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Controls on the ratio of mesozooplankton production to primary production in marine ecosystems

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ABSTRACT

An ecosystem model was used to (1) determine the extent to which global trends in the ratio of mesozooplankton production to primary production (referred to herein as the “z-ratio”) can be explained by nutrient enrichment, temperature, and euphotic zone depth, and (2) quantitatively diagnose the mechanisms driving these trends. Equilibrium model solutions were calibrated to observed and empirically derived patterns in phytoplankton biomass and growth rates, mesozooplankton biomass and growth rates, and the fraction of phytoplankton that are large ($> 5 \mu\text{m}$ ESD). This constrained several otherwise highly uncertain model parameters. Most notably, half-saturation constants for zooplankton feeding were constrained by the biomass and growth rates of their prey populations, and low zooplankton basal metabolic rates were required to match observations from oligotrophic ecosystems. Calibrated model solutions had no major biases and produced median z-ratios and ranges consistent with estimates. However, much of the variability around the median values in the calibration dataset (72 points) could not be explained. Model results were then compared with an extended global compilation of z-ratio estimates ($> 10\,000$ points). This revealed a modest yet significant ($r=0.40$) increasing trend in z-ratios from values ~ 0.01 – 0.04 to ~ 0.1 – 0.2 with increasing primary productivity, with the transition from low to high z-ratios occurring at lower primary productivity in cold-water ecosystems. Two mechanisms, both linked to increasing phytoplankton biomass, were responsible: (1) zooplankton gross growth efficiencies increased as their ingestion rates became much greater than basal metabolic rates and (2) the trophic distance between primary producers and mesozooplankton shortened as primary production shifted toward large phytoplankton. Mechanism (1) was most important during the transition from low to moderate productivity ecosystems and mechanism (2) was responsible for a relatively abrupt transition to values > 0.1 in high productivity ecosystems. Substantial z-ratio variations overlying these mean trends remained unexplained by these mechanisms. Potential sources of this variability include zooplankton patchiness, unresolved effects of advection and unsteady dynamics, unresolved shifts in mesozooplankton sizes and species, and unresolved aspects of zooplankton bioenergetics. Comparison of the modeled z-ratio patterns and mechanisms diagnosed herein with those obtained using models with expanded biological dynamics embedded in global circulation models will help further elucidate the causes of this variation.

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1. Introduction

Two pathways of carbon and energy flow within marine ecosystems are particularly relevant for understanding the impact of climate change on marine resources. The first is the biologically mediated export of organic carbon and nutrients between the ocean’s surface and depth (i.e., the “biological pump”). The second is the flow of energy between small, planktonic primary producers and larger marine organisms such as mesozooplankton and fish. Under-

standing controls on the second of these fluxes is a key step in predicting the impact of climate change on future fisheries production (Brander, 2007) and is the focus of this paper.

Both the ratio of export to primary production (i.e., the *e*-ratio) and the ratio of fisheries production to primary production have been shown to increase with primary productivity (e.g., Eppley and Peterson, 1979; Iverson, 1990). These trends have been linked to changes in the size distribution of phytoplankton (e.g., Dunne et al., 2005; Legendre and Rassoulzadegan, 1996; Ryther, 1969). Small phytoplankton ($SP, < 5 \mu\text{m}$ in equivalent spherical diameter—ESD) are prevalent in oligotrophic ecosystems, where their large surface area to volume ratios provide a critical nutrient scavenging advantage over larger cells (e.g., Chisholm, 1992; Munk and Riley, 1952). *SP* production fuels a tightly coupled microbial food web of

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slowly sinking particles, which minimizes export, particularly in warm waters, where accelerated bacterial rates favor the recycling of organic material within the euphotic zone (Azam et al., 1983; Kirchman, 2000; Laws et al., 2000). However, *SP* production may pass through several trophic links before reaching fish and only a small fraction is thought to contribute to fisheries production (Ryther, 1969). Large phytoplankton (*LP*, $>5\mu\text{m}$ ESD) are less effective nutrient scavengers than *SP*, but are also less susceptible to microzooplankton grazing (Hansen et al., 1994). *LP* (particularly large diatoms) generally prevail in highly productive regions characterized by frequent influxes of new nutrients (e.g., Margalef, 1978). Direct consumption of *LP* by mesozooplankton decreases the number of trophic steps between primary producers and fish. This creates the potential for highly productive fisheries if other phytoplankton loss mechanisms (e.g., sinking) do not prevent the transfer of this energy (Ryther, 1969).

Mesozooplankton form a key link between the planktonic food web and fish. While examples of regular scalings between mesozooplankton production and primary and/or “new” production within ecosystems exist (e.g., Roman and Gauzens, 1997; Roman et al., 2000) the robustness of such trends globally, the mechanisms that underlie them, and the influence of other variables such as water temperature, are less clear. For example, the ratio of mesozooplankton production to primary production (referred to as the *z*-ratio herein for brevity) has been estimated to increase from ~ 0.03 at the Bermuda Atlantic Time Series site (BATS, Roman et al., 2002; primary production $\sim 35\text{ mmol C m}^{-2}\text{ day}^{-1}$ at $\sim 20\text{--}25^\circ\text{C}$) to ~ 0.12 in the Arabian Sea (Roman et al., 2000; primary production $\sim 100\text{ mmol C m}^{-2}\text{ day}^{-1}$ at $25\text{--}28^\circ\text{C}$). This suggests a strong positive relationship between the *z*-ratio and productivity. However, the Hawaii Ocean Time Series (HOT) exhibits a higher *z*-ratio (~ 0.06) than BATS despite having a similar primary productivity and temperature (Roman et al., 2002). The central equatorial Pacific has mesozooplankton biomass comparable to that in BATS, but primary productivity and temperature similar to those in the Arabian Sea (Roman et al., 1995). Low mesozooplankton biomass also prevails in the very cold offshore waters of the Ross Sea despite considerable primary productivity in the austral summer (Tagliabue and Arrigo, 2003).

