Long-distance dispersal of a subantarctic brooding bivalve (*Gaimardia trapesina*) by kelp-rafting

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**Abstract**  The probability of successful dispersal by sessile benthic invertebrates is thought to strongly influence their geographic distribution and population genetics. Generally, species with long-lived planktonic larvae are expected to exhibit wider distribution patterns than those species which brood their young, due to their presumably greater potential for dispersal. In some cases, however, brooding species exhibit broad distributions and show evidence of genetic exchange with geographically distant populations. One potential factor that has been invoked as an explanation is dispersal by floating and rafting of adults and egg masses. Several studies have shown that it is possible for sessile adults to disperse on the order of several to many thousand kilometers by rafting on debris in ocean currents. With very few exceptions, however, direct evidence of rafting in the open ocean has been lacking. We present evidence of long-distance (1300 to 2000 km) dispersal of a brooding pelecypod, *Gaimardia trapesina* (Lamarck, 1819), in the Southern Ocean in the vicinity of Cape Horn, the Falkland Islands, and the antarctic island South Georgia (54°S; 37°W). Data on survival and fecundity rates of *G. trapesina* and the prevalence of kelp rafts collected during the austral winter of 1993 indicate that dispersal by rafting can occur over ecologically relevant time scales and could potentially serve as a significant means of genetic exchange between populations.

**Introduction**

Patterns in the geographic distribution and population genetics of benthic marine organisms depend critically on the frequency with which these organisms disperse gametes and offspring over ecologically relevant time scales (Strathmann 1974, 1985; Zinsmeister and Emerson 1979; Endler 1982; Scheltema 1986; Hellberg 1994; Kohn and Perron 1994; Worcester 1994). In particular, populations in geographically remote or otherwise inaccessible regions may be severely limited in the exchange of genetic material with other populations, and the degree to which genetic exchange occurs may be a direct consequence of the likelihood that adults, larvae, or eggs survive transport between populations. Thus, benthic invertebrates with a long-lived planktonic larval phase have generally been expected to disperse over longer distances than those species that have a short-duration pelagic larval stage or that brood young.

Despite the lack of a defined dispersal stage, at least some brooding invertebrates exhibit a fairly wide geographic distribution (Highsmith 1985; Jackson 1986). Johannesson (1988), for example, has shown that a brooding gastropod species (*Littorina saxatilis*) has a wider distribution than does a closely-related congener (*L. littorea*) with a pelagic larval phase. Furthermore, in a study of enzyme variation in the brooding clam *Lasaea* spp., O’Foighil and Eernisse (1988) found evidence of genetic exchange between geographically distant populations. In contrast, a similar study by Hellberg (1994) indicated very limited gene flow among populations of the coral *Balanophyllia elegans*, a species that lives attached to hard surfaces and has limited larval dispersal. However, genetic analysis revealed only a weak relationship between distance and gene flow, suggesting that some other mechanism of dispersal could occur at low levels (Hellberg 1994 and personal communication). These observations suggest that, in some cases, alternative means of dispersal such as floating and rafting by benthic animals may occur more frequently than previously expected (Johannesson 1988; Worcester 1994), but that the likelihood of transport may be strongly influenced by the local environment and the life history of the organism.

Several recent studies have examined the potential for dispersal by benthic invertebrates, algae and meiofauna by passive mechanisms, including rafting by adults and egg
masses on macroalgae, pumice and other floating debris (Gerlach 1977; Deysher and Norton 1982; Jokiel 1984, 1989; Highsmith 1985; Kohn and Perron 1994; Worcester 1994) drifting in the surface layers (Highsmith 1985; Martin and Chia 1991), and transport via human activity (Carlton 1987). Extrapolations of dispersal capability of sessile organisms based on current speeds and survival times under controlled conditions suggest that epibenthonic dispersal on the order of a few to many thousand kilometers may be possible (Zinsmeister and Emerson 1979; Deysher and Norton 1982; Jokiel 1984; Edgar 1987; Harrold and Lin 1989). For example, Jokiel (1984) demonstrated that coral colonies drifting into Hawaiian waters on volcanic pumice had traveled over 20,000 km at sea. Similarly, Worcester (1994) showed that rafting colonial ascidians recruited as successfully as did swimming larvae and were transported over substantially longer distances. However, comparatively little quantitative field evidence of rafting has been reported for most other regions of the world’s oceans (Scheltema 1977; Highsmith 1985), particularly over large distances of open ocean.

