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Potential effects of Global Climate Change on survival and growth of brown

trout (*Salmo trutta* L.): consequences of temperature and floods on young stages

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Abstract

Global Climate Change will increase precipitations in the temperate and Northern coast of Europe during winter and spring. In riverine ecosystems, precipitations affect strongly the discharge of running waters and, thus, it is predicted that streams will face more severe floods. Additionally, air and water temperature will increase all over the world. These new environmental conditions can alter the phenology of species and predator/prey interactions. Newborns of brown trout (*Salmo trutta* L.) start their exogenous feeding in March/April. This stage is a critical step as individuals undergo huge physiological and behavioral changes. To allow a good development and a high survival rate, preys have to be abundant, particularly during early ontogenesis when fish are most vulnerable to food scarcity and predation. In this thesis, experiments in controlled-environment were conducted to estimate the effect of water velocity on the drift of preferred prey taxa for salmonids and to understand the effect of temperature on the metabolism of alevins facing starvation. Experiments in semi-natural conditions were set up to better understand the effects of floods on invertebrate communities and on survival, behavior and growth of first-feeding alevins. Our data support that floods affect trout differently depending on when they start feeding (early or late spring) and the availability of prey in their environment.

Résumé

Le changement climatique devrait induire une augmentation des précipitations pendant l'hiver et le printemps dans les régions tempérées et la côte nord de l'Europe. Dans les écosystèmes fluviaux, les précipitations affectent fortement le débit des eaux courantes et les rivières subiront des crues plus sévères. En outre, la température de l'air et de l'eau augmenteront à travers le monde. Ces nouvelles conditions environnementales vont avoir des conséquences sur la phénologie des espèces et les interactions prédateurs/proies. Les jeunes truites fario (*Salmo trutta* L.) commencent leur alimentation exogène en mars/avril. Cette étape critique de leur cycle de vie induit d'importants changements aussi bien physiologiques que comportementaux. Pour permettre un bon développement des individus et un taux de survie élevé, les proies doivent être disponibles et abondantes, en particulier à ce moment de l'ontogénèse où les juvéniles sont vulnérables au manque de nourriture et à la prédation. Des expériences en milieux contrôlés ont été menées pour quantifier la sensibilité à la dérive de trois espèces d'invertébrés couramment consommées par les salmonidés en fonction de différentes modalités de vitesses de courant et pour évaluer l'effet de la température sur le métabolisme d'alevins en situation de jeûne. Des expériences en milieu semi-naturel ont été mises en place pour mieux comprendre les effets d'une crue sur la communauté d'invertébrés et sur la survie, le comportement et la croissance des alevins en première alimentation. Il apparaît que la crue impacte différemment les truites en fonction du moment de la saison auquel elles commencent à s'alimenter (au début ou à la fin du printemps) et de la productivité du système.

Resumen

Se espera que el cambio climático aumente las precipitaciones durante el invierno y la primavera en las regiones templadas y en la costa norte de Europa. En los ecosistemas fluviales, las precipitaciones influyen directamente al caudal y, por tanto, se espera que los ríos sufran inundaciones más severas. Además, la temperatura del aire y del agua aumentarán en todo el mundo. Estas nuevas condiciones ambientales afectarán a la fenología de las especies y a las interacciones depredador-presa. Los individuos jóvenes de la trucha común (*Salmo trutta* L.) comienzan su alimentación exógena en marzo/abril. Esta etapa crítica en su ciclo de vida conlleva importantes cambios fisiológicos y de comportamiento. Con el fin de permitir un buen desarrollo de los individuos y una alta tasa de supervivencia las presas deben ser abundantes, especialmente durante las primeras etapas, que son más vulnerables a la escasez de alimentos y la depredación. En esta tesis se llevaron a cabo experimentos controlados para cuantificar la sensibilidad de tres especies de invertebrados comúnmente consumidos por los salmónidos a la velocidad del agua, y, para evaluar el efecto de la temperatura sobre el metabolismo de los alevines en ayuno. Además, con otros experimentos en ambientes semi-naturales se ha tratado de comprender mejor los efectos de las inundaciones en las comunidades de invertebrados y en la supervivencia, comportamiento y crecimiento de los alevines en el comienzo de la alimentación exógena. Parece que las inundaciones afectan a la trucha de forma diferente dependiendo de cuándo llegan a esta fase (a principios o finales de la primavera) y la disponibilidad de presas en su ambiente.

Laburpena

Klima-aldaketaren aurreikuspenen arabera eskualde epeletan eta Europako iparraldeko kostaldean prezipitazioak handitu egingo dira neguan eta udaberrian. Prezipitazioek zuzenean eragiten dute ibaien emarien igoera, eta hala, ibaiek uholde gogorragoak jasango dituztela aurreikusten da. Horrez gain, airearen eta uraren tenperaturak mundu osoan egingo du gora. Ingurumen baldintza berri hauek espezieen fenologia eta harrapari/harrapakinen arteko elkarrekintzetan aldaketak sortuko dituzte. Amuarrain arruntak (*Salmo trutta* L.) martxo/apirilean hasten dira elikadura exogenoa erakusten. Bizitza-zikloaren etapa kritiko honek aldaketa garrantzitsuak dakartza fisiologian eta jokabidean. Aleen garapen egokia eta biziraupen-tasa handiak lortzeko, harrapakinak ugaria izan behar du, ontogeniaren lehen urratsetan batik bat, errekurtso eskasia eta predazioaren aurrean zaurgarrienak diren momentua bait da. Tesi honetan salmonidoek kontsumitzen dituzten hiru makroornogabe espezieek ur abiaduradi dioten sentsibilitatea estimatu zen. Bestalde, beste experimetu batean baraualdian zeuden alebinetan tenperaturak metabolismoan zuen eragina neurtu zen. Gainera, ornogabe komunitateetan eta elikatze exogenoan hasi berriak ziren alebinen biziraupenean, portaeran eta hazkundean uholdeek zuten eragina estimatu zen baldintza semi-naturaletan gauzatu ziren experimentuetan. Gure datuen arabera uholdeek eragin ezberdina dute amuarrainetan elikatzen hasten diren garaiaren arabera (udaberri hasieran edo bukaeran) eta inguruneak eskaintzen dien harapakin ugaritasunaren arabera.

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General discussion

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State of the art

Growing in running waters

Streams are classified according to channel geomorphology (size, width, depth) and volume of water discharged (Horton 1945; Strahler 1954, 1957). The smallest streams, namely first order streams, are located at the steepest parts of the watershed. The union of two first-order streams results in a second-order stream, and so on to sea; a sequence that entails important changes in functioning. Flowing waters have four distinct sources of energy (Allan & Castillo 2007; Giller & Malmqvist 1998). The first source comes from plants that use solar radiation *via* photosynthesis to produce instream (autochthonous) primary production. The other three sources of energy are imported into the running water system from the surrounding valley (allochthonous): coarse particulate organic matter ($CPOM - \emptyset > 1$ mm), fine particulate organic matter ($FPOM - 0.5 \, \mu m < \emptyset < 1$ mm) and dissolved organic matter ($DOM - \emptyset < 0.5 \, \mu m$) coming from the riparian vegetation or banks in the river. Then, autochthonous and allochthonous energy, in the form of organic matter, is transferred to consumers. The contribution of each source of energy varies along the river sections and changes the invertebrate community structure longitudinally, in a sequence that is known as the "River Continuum Concept" (RCC – Vannote et al. 1980). In headwater low order streams, most of the time dense canopies reduce the intensity of light and thus the amount of primary production. Then energy mainly comes from leaf inputs and invertebrate communities are principally composed by detritivores, mainly shredders. In mid-order streams, light conditions are improved and favour algal and macrophyte growth, stimulating the presence of grazers and scrapers. Finally, the scarce benthic light under the turbid waters of high order streams limit primary production again, and so, CPOM coming from the upstream parts are degraded in FPOM and consumed by the very abundant collectors. Then, instream energy availability is closely related to the light availability and to the transport of materials, which regulate primary (instream or in riversides) and secondary production (*i.e.* biomass production of both invertebrates and fish).

The perpetuation of species involves the individuals to grow, complete their developmental cycle and reproduce. They choose their habitat to maximize access to food, shelter or partners. Throughout the development their needs change and they may be forced to move from one habitat to another to optimise fitness. These habitat changes over the life of an organism are called "ontogenetic shifts" (Werner & Gilliam 1984). In nature, growth and survival of fish depend on several factors. As they are ectotherms, water temperature governs many physiological processes such as respiration, excretion and growth. The seasonality, the

abundance and the quality of food, within the constraints of the thermal regime, cause significant variability in fish production over time and space (Benke et al. 1988; Huryn 1996; Thompson & Beauchamp 2016) and appear as one of the main drivers that limit fish growth (Wildhaber & Lamberson 2004). As they grow, mortality risks are reduced. The number of potential predators that can feed on fish diminishes (Quinn & Peterson 1996; Sogard 1997), and they also become better competitors and swimmers (Young 2003), which guarantee their access to food (Ryer & Olla 1996), shelter (Harwood et al. 2002; Orpwood et al. 2003). However, individuals have to face events, which can slow down their growth and threaten their survival.

The Match-Mismatch Hypothesis

During the developmental cycle of species, some stages are more vulnerable to food scarcity. For example, the breeding period of the Atlantic puffin (*Fratercula arctica*) is synchronized with the peak of herring abundance, which are their main food items (Durant et al. 2003, 2005). The synchronization between prey availability and predator requirements increase the survival rate of chicks, while a mismatch would produce a weaker cohort and population. Hjort (1914) firstly suggested that mortality of marine fishes (cod, haddock and Norwegian spring herring) was probably due to food scarcity during larval and young fry stages, which were the most critical periods in fish development. In addition, Cushing (1969) noticed that the spawning timing of marine fishes (herring, plaice and cod) allowed the hatching of the eggs and then, the development of larvae when the zooplankton production was high. Indeed, releasing larvae during the spring or autumn peaks in plankton production resulted in high survival rate for the three species of interest (Cushing 1990).

Following these observations on terrestrial and marine species, the "Match-Mismatch Hypothesis" (MMH) emerged and states that critical periods during which predators need energy occur simultaneously with the peak availability of prey. This way, recruitment of predators is maximised. On the contrary, the higher the mismatch between food requirements and food availability, the lower the growth, survival and recruitment of predators (Durant et al. 2007; Woodward et al. 2010; Bewick et al. 2016). Mortality induced by prey scarcity is expected to be higher for fish larvae than for late stages because (*i*) larvae are not able to withstand prolonged fasting periods and (*ii*) smaller larvae are more susceptible to predation (Dou et al. 2005; Yokota et al. 2016). The mismatch between predator requirements and food availability can be due to the occurrence of disturbance, but, as far as we know, the MMH has never been tested in freshwater systems.

In Europe, projections for 2100 from the Intergovernmental Panel on Climate Change (IPCC) and from several studies modelling the consequences of Global Climate Change (GCC) on the precipitation patterns, forecast an increase in the magnitude and frequency of extreme hydrological events (Lehner et al. 2006; Dankers & Feyen 2008; IPCC 2014) as well as a modification of events timing (Blöschl et al. 2017). In southern Europe, average seasonal precipitations is predicted to increase from 5 to 40% during winter (from December to February – Figure 1), whereas the decrease of precipitation will induce low flows the rest of the year. In central and northern Europe, precipitations are expected to drastically increase during winter but also in spring (from December to May). It can also be noted that the mean discharge of rivers are predicted to increase outside periods of extreme flood. On the contrary, the summer season (from June to August) will be more arid and droughts will be more extreme almost everywhere in Europe. Additionally, climate scenarios forecast an air temperature increase of 3°C, which will induce an elevation of the river water temperature between 0.8 and 1.6°C (van Vliet et al. 2013; Bal et al. 2014).
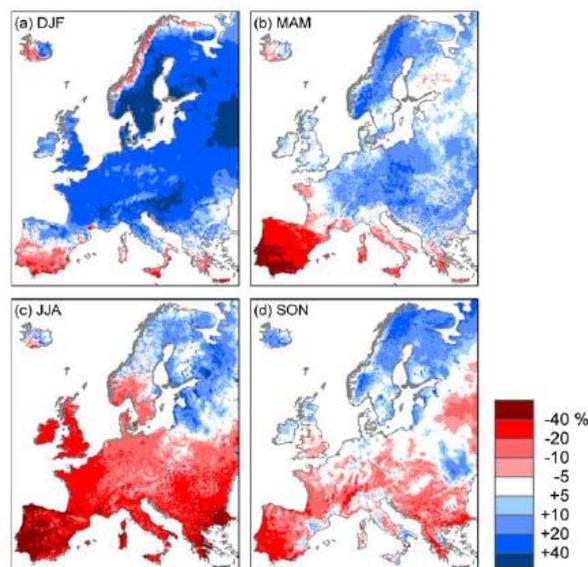
Figure 1 Predictions from Dankers & Feyen (2008) about the consequences of Global Climate Change in the average seasonal precipitation in (a) winter, (b) spring, (c) summer and (d) autumn in Europe.

In rivers, the increase of precipitations will increase the occurrence and the intensity of winter and spring floods. These new flow and temperature patterns can threaten the dynamic equilibrium of species. In particular, links between consumers and resources, which are often the result of a long co-evolution, might be weakened (Woodward 2009; Perkins et al. 2010;

Woodward et al. 2010). Consequently, the increase in stochastic events due to GCC may threaten the synchronization of species phenology and peaks in prey abundance may be shifted (advanced or delayed). Predators may then face higher mortality rates due to starvation during critical periods.

Brown trout (*Salmo trutta* L.) as a case of study

Repartition, ecological requirements and life cycle

Brown trout is indigenous to Europe, North Africa and western Asia (Klemetsen et al. 2003). It is present in many regions of Europe from north of Iceland, Scandinavia and Russia to South of the Mediterranean Sea. After many introductions, brown trout has now reached a world-wide distribution and is present in various biogeographic contexts (Elliott 1994). It is an important economical resource for professional and recreational fishing and it is frequently used as tourist attraction (Aas et al. 2000; Butler et al. 2009).

At the river scale, brown trout prefer upstream sections of rivers (Huet 1949, 1954), with well-oxygenated waters and neutral pH. Flow plays a major role in the distribution of individuals, supply of drifting invertebrates, redd oxygenation (Baglinière & Maisse 1991). They choose complex substrates that provide shelters from water velocity, predators and visual isolation between congeners (Armstrong et al. 2003). Lastly, brown trout is adapted to cool and quite narrow water temperature conditions (Elliott 1994).

Reproduction takes place from November to December, females dig a nest in the gravel, drop their eggs immediately fertilised by males and they cover the clutch with sediment. Eggs grow under the protection of gravel and they hatch around February, at 420 degree-days (*i.e.* the sum of the mean daily water temperature from the egg-laying). New-born alevins stay under the gravel, they feed on their yolk reserves. From March to April, when their yolk sac is almost exhausted (around 730 degree-days) alevins leave the protection of the redd and emerge in the water column to search for prey (Roussel & Bardonnet 2002). After spending at least one year in the river, juveniles can spend all their life in running waters ("riverine trout"), migrate to lake ("lake trout") or migrate to sea after physiological adaptations (smoltification; "sea trout" – Figure 2).
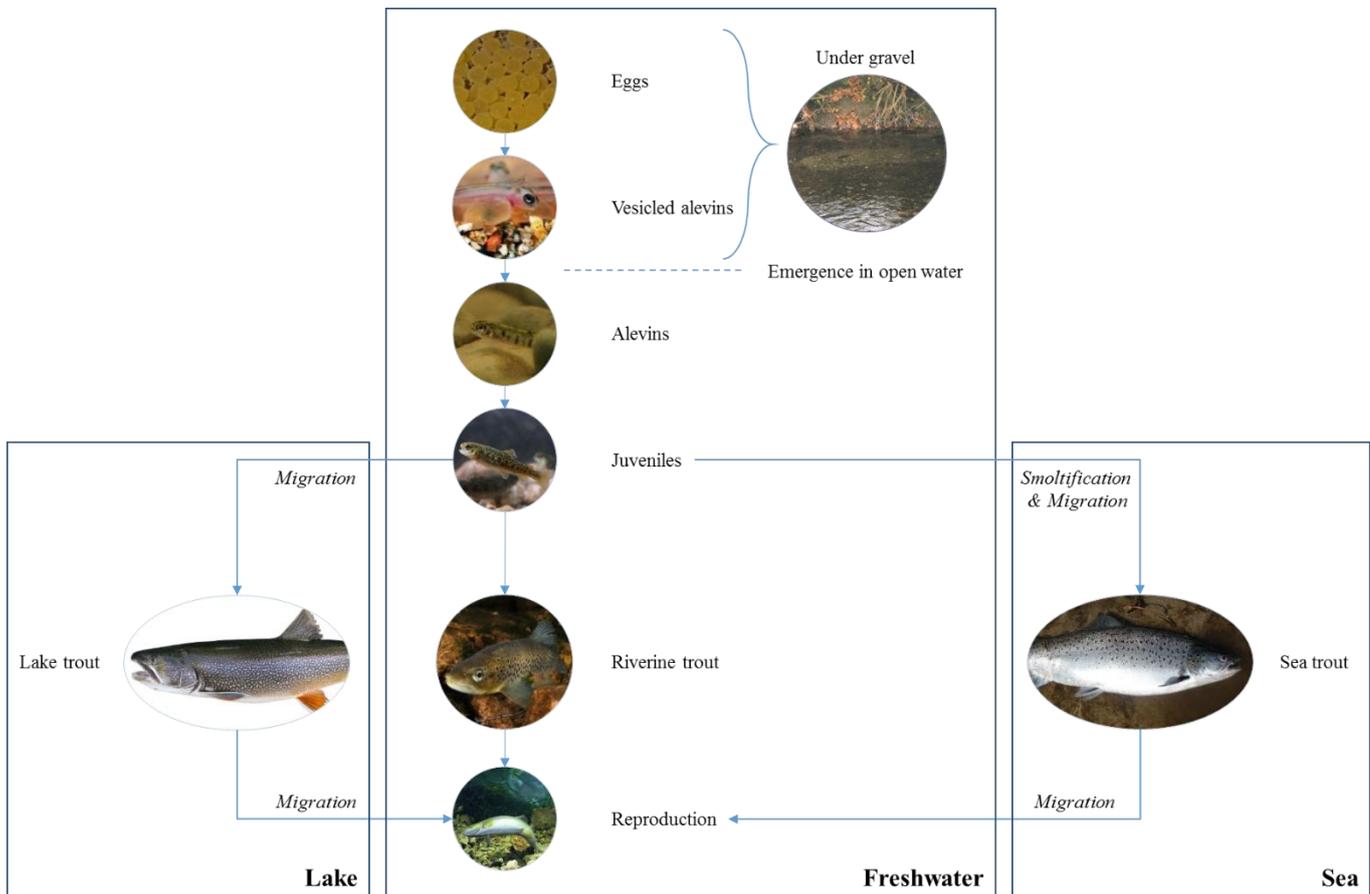
Figure 2 Life cycle of brown trout (Salmo trutta) according to life stages and to the different environments that the species is capable to use for growing (lake, freshwater and sea).

Emergence as a crucial step

The move from the under-gravel compartment to water column is called "emergence" and it is considered as a critical time for survival in brown trout with mortality rates as high as 90% (Elliott 1989). Alevins undergo huge behavioural and physiological changes (Einum & Fleming 2000; Skoglund & Barlaup 2006; Kennedy et al. 2008) and they must adapt quickly to a radically different environment. When they emerge, their yolk sac is almost exhausted and they shift to an exogenous feeding, which implies metabolic changes (Mennigen et al. 2013) and the establishment of the processes of digestion, absorption and assimilation (Dabrowski 1984). In addition to physiological changes, emergence involves behavioural modifications. Alevins need to maintain their position in the water column and catch prey that drift in water. Salmonids are territorial animals and a social hierarchy is established the week following emergence (Héland 1999). Alevins compete with congeners (conspecifics from the same clutch and those from surrounding redds) to access to the best hunting spots. They are "sit-and-wait" hunters (Elliott 1967; Cada et al. 1987; Giroux et al. 2000): they defend small territories (0.1–0.2 m² – Grant et al. 1998) close to shelters and near fast-flowing water that provide high quantity of prey. This strategy allows alevins to minimize their energetic expenditures while energy input is maximized by a large supply of food in the drift. These stations are energetically favourable

(Fausch 1984) and are generally chosen by dominant individuals (Jenkins 1969; Fausch 1984; Grant & Kramer 1990). The intensity of the competition depends greatly on the density of alevins. According to Elliott (1989), density exerts a selective pressure during 20-30 days after emergence. Under high density, the scarcity of favourable habitat and/or feeding resource would diminish the growth and then survival of alevins (Figure 3 – Elliott 1989; Milner et al. 2003).
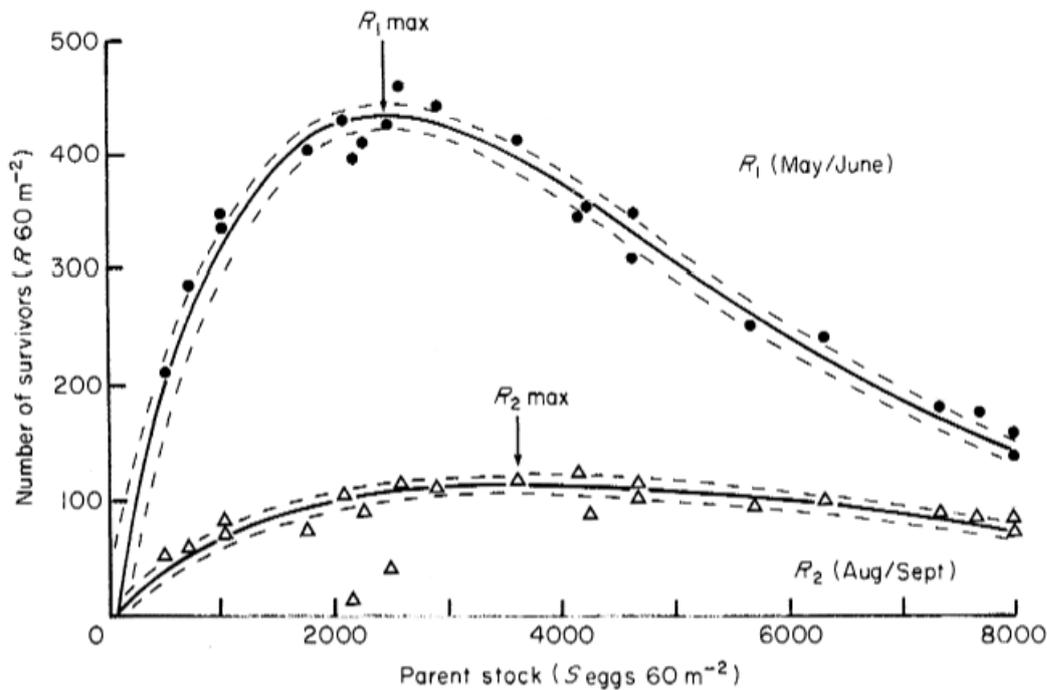
Figure 3 Relationship between parent stock (S eggs per 60 m²) and number of survivors (R fish per 60 m²) in May/June (black circles), August/September (empty triangles) – modified from Elliott 1989.

The timing of emergence influences density of alevins and depends on temperature, date of adult spawning and quantity of energy allocated by females to eggs (Armstrong & Nislow 2006; Régnier et al. 2013). Early emergence give access to the best hunting spots but fish are more vulnerable to predation and to hydrological events such as large floods (Einum & Fleming 2000). Late emerging alevins mingle with early emerging survivors and alevin densities may be high. This can decrease the predation risk of alevins by piscivore fish due to a dilution effect (Sogard 1997; Alvarez & Nicieza 2003) but intensify competition (Skoglund et al. 2011). Moreover, prey availability increases throughout spring, which should tend to favour alevins emerging later. First moments of salmonid life are crucial for growth and affect directly life history traits, strength of the cohort and population dynamics (Bacon et al. 2005; Wysujack et

al. 2009; Jonsson & Jonsson 2014). Then, understanding key factors acting on growth and survival of alevins is of main importance to improve our understanding on brown trout population functioning (Elliott 1986).

Diet of *Salmo trutta*

In open waters, brown trout (alevins and juveniles) feed mainly on "macroinvertebrates", which are organisms living in/on the top layer of river bed (Tachet et al. 2010) and larger than 0.5 mm at their adult stage. Macroinvertebrates are of main importance in ecosystem processes: they contribute to the processing of allochthonous and autochthonous organic carbon, influence periphyton growth and represent the main feeding resource for many fish and birds living near rivers (Quinn & Hickey 1990; Wallace & Webster 1996; Malmqvist 2002). Stream macroinvertebrates spend their larval stage in freshwaters, while the adult stage takes place in terrestrial systems after a nymphal transformation but some species (such as Mollusca, Crustacea, Oligochaeta and some Coleoptera) spend their entire life cycle in rivers. Macroinvertebrates colonize new habitats by drifting from upstream sources, crawling/swimming from adjacent substrates (including the hyporheic habitat) or adult flying (Mackay 1992). Their instream distribution and abundance depend on a variety environmental factors (Townsend et al. 2003). At the watershed scale, altitude, local climate, topography, geology and catchment vegetation drive the assemblage of invertebrates (Winterbourn 1981; Li et al. 2012). At the river scale, flow directly affects aquatic communities by influencing water quality, food sources, species interactions and the availability of diverse/heterogeneous habitats (Jowett & Richardson 1990; Quinn & Hickey 1990). Water physico-chemistry (temperature, pH, dissolved oxygen concentration) and nutrient availability can also heavily impact the survival, reproduction and growth of invertebrates (Stewart et al. 2000; Rawi et al. 2014).

Brown trout feed mainly on "drifting" aquatic larvae of invertebrates, which are carried by the current. However, brown trout exhibit flexible behaviour (Allen 1951; Ringler 1985; Waters 1988) and can adapt their hunting mode to maximize their energetic gain (Optimal Foraging Theory – OFT; Pyke et al. 1977). They can search prey in the benthos (Ware 1972) or they can pick up terrestrial invertebrates at the water surface (Dahl & Greenberg 1996; Huryn 1996; Nakano et al. 1999). The main factor driving trout prey selection is prey size. Salmonids are gap-limited predators (Sánchez-Hernández et al. 2011) and their access to food increases as the size of their mouth and oesophagus increases. Gut content analyses of newly emerged alevins revealed that prey were selected up to 0.50 mm width even if prey up to 2 mm width could be consumed (Bozek et al. 1994; Domagała et al. 2014) and between 2 and 5 mm length

(Wankowski 1989; Hubert & Rhodes 1992; Keeley & Grant 2001). Another important factor in prey selection is the morphological and behavioural features of invertebrates (Poff et al. 2006). According to these traits, the probability to be captured by a fish differs among taxa. Rader (1997) broadly reviewed traits affecting the availability of invertebrates for drift-feeding fish and all traits related to the propensity of invertebrates to drift are of main importance. Invertebrates intentionally drifting or those easily dislodged by the water current are more likely to be preyed. Moreover, flow exposure depends on the use of the habitat and shelters (Negishi & Richardson 2006; Fuller et al. 2010): invertebrates inhabiting the hyporheic zone are less susceptible to be carried away by the current than invertebrates living at the surface of stones (Ware 1972). The mobility (*i.e.* sessile, attached, crawling or swimming) and the shape (*i.e.* streamlined, cylindrical, dorsoventrally-flattened or spherical) of invertebrates also influence their probability to be washed by the flow as the drag force exerted by the water on individuals depends on their length, width and height (Naman et al. 2016; Schülting et al. 2016). However, the critical factor remains the abundance of the taxon in the system. An abundant taxon, prone to drift, is highly available for fish (Crespin de Billy & Usseglio-Polatera 2002).

Considering the catchability, drift propensity, abundance, energetic profitability of prey and size limitation of salmonid predators, Rader (1997) ranked first the Baetidae family (Order: Ephemeroptera), second the Simuliidae family (Order: Diptera) and third the Chironomidae family (Order: Diptera). Next, the most available prey were from the Ephemeroptera order (*i.e.* Heptageneidae, Ephemerellidae, Leptophlebiidae and Siphonuridae), and Crustacea (Amphipoda). Many researchers confirmed these findings and showed that Baetidae, Simuliidae and Chironomidae larvae were the most important food items in gut contents of brown trout in different geographical areas (McCormack 1962; Elliott 1967; Fahy 1980; Vignes & Heland 1995; Sánchez-Hernández et al. 2011 – Figure 4) and provided over 80% of the energetic inputs of new-borns alevins (Sánchez-Hernández et al. 2012).

Figure 4 Invertebrates most available and consumed by drift-feeding fish, including brown trout alevins. From left to right: Baetidae, Simuliidae and Chironomidae families. Photo from: http://lifeinfreshwater.net.

High discharge and the biota

The increase of discharge rises the scouring force of water on the bottom, called shear stress, and displaces the organisms downstream, which in turn alters the composition of instream communities (Leigh et al. 2015). The tight link between the discharge regime and macroinvertebrates has been described by many researchers. The optimal range of water velocities for invertebrates varies between 0.1 m s^{-1} and 0.6 m s^{-1}. Flow velocities higher than 0.7 m s^{-1} are not considered suitable for most macroinvertebrates (Gore et al. 2001; Li et al. 2009; Horta et al. 2009; Shearer et al. 2015).

In rivers, "hydropeaking" refers to frequent discharges pulses generated by hydroelectric power generation (Bratrich et al. 2004; Bretschko & Moog 1990; Bruno et al. 2013) and several studies showed that hydropeaking causes an increase in the number of macroinvertebrate drifting and a reduction of macroinvertebrate biomass and abundance in the benthos (Moog 1993; Céréghino & Lavandier 1998; Céréghino et al. 2002; Bruno et al. 2013; Miller & Judson 2014). Similarly, natural extremely large floods can reduce invertebrate abundances between 15 and 90%, while invertebrate diversity is reduced by 70% or not at all affected (Melo et al. 2003; Argerich et al. 2004; Mesa 2010). McMullen & Lytle (2012) conducted a meta-analysis for the link between flood events and changes in invertebrate communities with 41 studies spread across the world. Despite the differences in river type and regional climate, all these studies concluded that the total abundance of invertebrates as well as the abundance of the major groups of invertebrates significantly decrease immediately after floods. Moderate flow events have also been responsible for the reduction of invertebrate abundance and diversity by 90% and 25%, respectively (Theodoropoulos et al. 2017).

In brown trout, critical water velocities beyond which fish cannot maintain their position are 0.25 m s^{-1} for recently emerged alevins (body length around 3 cm – Heggenes & Traaen 1988; Bardonnet & Héland 1994) and 0.7 m s^{-1} for adults (around 21 cm – Heggenes 1988). High water velocities can alter recruitment (*i.e.* the juveniles incorporating the population) by

destroying redds, displacing individuals (Seegrist & Gard 1972; Wenger et al. 2011) or diminishing the abundance of suitable microhabitats for feeding and sheltering (Lobón-Cerviá & Mortensen 2005). Temporal variations in water velocity are known to limit survival and growth rates of the youngest juveniles (Lagarrigue et al. 2002; Korman et al. 2011). Lobón-Cerviá (2004; 2005) highlighted the importance of river discharge at the time of emergence and its influence on the population structure over the years. Indeed, year-to-year variation in river discharge at the time of emergence consistently matched recruitment rates, survival rates of mean cohort size and abundance of spawners. This phenomenon has been described for a variety of populations across the European range of brown trout (Elliott et al. 1997; Jensen & Johnsen 1999; Mäki-Petäys et al. 1999; Cattanéo et al. 2002, 2003). Similarly, numerous introduced populations across geographical (climatic) North American regions appear to be constrained by discharge variations (Strange et al. 1992; Nehring & Anderson 1993; Nuhfer et al. 1994; Latterell et al. 1998). Elwood & Waters (1969) suggested that declines in invertebrate populations caused by floods could reduce the food availability for fish causing an apparent decrease in their growth. However, it is difficult to disentangle the relative importance of these factors (*i.e.* diminution in habitat or trophic availability) in the mortality of alevins.

Synthesis and main objectives of this work

In brown trout, alevins emerge in spring, which currently matches with the increase in abundance of invertebrates in the drift (O'Hop & Wallace 1983; Romaniszyn et al. 2007; Leung et al. 2009) after the usually low abundances in temperate areas in winter (Brittain & Eikeland 1988). Besides, literature results seem to underscore a negative effect of hydrological events on both fish survival and growth. Because growth is highly density-dependant in salmonids (Jenkins et al. 1999; Vøllestad et al. 2002) one can suppose that the mechanism acting on 0^+ cohort following spates is related to low food availability (the Match-Mismatch Hypothesis), and/or suitable habitat availability. In this thesis, we carried out experiments which should help assessing to what extend Global Climate Change and more specifically the awaited increase in both spring temperature and precipitations might affect the post-emergence survival and growth of trout in relation to food shortage.
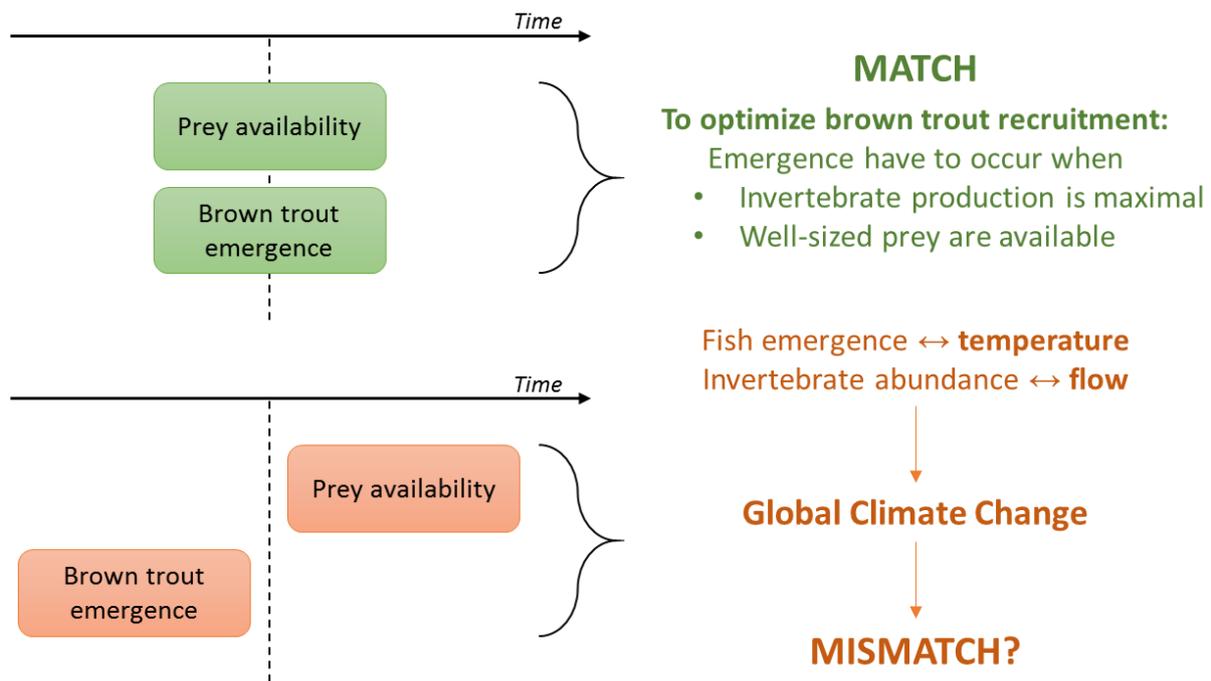
Figure 5 Invertebrates & brown trout: a Match-Mismatch Hypothesis case? Actually, prey availability matches with brown trout emergence (in green) but flow and temperature conditions should be modified by Global Climate Change and delayed prey availability inducing a decrease in brown trout recruitments (in orange).

This manuscript is composed of four chapters. The first chapter, based on an experimental study, investigates the drift propensity of three invertebrate taxa (*Baetis*, *Simulium* and *Chironomus*), which form the bulk of the diet of young salmonids. The second chapter, also conducted in a controlled environment, examines the metabolic pathways of just-emerged alevins facing starvation or a delayed first-feeding at 8 and 11°C. The third chapter relies on an experiment conducted in a semi-natural environment and tries to shed light on the consequences of an artificial flood on the invertebrates and on the survival, growth and behaviour of young trout at high density. The fourth chapter describes the consequences of a simulated flood on the invertebrate community and on the survival, growth and diet of trout alevins at low density. The last part of this manuscript draws a general discussion and proposes some hypotheses and future research pathways about the effect of Global Climate Change on young stages of salmonids.

Chapter I Drift of invertebrates: effects of taxa, water velocity, gravel bed quality and body size

Study context

In research areas focusing on drift-feeding fish, their growth is predicted from foraging and bioenergetic models. The Net Rate of Energy Intake of fish (NREI) is usually based on temperature and food availability (Hayes et al. 2000; Laliberte et al. 2016). Food availability is directly related to the density of drifting invertebrates and to water velocity. The increase in water velocity increases the invertebrate probability of being dislodged from the benthos and then, the number of drifting invertebrates (Brooker & Hemsworth 1978). However, Hayes et al. (2007) and Leung et al. (2009) emphasized that no studies provided an accurate estimation of the entry rate of invertebrates in the drift, which conditions the pertinence of the models. Moreover, Elliott (1971) investigated the distance travelled by invertebrates releasing them in running waters and he highlighted that an increase in water velocity carried the invertebrates further. Although this information is valuable for improving fish bioenergetic models, very few drift studies have attempted to predict invertebrate entry rate. To better understand the effect of floods on the food availability of salmonids, it is necessary to begin by understanding the response of invertebrates and their propensity to drift when facing water at various velocities.

Furthermore, the nature of the substrate is of prime importance. Stability of the gravel bed refers to its resistance to displacement and is generally proportional to particle size (Giller & Malmqvist 1998). Then, large particles increase the stability of the gravel bed, provide safe microenvironments and diminish accidental drift due to the dislodgment of invertebrates (Cobb et al. 1992). Number of shelters available for invertebrates depends on the number of interstices in the gravel bed, their size and the size of invertebrates (St Pierre & Kovalenko 2014).

In this experiment, we aimed to evaluate the drift propensity of three invertebrate taxa chosen because of their significant contribution to the diet of salmonid alevins: *Baetis* sp., *Simulium* sp. and *Chironomus* sp.. The variation of the drifting propensity was estimated in six indoor channels according to two environmental factors (water velocity and gravel bed quality) and a biotic factor (size of individuals).

Comparison of the propensity to drift for three invertebrate taxa: a laboratory study

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ABSTRACT

Invertebrate drift is an important ecological process but factors affecting the downstream displacement of invertebrates are difficult to appraise. The influence of water velocity on drift entry rates is still unclear and has rarely been quantified. In this study, we investigated the drift propensity of *Baetis*, *Simulium* and *Chironomus*. In experimental channels, invertebrates were submitted to low, moderate and high water velocities (14 cm s^{-1}, 30 cm s^{-1} and 40 cm s^{-1}) in either fine or coarse gravel beds. The drift was monitored for 24h to evaluate the effects of water velocity, gravel bed quality and invertebrate size on drift. Gravel bed quality had no effect. Small *Simulium* and *Chironomus* drifted more than larger ones, and drift was only positively related to water velocity for *Chironomus*. Accordingly, we presume that *Baetis* and *Simulium* were not constrained by the experimental conditions and drifted actively while *Chironomus* drifted passively.

Key words: invertebrates; modelling; water velocity; gravel bed quality; head capsule width; season.

Introduction

Invertebrate drift is defined as the downstream displacement of organisms and it is an important ecological process in lotic systems (Waters, 1965; Brittain & Eikeland, 1988). Drift contributes to the dispersal of invertebrate species across the water network, allows connection between habitats and facilitates recolonization processes. James et al. (2008) differentiate two drift categories: passive drift with animals unintentionally entering the water column and active drift with animals intentionally entering the water column.

Drift rate highly depends on abiotic (*i.e.* water chemistry – Hay et al., 2008, quantity of food – Ciborowski, 1983) and biotic (*i.e.* density of organisms – Lehmkuhl & Anderson, 1972; Walton et al., 1977, predation avoidance – Skinner, 1985; Sagar & Glova, 1992) factors and to determine the effect of each is extremely challenging. In addition, taxa respond differently according to their morphology, behaviour and ecology (Poff & Ward, 1991).

Many studies have attempted to investigate the effect of water velocity on invertebrate drift rate. The force exerted by the water on the river bed is called "shear stress" (Giller & Malmqvist, 1998; Vericat et al., 2008) and erodes mineral and biotic particles. The increase in water velocity within the channel increases the shear stress which then increases the risk of dislodgment and the passive transport of organisms downstream. Gibbins et al. (2007) observed the active drift of invertebrates up to a shear stress of 9 dynes cm^{-2} (1 dyne cm^{-2} = 1 Newton m^{-2}) and above this threshold, drift was mainly passive due to the displacement of the gravel. All sheltered invertebrates are inevitably carried away by the current when the gravel bed is scoured. High shear stress mobilises substrate and fine particles and results in a patchwork of both scoured and infilled stream beds (Carling, 1987; Lake, 2000; Matthaei & Townsend, 2000).

High water velocities recorded during extreme flow events increase passive drift and the number of drifting invertebrates (Bruno et al., 2016; Radford & Hartland-Rowe, 1971), with reductions in the abundance of benthic invertebrates ranging from 14 to 95% depending on the magnitude of the event (Matthaei et al., 1997; Nislow et al., 2002; Robinson et al., 2004). However, Theodoropoulos et al. (2017) highlighted the lack of studies that examined the response of freshwater communities to medium water velocities (*i.e.* outside flood periods) and Hayes et al. (2007) go further by pointing out that the entry rate of invertebrates in the drift has yet to be quantified.

Recently, Naman et al. (2016) investigated the response of invertebrates to flow disturbance (from 8 cm s^{-1} to 28 cm s^{-1}) according to channel architecture (flat *vs* concave channels) and taxa. The drifting community was comprised of a caddisfly (*Micrasema* sp.) and several taxa of Chironomidae, which for the most part, drifted passively. For the other drifting taxa, drift was primarily active. The shear stress exerted by the water was equal to 5 dynes cm^{-2} and not enough to dislodge invertebrates.

The quality of the gravel bed, especially the size of the particles, plays an important role by providing invertebrates with hydraulic refuges to avoid being dislodged. Results from field

studies failed to separate the effect of water velocity, depth and substratum quality on passive drift of invertebrates because to date, assessments have been done at the river scale (Lancaster, 1999, 2000). Most data stemming from studies that examined the role of specific habitat parameters on invertebrate drift were drawn from experiments under controlled conditions and showed a higher drift rate in small gravel compared to cobble for caddisflies, mayflies (Holomuzki & Biggs, 2003) and stoneflies (Long et al., 2011) when submitted to spates. According to these results, the size of the interstices, linked to invertebrate size, could play an important role in the availability of hydraulic refugia.

