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Differentiation of dispersive traits under a fluctuating range distribution in *Asellus aquaticus*

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Titel/Title:

Differentiation of dispersive traits under a fluctuating range distribution in *Asellus aquaticus*

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Sammanfattning/Abstract:

Knowledge about dispersion is of utmost importance for understanding populations' reaction to changes in the environment. Expansion of a population range brings with it both spatial sorting and over time, spatial selection. This means that dispersion rates increases over time at the expanding edge. Most studies have so far been performed on continuously expanding populations. This study aims to bring more knowledge about dispersal biology in dynamic systems. I studied dispersal traits in two permanent and two seasonal vegetation habitats of an isopod (*Asellus aquaticus*), for which differentiation between habitat types has previously been shown. I quantified differences in displacement (dispersal rate) and three morphological traits, head angle (body streamline) and leg of the third and seventh pair of legs. Isopods from the seasonal vegetation had higher displacement rates than animals from permanent vegetation. This inclines that mechanisms driving spatial selection in expanding population ranges also exist in dynamic systems. The more streamlined isopods found in seasonal sites further points towards spatial sorting by dispersion capability. Because no effect of permanence was found on leg length and there was no correlation between streamlining and displacement, the higher dispersion among animals from seasonal habitats most likely derives from behavioral differences.

Nyckelord/Keyword:

Asellus aquaticus, Dispersion, Dispersive traits, Habitats, Isopoda, Lake Tåkern, Spatial selection, Vegetation

Content

1 Abstract

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2 Introduction

The fragmentation and loss of natural habitats in modern times makes dispersion important for the preservation of species. Dispersion connects small populations into metapopulations and enables colonization of uninhabited patches (Hanski 1998). Knowledge about evolutionary as well as ecological causes to dispersion is crucial for understanding species' reactions to changes in the environment. It can also give insight into how the geographic distribution influences fitness and how this in turn is affected by heterogeneity in environment (Bowler & Benton 2005).

When a population range expands, sorting of individuals occur based on spatial dispersion. This spatial sorting enhances dispersive traits on the range edge due to assortative mating between individuals with high dispersive traits. Combined with density effects this leads to spatial selection for increase in dispersive traits on the expanding range. Consequently, dispersive capability decreases with distance to the expansion edge (Travis & Dytham 2002, Phillips et al 2008). There is further evidence of rapid adaptations of attributes which enhances dispersion in the invasion front compared to the range core, which likely occurs

due to spatial sorting (Cwynar & MacDonald 1987, Hughes et al 2007, Lindström et al 2013).

In *Asellus aquaticus* evolutionary differentiation can occur over small spatial distances in short time. This is observed in newly developed habitats with possibility for population growth (Hargeby et al 2004), which is crucial for fast evolution (Reznick & Ghalambor 2001). Furthermore, evolutionary change in such circumstances is dependent on heterogeneity in the habitat, which in turn is an important condition for genetic diversity in a population (Hargeby et al 2005).

In lakes where *A. aquaticus* is locally differentiated, the species is common in dense vegetation, but rare in unvegetated areas (Hargeby 1990). It can therefore be assumed that individuals found in locations where permanent vegetation is missing has either new- or recolonized the area after the vegetation has returned. Furthermore, it can be assumed that the range distribution of a population *A. aquaticus* varies with the seasons in environments which houses both permanent and seasonal vegetation.

In this study, I investigated if the differentiation of dispersive traits which is seen under continuous expansion (Lindström et al 2013) also exists when the population range fluctuates over the year. This was done in laboratory with individuals of *A. aquaticus* collected from two different habitats in Lake Tåkern, where there is evidence of differentiation between habitats (Hargeby et al 2004). In each habitat, collection was done from two sites, one with permanent and the other with seasonal vegetation. I expected to find that individuals found in the seasonal vegetation would have higher expression of dispersive traits than individuals found in the permanent vegetation, promoted by spatial sorting.

