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The ecology of plankton in biological oceanography: a tribute to Marta Estrada's task

Jordi Solé¹, Elisa Berdalet¹, Laura Arin¹, Lluïsa Cros¹, Maximino Delgado¹, Akira Kuwata²,
Clara Llebot³, Cèlia Marrasé¹¹Institute of Marine Sciences, ICM-CSIC. Passeig Marítim de la Barceloneta, 37-49, 08003 Barcelona, Catalonia, Spain.
E-mail: jsole@icm.csic.es²Tohokku National Fisheries Research Institute, Japan Fisheries Research and Education Agency, Shinhama-cho 3-27-5,
Shiogama, Miyagi, 985-0001, Japan.³College of Oceanic and Atmospheric Sciences, Oregon State University 104 COAS Administration Building Corvallis,
OR 97331-5503, USA.

Summary: Plankton ecology has been the object of intense research and progress in the last few decades. This has been partly due to technological advances that have facilitated the multidisciplinary and high-resolution sampling of ecosystems and improved experimentation and analytical methodologies, and to sophisticated modelling. In addition, exceptional researchers have had the vision to integrate all these innovative tools to form a solid theoretical background in ecology. Here we provide an overview of the outstanding research work conducted by Professor Marta Estrada and her pioneering contribution to different areas of research in the last four decades. Her research in biological oceanography has mainly focussed on phytoplankton ecology, taxonomy and physiology, the functional structure of plankton communities, and physical and biological interactions in marine ecosystems. She has combined a variety of field and laboratory approaches and methodologies, from microscopy to satellite observations, including in-depth statistical data analysis and modelling. She has been a reference for scientists all over the world. Here, her contributions to plankton ecology are summarized by some of her students and closest collaborators, who had the privilege to share their science and everyday experiences with her.

Keywords: phytoplankton ecology; taxonomy; functional structure of plankton communities; physical-biological interactions.

La ecología del plancton en la oceanografía biológica: un homenaje a la labor de Marta Estrada

Resumen: La ecología del plancton ha experimentado una intensa investigación y progreso en las últimas décadas. Esta se ha debido, en parte, a los avances tecnológicos que han facilitado la toma de muestras multidisciplinar y de alta resolución de los ecosistemas, la mejora de la experimentación y metodologías analíticas y el modelado matemático/numérico. El papel de investigadores excepcionales que han tenido la visión de integrar todas estas herramientas innovadoras a una sólida formación teórica en la ecología ha sido clave en este avance. A continuación hemos elaborado un resumen de la tarea de investigación llevada a cabo por la profesora Marta Estrada y su contribución pionera a diferentes áreas de investigación en las últimas cuatro décadas. Su investigación, en el marco de la oceanografía biológica, se ha centrado principalmente en la ecología del fitoplancton, su taxonomía y fisiología, la estructura funcional de las comunidades de plancton y las interacciones físicas y biológicas en los ecosistemas marinos. Ha combinado una variedad de enfoques y metodologías de campo y de laboratorio, desde observaciones por satélite, hasta el análisis en profundidad de datos estadísticos y el uso del modelado tanto analítico como numérico. La profesora Estrada ha sido una referencia para los científicos alrededor del mundo. Aquí, su contribución a la ecología del plancton la resumen algunos de sus alumnos y colaboradores más cercanos que han tenido el privilegio de compartir ciencia y vivencias con ella.

Palabras clave: ecología del fitoplancton; taxonomía; estructura funcional de las comunidades plantónicas; interacciones física-biología.

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INTRODUCTION

Professor Marta Estrada obtained her degree in Biology (1968) and in Medicine (1970) from the University of Barcelona. Her PhD thesis, “Studies on aquatic organism populations in a non-uniform environment” (“Estudios sobre poblaciones de organismos acuáticos en medio no uniforme”), was supervised by Ramon Margalef (1919-2004), the most important Catalan and Spanish ecologist, limnologist and biological oceanographer of the twentieth century (Estrada 2004). Estrada’s research, mainly focusing on biological oceanography, and in particular on the ecology of marine phytoplankton, is a direct continuation of some of the scientific lines developed by Margalef.

