Karl, 2007a).

Science is a world of ideas, and progress in science is limited ultimately by the emergence of new hypotheses and by the ability to test them (Pomeroy, 1981). In a thoughtful review entitled "The Inadequacy of Experiments in Marine Biology," Redfield (1958) concluded that ecosystem manipulation/perturbation experiments are essential if we ever hope to achieve the complete understanding of natural processes that is necessary for predicting the response to future climate change. However, he warned that complex marine systems needed to be thoroughly described and well understood before relevant experiments could be conducted. The recent establishment of the Center for Microbial Oceanography: Research and Education (C-MORE) as a hypothesis-testing complement to the HOT program has provided the incentive, and funding, to conduct field experiments and to initiate a genomics-based time-series measurement program that is now beginning its fifth year. The field experiments to date have focused on open-ocean phytoplankton blooms, the characterization and degradation of dissolved organic

10

Lesson 10: It is crucial to link hypothesis-testing field experimentation to existing time-series observation programs as a cost-effective, scientifically meaningful collaboration. The best site for in situ experimentation is one that is well characterized over a long period of time. The leveraged funding and new knowledge gained from the experimental program benefits the scientific value and relevance of time-series program investments.

matter, and controls on rates of nitrogen fixation (http://cmore.soest.hawaii.edu/cruises.htm). The nucleic acid-based (DNA and RNA) data will provide information on microbial community diversity, structure, and metabolic function (e.g., Frias-Lopez et al., 2008). In combination with the continuing HOT program observations of the physical, chemical, and biological properties of the NPSG habitat, these new complementary data sets will be invaluable indicators of microbial population variability and change. The future of this partnership holds great promise.

ROLE OF OCEANIC ECOSYSTEM MODELING

Oceanic ecosystem models, be they conceptual, statistical, or numerical stimulations, are useful and necessary tools for studying and understanding the complex interactions of natural ecosystems (Rothstein et al., 2006; McGillicuddy et al., 2010). There is great need to forecast ecosystem dynamics, including species interactions, biodiversity, and the metabolic state of the sea in a changing ocean environment. A major objective of oceanic ecosystem time-series programs is to provide data to initialize existing models and, if necessary, to improve model design. Strayer et al. (2003) proposed a useful classification scheme based on variability of natural ecosystems, including considerations of spatial heterogeneity, nonsteady-state dynamics, and nonlinear interactions. They go on to make the important point that models should be as simple as possible to describe the system under investigation but complex enough to capture all important processes; the selection of model type will largely depend upon the time-space scales of interest (Strayer et al., 2003). Partnerships between modelers and data originators have proven to be of great value in climate and ecosystem research, and should be further encouraged. The predictive skill of current models can be tested using time-series observations and results derived from at-sea experiments. An interdisciplinary team of marine scientists was recently established to examine some of the contemporary challenges; the PARtnership for Advancing Interdisciplinary Global Modeling (PARADIGM) program has already made substantial progress toward the goal of predictive marine microbial ecology (Rothstein et al., 2006).

Two of the main challenges confronting marine ecosystem modelers are: (1) current limitations of mechanistically based parameterizations of key processes, including solar energy capture and dissipation, nutrient flux processes, and controls on primary and secondary production, and (2) the ability to model mesoscale space and time variabilities that are now known to control carbon and related bioelemental fluxes in many open-ocean ecosystems (Doney, 1999). More recently, the marine microbial genomics revolution has fundamentally altered our views of many basic aspects of ecology and metabolism, and these discoveries must also be included in ocean simulations to provide the most accurate climate change projections (Doney et al., 2004). Environmental genomics, transcriptomics, and proteomics are beginning to provide new views of an old ocean; improved ecosystem models, and possibly new ecological theory, will be needed to fully capitalize on the new discoveries.

