BIOLOGICAL OCEANOGRAPHY

# Waves of invasion

Will the Southern Ocean's relentless waves undo Antarctica's ecological isolation? The discovery of a wayward piece of kelp and a simple numerical experiment set new expectations for the potential invasion of Earth's most isolated continent.

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The movement of individual organisms is a crucial component of all ecological and evolutionary processes, including those of growing concern to humans: invasive species, population responses to habitat modification and a rising extinction rate[1]. Our ability to make predictions about how these processes will respond to climate change is limited, in large part, by a lack of understanding of the mechanisms of organismal movement[1,2]. For animals, movement results from a complex interplay of sensory perception, orientation responses to internal and external stimuli, the biomechanics of locomotion and environmental conditions[1–3]. Even for the simpler cases, where the organisms' speed and direction of travel are determined entirely by wind or water currents, challenges in tracking that movement remain. Writing in *Nature Climate Change*, Ceridwen Fraser and colleagues show the importance of identifying the mechanisms of organismal movement in predicting the susceptibility of Antarctica's coastal ecosystem to biological invasion[4].

Biogeographic patterns are intrinsically tied to organismal movement[1] and, in the marine environment, movement is necessarily a function of ocean currents[3–6]. Accurately depicting ocean circulation is prerequisite to developing mechanistic models that can be used to predict the ecological processes that result from organismal movements[3,5,6]. Historically, the long-distance dispersal of marine organisms was thought to be common, as ocean currents were viewed as broad conveyors of drifting propagules[5]. With this model of ocean circulation in mind, the transoceanic movements of plankton (and even strong swimmers) were viewed as an inevitable consequence of life in the flowing ocean[5,6]. Panmixia was expected across marine regions and when it was not observed, differences in environmental conditions among sites (related to the ecological niche of species, for example) or processes such as competitive exclusion (that is, previous occupancy of a dominant species) were invoked[5,6].

