

MARINE BIOLOGICAL INVASIONS AS MODELS OF DISPERSAL: TRACKING SECONDARY SPREAD AND INTROGRESSIVE GENE FLOW

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ABSTRACT

A major limitation of genetic approaches to the study of ongoing dispersal is that site- or population-specific markers are rarely available. Over spatial scales that encompass transport of propagules, newly generated neutral polymorphisms will have been spread by prior dispersal. Marine biological invasions provide an alternative approach to the study of larval dispersal in two ways. First, primary invasions generally occur in one or few sites. The sources of recruits in subsequent range extension can therefore be traced. Second, invading species can inject novel genetic markers into native populations when hybridization is possible. Similarly, when the distribution of native and invading species overlaps narrowly, dispersal can be traced by the movement of hybrid genotypes from the hybrid zone. Dispersal of the invading barnacle *Elminius modestus* in Great Britain, the crab *Carcinus maenas* in California, and the green alga *Codium fragile* in New England are examples of the first approach. The unidirectional introgression of the mitochondrial genome of the native northern mussel *Mytilus trossulus* into invading populations of *Mytilus galloprovincialis* in southern California is an example of the second approach. Marine biological invasions are increasing in frequency and in these ways provide population biologists and geneticists with useful model systems.

RESUMEN

Una de las limitantes más importantes del estudio de la dispersión utilizando enfoques genéticos es que raramente se encuentran marcadores genéticos específicos, de sitios o de poblaciones. En escalas espaciales que abarcan el transporte de los diseminulos, los polimorfismos neutrales recientemente generados habrán sido diseminados por eventos de dispersión previos. Las invasiones biológicas en el medio marino proveen un enfoque alternativo al estudio de la dispersión; hay dos posibilidades. Primero, las invasiones empiezan generalmente en uno o pocos sitios, y las fuentes de reclutas pueden ser rastreadas después de una extensión del rango. Segundo, las especies invasoras pueden inyectar marcadores genéticos nuevos a las poblaciones nativas (siempre y cuando exista la posibilidad de hibridación). De la misma manera, cuando las especies nativas e invasoras traslapan de una manera marginal, la dispersión puede

ser rastreada por el movimiento de genotipos híbridos provenientes de la zona híbrida. El primer enfoque es ejemplificado por la dispersión del cirripedio invasor *Elminius modestus* en Gran Bretaña, el cangrejo *Carcinus maenas* en California y el alga verde *Codium fragile* en Nueva Inglaterra, y el segundo por la introgresión unidireccional del genoma de la mitocondria del mejillón noroeste nativo *Mytilus trossulus* en la población invasora del *Mytilus galloprovincialis* en el sur de California. Las invasiones biológicas en el medio marino han incrementado su frecuencia, y tal como se discutió anteriormente, proveen sistemas modelo útiles a los biólogos de poblaciones y genetistas.

INTRODUCTION

Dispersal is a key factor in the dynamics of marine populations because large numbers of marine species have planktonic life-history stages. Local populations are influenced by import and export of propagules, and it is insufficient to study local production and mortality. For this reason, there is great current interest in determining the fate of locally produced propagules and the source of recruits. Import and export of potential recruits will depend on transport mechanisms that operate over appropriate spatial scales (e.g., Farrell et al. 1991; Roughgarden et al. 1991).

Because variation in nucleic acids can resolve differences at individual, population, and species levels (Hillis and Moritz 1990), there has been much optimism that DNA-related approaches will allow population ecologists to uncover the sources of recruitment into local populations. However, a major limitation of genetic approaches to the study of ongoing dispersal is that site- or population-specific genetic markers are rarely available. Logically, newly generated neutral polymorphisms will have already been spread by prior dispersal over spatial scales that encompass transport of planktonic propagules. Current distributional patterns of genetic markers may indicate historical limits to dispersal (Avice et al. 1987) at large geographic scales, but will not provide sufficient resolution to discern patterns of dispersal among demographically linked populations. Direct oceanographic studies of movements of water masses offer one alternative to genetic approaches, but necessarily make simplifying assumptions about the behavior of larvae

(e.g., depth distribution and migration, duration of larval phase, time to competence to settle, etc.) that may vary in space, time, or across taxa. In this paper, I propose that marine biological invasions provide an alternative approach to the study of dispersal.

