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**THE GENERALITY OF ABUNDANCE-ENVIRONMENT RELATIONSHIPS IN
MICROHABITATS: A COMMENT ON LANCASTER AND DOWNES (2009)**

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ABSTRACT

We comment on a criticism of hydraulic preference models and instream habitat models. We provide evidence of the generality of many hydraulic preference models, which supports their use in instream habitat modelling even if the detailed mechanistic causes of the observed preferences are not fully known. We also reply to the assertion that preference models are not based on sound ecological theory. We identify unbalanced use of available knowledge and point out limitations relating to too detailed biological focuses.

KEY WORDS: instream habitat models, preference, niche, ecohydraulics

INTRODUCTION

In their paper "Linking the hydraulic world of individual organisms to ecological processes: putting ecology into ecohydraulics", Lancaster and Downes (2009) (henceforth "L&D") identify limits of hydraulic "preference" models for aquatic organisms (referred to as abundance-environment relationships AERs) and associated instream habitat models (referred to as habitat-based association models HAMs). In particular, they describe 1) some of the complexity of mechanisms that can lead to observed AERs, 2) potential spurious correlations among the environmental variables under study and others, 3) potential interaction with predation and competition and 4) potential effects of the environment on life history traits and population dynamics.

Though we agree with the need to better understand the complex biophysical interactions underpinning AERs, we disagree with the statement that "what HAMs based on AERs are

unlikely ever to do well is estimate or predict changes in population density". We do acknowledge that models are always a simplification, based on a compromise among complexity, relevance and realism. They can always be criticized for not being detailed enough or, on the contrary, being too complex to be of general interest. AERs and HAMs certainly follow this rule. They often have been criticised for not explaining all the mechanisms that lead to plastic density–environment association, or on the contrary for being too detailed for practical management applications (e.g. we cannot study hydraulic preferences of any life-stage at any moment in any stream). However, in responding to L&D we aim to illustrate the generality of many AERs, and therefore their usefulness in stream management even if the detailed mechanistic causes of the observed "preferences" are not fully known. We also reply to the criticism that AERs are not based on sound ecological theory and point out that L&D overuse un-representative examples. Finally, we suggest that the criticisms made of AERs also apply to the "good practice" research examples given by L&D.

MANY AERs ARE REMARKABLY GENERAL

L&D state that "agglomerating data" from comparative AER studies involving multiple sites "may result in a blurred, meaningless scatter of points or a very weak average response of questionable utility or ecological sense". We refute this statement and refer to a number of studies that have analysed observed relationships between animal density and microhabitat variables in several sites on repeated occasions (e.g. fish in France, Lamouroux *et al.*, 1999; invertebrates in small streams in France and Germany, Dolédec *et al.*, 2007; invertebrates and fish in New Zealand, Jowett and Davey, 2007; Jowett *et al.* 2008; invertebrates in large streams in France, Méricoux *et al.*, 2009). Concerning macroinvertebrates, the studies of

Dolédec *et al.* (2007) and Méricoux *et al.* (2009) provide a general picture of the degree of variation in AERs among sites and sampling occasions: many taxa, defined at different biological levels, have repeatable AERs at sites on rivers with different size, geology, water quality, community composition and other ecological characteristics; other taxa (examples in L&D and Méricoux *et al.*, 2009) have highly variable AERs. Specifically, of 151 taxa studied by Dolédec *et al.* (2007), 14 taxa have a generalised (site-averaged) AER that explains >50% of their log-density variations among microhabitats (within sites), and 40 taxa have AERs that explain >30% of their density variations. Two thirds of the variability in density explained by site-specific AERs are accounted for by a site-averaged, generalised AER in small German streams (Dolédec *et al.*, 2007), as well as in large French streams (Méricoux *et al.*, 2009).

