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Origins and dispersal of the Antarctic fairy shrimp

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Abstract: Passive dispersal has traditionally formed a fundamental component of biogeographical theories of the origin of the fauna that occupy the ice-free habitats of mainland Antarctica. But in the context of an emerging picture of endemism for many Antarctic terrestrial invertebrates, is there still a place for such stochastic processes in Antarctic biogeography? The case of the Antarctic fairy shrimp, *Branchinecta gaini* Daday 1910, may provide an answer - or, at least, an important exception to the rule. Although passive dispersal is certainly a stochastic and contingent phenomenon in Antarctica, the occurrence of *B. gaini* on the Antarctic Peninsula can only be explained satisfactorily by resort to this explanation. It is, at present, probably the best example of an Antarctic invertebrate with a biogeographic signature of passive - in particular, zoophoretic - dispersal.

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Introduction

Now that there is growing support and consensus for invertebrate faunal endemism on mainland Antarctica and the role of glacial refugia in their persistence (Convey & Stevens 2007, Convey *et al*. 2008, Pugh & Convey 2008), a more circumscribed understanding of the passive dispersal of invertebrates in Antarctica may be necessary. Although there is good evidence to suggest its contribution to the dispersal of micro-organisms and propagules (e.g. Skotnicki *et al*. 2001, Nkem *et al*. 2006), its involvement in the colonization of habitats by larger organisms may need a closer look. Thus, for example, although the passive dispersal of arthropods - Acari, Collembola - undoubtedly occurs, its contribution to the origins of these animals must probably now be ruled out, with attention re-directed to its contribution to Holocene and contemporary (‘Anthropocene’) distribution and dispersal patterns (see Hawes *et al*. 2007, 2008a).

In this paper, by way of supplemental note to the emerging picture of the origins of the fauna in glacial refugia on the Antarctic continent (e.g. Convey *et al*. 2008, Pugh & Convey 2008), I examine the unusual case of the Antarctic fairy shrimp, a species which is simultaneously the largest invertebrate of terrestrial Antarctica habitats (adult body size *c*. 16 mm), and the distribution of which, on the Antarctic Peninsula can, whatever the timescale, only have its origins in passive dispersal.

The Antarctic fairy shrimp, *Branchinecta gaini* Daday, 1910, is a freshwater crustacean, with a distribution that ranges from as far north as South America to half way down the Antarctic Peninsula (Fig. 1). Its active life stages cannot survive seawater or terrestrial exposure and yet they occur in habitats of isolated freshwater pools as small as *c*. 1 m^2 at Marguerite Bay on the Antarctic Peninsula (Hawes *et al*. 2008b), with distances between known freshwater habitats ranging from a few kilometres to hundreds of kilometres (Fig. 1). Thus, in the absence of contiguous pre-Holocene freshwater bodies stretching at least half the length of the Antarctic Peninsula, the only viable way for the fairy shrimp to have moved between habitats is in the dormant form of cysts. These cysts are highly resistant stages capable of surviving desiccation and low winter temperatures (Brendonck 1996, Peck 2004). However, as they are dormant metabolically (and are, of course, physically sessile), they are reliant on some form of foreign agency to move them between habitats - i.e. passive dispersal.

Vectors of passive dispersal

Antarctic biogeography has traditionally recognized four vectors of passive dispersal important to terrestrial biota: anthrochory (Pugh 1994), hydrochory (Hawes *et al*. 2008a), anemochory (Pugh 2003, Hawes *et al*. 2007), and zoochory (Pugh 1994, 1997). (Although strictly speaking, anthrochory is a branch of zoochory, it is most usefully considered separately, particularly in an Antarctic context where it is of interest to separate the effects of recent human arrival on the continent from ‘natural’ dispersal phenomena). There is nothing to suggest anthropogenic influence on the distribution of *B. gaini*. However, the latter three vectors are all circumstantially implicated in its dispersal. Although one must assume a state of polychory, the efficacy of each vector - even considered inferentially - may vary greatly. Thus in the context of the fairy shrimp, the relative influence of each factor may be ranked in ascending order from hydrochory (involvement limited to occasional local dispersal movements); to anemochory (involvement in both local and long distance dispersal, but highly stochastic); to zoochory (involvement in both local and long distance dispersal, potential for