3 Materials and methods

3.1 Study organism
Asellus aquaticus is a freshwater isopod which lives of fungi and bacteria associated with detritus. It is also known to feed on periphyton (Arakelova 2001). *Asellus aquaticus* is semelparous (reproduce only once before death) in Southern Scandinavia and has one or two generations per year (Økland 1978). However, populations in other regions is known to be iteroparous and reproduce more than once (Maltby 1991). *Asellus aquaticus* occurs in abundance in habitats of both *Phragmites australis* and *Chara tomentosa* (Eroukhmanoff & Svensson 2009). However, in habitats of macrophytes which die off during the winter the density of *A. aquaticus* is low, probably due to the slow colonization (Hargeby 1990).

Migration is not well studied in *A. aquaticus* and there is little information on how movement is related to individual variation in traits such as body size and length of legs. In other arthropods there is evidence for a connection between relative leg length and movement speed (Pearce-Duvet et al 2011) and the same has been found in other taxa during range expansion (Phillips et al 2006). Furthermore there is evidence of fluctuating asymmetry in land living isopods on the ischium and merus, which can arise from either environmental or genetic stress (Vilisics et al 2005).

3.2 Site description

Lake Tåkern is located in the western parts of Östergötland, 58°21´N, 14°5´E and covers an area of 44 km². The lake is eutrophic and was lowered in the 1840s. At the time of the experiment, the average water depth in summer is below 1 m, allowing submerged macrophytes to establish across all open water areas. Along the shoreline emergent vegetation covers roughly 30 % of the total lake area (Hargeby et al 2007). During the last century Lake Tåkern has shifted several times between submerged macrophyte and phytoplankton domination (Blindow et al 1993). A structural shift from macrophyte to phytoplankton occurred in 1995-1997 (Blindow et al 1998). Shortly afterwards the evergreen *Chara tomentosa* returned in discrete patches (Hargeby et al 2004). In recent years more submerged macrophytes, which wither during the winter, has colonized the lake bottom. Hence, during the most recent years there has been a blend of permanent and seasonally vegetated patches in the lake.

3.3 Experiments on displacement

Test animals were collected from Lake Tåkern on the 1st of April 2014 from two habitat groups with two locations respectively, one in permanent vegetation and one nearby, where only seasonal vegetation occurs. Coordinates in SWEREF 99 are shown in Table 1. Isopods were collected with hand nets in both the permanent reed (*Australis phragmites*) habitat and in the seasonally vegetated location nearby. In the permanent stonewort (*Chara tomentosa*) and the seasonally vegetated location isopods were gathered from vegetation, which was collected with rakes.

Table 1 *The four sites where test animals were collected in Lake Tåkern, on April 1:st 2014. Coordinates are in SWEREF 99.*

Coordinates	Permanent habitats		Seasonal habitas	
	Reed	Stonewort	Reed	Stonewort
Easting	E 489326	E 488354	E 489327	E 488381
Northing	N 6466122	N 6466846	N 6466172	N 6466810

Before separation in regard to sex, the test animals where kept two days at 15° C in polypropylene containers with water from Lake Tåkern. All further handling and storing was performed at this temperature. The test animals were kept in light conditions 14 hours and dark conditions 10 hours per day. After separation, the isopods from each location were kept in smaller polypropylene containers which partly consisted of nets instead of walls, inside larger containers. This made all test animals in each larger container share water with each other to minimize bias due to difference between containers regarding water quality or disturbance from pathogens. Each larger container included all four groups from each habitat. The isopods were given food in the form of decaying alder *(Alnus glutinosa)* leaves. Oxygenation was ensured with airpumps connected to diffusers. Each group of test animals was given a number for further studies (Table 2).

Table 2 *Assigned group number for different habitats of* A. aquaticus *and number of test animals used from each site. Collected from Lake Tåkern on April 1st 2014.*

Habitat	Permanent				Seasonal			
	Reed		Stonewort		Reed		Stonewort	
Sex	Males	Females	Males	Females	Males	Females	Males	Females
Group number	1	2	3	4	5	6	7	8
N° test animals	17	25	24	25	12	25	23	25

Test runs were performed in grey polypropylene pipes (2 m in length, 75 mm in diameter), which were cleaved lengthwise (Figure 1). Attached to the ends was transparent polypropylene, sealed with aquarium silicone glue. In order to save the plastic ends from mechanical stress and to ensure stability plastic strips was attached underneath the pipes. The distance from the center was written on the sides, in decimeters with centimeter decimals (Figure 1). The pipes were then placed on a flat surface and filled with boiled sand (Rådasand 0,8-1,2 mm Rådasand AB, Sweden) to such a level that it covered the bottom, approximately 0,5-1 cm in depth. Thereafter the pipes were filled with lake water to a depth of 2,5 cm and left over the night. The water in the pipes was replaced at the start of each test day. All lake water used in test runs had been collected at least 96 hours before use in order to prevent interaction from predatory cues, which have a considerable effect on *Asellus* in both reed and stonewort habitats (Harris 2013).

