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Could secondary flows make possible the cross-strait transport of passive floating organisms in the Strait of Gibraltar?

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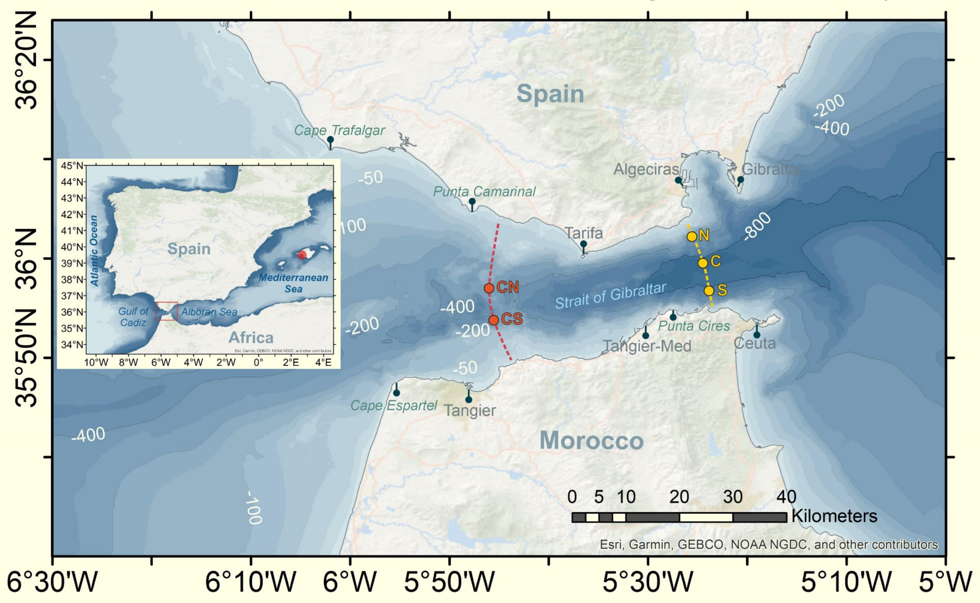
A biological invasion in the Strait of Gibraltar

Since the mid-2010s, the coasts around the Strait of Gibraltar (SoG) and neighboring basins are suffering from a **drastic invasion of *Rugulopteryx okamurae* (RO)**, a brown macroalga from the northwest Pacific Ocean. The alga appears to have reached Europe at the turn of the century with shipments of Japanese oysters imported for marine culture in a small Mediterranean lagoon of France. In 2015, it was identified for the first time on the south coast of the SoG, as a likely result of commercial exchanges with the port of Tanger-Med. However, it could have already been settled on the north coast at that time and not have been identified due to its resemblance to other algae of the area. Regardless of the precise route of entry, the alga has featured an unprecedented aggressive invasion and currently occupies the illuminated seafloor of extensive coastal areas on both shores of the SoG with the threat of monopolizing the sea rocky bottom to detriment of resident biota, given the favorable environmental conditions of the area.



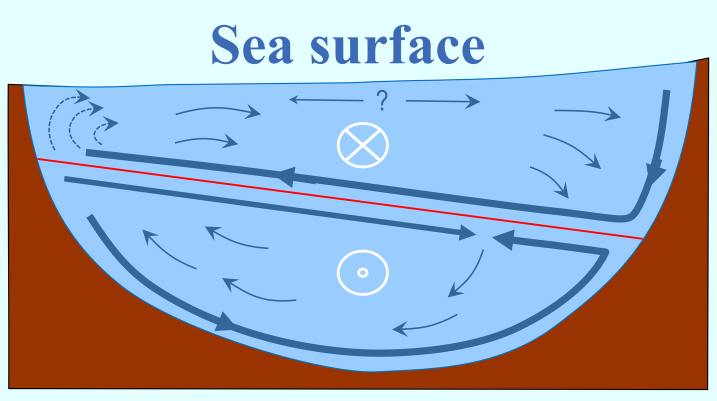
The explosive spread is favored by the fact that broken thalli act as seeding population as the specimens have vegetative propagules, which are found drifting at any depth in the SoG. The hypothesis that algae first settled in a shore of the SoG (the south one according to the scarce literature), opens the question of how they got to the opposite shore. A likely scenario is the heavy north-south traffic of ferries and commercial or fishing ships. Considering the huge capability of the alga to colonize any type of hard substrates, the eventual crossing attached to ship hulls, recreational boats or fishing nets is very feasible. Ballast waters from remote shipments cannot be ruled out either. Another possibility, however, is that the **algae managed to cross the Strait taking advantage of the hydrodynamics, without human intervention**. Such possibility is applicable to larvae and propagule of other marine species that last for weeks in the pelagic realm and opens new hypothesis about transport mechanisms between Lusitanian and Mauritanian biogeographical regions.