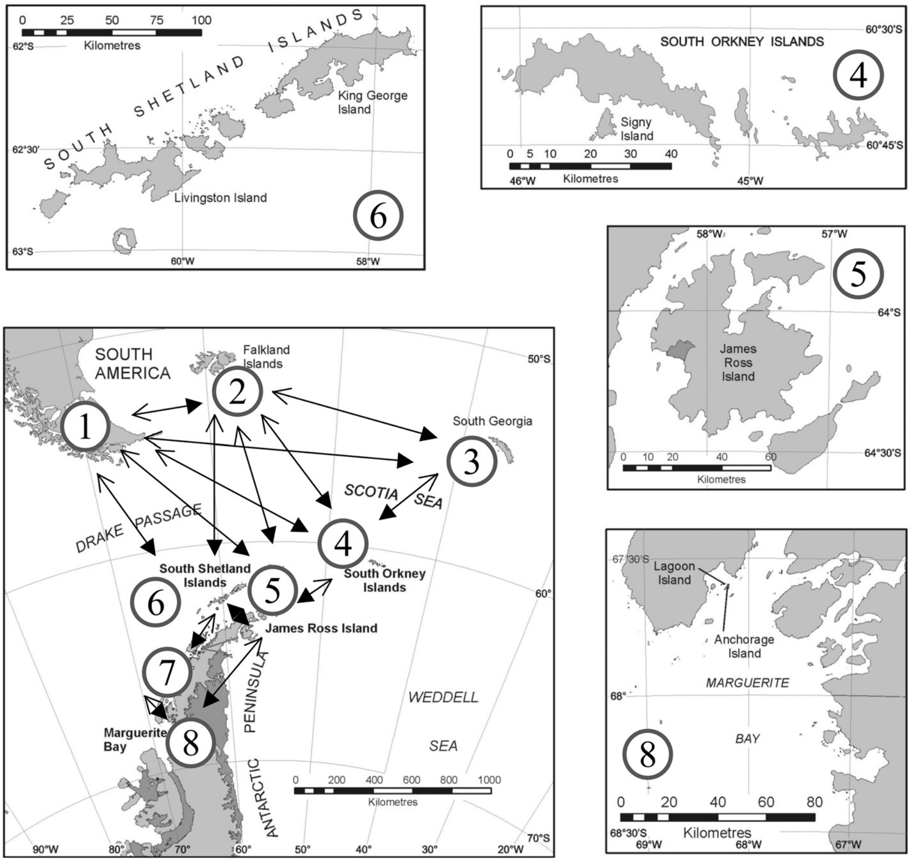

Fig. 1. The distribution of *Branchinecta gaini*: (1) Chile (Rogers *et al*. 2008), (2) the Falkland Islands (Weller 1975) (?), (3) South Georgia (Dartnall & Heywood 1980), (4) South Orkney Islands (5) James Ross Island (extinct), (6) South Shetland Islands (Pociecha 2007, Toro *et al*. 2007), (7) near Palmer Land (Bryant 1945) (?), (8) Marguerite Bay (Peck 2004, Hawes *et al*. 2008b, Hawes 2008). (Grey = land; dark grey = sea ice extent). Insets (4, 5, 6, 8) provide magnified maps of selected sites. Arrows indicate hypothetical population movements. So as not to assume uni-directional movements between populations, arrows are indicated in both directions: filled arrowheads indicate the direction of a source population, unfilled arrow-heads indicate the 'possibility' of reciprocal movements. Following Pugh *et al*. (2002), question marks next to references indicate records requiring further substantiation. Bryant (1945) records the *Branchinecta* found near Palmer Station as the South American species, *B. granulosa* - although given what we know about the distribution of *B. gaini* it is undoubtedly *B. gaini*. Multiple populations (indicative of local dispersal events) are definitely known from the South Shetland Islands, James Ross island, and Marguerite Bay - for the latter, on the two islands, Lagoon (1 population, 1 pool) and Anchorage (2 populations, *c*. 3 or 4 adjacent pools each) (TCH, personal observation) (see inset of (8)).

targeted transfer between suitable habitat). Each is considered below. It is to be noted that the wider literature on zoochory of aquatic invertebrates (including *Branchinecta*) suggests roles for both epi- and endozoochory. The latter, in fact, although not previously mentioned in an Antarctic context, may represent the most viable vector for the dispersal of *B. gaini*.