In the present work we focus on the drift of three invertebrate taxa that have different habitat preferences and locomotor behaviour: *Baetis* sp., *Simulium* sp. and *Chironomus* sp.. They are abundant in riverine ecosystems and they contribute significantly to the diet of drift-feeding fish (Sánchez-Hernández et al., 2011). In experimental channels we manipulated the size of the benthic insterstices using different sized substrates. We also considered the size of invertebrates. The interstice size-body interaction has rarely been related to drift propensity at the intra-specific level. Thus, the present study aims to quantify the propensity to drift according to taxa, water velocity, gravel bed quality and invertebrate size. We specifically tested the following hypotheses: 1) free swimming *Baetis* should actively drift more than *Simulium* (attached to the substrate with a suction cup) and *Chironomus* (buried under the substrate), 2) an increase in the water velocity should induce passive drift and increase the drift probability of invertebrates, 3) gravel size should mitigate passive drift with large particles diminishing drift probability of invertebrates, 4) large individuals should passively drift more than small ones due to scarcer shelter opportunities.

Material and Methods

Invertebrate collection

We collected invertebrates from two tributaries of the Nivelle River near Saint-Pée-sur-Nivelle (43°21' N, 1°33' W), on the 9th and the 10th of March and on the 19th and the 20th of October 2015. Baetids (*Baetis* sp.) were sampled from the Lapitxuri Brook, a pristine headwater stream. Simuliids (*Simulium* sp.) were sampled downstream from the spillway of a lake, in a fast-flowing brook characterised by a high percentage of fine sediment. Chironomids (*Chironomus* sp.) were purchased from Grebil (Arry, France). After collection, all invertebrates were kept in containers with aerated water at a constant temperature (*ca*. 13 ºC). Rocks with biofilm and conditioned leaves collected in the field were added to give them food and refuge until the start of the experiment, a few days later.

The experiments were conducted in 6 indoor channels (L: 150 cm, W: 10 cm and H: 12 cm) that were continuously fed in parallel by water pumped from a large outdoor reservoir (3000 m^3) filled with Nivelle River water. The water from the reservoir passed through a sand filter in order to remove most invertebrates, though we still recovered some small cyclops, oligochaetes and chironomids during the experiment. At this point, the only risk of confusion between the "experimental invertebrates" and the "natural invertebrates" concerned chironomids, but the larger size and the red colour of the reared taxon (*Chironomus* sp.) made it easy to separate wild from experimental animals. After the sand filter, water was sent to a 25 m^3 reservoir and pumped to a small reservoir (0.5 m^3) that fed by gravity the six experimental channels. The water level in the small reservoir was kept constant through an overflow. Water temperature followed natural changes, since water came from the outdoor reservoir and was registered every 15 min using a temperature logger (mini logger IIT, Vemco). Mean water temperature was 12.2ºC (± 0.37, SD) in March and 14.7ºC (± 0.50) in October. Light was controlled to mimic natural day and night rhythms. The lit period was chosen to match the natural photoperiod, and 30 min of progressive change in light levels were programmed to produce a 30 min period of dusk at 19:00 in March and 19:30 in October, and dawn at 6:30 in March and 7:30 in October. This results in quite similar L:D durations (12:11 in March and 11.5:11.5 in October).

Two types of gravel beds were created: a "fine" gravel bed (2-4 mm: 33%; 4-8 mm: 34%; 8-16 mm: 33%) and a "coarse" gravel bed (2-4 mm: 25%; 8-16mm: 50%; 20-31.5mm: 25%). Channels were filled to a depth of 3 cm for one gravel type, resulting in 3 fine and 3 coarse channels. Velocities were measured with a mini-velocimeter laid directly on the substratum (Schiltknecht, MiniWater®20 – Table 1, measure depth: 11 mm above the substratum). Three different flow levels were applied to both fine and coarse gravel channels: "low flow" (0.2 l s^{-1} ~ 14.3 cm s^{-1}), "medium flow" (4 times increase, 0.8 l s^{-1} ~ 29.8 cm s^{-1}), "high flow" (8 times increase, 1.6 l s^{-1} ~ 39.6 cm s^{-1}).

Experiments began at 9:00 and lasted for 27 hours. Between 9:00 and 10:00, 50 individuals from each taxon were added to each channel (no flow). A stepwise increase in non-scouring flow was carried out for one hour to avoid an abrupt and high amount of drift (Imbert & Perry, 2000). At 10:00, flow was opened at the low flow level for all channels, and remained at this level for two hours. From 12:00 to 13:00, the flow was increased every 15 min to mimic a

gradual increase in water velocity, up to the high flow in channels 1 and 2, and up to medium flow in channels 3 and 4 (Table 1). Channels 5 and 6 were kept at low flow.

Table 1 Water velocity (mean ± SD) for the 6 channels at the two trials.

Flow	Gravel bed	Water velocity in March (cm s^{-1})	Water velocity in October (cm s^{-1})
High	Coarse	36.71 ± 4.61	40.00 ± 2.38
High	Fine	43.86 ± 4.60	37.86 ± 2.27
Medium	Coarse	29.14 ± 4.85	29.86 ± 6.54
Medium	Fine	29.57 ± 6.11	30.57 ± 5.91
Low	Coarse	12.86 ± 4.56	17.71 ± 1.70
Low	Fine	14.29 ± 1.80	12.43 ± 2.23

From 10:00 onward, total hourly drift of invertebrates was gathered at the output of each channel in buckets equipped with two 10 x 10 cm openings closed by a 100 µm mesh net. During the period of increasing flow (12:15, 12:30 and 12:45) and for each non-sampled twilight time-frame (19:30 and 6:30 in March, and 19:30 and 7:30 in October), additional samples were taken. The last sample was taken on the second day at 12:00. A total of 33 drift samples were collected per channel and, at the end of the experiment, all invertebrates still present in the channels were recovered manually from the substratum (Table S1). Water velocity was also measured at this time, just prior to the recovery of the animals, longitudinally along each channel at 20 cm intervals.

All animals were stored in 70% ethanol and photographed under a binocular microscope (Olympus SZX16). Both Head Capsule Widths (HCW) and Body Lengths (BL – from the top of the head to the end of the abdomen) were measured with the software ImageJ (Abràmoff et al., 2004).

Statistical analyses

We did not account for missing individuals (equivalent to 12% of the individuals, including those not in the drift and those not recovered at the end). From the 1589 individuals that were collected and measured, we discarded animals collected before the beginning of the flow increase, *i.e.* during the settling period. Thus, 1396 individuals were used in the analyses and we assumed that the propensity/decision to drift of an individual was independent from that of the others. Raw data are shown in Figure 1.
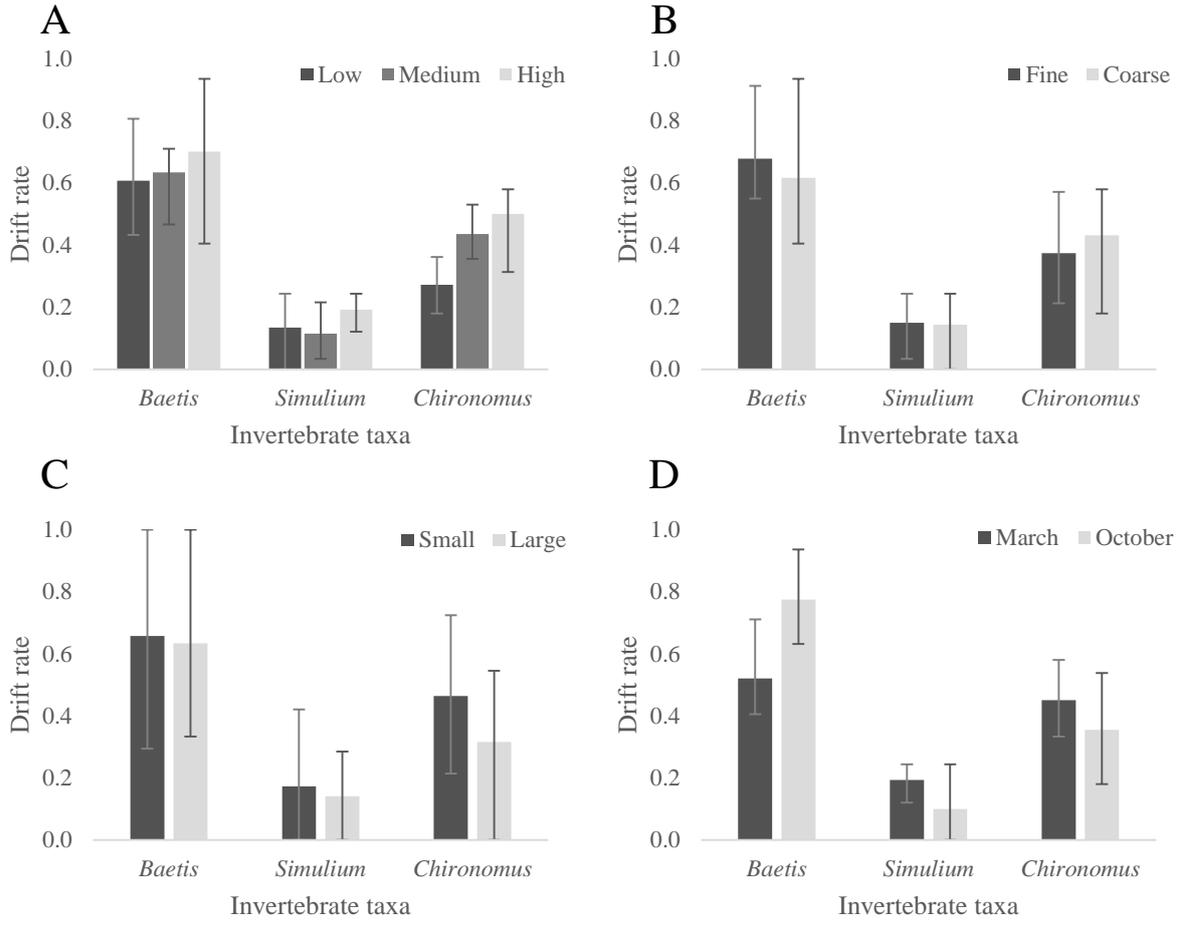
Figure 1 Average drift rate of the three invertebrate taxa according to water velocity (A: low flow in dark, medium flow in grey and high flow in light), gravel bed quality (B: fine gravel in dark and coarse gravel in light), head capsule width (C: small individuals in dark and large individuals in light) and season (D: March in dark and October in light). Bars indicate minimum and maximum drift rate values.

Data were then analysed using a modelling approach computed with OpenBUGS®. For each of the j taxon, if $p.D_i$ is the probability of drifting of the ith individual, we assume:

$$D_i \sim Bernoulli(p.D_i)$$

$$Logit(p.D_i) = \mu_{j[i]} + \alpha_{j[i]} V_i + \beta_{j[i]} H_i + \gamma_{j[i]} HCW_i + \eta_{j[i]} S_i + \delta_{l[i]}$$

Where $\mu_{j[i]}$ was the average drifting probability and $\alpha_{j[i]}$, $\beta_{j[i]}$, $\gamma_{j[i]}$ and $\eta_{j[i]}$ were fixed-effect parameters for water velocity (V_i), gravel bed quality (H_i), head capsule widths (HCW_i) or body lengths (BL_i) and season (S_i) respectively. A random effect (δ) was drawn from a common distribution:

$$\delta_{l[i]} \sim Normal(0, \sigma_\delta^2)$$

Parameters were given independent "weakly informative" priors (*i.e.* sampled in a normal distribution $N(0, 100)$ and for σ_δ in a truncated half-Cauchy $t(0, 1, 1)$ distributions – Gelman & Hill, 2006). Models were tested (Table 2) and the model with the lowest deviance information criterion (DIC) was selected (Spiegelhalter et al., 2002).

We used three independent chains, the first 10 000 iterations were discarded as an initial burn-in period. Then, 10 000 further iterations (resulting from one every ten runs) were performed. The convergence of the chains to their ergodic distribution was tested *via* the Gelman-Rubin (GR) diagnostics integrated in OpenBUGS®.

The significance of the parameters was tested with the step function implemented in OpenBUGS®. At each iteration for a variable X, step(X) equaled 1 if $X \geq 0$ and equaled 0 if $X < 0$. At the end of the run, if $P(X > 0)$ was lower than 0.1 or higher than 0.9, the parameter X was considered to be different from 0.

Results

The best model with the lowest DIC included the effect of water velocity (α), HCW (γ – instead of BL) and season (η), while the habitat (β) was excluded (DIC = 1573 – Table 2). Under our conditions, the gravel bed did not affect the drift probability for any taxa.

Table 2 Model selection based on minimum Deviance Information Criterion (DIC). Selected model is indicated by bold characters.

Model	Deviance	DIC	Estimated parameter number
$\text{Logit(p.D}_i) = \mu$	1645	1651	3.006
$\text{Logit(p.D}_i) = \mu + \alpha_{j[i]}V_i + \gamma_{j[i]}HCW_i + \delta_{l[i]}$	1517	1578	30.46
$\text{Logit(p.D}_i) = \mu + \alpha_{j[i]}V_i + \beta_{j[i]}H_i + \gamma_{j[i]}HCW_i + \delta_{l[i]}$	1515	1579	32.06
$\text{Logit(p.D}_i) = \mu + \alpha_{j[i]}V_i + \beta_{j[i]}H_i + \gamma_{j[i]}HCW_i + \eta_{j[i]}S_i + \delta_{l[i]}$	1520	1576	27.88
$\mathbf{\text{Logit(p.D}_i) = \mu + \alpha_{j[i]}V_i + \gamma_{j[i]}HCW_i + \eta_{j[i]}S_i + \delta_{l[i]}}$	**1521**	**1573**	**26**
$\text{Logit(p.D}_i) = \mu + \alpha_{j[i]}V_i + \gamma_{j[i]}BL_i + \delta_{l[i]} + \eta_{j[i]}S_i$	1525	1578	26.34

When submitted to low, medium and high water velocities, a taxa-specific drifting behaviour was observed (Figure 2). Although all three taxa followed the same pattern and increased their drift probability with water velocity, only *Chironomus* showed a significant relationship ($P(\alpha_C > 0) = 0.997$; $P(\alpha_B > 0) = 0.889$ and $P(\alpha_S > 0) = 0.841$ – Table 3). At low water velocity (10 cm s^{-1}), 44% of *Baetis*, 16% of *Simulium* and 26% of *Chironomus* drifted. At medium water velocity (30 cm s^{-1}), 53% of *Baetis*, 21% of *Simulium* and 45% of *Chironomus* drifted. At high velocity (40 cm s^{-1}), 58% of *Baetis*, 25% of *Simulium* and 55% of *Chironomus* drifted.
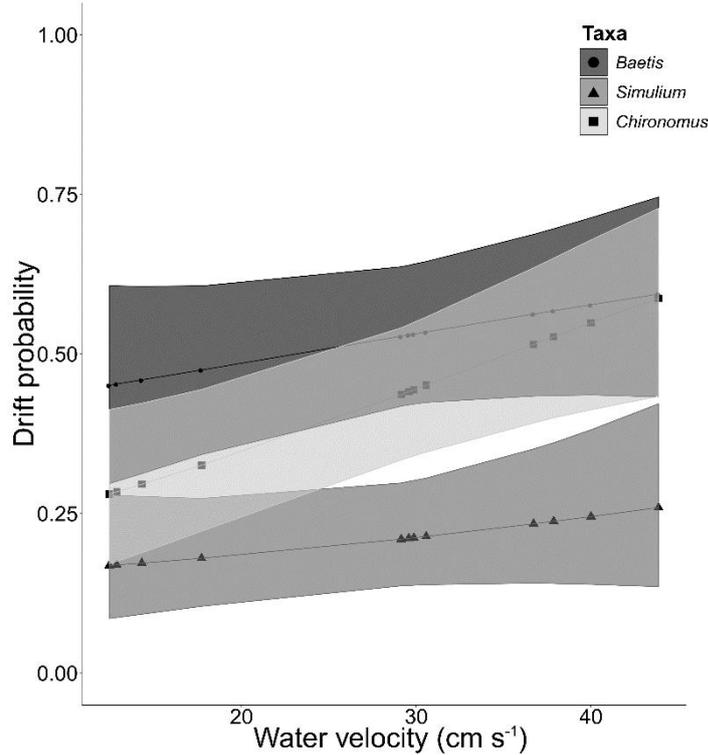
Figure 2 Model estimates of the drift probabilities of the three invertebrate taxa according to water velocity (cm s⁻¹). Shaded areas are the 95% probability intervals of posterior distributions.

Table 3 Main statistics of the posterior probability distribution functions of the free parameters. Parameters are considered significant when P(X > 0) is less than 0.10 or above 0.90 (in bold).

Parameters			Mean	SD	2.5%	Median	97.5%	P(X > 0)
Water velocity	α_B	*Baetis*	0.019	0.016	-0.012	0.019	0.051	0.889
	α_S	*Simulium*	0.018	0.018	-0.017	0.017	0.054	0.841
	α_C	*Chironomus*	0.042	0.014	0.014	0.042	0.071	**0.997**
HCW	γ_B	*Baetis*	0.183	0.655	-1.101	0.181	1.469	0.609
	γ_S	*Simulium*	-6.512	1.804	-10.130	-6.493	-3.008	**0.000**
	γ_C	*Chironomus*	-4.979	2.215	-9.316	-4.987	-0.656	**0.012**
Season	η_B	*Baetis*	1.208	0.341	0.552	1.203	1.900	**0.999**
	η_S	*Simulium*	-1.216	0.405	-2.031	-1.209	-0.443	**0.001**
	η_C	*Chironomus*	-0.253	0.309	-0.866	-0.253	0.356	0.200
SD of the random effects	σ_δ		0.396	0.129	0.158	0.390	0.667	1.000

Head capsule width was not related to the propensity to drift in *Baetis* (P($\gamma_B > 0$) = 0.609). *Simulium* showed a significant relationship between HCW and drift (P($\gamma_S > 0$) = 0.000), similar to *Chironomus* (P($\gamma_C > 0$) = 0.012), with small individuals drifting more than large ones in both cases (Figure 3).
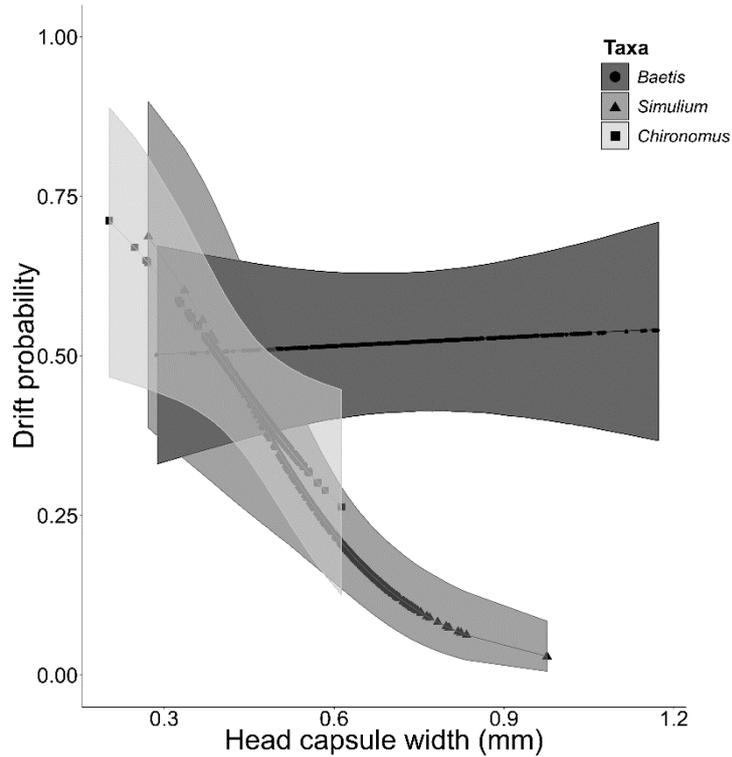
Figure 3 Model estimates of the drift probabilities of the three invertebrate taxa according to head capsule width (mm). Shaded areas are the 95% probability intervals of posterior distributions.

The effect of season on the drifting rates (η) was significant for *Baetis* and *Simulium* ($P(\eta_B > 0)$ = 0.999; $P(\eta_C > 0)$ = 0.200 and $P(\eta_S > 0)$ = 0.001). The drift probability of *Baetis* was higher in October than in March (0.522 in March and 0.782 in October – Figure 4) while the drift probability of *Simulium* was lower (0.206 in March and 0.073 in October). No pattern appeared in the estimations of δ and few values were different from 0 (Table S2), which indicates that no interactions were detected.
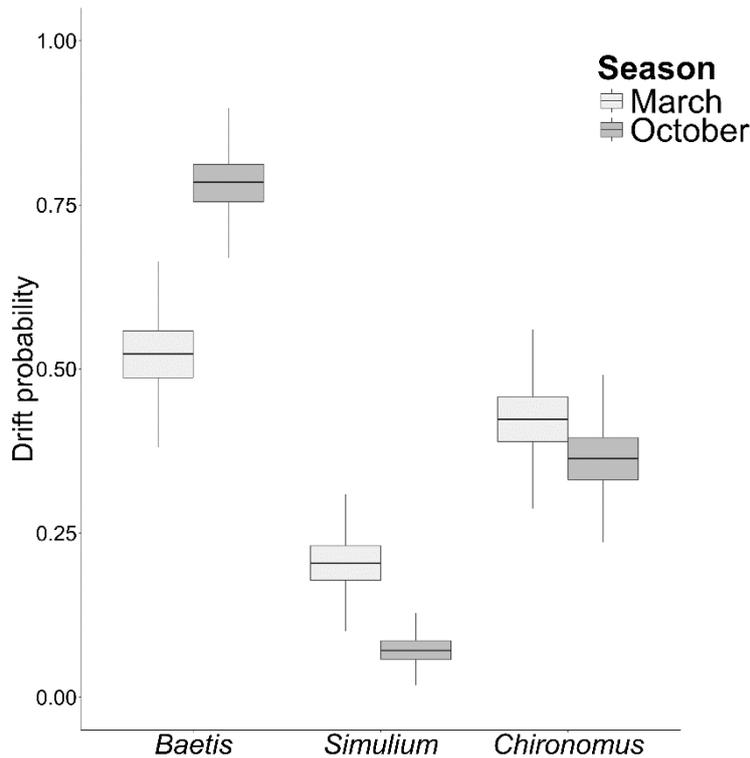
Figure 4 Model estimates of drift probabilities of the three invertebrate taxa according to the season for mean width individual and mean water velocity. Boxplots indicate the 1, 25, 50, 75 and 99 percentiles of posterior distributions.

Discussion

This experimental study provides a quantification of the drift rate for three taxa of invertebrates selected because of their abundance in riverine ecosystems and their potential contribution to drift-feeding fish (Sánchez-Hernández et al., 2011). The drift of *Chironomus* was positively related to water velocity while a positive, but non-significant, trend was observed for *Baetis* and *Simulium*. There was no effect of the substrate size (fine/coarse gravel bed) on any taxa and small *Simulium* and *Chironomus* drifted more than large ones. A seasonal effect was also detected, with *Baetis* drifting more in fall and *Simulium* drifting more in spring.

Under normal flow conditions, invertebrates are distributed along the river depending on their habitat preferences, their ability to cope with water velocity and their trophic requirements (Fjellheim, 1996; Rempel et al., 2000). *Baetis* is a rheophilic taxon and is commonly associated with medium flow habitat, between 25 and 50 cm s^{-1} (Tachet et al., 2010). They prefer stones that are exposed to water current, as this exposure allows them to feed on benthic microscopic algae and to benefit from the high dissolved oxygen levels of swift currents. Their location above the gravel bed and exposure to the current make them very prone to drift (Kohler, 1983, 1985). Accordingly, *Baetis* demonstrated the highest drift propensity among the three taxa

tested. Gibbins et al. (2005) highlighted that 50% of Baetis mayflies drifted with a fixed-bed sediment and that drift rate increased only when water current was strong enough to initiate bed-load transport. In the present experiment, flow was not high enough to mobilise the substrate to induce the passive drift of *Baetis*. As such, and in accordance with literature (Fonseca & Hart, 1996), we assume that in the present experiment the high drift rate of *Baetis* was largely active.

Simulium is the most rheophilic of the 3 taxa, as they demonstrate a preference for water velocities above 20 cm s^{-1} (Tachet et al., 2010), are able to withstand high flows around 90 cm s^{-1} (Finelli et al., 2002), and can be found in harsh conditions with water velocities around 300 cm s^{-1} (Phillipson, 1957; Wotton, 1985). Attached to rocks, they feed by catching fine particles in the water with their filter mandibles. Adapted to high water velocities, they drift more in slow than in fast waters (Fenoglio et al., 2013). In our experiment, they displayed the lowest drift rate and there was no significant relationship between their drift propensity and the tested water velocity gradient, which led us to presume that they drift actively. Indeed, exposed to experimental floods, Fingerut et al. (2015) showed that larval benthic densities of *Simulium* declined in microhabitats with near-bed velocities above 100 cm s^{-1}, much higher than velocities recorded under our conditions.

Chironomus is quite ubiquitous along the water velocity gradient (Tachet et al., 2010) and in the present experiment few individuals drifted under the lowest flow conditions. In running waters, they usually live buried in the substrate or within cocoons feeding on fine particulate organic matter (Berg, 1995). Without any morphological adaptations to cope with the drag force of the current, *Chironomus* was the only taxon that drifted significantly more when the water velocity increased and then, exhibited passive drift. In the field, many authors reported that a high proportion of the drifting community is composed of *Chironomidae* (Imbert & Perry, 2000; Kennedy et al., 2014; Robinson et al., 2004), which under flood conditions, respond as soon as the flow begins to increase. Despite this high sensitivity to flow, the analysis of long-term data (13-years) showed that chironomids are among the most resilient taxa of the community following catastrophic floods, in relation to their ecological traits (*i.e.* their abundance and their short life cycle – Woodward et al., 2015).

Taniguchi & Tokeshi (2004) emphasised the role of shelter availability in invertebrate size distribution, with larger proportions of small individuals in complex habitats. Some works have highlighted the importance of gravel bed quality in limiting the impact of disturbances such as floods and flow variations (Holomuzki & Biggs, 2003; Long et al., 2011). We did not find any

evidence of gravel bed quality impact on drift rate. As *Baetis* and *Simulium* drifted actively, habitat could not mitigate the effects of water velocity on the passive drift of these two taxa. However, considering that *Chironomus* are passive drifters, the lack of relation between drift rates and gravel bed quality could indicate that gravel bed quality was not different enough to induce a distinction between sheltering opportunities. Perhaps this result is due to the fact that we worked with small larvae (Figure S1 and S2) and that the size of the interstices provided by the fine gravel bed was too large to effectively limit sheltering opportunities.

No significant relationship between drift and head capsule width (HCW) was observed for *Baetis*, while *Simulium* and *Chironomus* HCW data showed a clear trend for larvae with small HCW to drift more. This could possibly be linked to a reduction in the ability of young individuals to access shelter due to lower locomotor abilities, at least in *Chironomus* larvae. Concerning *Simulium*, we emphasized that water velocities underwent in the present experiment were much lower than their preferred water velocity (Fingerut et al. 2015). Presumably, their drift was then active. Environmental conditions were good but low organic matter in the experimental channels may have motivated voluntary drift. It may have concerned in priority small *Simulium* since they need higher organic concentration than big ones to optimize their growth (Charpentier & Morin, 1994). *Baetis* are good swimmers, especially compared to the two Diptera used in this experiment. The lack of significant relationship between HCW and drift appears consistent with their swimming abilities, which may have given *Baetis* similar opportunities to reach shelters regardless of their developmental stage. When considering BL, results showed similar patterns to HCW, except for *Chironomus* (see Figure S1). Head capsule width is highly correlated with size in *Baetis* and *Simulium* but not in *Chironomus*. In *Chironomus*, the relationship between larval stages and body length is weak (Richardi et al., 2013). Thus, ontogenesis could be more relevant than larval body size in favouring drift for Diptera larvae. As far as we know, there is no literature linking invertebrate size to drift, except for daylight/night drifting differences. Drift rate of small individuals is higher during daylight while larger individuals drift more at night (Stewart & Szczytko, 1983; Allan, 1984; Bowles & Short, 1988), suggesting that small individuals are more likely to experience passive drift than large ones. In the present experiment, daylight and night-time drift levels were quite similar, but they were not interpreted because of the progressive depletion of invertebrates through time.

Unexpectedly, a seasonal effect on the drift of *Baetis* and *Simulium* was detected. *Baetis* drifted more in fall than in spring, while the opposite was observed for *Simulium*. The mean water

temperature was 2°C warmer in fall, and because invertebrates are ectotherms, this resulted in an increase in metabolism and activity. In addition, Kohler (1983) emphasised an increase in the feeding intensity in fall with *Baetis* more frequently observed on the surface of stones and more prone to drift. For *Simulium*, little information is available on their propensity to drift according to season. Stoneburner & Smock (1979) examined the composition of the drift over the course of a year in a California stream, and noted two peaks for Simuliid densities in drift. Two species of Simuliid were identified with one drifting preferentially in early spring and the second in fall, and these differences were assumed to be driven by their emergence dates. As Simuliids collected for our experiment were larger in March than in October (Figure S2), their higher drift rate in March might possibly be related to a time proximity with their emergence date at that time.

The present experiment was conducted in a closed system. This allowed natural processes such as immigration or the hatching of invertebrates to be avoided, which would have prevented the estimation of the drift entry rate. Ranging from 12 to 43 cm s^{-1}, water velocities obtained in this experiment are representative of conditions in the natural environment. *Baetis* and *Simulium* drifted actively and conditions were not stringent enough to induce significant passive drift. Ranging from 0.36 to 7.34 dynes cm^{-2}, shear stress experienced by invertebrates in our channels was lower than the 9 dynes cm^{-2} threshold needed to dislodge the invertebrates and to induce passive drift (Gibbins et al., 2007). Small *Simulium* demonstrated an abundance of drift, probably through active drift with low velocities driving the movement of individuals. In contrast, *Chironomus,* and specifically young stages, drifted passively.

This work provides the first accurate estimates of invertebrate drift entry rate. The accuracy of these rates are important because they allow the impacts of disturbances on invertebrate communities to be predicted, and they improve models of trophic interactions, such as those for drift-feeding fishes (Hayes et al., 2007).

Table S1 Step by step experimental procedure with the sample number and if it is included (Y) or not (N) in the model.

N° sample	Included in the model	12th of March 2015	Time	22nd of October 2015	N° sample	Included in the model
	N	Addition of invertebrates	09:00	Addition of invertebrates		N
1	N	Opening of the flow at low level	10:00	Opening of the flow at low level	1	N
2	N		11:00		2	N
3	N		12:00		3	N
4	Y		12:15		4	Y
5	Y	Gradual elevation of flow	12:30	Gradual elevation of flow	5	Y
6	Y		12:45		6	Y
7	Y		13:00		7	Y
8	Y		14:00		8	Y
9	Y		15:00		9	Y
10	Y		16:00		10	Y
11	Y		17:00		11	Y
12	Y		18:00		12	Y
13	Y	Dusk	19:00		13	Y
14	Y		19:30	Dusk	14	Y
15	Y		20:00		15	Y
16	Y		21:00		16	Y
17	Y		22:00		17	Y
18	Y		23:00		18	Y
19	Y		00:00		19	Y
20	Y		01:00		20	Y
21	Y		02:00		21	Y
22	Y		03:00		22	Y
23	Y		04:00		23	Y
24	Y		05:00		24	Y
25	Y		06:00		25	Y
26	Y	Dawn	06:30			
27	Y		07:00		26	Y
			07:30	Dawn	27	Y
28	Y		08:00		28	Y
29	Y		09:00		29	Y
30	Y		10:00		30	Y
31	Y		11:00		31	Y
32	Y	End of the experiment	12:00	End of the experiment	32	Y
33	Y	Recovery of the invertebrates settled in the channels		Recovery of the invertebrates settled in the channels	33	Y

Table S2 Probabilities of the random effects (the residuals) to be different from 0. Parameters are considered significant when P(δ[X] > 0) < 0.10 or P(δ[X] > 0) > 0.90 and are indicated in bold characters.

δ	Taxon	Flow	Season	Gravel bed	P(δ[X] > 0)
1	*Baetis*	High	March	Coarse	0.121
2	*Baetis*	High	March	Fine	0.381
3	*Baetis*	Medium	March	Coarse	0.323
4	***Baetis***	**Medium**	**March**	**Fine**	**0.924**
5	*Baetis*	Low	March	Coarse	0.442
6	*Baetis*	Low	March	Fine	0.753
7	*Baetis*	High	October	Coarse	0.842
8	*Baetis*	High	October	Fine	0.749
9	***Baetis***	**Medium**	**October**	**Coarse**	**0.097**
10	*Baetis*	Medium	October	Fine	0.297
11	*Baetis*	Low	October	Coarse	0.676
12	*Baetis*	Low	October	Fine	0.310
13	*Simulium*	High	March	Coarse	0.385
14	*Simulium*	High	March	Fine	0.233
15	*Simulium*	Medium	March	Coarse	0.505
16	*Simulium*	Medium	March	Fine	0.470
17	*Simulium*	Low	March	Coarse	0.765
18	*Simulium*	Low	March	Fine	0.665
19	*Simulium*	High	October	Coarse	0.891
20	*Simulium*	High	October	Fine	0.829
21	*Simulium*	Medium	October	Coarse	0.137
22	*Simulium*	Medium	October	Fine	0.391
23	*Simulium*	Low	October	Coarse	0.275
24	*Simulium*	Low	October	Fine	0.441
25	*Chironomus*	High	March	Coarse	0.681
26	*Chironomus*	High	March	Fine	0.370
27	*Chironomus*	Medium	March	Coarse	0.430
28	*Chironomus*	Medium	March	Fine	0.371
29	*Chironomus*	Low	March	Coarse	0.538
30	*Chironomus*	Low	March	Fine	0.634
31	*Chironomus*	High	October	Coarse	0.750
32	***Chironomus***	**High**	**October**	**Fine**	**0.099**
33	***Chironomus***	**Medium**	**October**	**Coarse**	**0.936**
34	*Chironomus*	Medium	October	Fine	0.504
35	*Chironomus*	Low	October	Coarse	0.209
36	*Chironomus*	Low	October	Fine	0.494
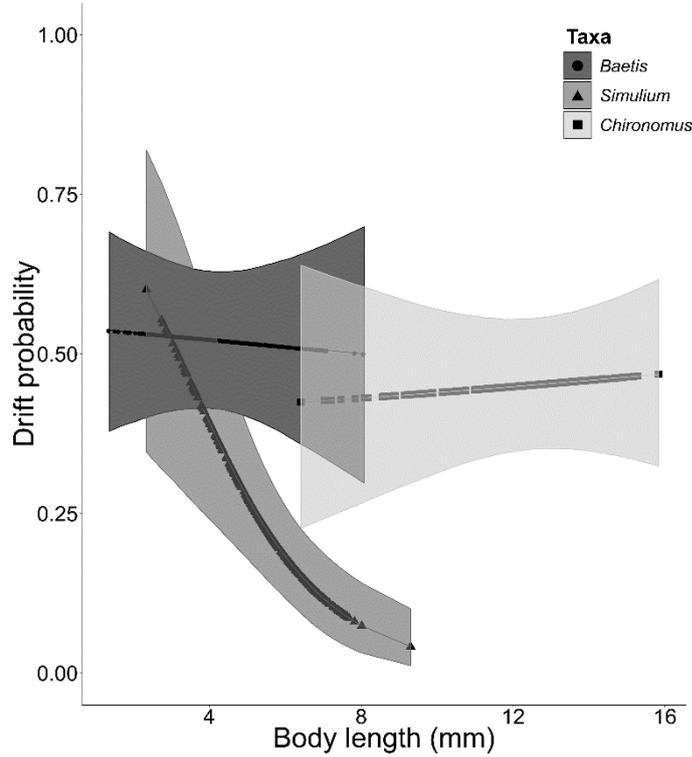
Figure S1 Estimates of the drift probabilities of the three invertebrate taxa according to body length (mm). Shaded areas are the 95% probability intervals of posterior distributions.
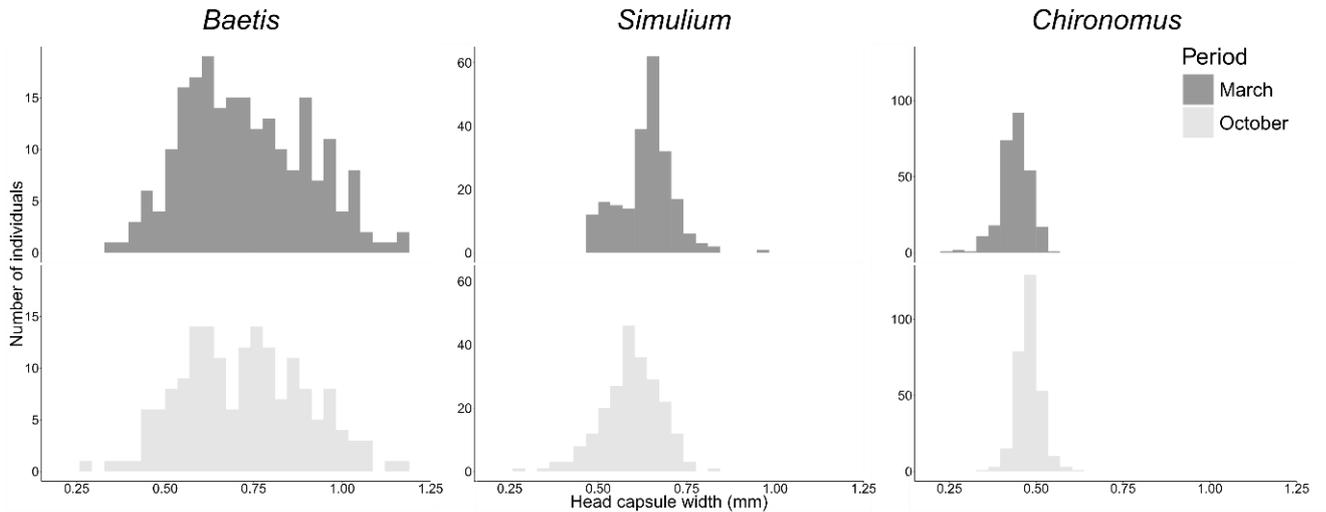
Figure S2 Distribution of the head capsule width (in mm) for the three taxa and the two trials. Differences in HCW between March and October were not significant for Baetis ($P(mean(HCW_{March}) > mean(HCW_{October}) = 0.671$). Simulium were larger in March ($P(mean(HCW_{March}) > mean(HCW_{October}) = 1.000$) and Chironomus were larger in October ($P(mean(HCW_{March}) > mean(HCW_{October}) = 0.000$).

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Table 1.1 Synthesis of the main results on the drift propensity of Baetis, Simulium and Chironomus according to water velocity, gravel bed, individual size and season.

Taxa	Mean drift probability	Water velocity 14, 30, 40 cm.s^{-1}	Gravel bed Fine vs. Coarse	Individual size Head capsule width	Season Spring vs. Autumn
Baetis	0.684	-	-	-	↗ Drift in Autumn
Simulium	0.128	-	-	Small individuals drift more *Active: not enough organic matter*	↗ Drift in Spring
Chironomus	0.363	↗ Water velocity ↗ Drift rate	-	Small individuals drift more *Passive: carried by the current*	-

Further considerations and discussion

Results included in the MS showed that head capsule width interfered with water velocity in *Chironomus* and *Similium* larvae propensity to drift. The model presented in the article estimated an effect of the individual head capsule width (HCW) by taxon (γ). To test our hypotheses about the drift propensity of small *Simulium* and *Chironomus* (*i.e.* small *Simulium* leaving actively the channels and small *Chironomus* carried by the current), the model was modified to estimate an effect of the individual size (HCW) by taxon and by water velocity modality.

Concerning *Simulium*, all the estimated parameters were negative (Table 1.2). The effect of HCW at low velocity (γ_{S1}) was significant (P(γ_{S1} > 0) = 0.000), while the effects at medium (γ_{S2}) and high velocities (γ_{S3}) were around the threshold of significance (P(γ_{S2} > 0) = 0.122; P(γ_{S3} > 0) = 0.096). γ_{S1} was significantly different from both γ_{S2} and γ_{S3} with probabilities of 0.022 and 0.030 respectively. γ_{S2} and γ_{S3} were equal (P(γ_{S2} > γ_{S3}) = 0.551). Small *Simulium* drifted more at low water velocities than at medium or high water velocities (Figure 1.1).

Concerning *Chironomus*, all the estimated parameters were negative (Table 1.1) but only γ_{C2} and γ_{C3} were significant (P(γ_{C1} > 0) = 0.468; P(γ_{C2} > 0) = 0.048; P(γ_{C3} > 0) = 0.013). γ_{C2} was not different from γ_{C3} and γ_{C1} (P(γ_{C1} > γ_{C2}) = 0.887; P(γ_{C2} > γ_{C3}) = 0.605) but γ_{C1} was significantly higher than γ_{C3} (P(γ_{C1} > γ_{C3}) = 0.939). There was no relationship between the head capsule width of invertebrate and the drift probability when the water velocity was low. However, small individuals drifted more in medium and high flow conditions (Figure 1.1). Results of this model supported the hypotheses proposed in the MS about the effect of individual head capsule width on the drift of invertebrates.

Table 1.2 Main statistics of the posterior probability distribution functions of the effect of the individual size (γ) by taxon (Simulium and Chironomus) and by water velocity modality (low, medium and high). Parameters are considered significant when P(X > 0) is less than 0.10 or above 0.90 (in bold).