Marine biological invasions are the arrival and establishment of marine organisms in geographic regions where they were previously absent (Carlton 1985, 1987, 1989). In historical times, most marine invasions have been human-mediated, and various modes of transport or release have been involved, including the hulls of ships, releases of aquarium specimens, and releases of aquaculturally important species and their epibionts (Carlton 1985, 1989). Today, the most important mode of invasion is untreated seawater used as ballast in ocean-going ships (Carlton 1985; Williams et al. 1988; Carlton and Geller 1993). Ships routinely take seawater into dedicated tanks and holds for extra weight and stability. This water is unprocessed, and contains virtually all organisms in the water column at the time of ballasting that can pass through a coarse sieve (ca. 2 cm), including the larvae of larger organisms. A recent study by Carlton and Geller (1993) showed that ballast water arriving in Oregon from Japan in 159 ships over a five-year period contained all major marine phyla, with the absence of sponges and ctenophores (the latter have now been observed in ballast water [J. T. Carlton, pers. comm.]). A minimum of 367 distinctly identifiable taxa were observed, with molluscs, polychaetes, copepods, cirripedes, and diatoms among the most abundant and most frequently released taxa. Because ballast water is carried from port to port, organisms can be entrained into a ship in coastal or estuarine waters, transported hundreds to thousands of kilometers (often to another continent), and released into other coastal or estuarine waters. In this way, natural biogeographic barriers are breached, and organisms may find themselves in environments physically and chemically similar to their home range.

Four characteristics of ballast-water-mediated transport make invasions an attractive alternative for the study of larval dispersal, because they make it possible to track range expansion of invading species, and to track genes introgressing into native populations. (1) Because of the association with shipping, initial invasions generally occur in one or few sites (ports). Therefore, subsequent range extensions of invading species can be easily traced to specific sources. (2) A broad taxonomic spectrum of marine organisms is transported in ballast water (Carlton and Geller 1993), so invading species that are similar to native species in terms of larval biology and reproductive phenology may be selected for study. (3) Invading species can inject novel genetic markers into native populations when hybridization is possible. Similarly,

when the distribution of native and invading species overlaps narrowly, dispersal can be traced by the movement of hybrid genotypes from the hybrid zone. (4) Marine biological invasions appear to be increasing in frequency (Carlton et al. 1990; Carlton and Geller 1993). Thus if each invasion is considered an "experimental" release, new invasions serve to replicate the dispersal experiment.

In the following section, I first discuss three examples of range extension from an area of primary invasion to illustrate the utility of this approach to the study of dispersal patterns. Next, I discuss the results of current research on the spread of the mitochondrial genome of a native species into allopatric populations of an invading species through a narrow hybrid zone.

RANGE EXTENSION OF INVADING SPECIES

Elminius modestus

Scheltema and Carlton (1984) summarize the history of invasion and spread of the Indo-Pacific barnacle *Elminius modestus* into Great Britain and Europe. *Elminius* was not known in Britain before 1940, and Crisp (1958) suggests that it was introduced during World War II. Between 1940 and 1945, this species became established in southeastern Britain, and then spread rapidly northward and westward. From examination of reports of the presence of *Elminius*, Scheltema and Carlton (1984 and citations within) estimate that *Elminius* spread at a rate of 20 to 30 km per year. The larval phase of *Elminius* is estimated as 17–34 days, depending on temperature, which would have easily allowed spread at this rate. By 1956, the species had arrived in Scotland and as far as northern Germany along the European coast. In this example, the source of settlers to previously unoccupied shore could be rather precisely inferred.