Hydrochory

Long-distance transport of *B. gaini* by water would require the existence of extensive contiguous networks of freshwater instead of the isolated and patchily distributed lakes and ponds that characterize the Antarctic Peninsula's ice-free regions. Short-range dispersal between adjoining pools rather than discrete populations undoubtedly occurs to some degree. The two populations on Anchorage Island (Fig. 1) occur as networks of closely associated pools at different elevations with considerable potential for run-off. At one of these sites, three pools formed a tiered group with a water channel connecting the top pool with the lower two pools. When the pools are full, it would be possible for free-swimming adults to be dispersed to the downstream pools. The transport of cysts would be particularly feasible. Elsewhere Brendonck & Riddoch (1999) have noted the propensity for cysts not buried in pool sediment to disperse by floating.

Anemochory

Winds have been implicated in the dispersal of other desiccation-resistant taxa, like nematodes and tardigrades, which have life stages amenable to passive dispersal

(Nkem *et al*. 2006). Given that pools occupied by *B. gaini* may dry out long before the onset of winter (Hawes *et al*. 2008b), there would be a temporal window of at least a month when the dry detrital substrate of the pools, impregnated with cysts, would be available for 'transport'. Brendonck & Riddoch (1999) were the first to directly demonstrate the aerial dispersal of viable eggs by *Branchinecta*, although they noted that such events were probably limited to short-range dispersal movements. Graham & Wirth (2008) have shown that even low wind velocities are capable of transporting pool sediments containing branchiopod cysts. Vanschoenwinkel *et al*. (2008) have underlined these findings by demonstrating that aerial dispersal is community-scale phenomenon (17 taxa, including *Branchinecta*, netted in wind socks), noting that although proving long-distance dispersal is difficult, if one assumes the occurrence of such events over long-time scales, it is by no means impossible. In the case of *B. gaini*, some degree of aerial dispersal is therefore not unlikely, but the scarcity of suitable habitat within ice-free areas which are themselves biological oases surrounded by ice and snow, means that successful long distance dispersal must be viewed as probabilistically very unlikely. Short-range dispersal movements, however probably occur to some degree, particularly between neighbouring pools.

Zoochory

The problem with both aerial and aquatic dispersal is not that it is impossible, but that the sheer scale of habitat isolation in ice-free Antarctica multiplies an already formidable degree of stochasticity in the dispersal-survival equation. Not only are pools 'patchy' within the ice-free habitat matrix, but only a small proportion of this matrix is itself suitable habitat for *B. gaini*. The existence of a means of dispersal that offers directed transfer between suitable freshwater habitats considerably improves the odds of success. Zoophoretic transport - accidental carriage by animals; in this case, birds - represents such a dispersal scenario for *B. gaini*. Freshwater bodies are an important focal point for birds in Antarctica as sites of aggregation and opportunities for bathing and drinking.

Epizoochory

The capture of organisms on the feet and feathers of birds has long been known to play a part in the dispersal of aquatic invertebrates (Darwin 1872, 1878). The accidental collection of *Branchinecta* cysts by birds in contact with pool sediments would be conducive to both short-range and long-distance movements – providing both means of transport and the potential for targeted transference between freshwater bodies.