CONTEMPORARY CHALLENGES AND OPPORTUNITY

Ocean time-series programs promote discovery, ignite hypothesis generation and testing, and provide unique opportunity for enhancing our understanding of natural ecosystems. All successful ocean time-series programs to date have been hybrids of routine observations and exciting cutting-edge, hypothesis-driven research. Indeed, this is a logical linkage because the serial observations feed directly into hypothesis generation, prediction, and experimentation, oftentimes leading to new observations. In this way, time-series programs act as intellectual flywheels that create and sustain ever larger, complementary programs where the scientific outcome of the integrated effort is much larger than the sum of its parts. The teams of collaborating scientists that emerge and the unique partnerships that are created add to the overall value of the time-series effort.

All successful time-series programs also have strong leadership, especially initially, but the truly impressive ones have multigenerational intellectual leadership that was passed on from senior to younger scientists without negative impact on the program as a whole. This program model is very important because the relevant time scale of many key ecological processes is longer than one academic lifetime. Because many modern time-series programs are transdisciplinary in their scientific missions, the leadership is often shared among disciplinary experts who collectively manage and promote the program among diverse science communities.

Human influence, mostly during the past century, on coastal and open-ocean ecosystems has been profound. Foremost among the deleterious impacts has been the accumulation of greenhouse gases in the atmosphere and surface ocean due to the accelerated use of carbon-based fuels mostly for energy generation. This has led to warming, enhanced stratification, acidification, and nutrient limitation of the surface waters of the open sea. The impact of these habitat changes on primary production, fish stocks, and the ability of the ocean to further sequester CO_2 or to perform other key ecosystem services is largely unknown. These are societal matters of great concern, and comprise the main justification for investments in ocean time-series programs. One relatively new area of research involves the search for leading indicators of probable regime shifts to predict climate impacts on ecosystem processes (Carpenter et al., 2008; Biggs et al., 2009). Warning signs, including wide swings in ecosystem dynamics, slower return rates following physical perturbations, and substantial changes in standard deviations of key variables, may hold predictive value for future ecosystem change (Carpenter et al., 2008). While this exciting research holds great promise and obvious societal value, field tests will require access to high-quality time-series data sets from diverse ecosystems.

Today, the global ocean network of coordinated time-series measurement programs has become the gold standard for detection of climate impacts on ecosystem processes. The OceanSITES project facilitates international coordination among ocean time-series efforts, including data management. The network includes moorings, as well as ship-supported observatories (Figure 7; http://www.oceansites.org). OceanSITES is well positioned to become the lead organization for the coordination of global, sustained ocean time-series programs. Furthermore, the ongoing Ocean Observatory Initiative (OOI), NSF's contribution to the US Integrated Ocean Observing System (IOOS), will deploy new technologies to create a novel deep-sea observatory network to improve our understanding of ocean variability. Finally, the IOC co-sponsored Global Ocean Observing System

