## Title

Introduction: Sensitivities of marine food webs and biogeochemical cycles to enhanced ocean stratification



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Preface

# Introduction: Sensitivities of marine food webs and biogeochemical cycles to enhanced ocean stratification

This issue contains papers from a workshop on "Sensitivities of food webs and biogeochemical cycles to enhanced ocean stratification", one of the topic areas explored at the second international meeting (IMBIZO II) of the Integrated Biogeochemistry and Ecosystem Research (IMBER) Program. IMBER has the general goals of advancing understanding and predictive capacity for the ocean's ecological and biogeochemical responses to global change. As one approach to moving this agenda forward, IMBIZOs (*imbizo* is a Zulu word for gathering of people) are held approximately biennially, bringing scientists together to review current knowledge and identify key questions for future research in three concurrent but interactive topical workshops.

IMBIZO II, broadly focused on regional oceanographic studies, was hosted in October 2010 at the Cretaquarium and Hellenic Center for Marine Research in Crete, Greece (Fig. 1). It involved 120 participating scientists from 26 countries who presented results and discussed outstanding issues relating to three areas: (1) the effects of varying elemental ratios and food quality in marine food webs; (2) large-scale regional comparisons of marine biogeochemistry and ecosystem processes; and (3) stratification effects on marine food webs and biogeochemical cycles. Contributions to Workshop #2 on research approaches and results of comparative ecosystem studies have recently been published as a special issue of *Journal of Marine Systems* (Hood et al., 2013). Here, we provide an introduction to the contributions from Workshop #3.

Increased stratification of the upper oceans is a predicted general consequence of global climate warming. The implications for food webs and biogeochemical cycling, however, remain poorly quantified and inadequately understood on regional to global scales. Enhanced thermal stratification can directly impact nutrient fluxes, metabolic rates and balances in the euphotic zone. Changes in the onset and strength of stratification can both increase or decrease the magnitude of seasonal production cycles, depending on environmental context. Possible ecological and biogeochemical sensitivities include: altered biomass, size structure, composition and diversity of the plankton community; timing effects on the coupling of production and grazing processes, trophic controls and reproductive cycles of key species; alterations in the ratios of nutrient availability, utilization and remineralization within the euphotic zone; and modified rates and pathways (particle flux, DOC, active migrations) of carbon and nutrient export out of the euphotic zone and through the underlying deep-sea water column. Significant uncertainties on many levels, including changing boundary inputs from adjacent systems (e.g. Rykaczewski and Dunn, 2010), make the net effects of such alterations, positive or negative, poorly resolved on regional bases.

The stratification workshop drew together perspectives from regional comparisons in the contemporary ocean, from paleo-reconstructions of past ocean conditions, and from models extending to future scenarios. Participants considered general organizing principles, major unknowns, and strategies for further study. Resulting recommendations emphasized the continuing need to improve understanding of regional ocean ecology and biogeochemistry and their interactions, but they also noted a need to focus attention on organisms/strategies that may be selected for by enhanced stratification (e.g. diazotrophs, mixotrophs, specialized niche diatoms, gelatinous suspension feeders and predators) and that can impact ocean biogeochemistry in significant ways. To better anticipate system responses, feedbacks and regional linkages associated with climate change, global models need to account explicitly for such unconventional strategies and more accurately reflect the coupled physical processes (land–ocean–air) that drive critical resource and population exchanges among and within regions.

Kemp and Villareal (2013) lead off the volume by challenging conventional wisdom that diatoms will greatly decrease with increased warming and stratification, leading to replacement by smaller phytoplankton and diminished productivity and carbon export. Their counter-argument considers specific diatom adaptations to low-light growth in the deep euphotic zone and diatom–diazotroph symbioses that afford niche advantages that maintain seed populations for opportunistic blooms. Evidence is presented from paleo-oceanographic as well as contemporary studies that diatoms with such strategies are often bloom and export dominants, even under strong stratification and oligotrophic conditions. Currently, such strategies are inadequately represented in parameterizations of diatom capabilities that go into most models of ocean ecosystems.

