

SUEZ CANAL MIGRATION AND MEDITERRANEAN COLONIZATION - THEIR  
RELATIVE IMPORTANCE IN LESSEPSIAN MIGRATION\*

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SUMMARY - The Suez Canal does not sort out propagules of benthic Red Sea species into successful and unsuccessful Lessepsian migrants; the currents are favourable for a Red Sea - Mediterranean crossing, and the Canal does not act as a genetic bottleneck. A successful colonizer should not necessarily originate in a diverse community and invade a less diverse one, neither should it be particularly competitive; the availability of a suitable habitat does not guarantee its colonization success, but an *r*-strategy constitutes a pre-adaptation for colonizing the Mediterranean.

Resumé - Le Canal de Suez n'effectue pas une sélection des propagules d'organismes benthiques de la Mer Rouge - en migrants Lessepsiens bon ou mauvais. Plutôt ce sont les courants qui agissent en faveur d'une passage Mer Rouge - Méditerranée et le Canal ne fonctionne pas comme un barrage génétique. Un colonisateur bien-réussi n'est pas nécessairement un ressortissant d'une communauté diversifiée qui pénètre une communauté moins diversifiée; aussi ne doit il pas être muni d'une capacité compétitive exceptionnelle. L'existence d'un habitat favorable n'est pas non-plus la garantie de son succès colonisateur. C'est une "*r*-strategy" qui constitue une pré-adaptation à la colonisation en Méditerranée.

Lessepsian Migration (Por 1977) is the process of colonization of the Mediterranean Sea by Red Sea species migrating through the Suez Canal. The presence of a viable, persistent population of a Red Sea species in the Mediterranean depends on the ability of propagules first to migrate through the Canal, then to colonize the new environment. The objective of this paper is to assess the contribution of these two processes to the final success of Lessepsian migrants.

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MIGRATION - It has been suggested that the high salinity of the Great Bitter Lake constitutes obstacle to many species. However, the Red Sea intertidal snail Cerithium caeruleum is more tolerant to high salinities than its sympatric congener C. scabridum, yet only the latter colonized the Mediterranean (Ayal & Safrieli 1983).

Since many benthic species migrate through the Canal by means of floating propagules, the currents of the Canal may determine migration success. Agur & Safrieli (1981) used a mathematical, hydraulic model (based on tidal predictions, barometric pressure, evaporation, salinity, run-off and wind data) that predicts the direction and velocity of the current along the Canal throughout the year, for simulating the movement of propagules floating in the Canal after being "introduced" (through a computer program) into the Canal entrance at Suez. Once introduced, the fate of each propagule was followed, either until it was "reabsorbed" into the Gulf of Suez, or until it emerged through the Mediterranean exit. These simulations revealed that once entering the Canal, a propagule has on the average 15% chances of emerging at the Mediterranean exit (45% at the peak of breeding season of most benthic Red Sea species), and the journey would last on the average 11 days (larval longevity of C. scabridum for example, is 3-4 times longer).

Thus, neither the chemical properties of the Canal, nor its currents sort out Red Sea species into colonizers versus non-colonizers. Yet, the Canal could constitute a genetic bottleneck by sampling only a small segment of the genetic variability existing in the Red Sea, hence for some species the propagules that manage to cross the Canal establish genetically inviable founding populations. The extent of the genetic variability in populations of C. scabridum (Pashtan & Ritte 1977) and of a colonizing intertidal mussel, Brachidontes variabilis (Lavee 1981) in the Red Sea was compared with that of their colonizing populations in the Mediterranean, through an electrophoretic analysis of enzymes. Only 8% and 7% of the Red Sea alleles of C. scabridum and of B. variabilis, respectively, have not been found in the Mediterranean populations of these species. Thus, we might have inferred that less than 10% of the genetic variability of the source populations has not been "sampled" by the Canal. However, 17% and 8% of the Mediterranean alleles, of the cerithiids and the mytilids, respectively, are "unique", i.e., we discovered them only in the Mediterranean but not in the Red Sea samples. It is unlikely that these alleles arose by spontaneous mutations; they presumably exist in the Red Sea in low frequencies, but in spite of their rarity they were sampled by the Canal, and then selected by the Mediterranean to become sufficiently common so as to be detected in our samples. In populations going through a genetic bottleneck mean heterozygosity and mean number of alleles should fall (Nei et al. 1975). However, there were no significant differences between populations of the source and the colonized area in mean heterozygosity, and in C. scabridum the mean number of alleles was

even 11% higher in the Mediterranean than in the Red Sea. Thus, the Canal could not have distorted the genetic structure of these colonizers to a point that will jeopardize their successful colonization.