Beaching of *RO* on the shore to the west (top picture) and east (middle picture) of Tarifa. The algae accumulated by tens of tons, must be removed, which requires a budget over 0.3M€/year. Bottom: algae attached to fishing nets of the "almadraba" (tuna fishing trap) deployed not far from the shoreline, few km west of Tarifa.

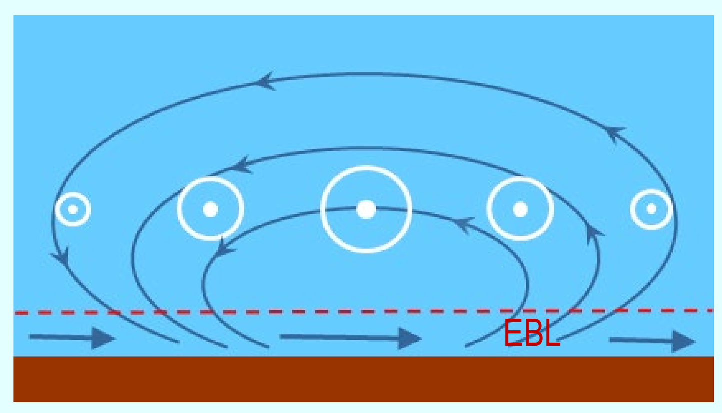
Hydrodynamic plausible mechanisms

The SoG holds a well-known two-way exchange to compensate for freshwater and buoyancy losses in the Mediterranean basin. It results in zonal-oriented currents that allows for easy west-to-east spreading of alga, carrying propagules out of the dimensions of the SoG well before they have chances to get to the opposite shore. Therefore, these currents behave like hydrodynamic barriers for cross-strait transport. A loophole for this constriction is the necessary vanishing of the along-strait current at the depth of the Atlantic-Mediterranean interface. **Should exist a cross-strait secondary flow at or nearby this depth** (figures below), **even if weak, the chances to successfully cross the SoG would be no null**.

