# THE RELATION OF REPRODUCTIVE MODES TO POPULATION GENETIC DIFFERENTIATION IN MARINE BIVALVES AND GASTROPODS

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## ABSTRACT

The purpose of this review is to determine if mode of reproduction in marine bivalves and gastropods is correlated with the pattern of population genetic differentiation. Two modes of reproduction, namely planktic (PT) and non-planktic development (NPT), have been defined. I compared the amount of genetic differentiation ($F_{st}$) among conspecific subpopulations over geographic distances between these two different reproductive modes. $F_{st}$ was recalculated using allele frequencies from 47 references, comprising 21 PT-bivalve, 15 PT-gastropod, and 11 NPT-gastropod species. The result is consistent with the hypothesis that PT species, which have the potential for greater gene flow, will show less differentiation among subpopulations (equal to low $F_{st}$). Conversely, NPT will increase the divergence among subpopulations (equal to high $F_{st}$). In addition, the linear discriminant function calculated by using both $F_{st}$ and geographic distance gives a possibility to predict mode of reproduction of a given species.

## INTRODUCTION

One major aim of population genetic studies is to describe the distribution of genetic variation and to find explanations for the observed patterns. Studies can be conducted on temporal or spatial scales or both. Some studies of genetic variation on temporal scale have been reported (*e.g.* Todd *et al.* 1988; Johannesson *et al.* 1995). However, many aspects have been studied on a spatial scales, and can be divided into biotic and abiotic components. Biotic components include of species characters, relationships with other species, recruitment and food availability (Johnson & Black 1984b; Hilbish & Koehn 1985; Borsa & Benzie 1996). Abiotic components may be regarded as environment factors such as salinity, temperature, pollutants and the stability of the habitat (Koehn *et al.* 1980; Fevolden & Garner 1986; Lavie & Nevo 1986; Lavie & Nevo 1987; Blot & Thiriot-Quievreux 1989; Johnson & Black 1991; Tatarenkov & Johannesson 1994). On the other hand, two mechanisms contribute to genetic variation: gene flow and natural selection (assuming that there is no influence of mutation). Organisms with a high capacity for dispersal should have a high potential for gene flow among conspecific populations. Furthermore, selective pressures (biotic and abiotic factors) will shape the genetic structure of populations in each particular area. Yamada (1989) regarded gene flow and selective pressures as homogenizing and differentiating effects, respectively.

Among these effective factors, modes of reproduction tend to play an important role influencing population structure via gene flow. An obvious reason is that most adult marine gastropods and bivalves have very limited dispersal ability. Thus, gene flow among populations relies mainly on dispersal capability of their larvae and gametes. Many schemes have been proposed to describe modes of reproduction in molluscs (Thorson 1950; Ockelmann 1965; Shuto 1974; Scheltema 1978; Jablonski & Lutz 1983). To discriminate two ends of dispersal ability, I prefer using planktic (PT) developers and non-planktic (NPT) developers, which are equivalent to pelagic and non-pelagic development described by Scheltema (1978). PT species include planktotrophic and some lecithotrophic developers. They spend a significant portion of their development time drifting in the water mass. In contrast, NPT species develop in egg capsules (oviparity) or within their parents (ovoviviparity) and hatch out as minute adults. Therefore, NPT species should have a restricted dispersal capacity. Due to the different gene flow capacity between reproductive modes, one may predict that species with high gene flow (PT) have little geographic variation among populations over large distances. Conversely, species with limited gene flow (NPT) should show distinct inter-population variation. This hypothesis has been tested in many studies (Snyder & Gooch 1973; Janson 1987; Yamada 1989; Ward 1990; Johannesson 1992; Hoskin 1997). However, most of these comparisons were limited to a few species or within a single genus.

In this paper, I compare genetic structure of marine bivalves and gastropods having two different reproductive modes, to test the hypothesis that species with PT will have lesser amount of genetic differentiation among populations compared to the ones with NPT. Moreover, I present the discriminant function as an alternative way to classify reproductive modes by using $F_{st}$ and geographic distance.

Table 1a. Species list of marine non planctic gastropods used for the comparison. # Loci represents a number of all loci examined and # Pop represents a number of sampling sites, populations or subpopulations. A row with " * " indicates that $F_{st}$ was recalculated from allele frequencies.