Figure 1 shows an example of a generalised AER for a rheophilic macroinvertebrate taxon that has a high transferability. Note that Figure 1 does not show the best example available, as "only" 37% of the density variation among microhabitats are explained by the generalised *Baetis* AER (this increases to 80% for some taxa in Dolédec *et al.*, 2007). Jowett and Davey (2007) also showed that generalised additive models explained about 50% of the abundance variation of benthic invertebrates taxa in 6 New Zealand rivers. Other examples of transferability can be found for fish. For example, Lamouroux *et al.* (1999) showed, for 24 species in six streams, that microhabitats with hydraulic conditions corresponding to high fish densities on average (according to generalised AERs) did contain more fish than other microhabitats in about 60% of the streams, and were never avoided in a given stream.

Assemblages at the local scale of microhabitats (e.g., sampled by Surbers) potentially depend on social behaviour, gregarism, predation, competition, physical history of the microhabitat, particle size and many other environmental drivers. In these conditions, the fact that

hydraulics have been demonstrated to explain >50% of density variations among microhabitats within multiple sites with contrasting characteristics is remarkable, and suggests the existence of strong causal mechanisms even if the details of these mechanisms are not fully known and deserve to be studied.

L&D cite M rigoux and Dol dec (2004) as an example of a single-stream study (the Ard che river in France) that assumes a limited tolerance of species and is not supported by empirical data. This assertion is strongly contradicted by another paper they cite (Dol dec *et al.*, 2007), where the most remarkable result is the consistency of AERs between the Ard che river in France (data from M rigoux and Dol dec, 2004) and a group of 12 German rivers, i.e. in streams of different countries independently surveyed by various teams at different seasons (Figure 2). The study of M rigoux *et al.* (2009) even goes further by showing consistency among preferences in small German and large French streams. Therefore, the study of M rigoux and Dol dec (2004) is not a study made "over a short gradient" (e.g., it spans nearly the whole range of shear stresses shown in Figure 1) but, on the contrary, a study that generated AERs of general relevance in independent contexts.

It is also surprising that Dol dec *et al.* (2007) and Statzner *et al.* (2008) are cited as papers that consider AERs as invariant, because the first paper essentially quantifies the variation in AERs across sites and dates, and the second paper does not address the subject at all. More generally, deriving generalised AERs does not imply that species have optimum, non-plastic, invariant AERs. On the contrary, studying the relevance of generalised AERs contributes to quantifying this plasticity. It is a prerequisite for understanding the causes of AERs variability and for identifying which of these models are appropriate for generic predictions.

THEORETICAL BASIS AND PREDICTIVE POWER OF AERs

AERs are firmly rooted in the niche concept that strongly influenced pioneer stream ecologists (Statzner, 2008). It has long been acknowledged that an ecological niche has multiple, interacting dimensions, and many of L&D's criticisms are merely restating this. For stream organisms, however, we also know that physical constraints typically play a predominant role in comparison to other niche dimensions. Early interest focused on velocity and, combining laboratory experiments and field observations nicely illustrated the ecological response of a blackfly across a velocity gradient (Figure 3). Thanks to ecohydraulics, we know today that the response of a filter-feeding blackfly species could be related to other hydraulic factors such as boundary layer conditions near its body, turbulence near its filter fans, transport rates of fine particles serving as food, lift and drag (e.g. Nikora, 2009). Finally, we also know that the response pattern of a specific larval blackfly potentially varies with its age/size (i.e. AER assessments at the family level as in L&D's Figure 2 are often scattered). Consequently, unravelling the "causal basis of the pattern" (L&D) shown in our Figure 3 would be extremely complex.

