In the pelagic ocean, plankton collectively outnumber, outweigh, and outgrow all other living creatures. Thus it is no surprise that plankton ecology has been important at the Bedford Institute of Oceanography (BIO) almost since inception. At that time, it was envisioned by the Atlantic Oceanographic Group of the Fisheries Research Board of Canada that “The proposed program will include phytoplankton and zooplankton sampling, allied physical and chemical measurements, and examining correlations between abundance of planktonic fish food organisms and concentrations of commercial fish stocks” (Prakash 1964). Over five decades, in pursuit of this deceptively straightforward goal of a mechanistic causal link from one end of the food chain to the other, plankton ecologists have come to face the complexity and perplexity of marine ecosystems. In so doing, the ethos of plankton ecology has expanded. Starting from the post-WWII modernism of the so-called endless frontier of science, the ethos now includes the postmodern worldview of sustainability underpinned by pillars that include integration of social and natural sciences, harmonization of social goals and research agenda, and public participation and judgment (Sarewitz 1996).

This article is the story of narrowly selected scientific milestones in plankton ecology at BIO. It draws from and expands upon previous personal accounts (Clarke et al. 2003, Harrison 2006), to present the contribution to knowledge and experience of biological oceanographic science at BIO. The narrative is developed from accounts in the peer-reviewed primary literature, the body of knowledge from which the milestones of science can be gleaned.

Our stories reveal a coalescence of what science philosophers recognize as distinct worldviews. One is described by the physics metanarrative of unifying the hydrosphere, atmosphere, geosphere, cryosphere, and biosphere through reductionistic approaches. The other is described by the ecology metanarrative of holistic ecosystems at risk to society (Doel 2009). With an apology to G. E. Hutchinson who can be said to have invented modern ecology (Slack 2010), we first set out the human theatre and then present the plankton ecology play. The play is in six acts, starting with a prolegomenon and ending with a post scriptum. The actors appear in segued vignettes in the dress of their scientific publications.

**ONTOGENETIC ESCALATOR**

Biological oceanography is not synonymous with plankton ecology, but the fundamental activity of observing and measuring plankton proper.
ties has been the mainstay of the progenitor BIO Biological Oceanography unit and its lineal descendants. In its early stage, this unit included research on benthic ecology, fisheries ecology, and bioacoustics, all of which were later placed into other organizational units as BIO expanded. The plankton ecology unit has been sustained by what might loosely be termed an ontogenetic escalator (Conover 1988) of successive waves of scientists who enter and exit the Biological Oceanography stage according to individual career ontogenies (Fig. 1).

The full roll-call of actors in this five decade enterprise extends very considerably beyond the 20 full-time staff research investigators appearing on the escalator. The complete list includes many technical and administrative personnel whose names appear in the collection of annual (or biennial) reviews of the Institute, and the numerous reports and documents published throughout the years. Many other scientific researchers (pre-doctoral and post-doctoral) have also stepped on and off the escalator, and some of them will be leading or supporting actors in the story to follow. It is evident that there has been a great flux of keen minds and diligent hands across the stage. The singular thread that weaves through a great length of this history is the administrative polymath M. Landry, who, like the rotating chain loop on an escalator keeps a group of people moving in perfect synchrony towards their destination.

PROLEGOMENON TO ECOLOGY AND BIOGEOGRAPHY

The desiderata for the founding studies of Biological Oceanography at BIO were “the description of pathways and measurement of amounts and rates of transfer of energy in the biological communities” and “the structure and degree of organization of the biological system in nature” for “it is these features of the system which control the availability of the energy for transfer, either as food for plants and animals or as catches for fishing vessels” (Dickie 1965). This was a prescription for seeking the ‘commonplace’ (in the sense of Allen et al. 2005) between disparate realities: on the one hand, rate-dependent dynamic processes of energy transfer, and on the other hand, rate-independent (but time-dependent) structures of organized communities. That is to say, this was the work needed to establish a common starting point in the discourse of ecological function and structure.

Even today, this founding challenge remains inviting and exciting, but it was early observational work in St. Margaret’s Bay, Nova Scotia, that decisively led the way towards important insights. A study of the 1969 spring phytoplankton bloom in this bay (Platt and Subba Rao 1970) became a test of the hypothesis that links production and diversity over successional phases of an ecological community. For the first time at BIO, the disciplines of physics (underwater optics), chemistry (element flux), and biology (species taxonomy) were simultaneously brought to bear on a question of plankton ecology. Although some degree of empirical justification was found to support the prediction that energy flow and species diversity are related, the enduring impact of this work lay in its perceptive conclusion that a distinction needs to be drawn between short-term and long-term responses of an ecological system. Confusion of many different time scales was an important weakness of ecological theories of the day.