Carcinus maenas

Ruiz and Grosholz (pers. comm. and submitted, 1994) have described the ongoing invasion of the European green crab, *Carcinus maenas*, in northern California. This crab, an important predator in its native range, was first discovered in 1989 in San Francisco Bay. *C. maenas* has planktonic zoea and megalopa larvae, as do other brachyuran crabs. Thus, this species may serve as a model for dispersal of native brachyuran species resident in San Francisco Bay. From 1989 to 1993, *Carcinus* were not observed outside of San Francisco Bay. But in January 1993, *Carcinus* were observed in Bodega Bay, north of San Francisco Bay. These sightings prompted Ruiz and Grosholz to investigate the intervening embayments of Drake's Estero, Bolinas Lagoon, and Tomales Bay, and crabs were found in each of these sites by the fall of 1993. Embayments north of Bodega Bay or south of San

San Francisco Bay (Princeton Harbor, Monterey Bay) have apparently not yet been invaded by *Carcinus* as of the winter of 1993–94.

Several interesting points arise from these observations. First, a lag of four years occurred before crabs were observed outside of San Francisco Bay. This may be attributable to a period of local population increase preceding sufficient larval production for successful export, transport, and colonization outside San Francisco Bay. Second, the spread of *Carcinus* has been exclusively in the northward direction. Although details of the reproductive phenology of *Carcinus* in San Francisco Bay are lacking, this may indicate predominately northerly surface currents at the time larvae are produced.

In summary, the secondary spread of *Carcinus* after invasion of San Francisco Bay unambiguously demonstrates that propagules produced there are the source of recruitment in Bodega Bay.

Codium fragile

Carlton and Scanlon (1985) describe the arrival and spread in New England of *Codium fragile* ssp. *tomentosoides*, a large and conspicuous green alga native to western Europe. Using evidence from herbarium collections, direct observations, interviews of shellfishermen and shellfish wardens, and literature reports, Carlton and Scanlon infer that *Codium* arrived first in Long Island Sound in or about 1956, possibly transported on the hulls of ships. Subsequent dispersal in the northwestern Atlantic Ocean apparently involved both human-mediated and natural dispersal mechanisms. Human-mediated dispersal may have included transfer on ships' hulls, on oyster shells, in fishermen's nets, and in packing material for lobsters and baitworm.

In the present context, natural dispersal is of greater interest. Natural dispersal may have been through motile gametes ("swarmers"), thallus fragmentation and drift, or rafting of entire plants. After transplantation on oysters to Chatham, on Cape Cod, in 1961, over the next 10 years *Codium* spread by natural dispersal mechanisms along the southern shore of Cape Cod. Dispersal to the north led to populations on the outer Cape by 1967. From Buzzards Bay, *Codium* moved through the Cape Cod Canal, arriving in Cape Cod Bay by 1972. Reports of *Codium* in Cape Cod Bay followed a chronological sequence consistent with bidirectional spread from the mouth of the Cape Cod Canal. *Codium* reached Provincetown in the northeast by around 1975 and Duxbury Bay in the northwest by 1981. This analysis, summarized from Carlton and Scanlon (1985), suggests that dispersal on both sides of the Cape Cod peninsula is not directional, though rates of spread may vary. For example, spread to the northeast was apparently more rapid than to the northwest in Cape Cod Bay.

TABLE 1
 Frequency of a Mitochondrial DNA Marker Indicative of *Mytilus trossulus* and *Mytilus galloprovincialis* in Populations from Alaska to Southern California

Site	<i>M. galloprovincialis</i>	<i>M. trossulus</i>	N
Shumagin Island, AK	0	100	20
Seattle, WA	0	100	23
Tillamook Bay, OR	0	100	54
Netarts Bay, OR	0	100	4
Yaquina Bay, OR	0	100	10
Coos Bay, OR	0	100	159
Humboldt Bay, CA	0	100	11
San Francisco Bay, CA	32.3	67.7	68
Monterey Bay, CA	72.4	27.6	58
Morro Bay, CA	51.6	48.4	31
San Diego Bay, CA	58.7	41.3	46
Japan (ballast water)	100	0	45

Data from Geller et al. 1994. For details on methods, see also Geller and Powers, in press.