Instead of trying to explain all variation, AERs for lotic invertebrates rely on general responses illustrated in our Figure 3: both flow decreases and increases beyond "normal" cause drift of most taxa (Dorier and Vaillant, 1953/54; Minshall and Winger, 1968), presumably because of respiratory problems at low flow (Ruttner, 1926; Ambühl, 1959) and of unbearable forces at high flow (Dorier and Vaillant, 1953/54). Between this minimum and maximum of the hydraulic niche dimension, specific instars (size groups) should have an optimum that varies across specific size groups and species. However, according to Liebig's "law of the minimum", one would not expect such hydraulic AER patterns when other factors

are too extreme. By citing an example from a stream site with extremely low slope and oxygen concentrations (extreme at the sediment surface: $<1 \text{ mg.l}^{-1}$; see Lancaster *et al.*, 2009) as an example of the limits of AERs, L&D have selected an untypical stream environment for which typically valid AERs must be obviously irrelevant.

Criticizing the predictive power of AERs and HAMs is easy because this criticism applies to most ecological models (Peters, 1991). Poor predictability is partly due to the complexity of ecological processes that potentially interfere in the niche of organisms and the difficulty in obtaining sound long-term datasets for testing actual population and community responses to environmental changes. However, there has been some evidence so far of successful predictions of density variations among sites, or before-after flow restoration, based on AERs/HAMs (Fuchs, 1994; Lamouroux *et al.*, 2002, 2006; Jowett and Biggs, 2008). For example, Fuchs (1994) used season- and size-specific AERs of invertebrate species from the nearest sites to predict 49% of the variation ($n=15$) in observed relative changes of population sizes after increasing the regulated discharge. Lamouroux *et al.* (2002) could partly predict associations between fish community traits and hydraulics in North American reaches from AERs observed at the microhabitat scale in France, i.e. using models built at another scale and in another continent, with distinct fish species.

AERs and HAMs may be correlative but they make sense in terms of biological trait adaptation to flow, e.g. the benefits of being small, streamlined, filter-feeders or attached in stressful habitats are interpretable (Lamouroux *et al.* 2004, Blanck *et al.* 2007). The consistency of niche-based AERs in different contexts, their actual validations and their physically-based interpretations support the idea that they reflect general causal relationships. Of course, there is some potential for developing more general AERs that are based on robust

physical principles, such as those suggested by Von Gelei (1928). His seminal paper discussed how Reynolds number and body shape (e.g. degree of streamlining) of an aquatic organism affect flow separation from its body and, in turn, the drag it experiences. The use of such variables in AERs has some potential because these variables can explain, similarly for different taxa, variation in flow separation (its location relative to body length; Statzner and Holm, 1989), fish drag (Sagnes and Statzner, 2009) and drift rates (Statzner and Borchardt, 1994). These examples suggest that putting hydraulics into ecohydraulics is at least as important as putting ecology into it.

L&D'S CRITICISMS OF AERs APPLY ALSO TO THEIR "EXAMPLES OF GOOD PRACTICE"

We support the importance of studying more detailed mechanisms such as the bioenergetics of filter-feeding insects or egg supply and their relations to flow (L&D's "examples of good practice"). These studies can identify key processes influencing population dynamics and biomechanical patterns of general relevance. However, the two examples provided by L&D in support of this point could be criticised, as AERs, for neglecting the complexity of the ecological processes or on the contrary, being too complex for use in management.

In their discussion of flow effects on feeding rate, growth rate and survival of filter-feeders, L&D focus on simuliids and hydropsychids. For the latter, we know that (1) net-building rates (proportion of filter nets to larvae) vary between 0-1 across species, seasons and/or instars; (2) net-building larvae that never build a net generally develop normally; and (3) beyond enabling filter-feeding, the nets have potentially four other functions for its builder (see Statzner and Bretschko, 1998). Increased growth rates can also generate higher drag, higher damage by

drifting particles and higher predation by fish, i.e. the effects of flow on feeding rate, growth and survival are not as direct as stated by L&D. Furthermore, relations between flow and feeding efficiency are likely highly variable due to additional complications cited by L&D (e.g. intraspecific competition for space, individual phenotypic plasticity of life history traits, behaviour) and others (e.g. thermal regime and its physiological effects, potential barriers to nutriment sources, interspecific predation, bed disturbance frequency and other dynamic hydraulic patterns). In this context, a modelled relationship between flow and feeding efficiency would be necessarily a simplification, partly based on correlation.