Schmoker and Hernández-León (2013) provide another example of marine food web response to increased stratification that runs counter to expectation. Their study region, the Canary Current, has experienced progressive warming and decreased productivity in recent decades. The surprising result of their fine-scale temporal sampling over two years of differing seasonal stratification is that picophytoplankton decease, rather than increase, in relative importance to total phytoplankton during the periods of water-column stability. Food-web path analysis, based on correlations among organisms occupying adjacent trophic levels, support, in part, a top-down explanation for this finding – picophytoplankton are controlled by microzooplankton grazers when they, in turn, are released from grazing pressure by reduced mesozooplankton predation during oligotrophy. Overall, results of the study indicate that small inter-annual differences in temperature and stratification can lead to important changes in pelagic community structure

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**Fig. 1.** Participants of IMBER IMBIZO II at the Hellenic Center for Marine Research in Crete Greece, 10–14 October 2010.

in subtropical waters through top-down as well as bottom-up impacts.

The complex network of channels and fjords in the Patagonian region of southern South America is the comparative research setting for González et al. (2013). Trophic fluxes near the heads of the fjords are dominated by heterotrophic nanoflagellates (HNF) and small copepods. Diatoms dominate on the ocean sides of the trophic gradients. Strong organic inputs from rivers and high spatial and seasonal variability make warming and stratification effects on system functions and carbon fluxes difficult to predict in this climate-sensitive region.

According to metabolic theory, seawater warming is expected to increase the metabolic and consumption demands of heterotrophic organisms relative to the production potential of phytoplankton (e.g. Chen et al., 2012). Though not designed as a test of theory, the article by Yoon et al. (2013) is nonetheless relevant to this trophic-coupling issue in its findings for the growth environment of Manila clam in a brackish subarctic lagoon in Japan. The approach combines numerical modeling of ecosystem responses with bioenergetic regulation of clam growth rate and biomass accumulation. Warming increases production of the Manila clam under the simulated conditions, but phytoplankton declines due to increased grazing pressure.

The three following articles (Heimbürger et al., 2013; Santinelli et al., 2013; Jones et al., 2013) comprise a regional focus on climate sensitivities of export mechanisms in the Mediterranean Sea. Heimbürger et al. (2013) compares 20 years of time-series data on particle export from the DYFAMED project in the Ligurian Sea, which link export efficiency to stratification via a seasonal but variable flush-down mechanism – winter convection and subsequent bloom. Export variability depends proximally on mixed layer depth, but is tied to various climate-sensitive drivers (temperature, rainfall, wind, atmospheric nutrient inputs) via complex relationships. For example, heating of Northwestern Mediterranean surface waters might, by itself, be expected to reduce convective mixing and consequently export. However, warming effects on stratification may be counter-balanced by concurrent drought or evaporative increase of salinity, enhancing deep wintertime mixing. Such complexities make it difficult to predict net effects at the present time.

Santinelli et al. (2013) and Jones et al. (2013) provide complementary perspectives on the dissolved organic carbon (DOC) contribution to export. First, Santinelli et al. (2013) compare two areas (southern Adriatic and Tyrrhenian Seas) with contrasting patterns of stratification and seasonal overturn, showing major differences in DOC export and depth distributions. The findings suggest that enhanced thermal stratification might further increase mixed-layer concentrations of DOC during stratified times of the year, but whether this would increase or decrease net export via the DOC pathway is unclear. Microbial transformations of DOC and possible salinity effects on stratification and deep-water formation are major uncertainties. With regard to microbial utilization, Jones et al. (2013) demonstrate that the composition of DOC in the Northwestern Mediterranean Sea varies seasonally and with depth, suggesting increased carbohydrate production by phytoplankton under stratified, oligotrophic conditions and subsequent utilization by microbes at depth. Further characterization of DOC constituents and utilization pathways is necessary to develop a mechanistic understanding of how this major pathway of carbon export could vary under climate-altered physical and trophic conditions.

Global ocean models sensitive to regional differences in dominant processes and organisms will ultimately be necessary to predict accurately the local responses of food webs and biogeochemistry to climate drivers, and their interactions among adjacent systems. Toyoda et al. (2013) take an important step in that direction by describing a Green's function optimization approach that improves simulations of seasonal and interannual variability in the lower trophic levels using NEMURO (Ecosystem Model for Understanding Regional Oceanography, Kishi et al., 2007). Although impacts of global warming are still poorly defined in terms of detailed impacts on circulation and stratification, such approaches provide some hope that relevant biology, including parameterizations for organisms/strategies that may be selected for by enhanced stratification, can be implemented into models to evaluate their potential impacts on future ocean scenarios.

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