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Invasion by the marine gastropod *Ocinebrellus inornatus* in France. II. Expansion along the Atlantic coast

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ABSTRACT: Dispersal ability is key to the spreading of exotic species to new areas. Herein, we focus on the expansion processes along the French Atlantic coast of an exotic marine gastropod, *Ocinebrellus inornatus*, first detected in the Marennes-Oléron bay in 1995. Unlike many aquatic invaders, *O. inornatus* lacks a swimming larval stage. This feature may reduce its ability to expand within the area of introduction unless counterbalanced by human-mediated spreading. By analyzing the genetic diversity at 7 allozyme markers, we compared the genetic diversity and structure of 9 French, 3 American and 5 Asian (native) populations. The genetic differentiation between populations within each area was low and of similar magnitude. However, a genetic isolation by coastline distances was detected in Asia only. We draw 2 main conclusions from these results. First, the settlement of new populations along the French Atlantic coast is not associated with drastic founder events. Second, expansion along the French coast is enhanced by oyster-farming activities.

KEY WORDS: Colonization · Introduced species · Direct-developing species · Population genetics · Allozyme markers · *Ocinebrellus inornatus*

INTRODUCTION

The increasingly high level of human activity has dramatically affected the natural geographic expansion of species by increasing the rate of biological introductions (Everett 2000). Biological invasion events can be arbitrarily separated into 2 main stages: (1) the introduction and settlement of the species over a restricted area, and (2) the demographic expansion of established populations across an increasing range via dispersal within the new environment (Vermeij 1996, Williamson 1996). Due to the ecological, political and economical outcomes of biological invasions, more and more studies are being devoted to deciphering the historical and biological processes underlying these 2 stages. This is not a trivial task, since invasive species are often detected many years after their introduction and during this time traces of the introduction and expansion events are progressively blurred by environmental variations and human activities. However, genetic imprinting of the invasion event can be detected by the use of specific population genetics tools with recently introduced populations (Sakai et al. 2001, Lee 2002). These tools have been successfully used in recent studies on invasive species (e.g. Villablanca et al. 1998, Davies et al. 1999, Duncan et al. 2001, Hellberg et al. 2001, Johnson et al. 2001, Dupont et al. 2003).

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Data on biological invasions can be used to determine the general biological attributes of invaders (Erlich 1989) and thus to improve the control and management of invading species (Bax et al. 2001, Kolar & Lodge 2001, Fagan et al. 2002). However, these biological attributes are highly variable, calling for additional research on invading species. Most studies on invading brackish or marine mollusks have been done on bentho–pelagic bivalves or gastropods with free-swimming larvae: e.g. the mussels *Dreissena polymorpha* and *D. quagga* (Geller et al. 1994, Stepien et al. 2002), the oyster *Crassostrea gigas* (Ó Foighil et al. 1998) and the slipper limpet *Crepidula fornicata* (Dupont et al. 2003). Little is known about the invasion of direct-developing marine mollusks, which do not have swimming larvae. This is unfortunate because this type of life-cycle has a direct effect on dispersal ability, a key factor in the long-term establishment and evolution of populations and species (Knowlton & Jackson 1993). Non-swimming larvae are less prone to dispersal, reducing the ability of exotic marine species to find new suitable habitats and extend their ranges. In *Littorina saxatilis*, this disadvantage has been shown to be balanced by an ability to rapidly colonize new sites (Johannesson 1988). A limited natural dispersal decreases the risks associated with primary introductions, but may be counterbalanced by human-mediated dispersal from which secondary introductions occur (Wolff & Reise 2002).

We studied the Asian oyster drill *Ocinebrellus inornatus*. This species constitutes an original biological model because it is a direct-developing marine gastropod. *O. inornatus* is native to the region between the Sakhalin and Kurile Islands and Japan, and to the region between northern China and southern Korea (Choe & Park 1997). The range of *O. inornatus* increased during the 20th century: it was detected in 1924 on the western coast of the United States (Puget Sound, Washington: Galtsoff 1929), and then 71 yr later on European coasts (Marennes-Oléron Bay, France: De Montaudouin & Sauriau 2000). Since the first years of detection in both introduced areas, the range of the gastropod has extended from Washington State to California (Carlton 1992) in the United States and from the Marennes-Oléron Bay to south Brittany in France (Goulletquer et al. 2002).

The first invasive stage (the introduction) of *Ocinebrellus inornatus* in France was investigated in a former study (Martel et al. in press). Based on mitochondrial DNA and allozyme polymorphism, we found that the populations from the primary introduction sites in France and the United States were closely related and substantially different from the native populations in Asia. From these results, we concluded that the most parsimonious scenario was that the source population of the French Atlantic coast was located in the United States. Herein, we report on the second stage of the invasion in France, namely the expansion of *O. inornatus* along the French Atlantic coast. When direct-developers lack a swimming larval stage, the natural spread of the species is expected to follow an isolation-by-geographical distance process. However, this process may be altered by stochastic human-mediated dispersal. To analyze the patterns and processes associated with the spread of *O. inornatus* in France, we compared the genetic architecture of French, American and Korean (native) populations. More specifically, we compared (1) the genetic diversity within populations, (2) the genetic differentiation between populations and (3) the level of genetic isolation according to coastline distances.