We suggest that L&D's discussion of egg supply is also unconvincing. Since the International Biological Programme we know that egg supply is generally not a bottleneck stage for extant riverine invertebrate populations (e.g. Edmondson and Winberg, 1971). Providing an example considered by L&D in their Figure 4, the mortality from egg supply to terrestrial adult (i.e. of aquatic stages) was 91% in the *Baetis (rhodani)* population of a German stream (Wernecke and Zwick, 1992). In addition, L&D's statement that the physical and hydraulic environment is very important to egg supply because egg masses are found on a minority of emergent rocks is not supported by two of the three examples illustrated in their Figure 4, where the relative frequency of velocities available and used by *Apsilochorema* and *Baetis* hardly differ. Finally, assessments of consequences of egg supply for populations would require egg identifications at the species level, which are notoriously difficult (note that the egg data in L&D's Figure 4 are for genera, not for species).

Studies at higher level of detail are useful for identifying the main mechanisms causing the observed preferences. However, ecohydraulics involve such a large variety of biological and physical processes that building predictive models of the effects of e.g., climate change on

populations (an objective cited by L&D) involving all contributing mechanisms is unrealistic at this time. Moreover, using the conventional tools of hydraulics and fluid mechanics for modelling the local hydraulic history undergone by individuals faces the complexity of both biological and hydraulic processes. In particular, constructing a general model for relating discharge management to the diversity of point hydraulics around individuals remains out of scope of predictive management tools. The 'good practice examples' described by L&D could be interesting pieces of research, but they would need generalisation, replication and validation before being of any use in practical stream management.

It is ultimately the predictive power of different models that will decide what is the most useful level of detail for building predictive management tools. In our view, some AERs represent a good compromise between parsimony, generality and ecological relevance for being useful in predictive approaches. For example, some simuliids and hydropsychids have strong, repeated, and interpretable association with high shear stresses, in small and large streams of different countries (e.g. Figure 2), and we cannot see any major reasons why these AERs should not be used to guide flow management in rivers. The test of several predictive approaches will also indicate which details of population dynamics are worth being included in HAMs. Meanwhile, it is incorrect to oppose HAMs and dynamic models, because most HAM applications are interpreted in a dynamic context, and HAMs based on AERs are sometimes explicitly used as part of population dynamic models (Statzner and Borchardt, 1994; Capra et al., 2003).

CONCLUSIONS

In summary, we think that L&D go much too far in their criticism of AERs. They use counterexamples without describing the general picture concerning the generality of AERs. They make a subjective use of the papers they cite and a too simplistic presentation of AERs as static, purely correlative models that are disconnected from theory and have little generality. We hope that this comment provides elements that will balance the debate on ecohydraulic tools. As any model, AERs and HAMs are necessarily based on simplifications of the real world. Their use requires warnings and they would benefit from a better knowledge of biophysical interactions. Nevertheless, many niche-based AERs show a strong repeatability, under different environmental and biological contexts, that clearly justifies their use in predictive instream habitat studies and management.

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FIGURE LEGENDS

Figure 1. Density of a mayfly (*Baetis rhodani*) as a function of bottom shear stress (FST hemisphere number of Statzner and Müller, 1989) in Surbers collected in 19 surveys made in 8 independent German streams at different seasons. The label in each frame indicates the river code and the sampling month. The bold line is an average model fit (common shape in all surveys); the thin line is a stream-specific one. Data are from Dolédec *et al.* (2007); methods are those of Dolédec *et al.* (2007) and Méricoux *et al.* (2009).