GENETIC INTROGRESSION AS AN INDICATOR OF DISPERSAL

The mussel *Mytilus galloprovincialis* is native to southern Europe and the Mediterranean Sea and has been introduced to many regions globally, including Japan, Hong Kong, Singapore, South Africa, and southern California (McDonald et al. 1991; Seed 1992). On the North American west coast, *M. galloprovincialis* occur from at least San Diego to the San Francisco Bay region (McDonald and Koehn 1988; Sarver and Foltz 1993; Geller et al. 1994). Although larvae of this species are regularly released into ports of the Pacific Northwest from the ballast water of ocean-crossing ships (Carlton and Geller 1993), these larvae apparently do not survive, and only the native mussel *Mytilus trossulus* is found in these sites (Geller et al. 1994). Both species are found in the San Francisco Bay region, and will apparently hybridize where overlap occurs (McDonald and Koehn 1988; Sarver and Foltz 1993). Geller et al. (1994) showed (table 1) the occurrence of the mitochondrial genome of *Mytilus trossulus* in southern California populations which analyses of allozymes indicated were purely composed of *Mytilus galloprovincialis* (McDonald and Koehn 1988; Sarver and Foltz 1993). This suggests the introgression of the mitochondrial genome across a species boundary, from native *M. trossulus* in the north to introduced *M. galloprovincialis* in the south.

One mechanism for mitochondrial introgression could be the production of hybrid larvae in the zone of overlap (San Francisco Bay), followed by transport to the south and backcrossing of settlers into pure *M. galloprovincialis* populations. Female hybrid larvae that are the product of male *M. galloprovincialis* and female *M. trossulus* will carry the *M. trossulus* mitochondrial genome. The mating of such hybrid larvae in a population of *M. galloprovincialis* will produce F₂ generation individuals that are

TABLE 2
 Expected and Observed Percent Frequencies of Alleles at
 Three Partially Diagnostic Loci, and of a Mitochondrial
 DNA Marker for *Mytilus trossulus*^a

Locus	Allele	<i>M.g.</i> ^b	<i>M.t.</i> ^b	Morro Bay	Mission Bay	Coos Bay
<i>Gpi</i>	86	0	0	0	0	0
	89	0	6	0	0	0
	93	0	24	0	0	5
	96	1	0	2	0	5
	98	0	56	2	7	45
	100	92	2	93	85	45
	102	0	10	4	9	0
	105	6	2	0	0	0
<i>Lap</i>	107	0	0	0	0	0
	92	0	6	3	0	5
	94	4	50	0	2	45
	96	69	28	70	56	45
	98	23	12	27	40	5
<i>Pgm</i>	100	4	4	0	2	0
	86	0	0	2	0	0
	89	5	0	0	2	0
	93	11	0	23	7	0
	100	54	10	48	64	10
	106	24	32	21	28	35
	111	4	52	4	0	50
114	2	6	2	0	5	
mtDNA marker				29	28	100

^aMorro Bay *N* = 28; Mission Bay *N* = 29; Coos Bay *N* = 10.

^b*M.g.* = *Mytilus galloprovincialis*; *M.t.* = *Mytilus trossulus*. Expected values are from McDonald and Koehn 1988.

mostly *M. galloprovincialis* in nuclear genotype, yet carry the *M. trossulus* mitochondrial genome. Actually, biparental inheritance and heteroplasmy of mitochondrial DNA has been shown in mussels (Fisher and Skibinski 1990; Hoeh et al. 1991; Zouros et al. 1992); thus the direction of crosses may not be important in determining whether hybrid larvae carry the *M. trossulus* mitochondrial genome. A test of this hypothesis is to characterize both nuclear and mitochondrial genotypes simultaneously from mussels from southern California populations. Table 2 presents preliminary data of this nature (J. B. Geller and D. Hedgecock, unpublished data). Populations from Morro Bay, Mission Bay (San Diego), and, for comparison, Coos Bay, Oregon, were surveyed for allelic frequencies at three enzyme-coding loci that are each partly diagnostic for *M. trossulus* and *M. galloprovincialis*. These mussels were also assayed for a mitochondrial marker diagnostic for *M. galloprovincialis* and *M. trossulus* (Geller et al. 1994; Geller and Powers, in press). As shown in table 2, around 28 percent of individuals from each of the southern California populations carried the mitochondrial genome of *M. trossulus*, while allelic frequencies for the populations were in general accordance with those reported by McDonald and Koehn (1988) for *M. galloprovincialis*. Coos Bay mussels all carried the mitochondrial genome of *M. trossulus* and also had allelic frequencies concor-

dant with those reported by McDonald and Koehn (1988) for *M. trossulus*. These data support the hypothesis of mitochondrial introgression and have implications for the directionality of larval dispersal.