We present evidence for potentially long-distance dispersal of a brooding pelecypod, Gaimardia trapesina, in the Southern Ocean in the vicinity of Cape Horn (South America), the Falkland Islands, and the subantarctic island South Georgia on dislodged rafts of the kelp Macrocystis pyrifera (Linnaeus). Rafts were presumed to have been transported eastward by the Antarctic Circumpolar Current (“West Wind Drift”), a predominantly unidirectional current running at 0.4 to 0.7 knots (0.75 to 1.3 km h⁻¹; United States Defense Mapping Agency 1988; Pickard and Emery 1990).

Mortensen (1925) first indicated the significance of the West Wind Drift to dispersal in the Southern Ocean, where he documented rafting by the sea star genus Calvasterias on floating Macrocystis sp. Through comparisons of species distributions, Fell (1962) extended this argument by suggesting that the spread of echinoderm species in the Southern Ocean was largely unidirectional, from west to east, and that this pattern was best explained by current-mediated dispersal. Evidence further suggests that the West Wind Drift has occurred at least since the late Cretaceous, and is therefore likely to have had a significant impact on the distribution of species on many subantarctic and antarctic islands (Fell 1967; Deacon 1982).

South Georgia and Gaimardia trapesina

The antarctic island South Georgia (54°S; 37°W) is located ~2000 km east of the southernmost region of South America (Cape Horn, ~53°S; 68°W), and 1300 km east-southeast of the Falkland Islands (52°S; 59°W; Fig. 1). Surface currents and winds between Cape Horn and South Georgia are dominated by the West Wind Drift (Deacon 1982). As a result, kelp dislodged from the region of Cape Horn and the Falkland Islands could potentially reach South Georgia, but only if it remained afloat and intact during the necessary travel time (Norton and Mathieson 1983; Edgar 1987), a minimum of 75 to 100 d at 0.5 knots (0.9 km h⁻¹), and most likely much longer due to transport in large-scale eddies. The potential for kelp rafts to serve as a significant means of transport for benthic invertebrates to South Georgia thus becomes a question of both the integrity of the raft and the probability of the associated epifauna surviving any physiological, hydrodynamic, and predatory stresses experienced while at sea. We present data on survival and reproductive capacity of invertebrates rafting on kelps in the vicinity of Cape Horn (Magellan region), the Falkland Islands, and waters adjacent to South
Georgia, and, in particular, focus on the bivalve *Gaimardia trapesina* due to its abundance, wide distribution, and the ease in determining its reproductive state.

*Gaimardia trapesina* (Fig. 2) is a common component of kelp-bed communities in nearshore subantarctic and antarctic waters (Dell 1964; Ralph and Maxwell 1977; Ojeda and Santileces 1984; Castiglia 1985). Despite the fairly high levels of endemism apparent on many islands in the Southern Ocean (Dell 1972), the genus *Gaimardia*, and in particular the species *G. trapesina*, exhibit a wide distribution throughout the Scotia Arc and beyond, including (but not necessarily limited to) Cape Horn, the Falkland Islands, South Georgia, Marion Island, and the Kerguelen Islands (Powell 1951; Fell 1962; Dell 1964, 1972; Ralph and Maxwell 1977; Blankley and Grindley 1985; Thiriot-Quiveux et al. 1988). As has been observed for many antarctic pelagic taxa (Nicol 1967) and other cold-water invertebrates (Thorson 1950), *G. trapesina* broods its young and has a free-living larval stage (Thiriot-Quiveux et al. 1988). Very little published information is available with regard to the biology of this species, although Ralph and Maxwell (1977) have demonstrated that *G. trapesina* shows no evidence of cold adaptation in terms of respiration rates.