Marta Estrada has published widely and led many projects. She has conducted field, laboratory and theoretical studies, combining biochemical, taxonomical and modelling tools. She has studied different freshwater ecosystems (lagoons and rivers in the Iberia Peninsula) and marine ecosystems in the Mediterranean (including the adjacent Barcelona coastal zone, the Ebro Delta and its bays, and open sea waters), across the Atlantic, in Arctic and Antarctic waters, in the Equatorial Pacific upwelling, and in the Indo-Pacific Ocean. Direct observation of nature—in particular thousands of microplankton samples—has provided her with a rich, comprehensive vision of ecosystems. She applied her outstanding skills in mathematics and modelling to understand the complexity of the links between organisms and their dynamics related to environmental forcing. Her perspective was multidisciplinary, integrating knowledge on physical, chemical, biological and geological properties of ecosystems. In the laboratory, she addressed microcosm and ecophysiology studies to elucidate the underlying mechanisms that operate at small scale and that can help to understand natural processes. With exceptional knowledge of phytoplankton taxonomy using optical microscopy, she also combined new tools in electron microscopy, flow cytometry and molecular techniques.

This paper aims to give a brief overview of Marta Estrada’s career, compiling the personal views of some of her PhD students and closest collaborators as a brief homage to the more than 40 years that she has dedicated to scientific research. Without the aim of being exhaustive, we have divided her work into four main areas.

COMBINING DIFFERENT APPROACHES TO BUILD A RELIABLE CONCEPTUAL FRAMEWORK

Estrada’s high level of curiosity to unravel the enigmas of nature, together with her multidisciplinary skills, enable her to address a wide range of questions using a wide range of approaches. From the very beginning of her career (Estrada 1972, Estrada and Wagensberg 1977), she applied mathematical tools such as time series and multiparametric analyses to quantitatively describe the apparent caprices of phytoplankton temporal and spatial variability. During her career she

combined these mathematical tools with experimental studies and fieldwork to address questions such as the importance of water hydrodynamics in phytoplankton composition. She examined the response of natural plankton assemblages to a combination of treatments in several experimental designs. The data obtained experimentally proved that nutrient-high turbulence favours the dominance of diatoms. These studies corroborated the conceptual ecological framework of Margalef’s Mandala (Margalef 1978, Margalef et al. 1979), which proposes a systematization of the functional morphology of phytoplankton on the basis of the supply of nutrients and the intensity of turbulence. Furthermore, the experiments pointed out the importance of initial conditions in the phytoplankton response to treatments (Estrada et al. 1987, 1988, Alcaraz et al. 1989). Estrada also inspected this question in the field. Analysing data from three legs of a winter NW Mediterranean survey, she observed that the dominance of diatoms increased as the intensity of stratification decreased (Estrada 1999, Estrada et al. 1999). In numerous field studies, she showed her interest in framing biological variability with physical processes. Here we cite some papers from her inspections in relation to upwelling (Estrada 1974, 1978, 1991), coastal processes (Estrada and Blasco 1979, 1985, Estrada and Marrasé 1987), fronts (Estrada 1991, Estrada and Margalef 1988), stratification (Estrada et al. 1992, Brink et al. 1995), eddy processes (Granata et al. 2004) and other physical processes (Morán et al. 1999, Llebot et al. 2011, Arin et al. 2013). She also helped to quantify the importance of plankton activity in biogeochemical fluxes under different conditions of nutrient and light availability. To address these questions she used a variety of approaches, ranging from experimental work (Estrada et al., 2003, Berdalet et al. 1992, 1994) to field work (Estrada 1979, Estrada et al. 1999), and different biogeochemical methodologies: phosphorus nutrient deficient inputs (Berdalet et al. 1996), biochemical relations with primary production (Berdalet et al. 1993b, Latasa et al. 1992, 2005), CO₂ links with frontal zones (Delgado and Estrada 1994), relationships of dissolved organic carbon with phytoplankton (Estrada and Morán 1996), DNA relative to biomass (Arin et al. 1999), excess of carbohydrate synthesis (Fraga et al. 1999), variability of photosynthesis parameters (Morán and Estrada 2001) and enzyme kinetics principles (Packard et al. 2004).