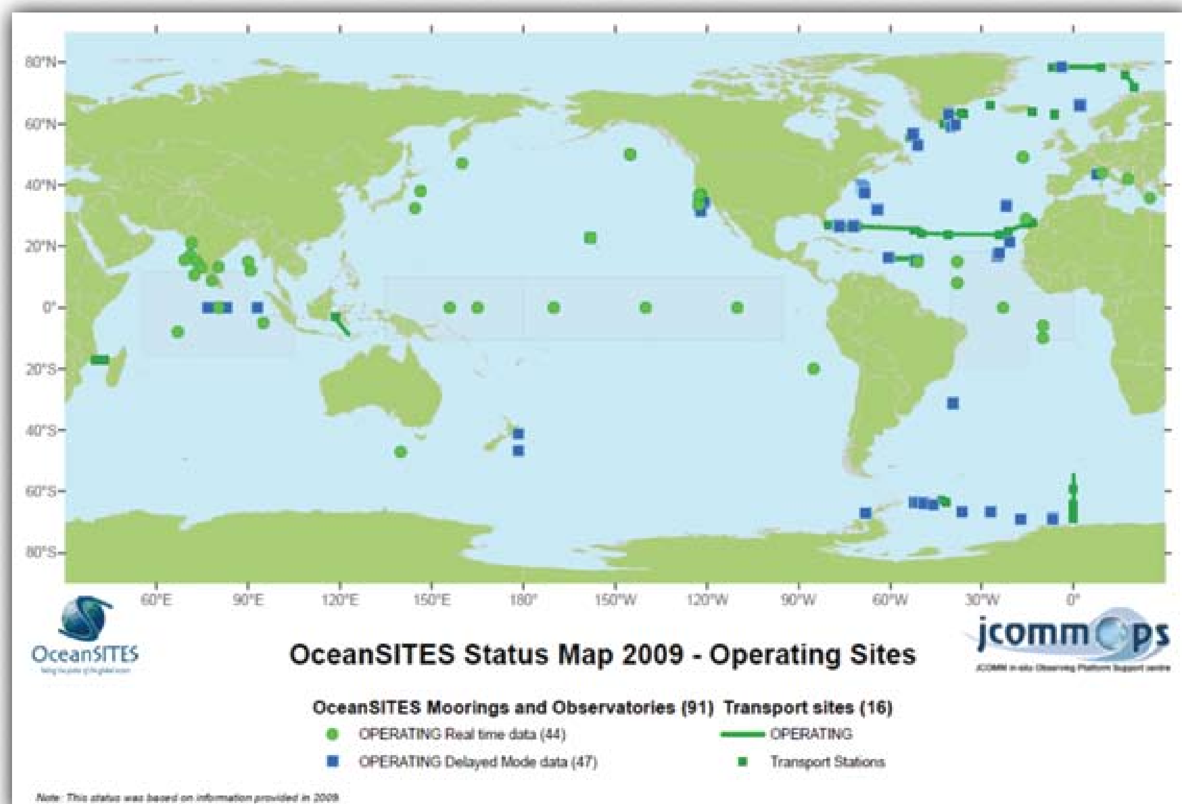

Figure 7. Map showing the geographical distribution of current ocean time-series sites, including moorings, observatories, and transport stations coordinated by the OceanSITES science and data management team. Additional activities are in various stages of planning so the global network is likely to expand in the near future. *From: http://www.oceansites.org*

(GOOS) will serve to integrate observations, data analysis, and modeling of the ocean as a whole (Hofmann and Gross, 2010), and may become the international clearinghouse for ocean knowledge to inform scientists, policymakers, and society. An important component, indeed the key to success, is data sharing and international collaboration. IOC has made major strides in the establishment of the International Ocean Data and Information Exchange (IODE) to facilitate this important mission (Glover et al., 2010).

Currently, there is a critical need to establish additional time-series measurement programs if we ever hope to achieve the ultimate goal of predicting the probable impacts of human-induced climate change. Ocean time-series programs of the future must embrace new methods, sensors, instruments, and other improvements in engineering and computation. Not unlike the movement away from an annual physical examination to track one's general health to a personalized, full genome sequence and computer-based surveillance of vital signs, ocean ecosystem programs are also on the verge of embracing novel, high-frequency observation systems. It should be a thrilling and productive next decade.

ACKNOWLEDGEMENTS

I thank Debbie Bronk, Kathy Tedesco, and Phil Taylor for their leadership and for the invitation to contribute to this special issue. Ocean time-series research is possible only through hard work and coordinated and unselfish efforts of teams of scientists, technicians, engineers, and logistical support staff. The HOT Team is second to none. Thanks also to Lisa Lum and Lance Fujieki for assistance with the preparation of this paper, and Paul Lethaby for the HOT program photographs. The research described herein was supported in part by NSF (HOT and C-MORE) and the Gordon and Betty Moore Foundation.

REFERENCES

Aiken, J., J. Fishwick, G. Moore, and K. Pemberton. 2004. The annual cycle of phytoplankton photosynthetic quantum efficiency, pigment composition and optical properties in the western English Channel. *Journal of the Marine Biological Association of the UK* 84:301–313.

Allen, E.J., and H.W. Harvey. 1928. The laboratory of the Marine Biological Association at Plymouth. *Journal of the Marine Biological Association of the UK* 15:735–752.

