

Contributions of Long-Term Research and Time-Series Observations to Marine Ecology and Biogeochemistry

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Annu. Rev. Mar. Sci. 2009. 1:279–302

First published online as a Review in Advance on
September 4, 2008

The *Annual Review of Marine Science* is online at
marine.annualreviews.org

This article's doi:
10.1146/annurev.marine.010908.163801

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1941-1405/09/0115-0279\$20.00

Key Words

climate change, plankton ecology, carbon cycle

Abstract

Time-series observations form a critical element of oceanography. New interdisciplinary efforts launched in the past two decades complement the few earlier, longer-running time series to build a better, though still poorly resolved, picture of lower-frequency ocean variability, the climate processes that drive variability, and the implications for food web dynamics, carbon storage, and climate feedbacks. Time series also enlarge our understanding of ecological processes and are integral for improving models of physical-biogeochemical-ecological ocean dynamics. The major time-series observatories go well beyond simple monitoring of core ocean properties, although that important activity forms the critical center of all time-series efforts. Modern ocean time series have major process and experimental components, entrain ancillary programs, and have integrated modeling programs for deriving a better understanding of the observations and the changing, three-dimensional ocean in which the observatories are embedded.

Πάντα ῥεῖ καὶ οὐδὲν μένει.

Everything flows, nothing stands still.

Heraclitus, ca. 500 B.P.

CPR: Continuous Plankton Recorder

CalCOFI: California Cooperative Fisheries Investigations

BATS: Bermuda Atlantic Time-series Study

HOT: Hawaii Ocean Time series

JGOFS: Joint Global Ocean Flux Study

WOCE: World Ocean Circulation Experiment

ILTER: Long Term Ecological Research

ENSO: El Niño-Southern Oscillation

INTRODUCTION

Awareness of change, the expression of difference over time, must be one of the first things humans regarded when consciousness of the world came into being. Magnuson (1990) noted that it is an unusually perceptive individual who "... senses with any precision changes occurring over decades." Magnuson considered that the slow pace of change was a major obstacle to understanding. The oceans offer other challenges: Most of their expanse is remote and inhospitable, and the coupling of time and space over multiple scales in a fluid medium further complicates the problem (Platt & Denman 1975). Except for selected nearshore locations, most ocean areas are sampled only sporadically in time and space.

Time-series observations have been a core strategy in oceanography for more than fifty years. By the time of his return from the Discovery Expedition in 1926, Sir Alister Hardy (1896–1985) recognized the importance of sampling over extended periods and large spatial scales for understanding change in ocean ecosystems. He established the Continuous Plankton Recorder (CPR) Survey in 1931 (Hardy 1935) and it continues today as one of the longest records of sustained ocean observations. The California Cooperative Fisheries Investigations Program (CalCOFI), the first and oldest multidisciplinary time series, was initiated in 1949 to investigate the massive collapse of the California sardine fishery (Ohman & Venrick 2003). Begun in 1955, Hydrostation "S" off Bermuda is the site of the longest-running continual study of oceanic hydrography. The logistical difficulty and great expense of conducting regularly repeated, spatially extensive surveys have caused interruptions and contractions in these efforts but at least they continue. Paradoxically, long-term time series are among the shortest lived of marine research projects (Duarte et al. 1992). Recognition of the importance of time-series observations as a valid and powerful research tool was reborn with the inception of the Bermuda Atlantic Time-series Study (BATS) and Hawaii Ocean Time series (HOT) stations by the Joint Global Ocean Flux Study (JGOFS) in 1988 (Fasham et al. 2001). JGOFS, the World Ocean Circulation Experiment (WOCE), and the Long Term Ecological Research Program (ILTER) initiated a new era in ocean time-series investigations. An analysis of the achievements of this period is the subject of this review.

This is not a comprehensive review of the history and results from ocean time series. Rather, we survey some of the longer and better-known examples to suggest what we have learned over the past two decades. We have identified three productive areas of contemporary oceanography in which time-series observations have been especially fruitful: detection and attribution of ecological responses to climate variability and climate change, understanding the ocean biogeochemical cycle of carbon and the biological pump, and informing predictive models with new concepts and new observations. We also selected these areas because of their importance for understanding climate change. By virtue of its large area and volume, heat capacity, and importance as a reservoir for inorganic carbon, the world ocean plays a critical role in climate regulation (Gruber & Sarmiento 2002). Ocean time series are especially valuable tools for detecting, mechanistically understanding, and predicting climate change.

ECOLOGICAL RESPONSES TO CLIMATE VARIABILITY

Climate Modes

Only a few biological time series have been carried out long enough to discern responses to longer-period modes of variability, such as the El Niño-Southern Oscillation (ENSO), Pacific

Decadal Oscillation (PDO), and the Northern and Southern Annular Modes (Cane 1986, Wang & Schimel 2003). As Wang & Schimel (2003) noted, climate modes present valuable opportunities for studying climate variability and impacts because several correlated climate variables vary systematically over large regions with predictable frequencies. Anthropogenic climate warming may be a manifestation of anthropogenically induced changes in the frequency and intensity of naturally occurring climate modes (Meehl et al. 2000, Timmermann et al. 1999). Searching for ecological responses to climate mode variability enables us to formulate testable hypotheses about the mechanisms of ecosystem change.

The CalCOFI program has sampled phytoplankton, zooplankton and fish distributions with species-level resolution, associated physical variables, primary production (PP), and nutrients over a 200,000 km² region off Southern California since 1949. Roemmich & McGowan (1995) documented a long-term (1951–1994) decline in the biomass of zooplankton in the region and related the decline to a parallel increase in water column stratification. These researchers estimated biomass from plankton displacement volume, the volume of water displaced by a plankton sample from a net haul. They suggested that reduced nutrient inputs via decreased upwelling resulted in lower production and food limitation of the zooplankton stocks. McGowan et al. (2003) attributed this trend principally to an abrupt shift in many climate, physical, and biological oceanographic properties from 1976 to 1978, corresponding to a change in the PDO state. They warned that “... significant changes in near-surface heat and freshwater balances can greatly alter marine community ecosystem structure and productivity, sounding the alarm to the potential impacts of a global warming trend.” (McGowan et al. 2003, p. 2579).

Lavaniegos & Ohman (2007) extended the earlier analyses, estimating the carbon biomass of specific zooplankton taxa over 1951 to 2005. They derived biomass estimates from taxon-specific regressions of carbon mass with body length measurements of individual organisms in various groups, then multiplied by the abundance of each group (**Figure 1**). The total carbon biomass did not change over the long-term, but observations confirmed the decline in displacement volume and the increase in stratification over the same period. The difference in the two biomass estimates is due to a decline in the abundance of pelagic tunicates, gelatinous organisms with very large volume to carbon ratios. Most of the carbon biomass in the samples is contributed by copepods, but most of the displacement volume is contributed by tunicates. Pelagic tunicate declines were confirmed by carbon biomass assessments. Why tunicates are declining is not known. These authors suggested the change could be a consequence of changes in circulation, namely decreasing equatorward transport from seed regions to the north. This explanation is in contrast to the bottom-up hypothesis proposed by McGowan and colleagues.