**Materials and methods**

All observations and collections were conducted between 28 May and 3 July 1993 (austral winter), aboard the R. V. "Nathaniel B. Palmer." (U.S. Antarctic Research Program Cruise S048) between South Georgia and Punta Arenas, Chile. Observations on kelp patch size and abundance offshore were conducted continuously during daylight hours (6 to 7 h daily) on the return trip to South America between 26 June and 29 June, using strip-transect methods. All kelp patches seen within 150 m to one side of the ship were recorded, along with their position and approximate dimensions. Nearshore observations (25 km offshore) were conducted using similar strip-transects while the ship ran parallel to the coast of South Georgia on 2 June, and most likely included kelps originating at South Georgia as well as other locations.

Data on survival rate and reproductive capacity of *Gaimardia trapesina* (Lamarck, 1819) transported on rafts were collected from 43 kelps taken from three rafts: Raft A (53°31'S; 62°45'W; closest raft to South America); Raft B (53°21'S; 56°35'W); and Raft C (53°44'S; 49°57'W; closest raft to South Georgia, Fig. 1). Kelps from each raft were obtained using a boat hook from the stern quarter of the ship, so any mobile fauna may not have been captured. As many kelps as possible were collected haphazardly from each raft (A: n=17, B: n=6, C: n=20). In general, sample size and collection locations were limited by adverse sea state conditions experienced during the return leg of the cruise.

Two measurements were used as indices of relative time since dislodgement: (1) mean kelp blade-length (a measure of deterioration; almost all blades lacked distal ends), and (2) percentage of branch points supporting the gooseneck barnacle *Lepas australis*. This species attaches to floating objects in the open ocean (Nilsson-Cantell 1930), and presumably settled after the kelp was dislodged (most barnacles were found at the base of blades at the branch point of the main stipe). The length of all blades (range of 0 to 36 blades per kelp) and the length of each kelp stipe were measured to the nearest centimeter. Blade lengths for each kelp were then averaged to yield a single value per blade for statistical analysis. Each kelp was completely surveyed for the presence and abundance of benthic epifauna. The maximum dimension of each *Gaimardia trapesina* was measured to the nearest 0.05 mm with a vernier caliper, and reproductive state (presence/absence of brooded young) was estimated by dissecting ten individuals from each raft. Two one-factor analyses of variance (Statview II) with Bonferroni correction for number of tests (n=2) were used to determine differences between indices of time at sea. Two additional ANOVAs were conducted to compare the relative abundance and size-frequency distributions of *G. trapesina* populations from each raft. A series of Student's t-tests with Bonferroni correction (n=3) was used to test for significant differences between pairwise (post hoc) comparisons within each significant ANOVA result.

**Results**

A total of 43 rafts were observed during the 4 d of offshore transects. Rafts ranged between 1 and 6 m in diameter with a mean of 2 m. Observations of kelp-raft abundance indicated a patchy distribution, but suggested that rafts were present throughout the open ocean between South America, the Falkland Islands, and South Georgia (Fig. 3). For example, on one occasion ten rafts were observed within a span of 35 km, but there then followed a complete absence of rafts for the next 45 km. This patchiness might reflect the distribution of meanders and eddies common to the polar Front Zone (Legeckis 1977).

Each kelp raft sampled was ≇ 2 m long × 2 m wide × 1 m deep and consisted of 100 to 200+ individual *Macrocytis pyrifera* plants. Rafts were composed almost entirely of *M. pyrifera*, and both smooth and corrugated blade morphologies were encountered (Fischer and Hureau 1985).
Table 1  Summary of characteristics of each raft sampled. Raft A was collected closest to Cape Horn (South America) and Raft C closest to South Georgia. Indices of time since dislodgement [mean blade length and percentage of branch points supporting pelagic Lepas australis ("% Lepas") ] generally suggest that the raft closest to South Georgia had spent a longer time at sea than had Rafts A or B, and maintained lower densities of Gaimardia trapesina m⁻² kelp stipe. Values are mean ± SD