Armstrong, F.A.J., and S. Tibbitts. 1968. Photochemical combustion of organic matter in sea water for nitrogen, phosphorus and carbon determination. *Journal of the Marine Biological Association of the UK* 48:143–152.

Atkins, W.R.G. 1922a. The hydrogen ion concentration of sea water in its biological relations. *Journal of the Marine Biological Association of the UK* 12:717–771.

Atkins, W.R.G. 1922b. The hydrogen ion concentration of sea water in its relation to photosynthetic changes. *Journal of the Marine Biological Association of the UK* 12:93–118.

Atkins, W.R.G. 1923. Note on the oxidisable organic matter of sea water. *Journal of the Marine Biological Association of the UK* 13:160–163.

Atkins, W.R.G. 1924a. On the thermal stratification of sea water and its importance for the algal plankton. *Journal of the Marine Biological Association of the UK* 13:693–699.

Atkins, W.R.G. 1924b. On the vertical mixing of sea-water and its importance for the algal plankton. *Journal of the Marine Biological Association of the UK* 13:319–324.

Atkins, W.R.G. 1926a. A quantitative consideration of some factors concerned in plant growth in water Part I. Some physical factors. *Journal du Conseil, Conseil permanent international pour l'exploration de la mer* 1:99–126.

Atkins, W.R.G. 1926b. A quantitative consideration of some factors concerned in plant growth in water. Part II: Some chemical factors. *Journal du Conseil, Conseil permanent international pour l'exploration de la mer* 1:197–226.

Atkins, W.R.G. 1926c. Phosphate content of sea water in relation to algal plankton. *Journal of the Marine Biological Association of the UK* 14:447.

Atkins, W.R.G. 1930. Seasonal variations in the phosphate and silicate content of sea-water in relation to the phytoplankton crop. Part V: November 1927 to April 1929, compared with earlier years from 1923. *Journal of the Marine Biological Association of the UK* 16:821–852.

Bidigare, R.R., F. Chai, M.R. Landry, R. Lukas, C.C.S. Hannides, S.C. Christensen, D.M. Karl, L. Shi, and Y. Chao. 2009. Subtropical ocean ecosystem structure changes forced by North Pacific climate variations. *Journal of Plankton Research* 31:1,131–1,139.

Biggs, R., S.R. Carpenter, and W.A. Brock. 2009. Turning back from the brink: Detecting an impending regime shift in time to avert it. *Proceedings of the National Academy of Sciences of the United States of America* 106:826–831.

Bond, N.A., J.E. Overland, M. Spillane, and P. Stabeno. 2003. Recent shifts in the state of the North Pacific. *Geophysical Research Letters* 30(23), 2183, doi:10.1029/2003GL018597.

Brewer, P.G., K.W. Bruland, R.W. Eppley, and J.J. McCarthy. 1986. The Global Ocean Flux Study (GOFS): Status of the U.S.GOFS program. *Eos, Transactions, American Geophysical Union* 67:827–832.

Butler, E.I., S. Knox, and M.I. Liddicoat. 1979. The relationship between inorganic and organic nutrients in sea water. *Journal of the Marine Biological Association of the UK* 59:239–250.

Carpenter, S.R., W.A. Brock, J.J. Cole, J.F. Kitchell, and M.L. Pace. 2008. Leading indicators of trophic cascades. *Ecology Letters* 11:128–138.

Chavez, F.P., J. Ryan, S.E. Lluch-Cota, and M. Niquen C. 2003. From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. *Science* 299:217–221.

Chelton, D.B., P.A. Bernal, and J.A. McGowan. 1982. Large-scale interannual physical and biological interaction in the California Current. *Journal of Marine Research* 40:1,095–1,125.

Church, M.J., C. Mahaffey, R.M. Letelier, R. Lukas, J.P. Zehr, and D.M. Karl. 2009. Physical forcing of nitrogen fixation and diazotroph community structure in the North Pacific subtropical gyre. *Global Biogeochemical Cycles* 23, GB2020, doi:10.1029/2008GB003418.