As goes time, so goes space. And so it was inevitable that questions arose about relevant scales in physical space. After all, if plankton are to be defined as organisms unable to maintain their distribution against the movement of water masses, how is this to be reconciled with their biological propensities for growth and motility? Are plankton no more than so-called passive scalars only to be regarded as diffusive contaminants in fluid flow? Obviously not, because at least in the vertical plane, where
turbulence permits, they are arranged quite nicely. How does this happen? This problem became tractable after a method was developed at the Scripps Institution of Oceanography for the continuous measurement of fluorescence from the chlorophyll pigment in living phytoplankton cells. For the first time, it was possible to map the spatial properties of both a physical water mass characteristic and a plankton characteristic at the same level of detail. Thus in 1973, water temperature and fluorescence were simultaneously recorded at 1 s intervals from sea water pumped aboard a ship travelling at 3 m/s in the St. Lawrence estuary for tens of kilometres at a run. The quantitative nature of physical-biological interactions in the sea became immediately apparent with an elegant covariability analysis of the data (Denman 1976). At times, phytoplankton are strongly distributed by physical mechanisms such as vertical displacements associated with internal waves or other non-uniform water motions with significant vertical transport. At other times, phytoplankton appear to grow fast enough so that structure on the kilometre scale in the horizontal is relatively long-lived despite the dispersive effects of the non-steady fluid motions. A picture thus emerged of spatial complexity in phytoplankton distributions that put to rest any notion of a facile or unique explanatory mechanism.

As both time and space together go larger in scale, so goes ecology towards biogeography. And so it became clear that organism life histo-

N. cristatus, N. sp.) can be mapped onto a typology of generalized life cycles. Species have adapted to the constraints of ice, temperature, salinity, light, and food (i.e., phytoplankton) availability by having one generation per year, several generations per year, or requiring more than one year per generation. Ecological processes of abiotic and biotic interactions affecting plankton organisms, populations, and communities thus nest hierarchically towards biogeographic processes of speciation, extinction, range expansion, or contraction.

The space-time vista of plankton ecology and biogeography explored in these and other related studies was foundational. This conceptual seascape became the commonplace for much research within Biological Oceanography at BIO and is the leitmotif for the story in this paper. It eventually led to a seminal turning point in oceanography when we, as Smith (1999) declared, moved from the multidisciplinarity of ‘The Oceans: Their Physics, Chemistry and General Biology’ (Sverdrup et al. 1942) to the interdisciplinarity of ‘The Ecological Geography of the Sea’ (Longhurst 1998).

CATALYSTS AND ENABLERS

It is a truism that technological innovations, both hard (instruments) and soft (methods), accelerate scientific progress. In Biological Oceanography, some of these developments lowered the barrier to rapid progress by catalysing a novel solution or by improving an existing approach; other developments enabled a breakthrough into new applications. While phytoplankton ecologists were making rapid progress at mapping chlorophyll with in situ fluorometers, zooplankton ecologists were likewise devising sampling systems capable of resolving the horizontal and vertical distributions of mesozooplankton and micronekton on small and intermediate scales. The requirements for such a system were met in the eponymous BIONESS (Bedford Institute of Oceanography Net and Environmental Sampling System), which is a multiple opening and closing net system equipped with environmental sensors (Sameoto et al. 1980). As BIONESS is towed, it is slowly lowered along an oblique path to the desired depth where animals are to be collected (Fig. 4). Ten nets are sequentially opened and closed at different depths to resolve vertical distribution. BIONESS can accommodate sensors for temperature, conductivity, fluorescence, depth, illumination, pitch, roll and yaw, and net closure together with internal and external flowmeters. An underwater camera and strobe flash can also be added to the top sides of the frame for the purpose of photographing the animals in front of the sampler to detect any signs of net avoidance. The successful operation of BIONESS in many studies provided the necessary depth-resolved estimates of mesozooplankton and micronekton abundance to consider questions of ecological distribution previously considered intractable. Here, a universal scientific innovation was created by in-house design and construction capacity within the BIO System Engineering and Metrology Groups.

Necessity was also the mother of the invention that led to what arguably might be considered an opening into vast new possibilities for phytoplankton field research. Faced with a problem that the characteristic time for phytoplankton acclimation is shorter than the usual time needed to measure the physiological process at sea, a device was developed to permit the measurement of the short time-scale response of phytoplankton photosynthesis to changes in available light (Lewis and Smith 1983). A temperature-controlled incubator was fabricated for measuring the amount of radioactive bicarbonate taken up by phytoplankton in a small volume of suspension (1 ml) over a short incubation period (20 min) with a sufficient number of samples (36) across a light gradient. The outcome was a plot of many data pairs showing the relationship between biological uptake of carbon-14 and available light, the so-called photosynthesis-irradiance (P-I) curve. The physical device, termed a photosynthetron, was modular in design so that later modifications (by the authors themselves and other researchers worldwide) were quite feasible. Most importantly, this innovation led to a rapid accumulation of data on the light-dependent parameters of photosynthesis that became the building block of a great deal of later work.

The photosynthetron promoted an extensive analysis of the functional dependence of photosynthesis on irradiance. The mathematical considerations required for this kind of analysis had already been established earlier (Jassby and Platt 1976), in which pragmatism dictated that the most suitable formulation ought to be based on the best fit between equation and data, and parsimony dictated that the only valid criterion

Figure 4. M. (Lewis) Kennedy deploying the BIONESS.
for judging the relative merits of the different formulations is their ability to describe data with the minimum number of well chosen parameters. Although revealing no new significant insight on the nature of the oceans, this work endures as a great catalyst in primary production research, being the most highly cited paper to date in the individual bibliographies of the co-authors.