Figure 1 *Five experimental halfpipes were used for the test runs, filled with Rådasand and water from Lake Tåkern. Cylinders made from polypropylene bottles were used as containers for the test animals before each run.*

The test runs were performed five at a time with immediate reruns making each individual run four times in total in the same pipe. Before the first run each individual was free to move in the pipe for five minutes. Thereafter, it was placed in a cylinder with neither bottom nor top in the center of the pipe for ten minutes before the test run was executed. This was done by carefully lifting the cylinder out of the water. Before each rerun, the last step, with ten minutes in the cylinder, was repeated. Test animals were taken from the eight groups (Table 2) in a systematical order. In the first run pipes one to five corresponded with the same groups. In the next run, group six to two filled the five pipes in the same order. In the third run groups three to seven filled the pipes in the same manner. This system was used continuous until 25 individuals from each group had performed the run. However, none of the male groups contained enough test animals throughout the experiment (Table 2). When a group with no individuals left was supposed to participate in the experiment, that pipe was left empty in the current run.

The test runs were spread over a period of ten workdays. Each day four series of tests were conducted, equaling 20 isopods with four runs each. For each test run the time it took an isopod to travel 90 cm in either direction from the center was

measured. If an isopod did not reach this distance in 15 min, the achieved distance from the center was instead noted.

3.4 Morphological analyses
After the displacement test was done each test animal was photographed alive with a Nikon Coolpix 4500 and was subsequently placed in carbonated water for euthanization. Thereafter, two legs were removed from each isopod and photographed, one from the third and seventh pair of legs, respectively. The test animals were then stored in -20° C to allow for additional photos and potential studies beyond this thesis. In rare cases isopods were only sedated during the incision, and were hence frozen to death.

Using the software ImageJ (Rasband 2013) ten body points were obtained from each test animal for further shape analysis such as body length. The angle between the legs on the first segment and the peak of the head was also measured with the software, this as an approximation of hydrodynamic characteristics (Eroukhmanoff & Svensson 2009). Using the same software, the length for each leg was measured, where ischium, merus and carpus was treated as one composite distance.

3.5 Statistics
The mean square displacement (r^2) is often used as a measure for random walk movements and was used as statistical unit for the dispersion experiment. It is calculated with the equation (1) where (d) equals displacement and (t) equals time.

$$r^2 = \frac{d^2}{t} \qquad (1)$$

Note that in runs where isopods completed the test there was only time that differed in the equation. However, when isopods did not reach the maximum distance only displacement separated them from other test animals that did not travel to the endpoints.

In order to achieve the relative leg length of each leg the equation (2) was used. The length of the three segments is represented as (l) and (b) stands for body length. In statistical analyzes the logarithm (base ten) of achieved relative leg length was used.

$$a = \frac{l}{b} \qquad (2)$$

For each of the four response variables, mean square displacement (MSD), head angle and length of legs number three and seven, an ANCOVA was performed with the logarithm (base 10) of body length as a covariate. The independent variables were habitat permanence (permanent and seasonal, habitat type (reed and stoneworts) and sex, all added as fixed factors.

The effect on mean square displacement from the other response variables were tested with a set of regressions, where the head angle and both relative leg lengths were used as independent factors on MSD, each in separate tests. Because sex showed a significant effect on every variable in the ANCOVA separate regressions were done for both genders.

All statistical tests were conducted in SPSS (IBM 2013) and all significance levels were $\alpha = 0.05$.

4 Results
There was a significant effect of permanence on MSD (Table 3), as animals from the seasonal category had a higher mean of MSD (13.4 % higher) than the permanent category. Gender had a highly significant effect on MSD, where males had a higher mean (38.3 % higher) compared to females. However, there were significant interactions between permanence, habitat and sex.