The primary objectives of this work are to (1) determine the extent to which observed cross-ecosystem patterns in the *z*-ratio can be explained by the equilibrium solutions of an ecosystem model forced solely by variations in nutrient enrichment, temperature, and euphotic zone depth, and (2) identify and quantify the importance of various parameters and mechanisms controlling these trends. Unexplained *z*-ratio variations will then be analyzed to suggest key model and observational improvements. The approach taken is similar to that employed by Laws et al. (2000) and Dunne et al. (2005) in their examinations of the influence of productivity and temperature on carbon export—equilibrium model solutions from a model with the basic structure of those currently embedded in global and regional circulation models are compared with and calibrated to global databases of observed ecosystem variables. While no ecosystem is ever truly at steady state, this approach is deemed an appropriate starting point for assessing broad-scale *z*-ratio patterns between vastly different ecosystems and provides a foundation for the effective analysis of highly complex ecosystem models in more dynamic settings.

2. Methods

2.1. Observed and derived ecosystem properties

Model solutions were analyzed as a function of three forcing variables: (1) euphotic zone depth (1% light level, Z_{eu} , m), (2)

euphotic zone temperature (T , $^\circ\text{C}$), and (3) an estimate of the flux of limiting nutrient into the euphotic zone (F_N , $\text{mmol N m}^{-2}\text{ day}^{-1}$) based on measured new production or export (see Section 2.1.1). The model was calibrated against directly observed or derived values in five quantities: (1) total phytoplankton carbon concentration ($SP+LP$, mmol C m^{-3}), (2) average phytoplankton growth rate (μ_p , day^{-1}), (3) fraction of phytoplankton that are *LP* (f_{LP}), (4) mesozooplankton carbon concentration (LZ , mmol C m^{-3}), and (5) mesozooplankton growth rate (μ_{LZ} , day^{-1}). Derived refers to the use of independent empirical and mechanistic models to obtain estimates based on other directly observed variables. The *z*-ratio can be calculated from these quantities as

$$z\text{-ratio} = \frac{\mu_{LZ} LZ}{\mu_p (SP+LP)} \quad (1)$$

Two compilations of ecosystem properties were used. The first is referred to as the “calibration compilation” (Section 2.1.1), which contained 72 estimates of the three forcing and five comparison variables from sites spanning a range of ocean environments (Fig. 1). It was used to calibrate the ecosystem model and as an initial basis for model evaluation and diagnosis. The second compilation is referred to as the “extended global *z*-ratio compilation” (Section 2.1.2). It combined satellite-based estimates of primary productivity, *in-situ* observations of mesozooplankton biomass, and empirical estimates of mesozooplankton growth to create a large set of *z*-ratio estimates to further evaluate global *z*-ratio trends.

2.1.1. Calibration compilation

The calibration compilation was constructed mainly from *in-situ* measurements gathered from the scientific literature by Dunne et al. (2005), with estimates of mesozooplankton biomass and growth added herein. It covers a range of oceanic and deep coastal regions (Fig. 1) and is provided in the online supporting material along with further details of its construction. Ecosystems with water depths $<100\text{ m}$ were omitted because the model cannot represent benthopelagic coupling. Briefly, $SP+LP$ was calculated from observed chlorophyll *a* (*Chl*) and *C:Chl* ratios. μ_p was estimated as the observed primary production divided by $SP+LP$. F_N was derived from various estimates of total carbon export (e.g., NO_3 -based new production, sediment trap fluxes

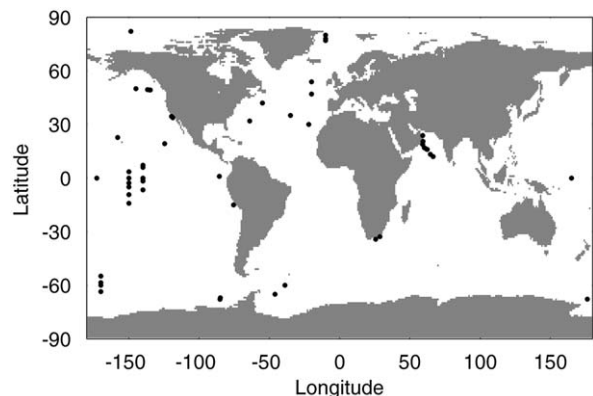


Fig. 1. Location of observations of ecosystem state in the calibration dataset. Some sites have multiple sets of data values that capture interannual and seasonal variability (see Dunne et al. (2005) and online supporting material for details). Mesozooplankton biomass data were gathered from O'Brien (2005), White et al. (1995), Roman et al. (2002, 1995, 2000), Stelfox et al. (1999), Le Borgne and Rodier (1997), Le Borgne et al. (1999), Madin et al. (2001), Landry et al. (2001), Harrison et al. (2001), Hopkins and Torres (1988), Boysen-Ennen et al. (1991), Brodeur et al. (1996), Atkinson and Shreeve (1995), Ashjian et al. (1995), Wheeler et al. (1996), Goldblatt et al. (1999), Sertorio et al. (2000), Tagliabue and Arrigo (2003), Urban-Rich et al. (2001), Gallienne et al. (2001), and Lenz et al. (1993).

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