HCW parameters	Taxon	Water velocity modality	Mean	P(X > 0)
γ_{S1}		Low	-12.520	**0.000**
γ_{S2}	*Simulium*	Medium	-3.400	0.122
γ_{S3}		High	-3.896	**0.096**
γ_{C1}		Low	-0.241	0.468
γ_{C2}	*Chironomus*	Medium	-6.517	**0.048**
γ_{C3}		High	-7.899	**0.013**
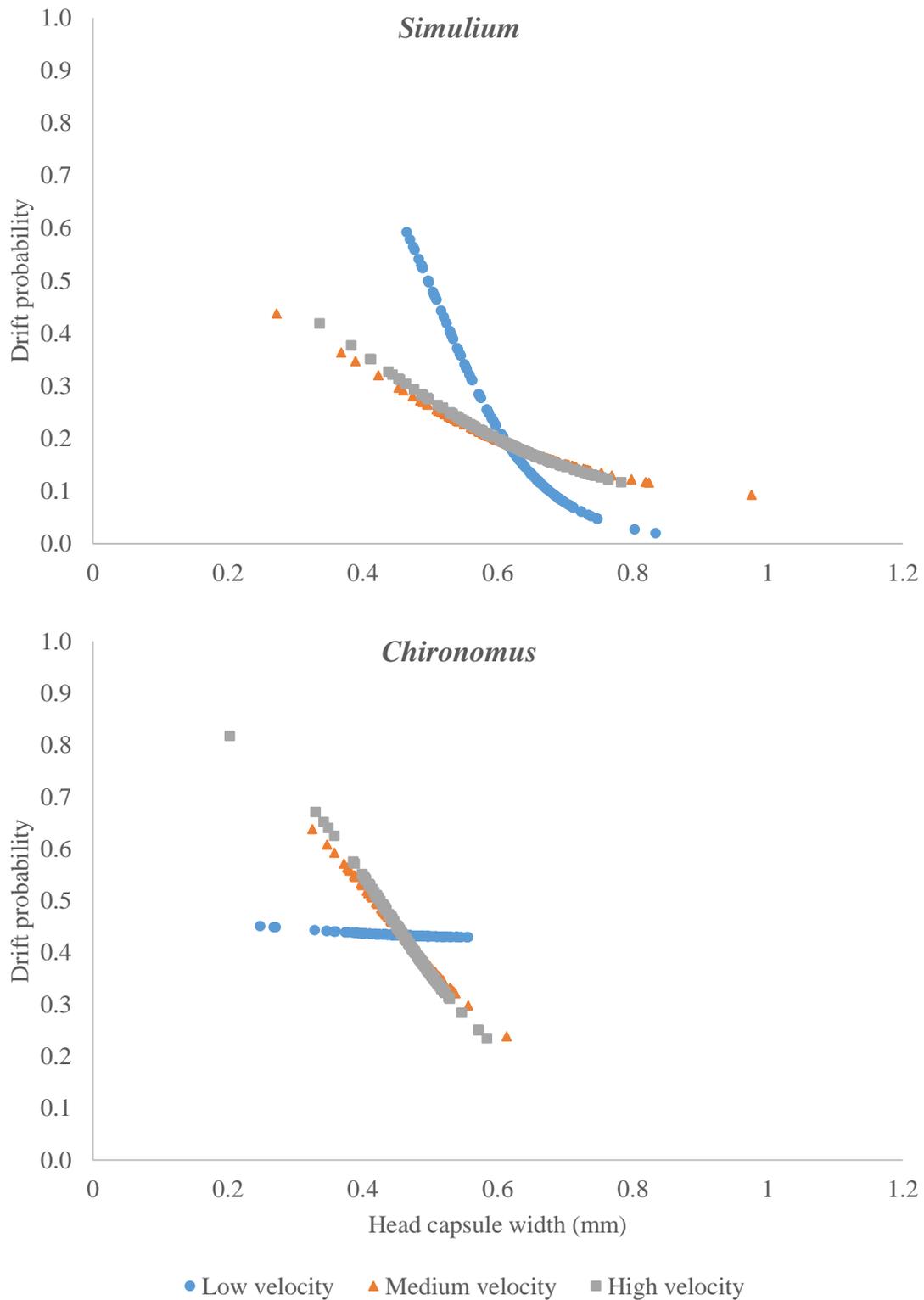
Figure 1.1 Model estimates of the drift probabilities of Simulium and Chironomus according to head capsule width (mm) at low (blue circles), medium (orange triangles) and high (grey squares) water velocities.

According to the present experiment, moderate water velocity induces passive drift of invertebrates even if bed load transport is not initiated. Then, besides the effect of catastrophic hydrological events that are known to deplete the benthos, an increase in the frequency of moderate floods may also affect their abundance.

For fish, the increase in water velocity increases the energetic costs to maintain hunting positions. They would possibly take advantage of an increase of food (especially *Chironomus*) up to a threshold (25 cm s^{-1} according to Heggenes & Traaen 1988 for alevins). However, it remains to be calculated if the increase in swimming expenditure is balanced by both the increase of energy intake and the decrease of the hunt efficiency. In anyway, at higher water velocities, they will try to shelter the time of the flood, without benefiting from the drifting invertebrates.

Then if the increase in floods frequency forecasted by Global Climate Change exacerbates the risk of depletion of benthic invertebrates it should lead to a decrease in food availability for carnivorous fish. This may especially affect 0^+ young salmonids for at least 4 reasons: *i*/ they start exogenous feeding in spring when the risk of flood events is still high (and this risk will increase with GCC), *ii*/ they are constrained by the small size of their oesophagus to small sized prey, *iii*/ they have much less reserve that large fish to face starvation periods, *iv*/ their swimming ability is limited at high water velocity.

Chapter II Effect of feeding conditions and temperature on growth and metabolism of alevins

The previous chapter highlighted that the increase in water velocity and flood frequency due to Global Climate Change should increase invertebrate drift (and especially of *Chironomus*). This might result in the depletion of the benthic invertebrate community, and on the drifting one as drifting invertebrates come from the benthos. For drift feeding fish, this means an increased risk to face periods of food scarcity.

When salmonid alevins emerge, they have almost exhausted the reserves of their yolk sac and they need to start feeding quickly (Johnson et al. 2013; Ladago et al. 2016). For many fish species, starvation during larval stage induces high mortality rates (Hunter 1981; Jonas & Wahl 1998) and it is an important driving force for 0^+ salmon (*Salmo salar*) survival (Kennedy et al. 2008) and growth (Ward et al. 2009). In the wild, most species regularly face periods of food deprivation and besides behavioural responses, they may adapt to the quantity of resources available by lowering their metabolism (McCue 2010). The basal metabolism of an organism, its environment (temperature) and the amount of its body resources (usually lipids), are important factors acting on its ability to face long period of starvation.

Whatever the organism, at the beginning of starvation, pancreas increases the secretion of glucagon and diminish the secretion of insulin, which trigger catabolism in the liver and mobilisation of reserves (Sundby et al. 1991). First, liver degrades glycogen in glucose *via* glycogenolysis pathway. Carbohydrates are then used by the brain and carbohydrate-dependent cells (*e.g.* red blood cells). However, salmonids are carnivorous fish and they have adapted their anatomy, physiology and metabolism to their natural diet, which contains few or no carbohydrates (Kamalam et al. 2017). They mainly synthesise glucose from non-carbohydrate precursors *via* gluconeogenesis (*i.e.* lactate, pyruvate and amino acids − NRC 2011). When stocks of carbohydrates are depleted, lipids are catabolised *via* the lipolysis pathway. Triglycerides contained in body fat release fatty acids in the blood, which are caught by the liver and oxidized in acetyl-Coenzyme A (acetyl-CoA) *via* the β-oxidation pathway. Acetyl-CoA is used for the synthesis of ketone bodies to feed muscles and the brain after transformation, or for energy synthesis. Finally, when carbohydrates and lipids are depleted, muscular proteins are mobilised. Muscles constitute the main protein mass and a reserve of amino acids. Muscle proteolysis releases amino acids in the blood that are catabolized by the liver *via* amino acid catabolism. Amino acid nitrogen components are eliminated in urea, while carbon skeletons are converted either into glucose *via* gluconeogenesis or into acetyl-CoA for the synthesis of energy. Acetyl-CoA obtained from the β-oxidation or from the catabolism of

amino acids is invested first in Krebs cycle and then in the respiratory chain for the synthesis of ATP (Figure 2.1 – Simpkins et al. 2003; Hecketsweiler & Hecketsweiler 2004). Synthesis of adenosine triphosphate (ATP) provides the energy needed for all the chemical reactions of metabolism. Fatty acid catabolism and amino acid catabolism can be activated sequentially but some organisms (and particularly larvae, as found in European plaice by Ehrlich 1974) can use them in conjunction to preserve the lipid reserve (and dispose of it longer) as it is the most cost-effective way to produce energy (Bar 2014).
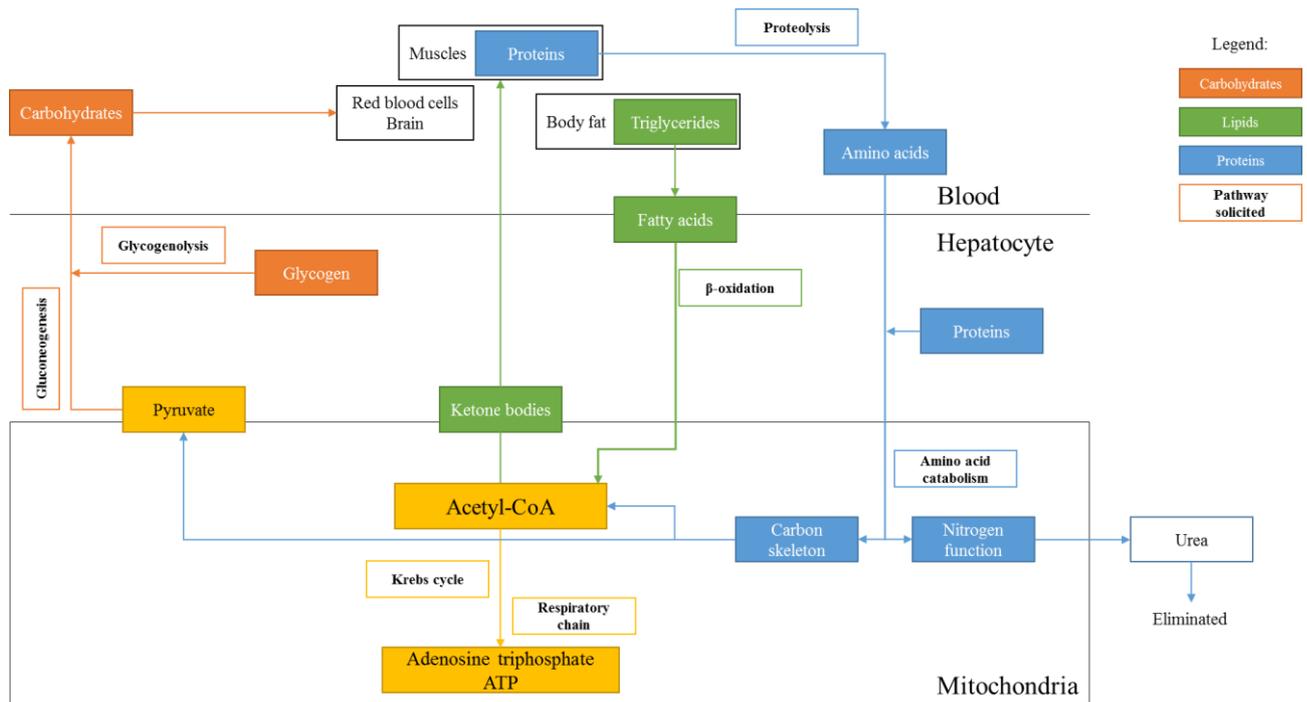
Figure 2.1 Metabolic flows for all living organisms (including salmonids) in fasting situation (modified from Hecketsweiler & Hecketsweiler 2004).

Temperature is an important factor that regulates the metabolism of organisms, especially in poïkilotherms, which do not regulate their internal temperature. Warmer temperatures increase their metabolism and so the reserve consumption rate. Therefore, Global Climate Change might affect young trout growth and survival through both a reduction in prey availability and an increase in metabolic loss. Thus in that chapter, we conducted an experiment in order to better understand the interactions of these two factors (prey availability and temperature) on young trout growth and metabolic pathways.

Effect of food shortage and temperature on 0[+] salmonids: a contribution to predict the effects of Climate Change

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ABSTRACT

In the present experiment, brown trout alevins were maintained at 8°C and 11°C at 3 conditions over a 9 day period from yolk sac exhaustion: fed *ad libitum*, starved or fed *ad libitum* after starvation. Whole body gene expressions for proteins involved in energy metabolism and the two primary proteolytic pathways were assessed and showed that proteasome and autophagy-related genes were over-expressed during and after starvation, particularly at 11°C. Our results suggest that higher temperature will intensify stress induced by starvation.

Key words: *Temperature, Salmo trutta, fry, starvation, prey, metabolism.*

Introduction

Climate Change (CC) will alter precipitation patterns (IPCC 2013) and will lead to an increase in winter/spring rainfall in most coastal areas of the north Atlantic. In freshwater ecosystems, rains are the primary source of running water discharge in rivers (Giller & Malmqvist, 1998) and with heavier and more frequent rainfall predicted, flooding events will become more frequent and intense in riverine systems. Further, CC will increase temperatures globally (IPCC 2013), which will affect metabolic rates, vital activities and growth of ectotherm organisms (Allan & Castillo, 2007).

Brown trout (*Salmo trutta* Linnaeus) alevins start their exogenous feeding in spring, which usually coincides with high prey availability (Romaniszyn et al., 2007). When the young trout emerge from the gravel, they have a limited amount of reserves and thus need to start feeding quickly to avoid mortality. Emergence is described as a critical period (Elliott, 1994), where high mortality rates occur (Elliott, 1986). More recent studies demonstrated that starvation during the critical period was an important driving force for 0[+] salmon (*Salmo salar*) survival

rates (Kennedy et al., 2008) and growth (Ward et al., 2009). The effect of temperature on metabolism is another factor affecting the survival of emerged salmonids. Régnier et al. (2013) showed that metabolic rate increased by 1.4-1.6 in response to a 4°C temperature increase for hatched brown trout. Thus, CC might affect young trout growth and survival through both a reduction in prey availability, as flood frequency and magnitude have the potential to drastically reduce the invertebrate community (Robinson et al., 2004), as well as through an increase in metabolic loss driven by rising temperatures.

While salmonid growth and survival at the swim-up stage have been relatively well studied (Bilton & Robins, 1973; Twongo & MacCrimmon, 1976; Koss & Bromage, 1990; Edsall et al., 2003), empirical data to assess the interaction between temperature and first-feeding are sparse. In addition, metabolic pathways activated at a molecular level by the starvation of early life stages have not yet been described.

The aims of the present study were to better understand young brown trout response to CC by (1) describing the consequences of starvation on their nutritional status, (2) testing their ability to recover from late first feeding and (3) analysing the effect of temperature on these phenomena (starving/recovering) by measuring growth and mRNA levels of genes involved in fatty acid/amino acid catabolism, as well as proteasomal and autophagy pathways.

Material and methods

Experimental features

Experimentation was conducted in the INRA experimental facilities (UMR Ecobiop, Saint-Pée-sur-Nivelle, France) authorized for animal experimentation (A640141). The experiments were in strict accordance with EU legal frameworks related to the protection of animals used for scientific research (Directive 2010/63/EU) and according to the National Guidelines for Animal Care of the French Ministry of Research.

Forty-two tanks (LxWxH: 50x25x30 cm), each equipped with an individual pump and a Perlon filter, were filled to 20 cm height with filtered water from the Nivelle River. Three pebbles (ø: 4-5 cm) were placed in each tank to serve as a place for the fish to shelter. Twenty one tanks were settled in each of two thermo-regulated rooms that were at 8°C (± 0.1 in the water) and 11°C (± 0.4 in the water). Natural nyctemeral light-dark regime was simulated, with a 6:30 to 19:00 lit period and two 30 min periods of gradual light intensity change mimicking dawn and dusk.

Fish sampling

On 30/12/2014, eggs were obtained through the artificial fertilization of gametes of wild brown trout caught in the Nivelle watershed (43°21' N, 1°33' W). Eggs and alevins were reared at 9.36°C (± 1.18) until complete yolk sac depletion (790 degree-days). Survival was high (up to 82%) and on 30/03/2015, 126 alevins were individually weighed and photographed under binocular (x 10), allowing for individual identification thanks to melanophore distribution patterns (Garcia de Leaniz et al., 1994). Each of the 42 tanks was allocated with a random batch of 3 fish. Ten additional alevins were settled in a bucket for 24h at each temperature in aerated water and killed on Day 0 (D_0). Live Chironomid larvae (Grebil, Arry, France) were distributed *ad libitum* from D_0 in 9 tanks at each temperature. Every morning, leftover food was removed and counted, and a known number of new larvae were then added. All tanks (fed F and starved S) received the same pipette disturbance from the feeding. On D_5, fish from 3 tanks from the fed (F_5) and starved conditions (S_5) at each temperature were measured, weighed, photographed and subjected to lethal anesthesia before being frozen in liquid nitrogen and stored at −80°C until analysis. Fish from another 3 tanks from the starved condition received food *ad libitum* (Delayed-feeding, DF). From D_5 to D_9, 6 fed tanks (F_9), 6 unfed tanks (S_9) and 3 delayed-feeding tanks (DF_9) remained. As some mortality occurred at D_9, the experiment was stopped.

Relative quantification of mRNAs levels for catabolic genes

mRNA levels were determined by quantitative real-time RT-PCR. The extraction of total RNA from whole alevins was performed using the Trizol reagent (Invitrogen, Carlsbad, CA, USA). One microgram of total RNA was used for cDNA synthesis. The SuperScript III RNaseH-Reverse Transcriptase Kit (Invitrogen) with random primers (Promega, Charbonniéres, France) were used. Primer sequences to amplify specific trout target genes (Seiliez et al., 2008, 2012; Panserat et al., 2017) are shown in the Supporting information (Table S1). Each PCR assay (Lightcycler 480, Roche Diagnostics, Neuilly-sur-Seine, France) included replicate samples (duplicates of reverse transcription and PCR amplification) and 2 negative controls (one with RNA but without RT enzyme and the other without RNA). For the analysis of mRNA levels, relative quantification of target gene expression was performed using the ΔCT method (Pfaffl, 2001). The relative gene expression of Luciferase was used for the normalization (Marandel et al., 2016).

Total length was calculated as the average of measurements from 3 different operators to the nearest 0.1 mm using ImageJ (Abràmoff et al., 2004). Weight gain (Wg) and length gain (Lg) were then calculated (eq.1):

$$Gain = \frac{Final - Initial}{Initial}$$

Wg and Lg were analysed using nonparametric Wilcoxon-Man-Whitney rank sum test.

Molecular analyses were performed on 72 individuals, 6 fish per condition and per temperature on D_0, on D_5 (F_5 and S_5) and on D_9 (F_9, S_9, and DF_9). mRNA levels were analysed using a Bayesian modelling approach with OpenBUGS®. Data were analysed separately according to temperature. If X_i is the expression of the ith individual, we assume:

$$log(X_i) \sim Normal(\mu_i, \sigma)$$

$$\mu_i = \mu + \alpha_{j[i]}$$

Where the mean of the log expression μ_i was modelled according to a global average (μ) and $\alpha_{j[i]}$ was a fixed-effect parameter for rearing conditions.

Bayesian computation

Parameters were given independent 'non informative' priors (*i.e.*, sampled in a normal distribution $N(0, 100)$ and for σ in a half-Cauchy $t(0, 1, 1)$ distributions – Gelman & Hill 2006). The convergence of three Markov Chain Monte Carlo (MCMC) chains to their ergodic distribution was tested for the model parameters *via* the Gelman-Rubin (GR) diagnostics. The first 10 000 iterations were discarded and then, 10 000 further iterations (thin = 10) were performed.

Results

Survival

No death was recorded in the fed group, and the same was true for all groups up to D_8. On D_9, 12 fish died: 4 at 8°C (S_9), 8 at 11°C (7 S_9 + 1 DF_9). The experiment was stopped and dead fish were not considered in further biometric and molecular analyses.

Biometric data

As expected, fed fish gained weight and starved fish lost weight (Fig. 1a). If weight gain on D_9 was higher than on D_5 for fed fish, no difference occurred among starved fish between the two

dates. Temperature did not change weight gain in fed fish. On the contrary, for starved fish weight loss was significantly increased by temperature increase (Wilcoxon test, p-value(S_5) and (S_9) < 0.01). The same tendency was observed for delayed fed fish (p-value(DF_9) = 0.059). DF_9 fish exhibited intermediate values between S_9 and F_9.

At the start of the experiment, fish measured 2.584 cm ($\pm$ 0.037) and weighed 0.106 g ($\pm$ 0.003), (box-plots, Fig. 1b). On average, F_9 fish were longer and heavier than S_9 ones, and DF_9 were in between, similar to results for weight gain (Fig. 1a). Weight/length relationships did not differ much among rearing conditions (Fig. 1b). However, it was noteworthy that at 11°C fish were usually shorter than at 8°C for a similar weight (Fig. 1b). Length gain values confirmed this point with higher gains at low temperature (8°C *vs* 11°C) for F_9 and DF_9 conditions (Wilcoxon test, p-value(F_9) = 0.01; p-value(DF_9) = 0.046; p-value(S_9) = 1).

During the feeding period, DF_9 fish ate as much as the fed fish (F_5 and F_9), but they grew less, especially at 11°C (Fig. 1c and 1d). For F_5 fish, the mean number of *Chironomus* eaten daily almost doubled at 11°C (8.08 on average *vs* 4.67 on average at 8°C) but it was not correlated with a better performance in growth. Results for F_9 showed the same trend (4.67 prey on average at 8°C and 8.08 at 11°C for a similar growth).
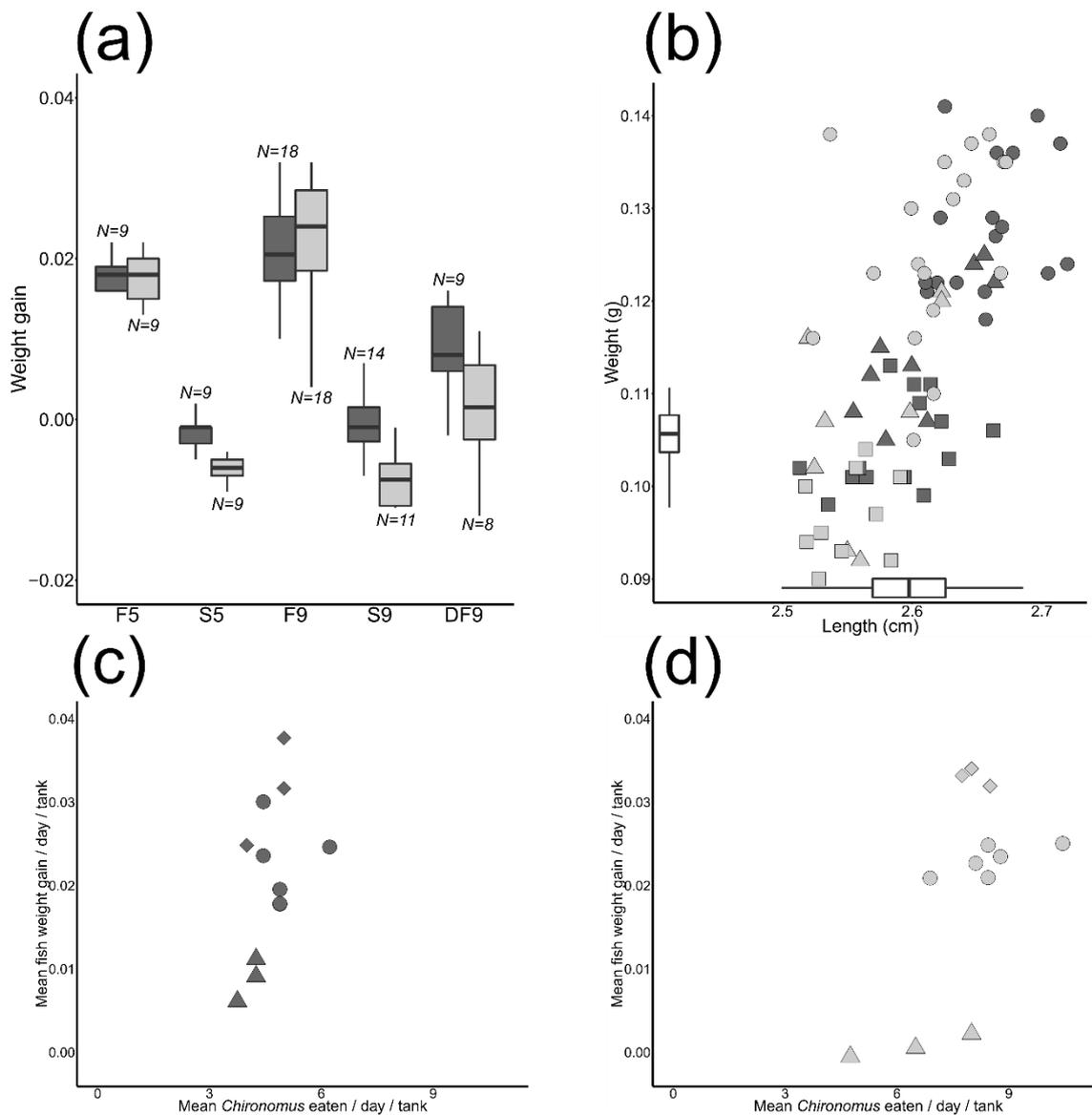
Figure 1 (a): Weight gain (WG = (final weight – initial weight) / initial weight) of emerged alevins according to rearing conditions. Boxplots indicate the 1, 25, 50, 75 and 99 percentiles. (b): Length (in cm) and weight (in g) of alevins after 9 days of growth. Boxplots indicate the 1, 25, 50, 75 and 99 percentiles of the initial measures of fish. The daily mean fish WG by tank for the fed conditions (F_9, DF_9 and F_5) according to the mean number of prey (Chironomus) eaten daily by tank at 8°C (c) and 11°C (d). Dark items represent alevins reared at 8°C and light items represent alevins reared at 11°C. Fed fish F_5 are represented in diamond, fed fish F_9 are in circles, delayed-fed fish DF_9 are in triangle and starved fish S_9 are in square.

mRNA levels for catabolic genes

All mRNA levels were usually above 0.5, except in some cases for genes involved in fatty acid catabolism at 11°C, and in proteasome and autophagy in fed fish (Table S2). Many of the differences between feeding conditions were found for genes involved in autophagy and proteasome pathways (Table 1, FC1 to FC8). On D_5 and at 8°C, starvation is associated with significantly higher mRNA levels for 4 of the 5 tested genes involved in proteasome and for 1

of the 5 tested involved in autophagy (Fold change, FC1 < 1, Table 1). At 11°C, mRNA levels for all the monitored proteasome/autophagy-related genes were significantly higher in S_5 than in F_5 (Table 1, FC2 < 1). On D_9, mRNA levels for autophagy and proteasome genes in S_9 were higher than in F_9 regardless of the temperature (FC3-FC4). For fish that were starved for 5 days before feeding (DF_9), mRNA levels for genes coding for autophagy and proteasome were in-between, *i.e.* they were more expressed than those in F_9 (FC5 and FC6) but less than those in S_9 (FC7 and FC8). In a comparison of gene expression at different temperatures, FC values were significant (0.9 < P < 1) in half of cases, and in all except one, mRNA levels were higher at 11°C (FC9 to FC13).

Concerning fatty acid catabolism (HOAD and CPT1 genes), FC values in mRNA levels between starved and fed fish were inconsistent between D_5 and D_9 (Table 1, FC1C2/C3C4). On D_5, mRNA levels were higher in starved fish when compared to fed fish (significant FC < 1), while lower on D_9 (significant FC > 1). Results for amino acid catabolism genes (GDH, ASAT, ALAT genes) were more congruent, indicating higher mRNA levels for these genes in fed fish compared to starved fish on both D_5 and D_9. For FC values in delayed-feeding (DF) fish and fed (F) fish (FC5-6), no significant values were reached for genes involved in fatty acid catabolism. Looking at amino acid catabolism, significant FC values were above 1 at 8°C, while they were less than 1 at 11°C, suggesting that mRNA levels for amino acid catabolic genes were higher in fed fish than in delayed fed fish at low temperature, while the opposite was observed at 11°C.

Comparing DF_9 fish with S_9 fish (Table 1, FC7-8) at 11°C, almost all of the mRNA levels for genes involved in catabolism (8 among 9 tested) were higher in DF_9. At 8°C only 2 differences for amino acid catabolism genes were observed, also in favour of S_9.

Concerning the impact of temperature, significant FC values (0.9 < P < 1) were observed in a quarter of cases, and all were > 1, suggesting that genes were expressed at a higher level at 8°C than at 11°C.

*Table 1 Comparison of the gene expressions among rearing conditions. Genes involved in fatty acid and amino acid catabolism, proteasome and autophagy were studied (pathways and genes were displayed in the first columns). Fold Changes (FC) were calculated by dividing the mean expression of the condition 1 by the mean expression of the condition 2. Significant differences are in bold and * means that P(Condition 1 > Condition 2) is between 0.90 and 0.95 and ** means that P(Condition 1 > Condition 2) is between 0.95 and 1.00.*

FC values		FC1	FC2	FC3	FC4	FC5	FC6	FC7	FC8	FC9	FC10	FC11	FC12	FC13
Pathways	Genes	F_5 / S_5 8°C	F_5 / S_5 11°C	F_9 / S_9 8°C	F_9 / S_9 11°C	F_9 / DF_9 8°C	F_9 / DF_9 11°C	S_9 / DF_9 8°C	S_9 / DF_9 11°C	F_5 / F_5 8/11°C	S_5 / S_5 8/11°C	F_9 / F_9 8/11°C	S_9 / S_9 8/11°C	DF_9 / DF_9 8/11°C
Proteasome	Fbx32	**0.10****	**0.14****	**0.20****	**0.11****	**0.55***	**0.19****	**2.82****	**1.64****	**0.55****	0.78	1.20	**0.70***	**0.41****
	MuRF1	**0.10****	**0.16****	**0.10****	**0.18****	**0.33****	**0.26****	**3.17****	**1.49***	**0.33****	**0.52****	**0.67***	1.14	**0.54****
	MuRF2	**0.20****	**0.14****	**0.12****	**0.06****	**0.48****	**0.12****	**3.97****	**1.88****	1.08	0.73	1.17	**0.61***	**0.29****
	MuRF3	**0.30****	**0.23****	**0.22****	**0.13****	**0.48****	**0.23****	**2.24****	**1.74****	**0.72****	**0.56****	1.21	**0.75***	**0.59****
	Znf216	0.84	**0.65****	**0.32****	**0.32****	**0.57****	**0.60****	**1.76****	**1.89****	1.05	0.82	0.69	**0.67***	0.72
Autophagy	atg4b	**0.38****	**0.18****	**0.10****	**0.08****	**0.28****	**0.12****	**2.73****	**1.63****	**1.45***	0.70	0.78	**0.56***	**0.34****
	atg12l	0.95	**0.75***	**0.49****	**0.51****	**0.67****	**0.66****	**1.37***	1.30	1.15	0.92	**0.64***	**0.66****	**0.62****
	SQSTM1	0.65	**0.70***	**0.33****	**0.21****	**0.43****	**0.52***	1.30	**2.48****	**0.78***	0.84	0.57	0.36	**0.69***
	Mul1	0.98	**0.81***	**0.49****	**0.68****	**0.47****	0.77	0.96	1.13	1.16	0.95	**0.58***	0.80	0.95
	Bnip3	0.42	**0.28****	**0.20****	**0.19****	**0.55****	**0.33****	**2.71****	**1.75****	1.03	**0.67***	0.82	**0.76***	**0.49****
Fatty acid catabolism	HOAD	1.21	0.98	**1.32***	**1.49****	1.31	0.93	0.99	**0.63****	**1.13***	0.92	**1.25****	**1.41****	0.89
	CPT1A	**0.62****	**0.44****	1.02	**1.76***	1.50	1.26	1.47	0.72	**2.26****	**1.59***	1.19	**2.04****	1.00
	CPT1B	**0.53****	**0.46****	0.91	**3.11****	1.02	1.08	1.12	**0.35****	1.31	1.13	**1.56***	**5.32****	**1.66****
Amino acid catabolism	GDH1	1.17	0.96	1.10	1.08	**1.33****	**0.80***	1.21	**0.74****	1.03	0.84	**1.13***	**1.12***	0.68
	GDH2	1.04	0.87	1.05	0.97	**1.28***	**0.75****	1.22	**0.78***	1.02	0.85	**1.10***	1.01	0.65
	GDH3	**1.65****	**1.30***	**1.39****	**1.82****	**1.44****	1.16	1.04	**0.64****	1.11	0.88	1.02	**1.33****	0.82
	ASAT1	**1.54****	**1.42****	1.17	**1.75****	**1.31****	1.21	1.12	**0.69****	0.97	0.90	0.93	**1.38****	0.85
	ASAT2	**1.23***	1.05	0.92	1.26	1.20	0.97	**1.31****	**0.77***	0.97	0.83	0.93	1.27	0.75
	ALAT	1.16	0.82	1.13	**1.37****	**1.57****	0.96	**1.38****	**0.70****	1.26	0.89	1.33	**1.61****	0.81

Discussion

This experimental study is the first to describe the influence of temperature and food depletion on mRNA levels of genes involved in the nutritional status of brown trout at the time of the first exogenous feeding. The transition from yolk reserves to exogenous feeding is a critical period for many fish, and may lead to high mortalities (Kennedy et al., 2008). Our data have clearly shown that in case of starvation, genes involved in autophagy and proteasome were highly expressed and it was boosted at 11°C. Surprisingly, the expression of genes coding for fatty acid and amino acid catabolism was not higher during starvation at 11°C (Table S2). These results are counter-intuitive and suggest that the regulation of these catabolic pathways may occur at different levels (*e.g.* post-transcriptional regulation; Salem et al. 2007), or that some other mechanisms such as hypometabolism are at work. This study has also demonstrated that young brown trout were able to feed and grow after 5 days of starvation. However, after this short period of starvation, mortalities were recorded at 11°C but not at 8°C, suggesting that in the wild, recovery would likely be uncertain at this temperature, even if food availability was restored. Finally, results demonstrated that at 8°C, food was more efficiently converted to tissue than at 11°C.

Energetic stress indicators: autophagy and proteasomal pathways at a molecular level

During nutrient restriction, metabolism changes to provide cellular energy *via* catabolic processes. Autophagy and proteasome are induced to mobilise energy and most often occur when essential nutrients are limited (Wing et al., 1995; Mizushima, 2007). To provide metabolic fuel, autophagy degrades all potential sources of energy (proteins, lipids and glycogen) and proteasome degrades skeletal-muscle proteins. In this regard, an induction of the expression of genes involved in both pathways can indicate energetic stress. The mRNA levels were greater in fish that were starved for 5 days and these differences were exacerbated at 9 days, highlighting the metabolic distress of starving fish. Consequences of starvation were still noticeable in delayed-fed fish although food input drove the majority of them back to a normal state. These results confirm that both pathways (autophagy and proteasome) are regulated by the feeding status (Robinowitz & White, 2010; Seiliez et al., 2010). Moreover, temperature exacerbates stress induced by starvation probably in relation with a higher standard metabolic rate (Régnier et al., 2013). More energy is needed to maintain vital functions and body reserves of alevins are probably rapidly depleted, which would explain a higher induction of these

catabolic pathways at 11°C, while recovery was not boosted at a sufficient rate to compensate when food was available again.

Recovery from delayed first exogenous feeding

Introduced by Blaxter & Hempel (1963), the "point-of-no-return" (PNR) is the threshold after which fish are still alive but too weak to feed. At 8 °C, no delayed-fed fish died and they were in an intermediate state, having gained weight when compared with starved fish, but exhibiting lower performance than fed fish. PNR value is largely dependent on temperature (McGurk, 1984; Dou et al., 2002). At 11°C, starvation over a 5-day period was an intense stress and all fish were not able to recover. At D_9, for delayed-fed survivors, results were mixed. Some gained weight, but some still had the same weight loss levels than starved fish, suggesting that they reached the PNR and would not be able to recover. Fish can exhibit compensatory growth after a period of food deprivation (Nicieza & Metcalfe, 1997), but the duration of the present experiment was probably too short to detect such a phenomenon. However, there were no evidences from prey consumption rate and catabolism that a catch-up growth may arise.

Feed utilisation at different temperatures

Because brown trout are ectotherms, their growth is linked to temperature. The best energy conversion efficiency into growth for *Salmo trutta* is around 9-10°C (Marr, 1966; Blaxter, 1969; Elliott & Hurley, 2001). Our results demonstrated a better food conversion in growth efficiency at 8°C when compared to 11°C (similar weight gain and catabolism, even though feed intake was higher at 11°C). In addition, length gain was higher at 8°C. Similar results for another salmonid were found by Malzahn et al. (2003) who highlighted hyperplasia phenomenon leading to longer coregonid fish in colder water.

In the context of CC, an increase of 3.2°C in air temperature will produce a moderate but sensible increase in stream water temperature from 1 to 2°C (Bal et al., 2014). Present results suggest that this may cause higher mortality rates during the critical period of emergence, especially when in conjunction with food shortage which is not a scarce event in the wild (Kennedy et al. 2008). Besides its effect on water temperature, CC will affect flow through changes in precipitation patterns. In winter and spring, higher flows will likely magnify the effect of temperature by reducing the availability of invertebrates both through habitat reduction (Kennedy et al. op. cit.) and invertebrate washout.

Acknowledgements

Table S1: Primers used for real time RT-qPCR analysis.