Habitat showed a significant effect on head angle, as animals from the reed category had a higher mean than the stonewort category. There was also a significant effect of permanence on head angle, as isopods from the seasonal category had a lower mean (1.6 % lower) than the permanent category. Gender had a highly significant effect, where males had a lower mean (5.7 % lower) compared to females. However, there was interaction between habitat and permanence.

Gender had a highly significant effect on 7th relative leg length, as males had a higher mean of relative leg length (28.7 % higher) than females. The effect of gender on 3rd relative leg length was highly significant, as males had a higher mean (7.1 % higher) compared to females.

Table 3 *Summary of four individual ANCOVAs on mean square displacement, head angle and two relative leg lengths as dependent variables, and permanence, habitat and sex as independent factors. The covariate was square body length in all four tests. Degrees of freedom for corrected total were 175 and one for all individual factors and interactions.*

	MSD		Head angle		Rel leg length (3)		Rel leg length (7)	
	F	P	F	P	F	P	F	P
Covariate								
Log Body length	2.33	0.129	2.95	0.088	3.85	0.051	2.85	0.093
Factors								
Permanence	7.60	**0.006**	5.16	**0.024**	0.57	0.451	0.11	0.736
Habitat	0.57	0.451	5.62	**0.019**	2.01	0.158	1.33	0.251
Sex	13.62	**<0.001**	48.45	**<0.001**	23.23	**<0.001**	333.61	**<0.001**
Interactions								
Permanence & Habitat	2.33	0.129	4.37	**0.038**	2.30	0.131	2.71	0.101
Permanence & Sex	1.13	0.289	0.40	0.530	1.67	0.199	0.82	0.368
Habitat & Sex	0.25	0.617	0.02	0.900	0.01	0.933	0.01	0.939
Permanence, Habitat & Sex	5.73	**0.018**	0.07	0.796	0.13	0.721	0.07	0.796

In MSD, the interaction between permanence, habitat and sex resulted from different response among the stonewort males (group three and seven) than the other groups (Figure 2 a,b). In stonewort males the mean MSD was unchanged whereas the mean for MSD was higher in the seasonal category for all other comparisons.

In the morphological trait head angle, stonewort females (group four and eight) had a slightly higher angle in the seasonal compared to the permanent category. In all other cases head angle was lower in the seasonal compared to the permanent group (Figure 2 c,d).