Lavaniegos & Ohman (2007) also examined potential relationships with climate variability. Using sequential tests for ecosystem regime shifts (Rodionov 2004), they concluded that neither displacement volume nor carbon biomass showed distinct changes corresponding to the 1976–1978 PDO shift. These aggregated measures of population responses were relatively insensitive to climate forcing, but many individual species of copepods and other groups showed abrupt shifts at this time. In contrast, the authors found that there were “appreciable declines” in both biomass measures during each of the major El Niños between 1958 and 1998, as diagnosed from local ENSO indices, including detrended sea level anomalies (DSLAs) and the Bakun upwelling index. Many individual zooplankton taxa also showed marked decreases in response to El Niños and increases during La Niñas. Changes were short lived, with most measures recovering by the following year. There were fewer and weaker correlations with remote and larger-scale ENSO indices [e.g., Southern Oscillation Index (SOI), Niño 3.4]. The largest response was not to PDO shifts in 1977 or 1989 but following the 1999 El Niño. Taken together, these analyses indicate the following: (a) the importance of having several alternative measures of ocean properties (e.g.,

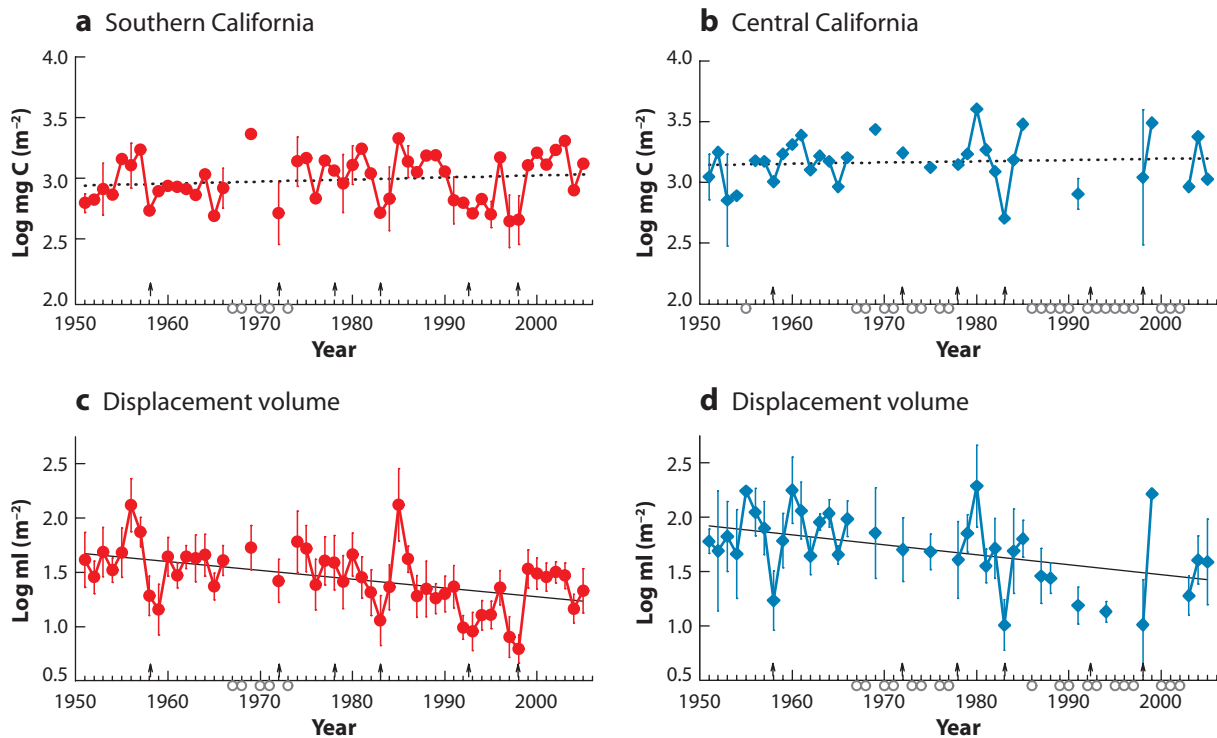


Figure 1

Interannual variation in total zooplankton biomass expressed as organic carbon (*a* and *b*) and displacement volume (*c* and *d*), from springtime California Cooperative Fisheries Investigations Program (CalCOFI) cruises from Southern California (SC) (*a* and *c*) and Central California (CC) (*b* and *d*). El Niño years are identified with upward facing arrows. Open circles below the *y*-axis indicate no springtime samples were available. From Lavaniegos & Ohman (2007) with permission from Elsevier.

carbon versus displacement biomass, DSLA versus SOI) and (*b*) the great value of multispecies, multitrophic-level observations for detecting and understanding change.

Regime Change

The discussion above highlights the difficulty in attributing species- and community-level changes to specific forcings and detecting ecological regime changes in response to longer-period climate variability (deYoung 2004, Hare & Mantua 2000). Even a greater than 50-year record is scant evidence for attributing causes of longer-term changes. An oceanographic regime is a period of a decade or more characterized by apparently stable annual mean biological and physical properties (MacCall 1996, Rebstock 2002), and a regime change is an abrupt shift or step-change in some group of properties following a stable period, and followed by another stable period in a new state (Beamish et al. 1999, Rebstock 2002). Accordingly, it takes at least a decade following a putative regime shift to document that shift. Regular sampling of the North Pacific subtropical gyre commenced in the late 1960s and became systematic with the initiation of the HOT site in 1988. Venrick et al. (1987) reported a doubling of water column chlorophyll in the oligotrophic central North Pacific after 1968 and postulated an ecosystem response to basin-scale changes in winds, circulation, and sea surface temperature. Venrick and colleagues (1987) hypothesized

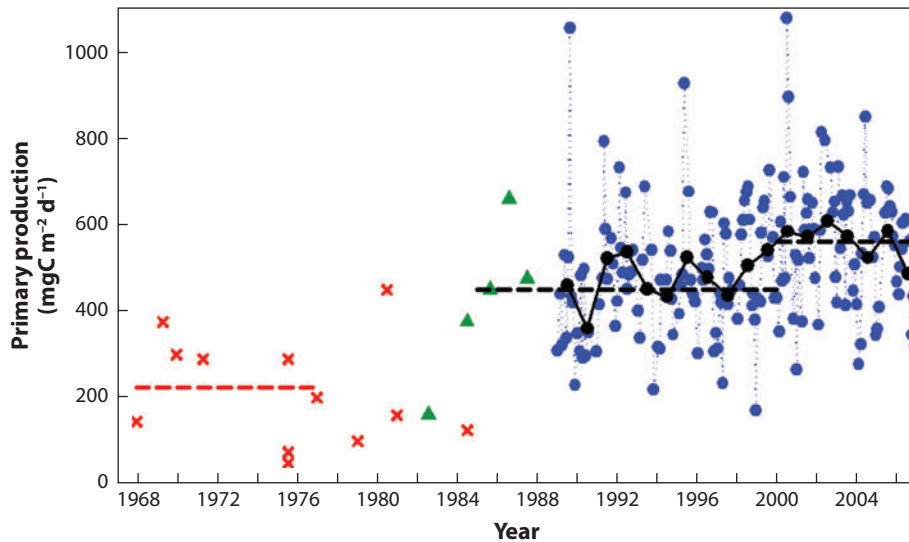


Figure 2

Primary production in the North Pacific Subtropical Gyre, 1968–2007. The red symbols show data collected from the CLIMAX region (Venrick et al. 1987) prior to development of trace-metal-free incubation techniques; the green and blue symbols show data collected after this development. The blue symbols show data from the Hawaii Ocean Time-series (HOT) station ALOHA ($22^{\circ} 45'N$, $158^{\circ} 00'W$). The horizontal dashed lines show the means for three observation periods. Pre-HOT data were digitized from Karl (1999). HOT data recovered from <http://hahana.soest.hawaii.edu/hot/hot-dogs/interface.html>.

that changes in the physical regime resulted in increased carrying capacity (increased PP) of the subtropical gyre system. Karl and colleagues (Cullen et al. 2002, Karl 1999, Karl et al. 1996, Karl & Lukas 1996) extended the observations reported by Venrick et al. (1987) and further elaborated the physical mechanism. PP rates averaged 200 to 250 $\text{mgC m}^{-2} \text{d}^{-1}$ before 1976, 450 $\text{mgC m}^{-2} \text{d}^{-1}$ for 1988–1999 and 562 $\text{mgC m}^{-2} \text{d}^{-1}$ for 2000–2006 (Figure 2). The 1977 PDO shift involved intensification of the Aleutian Low and increased westerly winds that cooled the upper 400 m, leading to deepening of the main thermocline extending into the gyre region, and enhanced nutrient flux into the euphotic zone. Interpretation of the extended PP record is complicated by several factors besides the obvious sparseness of the pre-1988 data. First, PP rates lower than 300 $\text{mgC m}^{-2} \text{d}^{-1}$ continued to be observed after 1977. Second, most pre-1986 data were collected using non-trace-metal-free incubations, known to contaminate some samples with inhibitory levels of copper (Fitzwater et al. 1982). Third, PP has shown a tendency to increase recently, raising the question of whether a new regime state will be reached, or if there ever was one.