MATERIALS AND METHODS

Sampling sites. We collected 9 French populations of *Ocinebrellus inornatus* (N = 347). These populations were compared with 3 populations from the United States (N = 87) and 5 populations from the native range (N = 146), along the South Korean coasts. In all cases, adult snails (characterized by a size larger than 25 mm) were collected from cultivation parks over a similar area (transect of less than 200 m in length). Upon collection, individuals were frozen at –80°C. Details of the sample sites and sampled populations are given in Table 1 & Fig. 1.

Table 1. *Ocinebrellus inornatus*. Characteristics of sampling locations: dates of sampling, population names (Pop) and number (N) of individuals analyzed

Site	Latitude	Longitude	Date (mo/yr)	Pop	N
France					
Chateau d'Oléron	45° 88′ N	1° 19′ W	12/2000	Chat	37
Saint-Trojan	45° 84′ N	1° 21′ W	01/2001	Troj	44
Fort Enet	45° 98′ N	1° 07′ W	01/2001	Fort	45
Fouras	45° 99′ N	1° 11′ W	01/2001	Fou	37
Ronce	45° 80′ N	1° 16′ W	02/2001	Ron	40
Rivedoux	46° 16′ N	1° 28′ W	03/2001	Riv	39
Estrée	45° 90′ N	1° 08′ W	04/2001	Est	29
Quiberon	47° 58′ N	3° 04′ W	11/2001	Qui	45
Bourgneuf	47° 04′ N	1° 96′ W	06/2002	Bour	31
United States					
Samish Bay	47° 31′ N	123° 02′ W	07/2002	Sam	34
Mud Bay	47° 04′ N	123° 00′ W	07/2002	Mud	31
Netarts Bay	45° 19′ N	124° 01′ W	07/2002	Net	22
South Korea					
KwagAnRi	35° 08′ N	129° 07′ E	03/2002	Anr	20
ChinSaPo	35° 10′ N	129° 12′ E	03/2002	Chi	39
Jinhae Bay	35° 00′ N	128° 51′ E	03/2002	Jin	22
Ilkwang Bay	35° 14′ N	129° 15′ E	03/2002	Kwa	38
TongAm	35° 11′ N	129° 13′ E	03/2002	Ton	27