As shown in both Figure 2 and 3, there were differences in response from the variables not mentioned specifically. This can be seen by comparing the gradients of the lines, when not equal, a difference in response is likely the cause.
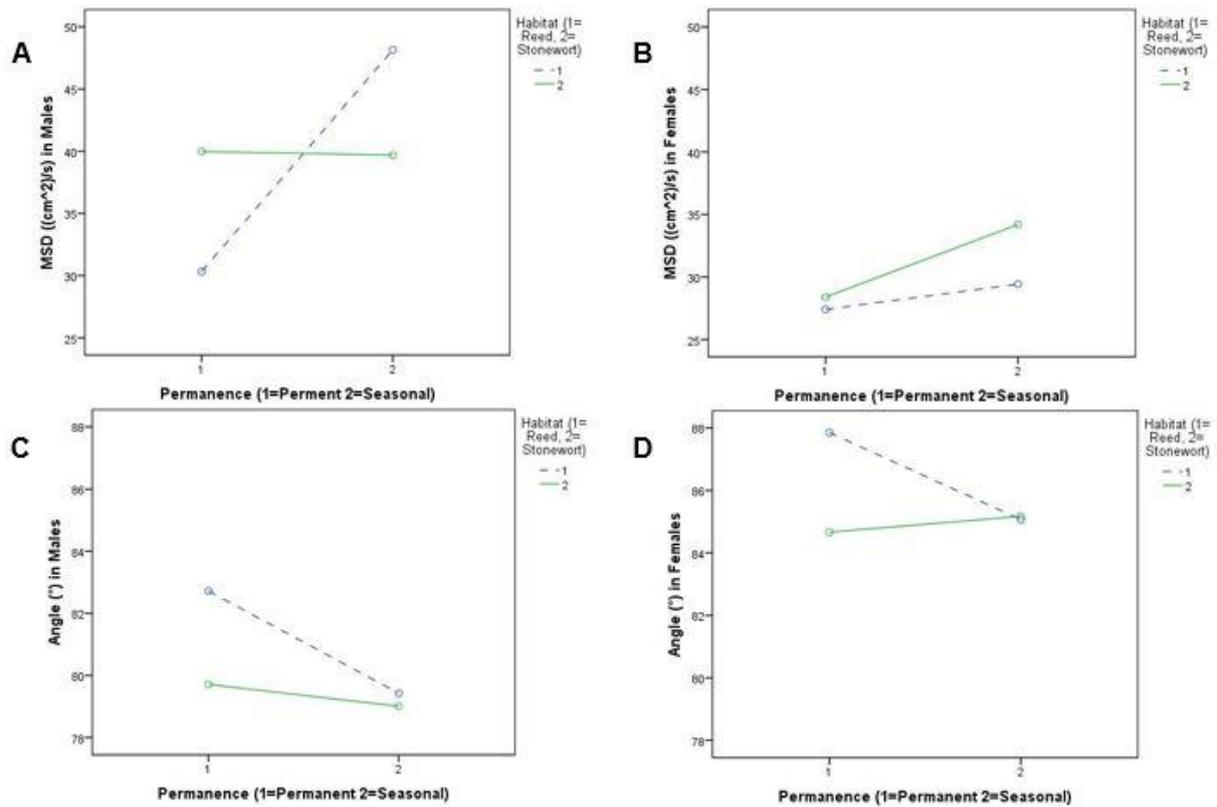
Figure 2 *Interactions between permanence and habitat on mean square displacement (A and B) and head angle (C and D) for males and females separately. Variables showed are in estimated marginal means. Intercepting lines points towards difference in effect from permanence between the habitat groups, thereby contributing to interaction. In the same manner differences in effect from gender can be seen with a comparison across figures.*
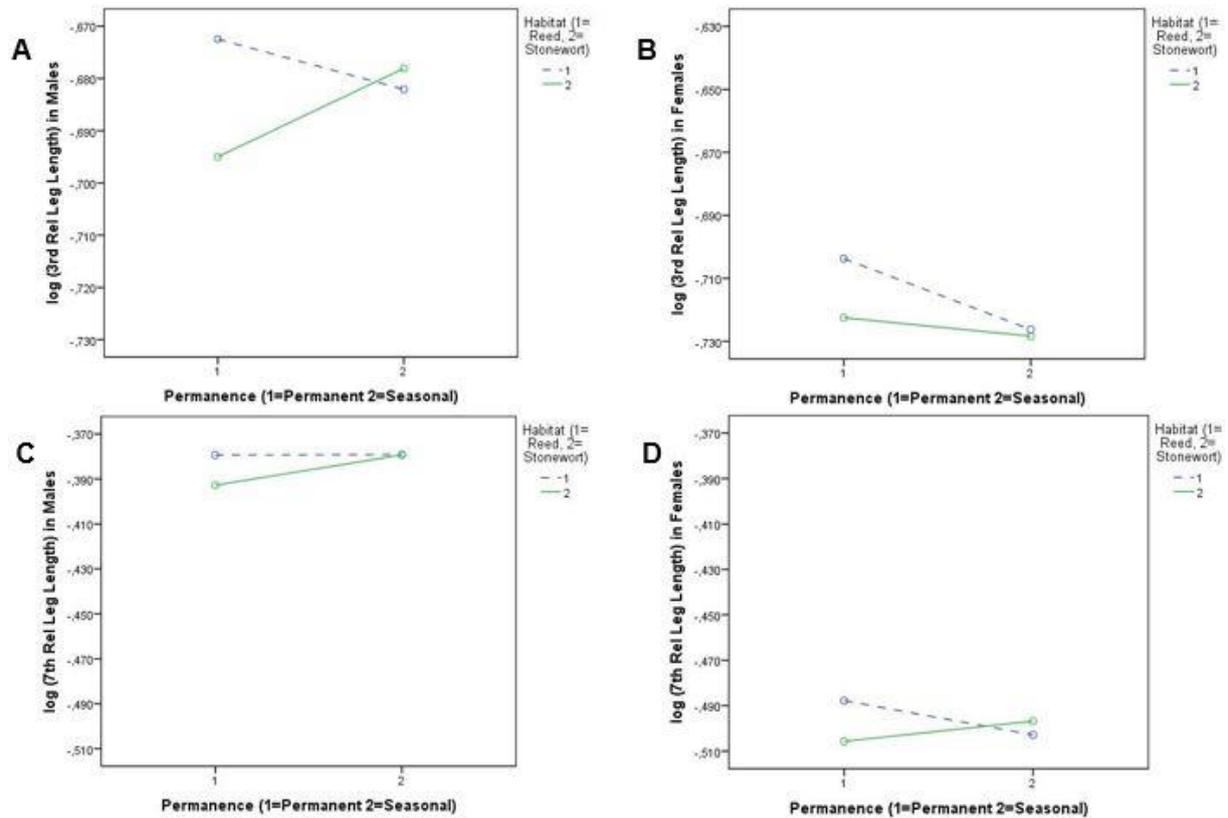
Figure 3 *The effect from permanence and habitat on 3rd relative leg length (A and B) and 7th relative leg length (C and D) for males and females separately. Variables showed are in estimated marginal means. Intercepting lines points towards difference in effect from permanence between the habitat groups, thereby contributing to interaction. In the same manner differences in effect from gender can be seen with a comparison across figures.*