STRUCTURE OF PHYTOPLANKTON COMMUNITIES RELATED TO ENVIRONMENTAL FORCINGS. FIELD STUDIES

Estrada studied the variability of the size structure and taxonomic composition of phytoplankton communities (Delgado et al. 1992, Estrada and Delgado 1990, Estrada et al. 1993) and their link with environmental dynamics (Morán et al. 2001). For instance, in the Mediterranean Sea Arin et al. (2002) showed how the short-term variability of the physico-chemical water conditions modulated the size structure of autotrophic communities. In the western Alboran Sea anticyclonic

gyre, for several days picoplankton (<2 µm in cell size, including picoeukaryotes and cyanobacteria) was dominant in the oligotrophic area of the centre of the gyre. In contrast, in the high hydrodynamic and eutrophic zone of the edge, the predominant fraction varied from nanoplankton (2–20 µm, mainly autotrophic flagellates) to microplankton (>20 µm, mostly diatoms) as a result of an injection of nutrients at the surface from upwelled deep waters. In a long-term variability (Arin et al. 2005) and a highly dynamic Mediterranean ecosystem (the Ebro shelf area), the picoplankton fraction was the main contributor to the autotrophic biomass (in terms of chlorophyll *a*) in the three seasons studied (winter, summer and autumn). The nanoplankton community showed the lowest variability among seasons, while microplankton was higher in winter than in the other seasons, supported by the intrusion of nutrients into the photic zone by intense vertical mixing and strong riverine inputs.

Estrada also participated in long-term studies about phytoplankton dynamics in a fixed observatory station in Barcelona harbour. An important finding derived from these studies was that coastal fertilization by offshore waters during atypical weather conditions (cold and dry winters) may be equal to, or more important than, continental fertilization and may introduce organisms typically thriving in open oceanic waters to coastal waters (Arin et al. 2013). In this situation, some of these taxa, in particular the foam-forming *Phaeocystis* sp., can proliferate, causing a considerable deterioration of coastal water quality (Arin et al. 2014).

Estrada also used multivariate analysis of organism abundances to explore the distribution of phytoplankton assemblages as a function of environmental conditions. A principal component analysis in an upwelling region of NW Africa, for example, showed that species belonging to the same taxonomic groups were strongly associated, reflecting a similar ecological response (Margalef and Estrada 1981). These analyses also contribute to the efforts to quantify the conceptual model of the Margalef Mandala, as noted above.

Principal component analysis was also used in Alfacs Bay (NW Mediterranean) to characterize the variability of the phytoplankton community related to physical and chemical forcings. The analysis revealed that freshwater influence was the main factor affecting the composition of phytoplankton species, and it also identified an assemblage of marine diatoms (in autumn) and a dinoflagellate group (in winter and early spring) as the main contributors to the seasonal variability of the phytoplankton community in the bay (Llebot et al. 2011).

Recently, Estrada led the study (Estrada et al. 2016) on the large-scale distribution patterns of the nano- and microphytoplankton collected from 145 oceanic stations during the Malaspina 2010 Expedition (December 2010–July 2011), which covered 15 biogeographical provinces across the Atlantic, Indian and Pacific Oceans between 35°N and 40°S. In general, the water column was stratified, the surface layers were nutrient-poor, and dinoflagellates, other flagellates and coccolithophores were dominant in the nano-

and microplankton community (including microalgae and heterotrophic protists), while the contribution of diatoms was only important in zones with shallow nutrient-rich waters such as the equatorial upwelling regions. The most striking composition contrast was found between the phytoplankton communities in the upper layers and those corresponding to the chlorophyll maximum depths, separated by tens of metres in the vertical dimension. In contrast, the structure and composition of phytoplankton communities were comparable over extensive transects of tropical and subtropical regions of the world's oceans. The study also showed differences among the phytoplankton communities in the sampled stations in Atlantic, Indian and Pacific waters due to a combination of ecological and historical factors.