**Non-planktic gastropods**

| Mode | Species | References | # Loci | # Pop. | Area |
|---|---|---|---|---|---|
| * | *Bedeva hanleyi* | Hoskin (1997) | 14 | 8 | SW Australia |
| | *Bembicium vittatum* | Johnson & Black (1991) | 5 | 25 | W Australia |
| | | Parsons (1996) | 26 | 17 | W Australia |
| * | *Cominella lineolata* | Hoskin (1997) | 25 | 9 | SW Australia |
| * | *Hydrobia totteni* | Davis et al. (1988) | 30 | 5 | New York |
| * | *Littorina arcana* | Ward & Warwick (1980) | 21 | 3 | Scotland |
| | *Littorina mariae* | Rolan-Alvarez et al. (1995) | 8 | 32 | NW Spain |
| | *Littorina mariae* | Tatarenkov & Johannesson (1994) | 28 | 21 | W Sweden |
| * | *Littorina obtusata* | Berger (1973) | 3 | 14 | NW Atlantic |
| | *Littorina obtusata* | Rolan-Alvarez *et al.* (1995) | 10 | 32 | NW Spain |
| * | *Littorina rudis* | Ward & Warwick (1980) | 21 | 6 | Scotland |
| * | *Littorina saxatilis* | Berger (1973) | 2 | 12 | NW Atlantic |
| | *Littorina saxatilis* | Janson & Ward (1984) | 15 | 11 | W Sweden |
| | *Littorina saxatilis* | Janson (1987) | 15 | 10 | W Sweden |
| * | *Littorina saxatilis* | Snyder & Gooch (1973) | 2 | 7 | Massachusetts |
| | *Nucella lamellosa* | Grant & Utter (1988) | 19 | 27 | NW USA |
| | *Nucella lamellosa* | Grant & Utter (1988) | 19 | 12 | Washington |
| * | *Nucella lapillus* | Day (1990) | 8 | 15 | UK |

Table 1b. Species list of marine planktic bivalves used for the comparison.

**Planktic bivalves**

| Mode | Species | References | # Loci | # Pop. | Area |
|---|---|---|---|---|---|
| * | *Aequipecten opercularis* | Lewis & Thorpe (1994) | 4 | 12 | UK |
|  | *Argopecten gibbus* | Krause *et al.* (1994) | 12 | 3 | SE USA |
| * | *Argopecten irradians* | Marelli *et al.* (1997) | 23 | 2 | Florida |
|  | *Bathymodiolus thermophilus* | Craddock *et al.* (1995) | 30 | 5 | Hot vents |
| * | *Cerastoderma edule* | Beaumont & Pether (1996) | 13 | 8 | UK |
|  | *Cerastoderma edule* | Hummel *et al.* (1994) | 7 | 8 | Europe |
|  | *Cerastoderma glaucum* | Hummel *et al.* (1994) | 7 | 9 | Europe |
|  | *Donax deltoides* | Murray-Jones & Ayre (1997) | 6 | 12 | E Australian |
|  | *Geukensia demissa* | Sarver *et al.* (1992) | 18 | 6 | N USA |
|  | *Geukensia granosissima* | Sarver *et al.* (1992) | 18 | 3 | N USA |
|  | *Macoma balthica* | Hummel *et al.* (1995) | 7 | 18 | France |
|  | *Macoma balthica* | Hummel *et al.* (1995) | 7 | 3 | The Netherlands |
| * | *Macoma balthica* | Nilsson (1987) | 4 | 12 | Baltic Sea |
| * | *Macoma balthica* | Meehan *et al.* (1989) | 11 | 2 | W USA |
|  | *Mytilus californianus* | Levinton & Suchanek (1978) | 2 | 41 | NW America |
|  | *Mytilus edulis* | Hummel *et al.* (1996) | 7 | 3 | Netherlands |
| * | *Mytilus galloprovincialis* | Quesada *et al.* (1995) | 15 | 21 | SW Europe |
|  | *Ostrea edulis* | Saavedra *et al.* (1993) | 22 | 11 | Europe |
| * | *Pecten maximus* | Beaumont *et al.* (1993) | 8 | 3 | France |
| * | *Pecten maximus* | Beaumont *et al.* (1993) | 8 | 7 | Scotland |
|  | *Pinctada margaritifera* | Benzie & Ballment (1994) | 17 | 7 | W Pacific |
| * | *Pinctada radiata* | Beaumont & Khamdan (1991) | 3 | 3 | Bahrain |
|  | *Potamocorbula amurensis* | Duda (1994) | 8 | 5 | San Francisco |
|  | *Tridacna derasa* | Macaranas *et al.* (1992) | 9 | 14 | W Pacific |
|  | *Tridacna gigas* | Benzie & Williams (1992a) | 8 | 6 | NE Australia |
|  | *Tridacna maxima* | Benzie & Williams (1992b) | 6 | 10 | NE Australia |
| * | *Tridacna maxima* | Kittiwattanawong (1997) | 4 | 3 | SW Thailand |