Cooper, L.H.N. 1938. Phosphate in the English Channel, 1933–1938, with a comparison with earlier years, 1916 and 1923–1932. *Journal of the Marine Biological Association of the UK* 23:181–195.

Corno, G., D.M. Karl, M.J. Church, R.M. Letelier, R. Lukas, R.R. Bidigare, and M.R. Abbott. 2007. Impact of climate forcing on ecosystem processes in the North Pacific Subtropical Gyre. *Journal of Geophysical Research* 112, C04021, doi:10.1029/2006JC003730.

Cushing, D.H., and R.R. Dickson. 1976. The biological response in the sea to climatic changes. *Advances in Marine Biology* 14:1–122.

DeLong, E.F., and D.M. Karl. 2005. Genomic perspectives in microbial oceanography. *Nature* 437:336–342.
Dickey, T.D. 1991. The emergence of concurrent high-resolution physical and bio-optical measurements in the upper ocean and their applications. *Reviews of Geophysics* 29(3):383–413, doi:10.1029/91RG00578.
Dickson, A.G., J.D. Afghan, and G.C. Anderson. 2003. Reference materials for oceanic CO_2 analysis: A method for the certification of total alkalinity. *Marine Chemistry* 80:185–197.
Dinsmore, R.P. 1996. Alpha, Bravo, Charlie… Ocean Weather Ships 1940–1980. *Oceanus* Fall/Winter:9–10. Available online at: http://www.whoi.edu/oceanus/viewArticle.do?id=2343 (accessed August 5, 2010).
Doney, S.C. 1999. Major challenges confronting marine biogeochemical modeling. *Global Biogeochemical Cycles* 13:705–714.
Doney, S.C., M.R. Abbott, J.J. Cullen, D.M. Karl, and L. Rothstein. 2004. From genes to ecosystems: The ocean's new frontier. *Frontiers in Ecology and the Environment* 2:457–466.
Dore, J.E., R.M. Letelier, M.J. Church, R. Lukas, and D.M. Karl. 2008. Summer phytoplankton blooms in the oligotrophic North Pacific Subtropical Gyre: Historical perspective and recent observations. *Progress in Oceanography* 76:2–38.
Dore, J.E., R. Lukas, D.W. Sadler, M.J. Church, and D.M. Karl. 2009. Physical and biogeochemical modulation of ocean acidification in the central North Pacific. *Proceedings of the National Academy of Sciences of the United States of America* 106:12,235–12,240.
Duarte, C.M., J. Cebrián, and N. Marbà. 1992. Uncertainty of detecting sea change. *Nature* 356:190.
Edwards, M., and A.J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430:881–884.
Franklin, J.F., C.S. Bledsoe, and J.T. Callahan. 1990. Contributions of the Long-Term Ecological Research program. *BioScience* 40:509–523.
Frias-Lopez, J., Y. Shi, G.W. Tyson, M.L. Coleman, S.C. Schuster, S.W. Chisholm, and E.F. DeLong. 2008. Microbial community gene expression in ocean surface waters. *Proceedings of the National Academy of Sciences of the United States of America* 105:3,805–3,810.
Glover, D.M., P.H. Wiebe, C.L. Chandler, and S. Levitus. 2010. IOC contributions to international, interdisciplinary open data sharing. *Oceanography* 23(3):140–151.
Gordon, D.C. Jr. 1970. *Chemical and Biological Observations at Station Gollum, an Oceanic Station Near Hawaii, January 1969 to June 1970*. Hawaii Institute of Geophysics Report, HIG-70-22, 44 pp.
Hansell, D.A. 2005. Dissolved organic carbon reference material program. *Eos, Transactions, American Geophysical Union* 86:318.
Harvey, H.W. 1926. Nitrate in the sea. *Journal of the Marine Biological Association of the UK* 14:71–88.
Harvey, H.W. 1928. Nitrate in the sea. II. *Journal of the Marine Biological Association of the UK* 15:183–190.
Harvey, H.W. 1934. Measurement of phytoplankton population. *Journal of the Marine Biological Association of the UK* 19:761–773.
Harvey, H.W. 1942. Production of life in the sea. *Biological Review of the Cambridge Philosophical Society* 17:221–246.
Harvey, H.W. 1950. On the production of living matter in the sea off Plymouth. *Journal of the Marine Biological Association of the UK* 29:97–137.
Harvey, H.W. 1955. *The Chemistry and Fertility of Sea Waters*. University Press, Cambridge, Great Britain, 224 pp.
Harvey, H.W., L.H.N. Cooper, M.V. Lebour, and F.S. Russell. 1935. Plankton production and its control. *Journal of the Marine Biological Association of the UK* 20:407–442.