Endozoochory

A less obvious but possibly more effective mode of phoresy may be the consumption (accidental and/or intentional) of cysts and/or gravid females by birds, followed by the voiding of undigested, viable cysts. The potential for targeted transference is the same as that of epizoochory, but the internal retention of cysts (potentially for several days) means that they are not reliant on the adhesive properties of pool sediment and may have greater potential for successful carriage on long distance flights. Although so far unexamined in an Antarctic context, the role of endozoochory in the dispersal of seeds and aquatic invertebrates (including Anostraca) elsewhere has been shown to be a viable and important dispersal vector (Bohonak & Jenkins 2003, Green & Figuerola 2005).

The ability of cysts to survive and hatch after digestion has been demonstrated on numerous occasions. Horne (1966) demonstrated that the hatchability of *Artemia salina* cysts was unaffected by *in vitro* manipulations of pH and treatments of chitinase, lipase, pepsin and trypsin. Proctor *et al*. (1967) showed the effectiveness of a small shorebird, the killdeer (*Charadrius vociferous*) as a potential dispersal agent: faeces collected 30 min after being fed the fairy shrimp *Streptocephalus texanus* produced successful hatchings in 28 out of 30 trials. Dispersal range would also be determined by retention time as well as resistance to digestion - although not tested in fairy shrimp, results from the halophilic anostracan, *Artemia salina*, showed retention times of 24 hr had no effect on hatching success (Proctor *et al*. 1967).

Renewed interest in the endozoochory of anostracans has provided further evidence of its effectiveness as a dispersal vector in a variety of 'hosts'. Bohonak & Whiteman's (1999) study of the dispersal of *Branchinecta coloradensis* by salamanders demonstrated the possibility of successful hatching of defecated cysts that had been consumed with their mother before being laid. Beladjal *et al*. (2007) showed that trout (*Salmo trutta*) assist in the upstream dispersal of the fairy shrimp (*Chirocephalus diaphanus*) with cysts capable of surviving trout ingestion. Likewise, Green *et al*. (2005) and Sánchez *et al*. (2007), hatching material collected from faeces and pellets, have provided further evidence that anostracans (in this case *Artemia*) are routinely dispersed via the gut passage of shorebirds.

Anostracans are included in the diet of many waterbirds (e.g. Green *et al*. 2005, Boros *et al*. 2006, Sánchez *et al*. 2007). Interestingly, further north in the sub-Antarctic, where there is greater avian diversity, *B. gaini* are a known component of the diet of the South Georgia pintail *Anas g. georgica* (Weller 1977). Although the South Georgia pintail is confined to South Georgia, given the well known role of ducks, in particular, as agents of passive dispersal (e.g. Green & Figuerola 2005) it seems reasonable to infer a role in the gene-flow of metapopulations on the island. Further south, the most likely candidates for avian vectors would be, but not confined to, skuas (*Catharacta maccormicki*), which are both omnivorous and known to frequent fairy shrimp pools. Although there is no published data on avian interactions with *B. gaini* in the maritime Antarctic, this reflects a lack of investigation, rather than a lack of evidence.

Current and historical distribution

No doubt in future years, molecular phylogeography will catch up with this largely neglected Antarctic animal, and help to put a timescale on its lake- and pool-'hopping' advance down the Antarctic Peninsula (Fig. 1). For the meantime, in the absence of such data, although it would be premature to dismiss an ancient connection - i.e. pre-Last Glacial Maximum (LGM) (20–18 000 yr BP) - to the continent, the circumstantial evidence agrees with Ralph (1967): 'The Antarctic environments in which it has been found have only been open to it for the last 10 000 years. This means that *Branchinecta* has colonized these areas from other freshwater habitats, presumably being distributed in the egg stage.'

Indeed, in the case of *B. gaini*, endemism seems to be less probable than the random processes of passive dispersal. Although cysts are certainly capable of surviving extended periods of dormancy, it seems highly unlikely that they could survive ice cover for the hundreds of years of maximum glacial cover. Likewise, although freshwater refugia may have persisted through glacial cycles (e.g. Hodgson *et al*. 2001, Cromer *et al*. 2006), the persistence of pools of *c*. 1 m^2 - typical of its occurrence on the islands of Marguerite Bay (Hawes *et al*. 2008b) - also seems highly unlikely and strongly suggests that, at least at the lower limits of its range, it is a mid- to late Holocene immigrant.