## MATERIALS AND METHODS

Data was obtained from 47 published studies, comprising 21 PT bivalve, 15 PT gastropod, and 11 NPT gastropod species (Table 1).

### *Obtaining $F_{st}$*

The fixation index $F_{st}$ (Wright, 1978) was employed to measure the amount of genetic differentiation among subpopu-lations. Values of $F_{st}$ range from zero to one. Values

Table 1c. Species list of marine planctic gastropods used for the comparison.

**Planktic gastropods**

| Mode | Species | References | # Loci | # Pop. | Area |
|---|---|---|---|---|---|
| | *Austrocochlea constricta* | Parsons (1996) | 26 | 17 | W Australia |
| | *Haliotis rubra* | Brown (1991) | 15 | 17 | SE Australia |
| | *Littorina brevicula* | Tatarenkov (1995) | 5 | 8 | The Sea of Japan |
| * | *Littorina irrorata* | Dayan & Dillon (1995) | 8 | 5 | E USA |
| * | *Littorina littorea* | Berger (1973) | 2 | 13 | NW Atlantic |
| | *Littorina littorea* | Janson (1987) | 14 | 9 | W Sweden |
| * | *Littorina littorea* | Johannesson (1992) | 15 | 13 | Europe |
| * | *Melarhaphe neritoides* | Johannesson (1992) | 15 | 13 | Europe |
| * | *Morula marginalba* | Hoskin (1997) | 11 | 9 | SW Australia |
| * | *Nacella concinna* | Beaumont & Wei (1991) | 7 | 4 | UK |
| * | *Rissoa violacea* | Oliverio (1994) | 20 | 2 | W Italy |
| | *Siphonaria jeanae* | Johnson & Black (1984a, 1984b) | 4 | - | SW Australia |
| | *Stramonita haemostoma canaliculata* | Liu *et al.* (1991) | 17 | 9 | S USA |
| | *Stramonita haemostoma floridana* | Liu *et al.* (1991) | 17 | 9 | S USA |
| * | *Strombus gigas* | Campton *et al.* (1992) | 19 | 5 | Florida |
| | *Tectus coerulescens* | Borsa & Benzie (1996) | 11 | 3 | NE Australia |
| | *Trochus niloticus* | Borsa & Benzie (1996) | 12 | 11 | NE Australia |

near zero indicate little genetic subdivision and values near one indicate high subdivision. The quantity of $F_{st}$ is approximately related to gene flow ($N_e$m) by the equation Fst ~ $1/(4N_e m+1)$ (Wright 1951). The weighted-$F_{st}$ over all subpopulations of a locus can be calculated from the folowing equations (Hartl, 1980).

$$F_{st} = \frac{\sum \bar{p}_i(1-\bar{p}_i)F_{st}^{(i)}}{\sum \bar{p}_i(1-\bar{p}_i)} \tag{1}$$

$$F_{st}^{(i)} = \frac{\left\lfloor H_T^{(i)} - \bar{H}_S^{(i)} \right\rfloor}{H_T^{(i)}} \tag{2}$$

$$H_T^{(i)} = 2\bar{p}_i(1-\bar{p}_i) \tag{3}$$

$$H_S^{(i)} = 2p_i(1-p_i) \tag{4}$$

| | |
|---|---|
| $Fst$ | is the weighted-$F_{st}$ for a given locus |
| $Pi$ | is frequency of allele "*i*" |
| $Fst^{(i)}$ | is the fixation index of allele "*i*" |
| $H_T^{(i)}$ | is the total heterozygosity |
| $H_S^{(i)}$ | is the heterozygosity for allele "*i*" in the subpopulation |
| $\overline{H}_S^{(i)}$ | is the average of $H_S^{(i)}$ over all subpopulations |

If there are many loci, a mean $F_{st}$ may be obtained by the bootstrap or jackknife techniques (Weir & Cockerham 1984). However, a simple average of $F_{st}$ over all loci was used in this paper.