Haury, L.R., C.L. Fey, and E. Shulenberger. 1994. Surface enrichment of inorganic nutrients in the North Pacific Ocean. *Deep-Sea Research* 41:1,191–1,205.
Hayward, T.L. 1987. The nutrient distribution and primary production in the central North Pacific. *Deep-Sea Research* 34:1,593–1,627.
Hayward, T.L. 1991. Primary production in the North Pacific Central Gyre: A controversy with important implications. *Trends in Ecology and Evolution* 6:281–284.
Hofmann, E.E., and E. Gross. 2010. IOC contributions to science synthesis. *Oceanography* 23(3):152–159.
Ives, A.R., and S.R. Carpenter. 2007. Stability and diversity of ecosystems. *Science* 317:58–62.
Johnson, K.S., S.C. Riser, and D.M. Karl. 2010. Nitrate supply from deep to near-surface waters of the North Pacific subtropical gyre. *Nature* 465:1,062–1,065.
Joint, I., M.B. Jordan, and M.R. Carr. 1997. Is phosphate part of the Russell Cycle? *Journal of the Marine Biological Association of the UK* 77:625–633.
Jordan, M.B., and I. Joint. 1998. Seasonal variation in nitrate:phosphate ratios in the English Channel 1923–1987. *Estuarine and Coastal Shelf Science* 46:157–164.
Karl, D.M. 1999. A sea of change: Biogeochemical variability in the North Pacific subtropical gyre. *Ecosystems* 2:181–214.
Karl, D.M. 2002. Nutrient dynamics in the deep blue sea. *Trends in Microbiology* 10:410–418.
Karl, D.M. 2007a. Microbial oceanography: Paradigms, processes and promise. *Nature Reviews Microbiology* 5:759–769.
Karl, D.M. 2007b. The marine phosphorus cycle. Pp. 523–539 in *Manual of Environmental Microbiology,* 3rd ed. C.J. Hurst et al., eds, American Society of Microbiology.
Karl, D.M., and R. Lukas. 1996. The Hawaii Ocean Time-series (HOT) program: Background, rationale and field implementation. *Deep-Sea Research Part II* 43:129–156.
Karl, D.M., and A.F. Michaels, eds. 1996. Ocean time-series: Results from the Hawaii and Bermuda research programs. *Deep-Sea Research Part II* 43(2–3).
Karl, D.M., and G. Tien. 1992. MAGIC: A sensitive and precise method for measuring dissolved phosphorus in aquatic environments. *Limnology and Oceanography* 37:105–116.
Karl, D.M., and G. Tien. 1997. Temporal variability in dissolved phosphorus concentrations in the subtropical North Pacific Ocean. *Marine Chemistry* 56:77–96.
Karl, D.M., and C.D. Winn. 1991. A sea of change: Monitoring the oceans' carbon cycle. *Environmental Science and Technology* 25:1,976–1,981.
Karl, D.M., R.R. Bidigare, and R.M. Letelier. 2001. Long-term changes in plankton community structure and productivity in the North Pacific Subtropical Gyre: The domain shift hypothesis. *Deep-Sea Research Part II* 48:1,449–1,470.
Karl, D.M., N.R. Bates, S. Emerson, P.J. Harrison, C. Jeandel, O. Llinas, K.-K. Liu, J.-C. Marty, A.F. Michaels, J.C. Miquel, and others. 2003. Temporal studies of biogeochemical processes determined from ocean time-series observations during the JGOFS era. Pp. 239–267 in *Ocean Biogeochemistry: The Role of the Ocean Carbon Cycle in Global Change*. M.J.R. Fasham, ed., Springer.
Keeling, C.D. 1998. Rewards and penalties of monitoring the Earth. *Annual Review of Energy and Environment* 23:25–82.
Mantua, N.J., S.R. Hare, Y. Zhang, J.M. Wallace, and R.C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78:1,069–1,079.
Matthews, D.J. 1916. On the amount of phosphoric acid in the sea-water off Plymouth Sound. *Journal of the Marine Biological Association of the UK* 11:122–130.
Matthews, D.J. 1917. On the amount of phosphoric acid in the sea-water off Plymouth Sound. II. *Journal of the Marine Biological Association of the UK* 11:251–257.
McGillicuddy, D.J. Jr., B. deYoung, S.C. Doney, P.M. Glibert, D. Stammer, and F.E. Werner. 2010. Models: Tools for synthesis in international oceanographic research programs. *Oceanography* 23(3):126–139.
McGowan, J.A., and P.W. Walker. 1985. Dominance and diversity maintenance in an oceanic ecosystem. *Ecological Monographs* 55:103–118.

