

Living in a fluid-dynamical landscape: how do marine predators respond to turbulence?

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Open ocean currents create a highly heterogeneous fluid-dynamical “sea-scape” that embeds ecological interactions and biogeochemical processes. The **coupling between marine ecology and biogeochemistry** and **ocean physics** occur at different spatio-temporal scales and through a variety of interactions that make disentangling the ecological and biogeochemical variability and the ocean physics a complex problem. In particular, **(sub-)mesoscale** (here defined as the spatio-temporal scale including the mesoscale and the upper boundary of the oceanic submesoscale - few days-months, 10-100 km) features like eddies and fronts shape the distribution of nutrients, physical properties and planktonic organisms into a highly contrasted environment. **Marine top predators**, that are generally able to move independently from the currents, hunt, navigate and make decision in an environment that changes at scales that are comparable with the ones of their foraging trips in the open ocean. At the same time, being at the top of oceanic trophic webs, top predators play a fundamental role in maintaining the structure and functioning of healthy marine ecosystems. In spite of their importance for marine ecosystems and of the recent technological development of bio-logging (i.e. deployment of autonomous recording tags on free-living animals) what influences marine predators’ movement at smaller spatial and temporal scales, such as the ones they experience during their foraging trips, is still largely unknown. In my doctoral research I analysed the interaction between marine top predators (elephant seals and macaroni penguins) and (sub-)mesoscale ocean dynamics. I focused on two research questions:

Q1. Does (sub-)mesoscale turbulence directly affect top predators? How can we evaluate the role of direct mechanical transport on top marine predators in respect to their swimming capabilities?

Q2. How does (sub-)mesoscale turbulence structure the dynamical and contrasted biological “sea-scape” that top predators navigate?

To address these questions, I combined in-situ **observations**, bio-logging data, remote-sensing, ecological **modeling** and a **Lagrangian approach** (i.e. based on the tracking of water parcels). To combine these heterogeneous datasets and model outputs and disentangle physical and biological factors I employed approaches from non-linear dynamics based on considering the **horizontal velocity field defined by ocean currents as a dynamical system**. In this framework, tools from dynamical systems theory such as the Finite Size Lyapunov Exponents analysis allow to extract key oceanographic features (such as fronts and eddy peripheries) and compare their spatial and temporal distribution with in-situ and remotely sensed observations of marine organisms and ocean properties.

The study has been focused on the sub-Antarctic region around the **Kerguelen Plateau** (Indian Sector of the Southern Ocean). This sector of the Southern Ocean provides a useful natural laboratory for this work in that (i) several marine predators species have large colonies on the island, (ii) the area is located in a highly dynamical ocean regime dominated by the Antarctic Circumpolar Current, (iii) the trophic web in the area is relatively simple and (iv) production is dominated by iron limitation, making it possible to disentangle physical and ecological effects.

First, I examined whether the mechanical effect of mesoscale currents on the **trajectories** of large fast-swimming marine predators is significant (Q1). With the help of a novel Lagrangian diagnostic, the “quasi-planktonicity index” (that is based on the approach of considering the horizontal current velocity field as a dynamical system) and measure of prey capture attempts from jaw accelerometers, I found that, in spite of what is often assumed, foraging marine predators are transported by the

horizontal ocean dynamics for a non-negligible part of their foraging trip. During these sections of their trips, marine predators invest their energy in deep diving and hunting rather than horizontally searching for profitable grounds. This movement pattern results in a “**quasi-planktonic**” behavior where animal horizontal trajectories do not differ significantly from the ones of simulated passive tracers or Lagrangian drifters. This phenomenon is more likely to occur on (sub-)mesoscale fronts and eddy peripheries that appear to be particularly favorable for animal foraging.

To address Q2, I focused on how mesoscale turbulence affects the distribution of ocean **productivity** (in particular, the distribution of **diatoms**) by combining a Lagrangian approach with previous biogeochemical and ecological knowledge of the region. A novel result is that waters that have been recently (~ 20 days) in contact with the Kerguelen plateau (which is assumed to be the major source of iron of the region) are more likely to manifest a phytoplanktonic community dominated by large diatoms. However, my results also suggest that other physical (e.g. fine scale dynamics, vertical circulation), biogeochemical (e.g. vertical structure in the distribution of iron) and ecological mechanisms (e.g. possible bistability of the system) may be important in determining what kind of phytoplankton dominates different water parcels. In particular, I focused on the possibility of a **bi-stable ecosystem** where, even for the same amount of iron, the phytoplanktonic community may be dominated by large diatoms or smaller phytoplankton depending on the initial population on the Kerguelen plateau. I parametrized a simple ecological model (a variation of the Lotka-Volterra differential equations) describing the phytoplankton community structure in the area to predict which dynamical niches are more favorable for high concentrations of diatoms. An interesting result of this study is that, using realistic values of the model parameters and for realistic initial conditions, measured during the Kerguelen Ocean and Plateau compared Study 2 (KEOPS2) survey in 2011, the phytoplanktonic ecosystem may present two stable states. The identification of the roles of different causes of variability in phytoplanktonic communities is important beyond the interest of phytoplankton itself. Coherently with observations in other regions of the Southern Ocean, a qualitative assessment of the regional food web, included in this thesis, shows that the growth of fish larvae and crustaceans (that occupy a large fraction of top predators’ diet) benefit from phytoplankton communities dominated by large diatoms. As consequence, mesoscale features and regions where large diatoms thrive are likely to develop the growth of fish and crustaceans and become favorable for marine top predators.

The results of my doctoral research challenged some major assumptions that are employed in the analyses of marine top predators' trajectories and supported and complemented the understanding of the interaction of physical and ecological drivers in iron fertilized regions. As a final result, the findings presented in this thesis have been used to estimate the location of a key foraging region for macaroni penguins from the Crozet archipelago (in the same sector of the Southern Ocean) and its inter-annual variability. This approach has been used for the design of **Marine Protected Areas** (MPAs) in the region of study and to my knowledge represent the first application of Lagrangian analyses (and of the use of diagnostics such as Finite Size Lyapunov Exponents) to MPA design.