*Measuring geographical distance*

In principle, a geographic distance among populations should be measured following the pathway of gene flow or direction of larval transportation. However, it is difficult to obtain a real direction of gene flow. Thus, I ignored modifying factors such as current direction, and estimated the geographic distances using the shortest pathway between conspecific. I measured geographic distance in four ways, according to island, archipelago, cape and bay models (Fig. 1). In the island model, a distance was simply measured between two populations. When more than two subpopulations were sampled in an archipelago, the greates diameter was used. A distance was measured along a coastline when land was considered as a barrier. Occasionally, sub-groups of sampling sites were separately compared for a proper distance measurement.

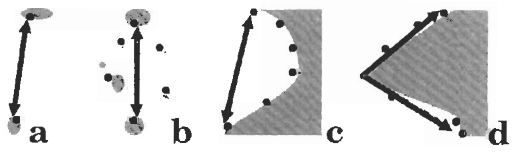

Figure 1. Models for measuring geographic distance among populations. Geographic distance was measured either between two islands (model *a*), between farthest samples from an archipelago (model *b*), across a bay (model c) or around a coastline (model *d*.).

*Data treatment and statistical test*

The observations ($F_{st}$ and geographic distances) were scaled by adding 1 and logarithmically transformed to normalize the distribution. However, a normal distribution was obtained only for geogra-phic distance data.Therefore, the $F_{st}$ data were treated with a nonparametric met-hod. Linear discriminant analysis was applied to distinguish PT and NPT using two variables, *i.e.* $F_{st}$ and geographic distance. Sen & Puri's nonparametric test (Sen & Puri 1968) performed was *a priori* to test an equality of covariance matrices ( which is required for

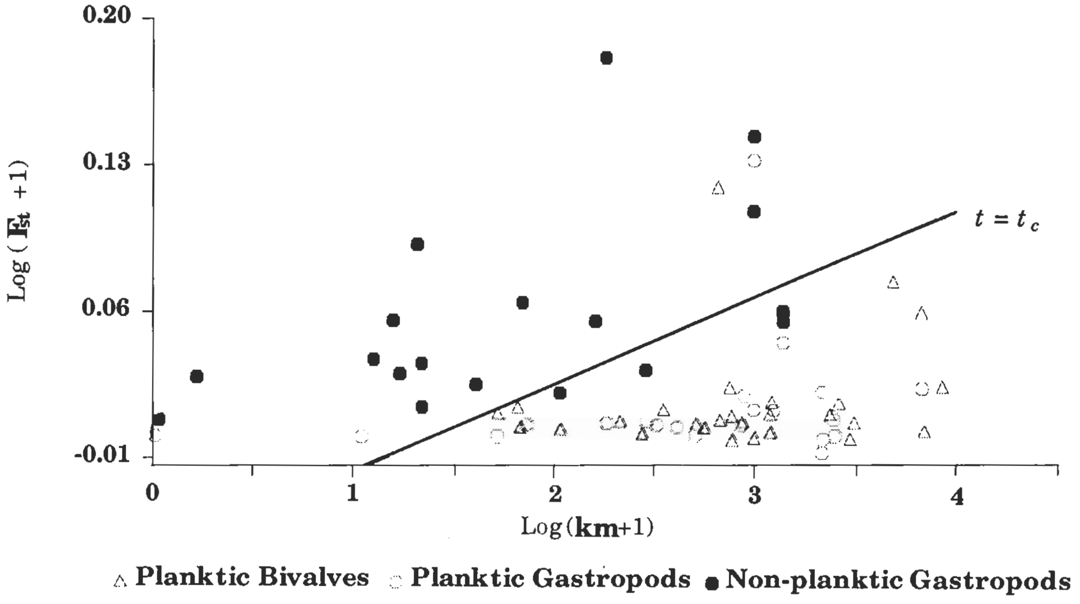

Figure 2. The linear discriminant function ($t = t_c$) as well as the plots of the amount of genetic differentiation among populations ($F_{st}$) and geographic distance (km) in logarithmic transformation between planktic and non-planktic species of gastropods and bivalves.