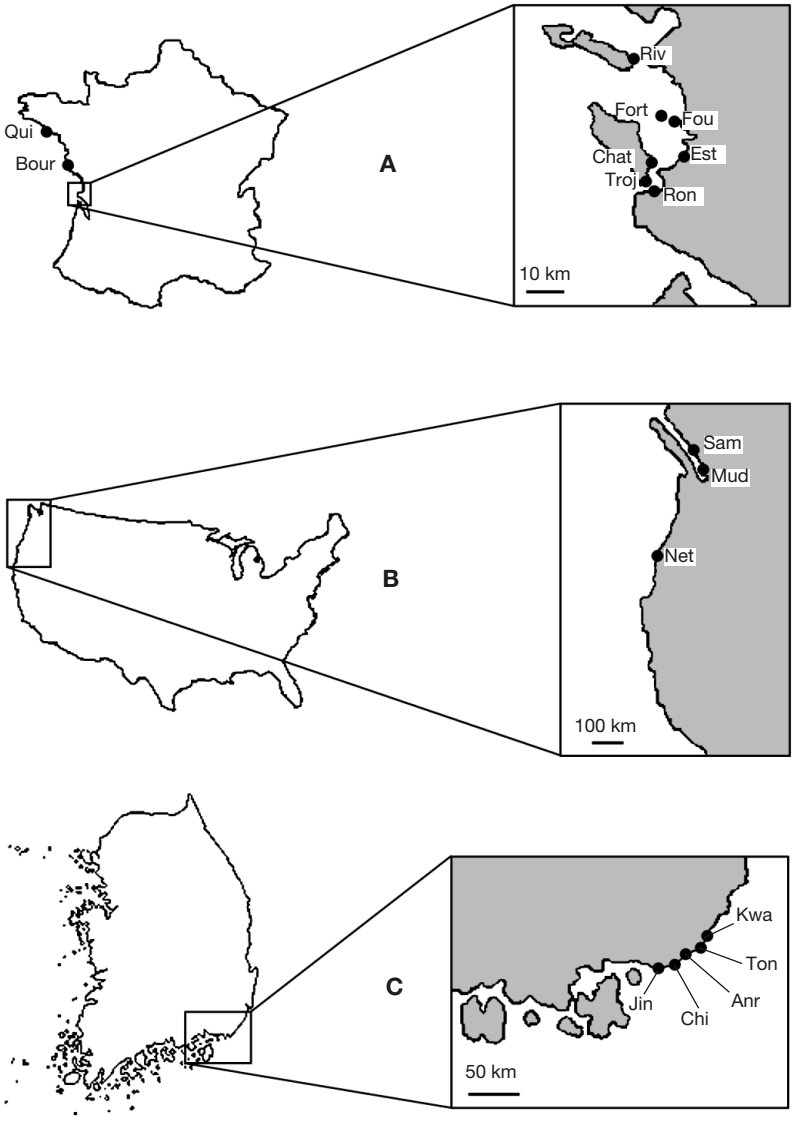

Fig. 1. Locations of sampling sites on (A) French Atlantic coast, (B) western coast of United States and (C) southern coast of South Korea. Site abbreviations (populations) as in Table 1

Electrophoresis. For each individual, a portion of the foot was homogenized in 100 µl Tris-EDTA (pH 6.8). The homogenates were centrifuged at 910 × *g* for 30 min at 4°C and then subjected to horizontal starch-gel electrophoresis. We studied 6 enzyme systems, adapted from Pasteur et al. (1987) and from Hillis & Moritz (1990), coded by 7 putative loci and allowing unequivocal genetic interpretation: phosphoglucomutase (PGM, EC 8.4.2.2), mannose-6-phosphate isomerase (MPI, EC 5.3.1.8), aspartate amino-transferase (AAT, EC 2.6.1.1) and triose phosphate isomerase (TPI, EC 5.3.1.1) for tris-borate-EDTA (pH 8.6) buffer; and fructo-kinase (FK, EC 2.7.1.4), malate-dehydrogenase (MDH, EC 1.1.1.37) in positive and negative migration for tris-maleate-EDTA (pH 7.4) buffer. Loci were numbered according to the decreasing anodal electromorph mobility in multiloci systems and alleles were assigned according to their relative distance from the most frequent allele (100) in French populations.

Data analysis. ***Genetic diversity in the populations:*** Linkage disequilibria between each pair of loci were tested at each locus and across all loci. Exact p-values were estimated using GENEPOP 3.2 (Raymond & Rousset 1995).

For each population we calculated the allele frequencies and several indices measuring the genetic diversity—the average number of alleles (N_{all}), the mean allelic richness (R_{all}, El-Mousadik & Petit 1996), the observed (H_o) and expected (H_e) heterozygozities (GENETIX 4.01, Belkhir et al. 2000, FSTAT 2.9.3, Goudet 1999). The departure from panmixia within each population was quantified by calculating the Weir & Cockerham's (1984) $\hat{f}$, a multilocus estimator of the fixation index F_{is}, with GENEPOP 3.2. Then, tests for deviation from Hardy-Weinberg expectations at each locus were computed within each population with GENEPOP 3.2. A permutation procedure was used to test for differences in H_o, R_{all} and $\hat{f}$ between the groups of French, American and Korean populations (i.e. by randomly permuting the entire samples among the 2 groups compared) using the FSTAT 2.9.3 software.

Genetic structure of populations within each area: Within each area, the genetic structure between populations was investigated by calculating the $\hat{\theta}$ estimator of F_{st} as described by Weir & Cockerham (1984), with GENEPOP 3.2. This estimator measures the correlation of genes within populations with respect to the correlation of genes between populations. F_{st} varies theoretically between 0 and 1; it is expected to be 0 when study samples belong to the same population or to genetically undifferentiated populations. Note that the $\hat{\theta}$ estimator of F_{st} can also be negative due to the computation of this estimator. When allelic differences occur between samples, F_{st} values are positive. A Fisher's exact-test was calculated with GENEPOP 3.2 to test for the null hypothesis of identity of the allelic distribution across populations. To determine the genetic relationships between populations, for each population pair, Reynolds' genetic dis-

tance (Reynolds et al. 1983) was calculated. Then, an unrooted consensus UPGMA tree (5000 bootstrap) was constructed with PHYLIP 3.5 (Felseinstein 1995) and visualised with TREEVIEW (Page 1996).

The isolation-by-distance model makes it possible to test patterns of dispersal using pairwise combinations of populations (Slatkin 1993). Given the lack of swimming larvae and that the study samples were collected in intertidal habitats, we used the coastline geographical distances (d) as measured from a map, and plotted ln (d) against $\hat{\theta}/(1 - \hat{\theta})$ estimates to compute a linear relationship, as recommended by Rousset (1997). A Mantel-like permutation procedure was used to test the null hypothesis of independence between genetic and geographic distances using GENEPOP 3.2. Isolation-by-distance patterns were not analyzed for the United States because of the limited number of sites.

RESULTS

Over the whole data set (N = 580 individuals), allozyme electrophoresis revealed 5 out of the 7 loci to be polymorphic: *Tpi*, *Mpi*, *Fk*, *Mdh1* and *Mdh2*, with 2, 6, 3, 4 and 2 alleles, respectively. In each population and over the 17 populations, we found no evidence of linkage disequilibria between pairs of loci. Allele frequencies for each population are given in Appendix 1.