HARMFUL ALGAL BLOOMS: A PARTICULAR CASE OF PHYTOPLANKTON ECOLOGY

The interest in harmful algal blooms (HABs) started early in Estrada's career, as a particular case of the phytoplankton life-forms selected by low turbulence and high nutrient availability in Margalef's Mandala. While the role of nutrients had been widely recognized as a main driver for plankton dynamics, including HABs, Margalef proposed for the first time the particular role of turbulence. Estrada's studies provided new insights into this role in the particular case of the bloom dynamics of dinoflagellates, a group that includes many species involved in HAB phenomena (Berdalet and Estrada 1993a, 2008, Estrada and Berdalet 1997). At the ecophysiological scale, Estrada hypothesized the direct impact of turbulence on dinoflagellate cells. This group of organisms showed reduced reproduction capacity under water column mixing conditions, while they tended to thrive under water column stability. In the laboratory, it was shown that small-scale turbulence could inhibit dinoflagellate cell division (Berdalet 1992), although the response was species-specific (e.g. Berdalet et al. 2007). Interestingly, benthic dinoflagellates such as the harmful species *Ostreopsis* cf. *ovata* and *Prorocentrum lima* could also exhibit differential responses to turbulence that would explain their temporal succession in the benthic community. Very recently, Estrada has been participating in a project that investigates the ecophysiological dynamics of *Ostreopsis* blooms on the Catalan coast.

More recently, using multi-species and low dimensionality mathematical models, Estrada improved the understanding of biological phenomena such as trophic and competitive interactions in plankton communities. For instance, predator-prey models and two- or three-equation models (low-dimensional models) were compared with multi-species models such as ERSEM (Baretta et al. 1995). With this approach, trophic relationships such as allelopathy and feeding preferences in the occurrence of plankton blooms and HABs of dinoflagellates were addressed (Solé et al. 2005, 2006a, b). These studies revealed that the toxicity in the inter-species competition models (allelopathy) has an effect only when the bloom has already started but not as a starting mechanism. Moreover, the toxicity affecting

trophic feeding interactions could be a mechanism that favours toxic species over a competitor with a higher intrinsic growth rate.

Using age-structured matrix population models, Estrada investigated the role of the different forms of phytoplankton life cycle (vegetative cells and cysts) in the occurrence and recurrence of HABs (Estrada et al. 2010). The study revealed that although cysts had a small effect on increasing bloom magnitude for an actively growing population of vegetative cells, cysts could be a safety mechanism for reintroducing the species when the vegetative cell population was driven to extinction by unfavourable environmental conditions.

INSIGHT INTO THE TAXONOMY AND LIFE CYCLE OF COCCOLITHOPHORES AND DIATOMS

Coccolithophorids are an important phytoplankton functional group characterized by their external covering of calcite scales or coccoliths (e.g. Young et al. 1999). These organisms have very complex haplo-diploid life cycles associated with different morphologies. Cros and Estrada (2013) showed how the alternation of life cycle stages and heteromorphology give coccolithophorids the capacity to exploit different ecological niches in the marine ecosystems. In particular, this capacity is an ecological strategy for surviving under different conditions in Mediterranean waters. In their study, Cros and Estrada found haploid holococcolithophores mainly in more oligotrophic upper layers, while the diploid heterococcolithophores inhabited relatively rich deeper waters.

Furthermore, holococcoliths have a higher Mg/Ca ratio than heterococcoliths (Cros et al. 2013), which predicts a lower preservation potential of holococcoliths because high-Mg calcite dissolves faster than low-Mg calcite. These characteristics could have paleoceanographic implications and consequences in relation to ocean warming and the increasing acidification of the world oceans (Gibbs et al. 2016). Estrada's interest in this phytoplankton group helped to show that some holococcolith structures (not present in all holococcoliths) can have the ability to scatter ultraviolet radiation (Quintero-Torres et al. 2006), suggesting a possible strategy of increasing the reflection of UV light away from the cell, thus enhancing the ability of the organism to live higher in the water column. The studies in Mediterranean waters led to the description of a new coccolithophore, *Picarola margalefii*, dedicated to Ramon Margalef (Cros and Estrada 2004), which is now the symbol of the Margalef Award for Ecology (Fig. 1) established by the Government of Catalonia in 2004 (<http://web.gencat.cat/en/generalitat/premis/premi-ramon-margalef/Guardo/index.html>).