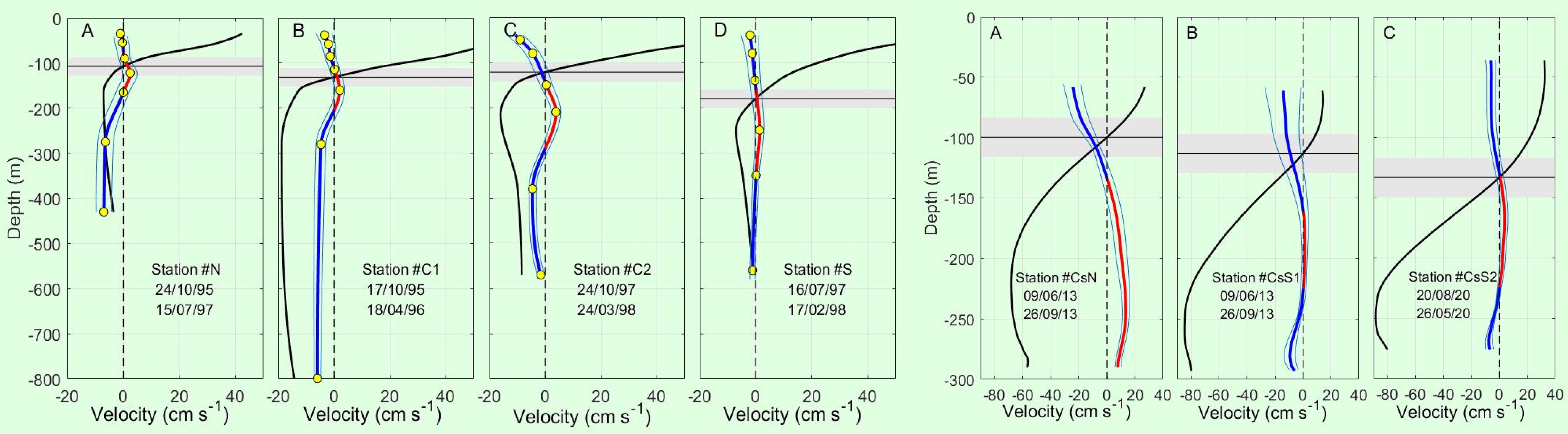
Scheme of a two-layer exchange through a channel of half-circular geometry (from Johnson and Ohlsen, 1994). Encircled white cross (dot) indicates flow into (out of) the page, mimicking the exchange through the SoG as seen from the Atlantic Ocean, with the north (south) shore in the left (right). Surface and interface (red line) slopes due to Earth rotation are disclosed. Thick arrows indicate the solid and interfacial boundary Ekman layers and thin arrows illustrate the return flow in the interior (secondary circulation).



Interior ageostrophic circulation (thin arrows) driven by convergence and divergence of Ekman transport (horizontal thick arrows) in the bottom Ekman boundary layer (EBL) beneath a spatially-variable jet flowing out of the page, whose strength is proportional to the size of the encircled dots. Ekman transport is proportional to this strength and changes along the EBL (different length of horizontal arrows), giving rise to an ageostrophic secondary circulation denoted by the thin continuous arrows.

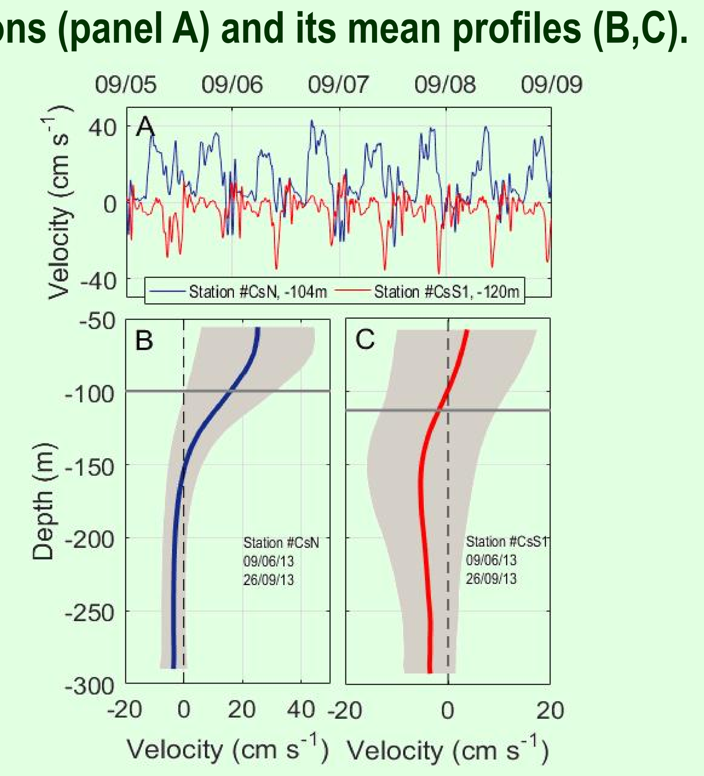


Mean vertical profiles of along-strait (black) and cross-strait (blue+red) velocity at the eastern (left) and Camarinal (right) sections from historical datasets (see stations in the map above). Horizontal black line is the interface of time-average null along-strait velocity *(from García-Lafuente et al., 2023)*