Going forward in the same direction, namely using observational data to solve for the parameters of a model in a parsimonious fashion, a very large step was made by the first application of inverse formalism to the estimation of fluxes in plankton food webs (Vézina and Platt 1988). Normally, starting with a compartmental model of the food web, the aim is to project state variables using known parameter values and initial conditions. However, the number of independent observations that can usually be made is far less than the number of parameters needed to describe the system. Given this fundamental limitation, the inverse method reverses that procedure by estimating parameters from observations of the state variables. Since there are more unknowns than observations, the solution is generally indeterminate. Unlike conventional curve-fitting (such as to P-I data), inverse methods offer the possibility of diagnosing model behaviour given that flow networks need to conserve mass, to satisfy basic biological constraints, and to be compatible with the observed structure of the food web. Importantly, inverse models are not meant to, and do not reveal new phenomena.

Discovery had to come from elsewhere – in this case from looking at plankton cells one by one with new electronic eyes. Unlike the BIONESS and the photosynthetron, the pedigree of the flow cytometer lies outside BIO. However, fluorescence-activated analysis of individual plankton cells in ocean waters using commercial off-the-shelf instruments manufactured for biomedical laboratory applications was no less a signature development at the Institute. The technique of measuring particles suspended in a very small volume of sea water utilizing the principle of wavelength-specific fluorescence emission following monochromatic excitation allows for rapid, accurate, and precise analysis of plankton cells of different kinds (Fig. 5). This enabling technology led to breakthroughs in several related areas of marine microbial ecology. These include the discovery of a previously undetected phytoplankton group (Li and Wood 1988) earlier predicted as a necessary closure element (Li et al. 1983), the reconciliation of the picophytoplankton size class by reductionistic analysis of its components (Li 1994), and the semi-automation of bacterioplankton enumeration (Li et al. 1995; Fig. 6).

In these advances, we see technology exerting a transformational effect on plankton ecology, leading to a broader exploration of the oceanographic space-time vista by seeking patterns of regularity at a variety of scales (Li 2009, Li and López-Urrutia 2013). From hours to weeks to seasons to years to decades, from the Compass Buoy location in Bedford Basin (Fig. 7) to a grid of stations on the Scotian Shelf to sampling transects across other large marine ecosystems, it is possible to discern cross-scale regularity in the way that phytoplankton respond to their environment (Li et al. 2010). In earlier times, confusion of many different scales was an important weakness of ecological thinking. Only recently are we able to peer through this confusion through multifocus lenses that range through these nested scales.

**PROCESSES AND MECHANISMS**

With visions of the big ecosystem picture never far from mind, the devil is inescapably in the mechanistic details. The processes are anabolic (such as nutrient assimilation, photon absorption, ingestion, and growth) and catabolic (such as respiration, excretion, egestion, and autolysis), all un-
under a strong degree of hydrodynamic control (such as mixing, turbulence, and advection), and made greatly complex by food web transfers, system feedbacks, and non-linear interactions. Storytelling and hand-waving are compelling semiotic devices; however, they fail to adequately portray the scientific groundwork that has been done by sheer tireless effort. So attention is now turned to some of those at BIO who have crafted the building blocks, but may sometimes be forgotten by those who later construct the edifice.

**Primary Production**

Primary production is *de novo* synthesis of living material from simple molecules using energy from light or chemicals. The biochemical process of photosynthesis can be measured by the consumption of reactant (carbon dioxide) or by the appearance of product (oxygen). The stoichiometric balance between carbon assimilation and oxygen evolution is seasonally variable in Bedford Basin (Irwin 1991), depending on several factors, including the chemical form of the inorganic nitrogen source.

Whether exogenous nitrogen is present as nitrate, ammonium, urea, or other organic form, phytoplankton have an essential need for this growth-limiting element. Although the kinetics of nutrient uptake and regeneration are complicated, they can be examined by comparative analysis of short-term isotope tracer experiments (Harrison 1983a, 1983b). These are processes underpinning a commonly observed pattern: namely the vertical separation in the water column between the depths of maximum chlorophyll and maximum primary production (Fig. 8). Phytoplankton biomass and metabolism are vertically ordered to a large extent on the balance between physically and biologically mediated supply of limiting nutrients (Harrison 1990).

In fact, biota and nutrients are vertically structured even at the centimetre scale of arctic sea-ice microbial communities. Compared to planktonic systems, vertical gradients in light and nutrients are highly intensified through sea ice, giving rise to compact distributions of ice algae at very much higher concentrations than in the underlying water. Variations in light and nutrient invoke acclimative physiological changes in the cellular composition of algae. These changes are the same for epontic and planktonic algae, except that the changes are expressed over centimetres within the ice and over meters in the water column (Smith et al. 1990). But the condition of extreme low photon flux at the bottom of the ice layer has given rise to a uniquely adapted obligate shade epontic flora. Experiments conducted in Resolute Bay using a photosynethron demonstrated that the optimal irradiance for resident ice algae is well within the dynamic range for the most energetically efficient photosynthesis (Cota 1985).

It is not surprising that algae are well adapted to their environment, whether under the ice in the epontic community, or in the phytoplankton community of the water column. Still, it is quite remarkable that for such a diverse group, the main characteristics of their photosynthetic physiology can be fairly well represented by a small number of apparently simple rules. One of the most pervasive relationships in biology is that between metabolic rate and body size. It turns out that such a relationship holds true even within a single taxonomic class. Thus, for diatoms, the relationship between photosynthesis and cell size is controlled by self-shading of chlorophyll a pigment and by the ratio of surface area to volume (Taguchi 1976).