Anthropogenic Warming

The scientific literature is now rich with examples of organisms across the phylogenetic spectrum and at all trophic levels that have responded to climate change in the past 50 years, paralleling the period of anthropogenic warming (McCarthy et al. 2001). The magnitude and pace of the 20th- to 21st-century warming are expected to produce novel climate conditions (no-analog climates) with combinations of temperature, precipitation, and seasonal variations that do not exist in the contemporary world (Fox 2007). The no-analog climates in turn are shuffling populations and

communities, possibly producing no-analog ecosystems. In the recent Intergovernmental Panel on Climate Change (IPCC) synthesis (Parry et al. 2007), terrestrial examples, especially studies of changing ranges for birds and plants, are most common, outnumbering marine and freshwater examples by 28,586 to 85! This must testify to the difficulty of detecting ecological change in the ocean. But there are also clear examples of changes in marine pelagic communities. Best documented are changes off of southern California: A 1400-year time series of planktonic foraminifera collected from sediments shows species shifts coincident with the 20th-century warming (Field et al. 2006). Fish, squid, kelp, seals, sea lions, and seabirds have also been affected by the increasing frequency of warm anomalies along the California coast (McGowan et al. 1998). Although globally coherent responses across many groups have been documented (Parmesan 2006), studies at the ecosystem level are less common. The CPR Survey shows changes in the North Atlantic at all trophic levels (Richardson & Schoeman 2004). Increases in ocean temperatures extending throughout the water column as well as air temperatures and reductions in sea ice have triggered extensive changes across trophic levels in the Bering Sea (Grebmeier et al. 2006). Declining benthic prey and their mammalian predators have been accompanied by a shift toward a pelagic-dominated food web with increased fish populations in the rich Bering system, site of several valuable commercial fisheries.

In all these cases, climate change has been implicated but the mechanisms of ecosystem response are less clear (Greenland et al. 2003). What is clear is that climate change causes ocean warming or changes in winds, circulation, and sea ice cover; these physical changes may directly influence regional species distributions. Even direct effects on individual species ranges may lead to complex changes at the community level. New species invasions may precede local extinctions, causing transient increases in species diversity (Walther et al. 2002). Such a species invasion is occurring along the Antarctic Peninsula, where the atmosphere has warmed in winter by almost 6°C since 1950, more than five times the global average (Vaughan et al. 2003). The paleorecord of species-specific penguin occupation suggests the recent warming is unique over at least the past few millennia and possibly longer (Domack et al. 2003, Smith et al. 1999). Chinstrap (*Pygoscelis antarctica*) and Gentoo penguins (*P. papua*) have successfully invaded the region, coexisting with long-resident Adélie penguins (*P. adeliae*) (Ducklow et al. 2007). The Adélies are in steep decline in the midpeninsular region; local populations have been reduced by approximately 70% since 1975.

The principal mechanism of ecological response to climate change appears to be trophic mismatch driven by differential changes in species phenologies, which disrupt the synchrony between species and their food or habitat resources (Cushing 1978). Changes in physical oceanographic processes (mixing, stratification, circulation, sea ice) mediate top-down effects of climate warming on foodwebs via trophic mismatches initiated at the upper trophic levels. The changes at higher trophic levels trigger trophic cascades that result in the reorganization of entire foodwebs. Phenology change and trophic mismatch may be particularly important in temperate and polar marine habitats where consumers depend on episodic pulses of primary and secondary production. The CPR Survey (1958–2002) found evidence for shifts in seasonal peaks of abundance in 34 of 37 planktonic consumer taxa that peaked under stratified (summer) conditions. In contrast, they found no change in the timing of the spring phytoplankton bloom of large diatoms that flourish in well-mixed, turbulent conditions. The result, overall, is a growing mismatch between diatoms and their consumers (Edwards & Richardson 2004). These changes and other climate-driven shifts in copepod biogeography, including the expansion of warm-water species poleward and the shrinkage in subarctic and arctic species ranges, have been implicated in the decline of North Sea cod stocks (Beaugrand et al. 2003).

In addition, the physical changes also affect rates and composition of the primary producers and corresponding prey abundance, thus indirectly affecting upper trophic level predators. An

alternative to the top-down model is that climate change induces bottom-up responses in lower trophic level populations. Examples include changes in phytoplankton size classes and krill reductions in response to declining sea ice (Atkinson et al. 2004, Fraser & Hofmann 2003, Moline et al. 2004). The reality is most likely a combination of both top-down and bottom-up interactions that vary in strength for different ecosystems and ecological measures.

BIOGEOCHEMISTRY AND THE BIOLOGICAL PUMP

Our view of ocean biogeochemistry and the net balance of carbon partitioning between the ocean and the atmosphere has changed profoundly over the past several decades with the establishment and analysis of long-term oceanographic time-series observations (Steinberg et al. 2001, Karl et al. 2001b). Understanding the basic processes that control ocean biogeochemistry on seasonal to decadal timescales ultimately improves our ability to predict the effects of climate change on ecosystems. Phytoplankton convert inorganic carbon into organic carbon that is transferred from the surface to the deep sea via sinking of particles, mixing of dissolved organic matter, and active transport by animals—collectively known as the biological pump (Ducklow et al. 2001, Volk & Hoffert 1985). This biologically mediated downward transport of organic carbon sequesters C in the ocean's interior. In this section we focus on some of the key contributions of time-series observations to our understanding of carbon and nutrient cycles in the ocean, and the transport of biogenic material to the deep sea.

Increase in Dissolved Inorganic Carbon in the Surface Ocean

Continuous measurements since the late 1950s at Mauna Loa, Hawaii indicate a steady increase in atmospheric CO₂ due to release of anthropogenic CO₂ and its accumulation in the atmosphere (e.g., Keeling et al. 1995). Direct evidence for increases in dissolved inorganic carbon (DIC) in surface ocean waters has come from time-series observations (**Figure 3**). In the North Atlantic subtropical gyre there is significant interannual variability in surface-ocean DIC and *p*CO₂ accumulation from the atmosphere due to physical forcing that is correlated with the North Atlantic Oscillation (NAO) (Bates 2001, Gruber et al. 2002). Over the decadal timescale, increases in DIC in surface waters at the BATS and Hydrostation S time series off Bermuda have increased at a rate that is in equilibrium with the anthropogenic CO₂ increase in the atmosphere (Bates 2007). Upward trends in surface seawater CO₂ have occurred at other sites in the North Atlantic, although some areas exhibit rates of CO₂ increase that are lower [Santana-Casiano et al. 2007 for the eastern subtropical Atlantic (ESTOC) near Gran Canaria] and some exhibit rates that are higher (Lefèvre et al. 2004; Olsen et al. 2003 for the subpolar gyre) than the expected oceanic equilibrium with anthropogenic CO₂ increase in the atmosphere, partly reflecting the period of observation (Bates 2007). In the North Pacific Ocean, time-series data from HOT in the subtropical gyre (Dore et al. 2003, Keeling et al. 2004) and station KNOT (Kyodo North Pacific Ocean time series) in the western subpolar region (Wakita et al. 2005) show rates of change of surface ocean DIC slightly higher than the expected oceanic equilibrium with anthropogenic CO₂ in the atmosphere. These increases in surface ocean DIC have led to measurable increases in ocean acidity, with a long-term secular decline of approximately 0.025 pH units over the past 20 years in the ocean near Bermuda (Bates 2007) and across much of the global surface ocean. Acidification alters seawater chemical speciation, and one well-known effect is the lowering of calcium carbonate saturation states, which impacts shell-forming marine organisms such as coccolithophores, foraminifera, and pteropods (Riebesell et al. 2000, Fabry et al. 2008). The broader influences on ocean ecology and biogeochemical cycles could be significant but are still poorly understood (Doney et al. 2009).