Pathways	Genes	Forward primer	Reverse primer
Proteasome	Fbx32	5'-TGCGATCAAATGGATTCAAA-3'	5'-GATTGCATCATTTCCCCACT-3'
	MuRF1	5'-CTGATTAGTGGCAAGGAGCTG-3'	5'-GTAAGGTGCTCCATGTTCTCG-3'
	MuRF2	5'-TGGAGGAGTCAGAGATGGCTA-3'	5'-TCCAGGTGGGAGATGTTAGTG-3'
	MuRF3	5'-ATGTCCATTGCAGGGACTCTA-3'	5'-AACTGGGGTAAGCCATTGTGT-3'
	Znf216	5'-AAGAGGGTGGGCCTCACAG-3'	5'-GACATCCTTTTGCCACTCGT-3'
Autophagy	atg4b	5'-TATGCGCTTCCGAAAGTTGTC-3'	5'-CAGGATCGTTGGGGTTCTGC-3'
	atg12l	5'-GATGGAGGCCAATGAACAGC-3'	5'-GCGTTTGAACTGAAAAGGGCTAA-3'
	SQSTM1	5'-AGCCCACTGGGTATCGATGT-3'	5'-GGTCACGTGAGTCCATTCCT-3'
	Mul1	5'-CCACGAGATGGAGGAGATGT-3'	5'-AGAGCGTTGTGGAAGCAACT-3'
	Bnip3	5'-CCTGTGACAGTCCTCCGAGA-3'	5'-CCACTTCACGTCTCCGTTCT-3'
Fatty acid catabolism	HOAD	5'-GGACAAAGTGGCACCAGCAC-3'	5'-GGGACGGGGTTGAAGAAGTG-3'
	CPT1A	5'-TCGATTTTCAAGGGTCTTCG-3'	5'-CACAACGATCAGCAAACTGG-3'
	CPT1B	5'-CCCTAAGCAAAAAGGGTCTTCA-3'	5'-CATGATGTCACTCCCGACAG-3'
Amino acid catabolism	GDH1	5'-AACTCCGCAGCGTCTCTTTCCCCAT-3'	5'-TCACCTCATCAACAGACACCTCTTCA-3'
	GDH2	5'-ATCAAGCCCTGCAACCACGTCCT-3'	5'-TCTTCACTGTAACGGATCCCCCCTTT-3'
	GDH3	5'-CTGCAACCATATACTGAGTGTATCGTTCC-3'	5'-ATGTCATCAGCGAGGCCAGGGCTTT-3'
	ASAT1	5'-TCAAGAGTGGCAGGAACATCA-3'	5'-AGCGTCTCTGAAGATGGGTGT-3'
	ASAT2	5'-TCTGTGCCCAGTCCTTCTC-3'	5'-GGAGGGTTGGACCAGGT-3'
	ALAT	5'-TGGGTGCGTACAGTGCCAGT-3'	5'-GACGCACCCTCACCACACAC-3'

Table S2: Mean and standard deviation of mRNA levels of genes involved in fatty acid/amino-acid catabolism and proteasome/autophagy pathways. From yolk sac exhaustion, 6 fish per condition were sampled at the beginning (D_0), after 5 days (F_5, S_5) and after 9 days (F_9, S_9, DF_9) of growth at 8°C and at 11°C. Gene expression level was normalized by the abundance of exogenous luciferase RNA and has no unit. The mean low expressions are in white, intermediate expressions in light grey and high expression in dark grey.

| Pathways	Genes	Initial Conditions - D_0				F_5				F_9				S_5				S_9				DF_9			
		8°C		11°C		8°C		11°C		8°C		11°C		8°C		11°C		8°C		11°C		8°C		11°C	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Proteasome	Fbx32	0.646	0.24	0.430	0.10	0.089	0.13	0.160	0.15	0.367	0.21	0.306	0.17	0.896	0.33	1.153	0.46	1.877	0.67	2.675	1.00	0.666	0.31	1.630	1.16
	MuRF1	0.508	0.09	0.335	0.08	0.101	0.04	0.302	0.18	0.247	0.14	0.371	0.22	0.964	0.40	1.848	0.84	2.384	0.81	2.088	0.99	0.752	0.47	1.401	1.05
	MuRF2	0.767	0.39	0.698	0.22	0.192	0.05	0.178	0.06	0.236	0.13	0.202	0.11	0.949	0.31	1.297	0.43	1.960	0.71	3.237	1.21	0.493	0.12	1.725	1.19
	MuRF3	0.799	0.12	0.652	0.09	0.341	0.04	0.472	0.17	0.389	0.12	0.321	0.13	1.149	0.38	2.067	0.59	1.801	0.53	2.388	0.90	0.803	0.36	1.369	0.65
	Znf216	0.754	0.21	0.753	0.14	0.621	0.11	0.591	0.17	0.480	0.15	0.697	0.29	0.744	0.14	0.905	0.25	1.485	0.65	2.203	0.27	0.843	0.27	1.164	0.61
Autophagy	atg4b	0.610	0.28	0.664	0.18	0.357	0.08	0.245	0.09	0.224	0.12	0.286	0.15	0.951	0.35	1.350	0.29	2.146	1.24	3.801	1.58	0.787	0.12	2.328	1.19
	atg12l	0.941	0.18	0.767	0.13	0.825	0.16	0.714	0.15	0.474	0.22	0.744	0.21	0.872	0.15	0.949	0.18	0.965	0.33	1.465	0.58	0.704	0.14	1.126	0.43
	SQSTM1	0.779	0.19	1.698	0.44	1.098	0.54	1.413	0.95	0.735	0.13	1.289	0.64	1.689	1.11	2.021	0.77	2.202	1.33	6.108	1.70	1.694	0.74	2.465	1.99
	Mul1	1.651	0.88	1.443	0.29	1.131	0.33	0.976	0.51	0.470	0.32	0.803	0.24	1.153	0.20	1.211	0.33	0.954	0.44	1.187	0.43	0.992	0.19	1.049	0.34
	Bnip3	0.678	0.27	0.570	0.15	0.320	0.08	0.310	0.10	0.355	0.17	0.435	0.20	0.754	0.20	1.117	0.31	1.742	0.95	2.305	0.53	0.644	0.09	1.319	0.80
Fatty acid catabolism	HOAD	1.418	0.56	1.710	0.41	1.208	0.32	1.067	0.35	0.872	0.32	0.696	0.27	0.997	0.18	1.089	0.46	0.660	0.27	0.467	0.17	0.665	0.10	0.745	0.15
	CPT1A	1.995	0.63	2.273	0.66	0.991	0.31	0.438	0.15	0.576	0.32	0.486	0.29	1.585	0.60	0.999	0.42	0.562	0.28	0.276	0.10	0.384	0.12	0.384	0.26
	CPT1B	1.510	0.37	1.670	0.40	0.652	0.21	0.499	0.15	0.747	0.37	0.478	0.20	1.228	0.30	1.089	0.36	0.818	0.38	0.154	0.09	0.732	0.20	0.442	0.10
Amino acid catabolism	GDH1	0.801	0.28	0.959	0.14	0.955	0.18	0.929	0.30	0.872	0.29	0.772	0.31	0.814	0.09	0.972	0.41	0.794	0.17	0.712	0.18	0.656	0.10	0.966	0.17
	GDH2	0.780	0.22	0.959	0.14	0.929	0.19	0.911	0.30	0.837	0.24	0.764	0.32	0.893	0.27	1.048	0.44	0.798	0.21	0.787	0.20	0.655	0.10	1.015	0.16
	GDH3	1.015	0.22	1.209	0.20	1.318	0.14	1.185	0.29	0.945	0.36	0.928	0.42	0.799	0.09	0.913	0.29	0.678	0.18	0.510	0.20	0.655	0.18	0.799	0.13
	ASAT1	0.921	0.24	1.017	0.13	1.163	0.21	1.199	0.30	0.898	0.35	0.970	0.40	0.757	0.08	0.845	0.32	0.766	0.20	0.554	0.11	0.685	0.12	0.803	0.08
	ASAT2	0.894	0.29	0.934	0.18	0.955	0.23	0.983	0.30	0.754	0.24	0.811	0.27	0.776	0.09	0.938	0.43	0.822	0.24	0.644	0.15	0.626	0.10	0.838	0.12
	ALAT	0.963	0.27	0.892	0.38	1.030	0.12	0.820	0.21	0.871	0.25	0.654	0.23	0.885	0.08	0.996	0.27	0.768	0.10	0.477	0.26	0.555	0.09	0.684	0.08

atg12l

SQSTM1

Mul1

Gene:Luciferase mRNA

Bnip3

HOAD

CPT1A

Gene:Luciferase mRNA
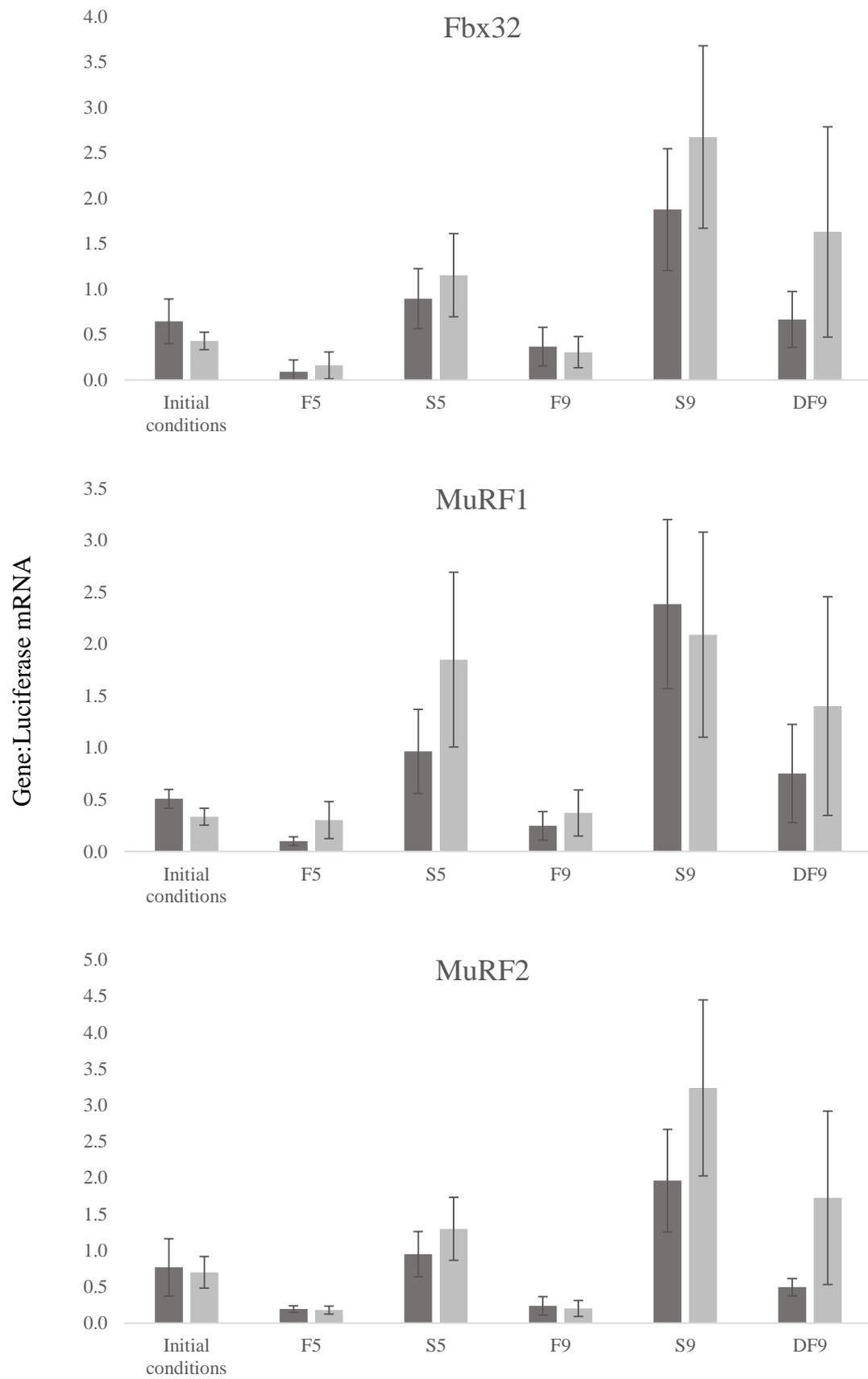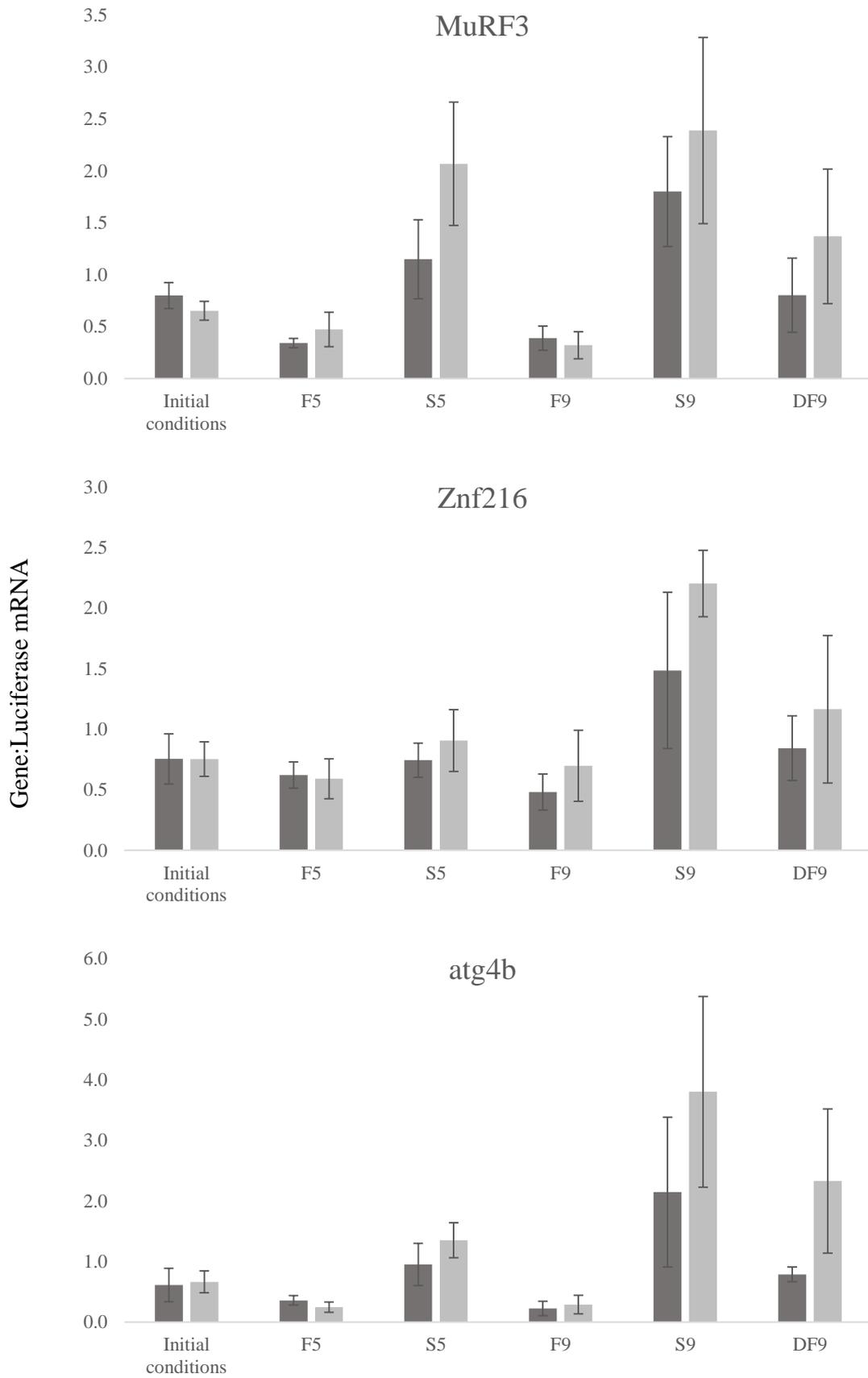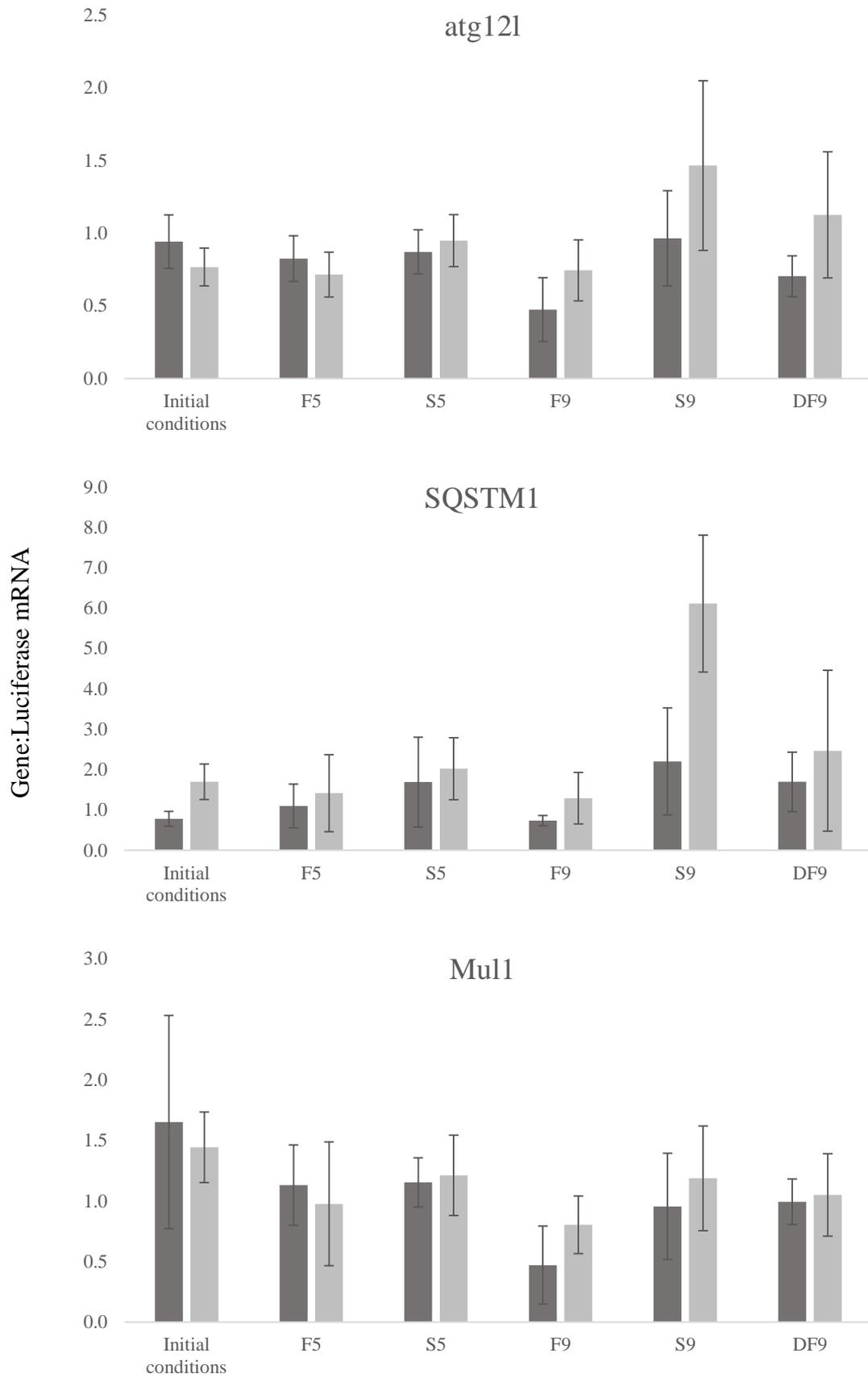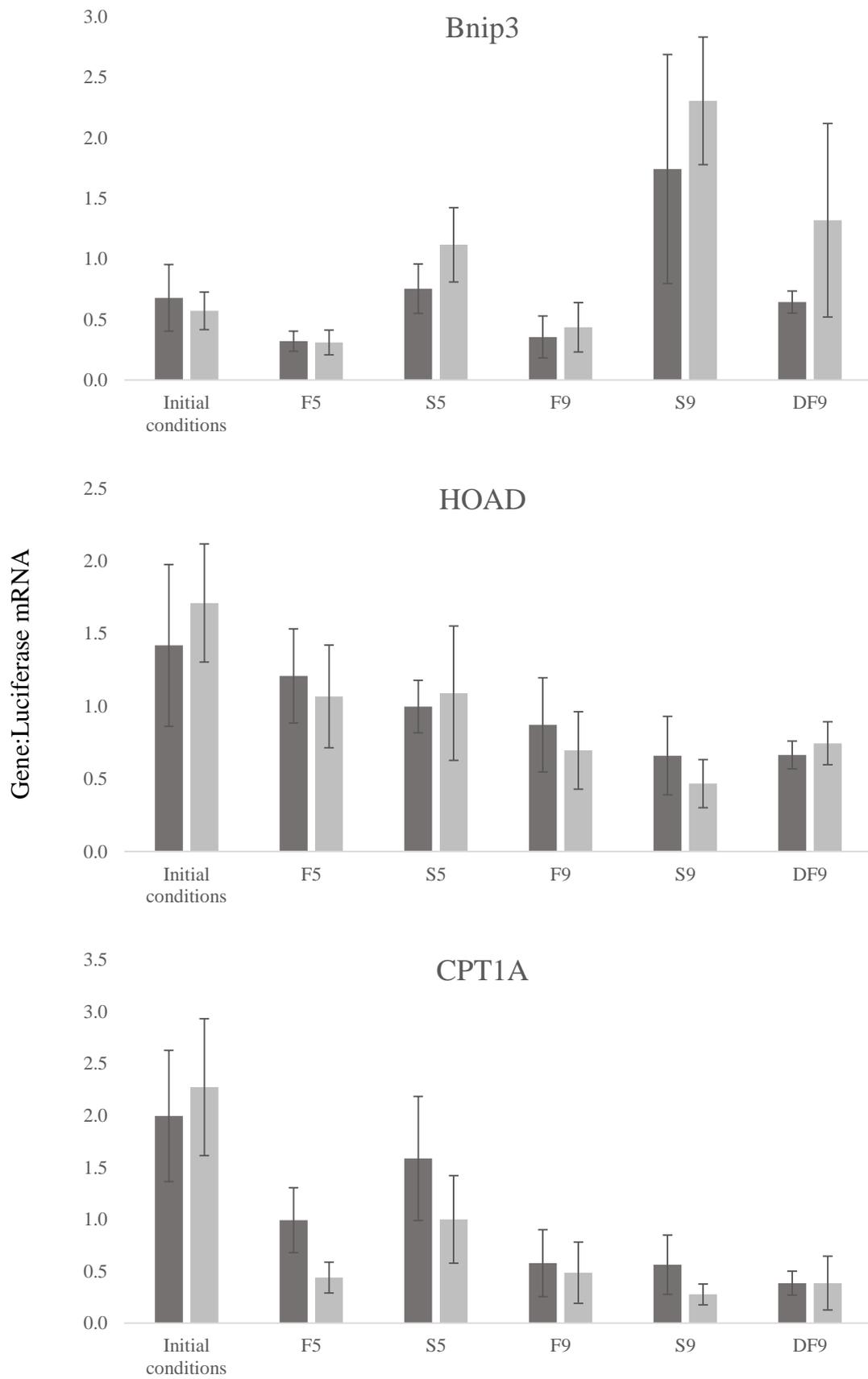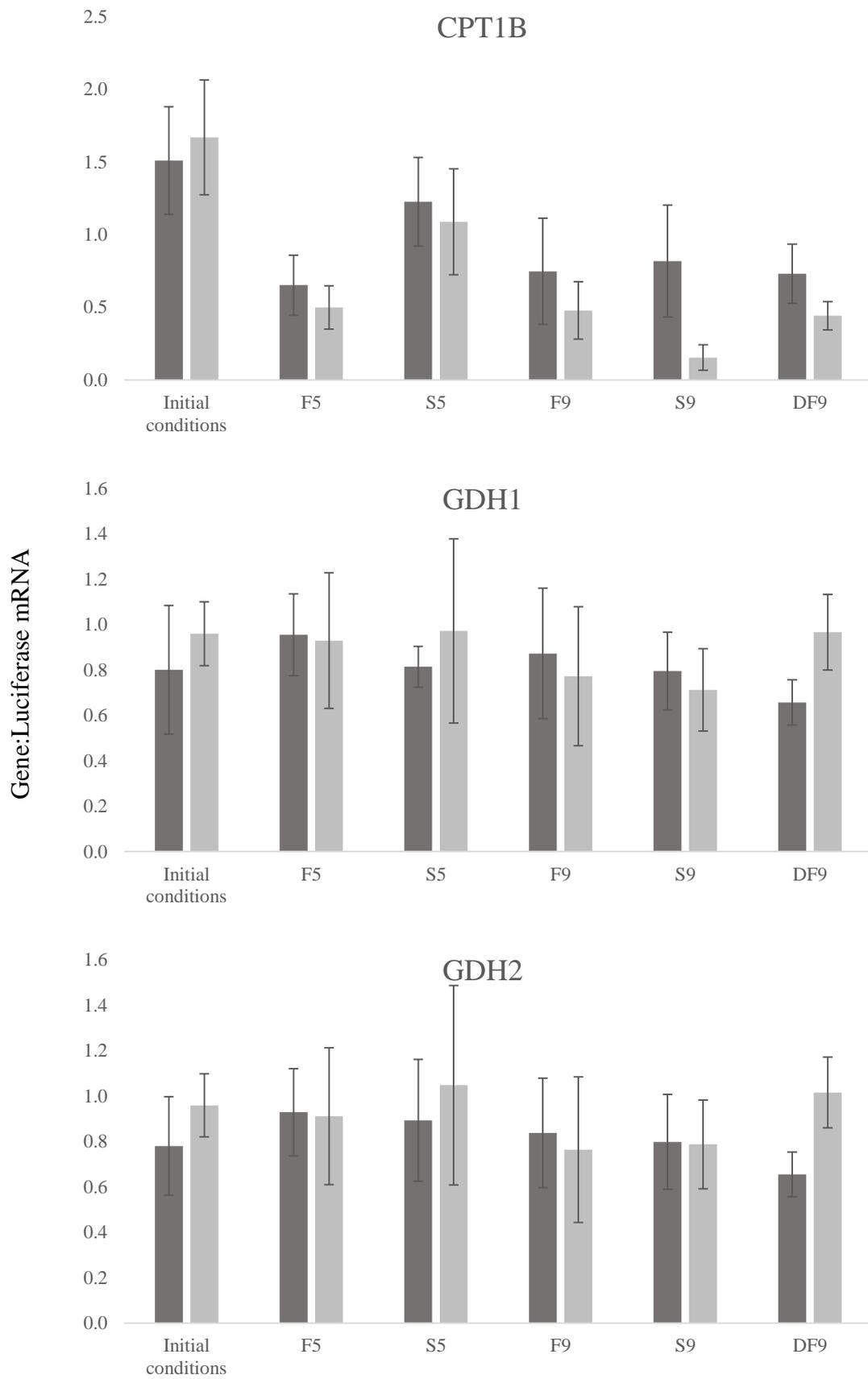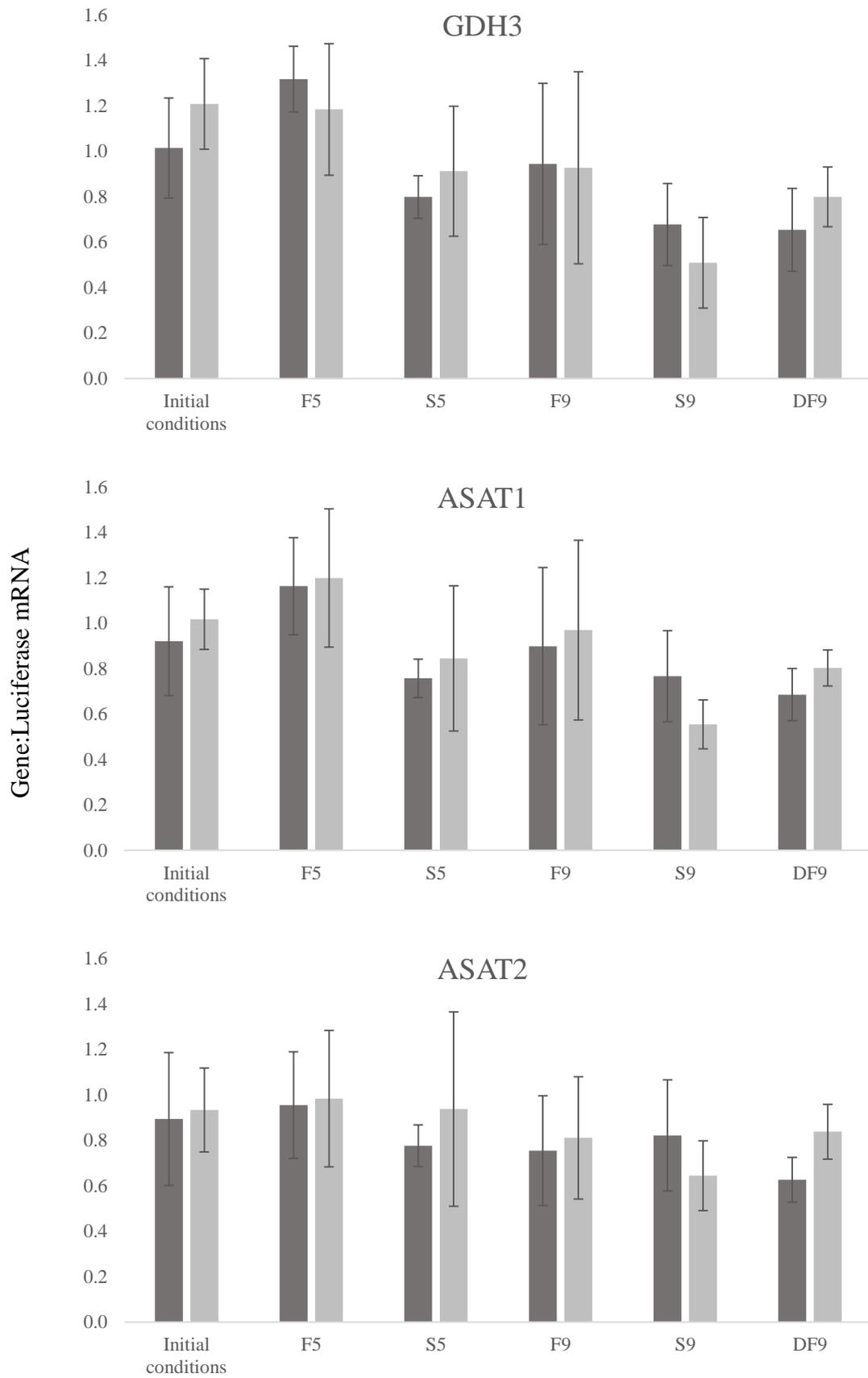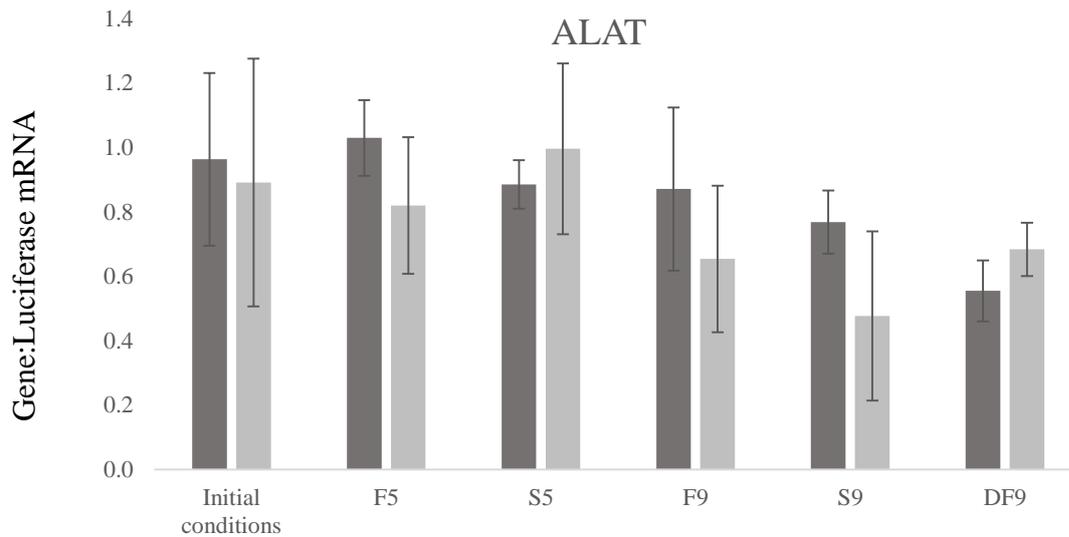
Figure S1 Mean and standard deviation of mRNA levels of genes involved in proteasome (Fbx32, MuRF1, MuRF2, MuRF3, Znf216), autophagy (atg4b, atg12l, SQSTM1, Mul1, Bnip3) pathways, fatty acid (HOAD, CPT1A, CPT1B) and amino-acid (GDH1, GDH2, GDH3, ASAT1, ASAT2, ALAT) catabolism. From yolk sac exhaustion, 6 fish per condition were sampled at the beginning (Initial conditions), after 5 days (F_5, S_5) and after 9 days (F_9, S_9, DF_9) of growth at 8°C (dark grey) and at 11°C (light grey). Gene expression level was normalized by the abundance of exogenous luciferase RNA.

Table 2.1 Synthesis of the main results on the growth and metabolism of starved and delayed first-feeding alevins at 8 and 11°C.

Temperature	Starvation		Delayed First-feeding
8°C	↘ Growth	Biometric data	Recovery
	Similar to F & DF fish *Body reserves still available?*	Lipid & AA catabolism	Similar to F fish
	+++	Autophagy & Proteasome	+
11°C	↘↘ Growth	Biometric data	Contrasted recovery
	↘↘ Gene expression *Reserves depleted? Hypometabolism?*	Lipid & AA catabolism	Intermediate state
	++++	Autophagy & Proteasome	++

Further considerations and discussion

In the present paper, analyses were focused on averages of mRNA levels according to conditions, while variance was not commented as an informative factor by itself because of the paper format chosen (brief communication). Because I thought it might brought interesting developments, I include this analysis here. After 9 days of experiment, standard deviation values of mRNA levels of genes coding for fatty acid and amino acid catabolism ranged from 0.09 to 0.42, while standard deviations of genes involved in proteasome and autophagy ranged from 0.11 to 1.99 (Figure 2.2). The important standard deviations of genes involved in proteasome and autophagy indicate that individual response to the treatment varied a lot. Considering weight as a reveller of stress induced by starvation (the individuals suffering most from starving being those losing more weight), we tested if the induction of these genes correlated with the weight. We hypothesised that the alevins suffering most from starvation should be those who had lost more mass and that they should be the individuals in which the expression of genes involved in proteasome and autophagy was maximized.
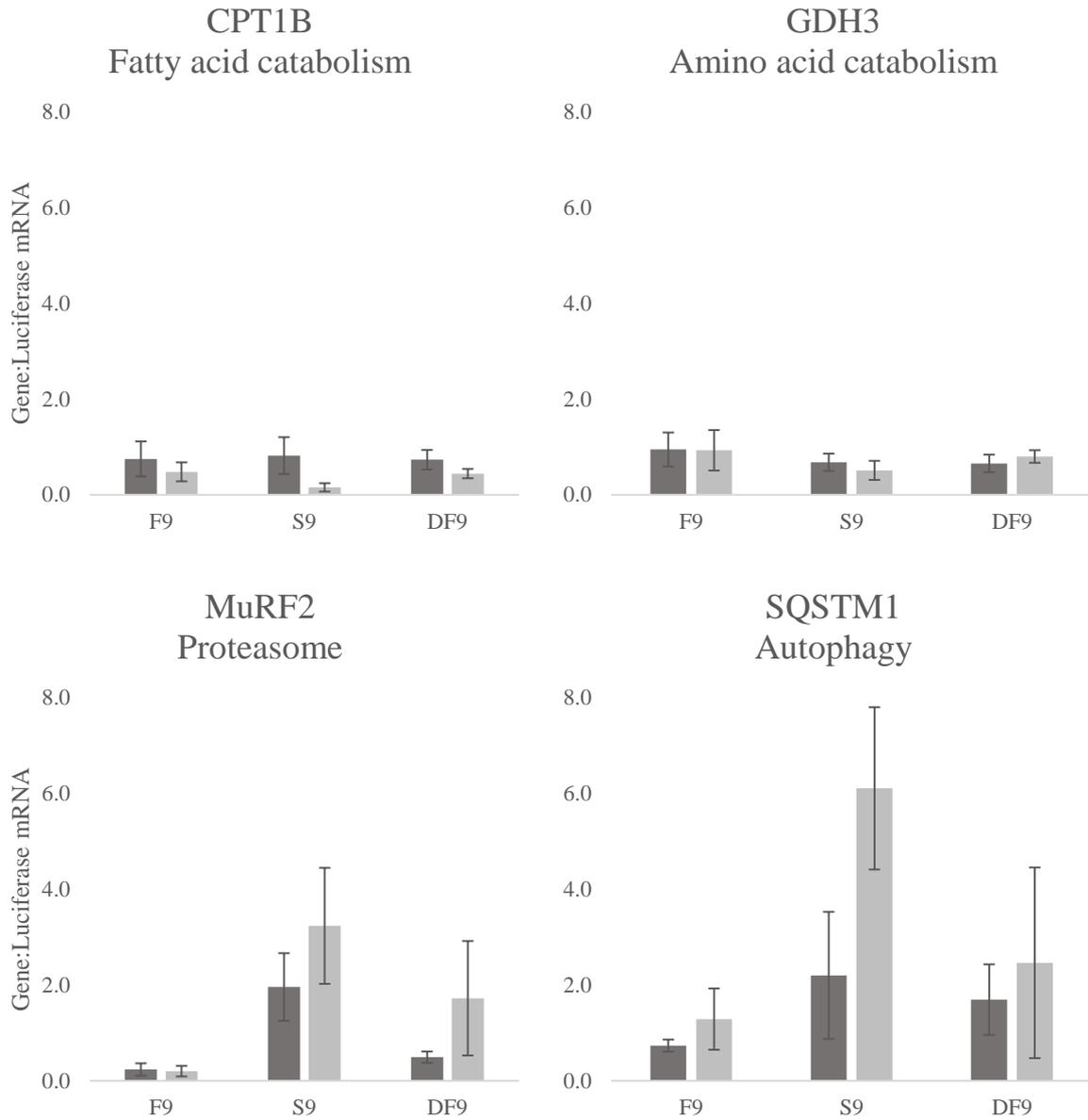
Figure 2.2 Mean mRNA levels of genes involved in fatty acid (CPT1B), amino acid catabolism (GDH3), proteasome (MuRF2) and autophagy (SQSTM1) according to the treatment (Fed F_9, Starved S_9 or Delayed-First feeding DF_9) after 9 days of experiment. mRNA levels were normalized by the abundance of exogenous luciferase RNA. Bars represent standard deviation. Alevins reared at 8°C are represented in dark grey and those reared at 11°C are in light grey.

Considering only data of the 9th day, correlations were tested with OpenBUGS® with estimations of coefficients for each j condition (F_9, S_9 and DF_9). If X_i is the mRNA level of the ith individual, we assumed:

$$X_i = a_{j[i]} \, Wg_i + b_{j[i]}$$

With $a_{j[i]}$ the slope coefficient and $b_{j[i]}$ the intercept, both estimated according to j conditions. Individual weight gain (WG_i) was calculated as follows:

$$WG_i = \frac{Final\ Weight_i - Initial\ Weight_i}{Initial\ Weight_i}$$

Fit of the correlation was calculated by dividing the variability unexplained by the correlation model with the variability observed in the data set as follows:

$$Fit = 1 - \frac{Variability\ unexplained\ by\ the\ model}{Variability\ of\ the\ data\ set}$$

When the fit was between 0.5 and 1, the correlation between mRNA levels and WG was good. When the fit was between 0 and 0.5, the correlation was intermediate and when the fit is negative, there was no correlation. For each condition (fed F_9, starved S_9 and delayed first-feeding DF_9), we tried to link individual weight gain with the expression of the autophagy and proteasome related genes. The fit represented the strength of the relationship, then a represented the direction of the relationship and b the intercept. A total of 30 relationships were tested (3 conditions x 10 genes).

For fed fish (F_9), considering 10 correlations between individual weight gain and mRNA levels, 8 fits were negative (Table 2.2). The majority of the parameters (7/10 intercepts and 8/10 slope coefficients) were equal to 0. This means that mRNA levels of genes involved in these pathways were very low and no relationship between weight gain (WG) and mRNA levels was observed. For starved fish (S_9), fits were intermediate, ranging from 0 to 0.30. 7 slope coefficients (a) were significantly lower than 0. For delayed first-feeding fish (DF_9), 9 fits were good, over 0.44 (except Mul1). 9 slope coefficients (a) were significantly lower than 0. It appeared that when fish face periods of food deprivation (S_9 and DF_9), the more they lost weight, the more genes involved in proteasome and autophagy were expressed. Moreover, whatever the gene considered, F_9 and S_9 constituted two distinct groups of individuals, while DF_9 made the link between F_9 and S_9 (Figure 2.3).

Fbx32

MuRF1

MuRF2

Gene:Luciferase mRNA

Individual Weight Gain (WG)

Temperature

	8°C	11°C
F_9	●	●
DF_9	▲	▲
S_9	■	■

Conditions

MuRF3

Znf216

Gene:Luciferase mRNA

atg4b

Individual Weight Gain (WG)