More generally, cost-benefit analysis of the energy balance involved in algal physiology confirms the competitive advantage of small cells over large cells due to enhanced catalytic efficiencies of growth and light absorption (Geider et al. 1986). Even within a single species, different ecological types are found that possess biochemical and physiological characteristics finely tuned to environmental conditions. By experimentation on different isolates of the same species collected from waters of different oceans, it was demonstrated that the cellular light-harvesting machinery and the quantum efficiencies for converting photons to biomass differ amongst strains of *Prochlorococcus marinus* according to the light environment of their particular native habitat (Partensky et al. 1993).

The physiological response of algae to their environment can however sometimes be counter-intuitive and seemingly maladaptive. For example, although high enzyme catalytic efficiency is a general metabolic adaptation to low habitat temperature, phytoplankton in arctic waters exhibit high activation energies (low efficiencies) for Rubisco, the catalyst of the primary carbon fixation process in photosynthesis. A possible explanation lies in hydrodynamics. It seems that in the Arctic, absolute temperature may be less important than the temperature structure of the water column in relation to irradiance, the limiting factors for growth, and the exploitative strategy of the characteristic species. Indeed, the enigmatic enzyme results can be understood as an opportunistic strategy that retains an energetically inefficient carboxylating metabolism but which can confer high reproductive rates under advantageous circumstances (Smith and Platt 1985; Fig. 9).

Clearly, vertical water movement that carries phytoplankton within a well-mixed layer bears important implications for photosynthesis in the resulting fluctuating light field. Deductions can be made by knowing, first, if the light field to which the freely circulating population is exposed is substantially more variable than that experienced by a contained population; and second, if the photosynthetic performance of phytoplankton in fluctuating light is different from the response measured in constant light (Gallegos and Platt 1985). These ideas were tested experimentally using a clever analog device that simulated vertical water motions (Gallegos and Platt 1982). Under conditions of moderate forcing such as in the Arctic, vertical mixing has little quantitative effect on water column primary production because the population is uniformly adapted to near-surface conditions.

From the Arctic to the subtropical Atlantic, questions were asked at BIO about how the intrinsic growth of phytoplankton is limited in the ocean. A great deal of evidence indicates that at ecological time scales, the availability of exogenous nitrogen is often limiting to the needs of phytoplankton. However, early studies from the Bermuda Biological Station and the Woods Hole Oceanographic Institution had suggested...
a possibility that iron is in fact the critical element in shortest supply. Results from those studies in the Sargasso Sea were inconclusive because artificial iron contamination of seawater by experimental manipulation could not be ruled out. These early results became even more enigmatic when others realized that iron limitation was indeed prevalent in other oceans (e.g., tropical and subarctic Pacific Ocean, Southern Ocean), but not the Atlantic Ocean because of differences in the stoichiometry of nutrient supply and phytoplankton demand. New experiments were therefore conducted in the Sargasso Sea with fastidious attention to metal-free techniques, leading to a conclusion that subtropical North Atlantic phytoplankton were indeed not limited by the supply of bioavailable iron (Subba Rao and Yeats 1984). Thus, we can now surmise that in these waters, purposeful enrichment with iron will generally not lead to enhanced fertility nor accelerated drawdown of carbon dioxide to mitigate atmospheric warming.

Nitrate supply to the upper water column is therefore of over-riding concern in North Atlantic primary production. The question then becomes economic: is the supply of nitrate from vertical flux sufficient to meet biological demand? To quantify supply, it is necessary to measure the concentration of nitrate (which is relatively easy) and the vertical eddy diffusivity (which is difficult). At BIO, shear probes that measure high-frequency fluctuations in the vertical gradient of horizontal velocity enable the dissipation rate of turbulent kinetic energy to be estimated (Oakey 1988). To quantify demand, concurrent measurements are required for primary production and nitrogen uptake. This type of study indicates the importance of turbulent mixing to new primary production, but other mechanisms such as upwelling cannot be ruled out, especially when supply does not meet demand as appears to be the case in summer on Georges Bank (Horne et al. 1996).

Supply of nitrogen can be met in another way, not from outside the system, but from within the biological community itself. This is possible because phytoplankton can use different chemical forms of nitrogen. The regeneration of ammonium by bacteria and other microheterotrophs supplies recycled nitrogen to support a significant proportion of primary production in Bedford Basin (LaRoche 1983) and the Scotian Shelf (Cochlan 1986). In fact, phytoplankton may prefer to utilize ammonium over nitrate even when the latter form is plentiful. Primary production supported by regenerated nitrogen (ammonium) tends to be packaged in small phytoplankton cells, whereas that supported by new nitrogen (nitrate) tends to packaged in large phytoplankton cells. These differences can lead to alternate secondary transformations further along the food chain.

Secondary Production
Secondary production is the assimilation of organic matter made available by primary producers to organisms that use the energy for maintenance, growth, and reproduction. By and large, a great deal of primary production is routed through the microbial food web of single-celled organisms (bacteria, archaea, protists). Much less of the primary production is transferred directly to multicellular animals, which are often portrayed in a stacked pyramid from herbivores, to carnivores, ending at an apex consumer. Indeed, it is often not realized that the largest reservoir of organic carbon in the ocean is in fact non-living. This carbon exists in various physico-chemical forms as dissolved, colloidal, or particulate entities in seawater (Kepkay 1994). To greater or lesser extents, according to their biochemical lability or recalcitrance, these entities are the organic substrates supporting secondary production of most bacteria and archaea.