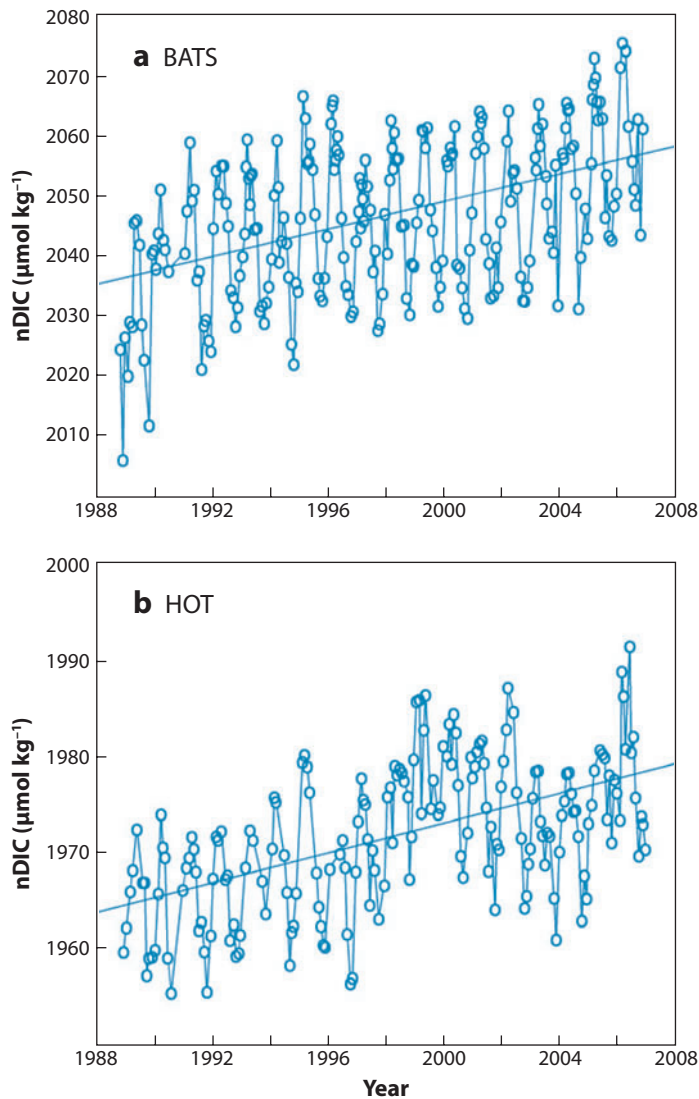


Figure 3

Long-term increase in surface-ocean dissolved inorganic carbon (DIC) at Bermuda Atlantic Time-series Study (BATS) and Hawaii Ocean Time series (HOT) sites. Mean of 0–45 m DIC normalized to surface salinity at each site (36.6 for BATS and 35 for HOT). Linear regression is significant at both sites ($P < 0.05$). Figure generated as in Karl et al. 2001b and Lomas et al. 2002 from data in the U.S. Joint Global Ocean Flux Study (JGOFS) database (<http://usjgofs.whoi.edu/jg/dir/jgofs/>).

Nutrient Limitation of Primary Production and Redfield Stoichiometry

The way we view the stoichiometry of elements and the processes that affect nutrient cycling in the ocean has changed considerably over the past several decades (Michaels et al. 2001). The demonstrations of the biogeochemical importance of N_2 fixation as a new nitrogen source and iron as a limiting micronutrient in large regions of the ocean are classic examples of major shifts that have occurred in some of the basic paradigms of our field. In particular, time-series studies

have taught us that relationships exist between patterns in nutrient distributions and climate over a range of timescales.

As discussed above, a shift in the PDO in 1977 led to a regime shift in the North Pacific subtropical gyre and an increase in primary production rates. This regime shift had a number of other important consequences, including an apparent shift in the phytoplankton community structure from larger eukaryotes (e.g., flagellates and to a lesser extent diatoms) to picoeukaryotes (e.g., prymnesiophytes and pelagophytes) and prokaryotes (e.g., *Prochlorococcus* and *Synechococcus*; Karl 1999). Associated with the shift in the PDO was an extended period of negative SOI post1980, favoring El Niño conditions, and resulting in increased stratification of the subtropical North Pacific gyre. The increased stratification has favored growth of N-fixing cyanobacteria such as *Trichodesmium* (Karl et al. 1995, Karl 1999), leading to a shift from the N-limited system that existed pre1980s, to the phosphorus- or iron-limited system that prevails today (Karl 1999, Karl et al. 2001a). This N₂-supported new production has led to non-Redfield C:N:P stoichiometry in surface waters, which in turn favors net C sequestration (Karl 1999, Michaels et al. 2001). However, recent evidence shows that *Prochlorococcus* in the subtropical North Pacific gyre is currently N limited and not P limited, suggesting a progressive shift away from P limitation (Van Mooy & Devol 2008).

Another major shift that has occurred in our understanding of biogeochemical budgets in the sea is the recognition that mesoscale processes play a significant role in nutrient supply to the upper ocean. Episodic, mesoscale eddy-driven upwelling supplies nutrients to the surface waters of the oligotrophic subtropical oceans that are estimated to account for a significant portion of the nutrients required for new production (Benitez-Nelson et al. 2007, McGillicuddy et al. 2007, McGillicuddy et al. 1998). Interpretation of time-series data is dependent upon our understanding of mesoscale spatial heterogeneity as these transient mesoscale features move across a fixed location in the ocean (McGillicuddy 2001). Passage of mesoscale eddies through the HOT and BATS sites resulted in large increases in surface nutrient and chlorophyll concentrations (Letelier et al. 2000, McNeil et al. 1999) and shifts in phytoplankton community structure (Letelier et al. 2000). Recent, comprehensive studies of mesoscale eddies in the subtropical North Atlantic and North Pacific have also demonstrated considerably enhanced nutrient injection and primary production, substantial diatom blooms, and elevated zooplankton biomass in comparison with the long-term record of biogeochemical properties at BATS and HOT (Benitez-Nelson et al. 2007, McGillicuddy et al. 2007). The biological and biogeochemical response varied considerably with eddy type, and although particulate organic carbon (POC) flux was not enhanced within the eddies, a variety of other mechanisms affected C export (Benitez-Nelson & McGillicuddy 2008).

Particle Flux to the Deep Ocean

We have learned much of what we know about the biological pump and transfer of particulate organic material from the surface ocean to the deep sea from long-term sediment trap studies. Deep-sea pelagic and benthic organisms are dependent on the rain of particles from above, and benthic time series have illustrated how communities respond to climate-induced changes in sedimentation.

POC flux measurements at the base of the euphotic zone are often poorly correlated with primary production in both the North Pacific and North Atlantic subtropical gyres (Steinberg et al. 2001, Karl et al. 1996). Although primary production and flux are not expected to be simultaneous processes (i.e., export follows production), even over longer portions of the time series the relationship is weak, invoking alternative export pathways (see below). A comparison of primary production and C flux at three subtropical time-series sites indicated considerably lower POC

flux and export ratio (POC export: primary production) across 200 m at ESTOC near the Canary Islands compared with BATS and HOT (Neuer et al. 2002). This lower ratio is suggested to be due to a lower input of new nitrogen at ESTOC, owing to a lack of both significant mesoscale eddy-induced upwelling of nutrients and N_2 fixation, compared with HOT and BATS (Neuer et al. 2002). A comparison of upwelling-dominated continental margin time series (Santa Barbara, Cariaco, and Guaymas Basins) showed that POC fluxes strongly correlated with mineral fluxes, lending support to the ballast hypothesis, which states that the export of POC to the deep ocean is determined, and can be predicted, by the rain of mineral ballast (Thunell et al. 2007). These and other factors that affect transport efficiency of POC as it sinks through the mesopelagic zone are of considerable importance to predictions of C sequestration in the deep sea (Buesseler et al. 2007).

Early important results from deep time-series sediment trap studies included the discovery of a coupling between surface seasonal patterns in primary production and the deep sea, resulting in a strong seasonality in deep-ocean particle fluxes, and the important role of episodic flux events in rapid transport of biogenic material to depth (Deuser 1986, Deuser & Ross 1980, Deuser et al. 1981). These early discoveries from the Oceanic Flux Program (OFP) sediment trap time series at 3200-m depth in the Sargasso Sea off Bermuda (begun in 1978) helped transform the long-held view that the deep sea was a relatively stable, invariable environment (Conte et al. 2001) (**Figure 4**). Since then, seasonality in deep particle fluxes has been found in numerous other time-series studies (Honjo & Manganini 1993, Karl et al. 1996, Lampitt & Antia 1997, Lampitt et al. 2001, Neuer et al. 1997, Smith et al. 2006, Takahashi et al. 2002). Episodic, short-lived, high-flux events in the deep sea that are not associated with the spring bloom are important in the delivery of highly labile organic material and can account for a significant proportion of the export flux of bioavailable C for mesopelagic and deep-sea benthic organisms (Conte et al. 1998). These episodic events have been linked to physical forcing such as physical perturbation by a mesoscale eddy (Conte et al. 2003).