atg12l

SQSTM1

Mul1

Gene:Luciferase mRNA

Individual Weight Gain (WG)
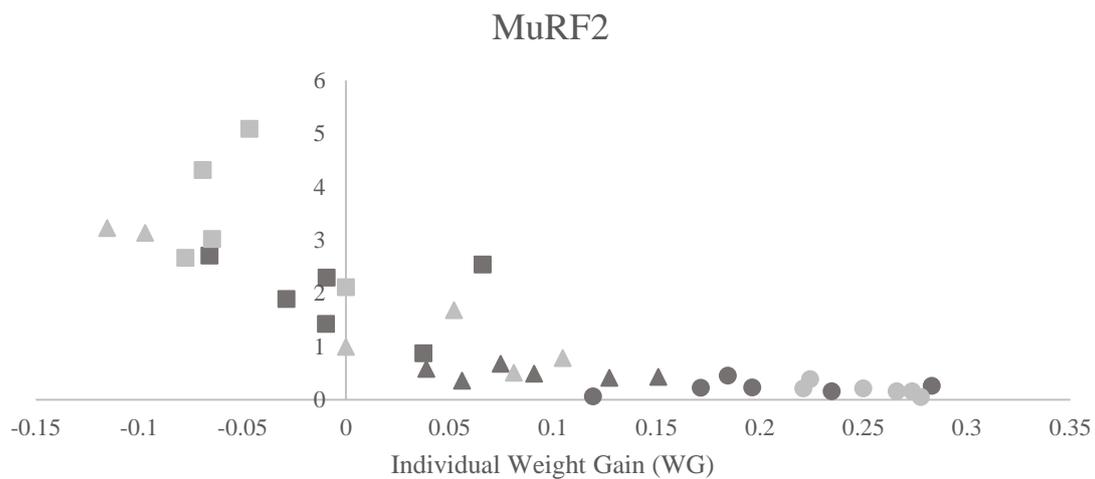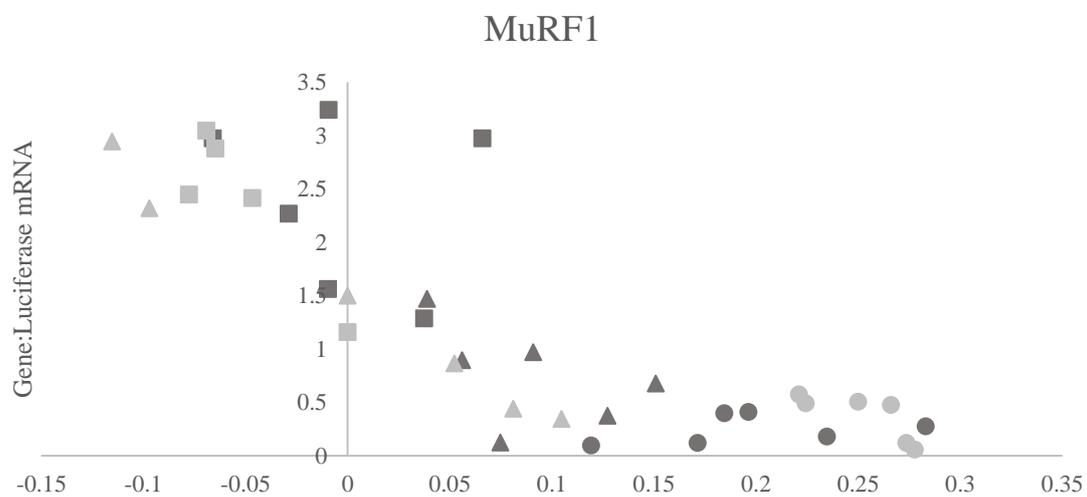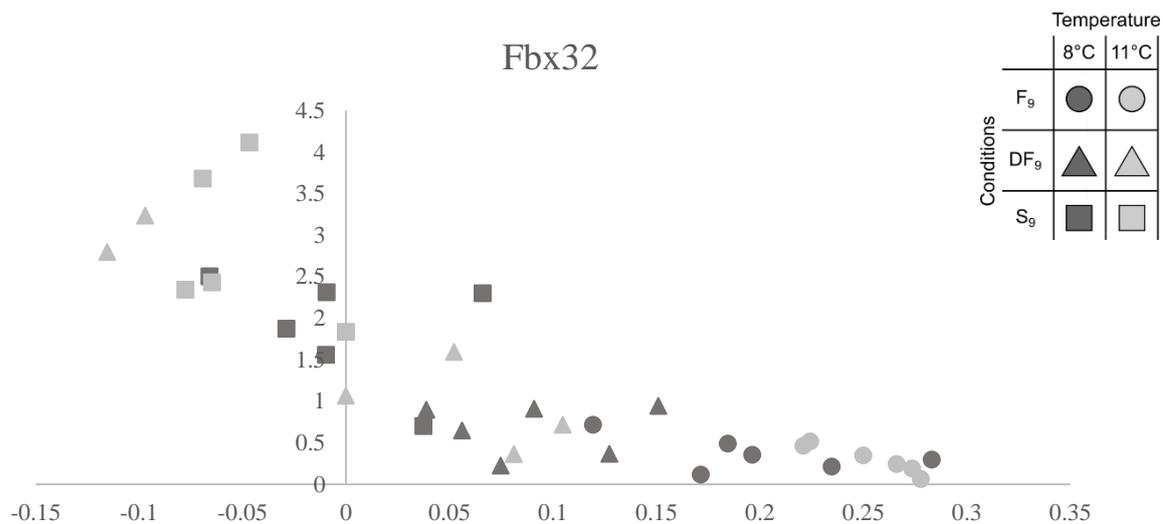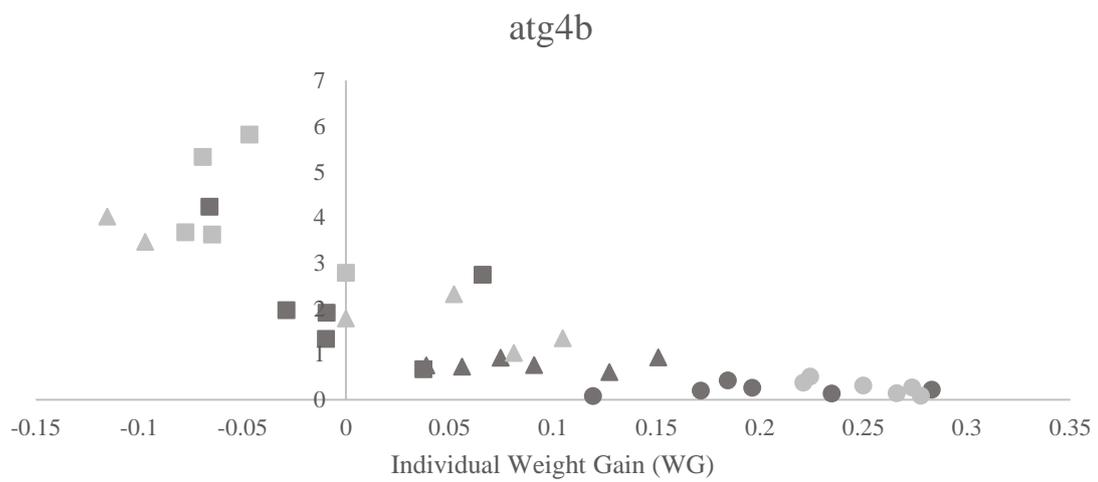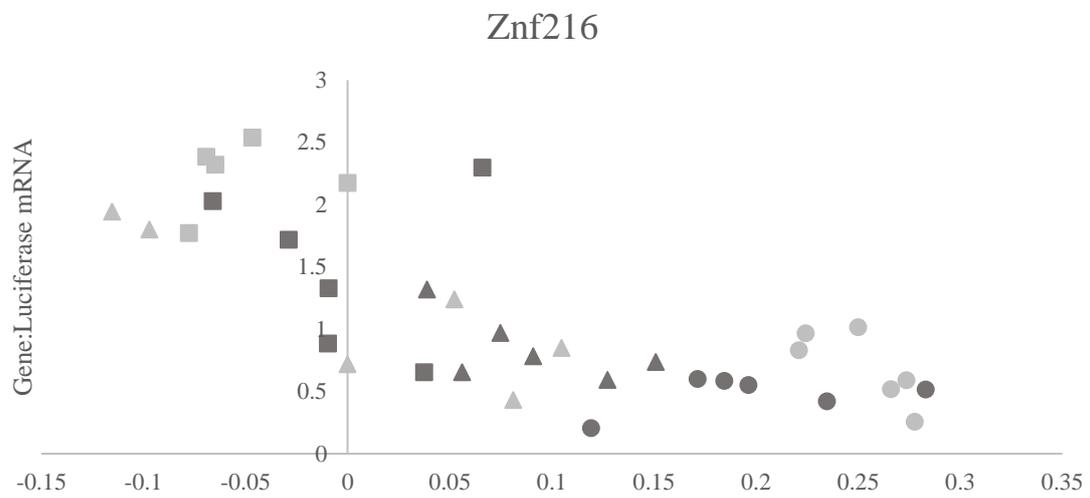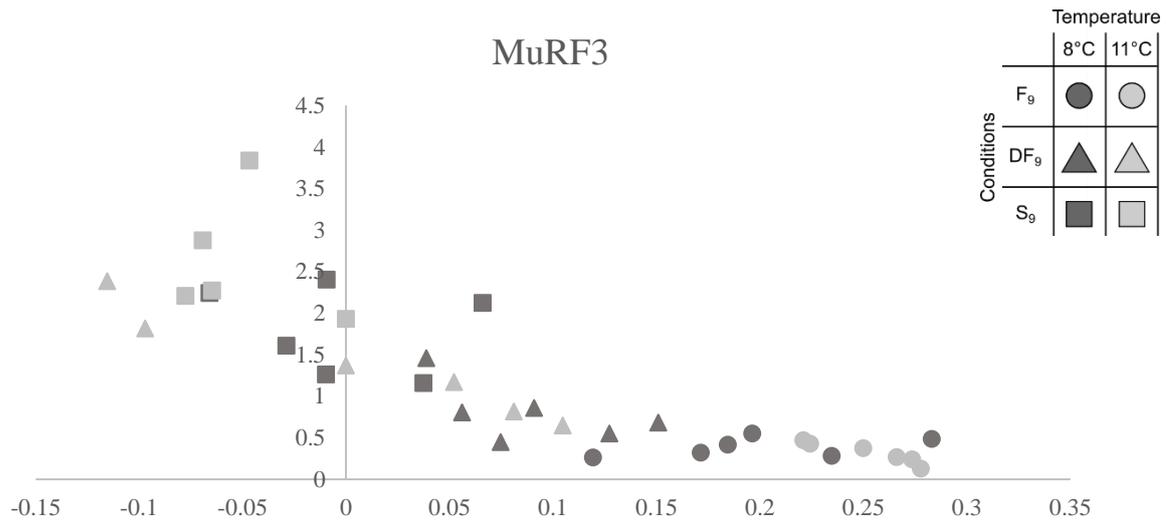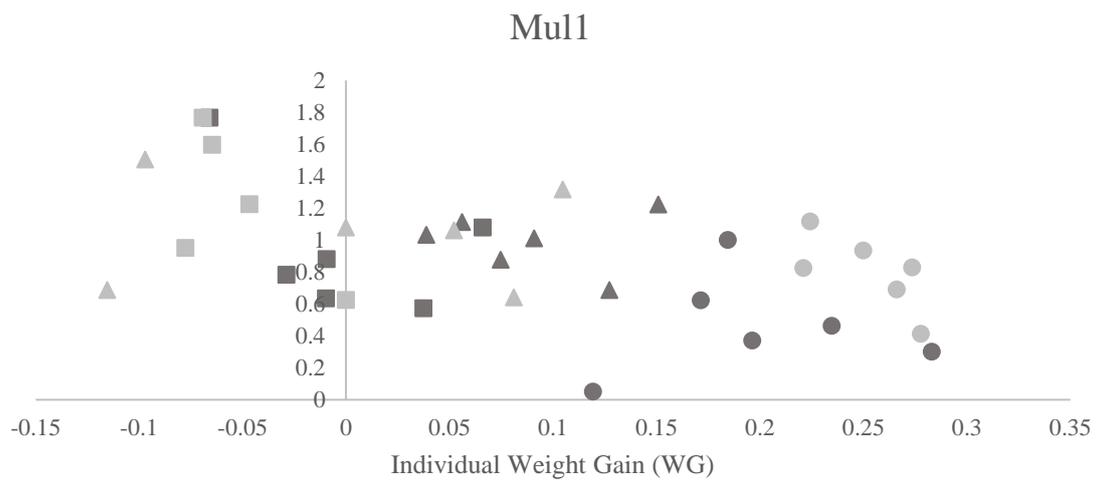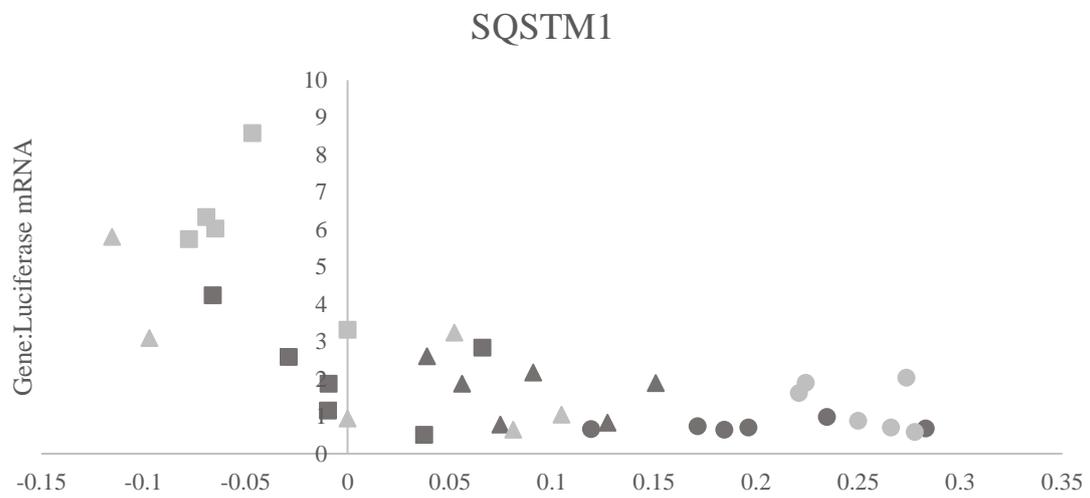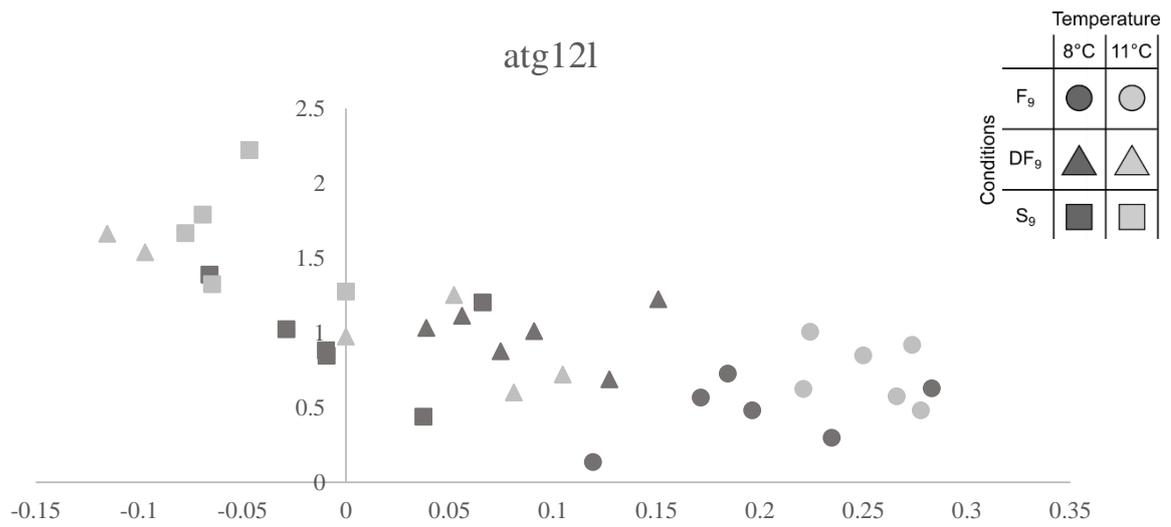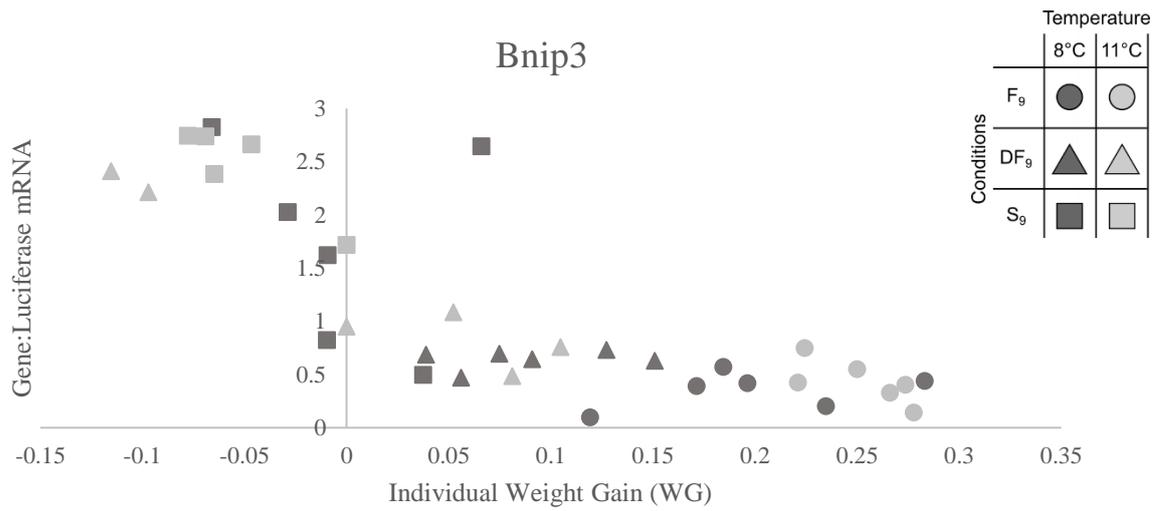
Figure 2.3 mRNA levels according to Individual Weight Gain for genes involved in proteasome (Fbx32, MuRF1, MuRF2, MuRF3 and Znf216) and autophagy (atg4b, atg12l, SQSTM1, Mul1, Bnip3) pathways. Dark items represent alevins reared at 8°C and light items represent alevins reared at 11°C. Fed fish F₉ are in circles, delayed-fed fish DF₉ are in triangle and starved fish S₉ are in square.

Table 2.2 Correlations between mRNA levels (Y) and individual weight gain (Wg; X) of alevins, mean of posterior probability distribution functions of a (the slope coefficient), b (the intercept) and fit of the models. Parameters were considered significant when P(X > 0) is less than 0.10 or above 0.90 (in bold).

| Conditions	Pathways	Genes	a	P(a > 0)	b	P(b > 0)	Equations	Fit
F_9	Proteasome	Fbx32	-2.33	**0.02**	0.86	**1.00**	Fbx32 = -2.329 Wg + 0.8606	0.29
		MuRF1	0.40	0.63	0.22	0.77	MuRF1 = 0.402 Wg + 0.2188	-0.15
		MuRF2	-0.22	0.39	0.27	**0.92**	MuRF2 = -0.2178 Wg + 0.2678	-0.16
		MuRF3	-0.42	0.31	0.45	**0.98**	MuRF3 = -0.4177 Wg + 0.4493	-0.14
		Znf216	0.86	0.70	0.39	0.85	Znf216 = 0.8641 Wg + 0.3935	-0.12
	Autophagy	atg4b	-0.02	0.49	0.26	0.88	atg4b = -0.01875 Wg + 0.2598	-0.16
		atg12l	2.19	**0.91**	0.12	0.63	atg12l = 2.187 Wg + 0.1172	0.08
		SQSTM1	2.14	0.75	0.53	0.76	SQSTM1 = 2.142 Wg + 0.5299	-0.08
		Mul1	1.41	0.75	0.32	0.75	Mul1 = 1.406 Wg + 0.3199	-0.09
		Bnip3	0.45	0.64	0.29	0.84	Bnip3 = 0.4489 Wg + 0.2939	-0.14
S_9	Proteasome	Fbx32	-7.97	**0.07**	2.14	**1.00**	Fbx32 = -7.969 Wg + 2.136	0.18
		MuRF1	-4.29	0.18	2.28	**1.00**	MuRF1 = -4.287 Wg + 2.279	0.00
		MuRF2	-8.63	**0.09**	2.42	**1.00**	MuRF2 = -8.627 Wg + 2.422	0.17
		MuRF3	-5.71	0.11	2.03	**1.00**	MuRF3 = -5.711 Wg + 2.034	0.09
		Znf216	-4.12	0.16	1.73	**1.00**	Znf216 = -4.124 Wg + 1.725	0.01
	Autophagy	atg4b	-11.75	**0.06**	2.81	**1.00**	atg4b = -11.75 Wg + 2.808	0.26
		atg12l	-5.88	**0.03**	1.14	**1.00**	atg12l = -5.88 Wg + 1.137	0.27
		SQSTM1	-11.72	**0.10**	3.63	**1.00**	SQSTM1 = -11.72 Wg + 3.626	0.21
		Mul1	-5.40	**0.03**	0.95	**1.00**	Mul1 = -5.399 Wg + 0.9494	0.26
		Bnip3	-7.21	**0.07**	1.89	**1.00**	Bnip3 = -7.207 Wg + 1.888	0.18
DF_9	Proteasome	Fbx32	-9.52	**0.00**	1.60	**1.00**	Fbx32 = -9.517 Wg + 1.596	0.70
		MuRF1	-9.25	**0.00**	1.51	**1.00**	MuRF1 = -9.253 Wg + 1.511	0.81
		MuRF2	-10.82	**0.00**	1.62	**1.00**	MuRF2 = -10.82 Wg + 1.616	0.77
		MuRF3	-6.45	**0.00**	1.39	**1.00**	MuRF3 = -6.451 Wg + 1.389	0.82
		Znf216	-4.78	**0.00**	1.23	**1.00**	Znf216 = -4.777 Wg + 1.227	0.64
	Autophagy	atg4b	-11.60	**0.00**	2.10	**1.00**	atg4b = -11.6 Wg + 2.102	0.74
		atg12l	-4.09	**0.00**	1.11	**1.00**	atg12l = -4.09 Wg + 1.107	0.76
		SQSTM1	-10.89	**0.01**	2.58	**1.00**	SQSTM1 = -10.89 Wg + 2.584	0.44
		Mul1	-0.31	0.38	1.04	**1.00**	Mul1 = -0.3092 Wg + 1.035	-0.15
		Bnip3	-6.89	**0.00**	1.31	**1.00**	Bnip3 = -6.891 Wg + 1.306	0.76

The results confirm that mobilisation of protein stored in muscles results in a loss of weight (Sandri 2010). Late access to food (DF_9) would induce a decrease in proteolytic activity for some alevins which would probably come back to a normal metabolic activity and survive, but the DF alevins with still high mRNA levels for these genes on the 9th day would probably die in the following hours/days. Further analyses measuring the expression of these genes on alevins in the wild could help to assess the starving situation of 0^+ fish. Indeed, if it is possible to use them as markers of metabolic stress, they would be an indicator of the alevin access to trophic resources.

According to the results of the present experiment conducted in controlled environment, alevins can survive only a 9-day period to starvation once the yolk sac is exhausted and warmer temperature clearly intensifies the metabolic distress. Consequently, survival and growth of salmonid alevins would be threatened by Global Climate Change because of the increase in starvation risk. However, these results should be considered with caution and may be difficult to transpose to the wild due to additional factors such as the cost of swimming, the risk of predation and the impact of competition and territoriality that may also increase.

Chapter III Consequences of Global Climate Change on the community of invertebrates, on the survival, growth and behaviour of first-feeding alevins at high density: flood simulation in a semi-natural environment

Previous chapters investigated factors triggering entry rate in the drift of invertebrates and the response of alevins to periods of food deprivation. Both were carried out under laboratory conditions. This third chapter attempts to connect the response of invertebrates with the response of alevins following a flood. In the field, heterogeneity of the environment makes difficult to separate the effect of floods from others abiotic factors. To overcome this, we used an experimental river fed naturally where some abiotic factors can be controlled (flow rate, water levels, gravel bed and the community of vertebrates).

Manuscript in preparation

Assessment of Global Climate Change on the community of invertebrates, on the survival, growth and behaviour of first-feeding alevins: flood simulation in a semi-natural environment

Introduction

Precipitation projections for 2100 from the Intergovernmental Panel on Climate Change (IPCC) forecast an increase of the average precipitation in Northern and Central Europe from October to March, while no change or a moderate reduction is expected in Southern Europe and Mediterranean (IPCC 2013). Then, Global Climate Change should increase precipitation during winter and spring in the northern distribution range of brown trout and freshwater ecosystems should face more frequent and extreme floods. Such events should lead to a decrease in the abundance of benthic invertebrates (Nislow et al. 2002; McMullen & Lytle 2012). As the number of invertebrates drifting is linked with benthic abundances (*i.e.* the benthic-drift hypothesis; McLay 1968; Hildebrand 1974; Kennedy et al. 2014), food availability for drift-feeding fish could be reduced. At the time of emergence, alevins have a limited amount of reserves and need to feed quickly to avoid mortality (Cushing 1972; Skoglund & Barlaup 2006). A desynchronization of species phenology could occur with a limited quantity of prey when alevins need to feed (*i.e.* the Match-mismatch hypothesis; Cushing 1990). Additionally, behaviour of alevins such as foraging activity, aggressive behaviours and dominance relationships could be modified by the scarcity of prey (Keeley 2000).

During reproduction, females dig nests in the gravel, drop hundreds to thousands of eggs immediately fertilised by males and they cover the clutch with gravel. As the development of the eggs depends largely on temperature, individuals of the same clutch are subjected to the

same conditions and hatch at the same time. Similarly, the emergence is quite synchronous between the individuals of the same clutch but also between the clutches laid simultaneously. Consequently, densities of just-emerging alevins can be very high (Jenkins et al. 1999). As salmonids are territorial species, alevins establish territories progressively (Grant 1997) and defend a feeding position to ensure a positive net energy balance and to optimise the energy gained. Territoriality and aggressive interactions can be noted as early as the first day after emergence (Kalleberg 1958) or 2.5 days after emergence (Titus & Mosegaard 1991). The size of the territory is related to the size of fish and alevins defend small areas (0.1–0.2 m² – Grant & Kramer 1990; Grant et al. 1998). However, the territory size and the intensity of the competition are influenced by other factors including competitor density, resource density and resource distribution in space and time (Brown 1964). The timing of the emergence plays an important role in competition and alevins emerging early can settle in more profitable position than congeners emerging later (Metcalfe & Thorpe 1992; Einum & Fleming 1999; Johnsson et al. 1999). The threshold model of feeding territoriality (Carpenter 1987) predicts that animals defend feeding territories according to the food abundance: when the food is too scarce, territorial individuals have a lower fitness compared to non-territorial ones; on the contrary, when food is superabundant, non-territorial individuals gain the same amount of food as territorial ones without paying the cost of defence (Grant et al. 2002; Brännäs et al. 2003; Imre et al. 2004).

The social hierarchy is organized by dominant individuals, subdominant and less aggressive, subordinate fish (Adams et al. 1998; Sloman et al. 2000). Generally, large individuals have the higher growth potential and dominate their congeners and the access to the best stream positions affording maximum potential profits (Chapman 1962; Mason & Chapman 1965; Fausch 1984). Indeed, high metabolic turnover rate is needed to allocate energy both to somatic growth and to territorial defence.

The diminution in prey availability would increase both territory size and foraging activity of alevins to increase encounter rate of prey (Biro et al. 2003) and maintain a constant abundance of food (Toobaie & Grant 2013). This would result in alevins emigration or death and a decrease in fish density when food abundance is low. Aggressive behaviour of young brown trout impacts their growth and survival and influence significantly the population dynamics (Biro et al. 2003) and it is necessary to consider events occurring at the individual level to understand these regulatory mechanisms (Titus 1990). Salmonid abundance is related to the individual territory size, consequently, any environmental factor affecting territoriality should affect

population density (Grant et al. 1998). Moreover, food availability for fish depends on the productivity of the system and it is established that productivity is low during winter and increases in spring when day length, brightness and temperature increase (Sumner & Fischer 1979; Nakano & Murakami 2001).

So, in order to assess the interaction between flood and some components of the ecosystem phenology (emergence timing and invertebrate production) on young salmonid performances, we conducted two experiments at different timing (early and late spring). In a semi-natural stream, we put first-feeding fish in large cages (to assess performances) and in small cages (to monitor behaviour). Then, we compared invertebrate production as well as alevins performances and behaviour according to the occurrence or the absence of a hydraulic disturbance (artificial flood) just before alevins release.

We aimed to test the following hypotheses:

1. Flood should diminish the abundance of invertebrates,

2. Flood should diminish food availability for fish, which should reduce growth and survival of alevins,

3. Flood should lead to an increase in alevins activity to search for prey and a more intense competition between congeners,

4. Ecosystem productivity should increase between early and late spring.

Material and Methods

Experimental design

The Lapitxuri semi-natural stream is a 2.80 m wide channel divided into 13 reaches of 10 m long each. Water is diverted from a tributary of the river Nivelle located near the French-Spanish border in the upstream part of the Nivelle watershed. Lapitxuri tributary is a typical trout brook characterized by a good water quality. We realized two trials of the same experiment, one in early and one in late spring. The experiment took place in two reaches of the artificial stream (30 m² each) located in the middle of its course (60 m downstream the flow entry). Flow was kept constant during the whole experiment (60 L s^{-1}). On 11/02/2016, three large cages (LxWxH: 100x100x50 cm − 1 m²; growth cages) and two small cages (LxWxH: 50x25x50 cm − 0.0125 m²; observation cages) were set up into each reach (Figure 1). The cages were buried 10 cm deep in the substrate. The particle size distribution was the same in all cages,

i.e. cobbles and pebbles ranging from 1 cm to 5 cm in size. The upstream and downstream gates of the cages (facing the water flow) were kept open to let the invertebrates colonise the cages until the beginning of the experiment. When fish were placed, they were closed to prevent the emigration of fish. The mesh size of the cages was 1 mm (even in the buried floor), except on the upstream gate, which was 2 mm to allow entering small invertebrates. Inside the cages water velocity was 5.16 cm s^{-1} (SD = 1.44) and water depth 12.57 cm (SD = 1.45) on average during the experiment. The large cages were used to study alevins growth and survival, while the small cages were used to study alevins behaviour. The observation cages were installed in front of the window of two underwater observation rooms. In the upstream reach, observation cages were located on the left bank at 4 m from the upstream limit of the reach. In the downstream reach, observation cages were located on the right bank at 2 m from the upstream limit of the reach (Figure 1).

Two trials took place, one in March (early spring) and one in April-May (late spring). Reach 1 (upstream) was used as Control Reach, whilst Reach 2 (downstream) was used as Impacted Reach (flood simulation). In the early spring (first trial) two growth cages were used in the "Control" and in the "Flood" Reaches. They were taken out before the second trial. Only one growth cage per reach was used in late spring (second trial).

To simulate the effect of a scouring flood, the out-flow coming from the flexible hose of a motor-pump was directed downward with a 30° angle to the gravel for 10 seconds, disturbing the gravel on a 20 cm wide and 50 cm long area. The flooding operation started at the right bank of the upstream end of the reach 2, then the pump was displaced by 20 cm to the left and used again for 10 seconds. This procedure was repeated over the entire width of the reach (14 times) and such transects were made every 50 cm to cover the entire area of the reach. The use of the motor-pump increased the mean water velocity to 97.74 cm s^{-1} (SD = 29.42) at 50 cm in front of the outflow. These velocities are comparable to velocities measured in the Nivelle river during a Q_{10} flood (*i.e.* a flood that has a 10% chance to occur due to its high intensity – see Figure S1 and Table S1 in Supplementary Information). After the flood simulation, the gravel bed was flattened again.

Fish processing

First-feeding alevins were randomly split in batches: four fish per batch for the observation cages and thirty-two alevins per batch for the growth cages. All of them were individually weighted, measured (total body length, BL), photographed for individual identification using melanophore distribution patterns (Garcia de Leaniz et al. 1994) and released in control and

impacted cage the same day, or the day after the artificial flood. Fish density in both growth and behaviour cages was 32 fish m^{-2}. At the end of the experiment, all the surviving alevins were manually recovered (after 22/21 days in the growth cages, and 21/15 days in small cages, Table 1) and left fasting 24h. They were then anaesthetised, individually weighted, measured (BL), photographed and subjected to a benzocaine lethal anesthesia.

In order to monitor individual behaviour, fish were marked with Visible Implant Elastomer (VIE) alongside the anal fin (Olsen & Vøllestad 2001). Three days before fish release, a forty fish devoted to the observation cages were anaesthetised and tagged. Three fluorescent VIEs were used (Orange, Green and Blue), together with the non-fluorescent white colour (Figure 1). On the release day, four fish per colour were chosen according to the quality of the mark. They were anaesthetised, weighted, measured and allocated to the four observation cages (each cage received four fish having a different VIE-tag colour). Behavioural surveys were done three times a day, every day during the establishment of the hierarchy (the first week) and every two days during the second week . Surveys were done around 10:00am, 1:00pm and 4:00pm. For each cage, the location of all fish was first noted on a tridimensional map of the cage. Then, focus observations started for each targeted fish for 5 minutes (successively) and the following behaviours were noted: (*i*) prevailing activity (2 states: resting on the substratum or swimming), (*ii*) number of catch prey attempts, (*iii*) distance of capture (3 categories: short < 2 cm, medium = 2-5 cm, long > 5 cm), and (*iv*) number of attacks given (4 types: intimidation, charge, nip or chase – Adams et al. 1995) or (*v*) reaction to attack (3 types: no reaction, fleeing, riposte).

Benthic invertebrate sampling

Immediately after the flood simulation (07/03/2016 and 21/04/2016) and at the end of the experiment (30/03/2016 and 12/05/2016), 3 invertebrate samples were randomly collected in growth cages. Sampling was carried out by burying a corer (ø: 13 cm) 10 cm deep in the substrate. Gravels and pebbles were then gently removed and the invertebrates in the pipe pumped, recovered in a 500 μm sieve and preserved in 70% ethanol. This was repeated 3 times per cage, providing 12 invertebrate samples for the early spring trial and 6 for the late spring one. Invertebrates were identified and assigned to different groups: Diptera, Trichoptera, Ephemeroptera, Mollusca, Coleoptera, Plecoptera, Oligochaeta, Crustacea and "Others".

The origin of the fish as well as the main environmental characteristics during each trial are summarized in Table 1.

Table 1 Date, conditions and events at each step of the experiment for both trials (in early spring and in late spring).

	1st trial – Early spring	2nd trial – Late spring
Origin of genitors	Wild Nivelle watershed	Produced by INRA experimental facilities (Lees-Athas)
Rearing temperature (°C)	9.00 (SD = 2.33)	8.58 (SD = 1.37)
Development of alevins (Degree-days) at the time of release	787	740
Flood simulation		
Mean water velocity (cm s^{-1})	86.37 (SD = 23.25)	109.37 (SD = 30.50)
Minimum water velocity (cm s^{-1})	51	51
Maximum water velocity (cm s^{-1})	150	217
Number of benthos samples	24	12
Observation period (days)	21	15
Number of surveys	40	36
Fish growth period (days)	22	21
Mean water temperature (°C)	10.58 (SD = 0.9)	12.33 (SD = 1.4)
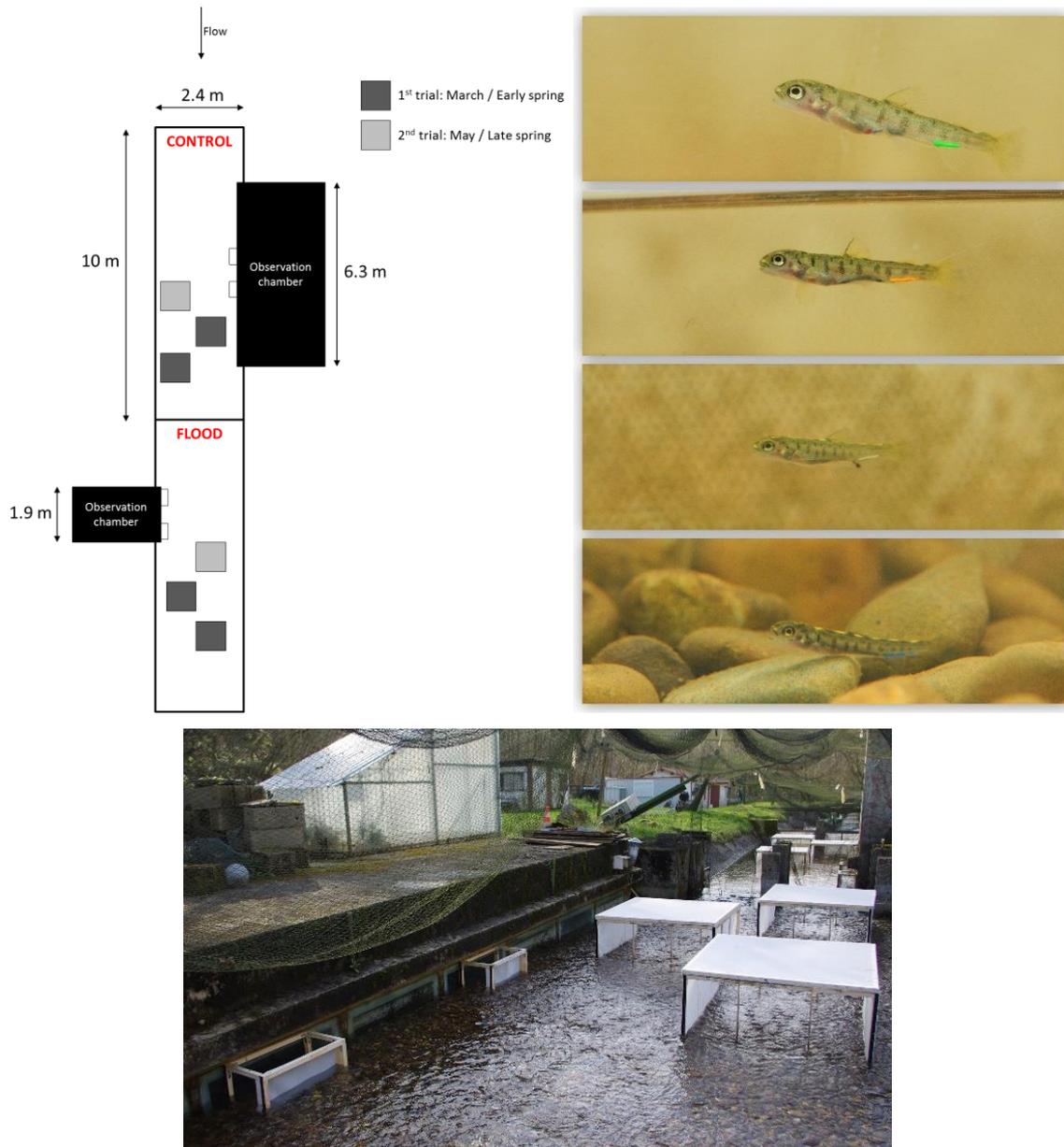
Figure 1 Experimental setup in the semi-natural Lapitxuri channel. The upstream reach was the control, while a flood was simulated in the downstream reach. Four cages were used for the growth of alevins in March/early spring (in dark grey) and two in April-May/late spring (in light grey). Behavioural surveys were conducted in additional small cages (not shaded), close to the observation chambers during the two trials with alevins tagged differently (top right photos). The picture shows an overview of the device.

Statistical analyses

Growth Cages

Abundance of invertebrates (number of individuals by sample) as well as the individual weight gain of alevins and fish productivity (sum of final weights) were analysed using a bayesian modelling approach computed with OpenBUGS®. We assumed that the variables of interest

followed a normal distribution. Then, the mean of the variable (μ.Variable) was modelled according to three parameters (Table 2): a fixed-effect relative to the flood (α), a fixed-effect relative to the season (β) and a fixed-effect relative to the interaction flood*season (γ). The logit of the probability of alevins survival was modelled with these same three effects.

*Table 2 Parameters taken into account according to the season and the condition. μ.Variable is the mean of the variable of interest, α represents the flood effect, β the second trial effect and γ the flood*second trial effect.*

		Season	
		1st trial (early spring)	2nd trial (late spring)
Conditions	Control	μ.Variable	μ.Variable + β
	Flood	μ.Variable + α	μ.Variable + α + β + γ

Abundance of invertebrates

If $Abond_i$ is the number of individuals counted in the ith sample, we assumed:

$$\mu.\log(Abond_i + 1)_i = \mu + \alpha \, Flood_i + \beta \, Season_i + \gamma \, Interaction_i$$

Where μ is the mean of the logarithm of the abundance of invertebrates, α is a fixed-effect parameter for the impact of the flood, β is a fixed-effect parameter for the season and γ is a fixed-effect parameter for the interaction flood*season. The same modelling treatment was applied to the total abundance of invertebrates and to the abundance per group (*i.e.* Diptera, Trichoptera, Ephemeroptera, Coleoptera, Plecoptera, Oligochaeta, Crustacea, Mollusca, and "Others").

Survival probability of alevins

We assumed that the alevins could not escape from the cage and so, not recovered alevins at the end of each trial were considered dead. Then, if $p.S_i$ is the probability of survival of the ith alevin, we assumed:

$$S_i \sim Bernoulli(p.S_i)$$

$$Logit(p.S_i) = \mu + \alpha \, Flood_i + \beta \, Season_i + \gamma \, Interaction_i$$

Where μ is the mean of the logit of the survival probability, α is a fixed-effect parameter for the impact of the flood, β is a fixed-effect parameter for the season and γ is a fixed-effect parameter for the interaction flood*season.

Individual weight gain of alevins

All the alevins were weighted at the beginning of each trial ($W.beg_i$) and all the survivors were weighted at the end ($W.end_i$). Photos allowed the individual recognition of alevins and then calculation of the individual Weight Gain (WG_i):

$$WG_i = \frac{W.end_i - W.beg_i}{W.beg_i}$$

Then, we stated that WG followed a normal distribution with $\mu.WG_i$ the mean and $\sigma.WG_j$ the standard deviation. We assumed:

$$\mu.WG_k = \mu + \alpha\ Flood_i + \beta\ Season_i + \gamma\ Interaction_i$$

Where μ is the mean of the individual weight gain of alevins, α is a fixed-effect parameter for the impact of the flood, β is a fixed-effect parameter for the season and γ is a fixed-effect parameter for the interaction flood*season.

Fish productivity

The final weights of alevins ($W.end_i$) were summed to obtain the fish production of each j cage ($Prod.Fish_j$).

$$\mu.Prod.Fish_j = \mu + \alpha\ Flood_j + \beta\ Season_j + \gamma\ Interaction_j$$

Where μ is the mean fish production, α is a fixed-effect parameter for the impact of the flood, β is a fixed-effect parameter for the season and γ is a fixed-effect parameter for the interaction flood*season.

Determination of hierarchy

Only One Side Attacks (OSA) were considered to establish the hierarchy matrix, *i.e.* attacks that induced a fleeing reaction or a gently sink underneath and downstream the aggressor (Katano 1985, 1990; Nakano & Furukawa-Tanaka 1994). Aggression Index (AI) was calculated for each alevin by dividing the number of OSA made (OSA+) by the number of OSA sustained (OSA-). Then, the AI was related to the positioning of the alevin in the cage and alevins were ranked. "A" was associated to the highest AI and an upstream positioning within the cage and referred to the dominant alevin. "B" was associated to the second highest AI and referred to the subdominant alevin. "C" and "D" was associated to the lowest AI and a downstream positioning within the cage and referred to the subordinates.

Following emergence, fish try to establish territories and start to feed. They have to learn how to swim in the water current, how to catch prey, and the hierarchy take a few days to be established. Alevins became progressively active and began to hunt and interact with their congeners over time. Therefore, δ represented the increase in the probability to be active or in the occurrence of discrete events (*i.e.* attempt to catch prey or aggressive interaction), δ_1 being the increase in control cages and δ_2 the increase in impacted cages. Difference between δ_1 and δ_2 was tested. Moreover, in the same reach, the second cage was positioned 2 meters downstream the first one, then a fixed-effect parameter λ relative to downstream cage positioning was also considered (Table 3).

Table 3 Parameters taken into account according to the condition and the position of the behavioural cage. μ.Variable is the mean of the behaviour of interest, δ_1 represents the increase in the control cages, δ_2 the increase in the impacted cages and λ the downstream cage position effect.

		Position of the behavioural cage in the reach	
		Upstream	Downstream
Conditions	Control	μ.Variable + δ_1	μ.Variable + δ_1 + λ
	Flood	μ.Variable + δ_2	μ.Variable + δ_2 + λ

If $p.A_k$ is the probability of being active (swimming in the water column) for an alevins during the kth survey, we assumed:

$$Activity_k \sim Benoulli(p.A_k)$$

$$Logit(p.A_k) = \mu + \delta_{Condition[k]}Time + \lambda\,Position_k$$

Where μ is the average of the logit of the probability of alevins to be active, δ is a fixed-effect parameter for the increase in activity over time and λ is a fixed-effect parameter for the position of the cage.

If $Hunt_k$ is the number of attempts to catch prey (the feeding activity) of an alevin during the kth survey of five minutes, we assumed:

$$Hunt_k \sim Poisson(\mu.Hunt_k)$$

$$\log(\mu.Hunt_k) = \mu + \delta_{Condition[k]}Time + \lambda\,Position_k$$

Where μ is the average of the logarithm of the numbers of attempts to catch prey in 5 minutes, δ is a fixed-effect parameter for the increase of the feeding activity over time and λ is a fixed-effect parameter for the position of the cage.

During a 5-minute survey, all the aggressive acts were summed, even if the focused alevins was the victim. An intimidation, a charge, a nip or a chase were equally considered as aggressive acts. Then, if Agg_k is the number of aggressive interactions during the kth survey of five minutes, we assumed:

$$Agg_k \sim Poisson(\mu.Agg_k)$$

$$\log(\mu.Agg_k) = \mu + \delta_{Flood[k]+1}Time + \lambda\,Position_k$$

Where μ is the average of the logarithm of the numbers of aggressive interactions in 5 minutes, δ is a fixed-effect parameter for the increase of the aggressive activity over time and λ is a fixed-effect parameter for the position of the cage.

Correlations between individual weight gain of alevins and (*i*) the number of surveys during which each alevin was actively swimming in the water column, (*ii*) the average number of attempts to catch prey by survey and (*iii*) the average number of aggressive interactions by survey were tested as previously described. Similarly, the number of surveys during which each alevin was actively swimming was linked to the average number of attempts to catch prey by survey and the average number of aggressive interactions by survey. Correlations were tested with OpenBUGS®. If Y_j was the individual weight gain or the alevin activity, we assumed:

$$Y_j = a\,Behaviour_j + b$$

Where Y_j is for each j alevin, the individual weight gain (WG_j) or the activity of alevins, a is the slope coefficient, $Behaviour_j$ is the behaviour of interest and b is the intercept. Fit of correlation was calculated by dividing the variability unexplained by the variability observed in the data set, as follows:

$$Fit = 1 - \frac{Variability\ unexplained\ by\ the\ model}{Variability\ of\ the\ data\ set}$$

When the fit is between 0.5 and 1, the correlation is good. When the fit is between 0 and 0.5, the correlation is intermediate and when the fit is negative, there is no correlation.

Parameters were given independent "weakly informative" priors. Following recommendations of Gelman & Hill (2007), μ, α, β, γ, a, b, δ_1, δ_2 and λ were sampled in a normal distribution, $N(0, 100)$. $\sigma_{\text{log.Abond}}$ and $\sigma_{\text{Prod.Fish}}$ were sampled in a half-Cauchy truncated distribution, $t(0, 1, 1)$. Hyperparameters of $\sigma.WG_j$ (B.σ.WG and E.σ.WG) were sampled in a gamma distribution, gamma(1, 1). We used each time three independent chains, the first 10 000 iterations were discarded as an initial burn-in period. Then, 10 000 further iterations (resulting from one every ten runs) were performed. The convergence of the chains to their ergodic distribution was tested *via* the Gelman-Rubin (GR) diagnostics integrated in OpenBUGS®. The significance of the parameters was tested with the step function implemented in OpenBUGS®. At each iteration for a variable X, step(X) equaled 1 if $X \geq 0$ and equaled 0 if $X < 0$. At the end of the run, if $P(X > 0)$ was lower than 0.1 or higher than 0.9, the parameter X was considered to be different from 0.

Results

Effect of the flood on the community of invertebrates

During the first trial (early spring), immediately after the artificial flood, Diptera, Ephemeroptera, Coleoptera, Plecoptera and the "Others" groups were less abundant in the impacted than in the control cages. The abundance of Mollusca and Crustacea increased, while the abundance of Trichoptera, Oligochaeta and the total abundance did not change (Figure 2 and Table 4 – α_1). At the end of the trial, the abundance of Diptera, Ephemeroptera, Coleoptera, Oligochaeta and the total abundance decreased in the impacted cages, while the abundance of Crustacea increased. The abundance of Trichoptera, Mollusca, Plecoptera and the Other invertebrates remained equal between the impacted and the control cages (α_2).