In a commentary on the place of microbial ecology in marine ecosystem science at the beginning of this century, L.R. Pomeroy (2001), a BIO Hunstman Award recipient, wrote: “Old paradigms die slowly, Thomas Kuhn told us mainly through the death of their adherents. Many fisheries scientists do not yet believe it, but the marine food web consisting principally of diatoms, copepods, and fishes is now generally seen as an occasional excursion from what is normally a microbial food web”. The Kuhnian assessment of science moving ahead one funeral at a time is rather dark, but perhaps mostly true. Exceptions are notable by their vigour (e.g., Longhurst 1998). Even in the eastern Canadian Arctic with large populations of charismatic apex consumers such as ursideans, cetaceans, pinnipeds, and seabirds, the flow of primary production through single-celled microbes can be substantial. Experimental measurements indicated that summer communities of ciliated protists in Jones Sound and Baffin Bay have the potential to consume up to about one half of the primary production on a daily basis. The transfer of energy and the recycling of nutrients assigned to this microbial community are evidently no less at high latitudes than at lower latitudes (Paranjape 1987).

The large pool of non-living carbon in particulate form did not escape the notice of those who study the diets of multicellular zooplankton. It was reasoned that if non-selective grazing is common among small copepods such as *Pseudocalanus minutus*, unsselective feeding based on available particle size should not distinguish between living and non-living particles if the sizes of the two fractions are similar. Thus, the feeding activities of such copepods should lead to maximum ingestion of those sizes of non-living particles which have the highest concentration in seawater, unless the particles are too small to be filtered. In a year-long test of this hypothesis in Bedford Basin, it was indeed shown that non-living particles cannot be considered only as a supplemental food source for small copepods, but that they are a basic food for *P. minutus* at all times (Poulet 1976).

The availability of food to zooplankton is highly variable over time. Yet, for digestion to occur, the appropriate enzymes must be active. Thus the length of time necessary to induce the enzymes may be a factor in adapting to increasing food supply. A strong test of the hypothesis that zooplankton feeding rates are associated with induction of digestive enzymes can be made during a phytoplankton bloom. Presumably, correlation between enzyme activity and food supply might be strongest during a period of accelerated primary production. In such a test carried out in Bedford Basin in the spring of 1977, this hypothesis was generally supported, but the results required careful interpretation because the structure of the zooplankton community underwent large changes (Mayzaud and Conover 1984).

A well-designed combination of experimentation and observation is the cornerstone of the scientific method. For the investigation of copepod feeding behaviour, it is important to know the state of the copepod gut at a place and time in the ocean (in situ), the response of the copepod under experimental manipulation (in vitro), and the rate of ingestion measured in the gut (in vivo) accounting for clearance and turnover (Head 1988; Fig. 10). A mechanistic understanding of food ingestion and egestion at the level of individual animals was an important step towards a wider appreciation of the strong impact that food availability exerts on the life history and population ecology of copepods.

Macroecological characterization of the copepod-phytoplankton linkage came from large scale multidisciplinary oceanographic programs. When the animal habitat is surveyed over a geographic area sufficiently large that distinct ecological sequences can be identified, the observations then constitute results from a pseudo-experiment in which nature itself has provided the changed conditions useful for strong inference. Thus in the Labrador Sea, the relationship between food supply and copepod development can be inferred by substituting a survey over space for a sustained sequence over time, invoking the ergodic principle. In nature’s pseudo-experiment, food (phytoplankton) is made available to the copepod at different levels, depending on place, but because of differences in time relative to the bloom. By measuring *Calanus finmarchicus* egg production rates and animal stage distributions in three areas of the Labrador Sea designated by the state of the phytoplankton bloom (early, mid- and late/post-bloom), it is clear that the timing of the spring bloom may have a significant impact on recruitment to the next generation (Head et al. 2000).

The importance of maintaining phase coordination between a dominant grazer such as *C. finmarchicus* and its dynamic forage is profound, especially in view of climate variability. Yet in the face of changing external conditions of temperature and phytoplankton availability, the proximate determinants of ontogenetic status remain an outcome of highly complex internal processes such as gonad maturation (Campbell and Head 2000). Mechanistic reductionism has its limits in complex adaptive systems.
 Processes and mechanisms explain cause and effect in plankton populations based on possibilities presented by initiating conditions. No less important are the constraints imposed by boundary conditions, but these need to be sought at a higher encompassing level, which might be called the biological seascape. The biological seascape denotes a spatial organization, but it has a broader connotation that recognizes the importance of biology to spatial architecture. A most vivid case of this is the shape of the vertical profile of chlorophyll $a$ in the ocean. A typology of the deep chlorophyll maximum layer can be constructed based on the interaction between hydrography and growth, behaviour, or physiological adaptation of phytoplankton, as well as the grazing effects of zooplankton (Cullen 1982). These class types constrain known possibilities, but the actual manifestation at any particular time or place cannot be confidently predicted because idiosyncratic contingencies lead to indeterminate outcomes.