Benthic time series show that deep-sea benthic communities rapidly respond to pulses of phytodetritus, resulting in increases in protozoan and metazoan abundance and sediment community oxygen consumption (Drzen et al. 1998, Smith et al. 2002). Climate fluctuations can also affect deep-sea communities through long-term variations in POC supply to the benthos. At Station M, located in the North Pacific California current upwelling region, POC flux reaching 3500-m and 4050-m depths is significantly correlated with several different Pacific climate indices (time-lagged by various intervals), including the basin-scale multivariate SOI, the NAO, and the Bakun upwelling index (Smith et al. 2006). Major changes were also observed at Station M in the dominant mobile, epibenthic megafauna at 4100 m, synchronous with a major ENSO event that occurred between 1997 and 1999 (Ruhl & Smith 2004), and were related to climate-induced changes in food supply noted above. Similar shifts in benthic community structure due to changes in food supply have been observed in the Porcupine Abyssal Plain in the northeast Atlantic (Billett et al. 2001).

Other Components of the Biological Pump

Export pathways once poorly constrained but now elucidated through time series and other studies include active C transport by zooplankton diel vertical migration and seasonal convective mixing of dissolved organic carbon (DOC). These processes are considerably variable in time and thus require long-term data sets to quantify their contribution to the biological pump.

Many species of zooplankton (and fish) that are resident in the mesopelagic zone during the day migrate into surface waters at night to feed, and descend again before dawn. This diel vertical

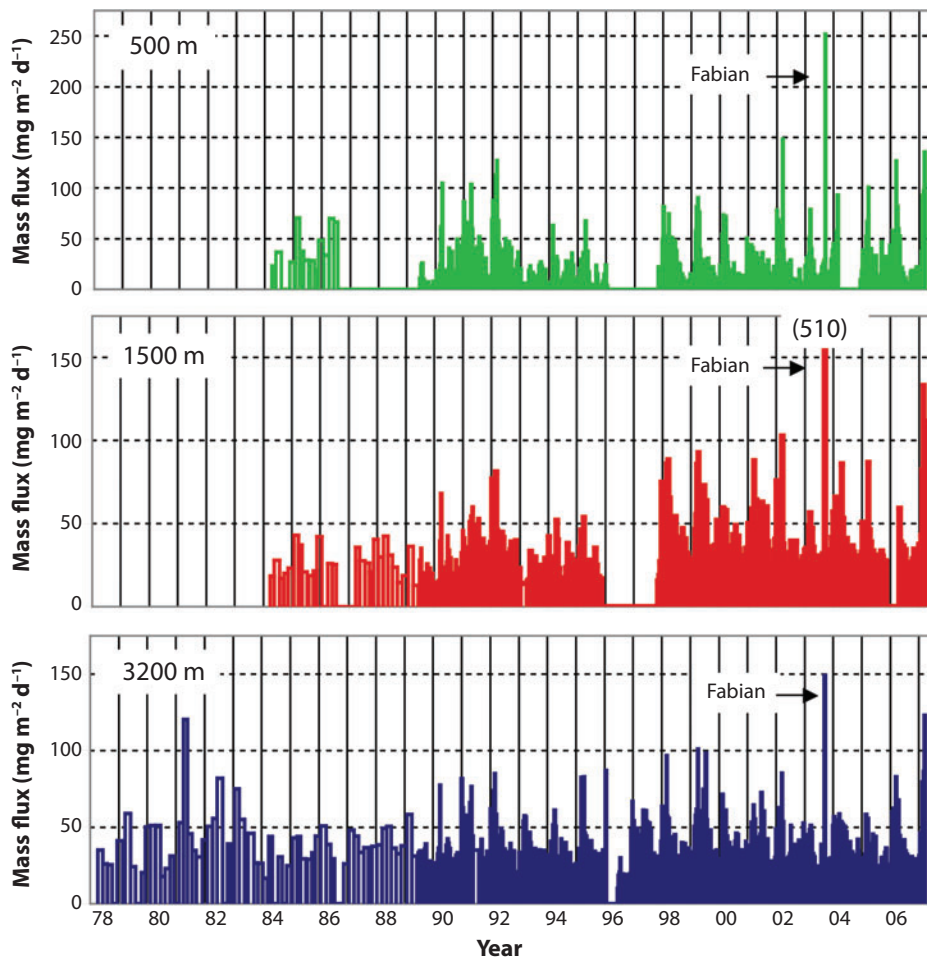


Figure 4

Deep-ocean sediment trap flux at the Oceanic Flux Program (OFP) time-series station in the Sargasso Sea. Note response to Hurricane Fabian in 2003. Data courtesy of Maureen Conte (OFP).

migration represents an active transport of C and nutrients to deep water, because zooplankton metabolize at depth the food they have ingested at the surface (Longhurst et al. 1990). In the North Pacific and North Atlantic subtropical gyres at HOT and BATS, on an annual basis active transport is equal to approximately 10–20% of the sinking particle flux. However, during times of high zooplankton biomass, such as spring, active transport is comparable to passive POC transport by sinking particles (Al-Mutairi & Landry 2001, Steinberg et al. 2000). In addition, a long-term increase in mesozooplankton biomass has been reported at both HOT and BATS (Sheridan & Landry 2004, Steinberg et al. 2008). At BATS this has led to an increase in migrator biomass, which in turn has increased active transport by diel migration and thus the efficiency of the biological pump (Steinberg et al. 2008).

Vertical advective supply of dissolved organic matter (DOM) from surface waters can represent a substantial flux of C to the oceans' interior and thus be an important component of the biological pump (Carlson et al. 1994, Emerson et al. 1997, Hansell & Carlson 2001, Hansell et al. 2002).

In the Sargasso Sea at BATS, export of DOC by vertical mixing can, depending on the depth of mixing, exceed vertical particle flux on an annual basis (Carlson et al. 2004, Hansell & Carlson 2001). The depth of vertical mixing in the North Pacific subtropical gyre at HOT is considerably shallower than at BATS; thus vertical export of DOC at HOT is comparatively lower (Emerson et al. 1997). The result is a higher annual export of total C at BATS than at HOT, despite the similar levels of primary production, vertical particle flux, and active transport by diel vertical migration at these two time-series sites (Lomas et al. 2002). Interestingly, DOC, like CO₂, is accumulating in the euphotic zone at both BATS and HOT, representing an additional and previously unforeseen carbon storage pool (Lomas et al. 2002).

INFORMING MODELS WITH OBSERVATIONS

The Synergy of Time Series and Models

Ocean ecological time series are attractive for numerical model development for many of the same reasons that they see wide usage in studies of interannual variability, climate change, and biogeochemical dynamics (Doney 1999). Steady-state descriptions of the ocean, for example the spatial contrasts between different biomes, are useful but can take us only so far. Without additional information on how the system responds in time to perturbations, we often cannot distinguish the balance of different factors that maintain the observed conditions. Fortunately there is a wide range of perturbations to ocean biology and chemistry, from storms and dust deposition events to the seasonal cycle, ENSO, decadal variability, and climate change (Boyd & Doney 2002). Encapsulating these dynamical insights into numerical models is a challenging, but critical, step in enhancing our conceptual understanding and improving our capability for ocean forecasting.

Biological modeling studies are inherently data limited. Observations are needed to build and test model parameterizations (e.g., for photosynthesis, grazing, respiration) and for evaluating model skill. Despite the wealth of data highlighted above, most of the upper ocean remains largely unobserved. Field oceanographers collect large amounts of water column stock and rate measures as part of targeted spatial surveys and process studies. But data sets from different cruises are disjointed in space and time, making it challenging to piece together a clear picture of temporal changes. Further, it can be difficult to intercompare data sets because of analytical and sampling issues. As a further complication, sometimes data are not readily available to other researchers. The advent of routine satellite ocean color sensors expands greatly our observational capabilities, but only a handful of biological variables are accessible with current remote sensing and then only for the near surface under clear-sky conditions.