Genetic diversity in each population

Data on within-population genetic diversity are summarized in Table 2. In all populations, the observed and expected heterozygosities were similar. Consequently, the estimates of $\hat{f}$-values did not reveal large excesses or deficits in heterozygotes. The largest discrepancies between the observed and expected heterozygozities were observed in the Chat (Chateau d'Oleron) population in France (H_e = 0.328 and H_o = 0.274) and the Jin (Jinhae Bay) population in South Korea (H_e = 0.269 and H_o = 0.182). However, the tests for deviations from Hardy-Weinberg expectations across the 5 loci were all non-significant even for Chat and Jin (p = 0.195 and 0.138 respectively, Table 2).

The range of the genetic diversity indices was similar in the 3 geographical areas. The mean number of alleles over loci (N_{all}) ranged between 1.714 and 1.857 in France, 1.714 and 2.000 in the United States, and 2.000 and 2.286 in South Korea (Table 2). The mean allelic richness over loci (R_{all}) ranged between 1.703 and 1.831 in France, 1.623 and 1.763 in the United States, and 1.776 and 2.067 in South Korea (Table 2). We found no statistical differences in H_o, R_{all} and $\hat{f}$ when comparing the French populations with the Asian populations (permutation procedure, p = 0.387, 1.000, 0.363, respectively) or when comparing the French populations with the American populations (permutation procedure, p = 0.998, 0.985, 0.652, respectively).

Population genetic structure within each area

The UPGMA tree (Fig. 2) showed that (1) Asian populations are separated from both the American and French populations with a bootstrap value of 71.38% and (2) French and American populations are mixed together.

In France, across the 5 loci and over all populations, we identified low but significant genetic differentiation ($\hat{\theta}_{overall} = 0.039$, $p < 10^{-5}$). The pairwise $\hat{\theta}$ values (Table 3A) showed that this differentiation was mainly due to the Bour (Bourgneuf), Riv (Rivedoux) and Est (Estrée) populations, which were significantly differentiated

Table 2. *Ocinebrellus inornatus*. Genetic diversity and heterozygote deficiency within populations (abbreviated as in Table 1). N: number of individuals; N_{all} and R_{all}: mean number of alleles and mean allelic richness over all loci, respectively. H_e, H_o: expected and observed heterozygozities, respectively. Multilocus estimator of fixation index F_{is} and exact probability ($p_{H\text{-}W}$) are also given (H-W: Hardy-Weinberg expectations)

Population	N	N_{all}	R_{all}	H_e mean	H_e SD	H_o mean	H_o SD	$\hat{f}$	$p_{H\text{-}W}$
France									
Chat	37	1.857	1.812	0.328	0.243	0.274	0.239	0.415	0.195
Troj	44	1.857	1.773	0.319	0.248	0.315	0.245	−0.117	0.537
Fort	45	1.857	1.784	0.315	0.245	0.292	0.242	0.118	0.549
Fou	37	1.857	1.831	0.351	0.252	0.344	0.249	−0.041	1.000
Ron	40	1.857	1.799	0.326	0.233	0.311	0.230	−0.013	1.000
Riv	39	1.857	1.799	0.306	0.233	0.260	0.230	0.182	0.262
Est	29	1.857	1.703	0.254	0.220	0.232	0.216	0.322	0.111
Qui	45	1.857	1.783	0.305	0.231	0.298	0.245	0.006	1.000
Bour	31	1.714	1.714	0.339	0.234	0.366	0.265	−0.288	0.152
United States									
Sam	34	1.857	1.763	0.317	0.229	0.316	0.225	0.143	0.477
Mud	31	2.000	1.752	0.320	0.241	0.318	0.237	0.045	1.000
Net	22	1.714	1.623	0.271	0.242	0.247	0.236	−0.068	1.000
South Korea									
Anr	20	2.286	1.936	0.317	0.266	0.336	0.260	−0.041	1.000
Chi	39	2.571	2.067	0.352	0.278	0.315	0.274	0.178	0.333
Jin	22	2.000	1.776	0.269	0.226	0.182	0.221	0.468	0.138
Kwa	38	2.143	1.818	0.277	0.250	0.286	0.247	−0.175	0.563
Ton	27	2.286	1.936	0.288	0.267	0.333	0.262	−0.130	1.000