During the second trial (late spring), the artificial flood decreased the abundance of all groups of invertebrates (α_1 and γ_1). At the end of the trial, the abundance of Diptera, Ephemeroptera, Crustacea, Coleoptera, Oligochaeta and the total abundance remained lower in the impacted cages, while the abundances of Plecoptera and Exogenous were higher. The abundance of Mollusca, Trichoptera and the Other invertebrates remained equal between the control and the impacted cages (α_2 and γ_2).

Whatever the conditions, there was a significant seasonal effect comparing the two trials. The abundance of Diptera, Trichoptera, Ephemeroptera, Oligochaeta, Crustacea, Others and the total abundance was higher in late spring than in early spring (β_1 and β_2).

The important information to better understand trophic availability concerns the main prey groups for 0^+ trout, *i.e.* Diptera and Ephemeroptera. For these groups (but still true for total abundances):

- Just after the flood and at the end of the trials, abundances in control were higher than in impacted cages in both early and late spring and these differences were more pronounced at the end of the trial than just after the flood,
- Abundances were much higher in late than in early spring for Diptera, which were ten times more abundant than Ephemeroptera.
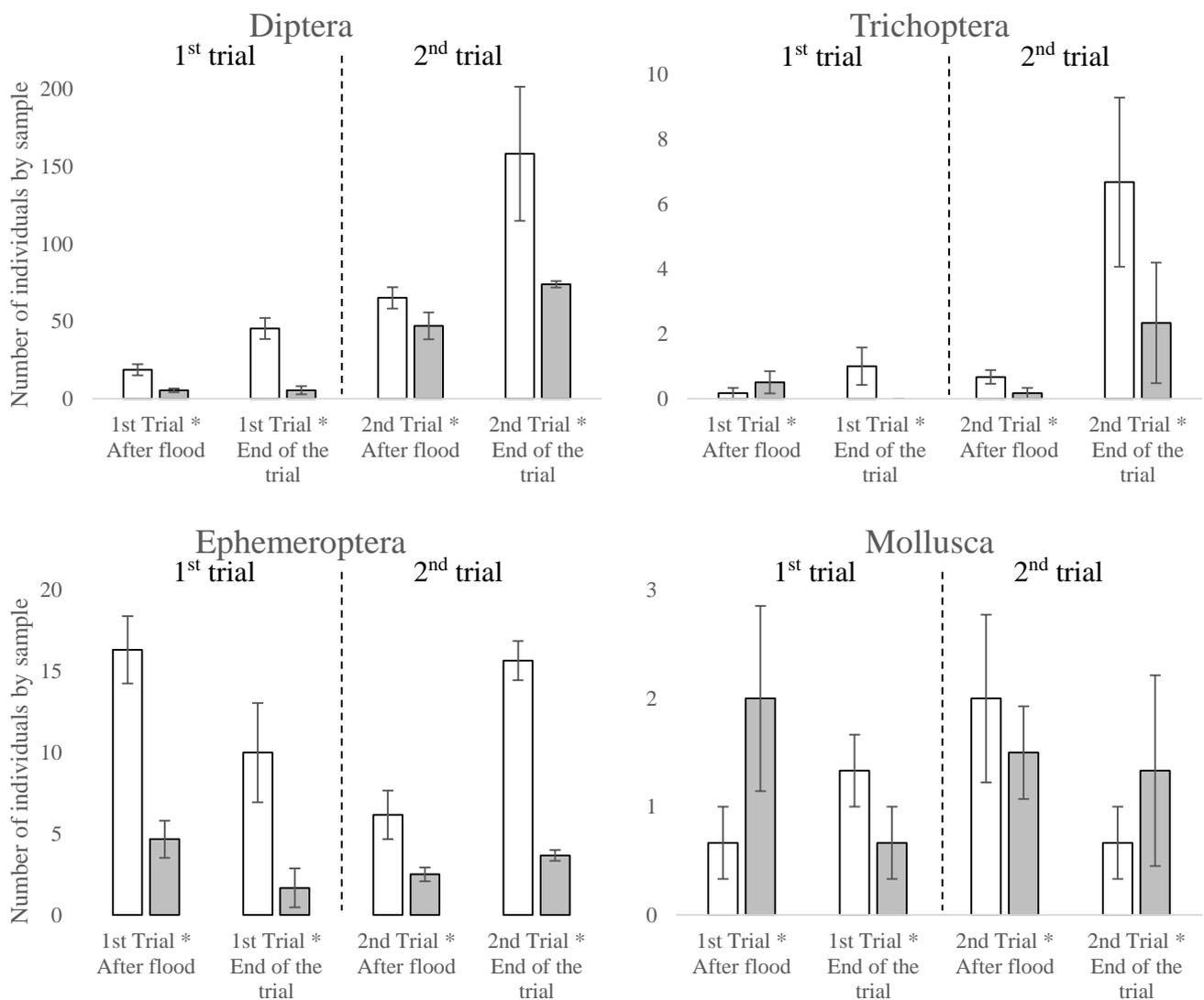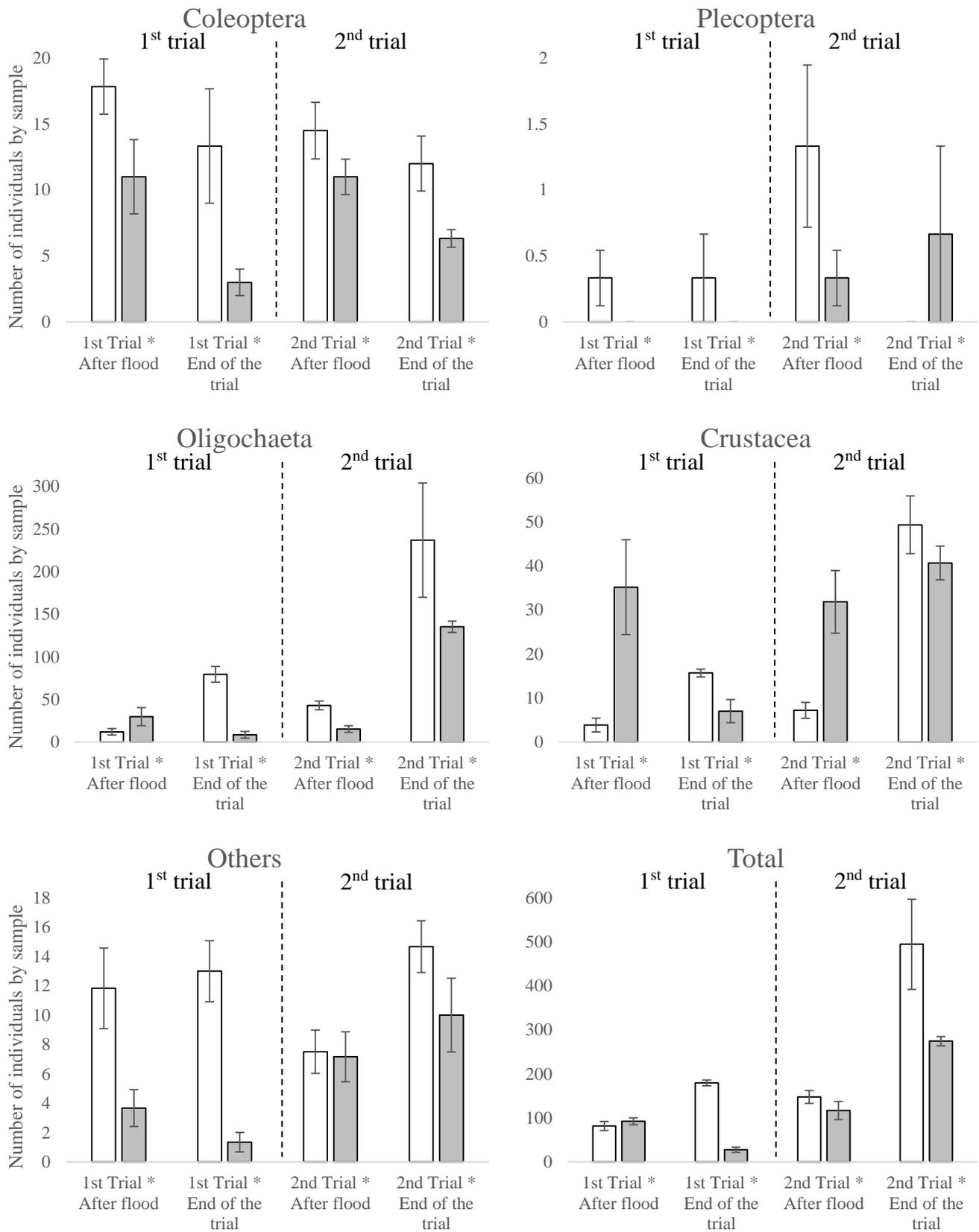
*Figure 2 Number of individuals per sample (average ± standard error) of the groups of invertebrates identified according to treatment (Control in white and Impacted by flood in grey) immediately and at the end of the trial.*

Table 4 Mean of the posterior probability distribution functions of the effect of the flood (α), season (β) and the interaction flood*season (γ) on the logarithm of the abundance of invertebrates. Effects were estimated for each group and for the total abundance, immediately after the flood and at the end of the trial. Parameters were considered significant when P(X > 0) is less than 0.10 or above 0.90 (in bold).

Groups	Immediately after the flood						At the end of the trial					
	α_1	$P(\alpha_1 > 0)$	β_1	$P(\beta_1 > 0)$	γ_1	$P(\gamma_1 > 0)$	α_2	$P(\alpha_2 > 0)$	β_2	$P(\beta_2 > 0)$	γ_2	$P(\gamma_2 > 0)$
Diptera	-1.245	**0.007**	0.926	**0.948**	-1.099	**0.084**	-0.388	**0.059**	0.834	**0.994**	-0.291	0.238
Trichoptera	0.180	0.773	0.478	**0.941**	-0.774	**0.038**	-0.346	0.143	1.423	**0.999**	-0.659	0.123
Ephemeroptera	-1.259	**0.002**	-0.478	0.151	-0.299	0.321	-0.642	**0.006**	0.956	**0.997**	-0.631	**0.066**
Mollusca	0.508	**0.946**	0.415	0.865	-0.874	**0.057**	-0.065	0.428	-0.429	0.169	0.290	0.683
Coleoptera	-0.591	**0.035**	-0.345	0.185	-0.637	0.123	-0.240	**0.079**	-0.160	0.219	-0.315	0.140
Plecoptera	-0.232	**0.082**	-0.001	0.498	0.000	0.500	-0.412	0.106	-0.640	**0.059**	0.774	**0.913**
Oligochaeta	0.635	0.887	2.013	**0.998**	-2.909	**0.002**	-1.112	**0.000**	1.628	**1.000**	0.651	**0.917**
Crustacea	2.083	**1.000**	1.519	**0.994**	-2.950	**0.001**	1.435	**1.000**	1.955	**1.000**	-1.613	**0.005**
Others	-1.134	**0.005**	0.184	0.651	-0.744	0.142	-0.115	0.360	0.690	**0.957**	-0.275	0.310
Total	0.138	0.795	0.819	**0.999**	-2.037	**0.000**	-0.280	**0.088**	1.176	**1.000**	-0.255	0.233

Effect of the flood on alevins

The survival probability was significantly higher in the control than in the impacted cages during the first trial (early spring – 0.609 *vs* 0.376 – P(α > 0) = 0.004 – Figure 3 and Table 5). The opposite was observed during the second trial (late spring), even if the ratio between the two survival levels was much lower (0.813 *vs* 0.937 – P(γ > 0) = 0.995).

At the beginning of the experiment, alevins weighted on average 0.117 g (SD = 0.007) at the first trial (early spring) and 0.078 g (SD = 0.008) at the second trial (late spring). After 21 or 22 days of growth, alevins weighted on average 0.118 g (SD = 0.015) at the end of first trial and 0.133 g (SD = 0.052) at the end of the second trial. Individual weight gain was higher in the control than in the impacted cages for both trials (0.028 *vs* -0.018 and 1.221 *vs* 0.237 – P(α > 0) = 0.100 and P(γ > 0) = 0.000).

Finally, there was no significant difference in fish productivity, but it tended to be higher in the control cages than in the impacted ones at both trials (2.349 *vs* 1.384 and 4.510 *vs* 2.928 – P(α > 0) = 0.110 and P(γ > 0) = 0.294). Whatever the considered variable, alevins performances were lower at the first trial than at the second one (P(β > 0) = 0.984, 1.000 and 0.964 for survival, individual weight gain and fish productivity).

Table 5 Mean of the posterior probability distribution functions of the effect of flood (α), season (β) and the interaction flood*season (γ) on the survival probability, on individual weight gain of alevins and on fish productivity. Parameters were considered significant when $P(X > 0)$ is less than 0.10 or above 0.90 (in bold).

Alevins performance	Parameters	Mean	P(X > 0)
	α	-0.963	**0.004**
Survival probability	β	1.086	**0.984**
	γ	2.373	**0.995**
	α	-0.046	**0.100**
Individual weight gain	β	1.192	**1.000**
	γ	-0.938	**0.000**
	α	-0.965	0.110
Fish productivity	β	2.161	**0.964**
	γ	-0.618	0.294

A
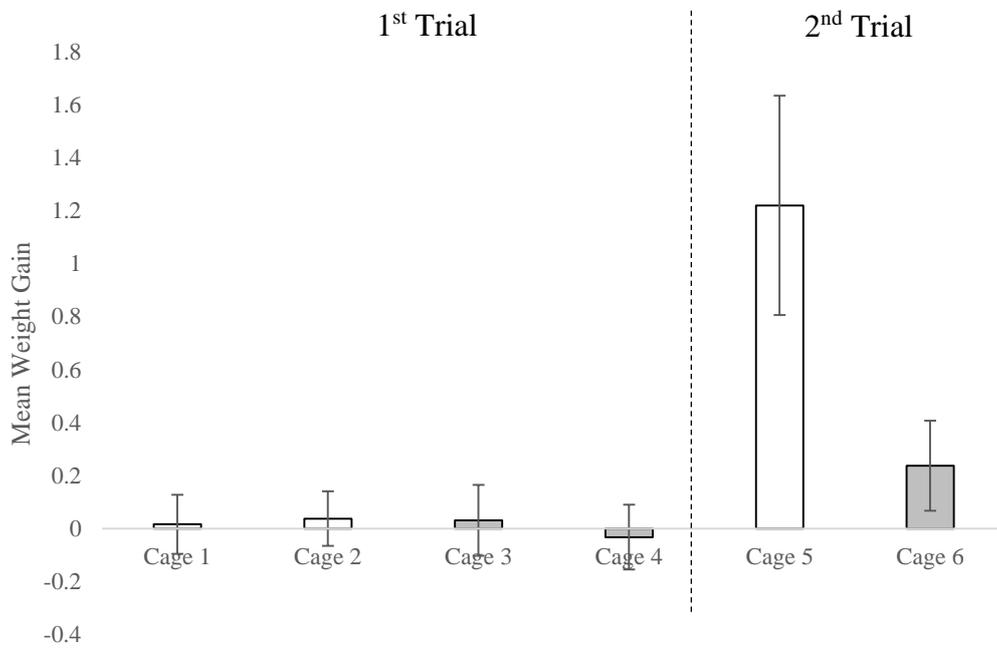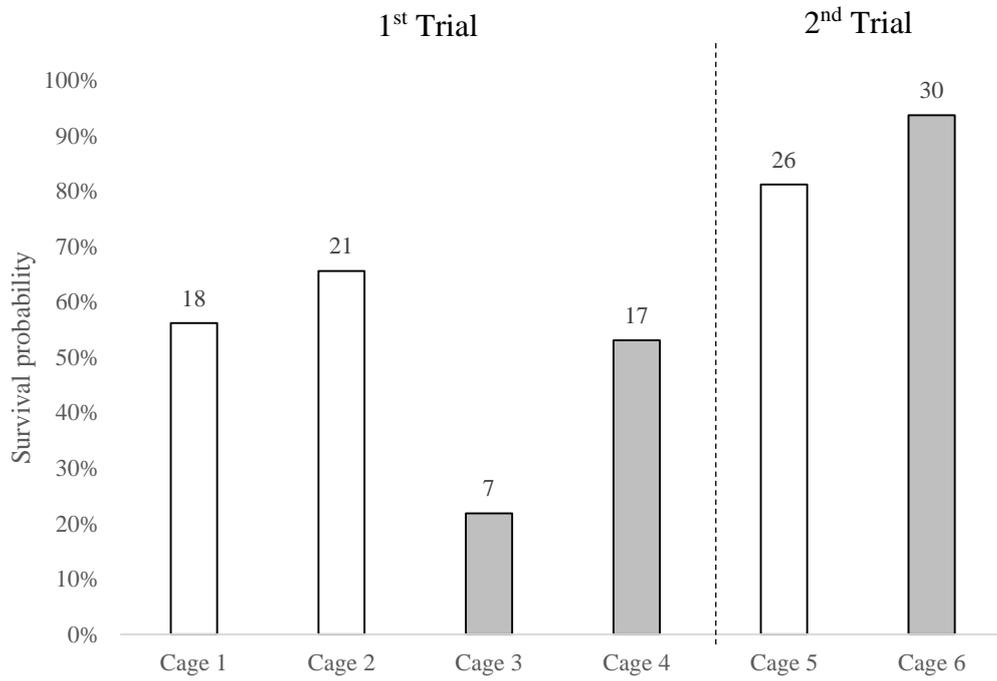
B

Figure 3 Raw data (A) of the survival probability and mean weight gain by cage and model estimates (B) of the survival probability, the individual weight gain and fish productivity in control (in white) and impacted (in grey) cages in the first and the second trial. Boxplots indicate the 1, 25, 50, 75 and 99 percentiles of posterior distributions. Significant differences are shown by *.

To sum up:

- Survival was low in early spring (50%) and high in late spring (80%),
- Growth was lower in early spring (close to zero) than in late spring (70% increase in weight),
- The artificial flood diminished the survival and growth in early spring,
- The artificial flood enhanced the survival, while the growth was low in late spring.

Behaviour of alevins

During the first trial (early spring), mortalities were recorded at the end of the 21 days of the observation survey, but we ignore when they arose. There was only 50% of survival with only two alevins surviving out on the four initially set up in each cage. Survivors grew, between 0.083 and 0.327 in the control and between 0.143 and 0.748 in the impacted cages (Table S2). Alevins appeared to do more attempts to catch prey in the control cages and there were also more aggressive interactions. However, because the number of alevins in the cage changed over time, it was not possible to analyse behavioural data for the first trial.

During the late spring surveys, we found a strong common pattern in the distribution of the four alevins within each cage. The dominant fish was positioned in the upstream part of the cage, immediately behind the net through which the invertebrates penetrated by drift into the cage. Then, the subdominant fish was positioned side by side or just downstream the dominant. The last two subordinates were generally positioned in the downstream part of the cage and accessed only to prey uncaught by the two upstream fish. The dominant and the subdominant fish gained the most weight and caught the most prey (Table 6), except in cage 2 in which differences in growth and feeding activity were less marked between alevins ranked B, C and D. There was no significant difference in average individual weight gain of alevins according to the conditions ($P(WG_{Flood} > WG_{Control}) = 0.818$).

Table 6 Initial and final weight, individual weight gain, mean number of feeding attempts by survey, One-Side-Attacks made (OSA+), sustained (OSA-), social rank and positioning of the alevins during the second trial (late spring) according to their cage of origin and the colour of their tag.

Condition	Cage	VIE tag	Initial Weight (mg)	Final Weight (mg)	Individual weight gain	Mean Number of feeding attempts by survey	OSA+	OSA-	Aggression Index	Rank	Social status	Position	
Control	1	Green	88	119	0.352	15.63	19	129	0.15	D	Subordinate	Middle	Bottom
		Orange	83	110	0.325	8.17	27	57	0.47	C	Subordinate	Downstream	Bottom
		Blue	70	151	1.157	14.86	139	4	34.75	A	Dominant	Upstream	Bottom
		White	93	165	0.774	12.03	74	69	1.07	B	Subdominant	Up/Mid	Surface
	2	Green	73	93	0.274	1.71	11	25	0.44	C	Subordinate	Up/Mid/Down	Bottom
		Orange	88	117	0.330	4.23	5	20	0.25	D	Subordinate	Middle	Bottom
		Blue	93	120	0.290	1.91	10	8	1.25	B	Subdominant	Downstream	Surface
		White	81	166	1.049	12.86	35	8	4.38	A	Dominant	Upstream	Bottom
Flood	3	Green	93	106	0.140	0.85	2	32	0.06	D	Subordinate	Downstream	Bottom
		Orange	89	224	1.517	17.58	30	4	7.50	A	Dominant	Upstream	Bottom
		Blue	85	167	0.965	10.94	20	9	2.22	B	Subdominant	Downstream	Surface
		White	73	127	0.740	8.06	23	30	0.77	C	Subordinate	Middle	Bottom
	4	Green	87	221	1.540	11.50	32	5	6.40	A	Dominant	Upstream	Bottom
		Orange	74	115	0.554	3.42	5	44	0.11	D	Subordinate	Downstream	Bottom
		Blue	75	86	0.147	1.97	3	9	0.33	C	Subordinate	Mid/Down	Bottom
		White	72	125	0.736	11.50	29	11	2.64	B	Subdominant	Mid/Down	Bottom

Over the 15 days of observation, the probability of activity, the number of attempts to catch prey and the number of aggressive interactions during a survey (five minutes) increased but the intensity of the increase always differed between the control and the impacted cages (Table 7).

Table 7 Mean of the posterior probability distribution functions of the increase in the activity probability or in the occurrence of discrete events (i.e. attempts to catch prey or aggressive interactions) over time (δ_1 being the increase in control and δ_2 in impacted cages) and the effect of cage positioning (λ). Parameters were considered significant when P(X > 0) is less than 0.10 or above 0.90 (in bold).

Behaviours	Parameters	Mean	P(X > 0)	P($\delta_1 > \delta_2$)
	δ_1	0.214	**1.000**	
Activity probability	δ_2	0.331	**1.000**	**} 0.002**
	λ	-1.483	**0.000**	
	δ_1	0.087	**1.000**	
Number of attempts to catch prey / survey	δ_2	0.076	**1.000**	**} 1.000**
	λ	-0.603	**0.000**	
	δ_1	0.197	**1.000**	
Number of aggressive interactions / survey	δ_2	0.135	**1.000**	**} 1.000**
	λ	-0.986	**0.000**	

Activity

Activity increased with time in both control and flood cages. Under impacted conditions, probabilities of being active were slightly higher (Figure 4).
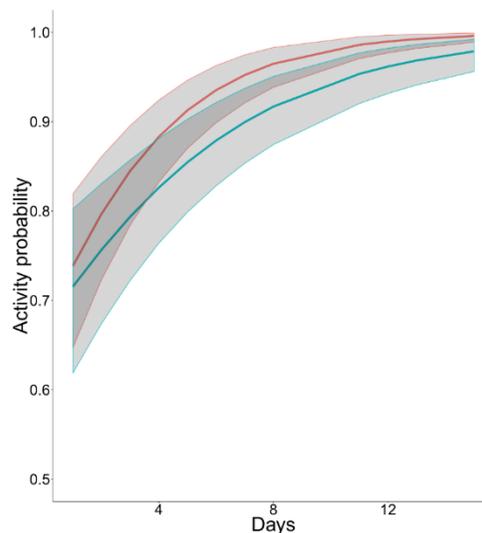
Figure 4 Model estimations of the probability to be active of an alevins according to time (in days) in the control (in blue) or in the impacted conditions (in red). Shaded areas are the 95% probability intervals of posterior distributions.

Feeding attempts

Number of feeding attempts increased with time in both conditions, but the increase was more pronounced under control conditions from day 3-4. Fish made on average 6 feeding attempts by survey on the first day, 11 *vs* 10 on the seventh day and 21 *vs* 18 on the fifteenth day (Figure 5).
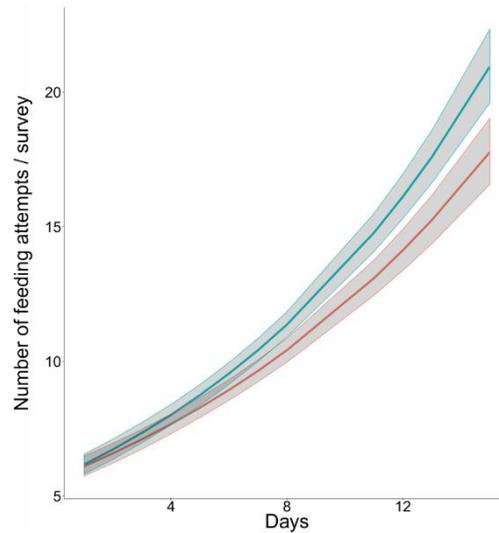
Figure 5 Model estimations of the number of feeding attempts during a survey (five minutes) according to time (in days) in the control (in blue) or in the impacted conditions (in red). Shaded areas are the 95% probability intervals of posterior distributions.

Capture distance

Alevins mostly sought prey around them (0-2 cm, 50.8% of total number of captures) but they also travelled intermediate distances (2-5 cm, 32.1%) or even longer (more than 5 cm, 17.1%). However, there was no significant difference in the temporal trend of the proportions of distances travelled by alevins between control and impacted conditions (Figure 6). It can only be noticed that short distance captures represented 80-90 % of the catches during the first 2 days in the control cages, whilst it established around 60% at the same time in the impacted cages.

Control   Flood
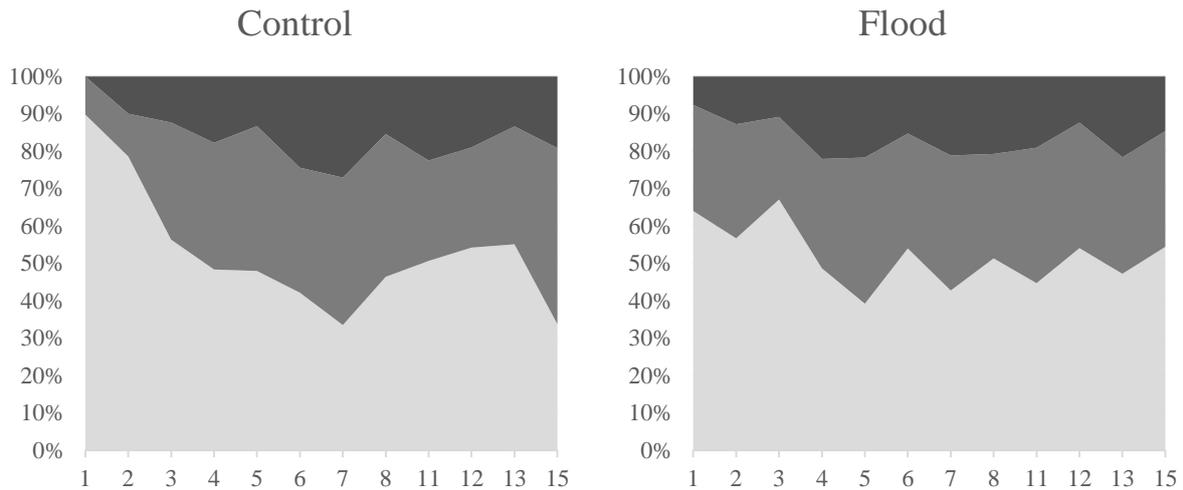
Figure 6 Proportion of short (< 2 cm – in light grey), medium (2-5 cm – in grey) and long (> 5 cm – dark grey) feeding attempts of alevins according to time (in days) in control and in impacted conditions.

Number of aggressive interactions

Aggressiveness increased with time in both conditions, but the increase was more pronounced under control conditions from the sixth day. Alevins made no attack on the first day, 1.5 *vs* 1 attack on the seventh day and 6.5 *vs* 2.5 attacks on the fifteenth day (Figure 7).
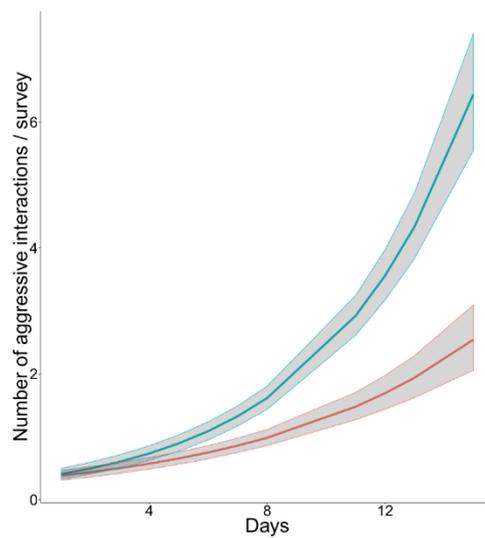

Figure 7 Model estimations of the number of aggressive interactions during five minutes according to time (in days) in the control (in blue) or in the impacted conditions (in red). Shaded areas are the 95% probability intervals of posterior distributions.

Relationship between behaviours

Individual weight gain was correlated with the activity of alevins as well as the average number of attempts to capture prey by survey. Activity of alevins seemed to be correlated with the

average numbers of attempts to capture prey by survey. In all three cases, the fit was higher than 0.50 and slope coefficients (a) were significantly positive (Table 8). The individuals which gained the most weight were the most active and they hunted the most (Figure 8). On the contrary, no link was established with aggressiveness.

Table 8 Correlations between individual weight gain (WG) and the number of survey noted active by alevins, the average number of attempts to catch prey by alevin and the average number of aggressive interactions by alevin. Activity of alevins was also related to the number of attempts to catch prey and the average aggressive interactions. Mean of posterior probability distribution functions of a (the slope coefficient) and b (the intercept) and fit of the models. Parameters were considered significant when P(X > 0) is less than 0.10 or above 0.90 (in bold).

Variable X	Variable Y	a	P(a > 0)	b	P(b > 0)	Equation	Fit
Activity	WG	0.046	**1.000**	-0.645	**0.033**	G = 0.04596 Activity + -0.645	0.534
Attempt to catch prey	WG	0.063	**1.000**	0.150	0.839	G = 0.06271 Catch.Prey + 0.1497	0.536
Aggressivness	WG	0.062	0.673	0.614	**0.998**	G = 0.06237 Agg + 0.6144	-0.082
Attempt to catch prey	Activity	1.216	**1.000**	18.290	**1.000**	Activity = 1.216 Catch.Prey + 18.29	0.692
Aggressivness	Activity	4.654	**0.991**	23.080	**1.000**	Activity = 4.654 Agg + 23.08	0.132
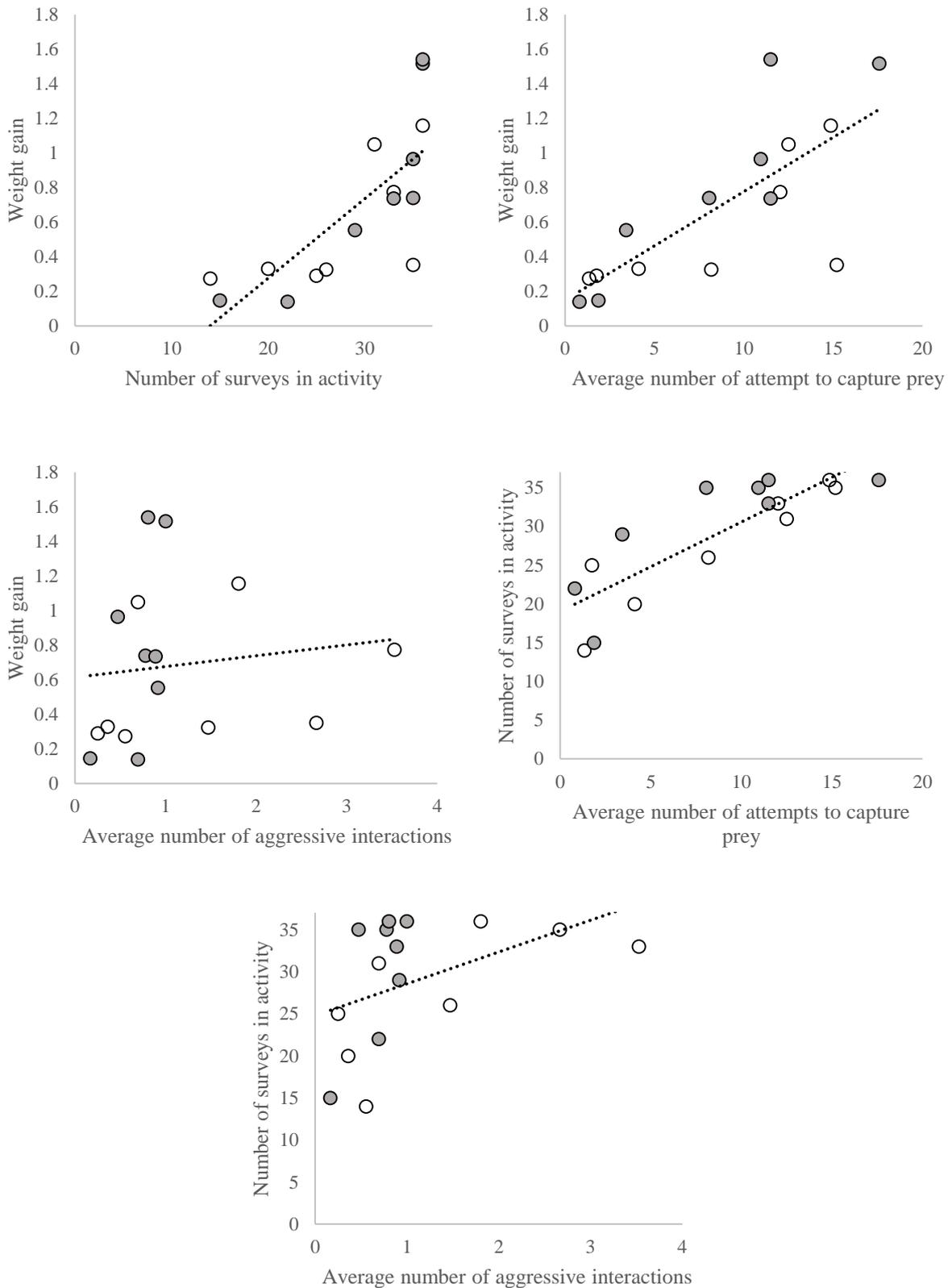
Figure 8 Individual weight gain (WG) according to the number of survey during which alevins were in activity, the average number of attempts to catch prey by alevins and the average number of aggressive interactions by alevins. Activity of alevins was also related to the number of attempts to catch prey and the average aggressive interactions. Empty circles represent alevins in the control cages, grey circles the alevins in the impacted cages and the dotted line the correlation.

Table 9 Synthesis of the main results on the effects of the artificial flood on invertebrate abundances (total and Diptera), alevin performances (survival and growth) and alevin behaviour (activity, feeding activity and competition) in early and late spring.

		Early Spring			Late Spring		
		Control		Flood	Control		Flood
Invertebrates	Abundances …						
	• Total	LOW	→	LOW	HIGH	↘	MODERATE
	• Diptera	LOW	↘	VERY LOW	HIGH	↘	MODERATE
	Recolonization	LOW	↘	NULL	HIGH	↘	MODERATE
Alevin performances	Survival	LOW *60 %*	↘	VERY LOW *40 %*	HIGH *80 %*	↗	VERY HIGH *95 %*
	Growth	NULL *0.03*	↘	NEGATIVE *-0.02*	HIGH *1.2*	↘	LOW *0.2*
Alevin behaviour	Activity probability					↗	
	Feeding attempts					↘	
	Strength of competition					↘	

Discussion

The experiment conducted in the semi-natural channel of the Lapitxuri highlighted that the artificial flood significantly impact the invertebrate community and the alevin performances and behaviour. However, the impact of the flood differed according to season.

Artificial flood and invertebrate abundances

In early spring, the artificial flood reduced the abundances of Diptera and Ephemeroptera to a third, while the total abundance of invertebrates remained more or less equal. In late spring, the artificial flood decreased by half the abundances of Diptera, Ephemeroptera and the total abundance. It is possible that the low abundances in early spring limited the impact of the artificial flood as observed in other streams when floods arose when invertebrate abundances were low (Arunachalam et al. 1991; Brewin et al. 2000). After twenty days, differences persisted. At that time abundances were the result of both recolonization processes and fish predation (Grosholz & Gallo 2006). Focusing on Diptera and Ephemeroptera, abundances remain lower in the impacted than in the control cages. However, the catch up was much quicker in late spring than in early spring. It could be due to an increase in system productivity that promotes the recolonization process as observed by Miller & Golladay (1996).

Artificial flood and performances of alevins

In early spring, the artificial flood diminished survival in large cages by 23% when compared to control. According to density-dependence mechanism this should reduce competition and promote growth. The growth of alevins was significantly but only slightly lower in the impacted cages. Therefore, the impact of trophic resources has probably been high enough to counterbalance the positive effect of density-dependence. Another possible explanation is that

mortalities occurred only shortly before the end of the experiment, before growth compensation. Then, the occurrence of a flood when the abundance of invertebrates is already low can seriously weaken the strength of the cohort. In late spring, the artificial flood increased unexpectedly the survival by 13%, while it diminished the individual weight gain. Density was higher in the impacted cages and then, the density-dependence mechanisms could partly explain the lower growth. Food availability probably might have had an effect also, since Diptera and Ephemeroptera were more abundant in control than in impacted conditions. It remains difficult to evaluate the respective impact of density and trophic resource limitation on alevin growth (see Supplementary Information Table S3, S4 and Figure S2 for details). The higher survival in impacted cages is surprising and it was probably linked to uncontrolled factors such as habitat availability. Indeed, it remains possible that the artificial flood, by washing fine sediment in between the gravels, favoured the visual isolation between 0^+ fish since they are very small during their first weeks of growth (23 mm long and 0.1 g on average for a first feeding alevins) and visual isolation is a well know factor that limits the strength of the competition in salmonids (Huntingford et al. 1993; Imre et al. 2002).

Artificial flood and behaviour of alevins

Alevins were seen swimming actively more often in the cages impacted by the artificial flood than in the control ones. This is consistent with Biro et al. (2003) who highlighted that in low food conditions, young trout (*Oncorhynchus mykiss*) needed to increase their activity to maintain a constant supply of food and then, grow. Present results confirm that when resource is scarce, young salmonids exhibit more risky behaviour, increasing their foraging effort and probably increasing the predation risk in the same time.

Our behavioural observations were in accordance with current knowledge: social status matched with the number of feeding attempts and with individual weight gain. The dominant fish was the largest at the beginning of the experiment in only one of the four cages. It suggests that the body condition of fish (weight and/or size) is rather the consequence of dominance than the cause as suggested by Metcalfe (1986). In the behaviour cages, the average individual weight gain did not differ between control and impacted cages, but inter-individual differences were higher in the impacted cages. At low food abundance, dominants monopolized most of the resource leaving a limited access to food for subordinates (Maclean & Metcalfe 2001; Höjesjö et al. 2002). The relationship between fish aggressiveness and food abundance is not yet clear. It has previously been argued that the strength of territorial defence depended on resource availability, with highest levels of territorial defence observed at intermediate levels

of food (Toobaie and Grant 2013). Accordingly, when food is scarce or abundant, the energetic cost of aggressiveness is greater than the benefit. However, results diverge: Symons (1968) and Slaney & Northcote (1974) found that frequency of aggressive encounter was greater at low prey level and during starvation. On the contrary, van Leeuwen et al. (2016) showed that the number of aggressions decreased at low food levels. Subordinates adopted an "energy minimizing" strategy (Johnsson et al. 1996), whereby they did not try to have a good feeding position and they avoided the energetic costs of both swimming against the water flow and potential battles over territories (van Leeuwen et al. 2016). Because investment in territorial defence can be costly for growth, Metcalfe et al. (1986) emphasized that the optimum strategy adopted by subordinate was minimizing energetic expenditures rather than maximizing food intake. This way, subordinates may continue to grow despite receiving a low level of food intake. This hypothesis is clearly strengthened by our results.

Artificial flood and season

In early spring, survival of alevins remained low (50% on average) and they did not gain weight. The same trends was recorded in the observation cages, at least concerning survival. It seems that the low invertebrate abundances impacted significantly the performances of alevins and cause their death. In contrast, in late spring, survival was quite high (90% on average) and their growth was positive, even if much lower in impacted than in control cages. Early emerging fish have less competition pressure to access to the best feeding spots and they can grow efficiently as far as the productivity of the system is not a limiting factor. When late alevins emerge, early survivors are favoured by their residence anteriority on territories (Huntingford & Garcia de Leaniz 1997; Cutts et al. 1999; Harwood et al. 2003). However, the results from the present experiment suggest that if early emerging fish suffer from food shortage, they would undergo high mortality rates as well as negative growth.

Conclusion

Throughout the spring season, temperature as well as sunshine duration and brightness increase and boost the primary production. Correlatively, the invertebrate production increased, the recolonization process was more effective and it partially compensated the flood effects. Therefore, the impact of a scouring flood on invertebrates might depend to a great extent on its timing (Robinson et al. 2004). That timing has to be taken into account when assessing the impact of flood on 0^+ trout since consequences on survival and growth were not of the same magnitude (harsh in early spring, light in late spring).
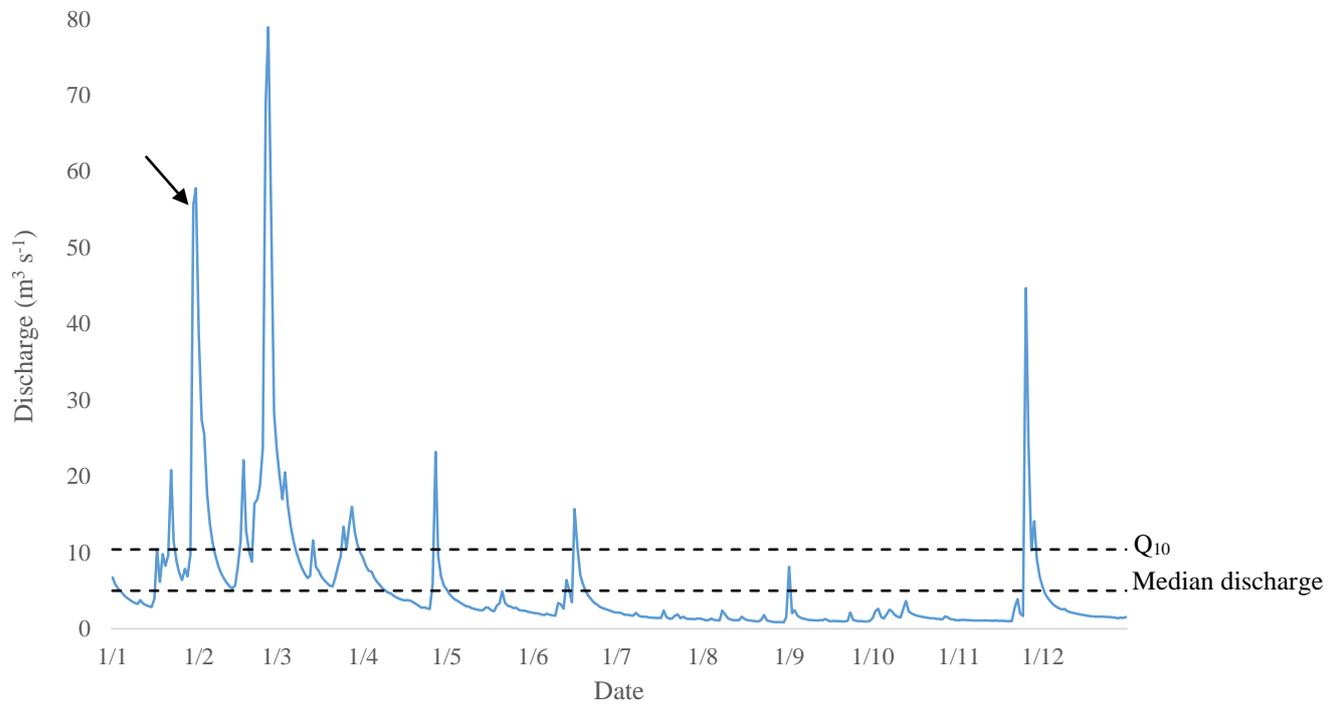
Figure S1: Discharge (in m^3 s^{-1}) on the Nivelle river during 2015. Water velocities were recorded on the Lapitxuri brook, a tributary to the Nivelle, the 30/01/2015. This date is represented by a dark arrow and dotted lines represent the Q_{10} and the median discharge of the Nivelle river.