In contrast, time-series records typically are collected in a single location (or confined region), are internally consistent, and are for the most part publicly available. Thus, modeling groups are drawn to time series (Evans 1999). Model-data interaction is, of course, two way because an integrated modeling component augments field programs. Even the best-sampled time series is not at sea continuously, especially for ship-based measurements, and cannot sample everything. Simulations can help fill in data gaps, whether in time or in variable space, and quantify the many biological processes left unconstrained from field observations (Daniels et al. 2006, Fasham et al. 1995).

Historical Context

Two seminal papers illustrate the state of ecosystem/biogeochemical modeling at the cusp of the JGOFS era. Frost (1987) applied a nutrient-phytoplankton-zooplankton (NPZ) mixed-layer

model with two zooplankton size classes to the eastern subpolar North Pacific (Ocean Station P), a region of high surface macronutrients but low and seasonally uniform phytoplankton biomass. Frost determined that mesozooplankton grazing by itself could not explain the lack of a seasonal bloom. He inferred a key role for microzooplankton, but field data were insufficient at the time to confirm this hypothesis. The low phytoplankton biomass at Ocean Station P and other high-nitrate, low-chlorophyll (HNLC) regions is now attributed to a combination of iron limitation on phytoplankton growth, particularly for bloom forming diatoms, and microzooplankton grazing (Boyd et al. 2007).

Fasham et al. (1990) developed a new ecosystem model for Hydrostation S off Bermuda to partition net primary production into the fractions due to new versus regenerated nitrogen sources. Fasham et al. (1990) found relatively high simulated f-ratios (new/total production) matched the available historical data, mostly from the 1960s. Their nitrogen-based model was noteworthy for a number of advances, including a prognostic bacteria-DOM microbial loop and adaptive feeding preferences for the zooplankton, which could ingest phytoplankton, bacteria, or detritus. The model became the foundation for a next generation of ocean biogeochemical simulations.

The JGOFS era saw a dramatic expansion in the duration, number, and biogeographical range of ocean time series (Kleypas & Doney 2001), driving a corresponding growth in numerical modeling. Below we highlight three major trends in the literature related to time-series modeling: improved physics, increased ecological and biogeochemical complexity, and more sophisticated model-data evaluation using data assimilation.

Simulating Upper Ocean Physics

The ocean is a turbulent, moving fluid, and ecological models of ocean time series need to either explicitly or implicitly take physics into account. Most early modeling efforts used smooth, often idealized, climatological seasonal cycles of mixed-layer depth, which governs nutrient supply, light supply, and photosynthesis (Evans & Parslow 1985). More realistic physics is required, however, for more detailed model-data comparisons and climate variability and climate change studies.

Local box models and 1-D models are cast as a set of time-varying advection-diffusion equations. The rate of change of each tracer χ , for example phytoplankton biomass or a nutrient concentration, is solved for at each point in space in terms of physical transport and biochemical transformations. In 1-D this can be written as:

$$\frac{\partial \chi}{\partial t} + \frac{\partial w \chi}{\partial z} - \frac{\partial}{\partial z} K_Z \frac{\partial \chi}{\partial z} + LHS_{lateral} = RHS_{bio}. \quad (1)$$

The second and third terms on the left-hand side are the advective and diffusive divergence terms, where w and K_Z are the vertical velocity and vertical diffusivity. The ecological-biogeochemical source/sink terms, along with the air-sea and water-sediment fluxes, are grouped into the right-hand-side term RHS_{bio} .

Mixed-layer models provide simulated seasonal and interannual time series of temperature, vertical velocity, mixed-layer depth, and/or vertical diffusivity (Large et al. 1994), which can be applied to transport biological scalars. Physical schemes are tested against field data, often biologically relevant, long time-series records such as Ocean Station P and BATS. Atmospheric forcing (winds, solar radiation, heat, and freshwater fluxes) is a challenge for 1-D physical models. Important developments include the increasing availability of high-quality data from moorings and the application of global atmospheric reanalysis and satellite data products (Doney 1996). The Regional Test-Bed Project developed a common 1-D modeling framework and physical forcing data sets for a number of ocean time-series locations (Friedrichs et al. 2007). Historical 1-D

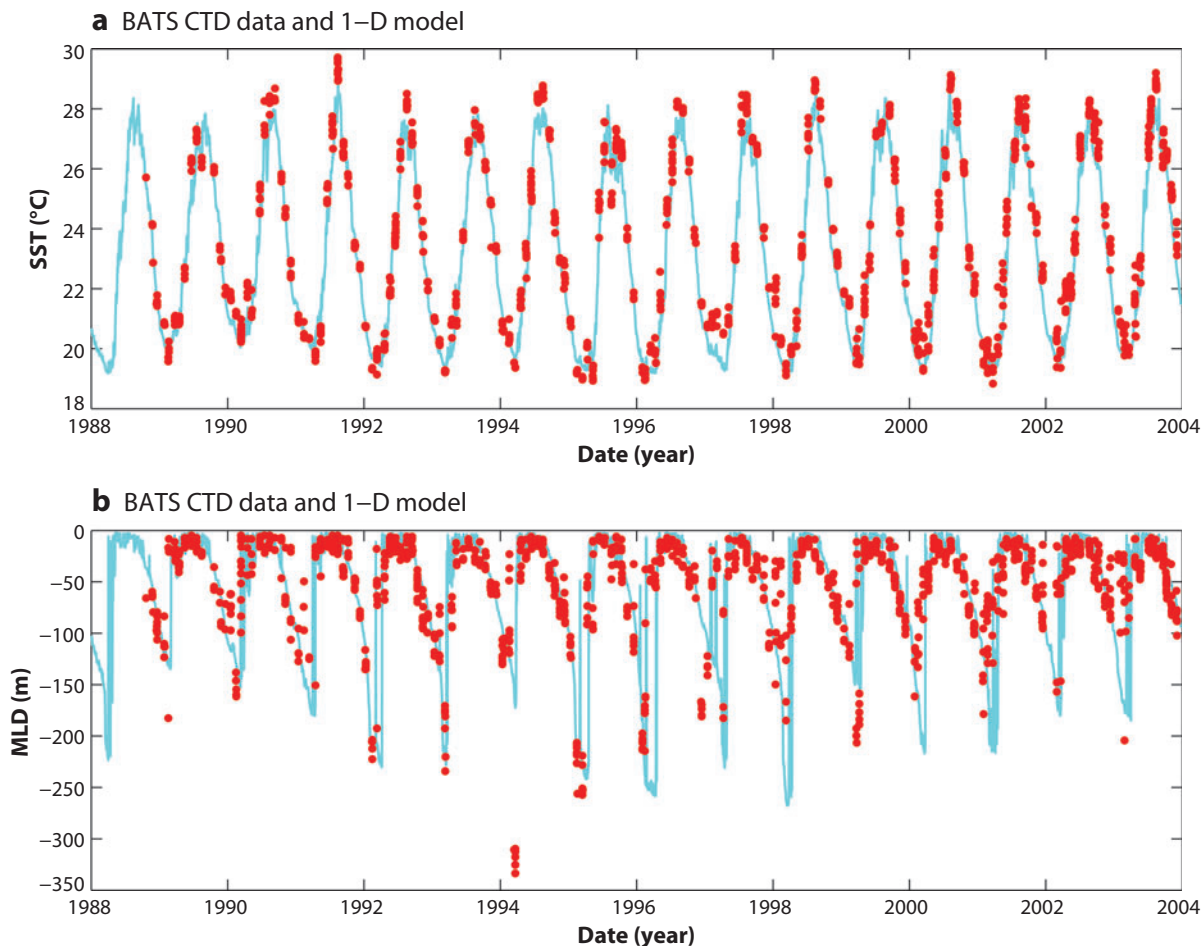


Figure 5

Seasonal and interannual variability in temperature (*a*) and mixed layer depth (*b*) from the Bermuda Atlantic Time-series Study (BATS) site. Observations are marked by red dots and results from the 1-D physical model are denoted by the blue line. SST, sea surface temperature; MLD, mixed layer depth. Figure generated as in Doney (1996) and Glover et al. (2002).

simulations have been constructed to document physical and biological interannual variability at time-series stations (Glover et al. 2002, McClain et al. 1996) (Figure 5).