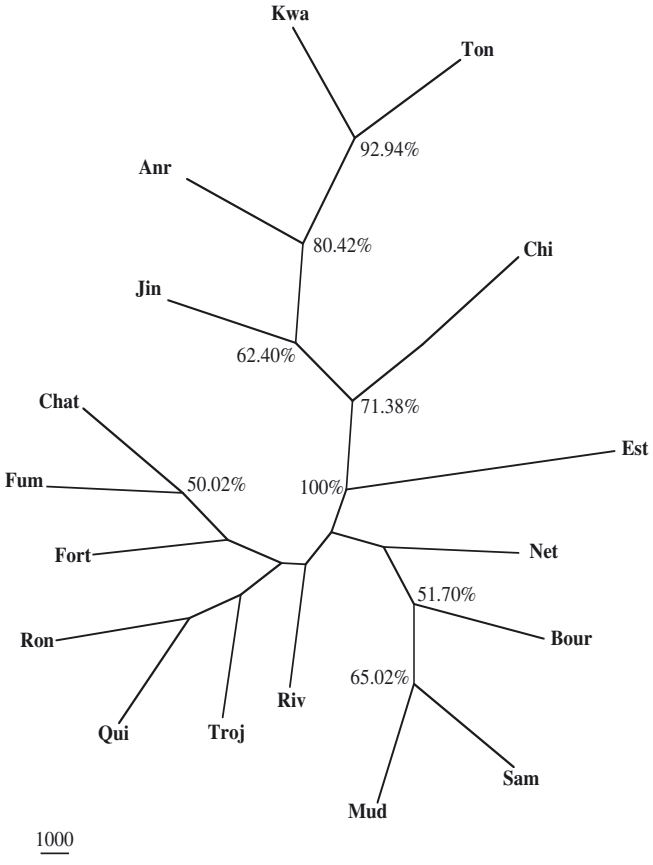

Fig. 2. *Ocinebrellus inornatus*. Unrooted UPGMA tree, showing relationships between populations from native and introduced areas. Bootstrap values >50% are indicated at each node. Site abbreviations (populations) as in Table 1

($0.027 < \hat{\theta} < 0.151$; $p < 10^{-3}$ for all comparisons) from the other populations. These 3 populations were also substantially differentiated from each other ($\hat{\theta}_{Est\text{-}Riv} = 0.057$, $p < 10^{-3}$; $\hat{\theta}_{Est\text{-}Bour} = 0.117$, $p < 10^{-5}$; $\hat{\theta}_{Bour\text{-}Riv} = 0.092$, $p < 10^{-5}$). The difference between Bour and the other populations may be explained by its location, as Bour is separated by more than 300 km of coastline from the Marennes-Oléron Bay and by around 100 km from Qui (Quiberon). However, isolation by geographical distance cannot explain the genetic differentiation between both Est and Riv and Fou (Fouras), Fort (Fort Enet), Chat, Troj (St. Trojan) and Ron (Ronce). Indeed, all these populations were collected in the Marennes-Oléron Bay and were separated by no more than 40 km of coastline. The absence of relationship between genetic differentiations and geographical distances is also illustrated by the Qui population which, despite being located more than 300 km away from the Marennes-Oléron bay, was not significantly differentiated from For, Troj and Ron, and was only slightly differentiated from Chat, Est, Riv and Fou (Table 3A). Consequently, it was not surprising that we failed to detect any evidence of an isolation-by-distance pattern over all populations collected in France (slope = −0.002, $R^2 = 0.004$, $p = 0.633$; see Fig. 3A).

Only 3 populations were collected in the United States. Over them and across all loci, we found a low but significant genetic differentiation ($\hat{\theta}_{overall} = 0.014$, $p = 0.030$). The 2 closest populations, Sam (Samish Bay) and Mud (Mud Bay), were not differentiated from each other ($\hat{\theta}_{Sam\text{-}Mud} = -0.005$, $p > 0.05$, Table 3B). Both populations were more differentiated from the Net

Table 3. *Ocinebrellus inornatus*. Allelic differentiation between pairs of populations across all loci within (A) France, (B) United States and (C) South Korea. $^{*}p < 5 \times 10^{-2}$; $^{**}p < 10^{-3}$; $^{***}p < 10^{-5}$

(A)	Chat	Troj	Fort	Fou	Ron	Riv	Est	Qui
Troj	0.032*							
Fort	0.002	0.011						
Fou	0.002	0.035**	0.011					
Ron	0.013	0.005	0.013	0.028*				
Riv	0.040**	0.052***	0.058***	0.073***	0.011*			
Est	0.132***	0.068***	0.095***	0.151***	0.058***	0.057**		
Qui	0.031*	0.005	0.010	0.046**	−0.003	0.027*	0.035*	
Bour	0.064***	0.027*	0.054***	0.039**	0.027*	0.092***	0.117***	0.044**
(B)	Sam	Mud						
Mud	−0.005							
Net	0.038*	0.016						
(C)	Anr	Chi	Jin	Kwa				
Chi	0.011							
Jin	0.045**	0.073***						
Kwa	0.001	0.040**	0.028*					
Ton	−0.002	0.042**	0.037*	−0.010				