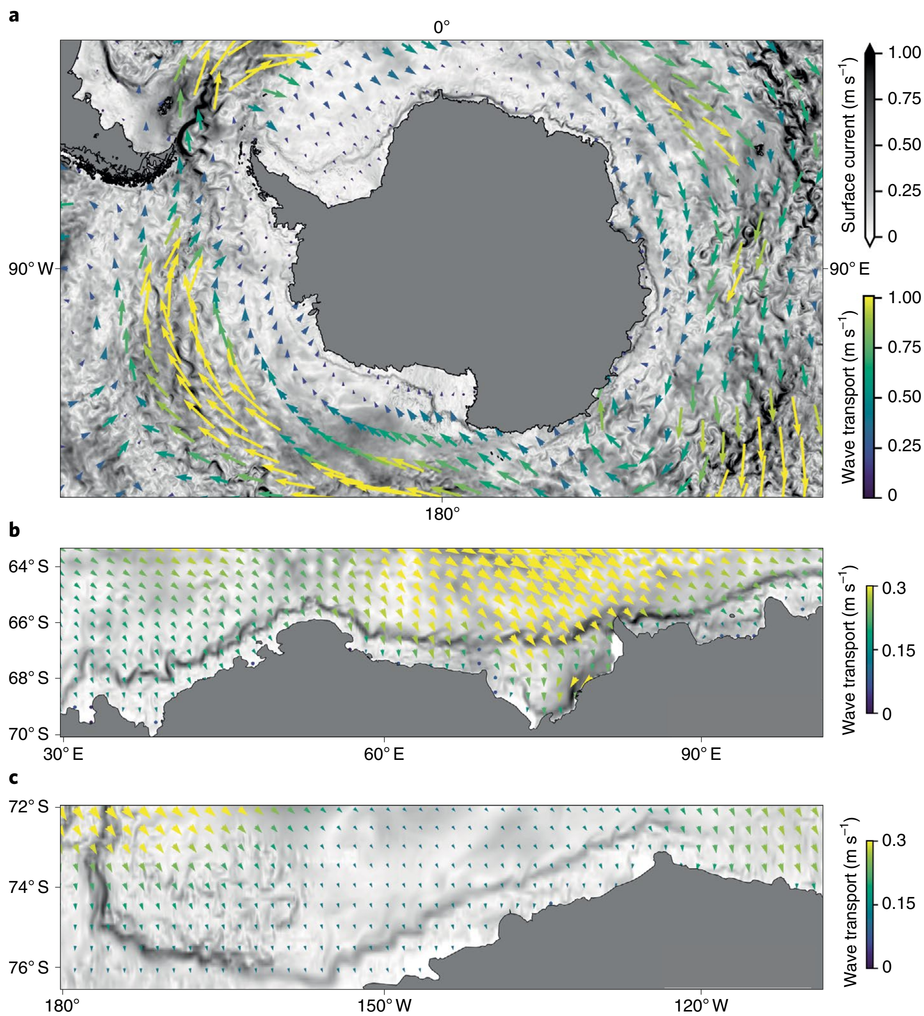


**Fig. 1 | Maps of surface currents and wave transport in the Southern Ocean. a**, Surface currents in the Southern Ocean result in oceanic fronts that reduce north–south transport between the global ocean and coastal Antarctica (darker lines). However, wave-induced transport (Stokes drift) results in transport across these apparent barriers. **b**,**c**, Different areas along Antarctica's coast where wave-induced transport results in the crossing of oceanic fronts. Ocean currents are based on HYCOM ouput and wave transport is from the Wave Watch III model[4], both depicting conditions on 15 August 2012.

As our ability to measure aspects of ocean currents at high resolution has improved, the view that local retention typically predominates over long-distance transport has emerged[6,7]. A key physical constraint responsible for retention is the frontal zones that delineate coastal and oceanic waters. Oceanic fronts are established where water masses with different physical properties meet[7]. Owing in part to Earth's rotation, flow is directed along the front rather than across it. Coastal areas throughout the globe are flanked by oceanic fronts, which typically act as barriers to transport[7].

A series of such fronts encircle Antarctica (notably the Antarctic Shelf–Slope Front[7] and the Polar Front[8]) and have been implicated as an important mechanism for limiting biological exchange with the global ocean. These oceanic fronts, combined with the freezing coastal temperatures, are thought to isolate the Antarctic ecosystem from species and populations that occupy more northern latitudes. Fronts provide the first line of defence to impede invasion, and the harsh environment of Antarctica snuffs out any lucky propagule brought between the webbing of a bird's foot[9] (or in the tread of a researcher's or tourist's boot).

The study by Fraser and colleagues provides a different set of expectations[4]. They found unusual pieces of kelp on the coastline of Antarctica. They bore signs of drifting a long time at sea (evidenced through barnacle growth). A nearly exhaustive analysis of the genetics of the specimens in relation to kelp populations skirting the Southern Ocean indicated the source populations were probably Kerguelen (49° S) and South Georgia (54° S), more than 20,000 km distant from the site of beaching[3]. How had this kelp arrived through the bulwark of frontal zones? An elegant set of numerical experiments shows waves to be responsible.

Using the surface layer of the global Hybrid Coordinate Ocean Model (HYCOM) the authors are able to simulate the drift of kelp from the islands of Kerguelen, South Georgia, Cape Horn and Macquarie (potential source populations of kelp). HYCOM performs well at portraying the main ocean circulation features, such as fronts and eddies[10]. However, other physical processes that are not accounted for in HYCOM[3] occur at the ocean surface, and may play an important role in organismal movement. Such processes include direct momentum transfer to floating material from the wind (that is, windage) and residual transport due to waves (Stokes drift)[3,11]. As expected, in HYCOM simulations virtual kelp remained north of the major oceanic fronts, but when the velocity imparted by waves (in some regions>20 cm $s^{-1}$) was added, an entirely different picture emerged: transport across the Antarctic fronts was common and persistent (Fig. 1).

Interestingly, this finding comes on the heels of another study that showed alarming amounts of microplastic landward of the Antarctic Polar Front[8]. A reasonable hypothesis is that the same wave-induced transport that allows kelp to reach Antarctica also facilitates the movement of debris from distant centres of large human populations into this ecosystem. Given the massive waves in the Southern Ocean (Fig. 1), species and objects with long drift times are likely to make it past oceanic fronts. Thus, it seems that the present level of ecological endemism in Antarctica is more due to its harsh climate than its lack of connectivity with the rest of the ocean. As Antarctica's climate warms, kelp and a variety of other species rafting at the ocean surface seem poised to invade.

Important questions remain. Waves result in transport across fronts (increasing invasion potential), but do they also increase the sinking rate of objects at the surface (thereby decreasing invasion potential)? How do the shape, drag and windage coefficient of different objects influence their transport across the ocean surface? Further research is required to resolve the effects of physical transport processes at the air–sea boundary, the conditions that influence movement, and the sensitivity of predictions of various ecological processes to their inclusion in models[11]. Fraser and colleagues[4] show that close collaboration between ecologists and physical oceanographers will be required to yield the information needed. ❐

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