In males, there was a significant correlation between 7th relative leg length and MSD ($R^2 = 0.066$; $P = 0.025$; df = 75) (Figure 4). In all other cases there were no correlation ($P > 0.40$; $R^2 < 0.01$; $df_{males}=75$, $df_{females}=99$).
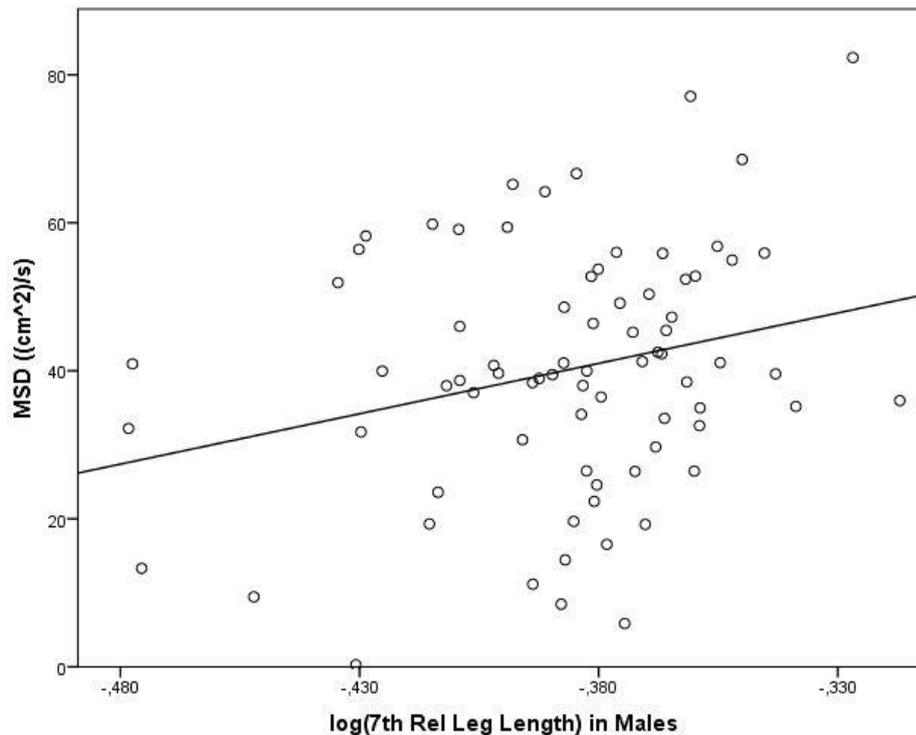
Figure 4 *Relationship between mean square displacement and 7th relative leg length in males shows a positive correlation. The values for relative leg length are logarithmic.*