Lateral (3-D) ocean circulation effects in Equation 1 are hidden in the unspecified left-hand-side term $LHS_{lateral}$. Unfortunately, local time-series data sets often provide little guidance on the magnitude (or even sign) and temporal variations of these lateral divergence terms (e.g., the net supply of nitrate from horizontal currents). Oftentimes these terms are simply ignored, at the peril of the simulation and the science. To compensate, lateral divergence terms estimated from 3-D simulations can be applied to local 1-D cases (Friedrichs et al. 2007). However, this practice may introduce new errors because 3-D simulations do not always perform well in direct comparisons against local data sets (Doney et al. 2008, Lima & Doney 2004, Oschlies et al. 2000). Also, even if the simulated seasonal cycle looks reasonable, the underlying balance between lateral nutrient supply and vertical nutrient supply, for example, may be incorrect (Fasham et al. 1993, McGillicuddy et al. 2003).

The ubiquitous, and often aliased, mesoscale variability in time-series records is another challenge for data interpretation and numerical modeling (Glover et al. 2002). Eddies affect ecology in a number of ways; for example they stimulate productivity in oligotrophic regions by injecting nutrients from the thermocline into the euphotic zone. Siegel et al. (1999) proposed an approach for BATS to estimate thermocline vertical displacements using satellite altimeter data. McGillicuddy & Kosnyrev (2001) took the next step, assimilating altimeter data into a regional-scale eddy-resolving model, from which lateral divergence fields can be estimated for 1-D studies.

Food Web and Biogeochemical Complexity

As one might expect, the wealth of new time-series data demonstrated a significant number of flaws in model formulations. In response, marine ecosystem models have evolved in complexity. Whereas the Fasham model (Fasham et al. 1990) followed only nitrogen and incorporated single groups for phytoplankton and zooplankton, today's state-of-the-art model often incorporates multiple limiting nutrients (e.g., nitrogen, phosphorus, silicon, and iron), multiple phytoplankton functional groups (e.g., pico/nanoplankton, diatoms, calcifiers, nitrogen fixers), and size-structured zooplankton (Hood et al. 2006, Le Quere et al. 2005, Moore et al. 2002). Simply adding more features, however, does not guarantee a more skillful model (Denman 2003). Selected examples drawn from BATS illustrate the synergy between ecosystem model advances and time series.

Numerous model studies target the BATS time series (1988–present) in the seasonally stratified and oligotrophic (low-nutrient) waters near Bermuda. The BATS data over the 1990s differed substantially from the 1960s data used by Fasham et al. (1990). Weaker nutrient inputs from winter convection together with high net primary productivity and low export flux into sediment traps result in simulations with substantially more regeneration in the upper ocean (lower *f*-ratio) (Doney et al. 1996). The picture of a low export system, however, is inconsistent with the measured large seasonal drawdown of surface water DIC (Michaels et al. 1994), which appears to have a biological origin on the basis of ¹³C data (Gruber et al. 2006). Subsequent BATS 1-D model studies have focused on mechanisms that could explain these discrepancies by decoupling upper ocean carbon and nitrogen cycles. Potential mechanisms include nitrogen fixation and nitrification as alternative sources of new and regenerated nitrogen at BATS (Hood et al. 2001), variable elemental stoichiometry, DOM export, and differential particle remineralization (Anderson & Pondaven 2003, Mongin et al. 2003). Other simulations exploit BATS observations on other biogeochemical cycles, including iron speciation (Weber et al. 2005) and organic sulfur dynamics (Toole et al. 2008). Although not targeted specifically at BATS, a number of modeling efforts are underway on how to incorporate the rapidly growing wealth of new molecular and genomic data on marine microbes and plankton into ecological simulations (Doney et al. 2004, Follows et al. 2007).

Bermuda data also provide an important venue for data assimilation experiments that use ocean ecosystem models. Many model parameters are not well constrained from field and laboratory data, and it is often unclear whether a poor model-data fit reflects inherent problems with a particular model structure or simply a poor choice of model parameters. Adjusting the parameters by hand is laborious and typically inconclusive. Fortunately, more formal inverse or assimilation methods are available to find the set of parameters that best fits the observations of a given model (Fasham et al. 1995), or in some cases to determine that a particular model is incapable of capturing the observations no matter what parameters are used (Fennel et al. 2001a, Spitz et al. 1998). Several of the assimilation studies at BATS used the Fasham model as a baseline, making modifications to parameter values, model functions (e.g., allowing for variable chlorophyll to nitrogen in phytoplankton), or increasing/reducing the number of model variables (Hurtt & Armstrong 1996, Spitz et al. 2001).

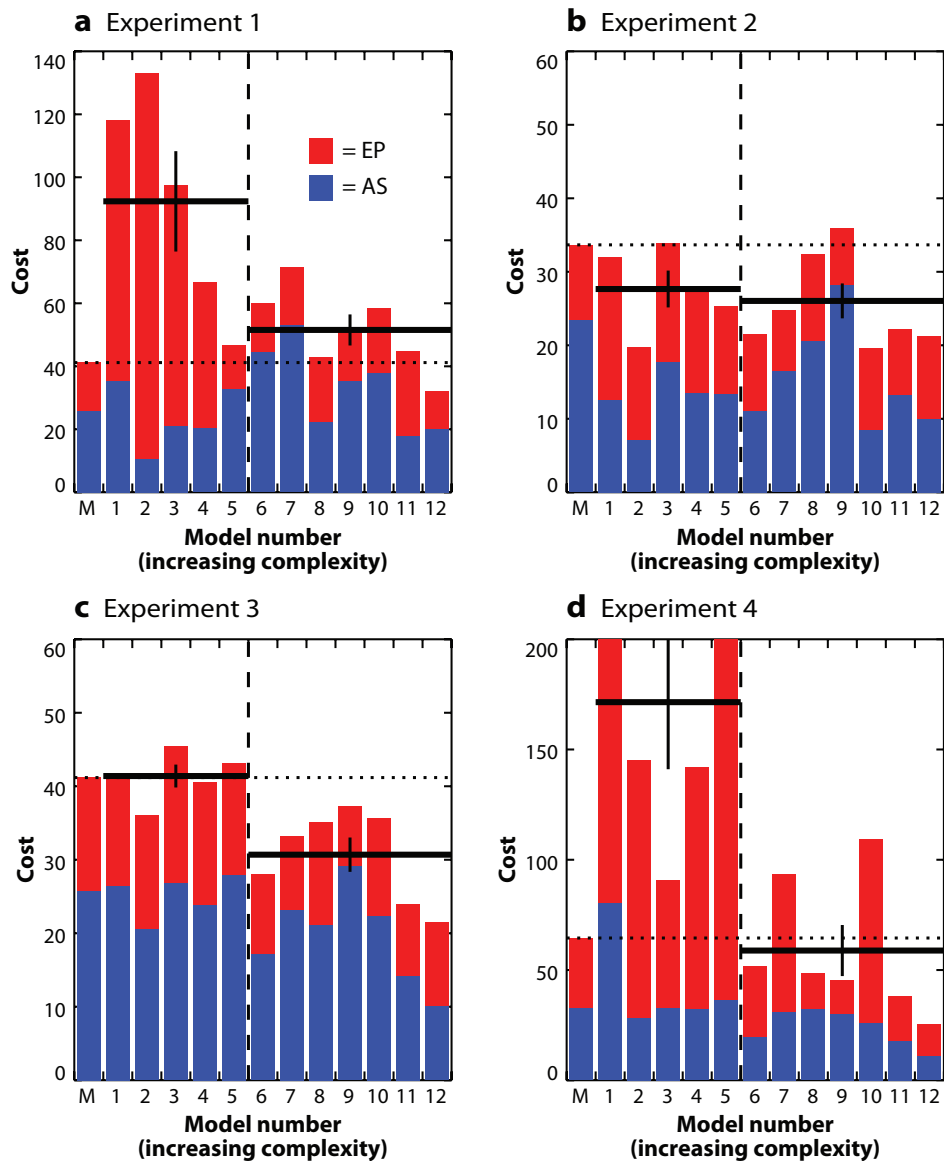


Figure 6

Cost function as a function of model number. A vertical dashed line separates the single-P models (Models 1–5) from the multi-P models (Models 6–12). Red bars represent the equatorial Pacific (EP) component; blue bars represent the Arabian Sea (AS) component. Bars lower than the dotted horizontal line (cost of Mean Model “M”) indicate that the model-data misfit is lower than that computed from the mean of the observations. Cost values are not significantly different if they vary by less than two. Two solid horizontal lines represent mean cost for the single-P and multi-P models, respectively; error bars illustrate one standard error. Note change in scales between panels: (a) Experiment 1: no optimization, (b) Experiment 2: individual optimization, (c) Experiment 3: simultaneous optimization, and (d) Experiment 4: cross-validation (portability experiment). Reprinted from Friedrichs et al. (2007). P, phytoplankton functional group.