<table>
<thead>
<tr>
<th>Raft</th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kelps/raft</td>
<td>17</td>
<td>7</td>
<td>20</td>
</tr>
<tr>
<td>Stipe length</td>
<td>5.39 ± 4.95</td>
<td>4.31 ± 1.97</td>
<td>2.61 ± 1.71</td>
</tr>
<tr>
<td>Blade m⁻¹ stipe</td>
<td>3.45 ± 2.25</td>
<td>4.93 ± 5.96</td>
<td>3.24 ± 2.84</td>
</tr>
<tr>
<td>Blade length</td>
<td>25.62 ± 15.78</td>
<td>24.33 ± 15.72</td>
<td>11.91 ± 10.30</td>
</tr>
<tr>
<td>% Lepas</td>
<td>43.93 ± 18.49</td>
<td>41.18 ± 22.98</td>
<td>51.05 ± 16.91</td>
</tr>
<tr>
<td>G. trapesina m⁻² stipe</td>
<td>5.73 ± 22.15</td>
<td>2.31 ± 3.35</td>
<td>1.64 ± 3.03</td>
</tr>
</tbody>
</table>

The relative abundance of Gaimardia trapesina (number of individuals per m kelp stipe) was lowest nearer South Georgia, but was also highly variable and showed no significant trend with distance from South America (Table 1, F=0.41, p=NS). Maximum shell length was significantly shorter on the raft closest to South Georgia (Raft C) and was highest for Raft B (Fig. 4; F=53.56, p≤0.0001; all pair-wise comparisons significant at p≤0.0001). Dissection revealed that G. trapesina from all three rafts contained high numbers of brooded young (upwards of several hundred per individual; number of individuals with young: Raft A=7/10, B=10/10, C=9/10).

With the exception of Lepas australis, which were found primarily at the branch points of the kelp stipe, most organisms were located on the blades of the kelp. In general, the percentage of the blade covered was highly variable, and consisted primarily of Gaimardia trapesina, L. australis and spirobid polychaetes. An unidentified species of hydroid was common (up to 50% cover) on several blades from each raft, as was a bryozoan later identified as Membranipora hyadesi (J.E. Winston personal communication).

Discussion and conclusions

Rafting on algae has commonly been invoked as a means by which sessile benthic invertebrates can disperse and colonize new habitats (Highsmith 1985 and references therein). The probability of successful dispersal by rafting is likely to be influenced by the availability of rafts, as well as the ability of organisms to utilize them. Organisms living on benthic macroalgae in areas where dislodgement occurs frequently thus may be more likely to disperse by rafting than organisms inhabiting hard substrata (e.g. Hellberg 1994; Worcester 1994). Highsmith has suggested that the relatively high diversity of brooding invertebrates in high latitudes may result in part from an increase in rafting op-
portunities compared to the tropics due to the higher abundance of large macroalgae in high latitudes. The results of the present study support this hypothesis and tentatively suggest that dispersal by rafting could occur commonly in the Southern Ocean. To the best of our knowledge, this study represents the first reported collection of rafted invertebrates from an offshore location (>200 km, Arnaud et al. 1976) in the region.

Our data indicate that *Gaimardia trapesina* are able to survive transport across a large portion of the distance between South America and South Georgia, and are able to maintain brooded young during this time. Furthermore, observations suggest that potentially large numbers of rafts can reach the open ocean. Thus, over geologic time, *G. trapesina* are likely to have been spread throughout and beyond the Scotia Arc by rafting. It is also probable that populations on South Georgia experience fairly frequent recruitment from populations from Cape Horn and/or the Falkland Islands. Genetic analysis is obviously necessary for confirmation.

Despite potential mortality factors, large numbers of *Gaimardia trapesina*, bryozoans, sponroids, and hydroids can survive transport on kelps well, even apparently over a period of several months. Given its persistence over geologic time, the West Wind Drift has probably served as a significant means of dispersal for brooding invertebrates that are capable of surviving transport between shores throughout the Southern Ocean, and probably accounts for the widespread distribution of *G. trapesina*. Furthermore, the prevalence of algal rafts in the area surveyed suggests that genetic exchange may occur over ecologically relevant time scales, which is likely to be significantly influenced by the unidirectional nature of the West Wind Drift.

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