Michaels, A.F., and A.H. Knap. 1996. Overview of the US JGOFS Bermuda Atlantic Time-series Study and the Hydrostation S program. *Deep-Sea Research Part II* 43:157–198.

Mills, E.L. 1989. *Biological Oceanography: An Early History, 1870–1960*. Cornell University Press, Ithaca, New York, 378 pp.

Østerhus, S., I. Skjelvan, and T. Gammelsrød. 2009. Weather ship station M in the Norwegian Sea "Polarfront": The flagship of climate research. IOP Conference Series: *Earth and Environmental Science* 6:032022.

Overland, J.E., D.B. Percival, and H.O. Mofjeld. 2006. Regime shifts and red noise in the North Pacific. *Deep-Sea Research Part I* 53:582–588.

Pinkerton, M.H., S.J. Lavender, and J. Aiken. 2003. Validation of SeaWiFS ocean color satellite data using a moored databuoy. *Journal of Geophysical Research* 108(C5), 3133, doi:10.1029/2002JC001337.

Platt, T., W.G. Harrison, M.R. Lewis, W.K.W. Li, S. Sathyendranath, R.E. Smith, and A.F. Vezina. 1989. Biological production of the oceans: The case for a consensus. *Marine Ecology Progress Series* 52:77–88.

Polovina, J.J., G.T. Mitchum, N.E. Graham, M.P. Craig, E.E. DeMartini, and E.N. Flint. 1994. Physical and biological consequences of a climate event in the central North Pacific. *Fisheries Oceanography* 3:15–21.

Polovina, J.J., E.A. Howell, and M. Abecassis. 2008. Ocean's least productive waters are expanding. *Geophysical Research Letters* 35, L03618, doi:10.1029/2007GL031745.

Poole, H.H., and W.R.G. Atkins. 1937. The penetration into the sea of light of various wave-lengths as measured by emission or rectifier photo-electric cells. *Proceedings of the Royal Society of London B* 123:151.

Pomeroy, L.R. 1981. Microbial processes in the sea: Diversity in nature and science. Pp. 1–23 in *Heterotrophic Activity in the Sea.* J.E. Hobbie and P.J.leB. Williams, eds, Plenum Press.

Redfield, A.C. 1958. The inadequacy of experiment in marine biology. Pp. 17–26 in *Perspectives in Marine Biology*. A.A. Buzzati-Traverso, ed., University of California Press.

Reid, P.C., J.M. Colebrook, J.B.L. Matthews, J. Aiken, and Continuous Plankton Recorder Team. 2003. The Continuous Plankton Recorder: Concepts and history, from Plankton Indicator to undulating recorders. *Progress in Oceanography* 58:117–173.

Riser, S.C., and K.S. Johnson. 2008. Net production of oxygen in the subtropical ocean. *Nature* 451:323–325.