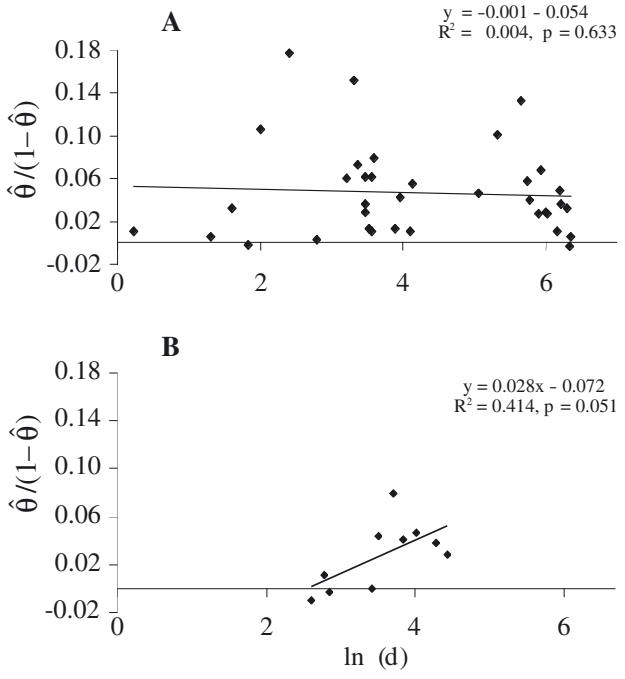

Fig. 3. *Ocinebrellus inornatus*. Isolation-by-distance graphs showing pairwise genetic distances $\hat{\theta}/(1-\hat{\theta})$ plotted against geographic distances, ln(*d*) in (A) France and (B) South Korea

(Netarts Bay) population ($\hat{\theta}_{Sam\text{-}Net} = 0.016$, $p = 0.078$ and $\hat{\theta}_{Mud\text{-}Net} = 0.038$, $p < 0.05$, Table 3B). This latter population was collected in the Netarts Bay, which is located about 500 km south of the Samish and Mud Bays. Due to the small number of populations sampled in the United States, we did not carry out an isolation-by-distance analysis in this area. However, it is noteworthy that Sam was not significantly differentiated from Net despite the large geographical distance separating these 2 populations.

As in the 2 other areas, the genetic differentiation over the 5 populations collected in South Korea was low ($\hat{\theta}_{overall} = 0.029$) but significant ($p < 10^{-5}$). In contrast to the situation along the French Atlantic coast, this genetic differentiation was not due to specific populations. This is illustrated by the fact that none of the 5 populations were differentiated from all the other populations (Table 3C). Genetic isolation was correlated with coastline distances (slope = 0.028, $R^2 = 0.414$, Fig. 3B). However, due to the small number of populations, the slope was on the border of being significantly different from zero ($p = 0.051$).

DISCUSSION

Following the primary introduction step, dispersal is a key stage for the extension of exotic species to other suitable habitats (Geller 1994, Sakai et al. 2001), and the bentho-pelagic larval stage is thought to be particularly favorable for the dispersal of marine invertebrates. In this study, we examined factors involved in the expansion of *Ocinebrellus inornatus*, a direct-developing species that lacks a free-swimming larval stage.

Direct-developing marine species are much less affected by hydrodynamic conditions (e.g. tidal residual, wind-driven and density currents) than species with free-swimming planktonic larvae (Pechenik 1999, Ellien et al. 2000). Their lower dispersal rate and fecundity than bentho-pelagic species (Arndt & Smith 1998) could generate a higher rate of gene flow between populations of marine mollusks with a free-swimming larval stage than between populations without such a stage. Accordingly, populations of direct-developing muricid species can be genetically structured over restricted areas, as reported for *Bedeva hanleyi* (Hoskin 2000). We observed a similar pattern for *Ocinebrellus inornatus* over its native range, with a low ($\hat{\theta}_{overall} = 0.029$) but significant genetic differentiation over populations. In addition, in this area genetic differentiation was correlated with coastline distance between populations, suggesting that dispersal occurs across short distances and through successive events (i.e. following a step-by-step process along the coastline). When we compared these data with those gathered in both France and the United States, 2 main results emerged: (1) the genetic structure was of the same magnitude as in the native area, and (2) no isolation-by-distance pattern was observed in France, unlike in the native range.

During the invasion process, 2 events are likely to increase the genetic divergence among populations within the invaded area compared with the native range. First, populations are often founded by a limited number of individuals (i.e. founder events), and the associated local genetic drift is likely to induce genetic heterogeneity between newly established populations (Slatkin 1977). Second, recurrent introduction events from genetically differentiated source populations may also increase the genetic differentiation between newly settled populations. In agreement with these theoretical hypotheses, a higher level of genetic structuration has been reported in introduced versus native populations of the starling *Sturnus vulgaris* (Ross 1983), the fly *Rhagoletis completa* (Berlocher 1994) and the land snail *Theba pisana* (Johnson 1988). However, *Ocinebrellus inornatus* populations collected in the 2 introduced areas were not more structured than those collected in the native range. For sampling areas of similar size, the genetic differentiation in the United States ($\hat{\theta}_{overall} = 0.014$) and France ($\hat{\theta}_{overall} = 0.039$) was of the same magnitude as in South Korea ($\hat{\theta}_{overall} =$