A huge step was then taken towards a global organization of the biological seascape by construction of a typology for seasonal cycles of pelagic production and consumption (Longhurst 1995). The well-known Sverdrup critical depth concept for the induction of phytoplankton growth forced by local mixing and light is the starting point for the seasonal evolution of primary production, and this is very much related to regional oceanography. However, the accumulation or loss of phytoplankton biomass is influenced by secondary processes, such as variation in the size of the herbivore population at the start of the bloom. In extending the Sverdrup model to all parts of the ocean, a typology of plankton cycles is necessary that describes a continuum from strongly seasonal regions with seasonal recharge of photic zone nutrients to weakly seasonal regions where nutrient renewal of the photic zone is slow or episodic and where productivity is largely fuelled by internal nutrient regeneration. Along this continuum, phytoplankton and zooplankton exhibit characteristic features of ecological structure and function that arise as outcomes of systemic behaviour.

A full exposition of this organizational scheme into a rational partition of the global ocean was a landmark in many respects. At its root, this ecological geography (Longhurst 1998) addresses the fundamental issues of pelagic ecology and biogeography, which distill to whether, at some level of probability, a deduction may be made about the characteristic features of any region. Here, the definition of region is crucial since it determines the scale of the biological seascape. By placing the typology of seasonal plankton cycles into the context of regional oceanography, characteristic features of ecology can be discerned at two hierarchical scales. The higher level comprises a small number of large compartments (biomes), and the lower level comprises a large number of smaller compartments (provinces).

The first application of this geographic approach was the computation of regionally and seasonally differentiated primary production in the North Atlantic using local algorithms of a light-dependent model of photosynthesis combined with satellite-derived chlorophyll data (Sathyendranath et al. 1995). In a tour de force of reductionism, whereby the whole is constructed from the sum of its parts, the total annual production for the North Atlantic basin of 10.5 gigatons of carbon per year has been computed as the sum of values from 19 separate geographic compartments. The partitioning respects the realities of regional diversity in ocean ecology, and the summation achieves an integration for the basin. Like the Cullen typology of chlorophyll profiles, the Longhurst (1998) typology of pelagic ecosystems constrains possibilities but admits indeterminacy at fine local scales.

It is possible to operationalize the Longhurst typology for ecological characterization at local time and place, but this requires a computation algorithm based on statistical analysis of geophysical and biological data to delineate irregular dynamic boundaries of the provinces in real time. Thus, instead of climate averaging into a static arrangement of provinces with rectilinear boundaries, high resolution satellite data on sea-surface temperature and ocean colour are used in an objective statistical method for accurately defining the boundaries (Devred et al. 2007). With a spatial resolution of 2.25 km$^2$ (1.5 x 1.5 km), this approach down scales the seascape towards what might be measured from ships at sea.

In so doing, the distinction between a partition and a continuum approach becomes increasingly blurred, emphasizing that the approaches are not mutually exclusive. On the one hand, biomes and provinces highlight ecological regularities, or in other words, the general constraints drawn by the rules of nature’s necessity. On the other hand, a macroecological continuum represented by a very large ensemble of interacting biological units highlights a statistical manifestation covering the range of known possibilities allowed by nature’s flexibility. The pattern of plankton diversity and water stratification revealed in ecological partitions is a motif no less evident when the biological seascape is drawn upon the shapes and boundaries of statistical distributions of phytoplankton in the North Atlantic (Li 2002).

The indicators of the structure and functioning of environmental systems at large spatial and temporal scales (i.e., macroenvironmental indicators) have potential to provide scientific insights and policy guidance, but must be carefully selected for scientific credibility to the public, for salience to decision makers, and for legitimacy to all stakeholders (Orians and Policansky 2009). All of these considerations were important in the scientific advice delivered to shape a conservation strategy for a large submarine canyon (The Gully) on the eastern Scotian Shelf (Harrison and Fenton 1998). The strategy includes environmental monitoring with regional coverage of a large number of measured variables, among which some plankton indicators serve as diagnostic clues for the status and trends of the ocean. Year-to-year changes in phytoplankton and zooplankton can be scored to indicate complex ecological processes (Harrison et al. 2009), forming the nexus between driving forces and pressures on the one hand, and impacts and responses on the other hand (Shackell 2011). At the 50-year mark of BIO, we have a 50-year record of phytoplankton and zooplankton in the Northwest Atlantic (Head and Pepin 2010), which leads us into the future.

**ECOLOGICAL FUTURES**

Ecological futures, that is the futures of ecological systems, are the future consequences of present choices. At this point, scientific research moves from the work station to the town hall. Here, scientists try to build an ecology of the “long now” (Carpenter 2002) for management facilitators,
policy thinkers, and decision makers. In common parlance, “now” means yesterday, today, and tomorrow; “yesterday” means last year, this year, and next year. Thus, “long now” can mean last decade, this decade, and next decade, or even longer. It emphasizes that past events shaped present ecosystems, and that current actions influence future states. Nowadays, plankton ecology at BIO is an ecology of the “long now”. Following a decade of Joint Global Ocean Flux Study (JGOFS) out of which ocean ecology and biogeochemistry became inextricably intertwined, the birth of systems-based observation networks to record the “long now” was realized. Thus emerged the Atlantic Zone Monitoring Program (AZMP) for the Scotian Shelf and adjoining shelf areas, the Atlantic Zone Off-shelf Monitoring Program (AZOMP) for continental slope and deeper waters of the northwest Atlantic, and the Bedford Basin Monitoring Program (BBMP) for the harbour waters that give BIO its name.