Rodriguez, F., E. Fernandez, R.N. Head, D.S. Harbour, G. Bratbak, M. Heldal, and R.P. Harris. 2000. Temporal variability of viruses, bacteria, phytoplankton and zooplankton in the western English Channel off Plymouth. *Journal of the Marine Biological Association of the UK* 80:575–586.

Rothstein, L.M., J.J. Cullen, M. Abbott, E. Chassignet, K. Denman, S. Doney, H. Ducklow, K. Fennel, M. Follows, D. Haidvogel, and others. 2006. Modeling ocean ecosystems: The PARADIGM program. *Oceanography* 19:17–45. Available online at: http://tos.org/oceanography/issues/issue_archive/issue_pdfs/19_1/19.1_rothstein_et_al.pdf (accessed August 4, 2010).

Russell, F.S., A.J. Southward, G.T. Boalch, and E.I. Butler. 1971. Changes in biological conditions in the English Channel off Plymouth during the last half century. *Nature* 234:468–470.

Saba, V.S., M.A.M. Friedrichs, M.-E. Carr, D. Antoine, R.A. Armstrong, I. Asanuma, O. Aumont, N.R. Bates, M.J. Behrenfeld, V. Bennington, and others. 2010. Challenges of modeling depth-integrated marine primary productivity over multiple decades: A case study at BATS and HOT. *Global Biogeochemical Cycles* 24, doi:10.1029/2009GB003655.

Sabine, C.L., H. Ducklow, and M. Hood. 2010. International carbon coordination: Roger Revelle's legacy in the Intergovernmental Oceanographic Commission. *Oceanography* 23(3):48–61.

Southward, A.J. 1960. On changes of sea temperature in the English Channel. *Journal of the Marine Biological Association of the UK* 39:449–458.

Southward, A.J. 1974. Changes in the plankton community of the Western English Channel. *Nature* 249:180–181.

Southward, A.J. 1980. The western English Channel: An inconstant ecosystem? *Nature* 285:361–366.

Southward, A.J. 1995. The importance of long time-series in understanding the variability of natural systems. *Helgolander Meeresuntersuchungen* 49:329–333.

Southward, A.J., and E.K. Roberts. 1987. One hundred years of marine research at Plymouth. *Journal of the Marine Biological Association of the UK* 67:465–506.

Southward, A.J., G.T. Boalch, and L. Maddock. 1988. Fluctuations in the herring and pilchard fisheries of Devon and Cornwall linked to change in climate since the 16^{th} century. *Journal of the Marine Biological Association of the UK* 68:423–445.

Stommel, H. 1963. Varieties of oceanographic experience. *Science* 139:572–576.

Strayer, D., J.S. Glitzenstein, C.G. Jones, J. Kolasoi, G.E. Likens, M.J. McDonnell, G.G. Parker, and S.T.A. Pickett. 1986. Long-term ecological studies: An illustrated account of their design, operation, and importance to ecology. Occasional Publication of the Institute of Ecosystem Studies, No. 2. Millbrook, New York.

Strayer, D.L., H.A. Ewing, and S. Bigelow. 2003. What kind of spatial and temporal details are required in models of heterogeneous systems? *Oikos* 102:654–662.

Sverdrup, H.U., M.W. Johnson, and R.H. Fleming. 1946. *The Oceans*. Prentice-Hall, Englewood Cliffs, NJ, 320 pp.

Swanson, F.J., and R.E. Sparks. 1990. Long-term ecological research and the invisible place. *BioScience* 40:502–508.

Valdés, L., L. Fonseca, and K. Tedesco. 2010. Looking into the future of ocean sciences: An IOC perspective. *Oceanography* 23(3):160–175.

Venrick, E.L. 1990. Phytoplankton in an oligotrophic ocean: Species structure and interannual variability. *Ecology* 71:1,547–1,563.

Venrick, E.L., J.A. McGowan, D.R. Cayan, and T.L. Hayward. 1987. Climate and chlorophyll *a*: Long-term trends in the central North Pacific Ocean. *Science* 238:70–72.