Profiles show mid-depth layers of positive cross-strait velocity (red line) and of negative velocity above and below (blue line). South-to-north connection could happen in the intermediate layer and north-to-south transport within the surface or deep layers. For a cross-strait velocity of ~5 cm/s (4 km/day), at least four days are necessary to cross the SoG at its narrowest section (~14 km). In the deep layer, along-strait velocity changes with depth and location, increasing from few tens of cm/s in the east to nearly 1 m/s in the west. Even with a moderate spatial mean of 40 cm/s, along-strait displacements in four days would be close to 150 km, well above the SoG dimensions. More unfavorable considerations apply to the surface layer. Only by remaining close to the interface, the algae could have chances to cross the SoG.

Vertical velocity near the interface at Camarinal stations (panel A) and its mean profiles (B,C).



Tidal semidiurnal fluctuations (panel A) are larger than algae sedimentation velocity, and are able to displace them up. Panels B,C show that, nearby the interface, upward (downward) advection is more likely to occur in the north (south).

Assessing the hydrodynamic connection hypothesis.

Let us consider one of the shores of the SoG with algae settlements while the other is free of them. The successful colonization of the later requires not only the existence of cross-strait flows, but also other set of concomitant circumstances. Availability of products to be transported is the first one. They must sink to the interface depth, be carried to the other shore and then advected by vertical velocity up to the illuminated layer in order to settle and thrive. Algae density and flow vertical velocity come into play. *RO* is very slightly denser than seawater, so they have sedimentation velocities of 1 to 4 cm/s in calm conditions, depending on the size and shape of thalli. But such small density difference makes the algae be easily displaced in the vertical many tens of meters by the vertical velocities of short-scale hydrodynamic features generated by flow-topography interaction around Camarinal sill (right panel above).

The journey will take days to weeks and be done in weak light or no-light conditions. The colonization success will depend on whether or not the algae arrive in good conditions for reproduction after the journey. ***RO* collected in Tarifa placed in darkness inside a culture chamber of nutrient-rich seawater at 17°C were able to recover partially and reactivate their metabolism when re-exposed to light after 13 days**. Rosas-Guerrero et al. (2018) observed that adult thalli had survival rates between 80-100% after being cultivated in dark conditions for three weeks. These experiments suggest real chances for colonizing the new region of arrival after such a hard journey.

The successful connection, however, relies on a chain of circumstantial links. Algae should be ripped out from the seafloor by natural (wind or current-induced turbulence) or human (fishing) agents in the surface illuminated layer in the colonized shore. Propagules or spores must be horizontally displaced offshore and vertically to the depths of the interface. Once there, they should cross the SoG and reach the opposite continental slope, be raised to the surface layer and displaced to the new shore. The process will take weeks and be done under extreme low light conditions. Each and every of these contingencies are surmountable. Their concatenation in a single experiment, however, is extremely improbable. **It is only the massive amount of available specimens for transport that can provide a number of successful connections**. Even if the number is small, it would suffice to colonize the new ecosystem taking into account the huge adaptability of the algae. Studies based on high resolution fully 3D numerical models coupled to accurate advection schemes, currently in progress, would help to support or reject the hypothesis of hydrodynamic connection.

Johnson, G.C., and D.R. Ohlsen (1994). Frictionally modified rotating hydraulic channel exchange and ocean outflows. J. Phys.Oceanogr., 24, 66-78,
García-Lafuente et al. (2023) Could secondary flows have made possible the cross-strait transport and explosive invasion of Rugulopteryx okamurae in the Strait of Gibraltar? PLoS ONE 18(5): e0285470.
Rosas-Guerrero, J., Y.E. Meco, and M. Altamirano (2018). Could Rugulopteryx okamurae (Dictyotales, Ochrophyta) have been introduced by ballast waters? Algas, 54, 52.