Table S1: Water depth (in cm) and water velocities (in m s⁻¹) recorded on the Lapitxuri brook (the 30/01/2015).

	Lapitxuri brook – 30/01/2015 – Nivelle discharge = 55.6 m³ s⁻¹											
	Section	1	2	3	4	5	6	7	8	9	10	11
	Water depth (cm)	13	13	30	32	38	47	50	62	70	50	30
Water velocity (m s⁻¹) at	80% water depth	0.45	0.48	0.66	0.79	0.83	0.89	0.82	0.87	0.66	0.62	0.38
	40% water depth			0.55	0.63	0.82	0.87	1	1.06	0.83	0.72	0.37
	20% water depth			0.5	0.54	0.75	0.7	0.93	1.09	0.82	0.6	0.43

Table S2 Number of surveys, initial and final weight, individual weight gain, mean number of feeding attempts and of aggressive interactions of the alevins by survey during the first trial (early spring) according to their cage of origin and the colour of their tag.

Condition	Cage	VIE tag	Number of surveys	Initial weight (mg)	Final weight (mg)	Individual weight gain	Mean feeding attempts by survey				Mean number of aggressive interactions by survey		
							Short	Medium	Long	Total	Attacks made	Attacks sustained	Total
Control	1 Up	Green	40	110	146	0.327	3.40	4.28	3.43	11.10	2.18	0.03	2.20
		Orange	40	117	127	0.085	2.90	2.25	1.35	6.50	0.43	2.35	2.78
		Blue	13	86	-	-	0.54	0.00	0.08	0.62	0.00	0.69	0.69
		White	2	109	-	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	2 Down	Green	40	121	131	0.083	3.25	3.03	2.68	8.95	0.45	0.25	0.70
		Orange	40	118	153	0.297	3.25	2.53	1.48	7.25	0.98	1.03	2.00
		Blue	36	120	-	-	2.33	1.39	0.89	4.61	0.22	0.33	0.56
		White	35	118	-	-	2.91	2.80	1.69	7.40	0.57	0.17	0.74
Flood	3 Up	Green	31	114	-	-	0.81	0.23	0.00	1.03	0.03	0.13	0.16
		Orange	39	98	112	0.143	3.21	3.28	1.67	8.15	1.00	0.03	1.03
		Blue	23	97	-	-	1.96	0.57	0.35	2.87	0.04	0.39	0.43
		White	35	107	187	0.748	2.31	1.94	1.51	5.77	0.14	0.74	0.89
	4 Down	Green	40	114	136	0.193	3.43	2.80	2.00	8.23	0.43	0.68	1.10
		Orange	40	115	141	0.226	4.48	3.15	2.00	9.63	1.30	0.38	1.68
		Blue	32	108	-	-	2.81	1.41	0.88	5.09	0.06	0.41	0.47
		White	35	110	-	-	3.06	3.03	2.26	8.34	1.40	0.51	1.91

Supporting information: Relationship between the invertebrate abundances and alevin performance

We assessed the strength of link between the mean abundances of invertebrates and (*i*) the survival, (*ii*) the average individual weight gain, and (*iii*) the fish productivity. We tested 60 relationships (10 invertebrate groups x 3 fish performance variables x 2 times, just after the disturbance and at the end of the trial). Correlations were tested with OpenBUGS®. If Y_j was the fish variable of the jth cage, we assumed:

$$Y_j = a\ Abond_j + b$$

Where Y_j is for each j cage, the number of survivors (S_j), the average individual weight gain ($WG_{j[i]}$) or the fish productivity (Prod.Fish$_j$), a is the slope coefficient, Abond$_j$ is the average of abundance of invertebrates by cage and b is the intercept. Fit of correlation was calculated by dividing the variability unexplained by the variability observed in the data set, as follows:

$$Fit = 1 - \frac{Variability\ unexplained\ by\ the\ model}{Variability\ of\ the\ data\ set}$$

When the fit is between 0.5 and 1, the correlation is good. When the fit is between 0 and 0.5, the correlation is intermediate and when the fit is negative, there is no correlation.

Immediately after the flood, abundances of invertebrates fitted with fish performances in 23% of the cases (7/30, fit > 0.500 – Table S3). At the end of the trials, final invertebrate abundances fitted with fish performances in 63% of the cases (19/30, fit > 0.500 – Table S4). Usually positive, the links happen to be negative in five cases but only one link was significantly negative: between fish productivity and abundances of Diptera. Focusing on final Total abundance, and on Diptera and Ephemeroptera (the two groups among which are the main food items of newborn alevins), correlations with the weight gain of alevins were positive and significant (Fit = 0.888, 0.914 and 0.712 respectively – Figure S2). However, they were highly influenced by one point (Control cage in the second trial) characterized by abundances especially high. When this point was not taken into account, correlation was still significant for total abundance (Fit: 0.851; a = 0.0015; P(a > 0) = 0.995), but no more for Diptera and Ephemeroptera (Fit = -0.712 and -2.325, respectively).

Table S3 Correlations between fish variable (Y) and invertebrate abundances after the flood (X), mean of posterior probability distribution functions of a (the slope coefficient) and b (the intercept) and fit of the models just after flood simulation disturbance. Parameters in bold are significant (when P(X > 0) is less than 0.10 or above 0.90).

Variable Y	Variable X	Groups	a	P(a > 0)	b	P(b > 0)	Equation	Fit
Number of surviving alevins by cage S	Number of invertebrates After the flood	Diptera	0.591	**0.967**	7.438	**0.969**	S = 0.591 Diptera + 7.438	0.574
		Trichoptera	-1.515	**0.086**	14.880	**0.997**	S = -1.515 Trichoptera + 14.88	0.580
		Ephemeroptera	0.201	0.820	8.719	**0.957**	S = 0.2005 Ephemeroptera + 8.719	0.313
		Mollusca	3.306	0.870	8.436	**0.964**	S = 3.306 Mollusca + 8.436	0.407
		Coleoptera	1.084	**0.998**	0.362	0.546	S = 1.084 Coleoptera + 0.3619	0.832
		Plecoptera	0.026	0.493	11.480	**0.990**	S = 0.02616 Plecoptera + 11.48	0.342
		Oligochaeta	0.026	0.515	11.100	**0.971**	S = 0.02557 Oligochaeta + 11.1	0.256
		Crustacea	0.128	0.772	9.943	**0.982**	S = 0.1276 Crustacea + 9.943	0.289
		Others	0.053	0.660	10.420	**0.980**	S = 0.05349 Others + 10.42	0.251
		Total	0.122	**0.960**	4.947	0.854	S = 0.1218 Total + 4.947	0.525
Mean Individual Weight Gain by cages WG	Number of invertebrates After the flood	Diptera	0.025	**0.974**	-0.168	0.223	WG = 0.02543 Diptera + -0.1681	0.459
		Trichoptera	0.844	**0.922**	-0.079	0.386	WG = 0.844 Trichoptera + -0.0787	0.076
		Ephemeroptera	0.000	0.500	0.251	0.713	WG = -0.0001604 Ephemeroptera + 0.2508	-0.649
		Mollusca	-0.023	0.469	0.280	0.737	WG = -0.02336 Mollusca + 0.2798	-0.641
		Coleoptera	-0.005	0.459	0.308	0.684	WG = -0.004779 Coleoptera + 0.3083	-0.637
		Plecoptera	1.022	0.766	0.080	0.598	WG = 1.022 Plecoptera + 0.08009	-0.386
		Oligochaeta	0.014	**0.970**	-0.143	0.261	WG = 0.01387 Oligochaeta + -0.1428	0.416
		Crustacea	-0.003	0.417	0.303	0.802	WG = -0.003036 Crustacea + 0.3032	-0.638
		Others	0.038	0.782	-0.037	0.467	WG = 0.03778 Others + -0.03725	-0.402
		Total	0.007	**0.942**	-0.404	0.166	WG = 0.00711 Total + -0.404	0.189
Fish Productivity by cages Prod	Number of invertebrates After the flood	Diptera	-0.536	0.172	11.800	**0.952**	Prod = -0.5361 Diptera + 11.8	0.040
		Trichoptera	4.990	**1.000**	0.312	0.628	Prod = 4.99 Trichoptera + 0.3116	0.978
		Ephemeroptera	0.428	0.898	3.072	0.701	Prod = 0.4279 Ephemeroptera + 3.072	-0.034
		Mollusca	-1.819	0.332	9.490	**0.921**	Prod = -1.819 Mollusca + 9.49	-0.111
		Coleoptera	-0.522	0.226	13.490	**0.925**	Prod = -0.5224 Coleoptera + 13.49	0.068
		Plecoptera	14.100	**0.969**	3.602	0.805	Prod = 14.1 Plecoptera + 3.602	0.503
		Oligochaeta	-0.152	0.312	9.922	**0.913**	Prod = -0.1516 Oligochaeta + 9.922	-0.159
		Crustacea	-0.196	0.226	9.917	**0.940**	Prod = -0.1961 Crustacea + 9.917	-0.116
		Others	0.288	**0.941**	3.862	0.778	Prod = 0.2876 Others + 3.862	0.117
		Total	-0.264	**0.010**	25.580	**0.997**	Prod = -0.2642 Total + 25.58	0.819

Table S4 Correlations between fish variable (Y) and invertebrate abundances at the end of the trials (X), mean of posterior probability distribution functions of a (the slope coefficient) and b (the intercept) and fit of the models at the end of the trials. Parameters in bold are significant (when P(X > 0) is less than 0.10 or above 0.90).

| Variable Y	Variable X	Groups	a	P(a > 0)	b	P(b > 0)	Equation	Fit
Number of surviving alevins by cage S	Number of invertebrates At the end of the trials	Diptera	0.094	0.887	10.490	**0.986**	S = 0.09432 Diptera + 10.49	0.649
		Trichoptera	-0.356	0.323	14.440	**0.998**	S = -0.3557 Trichoptera + 14.44	0.621
		Ephemeroptera	-0.002	0.455	13.750	**0.997**	S = -0.002252 Ephemeroptera + 13.75	0.582
		Mollusca	0.667	0.691	12.030	**0.988**	S = 0.6673 Mollusca + 12.03	0.581
		Coleoptera	0.611	**0.915**	7.091	0.894	S = 0.6105 Coleoptera + 7.091	0.654
		Plecoptera	3.934	0.850	10.480	**0.988**	S = 3.934 Plecoptera + 10.48	0.661
		Oligochaeta	0.221	**0.956**	9.253	**0.984**	S = 0.2205 Oligochaeta + 9.253	0.727
		Crustacea	-0.090	0.254	14.930	**0.998**	S = -0.08984 Crustacea + 14.93	0.648
		Others	-0.005	0.401	13.960	**0.997**	S = -0.004778 Others + 13.96	0.598
		Total	0.052	0.875	8.776	**0.945**	S = 0.05168 Total + 8.776	0.627
Mean Individual Weight Gain by cages WG	Number of invertebrates At the end of the trials	Diptera	0.011	**0.999**	-0.602	**0.006**	WG = 0.01121 Diptera + -0.6015	0.914
		Trichoptera	0.188	**1.000**	-0.083	0.107	WG = 0.1882 Trichoptera + -0.08306	0.939
		Ephemeroptera	0.090	**0.991**	-0.296	**0.076**	WG = 0.08964 Ephemeroptera + -0.2962	0.712
		Mollusca	-0.483	**0.090**	0.978	**0.943**	WG = -0.4834 Mollusca + 0.9781	0.027
		Coleoptera	-0.006	0.469	0.323	0.633	WG = -0.006134 Coleoptera + 0.3234	-0.631
		Plecoptera	-0.442	0.146	0.545	**0.923**	WG = -0.442 Plecoptera + 0.5448	-0.197
		Oligochaeta	0.005	**0.994**	-0.169	0.123	WG = 0.005161 Oligochaeta + -0.1686	0.773
		Crustacea	0.017	**0.904**	-0.221	0.284	WG = 0.01688 Crustacea + -0.2214	-0.005
		Others	0.110	**0.971**	-0.742	**0.068**	WG = 0.1102 Others + -0.7421	0.425
		Total	0.003	**0.998**	-0.427	**0.012**	WG = 0.003139 Total + -0.4272	0.888
Fish Productivity by cages Prod	Number of invertebrates At the end of the trials	Diptera	-0.333	**0.014**	21.350	**0.996**	Prod = -0.3325 Diptera + 21.35	0.724
		Trichoptera	5.049	**1.000**	-0.080	0.466	Prod = 5.049 Trichoptera + -0.07976	0.977
		Ephemeroptera	0.188	**0.996**	2.488	0.767	Prod = 0.1877 Ephemeroptera + 2.488	0.657
		Mollusca	3.988	**0.965**	-0.116	0.489	Prod = 3.988 Mollusca + -0.1155	0.267
		Coleoptera	0.142	0.555	6.813	0.783	Prod = 0.1418 Coleoptera + 6.813	-0.217
		Plecoptera	4.670	0.772	4.737	0.771	Prod = 4.67 Plecoptera + 4.737	-0.062
		Oligochaeta	-0.180	0.260	11.400	**0.924**	Prod = -0.1801 Oligochaeta + 11.4	-0.049
		Crustacea	-0.353	0.140	12.100	**0.962**	Prod = -0.3531 Crustacea + 12.1	0.094
		Others	0.127	**0.999**	1.887	0.744	Prod = 0.1274 Others + 1.887	0.761
		Total	-0.099	0.132	17.900	**0.955**	Prod = -0.09919 Total + 17.9	0.313
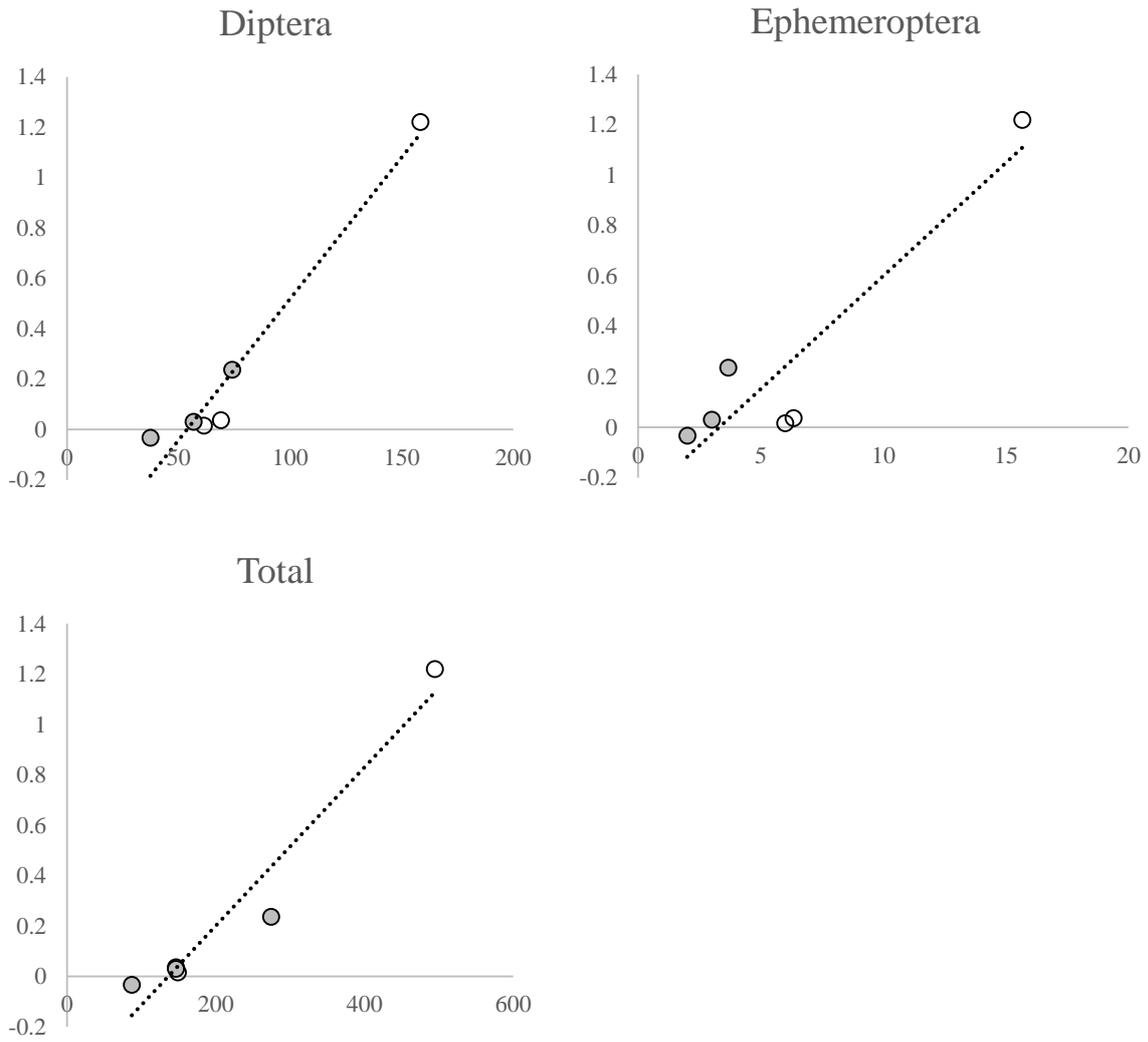
Figure S2 Average individual weight gain of alevins by cage according to the average abundance of Diptera, Ephemeroptera and the total invertebrates by cage at the end of the trials. Empty circles represent the control cages, grey circles the impacted cages and the dotted line the correlation.

Chapter IV Consequences of Global Climate Change on the community of invertebrates, on the survival and growth of first-feeding alevins at low density: flood simulation in a semi-natural environment

Introduction

The previous experiment emphasised that hydrological disturbances decreased the food availability for fish but the consequences at the fish level depended on the productivity of the system. These results stemmed out from an experiment at high fish density (32 fish m^{-2}) and one may wonder on the persistence of these effects on the fish population at low alevins density. According to literature, mortality rate at low density is mainly density-independent while density-dependent growth still occurs (Jenkins et al. 1999; Grant & Imre 2005; Imre et al. 2005).

A protocol was set up in the experimental channel of the Lapitxuri in late spring to look at the performances of alevins at low density. A flood was simulated in four half-reaches, while four others were not impacted and used as control. Immediately after the flood, invertebrates were sampled and just-emerged brown trout alevins were introduced in all reaches at low fish density (2.6 fish m^{-2}). After 33 days, the surviving alevins were recovered and invertebrates were sampled. We aimed to test the following hypotheses:

1. Flood should diminish the abundance of invertebrates,

2. Flood should diminish growth of alevins, but not survival,

3. A relationship between the abundance of invertebrates and growth is awaited.

Material and Methods

The experimental channel of the Lapitxuri and experimental design

The experiment was conducted from April to the end of May 2015 in an experimental channel fed by the Lapitxuri brook, a tributary of the Nivelle river in south-western France (43°16' N, 1°28' W). Four reaches (10 m long and 2.8 m wide) were used for the experiment, two located at 30 meters and two at 80 meters downstream the flow entry (Figure 4.1). Each reach was divided longitudinally by a tarpaulin wall in two half-reaches of 14 m² (10 m long and 1.4 m wide). Upstream and downstream movements of fish were prevented by nets, and traps at the end of downstream nets allowed to catch drifting fish. Aerial nets protected fish from avian predation. Gravel bed was constituted by cobbles and pebbles, substrate particles ranging approximately from 1 to 5 cm. The average mid-water velocity was maintained during the whole experiment at 12.4 cm s^{-1} (SD = 3.9 – calculation based on the absolute value of velocity measurements) and the mean water temperature during the experiment was 13.34°C (SD = 1.04). Abiotic conditions in the channel were close to optimal environment for young trout in terms of substratum quality, water quality and temperature values (Roussel & Bardonnet 1997,

2002; Heggenes et al. 1999). Food supply was provided by invertebrate drift from the Lapitxuri brook and by the production of the channel itself. To recover fish from a previous experiment, an electrofishing was conducted in the totality of the channel on 14/04/2015. On 15/04/2015, a flood was simulated with a motor-pump in the 4 left-bank reaches (Figure 4.1). The motor-pump was used at the extreme right point during 5 seconds, then the pump was displaced by 20 cm to the left and used again during 5 seconds. This procedure was repeated over the entire width of the impacted reach (7 times) and such transects were made every 50 cm to cover the entire length of each impacted reach. The use of the motor-pump increased the water velocity up to 92.2 cm s^{-1} (SD = 18.9) on average, ranging from 45 to 146 cm s^{-1} in the 50 cm in front of the outflow. After the flood simulation, the gravel bed was flattened again.

Figure 4.1 Experimental design set up in the semi-natural channel of the Lapitxuri. Eight reaches were used. Four reaches were impacted by the flood (left bank – in grey) and four reaches served as controls (right bank – in white).

Fish sampling

On 16/01/2015, eggs were obtained through the artificial fertilization of gametes of wild brown trout caught in the Nivelle watershed (43°21' N, 1°33' W). Eggs and alevins were reared at 8.33°C (SD = 1.40) until complete yolk sac depletion (752 degree-days; survival: 92%). On 16/04/2015, 40 randomly selected alevins were individually weighed and measured to

characterize the biometry of the batch. Then, remaining individuals were randomly split into eight groups of 37 alevins and released in the eight experimental reaches of the Lapitxuri semi-natural stream. The fish density in each reach was of 2.6 fish m^{-2} (~8% of the density used for the previous experiment). Downstream traps were checked every morning, and after counting, fish were immediately released back into the reach they came from. After 33 days of growth, surviving alevins were recovered by successive removal of electrofishing (19–22 May). They were weighted, measured and subjected to a benzocaine lethal anesthesia. Eight alevins of each reach were randomly selected and all invertebrates contained in their stomachs were identified to family level when possible and counted. Then a total of sixty-four gut contents were analysed.

Benthic invertebrate sampling

Immediately after the flood simulation (15/04/2015) and at the end of the trial (19/05/2015), 3 invertebrate samples by reach were randomly collected using a Surber net (30 cm x 30 cm, 500 µm mesh). Samples were preserved in 70% ethanol. Invertebrates were identified and assigned to different groups: Diptera, Trichoptera, Ephemeroptera, Mollusca, Coleoptera, Plecoptera, Oligochaeta, Crustacea and Exogenous.

Statistical analyses

Abundance of invertebrates as well as the logit of the alevins survival probability, alevins individual weight gain and fish productivity (sum of final weights) were analysed using a bayesian modelling approach computed with OpenBUGS®. All the models were built with the same logic: we assumed that the variables of interest followed a normal distribution. Then, the mean of the variable (µ.Variable) was modelled according to two parameters: a fixed-effect relative to the flood (α) and a random effect relative to each j reach (β$_j$), which integrated all the potential sources of variation other than the flood. The number of prey ingested by alevin followed a Poisson law and the mean (µ.Prey) was modelled according to these same two effects (α and β$_j$).

Abundance of invertebrates

If Abond$_i$ is the number of invertebrates counted by sample, we assume:

$$\mu.\log(Abond_i + 1)_i = \mu + \alpha\ Flood_i + \beta_{j[i]}$$

Where µ is the average of the logarithm of the invertebrate abundance, α is a fixed-effect parameter for the impact of the flood and β is a random effect corresponding to each j reach. The same modelling treatment was applied to the total abundance of invertebrates as well as to

the abundance of each group identified (*i.e.* Diptera, Trichoptera, Ephemeroptera, Mollusca, Coleoptera, Plecoptera, Oligochaeta and Crustacea) and for exogenous individuals.

Survival probability of alevins

For each j reach, number of survivors S_j is estimated from the number of fish caught at each electrofishing passage ($C1_j$, $C2_j$, $C3_j$ and $C4_j$), the number of remaining fish after each passage ($R1_j$, $R2_j$ and $R3_j$) and the fish efficiency ($p.F_j$):

$$C1_j \sim Binomial(p.F_j, S_j)$$

$$R1_j = S_j - C1_j \; ; \; C2_j \sim Binomial(p.F_j, R1_j)$$

$$R2_j = R1_j - C2_j \; ; \; C3_j \sim Binomial(p.F_j, R2_j)$$

$$R3_j = R2_j - C3_j \; ; \; C4_j \sim Binomial(p.F_j, R3_j)$$

Then, if $p.S_j$ is the probability of survival in the j reach and N_j the number of fish introduced in each reach at the beginning of the experiment, we assume:

$$S_j \sim Binomial(p.S_j, N_j)$$

$$\mu.Logit(p.S_j) = \mu + \alpha\,Flood_j + \beta_j$$

Where μ is the average of the logit survival probability, α is a fixed-effect parameter for the impact of the flood and β is a random effect corresponding to each j reach.

Individual weight gain of alevins

The initial weight (IW) of the 40 alevins sub-sampled at the beginning of the experiment allowed to estimate the mean ($\mu.IW$) and the standard deviation ($\sigma.IW$) of the alevins initial weight distribution. For each k survivor recovered at the end, its initial weight ($W.Beg_k$) was drawn in the alevin initial weight distribution (according to $\mu.IW$ and $\sigma.IW$), while its final weight was known ($W.End_k$). By j reach, the standard deviation of the final weight of alevins ($\sigma.W.End_j$) was also modelled to test if the flood affected the variability of alevins final weight.

Individual weight gain (WG_k) was obtained by dividing the difference between the final weight and the initial weight by the initial weight. Then, we assume:

$$\mu.WG_k = \mu + \alpha\,Flood_k + \beta_{j[k]}$$

Where μ is the average weight gain of alevins, α is a fixed-effect parameter for the impact of the flood and β is a random effect corresponding to each j reach.

For each j reach, the final weights were summed to obtain the fish production per reach (Prod.Fish$_j$).

$$\mu.Prod.Fish_j = \mu + \alpha\, Flood_j + \beta_j$$

Where μ is the average fish production, α is a fixed-effect parameter for the impact of the flood and β is a random effect corresponding to each j reach.

Relationship between the community of invertebrate and alevins

We linked (*i*) the number of surviving alevins by reach, (*ii*) the average individual weight gain of alevins by reach and (*iii*) fish productivity by reach according to the average invertebrate abundance by reach immediately after the flood or at the end of the experiment (33 days after). Then, 60 relationships were tested (10 invertebrate groups x 3 variables for alevin performances x 2 times). Correlations were tested with OpenBUGS®. If Y_j was the variable of the jth reach, we assume:

$$Y_j = a\, Abond_j + b$$

Where Y_j is the number of survivors by reach (S_j), the fish weight gain by reach ($WG_{j[i]}$) or the fish productivity by reach (Prod.Fish$_j$), a is the slope coefficient, Abond$_j$ is the average invertebrate abundance by reach and b is the intercept.

Fit of the correlation is calculated by dividing the variability unexplained by the correlation model with the variability observed in the data set, as follows:

$$Fit = 1 - \frac{Variability\ unexplained\ by\ the\ model}{Variability\ of\ the\ data\ set}$$

When the fit is negative, there is no correlation. When the fit is between 0 and 0.5, the correlation is intermediate. When the fit is between 0.5 and 1, the correlation is good.

Gut contents

For the description of the diet, data were pooled according to conditions (control *vs*. impacted). The total number of prey (N), the relative abundance (A) and the occurrence of prey in fish (F, where the number of alevins containing this kind of prey is divided by the total number of alevins sampled) were calculated for each family.

Total number of prey ingested by alevins and the number of individuals of Chironomidae and Baetidae families (which are the main food items just-emerged alevins) were analysed. Then, if Prey$_l$ is the number of prey ingested by the lth alevins, we assume:

$$Prey_l \sim Poisson(\mu.Prey_l)$$

$$\log(\mu.Prey_l) = \mu + \alpha\ Flood_j + \beta_j$$

Where µ is the average number of prey ingested, α is a fixed-effect parameter for the impact of the flood and β is a random effect corresponding to each j reach.

Bayesian computations

Parameters were given independent "weakly informative" priors. Following recommendations of Gelman & Hill (2007), µ, α, µ.IW, σ.IW, a and b were sampled in a normal distribution, N(0, 100). β_j were drawn in a normal distribution, N(0, σ_β^2), with σ_β sampled in a truncated half-Cauchy distribution, t(0, 1, 1). p.F$_j$ were sampled in a beta distribution, beta(1, 1). Hyperparameters of σ.W.End$_j$ (B.σ.W.End and E.σ.W.End) were sampled in a gamma distribution, gamma(1, 1). We used each time three independent chains, the first 10 000 iterations were discarded as an initial burn-in period. Then, 10 000 further iterations (resulting from one every ten runs) were performed. The convergence of the chains to their ergodic distribution was tested *via* the Gelman-Rubin (GR) diagnostics integrated in OpenBUGS®. The significance of the parameters was tested with the step function implemented in OpenBUGS®. At each iteration for a variable X, step(X) equaled 1 if $X \geq 0$ and equaled 0 if $X < 0$. At the end of the run, if P(X > 0) was lower than 0.1 or higher than 0.9, the parameter X was considered to be different from 0.

Results

Effect of the flood on the community of invertebrates

Immediately after the artificial flood, most invertebrate groups and the total abundance of invertebrates were negatively impacted (except Mollusca – Figure 4.2). However, this tendency was never significant (except for Coleoptera (P(α_1 > 0) = 0.054, Table 4.1). At the end of the trial, all groups (except Diptera) were still less abundant in the impacted reaches, but again differences were not significant, (except for Ephemeroptera and Mollusca (P(α_2 > 0) = 0.037 and 0.052 respectively).
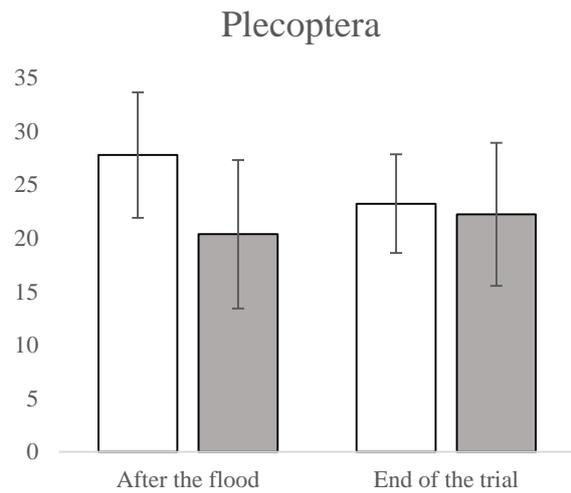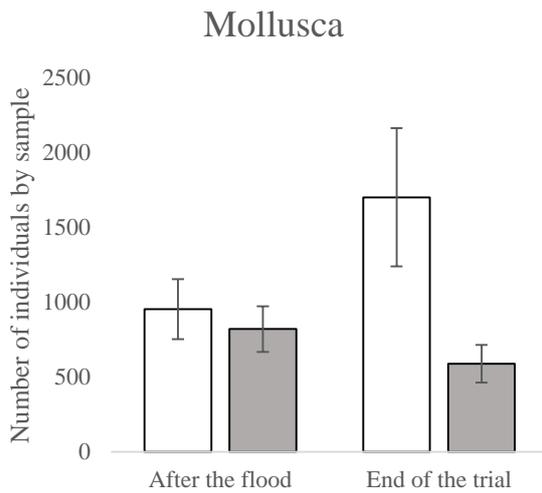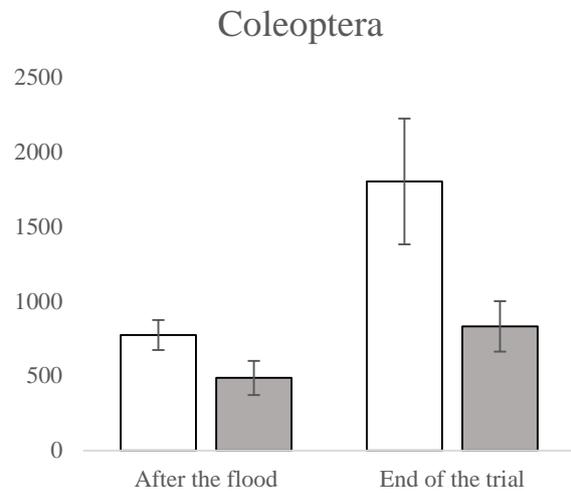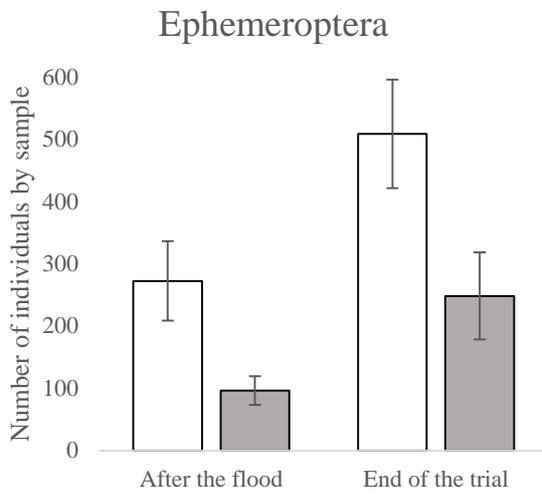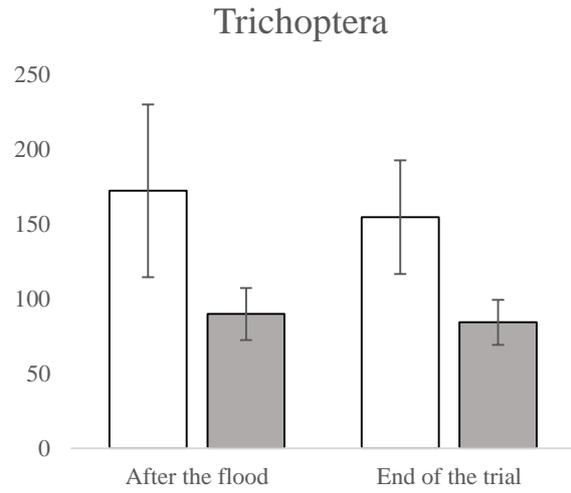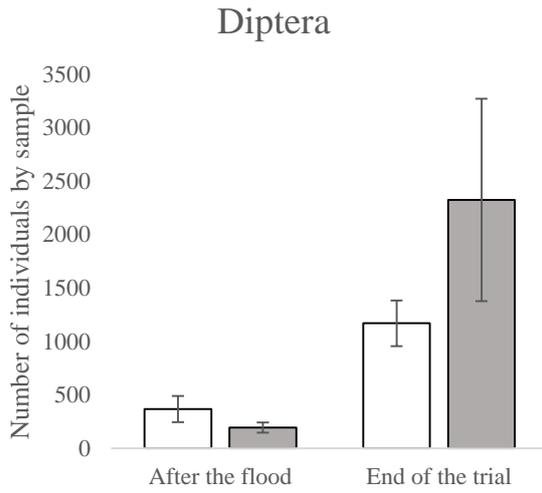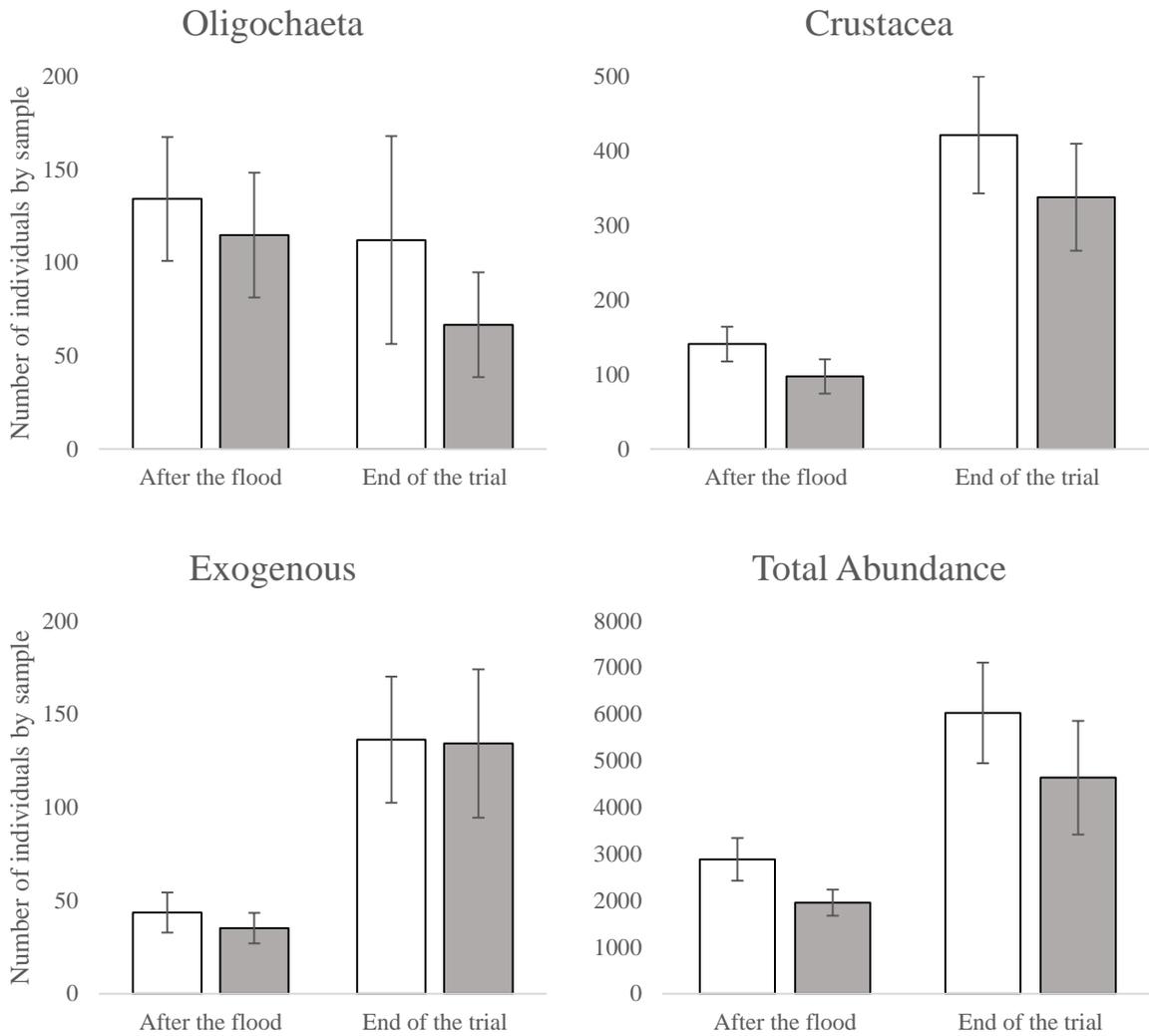
Figure 4.2 Number of individuals per sample (average ± standard error) of the groups of invertebrates identified according to treatment (Control in white and Impacted by flood in grey) immediately and at the end of the trial.

Table 4.1 Mean of the posterior probability distribution functions of α, the effect of flood on the logarithm of the abundance of invertebrates. The effect was estimated for each group and for the total abundance, immediately after the flood and at the end of the trial. Parameters were considered significant when P(X > 0) is less than 0.10 or above 0.90 (in bold).

Groups	After the flood		End of the trial	
	α_1	$P(\alpha_1 > 0)$	α_2	$P(\alpha_2 > 0)$
Diptera	-0.375	0.264	0.078	0.553
Trichoptera	-0.440	0.163	-0.724	0.117
Ephemeroptera	-0.844	0.156	-1.307	**0.037**
Mollusca	0.015	0.512	-1.282	**0.052**
Coleoptera	-0.680	**0.054**	-0.737	0.122
Plecoptera	-0.500	0.246	-0.565	0.208
Oligochaeta	0.014	0.503	-0.763	0.232
Crustacea	-0.185	0.370	-0.616	0.196
Exogenous	0.060	0.545	-0.402	0.281
Total	-0.301	0.186	-0.519	0.168

Effect of the flood on alevins

Survival probability reached 84% in the control and only 63% in the impacted reaches (Figure 4.3). At the beginning of the experiment, the batch of 40 alevins weighted on average 0.104 g and the SD was low (0.004). At the end of the trial (33 days of growth), fish were lighter in the control (0.459 g on average), than in the impacted reaches (0.505 g). Accordingly, weight gain was lower in the control (3.411) than in the impacted reaches (3.854). In addition, alevins weights were more homogenous in the impacted reaches ($SD_{F1} = 0.060$, $SD_{F2} = 0.065$, $SD_{F3} = 0.087$ and $SD_{F4} = 0.090$), than in the control ones ($SD_{C1} = 0.098$, $SD_{C2} = 0.104$, $SD_{C3} = 0.092$ and $SD_{C4} = 0.113$). Finally, fish productivity reached on average 13.23 g in control reaches and only 11.31 g in the impacted ones.

To sum up, alevin survival probability and fish productivity were significantly lower in the impacted reaches than in the control ones ($P(\alpha > 0) = 0.012$ and 0.084, respectively – Table 4.2), while individual weight gain was higher ($P(\alpha > 0) = 0.907$).