5 Discussion

5.1 Analysis

The results largely fits with our predictions, thus supporting the notion that spatial selection is important also in this system with a seasonally expanding and retracting range distribution. There was a higher rate of displacement in individuals from seasonal vegetation compared to permanent vegetation. The same mechanism of spatial sorting, seen in continuous expanding populations, seems to appear even when the range distribution is fluctuating. This is based on the assumption that the seasonal sites in dynamic systems can equate the expansion edge in expanding populations. Spatial selection probably occurs, but doubtfully with the acceleration over time seen by Lindström et al (2013), because the offspring in the seasonal vegetation probably needs to reach a permanent habitat in order to survive the winter. Because *A. aquaticus* can be expected to be semelparous and reproduce once or twice a year in the lake (Økland 1978), this means that a maximum of two subsequent generations may reproduce in the seasonal vegetation before finding a permanent patch is a requirement. Because survival against predation increases with habitat complexity (Mattila 1992, Diehl & Kornijów 1998) the seasonal vegetation provides poor shelter and thus reduced survival chances during winter.

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As male isopods are known to be more active than females (Huang & Sih 1990), it was not surprising that they dispersed at a higher rate than females. In line with this reasoning, Bertin et al (2002) propose that males could have characteristics that enhance their movement, especially regarding their legs. My results with higher relative leg length in males fits well with this suggestion. The higher displacement found in males can thus be explained by the higher activity, but Harris et al (2011) shows that males also are more prone to take risks.

The difference in head angle between reed and stonewort habitats contradicted the studies done by Eroukhmanoff & Svensson (2009), where the stonewort isopods had the higher head angle. The difference found between permanent and seasonal sites regarding head angle means that animals found in the seasonal sites require less propulsion force for the same movement speed as the animals with higher angle in the permanent sites (Eroukhmanoff & Svensson 2009). Since males are more active than females the difference between sexes regarding head angle is logical. The lower angle in males means that they probably can travel more cost efficiently.

Since there was no significant effect of permanence on leg length, this indicates that the higher displacement seen in animals from the seasonal sites does not derive from longer legs. There was however a difference in head angle between the permanence categories, which points out a more hydrodynamic body profile in the seasonal sites. As there was no obvious correlation between head angle and displacement it is unlikely that the higher displacement can be explained entirely by the difference in morphology. The higher displacement can likely be explained by differences in behavioral rather than morphological traits. There is no experiment to investigate this statement in this study. However, Barton et al (2012) proposes that behavior which enhances expansion benefits more from selection on an expanding range, than behavior which promotes survival. It is unclear if the same benefits are achieved in dynamic systems.

The lack of significant correlation between displacement and other test variables should not necessary be interpreted such that these variables have no impact on displacement. The displacement experiment in this study likely suffered from measuring on a scale too small and therefore inaccurate estimations might occur (Westerberg et al 2008). It is also important to recognize that the displacement test unlikely was long enough to cope with several behavior modes. This can lead to misleading comparisons as individuals might shift between behaviors and thus over time disperse at completely different rates (Lindström et al 2013). However, the author would like to emphasize, this should not be interpreted as that the significant results are without value. On the contrary, the results largely fit with the predictions, thus supporting the hypothesis that differentiation of dispersive traits occur also in the habitat system with permanent and temporal habitats.

As there are several interactions between factors in the study, the results are rather complex to analyze. In order to secure more firm knowledge about dispersion in dynamic systems further research should probably focus more on one habitat and gender at a time, as differences between habitat and sexes interfere with difference depending on permanence.

5.2 Societal and ethical considerations

The thesis focused on basic research with the intent to bring greater understanding to dispersal biology in dynamic systems. A better understanding of dispersion mechanics in *Asellus* might provide useful insight into how fragmentation as an ecosystem function can be affected, both naturally and artificially. As conclude by Bowler and Benton (2005), dispersal behavior affects how well a population will handle threats such as fragmentation, climate change and invasion of alien species. Thus with further research in connected areas a better understanding of biodiversity might be achieved, which in turn is important for ecosystem services (Balvanera et al 2006).

There are some ethical aspects of the project. During handling and termination there was a strife for as little stress for the test animals as possible, without hampering the scientific result. However, the method to use carbonated water as a mean to kill the animals should probably not be used again if unaltered. Probably, a version with higher concentration would not fail. The fieldwork in Lake Tåkern could disturb the rich birdlife in the area. The fieldwork was limited to a short time and care was taken no to work unnecessarily near colonies, therefore the damage to the birdlife is assumed to be minimal. Permission to work in the area was granted by the county administrative board of Östergötland.

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