Is it possible to establish a chained link of attribution to assess whether a specified set of drivers are the cause of an observed change in a specific system? When anthropogenic radionuclides are released from nuclear reprocessing plants into the English Channel or the Irish Sea, they are carried by ocean circulation on a relentless journey. They pass through the North Sea into the Norwegian Sea, then the Barents Sea, and into the Arctic Ocean, flowing through the Kara Sea, the Laptev Sea, over the Lomonosov Ridge, the Mendeleyev Ridge, around the Beaufort Sea, out of the Arctic through the Fram Strait, around Greenland, to the Labrador Sea, and onward. The journey takes many years, but it can be documented by measuring the radionuclides at fixed stations as the water flows by as time passes (Smith et al. 2011, Smith 2014). The future of a radionuclide particle released into the English Channel many years ago can be determined with fair confidence by making measurements today.

The transit of Arctic origin water continues down the Labrador Shelf and eventually arrives on the Scotian Shelf, but not before mixing with waters from rivers, from the Gulf of St. Lawrence, and from offshore. Unlike salt which is conserved, other chemical constituents such as nutrients and oxygen are not conserved during transit, being consumed or produced by biochemical processes over time. The Arctic signature of non-conservative inorganic entities in waters arriving on the Scotian Shelf is modified (Yeats et al. 2010). The complex interaction between temporarily variable advective and biogeochemical processes generates an ensemble of possible future outcomes for oxygen or nutrient concentrations. The challenge will be to designate the probable from the possible.

Are future states ineluctably pre-determined? Processes and mechanisms explain material, formal, and efficient causes. It is tempting to draw a deterministic future from these, but we would be wrong to do so. By this, we do not mean to tread into the teleology of final causation, although this should not be necessarily anathematic. The point we wish to make is that though ecosystem processes may not be random, they are indeterminate because organisms, unlike radionuclides or even nutrients and oxygen, are adaptive entities nested hierarchically in complex systems.

Futures cannot be observed. We can only forecast, predict, project, and explore scenarios. Empirical long-term scientific observations are the only validation that a storyline about futures is plausible, coherent, and consistent. In the Gulf of Maine, an observational time series approaching 50 years in duration records the history of the copepod community there. Changes in species diversity were greatest on interannual scales, intermediate on seasonal scales, and smallest across regions, in contrast to abundance patterns, which suggests that zooplankton diversity may be a more sensitive indicator of ecosystem response to interannual climate variation than zooplankton abundance (Johnson et al. 2011). With climate projections of a less saline more stratified surface ocean layer with possible consequent changes in the phytoplankton community, a future of a bottom-up induced change in zooplankton diversity seems plausible.

Plausible, yet uncertain, because another part of the story has yet to be considered, and that is from the top down. On the western Scotian Shelf, a decline in average body size of aggregate top predators (mainly finfish) was the dominant factor associated with the increase in prey species biomass (planktivores). In turn, declines in the abundance of larger zooplankton and increases in phytoplankton concentrations were weakly associated with the increase in prey species, suggesting that a weak trophic cascade has occurred. On the other hand, growing conditions for prey fish might have been enhanced by increased stratification (Shackell et al. 2010). Size-selective harvesting at the top of the food chain concurrent with changing climatic conditions propagating from the bottom up may lead to indeterminate ecological futures.

Scientific conjectures on ecological futures are the future of plankton ecology at BIO. Fifty years of ocean research and monitoring have prepared us well for this. As Smith (1999) presumed, it is not the snow, fog, and mud in Nova Scotia that will allow these salient conjectures to be made with credibility and legitimacy; instead it will be the creation of a reservoir of scientific knowledge that is shaped by societal norms in culture, politics, and economics. The paradox of creativity (Martin 2007) conveys a well-known ironic truth: that non-moral desires of self-fulfillment such as curiosity, truth-seeking, and appreciation of nature’s beauty (all tempered by conscience) are often a more effective path to moral benefits contributing to the well-being of human society than is directed service.

POST SCRIPTUM

A contrast between the denotation and the connotation of Bedford Institute of Oceanography is important. On the one hand, the denotatum has always been immutable: BIO is an eponymous organization for the natural science of the oceans. Arguably, this denotation has been more apt for biological oceanography than for any other discipline at the Institute since there has been a continuity of plankton research in the waters of the Bedford Basin itself, from early experiments in the 1960s to the ongoing plankton monitoring program in the 2010s.

On the other hand, the connotation of BIO mutates according to what is signified by prevailing bureaucratic culture as “doing science”. Science in the public interest is inherently a partially contradictory enterprise involving tensions between public goods and commercial goods, between development and conservation, between departmental mandates and political-economic imperatives, between macro and micro management policies, and between the department and its stakeholders (Doern and Kinder 2007). Viewing public sector science as an economic enterprise based on a market model of supply and demand in the community of knowledge challenges normative core science values (Hasselberg 2012). In other words, the meaning of “science” is made in ever changing contexts. Here, a semantic clarification by Day (2008) is helpful: “What we understand as science consists of three separate and distinct aspects, a dynamic body of knowledge (scientage), a process (scientody), and a profession (scientistry). This three-in-one works together in a unified manner that should be recognizable to the sufficiently educated, wherein the body of knowledge reigns supreme, the process offers the only way to the body of knowledge, and those who blaspheme against the profession will not be forgiven.”