0.029). We also did not observe significant genetic disequilibrium between loci or significant heterozygote deficiencies, which are expected in the case of strong Wahlund effects (i.e. mixing of genetically differentiated subpopulations). These results suggest that the introduction and the subsequent expansion range of *O. inornatus* along the French and American coasts were not due to the mixing of founders originating from genetically differentiated source populations. Moreover, the fact that genetic differentiation was low in France suggests that the establishment of new populations along coasts did not involve a limited number of individuals. These conclusions are in agreement with our previous results on mitochondrial DNA and allozyme markers (Martel et al. in press). These analyses suggest that during the introduction stage, limited genetic drift effects occurred in France and the United States associated with the settlement of new populations.

Although the level of genetic differentiation among *Ocinebrellus inornatus* populations was the same in France and Asia, the spatial pattern of this differentiation was not. Whereas genetic and coastline distances were correlated in South Korea (slope = 0.028, R^2 = 0.414), we found no evidence for such a correlation among the introduced populations collected in France (slope = −0.002, R^2 = 0.004). This suggests that, in France, the limited dispersal ability of *O. inornatus* is counterbalanced by long-distance dispersal due to human activities (Buchan & Padilla 1999, Roy & Sponer 2002). This is exemplified by the genetic homogeneity between the Qui population and several populations from the Marennes-Oléron Bay, located 300 km apart. Gene flow over such large distances is unlikely to be due to natural dispersal given the absence of free-swimming larvae and the recent establishment of these populations (<10 yr). Similarly, the Bour population was significantly genetically differentiated from all the other populations including Qui, which would be an unexpected result if range extension were due to a step-by-step colonization of the coastline from Marennes-Oléron toward the north. Human-mediated transfer may also have occurred in the United States, where the sample from Netarts Bay (Net) was not significantly differentiated from the Mud population located 500 km away.

The extension of the range of exotic species in the areas of primary introduction is often tightly linked to human activities, for example through the transportation of larvae in ballast water (e.g. various species of fishes: Wonham et al. 2001) or the fouling of algae sporophytes on the hulls of boats (e.g. *Undaria pinnatifida*: Hay 1990). Bivalve farming may also have a significant impact on the transport of exotics and in shaping the genetic structure of populations of exotics between shell-farming areas (e.g. *Crepidula fornicata*: Dupont et al. 2003, Wolff & Reise 2002). In France, oysters are mainly cultivated on bags that are laid on oyster tables and often contain juvenile and adult *O. inornatus* (C. Martel & S. Robert pers. obs). To improve growth rates, growers regularly move oyster bags from farm to farm. The movements are facilitated by the fact that oyster farmers often possess several farming parks scattered within the Marennes-Oléron Bay. Furthermore, 10 to 15% of the oyster farms located in south Brittany also belong to oyster farmers from Marennes-Oléron (French marine governmental institution pers. comm.). These human-mediated movements provide effective means of transporting the Asian drills, generating long-range dispersal. As the transfer of oysters is not related to coastline distances it may have not only decreased the genetic differentiation between populations but also impeded the isolation-by-distance pattern that would have been produced by the natural dispersal of *O. inornatus*. Theoretical analyses have recently shown that even when long-distance dispersal is rare, it has major implications for the speed at which the geographic range of a population expands (Neubert & Caswell 2000). Moreover, invasion speed is a critical parameter of invasion dynamics and, thus, management policy and long-distance dispersal are generally due to stochastic events that cannot be easily included in models and predictions (Hengeveld 1994, Shigesada & Kawasaki 1997).

If the absence of an isolation-by-distance pattern among the French populations is truly the consequence of oyster-farming practices, why was such a pattern not detectable among the South Korean populations where oyster-farming also occurs? This may be due to differences in bivalve farming methods. In Asia, as is currently the case in France, oysters were traditionally cultivated on oyster tables. Some decades ago, this practice was modified to decrease damage by Asian drills (C. K. Kang, National Institute of Development and Aquatic Research, South Korea, pers. comm.). Currently, most Asian growers use strings of oysters hung on trellises (Cahn 1950, Shaw 1974). As these trellises do not touch the ocean bed, drills cannot climb onto them and attack cultivated oysters. This change in cultivation practices means that Asian drills now feed almost exclusively on wild oysters, thus suppressing human-mediated long-distance dispersal. Hence, *Ocinebrellus inornatus* is apparently not a recognized enemy of oysters in Japan (McLeod Chapman & Banner 1949).