The direction of mitochondrial introgression is asymmetric, occurring only from *M. trossulus* to *M. galloprovincialis*. This can be explained in two ways: first, hybridization may be asymmetrical, in that *F*₁ hybrids may be viable only when they are products of a crossing between female *M. trossulus* and male *M. galloprovincialis*. If this were the case and if mitochondrial inheritance in mussels were mostly maternal, then transport of hybrid larvae could be bidirectional, but introgression detectable only in southern populations. Reports of biparental inheritance in crosses between *Mytilus galloprovincialis* and *M. edulis*, if extrapolated to crosses between *M. galloprovincialis* and *M. trossulus*, render this hypothesis unlikely (Hoeh et al. 1991; Zouros et al. 1992). An alternative explanation is that transport of hybrid larvae is predominately to the south. If so, the absence of *M. galloprovincialis* mitochondrial genomes in northern *M. trossulus* populations can be explained by the absence of a transport mechanism. Hybrid larvae carrying the mitochondrial genome of *M. trossulus*, *M. galloprovincialis*, or both, may be carried to southern populations, resulting in detection of the *M. trossulus* mitochondrial genome in those populations.

This proposed pattern of larval transport to the south seems contradictory to that seen in *Carcinus maenas*, described above, in which transport from San Francisco Bay appeared to be to the north. However, *Mytilus* from embayments immediately north of San Francisco were not sampled in the survey of mitochondrial genotypes, and analysis of allozymes indicates the presence of *M. galloprovincialis* in those populations (McDonald and Koehn 1988). Thus the distributions of *C. maenas* and *M. galloprovincialis* in the region north of San Francisco Bay are concordant. Neither species appears north of Bodega Bay. For *C. maenas*, insufficient time may explain its absence farther north, but *M. galloprovincialis* has been established in San Francisco Bay much longer, perhaps since the 1930s. The failure of *M. galloprovincialis* to spread north, or the failure of its mitochondrial genome to introgress into northern *M. trossulus* populations, suggests either lack of transport farther north, the lack of suitable habitat north of Bodega Bay, or a combination of both. If the introgression of the *M. trossulus* genome into southern *M. galloprovincialis* populations is mediated by southward movement of hybrid larvae, *Carcinus maenas* should eventually spread to the south.

CONCLUSION

These cases illustrate the utility of marine biological invasions for the study of ongoing dispersal over geo-

graphic scales relevant to population dynamics. Invasions involving large and easily identified organisms such as *Elminius modestus*, *Carcinus maenas*, or *Codium fragile* offer the most tractable systems for dispersal studies. However, many invading species are small, inconspicuous, or taxonomically understudied (Carlton and Geller 1993). Although these species are less attractive for dispersal studies, they are often highly abundant in the ballast water of ships. For these species, genetic characterization can allow study of their dispersal from an initial site of invasion. Some invading species are closely related to native species (i.e., congeners). In these cases, hybrid larvae produced in sites of invasion are "genetically marked" for their site of origin. Also, hybridization allows non-native genes to introgress into native populations (Geller et al. 1994). Thus invasions can serve simultaneously as models of dispersal and gene flow.

Marine invasions appear to be on the increase: Carlton et al. (1990) estimate that there is currently at least one successful invasion of San Francisco Bay each year. Although invasions can be deleterious to native organisms and should not be encouraged or celebrated, the association with shipping will continue to propagate invasions for the foreseeable future. Population biologists and geneticists have an opportunity to gain useful knowledge from this inadvertent modification of native communities.

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