Modeling emphasis varies by biogeographical regime. Nitrogen fixation is a major focus for the permanently oligotrophic HOT site off Hawaii (Fennel et al. 2001b), and iron limitation on phytoplankton growth is central to simulations in HNLC regions for Ocean Station P (Denman & Pena 1999), equatorial Pacific (Friedrichs 2001), and Southern Ocean Kerfix (Fasham et al. 2006). Bloom dynamics of fast-growing diatoms is critical for temperate regions, North Atlantic Bloom Experiment (Fasham et al. 1995), and KNOT in the western North Pacific (Fujii et al. 2002), as well as coastal upwelling systems such as Monterey (Gruber et al. 2006, Olivieri & Chavez 2000). A key question is whether any single model with a uniform set of parameters can capture the diverse behavior observed globally at local study sites (Laws et al. 2000, Moore et al. 2002). Some optimism is perhaps warranted. For example, Friedrichs et al. (2007) found that models with multiple functional groups and size classes are more portable across marine biomes (Figure 6). Moreover, in a 3-D North Atlantic simulation optimized to local station data, Oschlies & Schartau (2005) observed significant basin-scale improvement, even at locations not included in the optimization.

FUTURE ISSUES

National and international scientific planning efforts (e.g., Doney et al. 2004) consistently rank ocean ecological and biogeochemical time series as high priorities. However, a number of challenges confront the scientific community in their attempts to establish and, perhaps even more difficult, maintain research-quality ocean time-series programs. Issues range from the technical and logistical to the political and financial. Scientific demands will only intensify as we attempt to better understand how ocean ecosystems will change in response to future anthropogenic impacts and exploitation. Several key elements for ocean time series can be identified:

1. Existing ocean time-series efforts need to be maintained and, in many cases, expanded with routine sampling of additional biological properties, particularly on community structure, food web dynamics, and mesopelagic processes.
2. New time-series observation programs need to be initiated in critical, undersampled ocean regions, including regions sensitive to climate change and human impacts such as the temperate northern hemisphere, the Southern Ocean, and the heterogeneous coastal ocean. One approach would be to aggressively add biological and chemical instrumentation to the growing global network of open-ocean and coastal moorings, for example coordinated through the international OceanSITES program (<http://www.oceansites.org/>) or the emerging U.S. Ocean Observatories Initiative (OOI) (<http://www.orionprogram.org/OOI/default.html>).
3. The high-frequency time and space variability around time-series sites should be better characterized via the use of satellite and airborne remote sensing, autonomous moorings, gliders, and in situ sensors. These rich field and remote data streams should be combined with numerical simulations via data assimilation to create truly integrated observing systems.
4. Targeted process studies should be conducted in the vicinity of time series to better elucidate physical transport mechanisms and quantify the contributions of non-local processes to biogeochemical budgets on what are essentially Eulerian time records.

5. The scope of time-series observations should be broadened to include more extensive use of repeat transect observing programs on Antarctic resupply ships, mooring turn-around vessels, commercial ships, and cruise ships that routinely transit the same routes (e.g., Wanninkhof et al. 2007). International coordination could be facilitated through the International Ocean Carbon Coordination Project (IOCCP) (<http://www.ioccp.org/>) or similar groups.
6. New funding approaches are required that blend the stable, long-term support of operational funding with the requirement of delivering research-quality climate or earth system data records. Although much of the value in time series comes from their continuity and longevity, funding at present is commonly tied to repeatedly identifying “new” science questions and hypotheses.
7. Cross-site comparisons, data synthesis, and numerical modeling efforts should be strongly encouraged. An important first step will be the development of more systematic data management approaches (Glover et al. 2006) to ensure that the wealth of international time-series data is publicly available via centralized data portals and easily accessible in consistent electronic formats.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We acknowledge the dedicated multitude that forms the backbone of long-term oceanographic time series; much credit for these rich data sets is due to them. H.W.D. was supported by NSF grant OPP-0217282. S.C.D. was supported by the Center for Microbial Oceanography Research and Education (C-MORE; NSF CCF-424599). D.K.S. was supported by NSF grant OCE-0628444.

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Contents

Wally's Quest to Understand the Ocean's CaCO ₃ Cycle <i>W.S. Broecker</i>	1
A Decade of Satellite Ocean Color Observations <i>Charles R. McClain</i>	19
Chemistry of Marine Ligands and Siderophores <i>Julia M. Vraspir and Alison Butler</i>	43
Particle Aggregation <i>Adrian B. Burd and George A. Jackson</i>	65
Marine Chemical Technology and Sensors for Marine Waters: Potentials and Limits <i>Tommy S. Moore, Katherine M. Mullaugh, Rebecca R. Holyoke, Andrew S. Madison, Mustafa Yücel, and George W. Luther, III</i>	91
Centuries of Human-Driven Change in Salt Marsh Ecosystems <i>K. Bromberg Gedan, B.R. Silliman, and M.D. Bertness</i>	117
Macro-Ecology of Gulf of Mexico Cold Seeps <i>Erik E. Cordes, Derk C. Bergquist, and Charles R. Fisher</i>	143
Ocean Acidification: The Other CO ₂ Problem <i>Scott C. Doney, Victoria J. Fabry, Richard A. Feely, and Joan A. Kleypas</i>	169
Marine Chemical Ecology: Chemical Signals and Cues Structure Marine Populations, Communities, and Ecosystems <i>Mark E. Hay</i>	193
Advances in Quantifying Air-Sea Gas Exchange and Environmental Forcing <i>Rik Wanninkhof, William E. Asher, David T. Ho, Colm Sweeney, and Wade R. McGillis</i>	213

Atmospheric Iron Deposition: Global Distribution, Variability, and Human Perturbations <i>Natalie M. Mahowald, Sebastian Engelstaedter, Chao Luo, Andrea Sealy, Paulo Artaxo, Claudia Benitez-Nelson, Sophie Bonnet, Ying Chen, Patrick Y. Chuang, David D. Cohen, Francois Dulac, Barak Herut, Anne M. Johansen, Nilgun Kubilay, Remi Losno, Willy Maenhaut, Adina Paytan, Joseph M. Prospero, Lindsey M. Shank, and Ronald L. Siefert</i>	245
Contributions of Long-Term Research and Time-Series Observations to Marine Ecology and Biogeochemistry <i>Hugh W. Ducklow, Scott C. Doney, and Deborah K. Steinberg</i>	279
Clathrate Hydrates in Nature <i>Keith C. Hester and Peter G. Brewer</i>	303
Hypoxia, Nitrogen, and Fisheries: Integrating Effects Across Local and Global Landscapes <i>Denise L. Breitburg, Darryl W. Hondorp, Lori A. Davias, and Robert J. Diaz</i>	329
The Oceanic Vertical Pump Induced by Mesoscale and Submesoscale Turbulence <i>Patrice Klein and Guillaume Lapeyre</i>	351
An Inconvenient Sea Truth: Spread, Steepness, and Skewness of Surface Slopes <i>Walter Munk</i>	377
Loss of Sea Ice in the Arctic <i>Donald K. Perovich and Jacqueline A. Richter-Menge</i>	417
Larval Dispersal and Marine Population Connectivity <i>Robert K. Cowen and Su Sponaugle</i>	443

Errata

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