Figure 2. The average "preferred" bottom shear stress in the Ardèche river in France (data from Méricoux and Dolédec, 2004) predicts the average "preferred" bottom shear stress observed in German streams (data from Dolédec *et al.* 2007), for 20 taxa involved in both studies ($R^2 = 0.68$, $P < 0.001$). Some taxa, defined at different biological levels, are indicated as labels. Redrawn from Dolédec *et al.* (2007), where methods are detailed.

Figure 3. Population loss by drift and density on artificial substrates (all relative to their maximum) of larval blackflies (*Simulium ornatum*) across a velocity gradient (in the field, for available conditions) (redrawn after data in Phillipson, 1956).

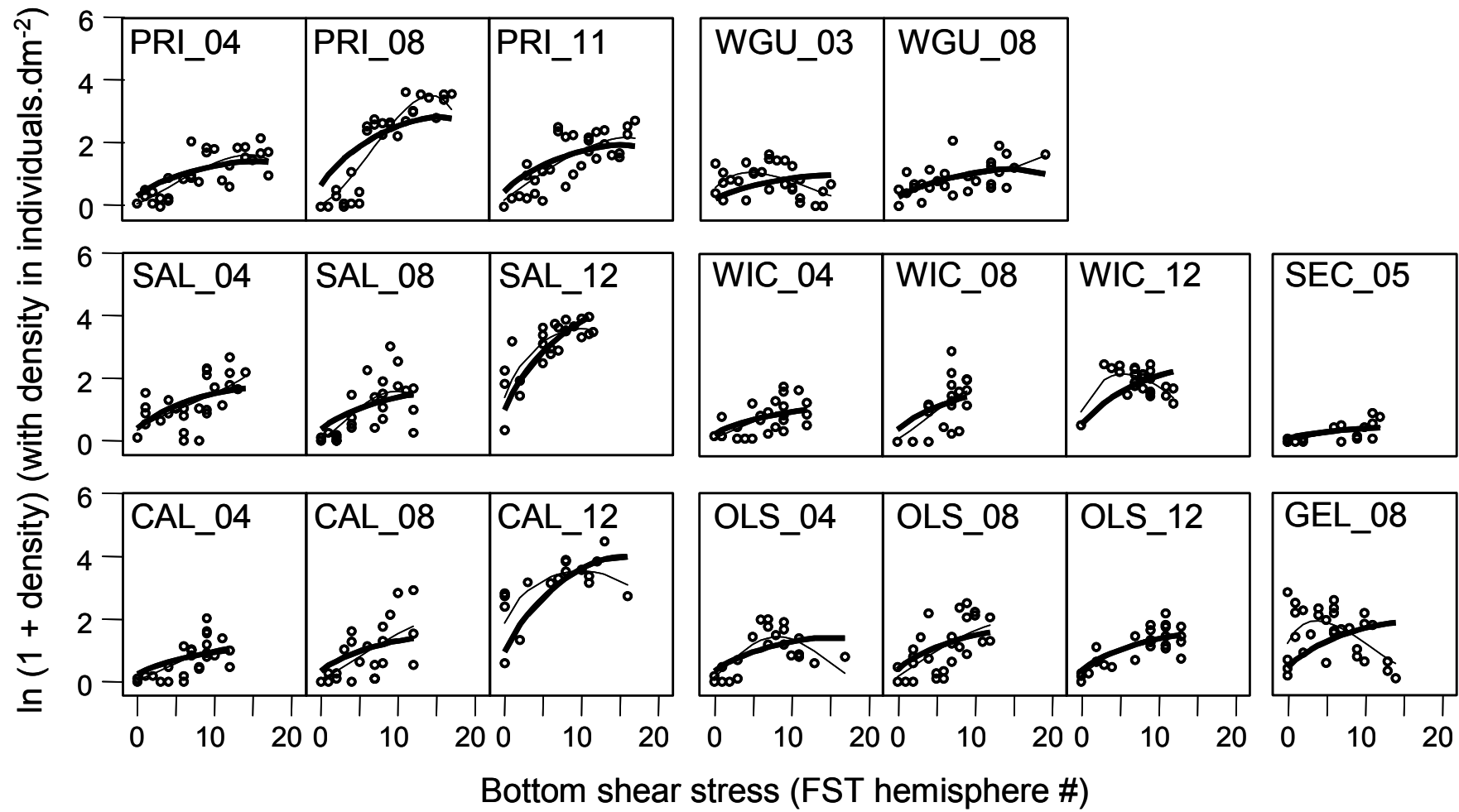


Figure 1. Lamouroux *et al.*

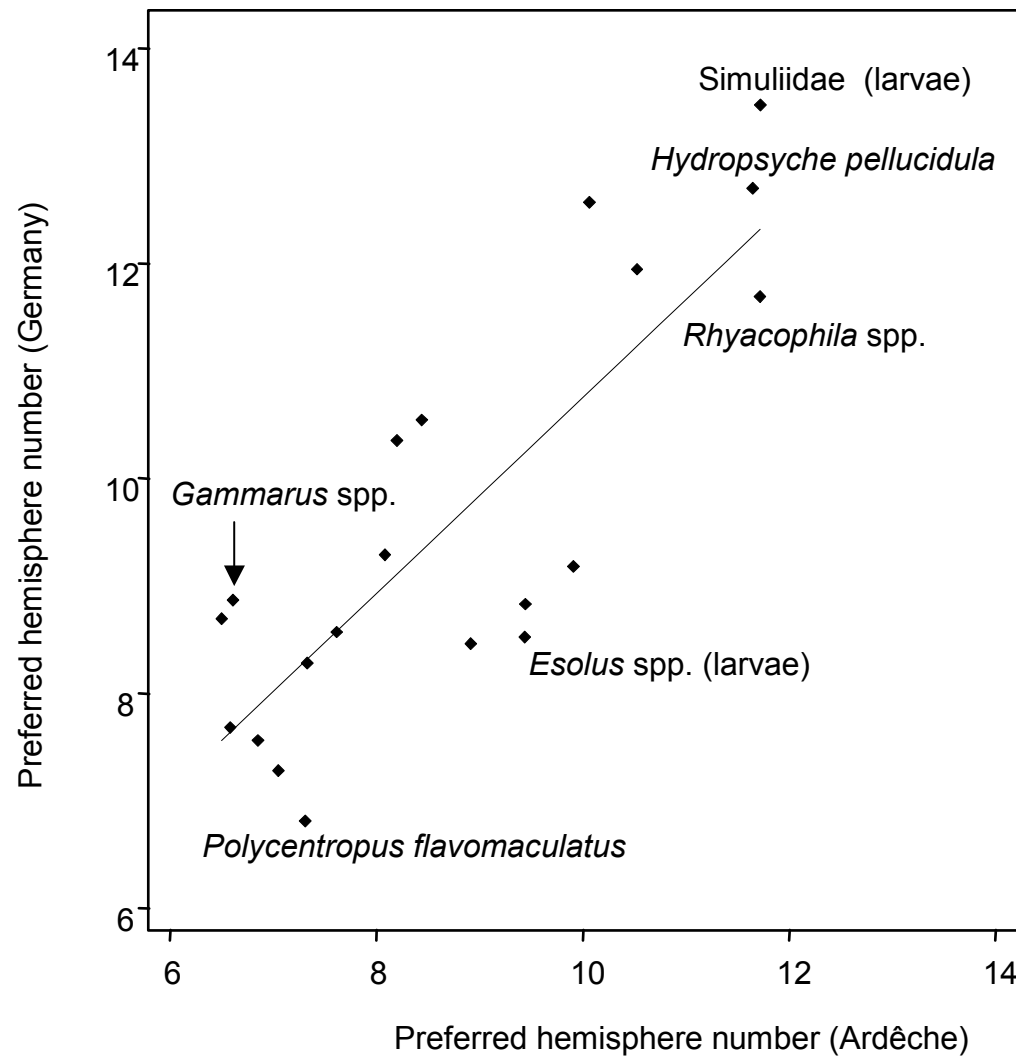


Figure 2. Lamouroux *et al.*

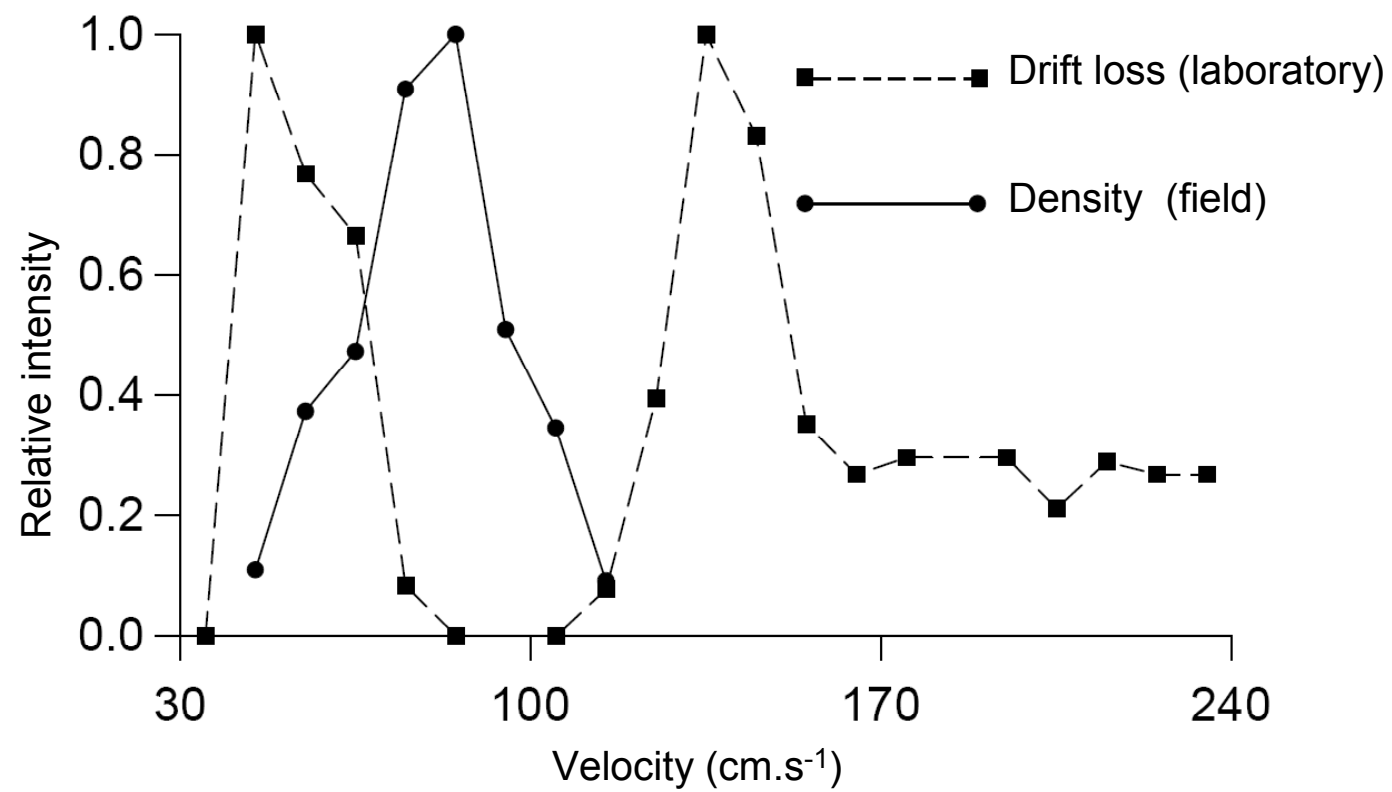


Figure 3. Lamouroux *et al.*