calculating linear discriminant functions) between groups. The linear discriminant function was performed and significant test of the function was obtained by using Hotelling's $T^2$ test. The correctness (power to classify correctly) of the linear discriminant function was tested with known-reproductive-mode species (the observations in this study) and calculated as a percentage. This stepwise procedure was explained by Tacq (1991) and Rencher (1995). In addition a Kruskal-Wallis test (Sokal & Rohlf 1995) was applied to test the difference of $F_{st}$ between the two reproductive modes.

## RESULTS

The two modes of reproduction are well discriminated ($p<0.001$). The assumption of linear discriminant function was fulfilled, since the same covariance matrices were found in the two reproductive modes.

The discriminant function is $t = 2.378^* \mathrm{Log}(\mathrm{km}+1)-56.91^*\mathrm{Log}(F_{st}+1)$ and $t$ critical value ($t_c$) is 3.311. If $t<t_c$, an observed species is considered as NPT while when $t>t_c$ it indicates PT. By back testing to the observations in this study, 88% of the cases were correctly classified. The correctness is higher in PT (92%, n=48) than in NPT species (78%, n=18).Note that, the function should not be applied with geographic distance less than 20 km, because it will then classify all data as NPT. The separation between reproductive modes is shown in Fig 2.

There is no significant difference between PT bivalves and PT gastropods. The mean $F_{st}$ over all geographic distances with 95% confident limits are $0.044 \pm 0.023$ and $0.152 \pm 0.061$ in PT and NPT species, respectively. The observed geographic range among conspecific populations of PT and NPT species are 0.05–8500 km and 0.1–1394 km, respectively. In addition,significant difference of $F_{st}$ ($p<0.001$) was obtained by the Kruskal-Wallis test.

## DISCUSSION

As mentioning earlier, population genetic structure is influenced by many factors. However, this study shows that mode of reproduction, which in turn determines the amount of gene flow, plays an important role than other factors. This study found that most of PT have very low $F_{st}$. Two exceptional observations with high $F_{st}$ in PT were reported by Meehan *et al.* (1989) and Parsons (1996). Meehan *et al.* (1989) suggested that the studied populations of *Macoma balthica* might have diverged as sibling species. If this is true, the data from their studies may be discounted (for the current hypothesis). Parsons (1996) explained the high $F_{st}$ in PT *Austrocochlea constricta*, as a result of strong selection among generations in a highly heterogenous habitat. Thus, the role of reproductive modes (gene flow) in this case was deviating from the realized potential.

Generally, reproductive mode must be observed directly from reproductive behaviour, which may be difficult. For instance the case of the bivalves living in hot vents which are very hard to observe *in situ,* or an animal can not be successfully bred and spawned in captivity. Thus other means have been proposed to identify modes of reproduction, *e.g.* using morphology and size of protoconch in gastropods and prodissoconch in bivalves, the amount of yolk, egg size, *etc.* (Thorson 1950; Mileikovsky 1974; Jablonski & Lutz 1983).

This study now presents a new tool to recognize reproductive modes using the linear discriminant function. However, one should realize that the data in this review were obtained from protein electro-phoresis and that results may depend on choice of polymorphic loci to be analyzed, interpretation of zymogram, and staining procedure. Despite these problems, the present results have shown the potential of employing allozyme diversity to classify reproductive modes in marine bivalves and gastropods.

For further investigation of the role of reproductive modes, more data are required and other indices could be calculated. A comparison between repro-ductive modes could possibly be expanded to other groups of organisms. The information from DNA analysis should be added. Other genetic indices *e.g.*, genetic distance, or other approaches such as multivariate analysis should be used. Althought, this study emphasized the amount of genetic differentiation, other aspects such as the amount of genetic variation, percentage of polymorphic loci and heterozygosity should be investigated.

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