In summary, comparison of the population genetics of *Ocinebrellus inornatus has* provided interesting clues about expansion patterns. First, the establishment of new populations along the French Atlantic coast was certainly not the result of introduction events originat-

ing from genetically distinct source populations, and the range expansion stage was not associated with strong genetic drift effects (i.e. founding effects). Second, the expansion of *O. inornatus* within and outside Marennes-Oléron Bay was certainly enhanced by oyster-farming activities, counterbalancing the naturally limited dispersal of this direct-developer. Therefore, when trying to manage or eradicate oyster drills, it is important to take into account these farming activities to avoid dispersal between managed and non-managed areas (Myers et al. 2000). This situation is interesting when compared with that of *Crepidula fornicata*, another exotic gastropod introduced into Europe with the oysters *Crassostrea virginica* and *C. gigas* (Blanchard 1997). *Crepidula fornicata* is a bentho–pelagic species, and its current distribution can be partly explained by its natural dispersal ability through a free-swimming larval stage (Dupont et al. 2003). Finally, our understanding of the dynamics of expansion of *O. inornatus* can be improved by comparing its effective dispersal with that of the European drill *Ocenebra erinacea*. These species, both of which belong to the Muricidae family, occur in sympatry and compete for resources (marine bivalves) but exhibit different life cycles (i.e. *O. erinacea* is a direct-developer with a 3 to 5 d swimming larvae: Fretter & Graham 1972, Gibbs 1996). It would be of interest to compare both species and the effects of having a free-swimming larval phase or being a direct-developer on the evolution of the 2 species on the French Atlantic coast.

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Appendix 1. *Ocinebrellus inornatus*. Allele frequencies at each locus for each population in the 3 geographical areas. N: number of individuals. Populations abbreviated as in Table 1

	N	*Tpi*		*Mpi*						*Fk*			*Mdh1*				*Mdh2*	
		80	100	50	60	70	80	90	100	80	100	120	70	80	100	120	80	100
France																		
Chat	37	0.473	0.527	0.000	0.230	0.000	0.000	0.000	0.770	0.310	0.541	0.149	0.000	0.514	0.487	0.000	0.230	0.770
Troj	44	0.409	0.591	0.000	0.443	0.000	0.000	0.000	0.557	0.455	0.443	0.102	0.000	0.341	0.659	0.000	0.125	0.875
Fort	45	0.533	0.467	0.000	0.333	0.000	0.000	0.000	0.667	0.311	0.567	0.122	0.000	0.411	0.589	0.000	0.122	0.878
Fou	37	0.581	0.419	0.000	0.284	0.000	0.000	0.000	0.716	0.364	0.460	0.176	0.000	0.460	0.540	0.000	0.324	0.676
Ron	40	0.325	0.675	0.000	0.375	0.000	0.000	0.000	0.625	0.325	0.575	0.100	0.000	0.375	0.625	0.000	0.225	0.775
Riv	39	0.167	0.833	0.000	0.346	0.000	0.000	0.000	0.654	0.167	0.577	0.256	0.000	0.449	0.551	0.000	0.218	0.782
Est	29	0.224	0.776	0.000	0.621	0.000	0.000	0.000	0.379	0.086	0.655	0.259	0.000	0.241	0.759	0.000	0.052	0.948
Qui	45	0.367	0.633	0.000	0.400	0.000	0.000	0.000	0.600	0.267	0.600	0.133	0.000	0.289	0.711	0.000	0.133	0.867
Bour	31	0.452	0.548	0.000	0.517	0.000	0.000	0.000	0.483	0.500	0.500	0.000	0.000	0.274	0.726	0.000	0.403	0.597
USA																		
Sam	34	0.382	0.618	0.000	0.441	0.000	0.000	0.000	0.559	0.242	0.697	0.061	0.000	0.191	0.809	0.000	0.427	0.573
Mud	31	0.468	0.532	0.000	0.436	0.016	0.000	0.000	0.548	0.355	0.597	0.048	0.000	0.145	0.855	0.000	0.371	0.629
Net	22	0.500	0.500	0.000	0.205	0.000	0.000	0.000	0.795	0.454	0.546	0.000	0.000	0.046	0.955	0.000	0.432	0.568
South Korea																		
Anr	20	0.750	0.250	0.000	0.100	0.000	0.470	0.350	0.080	0.075	0.475	0.450	0.000	0.050	0.900	0.050	0.350	0.650
Chi	39	0.564	0.436	0.026	0.128	0.000	0.321	0.385	0.140	0.128	0.564	0.308	0.013	0.090	0.833	0.064	0.269	0.731
Jin	22	0.909	0.091	0.000	0.091	0.000	0.590	0.296	0.023	0.000	0.682	0.318	0.000	0.318	0.682	0.000	0.182	0.818
Kwa	38	0.842	0.158	0.000	0.171	0.000	0.513	0.303	0.013	0.052	0.632	0.316	0.000	0.066	0.934	0.000	0.316	0.684
Ton	27	0.870	0.130	0.019	0.148	0.000	0.482	0.333	0.018	0.093	0.593	0.315	0.000	0.074	0.926	0.000	0.389	0.611

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