Extended abstract

Going against the flow: how marine invasions spread and persist in the face of advection[1]

James E. Byers and James M. Pringle

Byers J. E., and Pringle J. M. 2008. Going against the flow: how marine invasions spread and persist in the face of advection. – ICES Journal of Marine Science, 65: 723–724.

Keywords: *Carcinus maenas*, climate change, coastal transport, diffusion, Lagrangian framework, upstream movement.

Received 21 October 2007; accepted 27 December 2007; advance access publication 17 March 2008.

J. E. Byers: Department of Zoology, University of New Hampshire, 46 College Road, Durham, NH 03824, USA. J. M. Pringle: Department of Earth Sciences, and the Institute of Earth, Oceans, and Space, University of New Hampshire, Durham, NH 03824, USA. Correspondence to J. E. Byers: tel: +1 603 8620006; fax: +1 603 8623784; e-mail: jebyers@unh.edu

The factors that set the range limits of species are poorly understood. This uncertainty is even more pronounced for species living in moving fluids such as the coastal ocean. Often, ecologists have the superficial impression that ocean currents are an energetically efficient dispersal mechanism. Although this statement is true, these same currents present a very real challenge to an organism. How does a species in such an advective environment avoid being moved downstream in successive generations and thus be swept out of its habitable domain after only a handful of years? In the original version of this paper (Byers and Pringle, 2006), we identified a quantitative relationship that determines whether a coastal species with a benthic adult stage and planktonic larvae can be retained within its range and invade in the direction opposite to the mean current experienced by the larvae (i.e. upstream). The derivation of the retention criterion extends prior riparian results into the coastal ocean by formulating the criterion as a function of observable oceanic parameters, by focusing on species with obligate benthic adults and planktonic larvae, and by quantifying the effects of iteroparity and longevity. By placing the solutions in a coastal context, the retention criterion isolates the role of three interacting factors that counteract downstream drift and set or advance the upstream edge of a marine species' distribution. First, spawning over several seasons or years exposes the larvae to increased variation in the currents encountered and so enhances retention. Second, for a given rate of population growth, species with a shorter pelagic period are better retained and should be more able to spread upstream. In other words, as planktonic duration increases, the net movement of the plankton increasingly conforms to the probabilistic motion of the current, which by definition is in the downstream direction. Third, prodigious larval production improves retention. Most larvae are swept downstream, with only a small fraction remaining at the upstream edge. Therefore, long-distance downstream dispersal may be a by-product of the many propagules necessary to ensure sufficient local recruitment and persistence of a population in an advective environment.

Life histories of organisms must include a combination of these traits that minimize downstream advection by the mean currents or that maximize the variability of this advection to retain essential upstream populations. (Larval behaviour via vertical positioning can also enhance retention, but typically only if the variability in currents encountered by the larvae is increased relative to the mean.) All species must adhere to some of these tenets, and clearly some of these will be harder to satisfy for recently introduced species. Specifically, new invaders tend to have small populations (and therefore low population-level propagule production) and limited distribution (implying that the population as a whole is less able to benefit from spatial variability in flows).

The theory does suggest where invasions will be very successful: in upstream retention zones, a role often played by estuaries. This is so because these areas are not typically subject to alongshore advection and so can be excellent retention centres and persistent sources of larvae that can exit the estuary and readily supply downstream areas of the coast. This supply of larvae can take place, in fact, without the parent estuarine population itself ever being in danger of being displaced downstream.

Interspecific interactions, like competition, can also be incorporated into our theory, with the general effect that maintaining or advancing the upstream edge of a species' distribution becomes even harder. Now, a species is fighting not only physical processes, such as advection, that move it downstream, but also biotic interactions from upstream competitor species. Upstream

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[1] Much of the material discussed here is based on the manuscript by Byers and Pringle (2006) in Marine Ecology Progress Series, 313 (see References).

competitors should have a great advantage because they easily swamp downstream sites with their larvae. In contrast, the downstream species struggles to maintain itself at its upstream edge, usually returning only small numbers of larvae. Therefore, any competitive outcome based on numerical advantage will greatly favour the upstream species. For the downstream species to persist despite such a numerical disadvantage in larvae, it must have a superior *per capita* competitive ability that is able to compensate for the extent to which its larvae are being swept downstream. If not, the downstream species will slide quickly downstream in just a few generations, to the point at which the number of larvae that survive to adulthood is sufficient to satisfy the retention criterion.

We are currently testing several tenets of this theory on the coastline of northeastern North America using the introduced European green crab (*Carcinus maenas*). The species was introduced to the mid-Atlantic coast of the US in the early 1800s, and has subsequently spread >1000 km upstream, where the invasion seemingly stalled in the 1960s around Halifax, Nova Scotia. Owing to the increased time needed for larval development as water temperature decreases, our calculations suggest that this stopping point for the invasion was natural, because *C. maenas* could not spread on its own farther north (upstream) than Halifax. However, in the 1990s, *C. maenas* populations suddenly expanded farther north into the Canadian Maritimes. Roman (2006) elegantly demonstrated that the new expansion was driven by a new introduction of *C. maenas* to northern Canada from Europe that possessed distinct haplotypes from the older established population in North America. We contend that, once inoculated farther north of Halifax by humans, *C. maenas* could be retained and even expand because of the presence of upstream retention zones throughout the Canadian Maritimes, e.g. the Straight of Canso and the Bras d'Or Lakes. Moreover, once anchored there, these upstream *C. maenas* populations should then flood downstream areas with their propagules and have a great competitive advantage over downstream populations, which, we predict, they will eventually displace. This replacement can readily be tested thanks to the distinctive genetic signatures of *C. maenas* in the upstream and downstream positions. If the competitive dominance of the upstream populations is correct, the distinctive haplotypes currently found only in the upstream northern end of *Carcinus*' introduced range should come to dominate throughout the entire range (Pringle and Wares, 2007). We are now completing genetic sampling of *C. maenas* to evaluate the spread of the northern haplotypes over the past 7 years.

Advection is a dominant force on life in the ocean. Clearly, if we are to understand marine invasions better, we must understand how species, both native and introduced, have been shaped to deal effectively with this force. Therefore, the question of interest is perhaps not, "how has the planktonic life cycle been shaped to promote dispersal?", but rather, "how do species persist in spite of a planktonic life history?" In specific regard to biological invasions, our theory helps to identify the most influential areas to population establishment and persistence along a coastline, as well as general characteristics that may make an invader more likely to succeed in an advective environment.

References

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doi:10.1093/icesjms/fsn012