The best palaeolimnological evidence to date is that from Signy Island, South Shetland Islands where *Branchinecta* eggs from Holocene lake sediments paint a picture of post LGM arrival (Jones *et al*. 2000). During the LGM most of Signy is believed to have been covered by the South Orkney Ice Cap (Sugden & Clapperton 1977) with lake formation following deglaciation *c*. 7000 BP (Jones *et al*. 2000). The islands nearest to the tip of the Antarctic Peninsula (South Orkney Islands, South Shetland Islands) can reasonably be assumed to be the 'source' population for community establishment further down the Peninsula. As to the 'source' population for the first Holocene arrivals, one must, given the distributional data currently available, infer a sub-Antarctic and/or South American point of origin. Although a couple of records need verification (see legend for Fig. 1) and there are no doubt unrecorded populations, the distributional data for the Maritime Antarctic is unequivocal in its implication of a 'stepping-stone' picture of *B. gaini's* dispersal south.

It should be emphasized however, that typical of an animal dependent on both stochastic dispersal processes and specific environmental conditions - particularly freshwater (Hawes *et al*. 2008b) and organic-rich sediments (Paggi 1996) - its incursion into Antarctica should not be considered necessarily linear or progressive with time. The most favourable conditions for its persistence on Signy, for example, were between *c*. 3800–1200 BP (Jones *et al*. 2000). Likewise the extinction of 'sink' populations has been documented in the sediment cores of James Ross Island on the eastern side of the Peninsula (Björck *et al*. 1996). In this regard, an interesting question is whether the temporal segregation of egg abundance in sediments of the different lakes analysed on James Ross Island (Björck *et al*. 1996), represents not just changing pool chemistry, but also metapopulation dispersal dynamics?

A 'non-Antarctic' life history strategy?

Perhaps the greatest argument against endemism is its life history strategy, which shows little evidence of 'Antarctic' adaptations (*sensu* Convey 1996, Peck *et al*. 2006) - although its feeding behaviour may suggest some divergence from *Branchinecta* that are strictly filter feeders (Hawes 2008). Most Antarctic invertebrates occupying terrestrial habitats exhibit slow, seasonally interrupted lifecycles. By contrast, *B. gaini*, facilitated by metabolic eurthythermy (Peck 2004, Pociecha 2007), squeezes its entire active life cycle into the narrow temporal window of positive temperatures and liquid water availability provided by the Antarctic summer (Jurasz *et al*. 1983, Hawes *et al*. 2008b). This 'ruderal' strategy (*sensu* Grime 1977), does not, of course, necessarily preclude Antarctic origins. However, that a large invertebrate like *B. gaini* should have such a life history strategy in Antarctica is, at the very least, highly unusual. The parsimonious explanation is that we have an example of an animal that has not 'adapted' to Antarctica, so much as the 'opportunistic' character of its pre-existing life history strategy - shared by all other *Branchinecta* (e.g. Hildrew 1985, Bohonak & Whiteman 1999, Brendonck & Riddoch 2000) - has allowed it to colonize and occupy Antarctica. Their success at the edges of Antarctica's extreme environment may be attributed simultaneously to the metabolic flexibility of their active life-stages and their dispersal-friendly dormant stage.

Conclusion

As the only fairy shrimp in Antarctica, *B. gaini's* reliance on foreign agencies to move it between freshwater bodies makes it an exemplar of passive dispersal in Antarctica and, as such, an important footnote to any picture of the biogeography of the fauna of the continent. Although the evidence remains, for the moment, circumstantial, it would seem that there is no other way this species can have got to where it is today. This does nothing to obviate the emerging picture of Antarctic endemism, but it does provide a useful reminder of the viability of passive dispersal in Antarctica. Although there are probably many more organisms that could survive, and perhaps even thrive in maritime Antarctica, there are few that can penetrate the isolation of its ice-free habitats. Every species and community has its own biogeographic story; the Antarctic fairy shrimp is perhaps the best example we have of a species that has successfully hitchhiked into and across a part of Antarctica.

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