## Micro-scale patchiness enhances trophic transfer efficiency and potential plankton biodiversity

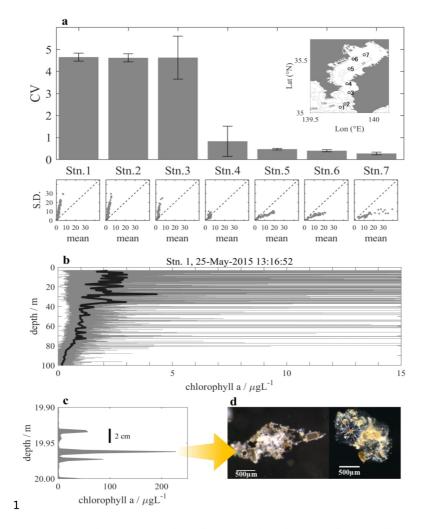
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Recent observations have revealed ubiquitous intermittency in phytoplankton distributions at the micro (mm) scale, and a few recent modelling studies have suggested that this micro-scale variability impacts plankton ecosystem dynamics and biodiversity. Modelling is an essential tool for studying complex food webs, by linking the observed ecological patterns with experimental findings to understand mechanisms and make future predictions. However, so far almost all ecosystem models have been developed based on the mean-field approach, i.e. assuming well mixed environmental conditions within each discretely resolved grid cell. Although this is reasonable for examining patterns at the meso- (km) to global scales, it is not realistic for plankton, which experience micro-scale variability in aquatic environments where predator-prey overlap can substantially enhance trophic transfer. Similar to a recent study that addressed variability at the scale of ocean fronts, we have recently used Reynolds decomposition and truncated Taylor series to develop 'moment closure' models accounting for micro-scale variability in the distributions of Nutrients and Phytoplankton (NP closure model), and also Zooplankton (NPZ closure model). Compared to conventional ecosystem models based on the mean-field approach, these closure models yield qualitatively different dynamics.

Using a generalized plankton ecosystem modelling framework, including models of differing trophic complexity and with different grazing functional responses, we investigate how micro-scale variability affects plankton biodiversity and ecosystem function. Specifically, we apply the closure modelling approach to test the functional forms often assumed in ecosystem models against observed micro-scale intermittency as quantified by the coefficient of variation (CV) (ratio of standard deviation to mean) of micro-scale fluorescence field, which is a proxy for phytoplankton biomass. With both saturating and non-saturating grazing functions and in all model configurations considered, we find that micro-scale variability consistently supports the highest trophic level present, i.e. enhances Tansfer Efficiency, and expands the model stability domain, potentially sustaining biodiversity by allowing species with a wider range of trait values to coexist. Based on our observations and model results we hypothesise a novel answer to the "paradox of the plankton" (Hutchinson, 1961) for such calm, low-nutrient oceanic environments: Heretofore under-appreciated high levels of micro-scale variability may explain the great diversity of plankton present in these vast low-nutrient regions of the ocean.

Keywords: plankton, turbulence, microstructures, ecosystem models



2 **Figure**: (a) Observation stations (open, numbered circles) in Tokyo bay, *CV* estimates (bar 3heights, with error bars indicating 99% confidence intervals) and corresponding scatter 4plots of observed standard deviation vs. mean of fluorescence data from each station 5(dotted lines showing one-to-one relationships). (b) Raw data (thin grey lines) and 1 m 6average values (thick black lines) from a vertical fluorescence profile acquired at stn. 1 by 7the laser sensor, which was calibrated with *in situ* water samples to obtain values in *g* 8chl L<sup>-1</sup>. (c) A subset of peaks from the same profile around 20 m depth. Vertical thick black 9bar indicates a scale bar of 2 cm height. (d) Images of typical aggregates.

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