Marta Estrada has also shed light on the taxonomy and life cycle of diatoms, which are responsible for 40% of marine global primary production. They have a characteristic rigid silicified cell wall, with most species going through a cycle of diameter size decline and size restoration (usually by auxospore formation). Originally it was thought that this was a consequence

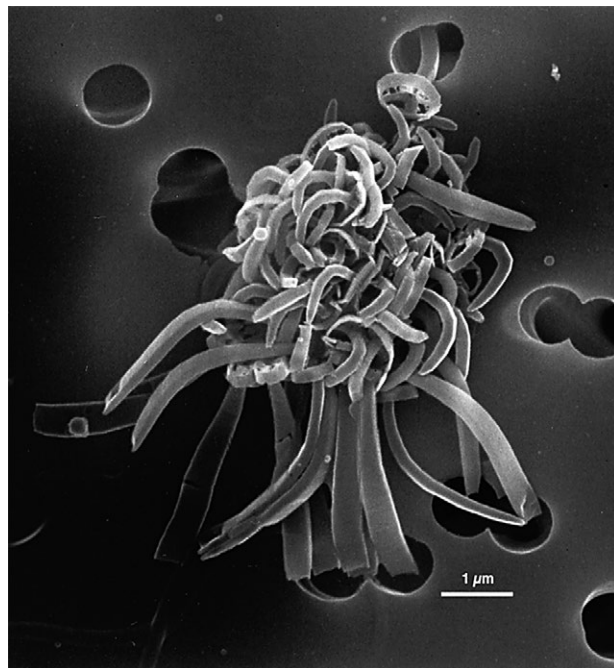


Fig. 1. – The new coccolithophorid *Picarola margalefii* dedicated to Ramon Margalef (Cros and Estrada 2004), symbol of the Margalef Award for Ecology established by the Government of Catalonia in 2004.

of having a rigid cell wall, but we now know that it is actually related to a sophisticated clocking mechanism for timing the length of their life cycles over periods longer than a year. In the case of one of the smallest diatoms, *Minidiscus comicus*, which is near the theoretical minimum volume for eukaryote cells, the question was whether they could still use this mechanism. Estrada contributed to the study by Jewson et al. (2016), which shows how *M. comicus* has adapted to the decline in diameter by changing its cell shape (at division) from discoid to spherical, thus maintaining its cell volume. This finding demonstrates the remarkable adaptability of diatoms in this case, enabling them to colonize and survive in an often overlooked habitat, oceanic nanoplankton.

HAPPY YEARS WITH PHYTOPLANKTON ECOLOGY AND MARTA ESTRADA

The authors of this article have spent many years with Marta Estrada, who has been for all of us “our Marta”. We have shared 10 to 35 years of our lives with Marta and with phytoplankton... We have learnt about phytoplankton ecology working at sea, calm and rough, either close to our home in the Mediterranean or very far away.

In addition to serious and strict science, we have also shared our personal lives with someone who is extraordinary, generous, hardworking and wise.

... Someone who knows that high pressure and temperature make the most beautiful gems, so effort and perseverance give the best result...

... Someone who has a refined sense of humour to make us understand that humans are like phytoplankton cells, some (almost) naked and fragile, while others

are nicely and sophisticatedly dressed or armoured: diatoms on glasshouses of silica, coccolithophores with strong walls of calcium carbonate, dinoflagellates wearing fancy cellulose plates, soft flagellates like sweet jelly candies...

... Someone who can always find some funding to pay for the most important necessities of life...

... Someone who always differentiates "maybe" from the "definitely" in a simple way...

... Someone who will turn the puzzled ideas of her students and contributors into a coherent story...

... Someone who will respect opinions and diversity among humans, as a common component of natural selection...

... Someone who believes that observing nature through the microscope is a mirror of humanity and a fantastic road to happiness.

For all of this, thank you Marta!

We are your children forever.

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