In most of 50 years, “doing the science” of plankton ecology at BIO has been a tripartite success of knowledge, process, and profession. This account has shown that the success was a result of creative work undertaken on a systematic basis to increase the stock of knowledge (that is to say, research and development, R&D), aided to some extent by complementary activities (that is to say, related science activities, RSA) that extend R&D towards socio-economic outcomes.

To prognosticate, it has not escaped our attention that ecosystem theory (Holling 2001) predicts that after growth through innovation, followed by consolidation through capitalization, any complex system becomes susceptible to catastrophic collapse due to rigidity, inflexibility, and brittleness. The complex demands of postmodern scientity on a shrinking scientistry (Fig. 1) faced with an expanding scientage may be a harbinger of Holling’s omega phase. To ensure continuing perdurance of biological oceanography at BIO, it will be important to insist that science as a profession remains noble to its practitioners in the face of “narrow mandates and over-zealous accountability regimes in government” (Nicholson 2011), and that science as process is undertaken by stunted professionals assiduously engaged in the changing and growing edifice of knowledge. This insistence is a necessary, but sadly insufficient condition to ensure that in the coming years, there will always be oceanographers engaged in voyages of oceanographic discovery at the Bedford Institute of Oceanography.
ACKNOWLEDGEMENTS

This paper is dedicated to all those now passed away who were associated with the Biological Oceanography group. The Government of Canada has supported plankton ecological research at the Bedford Institute of Oceanography since its inception. I thank Glen Harrison and Erica Head for their help in the preparation of this article, and also Alan Longhurst, Ken Denman, and Charles Hannah for their comments on the draft, but all shortcomings are mine alone. The editorial advice and encouragement received from the editors is much appreciated.

REFERENCES


Nicholson, P.J. 2011. The value of marine research. keynote address, Dalhousie University Oceanes Week gala dinner, 4 June 2011. Dalhousie University, Halifax, NS.


BIO-Oceans Association announces the publication of a major treatise reviewing the history and marine research accomplishments at Canada’s Bedford Institute of Oceanography over five decades primarily in the Atlantic and Arctic Oceans

VOYAGE OF DISCOVERY

Fifty Years of Marine Research at Canada’s
Bedford Institute of Oceanography

Edited by
D.N. Nettleship, D.C. Gordon,
C.F.M. Lewis and M.P. Latremouille

Voyage of Discovery summarizes BIO research results on the oceanography of Arctic and Eastern Canada. In a series of 48 papers by past and present research staff from all oceanographic disciplines at BIO, the history of Canadian oceanography before BIO and a broad cross section of the Institute’s work spanning five decades are featured with particular emphasis on contributions to Canadian and global understanding/management of the marine environment.

Divided into 12 sections with a Preface and Epilogue, Voyage of Discovery is the most extensive overview of the history and scientific accomplishments of the Bedford Institute of Oceanography under one cover: Historical Roots, Arctic Studies, Ocean Life, Ocean Circulation and Chemistry, Hydrography and Seabed Mapping, Geological Oceanography, Fisheries-Ecosystems-Aquaculture, Marine Contamination, Technology and Instrument Development, Energy Developments, BIO and the Law of the Sea, and The BIO Experience. This book’s well-written and illustrated accounts will appeal to a broad readership from professional oceanographers and environmental/resource managers and decision-makers to marine science students and lay persons interested in the Arctic and Atlantic oceans, and their present status and future welfare.

Hardcover, text on premium 8.5 x 11 inch glossy 100 lb Sterling paper with sewn binding.
460 pages, 2.2 kg. Price: $35.00 Cdn/US plus shipping ISBN 978-0-9936443-0-6
BIO-OA Publication: November 2014

ORDER FORM

To order one or more copies of Voyage of Discovery, please complete order form below and send with payment (money order, cheque, credit card) or purchase order (for libraries, institutions, universities) to: ‘BIO-Oceans Association (VOD), c/o Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

Please send me ........ copies of Voyage of Discovery at $35 Cdn/US per copy ($36 if charged to credit card) plus cost of shipping per book (mailer & postage) if not to be picked up at BIO: Atlantic Canada, $13; Quebec & Ontario, $15; MB, SK, AB and BC, $17; Territories, $24; United States, $26; Europe, $34; and elsewhere, $39. For additional information: e-mail ‘bio.oceans@bedfordbasin.ca’ or phone 902-826-2360. Manner of delivery: [ ] pickup at BIO or [ ] send by mail.

Method of payment: [ ] I enclose cheque/money order (payable to BIO-Oceans Association) Amount: $ ________ Cdn/US
[ ] I wish to pay by credit card (circle type): VISA MC AMEX JCB Discover
Card Details: Account # Expire Date Security Code
Postal/Zip Code on billing address for card Phone #
Name E-mail address
Delivery name and address:________________________________________________________________________________________
________________________________________________________________________________________
________________________________________________________________________________________

With many thanks for your order from BIO-Oceans Association