COLONIZATION - If the Suez Canal neither constitutes a chemical barrier, nor a genetic bottleneck for Red Sea migrants, and its currents allow for a rapid flow of Red Sea propagules to the Mediterranean, why then out of the hundreds of Red Sea species with pelagic larvae, only ca 130 (Por 1977) successfully colonized the Mediterranean? For example, C. caeruleum which exhibits great ecological similarity to the colonizer C. scabridum (Ayal & Safriel 1983) should have migrated easier than the colonizer. However, though both have been found in the Canal, only C. scabridum has colonized the Mediterranean. Similarly, Modiolus auriculatus, the Red Sea mytilid which is ecologically similar to the mytilid B. variabilis, has occasionally migrated through the Canal, but has not colonized the Mediterranean (Safriel et al. 1980). Note that when a genetic bottleneck exists, only species with large genetic variability maintain a sizeable part of it after going through the Canal, sufficient for colonizing successfully, whereas species with low genetic variability in the Red Sea will be unsuccessful, even if they manage to cross the Canal. However, since the Canal does not constitute a genetic bottleneck colonizers and non-colonizers need not differ in the extent of genetic variability they maintain in the Red Sea. A comparison of electrophoretic variability of Red Sea populations of colonizing species, with that of their closely related non-colonizing species (Table 1) could not point at significant difference. Thus, the success in colonization does not depend on electrophoretic variation.

Table 1 - Electrophoretic analysis of colonizers and non-colonizers in the Red Sea

	Cerithiids		Mytilids	
	Col.	Non-col.	Col.	Non-col.
No. of examined loci	20	2	17	16
Mean No.alleles/loc.	4.45	3.86	5.88	5.87
Heterozygosity/locus	0.66	0.68	0.59	0.63

Since the biota of the eastern Mediterranean is regarded as "impoverished", it has been suggested that Red Sea species are "diffusing" through the Canal to fill-in "empty ecological niches" in the Mediterranean (Por 1977). Indeed, there are 6 intertidal cerithiid species in the Gulf of Suez and only one

indigenous species in the eastern Mediterranean. However, though there are 3 intertidal mytilids in the Gulf of Suez, but 4 species in the eastern Mediterranean (Safriel *et al.* 1980), a Red Sea mytilid invaded the Mediterranean mytilid community, whereas none of the Mediterranean mytilids have colonized the Red Sea.

It has been also suggested that Red Sea species have high competitive ability relative to Mediterranean species, on the grounds that species from highly diverse communities are competitively superior to those from less diverse ones (Briggs 1968). Our studies revealed that *C. scabridum* is competitively superior to its closely related Mediterranean indigenous species *C. ruppestre* and is 10 times commoner in the habitats they share. However, *B. variabilis* is competitively inferior to its closely related Mediterranean indigenous species *Mytilaster minimus*, the latter being 200 times commoner in the habitats they co-occupy.

Could it be that the two non-colonizing molluscs did not colonize simply because they had not found suitable habitats in the Mediterranean? At least *C. caeruleum* could have found a suitable habitat since its habitat range is wider than that of the colonizing cerithiid (Ayal & Safriel 1983), yet it has not colonized. What are then the problems in colonizing the Mediterranean that *C. caeruleum* and other species could not overcome?

A common feature to all colonizations preceded by migration through a narrow passageway is the small size of the founding population. It is therefore vulnerable to random extinction, either through "demographic stochasticity" in uniform and stable environments, or through "environmental stochasticity" in non-uniform and fluctuating environments, especially at the initial stage of colonization. A potential for rapid population growth expressed by high  $r$  (intrinsic growth rate at low densities), would shorten the time during which a colonizing population, threatened by demographic stochasticity, is exposed to the risks of environmental stochasticity. Thus, a high  $r$  (and associated features of the " $r$ -strategy") is a preadaptation for all kind of colonizations (Safriel & Ritte 1983). Indeed, each of the two colonizing molluscs is an " $r$ -species" relative to its non-colonizing mate (Table 2).

To conclude, the Canal constitutes a narrow passageway that samples only a minute portion of the available propagules and allows the successful passage of only few at a time. Therefore founding colonies are small and their persistence time depends on their ability to grow fast. Note that the non-colonizing cerithiid has a high fecundity and it is likely that the disparity in age of first reproduction between the two determines their difference in colonization success: A founding colony of *C. scabridum* produces propagules to colonize adjacent habitat patches within a year, whereas that of *C. caeruleum*, if it does not perish, only after three years. By that time most patches in the surroundings are already occupied by *C. scabridum*, which has the upper hand in this type of "migration and extinction" competition. Thus, *C. caeruleum* could have colonized the Mediterranean were it not living in the Red Sea together with a closely related but potentially better colonizing species.

Table 2 - Demographic features of colonizers vs non-colonizers

	Cerithiids		Mytilids	
	Non-col.	Col.	Non-col.	Col.
Mean size of adults(mm)	28	18	35	20
Age of 1st reproduction(y)	4	1		
Size at maturation(mm)			18	8
Generation time(y)	7.3	2.1		
Max.No.eggs/fem.d(thousands)	25	13		
r-value(per year)*	1.6	0.9		

\* For larval survivorship of 0.001 (Ayal & Safriél 1982).

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