Table 4.2 Mean of the posterior probability distribution functions of α, the effect of flood on the survival probability, on individual weight gain of alevins and on fish productivity. Parameters were considered significant when P(X > 0) is less than 0.10 or above 0.90 (in bold).

| Effect of the flood (α) on …	Mean	$P(\alpha > 0)$
Survival probability	-1.169	**0.012**
Weight gain	0.443	**0.907**
Productivity	-1.923	**0.084**
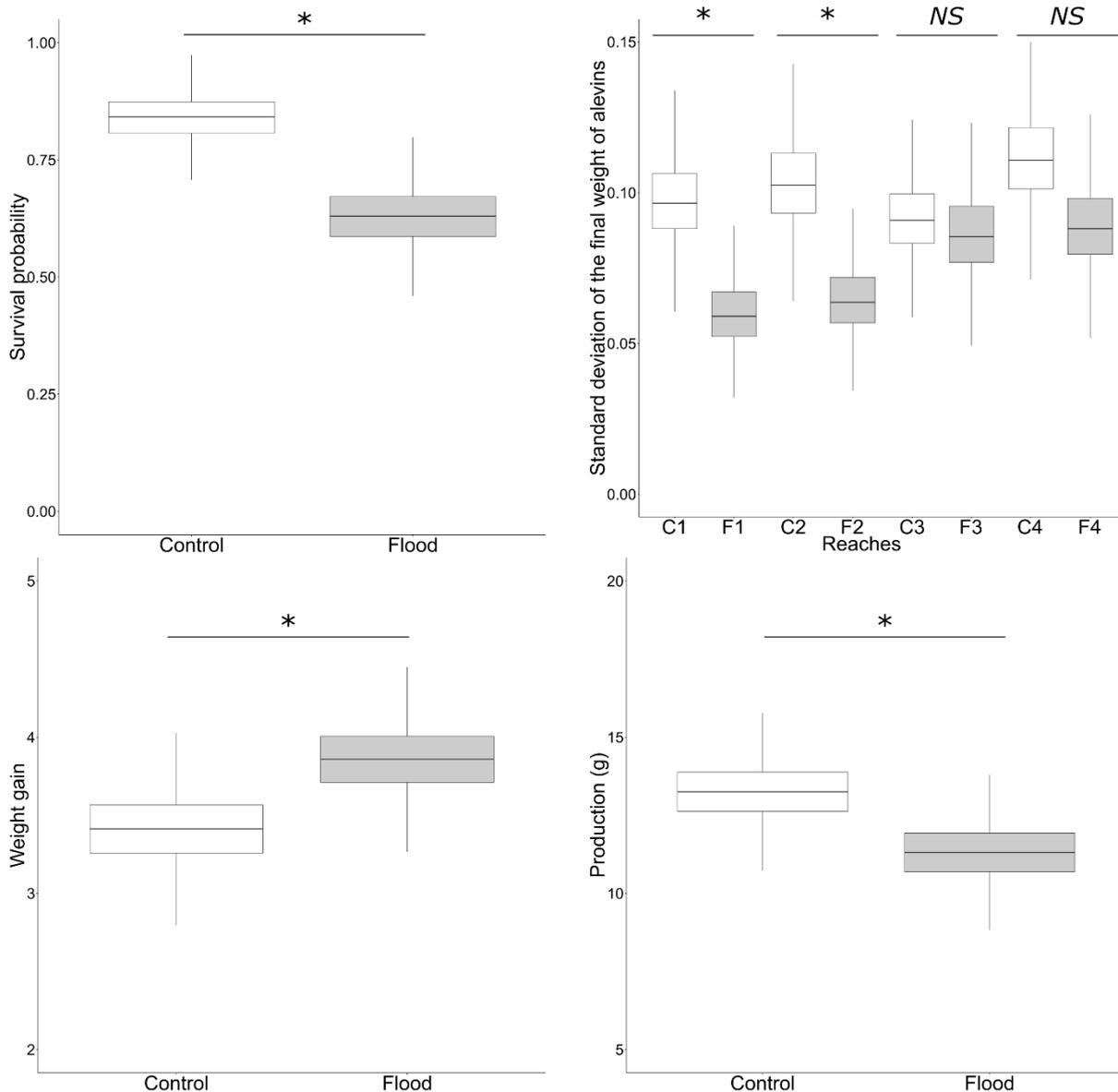
Figure 4.3 Model estimates of the survival probability, of standard deviation of the final weight, of weight gain of alevins and of fish productivity of control (in white) and impacted by flood reaches (in grey). Boxplots indicate the 1, 25, 50, 75 and 99 percentiles of posterior distributions. Significant differences are shown by *.

Relationship between the community of invertebrate and alevins

Alevins performances (number of survivors, average individual weight gain, fish productivity) were related to the abundances of each invertebrate group (10 groups: Diptera, Trichoptera, Ephemeroptera, Mollusca, Coleoptera, Plecoptera, Oligochaeta, Crustacea, Exogenous and Total) both immediately after the flood (Table 4.3) and at the end of the trial (Table 4.4), then 60 relationships were tested. On the 60 relationships tested, 45 fits of correlations were negative and 15 fits were positive but lower than 0.50. This meant that the link between the variables tested was low or inexistent. Focusing on Diptera and Ephemeroptera orders, despite the poor

quality of the correlations, on 12 relationships, the slope coefficient was significantly positive five times ($P(a > 0) > 0.9$) and significantly negative once ($P(a > 0) < 0.1$), leading to the following hypotheses: the initial abundance of Diptera and Ephemeroptera increased the survival and the productivity of fish (Table 4.3). However, the growth of alevins decreased the abundance of Ephemeroptera at the end of the trial (Table 4.4).

Table 4.3 Correlations between invertebrate abundances immediately after the flood (X) and fish variable (Y), mean of posterior probability distribution functions of a (the slope coefficient) and b (the intercept) and fit of the models. Parameters were considered significant when P(X > 0) is less than 0.10 or above 0.90 (in bold).

Fish variable (Y)	Invertebrate variable (X)	Groups	a	P(a > 0)	b	P(b > 0)	Equations	Fit
Number of surviving alevins by reach S	Abundance of invertebrates by reach Immediately after the flood	Diptera	0.009	**0.912**	23.890	**1.000**	S = 0.008572 Diptera + 23.89	-0.198
		Trichoptera	0.028	**0.951**	22.680	**1.000**	S = 0.02825 Trichoptera + 22.68	-0.127
		Ephemeroptera	0.016	**0.967**	23.510	**1.000**	S = 0.01583 Ephemeroptera + 23.51	0.034
		Mollusca	0.008	**0.943**	19.440	**0.996**	S = 0.007867 Mollusca + 19.44	-0.400
		Coleoptera	0.011	**0.973**	19.530	**0.998**	S = 0.01103 Coleoptera + 19.53	-0.164
		Plecoptera	0.198	**0.952**	21.610	**0.999**	S = 0.198 Plecoptera + 21.61	-0.191
		Oligochaeta	0.040	**0.917**	21.340	**0.999**	S = 0.03996 Oligochaeta + 21.34	-0.372
		Crustacea	0.067	**0.990**	18.700	**0.999**	S = 0.06662 Crustacea + 18.7	0.068
		Exogenous	0.102	**0.915**	22.290	**1.000**	S = 0.1021 Exogenous + 22.29	-0.324
		Total	0.003	**0.969**	20.230	**0.999**	S = 0.002573 Total + 20.23	-0.167
Average individual weight gain of alevins by reach WG	Abundance of invertebrates by reach Immediately after the flood	Diptera	0.000	0.750	3.518	**1.000**	WG = 0.0004204 Diptera + 3.518	-0.236
		Trichoptera	0.001	0.618	3.567	**1.000**	WG = 0.0005287 Trichoptera + 3.567	-0.333
		Ephemeroptera	0.000	0.616	3.587	**1.000**	WG = 0.0002745 Ephemeroptera + 3.587	-0.326
		Mollusca	0.000	0.838	3.226	**1.000**	WG = 0.0004618 Mollusca + 3.226	-0.108
		Coleoptera	0.000	0.663	3.477	**1.000**	WG = 0.0002509 Coleoptera + 3.477	-0.304
		Plecoptera	0.001	0.537	3.610	**1.000**	WG = 0.001053 Plecoptera + 3.61	-0.344
		Oligochaeta	0.000	0.554	3.589	**1.000**	WG = 0.0003731 Oligochaeta + 3.589	-0.337
		Crustacea	0.000	0.511	3.628	**1.000**	WG = 0.00007267 Crustacea + 3.628	-0.346
		Exogenous	0.007	0.835	3.374	**1.000**	WG = 0.006682 Exogenous + 3.374	-0.121
		Total	0.000	0.738	3.417	**1.000**	WG = 0.00009113 Total + 3.417	-0.258
Fish productivity by reach Prod	Abundance of invertebrates by reach Immediately after the flood	Diptera	0.003	**0.950**	11.440	**1.000**	Prod = 0.003001 Diptera + 11.44	0.159
		Trichoptera	0.009	**0.956**	11.160	**1.000**	Prod = 0.008547 Trichoptera + 11.16	0.177
		Ephemeroptera	0.005	**0.979**	11.330	**1.000**	Prod = 0.00519 Ephemeroptera + 11.33	0.344
		Mollusca	0.002	**0.942**	10.320	**1.000**	Prod = 0.002216 Mollusca + 10.32	0.088
		Coleoptera	0.003	**0.964**	10.360	**1.000**	Prod = 0.003065 Coleoptera + 10.36	0.204
		Plecoptera	0.044	0.886	11.220	**1.000**	Prod = 0.04409 Plecoptera + 11.22	-0.035
		Oligochaeta	0.007	0.801	11.380	**1.000**	Prod = 0.007145 Oligochaeta + 11.38	-0.173
		Crustacea	0.017	**0.968**	10.280	**1.000**	Prod = 0.01685 Crustacea + 10.28	0.224
		Exogenous	0.032	**0.941**	11.010	**1.000**	Prod = 0.03226 Exogenous + 11.01	0.106
		Total	0.001	**0.973**	10.410	**1.000**	Prod = 0.0007759 Total + 10.41	0.271

Table 4.4 Correlations between invertebrate abundances at the end of the trial (X) and fish variable (Y), mean of posterior probability distribution functions of a (the slope coefficient) and b (the intercept) and fit of the models. Parameters were considered significant when P(X > 0) is less than 0.10 or above 0.90 (in bold).

Fish variable (Y)	Invertebrate variable (X)	Groups	a	P(a > 0)	b	P(b > 0)	Equations	Fit
Number of surviving alevins by reach S	Abundance of invertebrates by reach At the end of the trial (33 days)	Diptera	-0.001	0.213	27.850	**1.000**	S = -0.0008931 Diptera + 27.85	-0.046
		Trichoptera	0.037	**0.954**	22.060	**1.000**	S = 0.03713 Trichoptera + 22.06	-0.164
		Ephemeroptera	0.017	**0.994**	20.400	**1.000**	S = 0.01676 Ephemeroptera + 20.4	0.250
		Mollusca	0.004	**0.993**	21.840	**1.000**	S = 0.004215 Mollusca + 21.84	0.283
		Coleoptera	0.002	**0.939**	23.050	**1.000**	S = 0.002463 Coleoptera + 23.05	-0.172
		Plecoptera	0.262	0.877	20.470	**0.995**	S = 0.2616 Plecoptera + 20.47	-0.566
		Oligochaeta	0.019	0.808	24.520	**1.000**	S = 0.01855 Oligochaeta + 24.52	-0.339
		Crustacea	0.016	**0.934**	20.260	**0.997**	S = 0.01626 Crustacea + 20.26	-0.393
		Exogenous	0.017	0.756	23.820	**0.999**	S = 0.0173 Exogenous + 23.82	-0.475
		Total	0.001	0.897	21.930	**0.999**	S = 0.0008152 Total + 21.93	-0.415
Average individual weight gain of alevins by reach WG	Abundance of invertebrates by reach At the end of the trial (33 days)	Diptera	0.000	0.851	3.412	**1.000**	WG = 0.0001282 Diptera + 3.412	-0.095
		Trichoptera	-0.002	0.128	3.916	**1.000**	WG = -0.00239 Trichoptera + 3.916	-0.046
		Ephemeroptera	-0.001	**0.081**	4.015	**1.000**	WG = -0.001018 Ephemeroptera + 4.015	0.104
		Mollusca	0.000	**0.029**	4.007	**1.000**	WG = -0.0003253 Mollusca + 4.007	0.344
		Coleoptera	0.000	**0.057**	3.937	**1.000**	WG = -0.0002251 Coleoptera + 3.937	0.185
		Plecoptera	0.008	0.659	3.454	**1.000**	WG = 0.008094 Plecoptera + 3.454	-0.307
		Oligochaeta	-0.002	0.171	3.794	**1.000**	WG = -0.001739 Oligochaeta + 3.794	-0.129
		Crustacea	-0.001	0.186	3.966	**1.000**	WG = -0.0008761 Crustacea + 3.966	-0.147
		Exogenous	0.000	0.483	3.646	**1.000**	WG = -0.00006981 Exogenous + 3.646	-0.351
		Total	0.000	0.222	3.871	**1.000**	WG = -0.00004401 Total + 3.871	-0.198
Fish productivity by reach Prod	Abundance of invertebrates by reach At the end of the trial (33 days)	Diptera	0.000	0.184	12.880	**1.000**	Prod = -0.0003482 Diptera + 12.88	-0.077
		Trichoptera	0.004	0.693	11.830	**1.000**	Prod = 0.003705 Trichoptera + 11.83	-0.244
		Ephemeroptera	0.003	0.880	11.220	**1.000**	Prod = 0.002825 Ephemeroptera + 11.22	-0.054
		Mollusca	0.001	0.826	11.590	**1.000**	Prod = 0.0005948 Mollusca + 11.59	-0.138
		Coleoptera	0.000	0.579	12.110	**1.000**	Prod = 0.0001153 Coleoptera + 12.11	-0.264
		Plecoptera	0.021	0.619	11.810	**1.000**	Prod = 0.02081 Plecoptera + 11.81	-0.275
		Oligochaeta	-0.001	0.422	12.360	**1.000**	Prod = -0.001085 Oligochaeta + 12.36	-0.258
		Crustacea	0.001	0.618	11.870	**1.000**	Prod = 0.001065 Crustacea + 11.87	-0.268
		Exogenous	-0.001	0.457	12.350	**1.000**	Prod = -0.0005867 Exogenous + 12.35	-0.264
		Total	0.000	0.518	12.190	**1.000**	Prod = 0.00001373 Total + 12.19	-0.277

Gut contents

All the sixty-four alevins had prey in the stomach. The number of preys ingested was 1.5 lower in the control reaches when compared to the impacted ones (Table 4.5). The Chironomidae family was found in 100% of alevins from the control reaches and in 96.9% of alevins from the impacted ones. Chironomidae represented 68.3% and 76.1% of the prey consumed in the control and impacted reaches, respectively. Baetidae was the second most represented group (17.5% of prey in the control and 12.7% in the impacted reaches). The other groups represented less than 3% of the total amount of prey ingested.

Model estimations highlighted that fish consumed significantly less prey in the control (12.3 prey on average) than in the impacted reaches (17.4 prey on average, $P(\alpha > 0) = 0.998$ – Figure 4.4). Accordingly, fish ate significantly less Chironomidae in the control (8.4 in average) than in the impacted reaches (13.2 in average, $P(\alpha > 0) = 993$ – Figure 4.4). However, there was no difference in the number of Baetidae ingested (2.1 vs 2.2 respectively, in the control and in the impacted reaches – $P(\alpha > 0) = 0.559$).

Table 4.5 Diet composition. Number of prey (N), relative abundance (A) and frequency of occurrence in fish (F) in the control and in the impacted reaches.

|	Control			Flood		
	N	A (%)	F (%)	N	A (%)	F (%)
Diptera						
Chironomidae	269	68.3	100	424	76.1	96.9
Simuliidae	8	2.0	21.9	5	0.9	15.6
Empididae	-	-	-	1	0.2	3.1
Brachycera	-	-	-	1	0.2	3.1
?	2	0.5	6.3	1	0.2	3.1
Trichoptera						
Polycentropodidae	7	1.8	18.8	9	1.6	21.9
Philopotanidae	-	-	-	1	0.2	3.1
Hydropsychidae	1	0.3	3.1	3	0.5	9.4
Psychomyiidae	-	-	-	1	0.2	3.1
?	5	1.3	15.6	5	0.9	12.5
Ephemeroptera						
Baetidae	69	17.5	87.5	71	12.7	71.9
Heptageniidae	3	0.8	9.4	4	0.7	6.3
Ephemerellidae	11	2.8	21.9	3	0.5	9.4
Caenidae	1	0.3	3.1	-	-	-
?	1	0.3	3.1	1	0.2	3.1
Coleoptera						
Elmidae	1	0.3	3.1	2	0.4	6.3
Amphipoda						
Gammaridae	2	0.5	6.3	3	0.5	6.3
Isopoda						
Asellidae	3	0.8	9.4	-	-	-
Oligochaeta	1	0.3	3.1	-	-	-
Others						
Hydracaria	4	1.0	3.1	6	1.1	6.3
Hemiptera	-	-	-	1	0.2	3.1
Nematoda	-	-	-	5	0.9	3.1
?	1	0.3	3.1	1	0.2	3.1
Exogenous	5	1.3	15.6	9	1.6	25.0
Total	394			557		
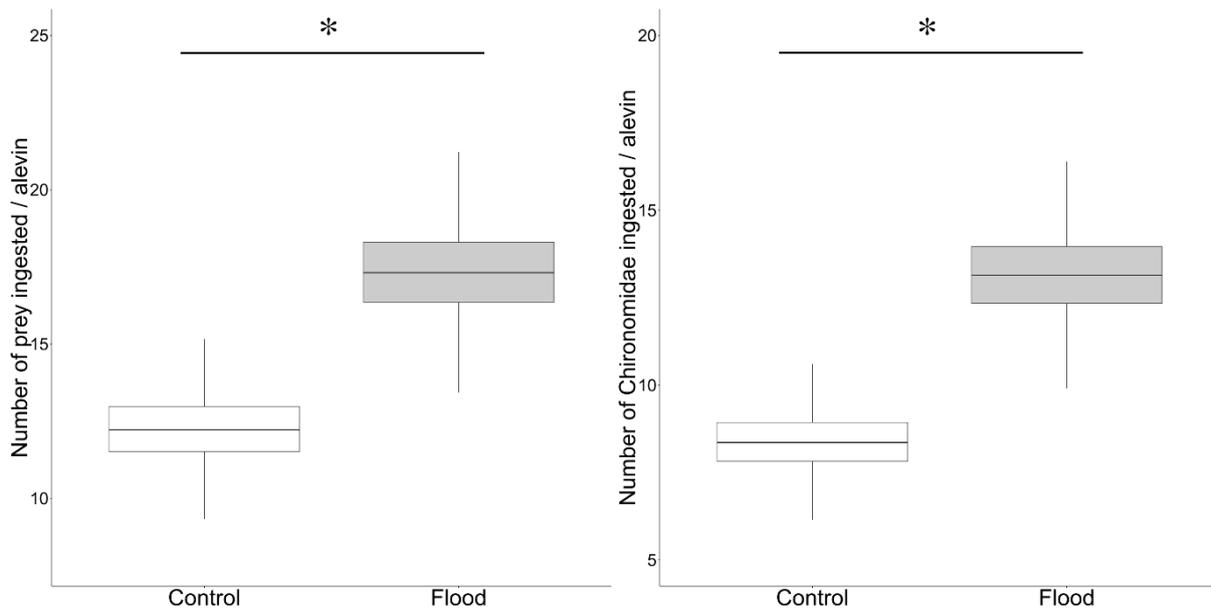
Figure 4.4 Model estimations of the number of prey ingested and the number of Chironomidae ingested by alevins in the control (in white) and in the impacted (in grey) reaches. Boxplots indicate the 1, 25, 50, 75 and 99 percentiles of posterior distributions. Significant differences are shown by *.

Table 4.6 Synthesis of the main results on the effects of the artificial flood on invertebrate abundances (total and Diptera), alevin performances (survival and growth) and alevin diet (number of prey eaten and number of Chironomids eaten) in late spring.

		Late Spring		
		Control		Flood
Invertebrates	Abundances …			
	• Total	MODERATE	→	MODERATE
	• Diptera	HIGH	↗	VERY HIGH
	Recolonization	HIGH	↗	VERY HIGH
Alevin performances	Survival	HIGH *85 %*	↘	MODERATE *60 %*
	Growth	HIGH *3.4*	↗	VERY HIGH *3.9*
Alevin diet	Number of prey	*12*	↗	*17*
	Number of Chironomids	*8*	↗	*12*

Discussion

We failed at pointing out a significant effect of the artificial flood on the community of invertebrates. There was a high variability among the 3 samples characterizing a given reach, and this is probably why results were not significant. Thus, despite the homogeneity of the reaches in terms of water velocity, depth and gravel size, this suggests a huge heterogeneity in

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spatial distribution of invertebrates as observed in the field (Downes et al. 1995; Heino et al. 2004). Nevertheless, the repeated trend for every taxa was a decrease in abundance in the impacted reaches and this trend persisted thirty-three days after the flood (except concerning Diptera). Because Diptera are essential in fish diet (see gut contents results), they deserve a specific attention. In control reaches, Diptera abundances double during the May month, probably in accompaniment to the increase in primary productivity and temperature. This happened also in the impacted reach, the average effect was much higher (more than 10 times increase), even if quite heterogeneous among reaches. All groups of invertebrates showed the same trend but Diptera was the only group exhibiting such a high increase in the impacted reaches.

As there was no significant impact of the artificial flood immediately afterwards, it was not expected to detect differences at the end of the trial, thirty-three days later. However, there were significantly less Ephemeroptera and Mollusca in the impacted reaches. Although there was no significant difference immediately after the disturbance, enough adults could have been displaced and/or the clutches hooked to the gravel (Gaino & Rebora 2001; Tachet et al. 2010) could have been decimated, weakening the next generation of these two orders.

Surviving alevins were more homogenous in weight in the impacted reaches than in the control ones. It is likely that the lack of food affected first the weaker ones, which would die because of their inability to establish a feeding territory and a lower amount of reserves than bigger alevins. This hypothesis is supported by Good et al. (2001) who concluded that early mortality associated with hydroclimatic events was high for small Atlantic salmon as they were not strong enough to survive. Then, massive mortalities caused by hydrological events reduce variability in individual growth rate (Vincenzi et al. 2012). The higher weight gain of alevins in impacted reaches than in the control ones could be related to density-dependent mechanisms with few survivors sharing the same amount of resources. Another explanation may rely on the difference in habitat availability. Indeed, floods mobilise fine particles filling the interstices of the gravel bed (Kondolf & Wilcock 1996; Mürle et al. 2003; Lepori & Hjerdt 2006), which maintain the heterogeneity of the substrate and provide shelters. Habitat heterogeneity increases the visual isolation between alevins and reduces the strength of the aggressive interactions (Kalleberg 1958; Bolliet et al. 2005). The combined effect of a diminution in the numbers of competitors and a heterogeneous habitat may have enhanced fish growth (Letcher & Terrick 1998). Gut content analyses highlighted a higher number of prey ingested by alevins in the impacted than in the control reaches and a large amount of these prey were Chironomidae. Cross et al. (2011)

found that a flood in the Colorado River (USA) decreased the number of benthic invertebrates while the production of rainbow trout (*Oncorhynchus mykiss*) increased. The trout production was mainly supported by invertebrates from the Simuliidae and the Chironomidae families, which both represented 50% of the prey ingested. They suggested that the flood created favourable conditions for age-0 trout: the scouring of the benthos associated with the flood enhanced the quality of the habitat and increased the production of Simuliidae and Chironomidae, which need a clean substrate for attachment. These taxa are also the pioneers at the recolonization time after hydrological disturbances (Otermin et al. 1998). Despite the absence of significant difference in the invertebrate community, it can be argued that the Chironomidae preferentially colonized the impacted reaches because the habitat was of better quality but the intrinsic variability of the experimental channel masked this phenomenon. Therefore, the increase in Diptera in the impacted reach may have also favour growth. However, the highest growth of alevins did not compensate for their lower survival and fish productivity was reduced by the impacted reach.

We predicted that reaches with a good food availability (high abundance of invertebrates) would enable the settlement of a stronger fish population (high numbers of survivors, high average weight gain and high productivity) but it was difficult to put forward this kind of relationship. Although abiotic factors were controlled and the habitat simplified compared to natural environment, the invertebrate community was unevenly spread and the heterogeneity in the invertebrate distribution limited the information provided by benthic samples. Additionally, Weber et al. (2017) demonstrated that measuring the biomass of invertebrates drifting was more accurate to estimate food supply for fish. Even if there is a link between benthic invertebrates and drifting invertebrates, direct relationship between benthic community composition and the productivity of salmonids is not well established (Fausch et al. 1988). Moreover, sampling at a given time does not reflect the dynamics of the invertebrate population and the food availability on the 33 days that lasted the experiment. More accurate analysis taking into account only small larvae of Chironomidae, Simuliidae and Baetidae might improve our understanding of the mechanisms at work.

Conclusion

The impact of the artificial flood was low on the invertebrate assemblage, while it was obvious on brown trout young stages. At low fish density (2.6 fish m^{-2}), the artificial flood decreased fish survival and improved fish growth (probably in relation with a mix between habitat, density and food availability). Despite our inability to identify the proximal factors underpinning fish

performances, emergence appears to be a critical stage, highly sensitive to hydrological disturbances since even at low density, and with relatively low impact on benthic invertebrates, fish productivity was negatively impacted.

General discussion

In the following section, I will highlight how results from different chapters complement each other to answer the original question: what could be the consequences of Global Climate Change (GCC, and notably an increase in temperature and flood frequency/intensity) on the trophic availability in invertebrate larvae for young trout stages. Then, the discussion will go through a more speculative part on the potential evolutionary consequences of GCC on salmonid phenology, before concluding on some perspectives.

Studying the ecological consequences of a flood by sampling in the wild is a tricky challenge. Indeed, because of the unpredictability of floods it is highly hazardous to gather enough points to assess the effects of flood on young emerging salmonids within a 3-year study. In addition, the instream habitat heterogeneity can mask or modify the effect of a disturbance. For all these reasons, we worked in a semi-natural environment. These experiments allow to evaluate the consequences of a flood in a context where invertebrate production and renewal is very close to the wild. The simulation of the flood with a motor pump created a flush that disturbed the gravel like a scouring flood. However, the impact of the simulated flush was restricted both in space and time. In addition, abiotic factors characterizing natural floods such as the gradual increase in water level and in turbidity were not reproduced. These cues annunciate the flood to the biota, which can shelter (Doeg & Milledge 1991; Suren & Jowett 2001). However, in the case of a scouring flood, the substratum is mobilised and most of the invertebrates are dislodged, including the sheltered ones. Water velocities obtained by the use of the motor pump were probably of the same order than velocities observed during natural scouring floods. Invertebrate species responded quite differently to the flood disturbance, but at least for Diptera and Ephemeroptera, densities were reduced.

In the chapters 3 and 4, we conducted experiments at two fish contrasted densities. In nursery streams, clutches are aggregated and it can result in high fish densities on the spawning grounds (Elliott 1989). We worked at 32 and 2.6 fish m^{-2} and this last value corresponds to the carrying capacity in 0$^+$ trout of the Lapitxuri semi-natural stream after emigration post-emergence (A. Bardonnet, pers. com.). Analyses of alevin performances in late spring were quite disrupting between high (cages experiment) and low (reach experiment) density as the impacts of the flood diverged. At low density, survival was lower and growth higher in the impacted condition when compared to control, while the opposite was observed at high density. In addition, survival rates were quite similar according to density in the control conditions (0.84 at low density *vs* 0.81 at high density) but survival was much lower at low density in flooded conditions (0.63 at low density *vs* 0.94 at high density). Looking at weight gain, growth performances were 5 times

higher at low density in control, and even more in the impacted conditions. One possible explanation of such pattern may lie in the rhythm of the invertebrate recolonization process. Invertebrates sampling differed between low and high density protocol, preventing the comparison of abundances. However, we can compare differences in the pattern of abundances between the start and the end of the experiment. At high fish density, the flood diminished the abundances of Diptera immediately after the disturbance and one month later, Diptera did not recolonize and their abundance keep on declining, while the opposite was observed at low fish density. This was probably due to a high fish predation rate decreasing the Diptera abundances in the cages. In the reaches, fish density was too low to affect Diptera abundances and allowed the course of the recolonization process. We can then hypothesize that at the start of the experiment, the abundances of good sized preys, mainly chironomids, in the cage (high density) and in the reach (low density) were similarly low. However, prey were easy to catch in the cages because water velocity was lower, hunting surface was restricted and the prey shelters was limited to a small gravel layer. Therefore, alevins in the reaches were more likely to face a period of starvation leading to mortality than in the cages. Later, Diptera dramatically decreased in the cages, limiting fish growth. In the reach, the recolonization process was very efficient leading to the replenishment of Diptera and to excellent growth performances (confirmed by the number of chironomids in the gut content).

Of course, this scenario is speculative and many uncontrolled factors might have shape our results. Among them, temperature was on average one degree higher during the low density experiment and it may have interact. Water temperature averaged 10.2, 12.3°C at high density (chapter 3) and 13.3°C at low density (chapter 4). The last value is close to the upper thermal tolerance of alevins (Ojanguren & Braña 2003; Lahnsteiner 2012), and it may have increased the mortality rate of starving fish (as observed in chapter 2). Temperature may also interfere with growth. However in chapter 2 we observed no difference in growth between 8 and 11°C for fish fed *ad libitum* (despite the fact that they almost double the food intake at warm temperature). In addition, after a delayed access to food, alevins were more capable to resume a normal diet and growth was higher at low temperature (12% differences in growth catch-up between the two temperatures). This was quite surprising and could be due to the short duration of the experiment, but it could also be the consequence of a growth optimum closer to 8 than to 11°C in trout early ontogenesis (Elliott & Elliott 2010).

Fish growth and survival are linked in a complex and hardly predictable manner and the intensity of the density-dependent mechanisms partially enlighten the results of the Lapitxuri

experiments. At high population abundance, space is limited and density-dependent mortality and emigration occur. At low population abundance, mortality rate is mainly density independent while density-dependence only operates on growth during the earliest time period (Jenkins et al. 1999; Grant & Imre 2005; Imre et al. 2005; Lobón-Cerviá 2007). It was only during a second time period that density-dependence operates on both growth and mortality. This way, the population can persist after catastrophic disturbances and recover quickly, which reduces the extinction risk of stream dwelling salmonid populations in variable environments. Vincenzi et al. (2008) pointed out that the population abundance of marble trout (*Salmo marmoratus*) was diminished by severe floods, while growth of surviving juveniles was stimulated. This phenomenon was linked to both high food supply and low competition due to a low population density following the event. Moreover, females were larger to sexual maturity and produced more eggs. The increase in fertility allowed the population to recover fast and to be highly resilient.

Throughout spring, temperature, sunshine and brightness duration increase and initiate both primary and secondary production. Consequently, stream productivity is higher in late spring than in early spring. Emergence is spread during spring and according to literature (e.g. Einum & Fleming 2000), the timing of salmonid emergence is under high selective pressure. The timing of emergence is the result of a trade-off between food and territory availabilities (Bromage et al. 2001; Letcher et al. 2004 – Figure 1). Alevins emerging in early spring undergo harsh environmental conditions with a reduced amount of food. However, the low density of alevins allows them to establish feeding territories on the best hunting spots, giving them a growth advantage. In contrast, alevins emerging in late spring face good environmental conditions with an abundant amount of food but the number of territories available in optimal habitat is limited and intensifies the strength of the competition between congeners. The prior residency of the early emergent alevins gives them a significant advantage (Johnsson et al. 1999; Harwood et al. 2003). These mechanisms maintain a variability in the timing of emergence but this could be disrupted by Global Climate Change.
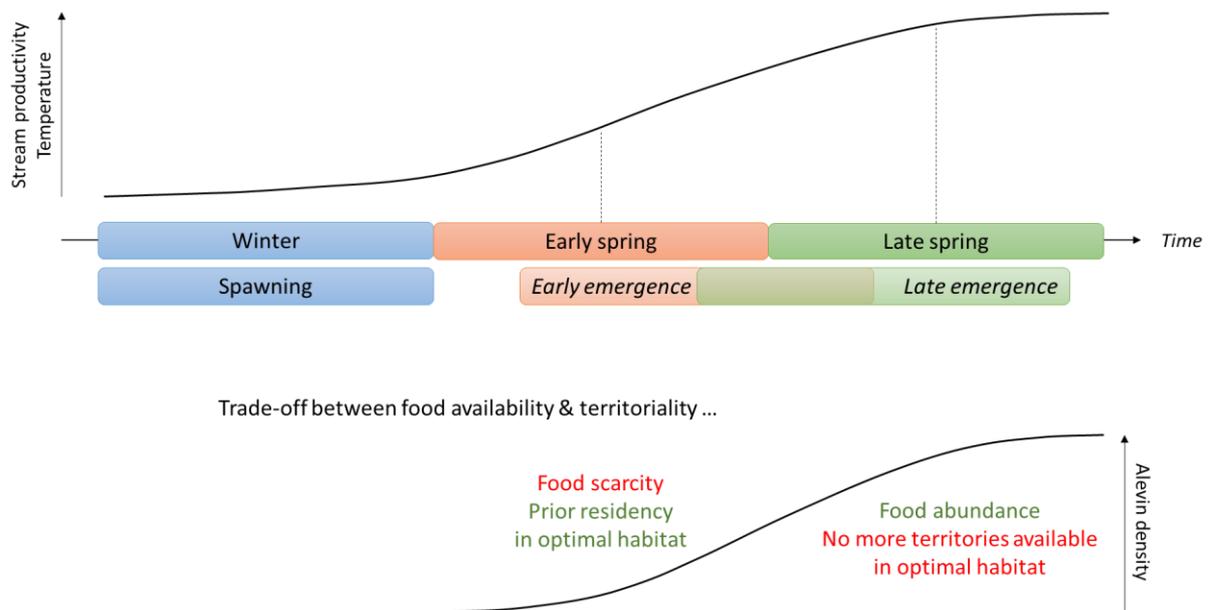
Figure 1 Stream productivity increases during the spring. Emergence is spread from early spring to late spring and alevin density is a trade-off between food availability and territoriality.

Currently, prey availability matches with the timing of emergence. GCC should increase the intensity and the frequency of stochastic hydrologic events such as catastrophic floods. This could directly diminished the production, the abundances of stream invertebrates by displacing and killing them and consequently, reduced the prey availability for carnivorous fish. Additionally, GCC should increase the temperature and affect the phenology of brown trout, including the timing of emergence. As brown trout is an ectotherm, warmer temperature will reduce the development duration and advance the timing of emergence. Consequently, GCC should delayed the peak of prey availability while the emergence date should be advanced (Figure 2).
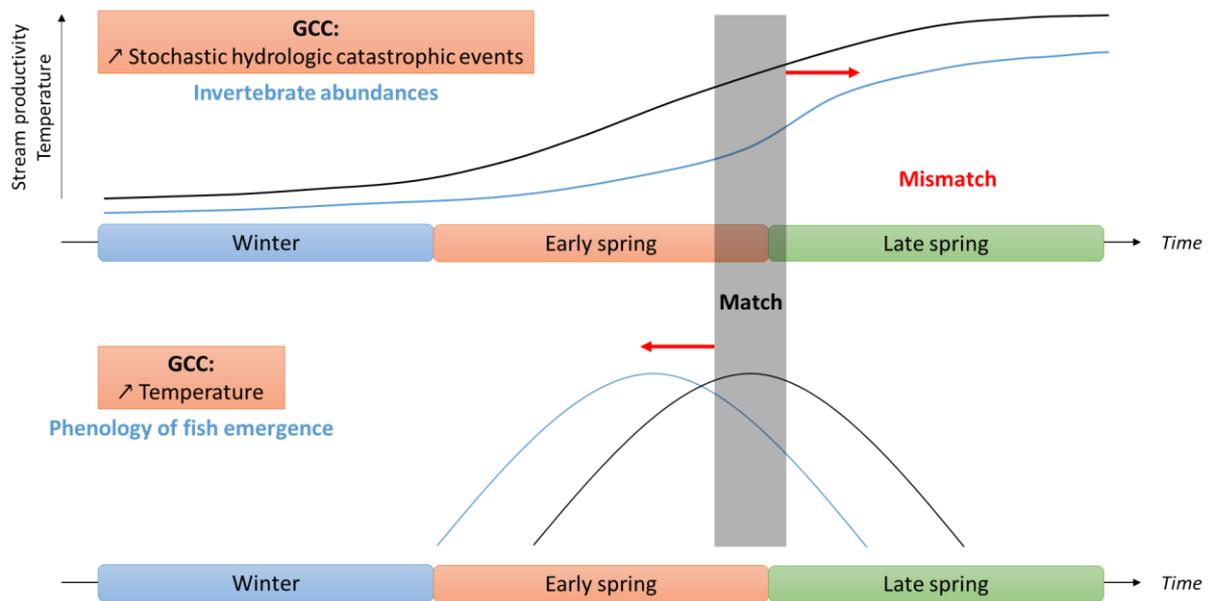
Figure 2 Currently, fish emergence timing matches with invertebrate abundance (in black) but Global Climate Change should delay the increase in invertebrate abundance and advance the emergence date (in blue) and create a mismatch between prey availability and predator requirements (in red).

Nevertheless, temperature affects the whole ecosystem metabolism. According to Woodward et al. (2010), warmer temperature should put forward the initiation of both primary and secondary productivity. Therefore, a move forward in the emergence date might be supported by an earlier primary production (Demars et al. 2011) and a higher leaf decomposition rate (Pereira et al. 2017), leading to high invertebrate production. Invertebrate drift should also be enhanced: "mechanically" with the increase in invertebrate abundance, and also in relation to drifting behaviour. Results from chapter 1 suggested that *Baetis* drift may depend on temperature. This experiment was not designated to look at the effect of temperature, but differences in temperature (12.2 *vs* 14.7°C) accompanied the spring and autumn trials. In the autumn trial, the warmest, *Baetis* drift rate was increased by nearly a third (26%). The increase in temperature could then mitigate the negative effect of flood on invertebrates.

Temperature should also affect the proximal mechanisms affecting the timing of emergence (Figure 3). We know that an increase in temperature will at first reduce the time needed for the embryo-larval development as an immediate physiological response to temperature. This will lead to an earlier emergence date. The quicker development of the embryo-larval stages can be compensated by a delay in the spawning season, which depends strongly on the photoperiod and falling autumn temperature (Beacham & Murray 1990; Van Der Kraak and Pankhurst 1997; Pankhurst & Porter 2003; Pankhurst & King 2010; Pankhurst & Munday 2011). Literature

suggests that genitors adjust the spawning date to match the emergence with favourable conditions of water flow, temperature and food supply (Crozier et al. 2008). Hence, Unwin et al. (2000) demonstrated that later spawning occurs in chinook salmon populations where embryos develop in warmer water. Similarly, Webb & McLay (1996) highlighted that spawning time of Atlantic salmon varied along an altitudinal gradient in Scotland rivers. At high altitudes, temperatures were lower and salmons spawned earlier. The same trend was observed by Warren et al. (2012), warmer temperatures delayed spawning of brook trout (*Salvelinus fontinalis*) to coincide the date of emergence with the peak of prey production. These two phenomenon (*i.e.* a quicker development associated with a delayed spawning season) could compensate each other but it is still difficult to say whether the emergence date will be changed. The third mechanism affecting the timing of emergence is the variation in egg size. Johnston & Legget (2002) demonstrated that warmer temperature increased the egg size but this affects the survival of eggs. Large eggs are stenotherm (Régnier et al. 2013). Moreover, maximal egg size is related to the female size (Hendry & Day 2003) and maternal fitness is a trade-off between egg size and egg number (Einum et al. 2002). Then, warmer temperature should increase the mortality rate of large eggs and the egg size increase should decrease the egg number. The pre-emergence mortality should be higher, resulting in fewer emerging fish. However, large eggs develop faster and emerge early (Einum et al. 2002; Rollinson & Hutchings 2010). Early emerged alevins have higher metabolic rates (Régnier et al. 2012a) and the energy conversion efficiency into growth is higher for large eggs than for small eggs (Régnier et al 2012b), which produces larger alevins. These four factors should support post-emergence survival and confer a competitive advantage to alevins hatching from large eggs but it is difficult to evaluate if the strategy to produce large eggs should be favoured by GCC.

**Effects of Global Climate Change on Emergence: Proximal mechanisms**
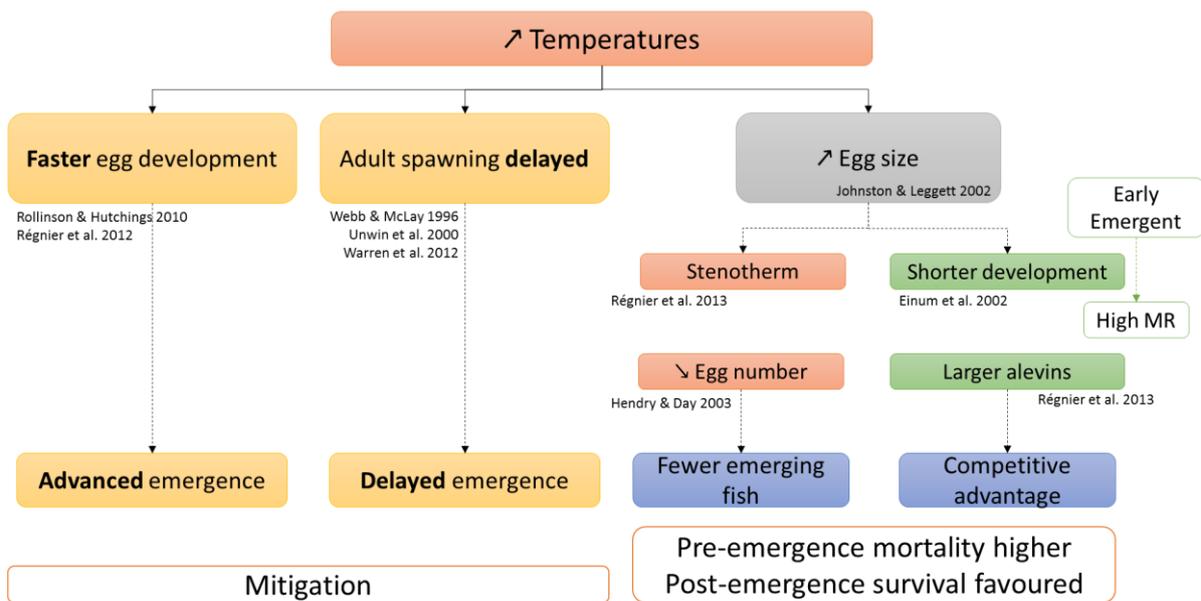
Figure 3 Effects of Global Climate Change on the proximal mechanisms affecting the emergence date (i.e. the egg development duration, the timing of the spawning season and the size of the eggs).

GCC should also be a selective force by selecting individuals according to their temperaments or personalities, which induce individual differences in exploration and activity (Le Galliard et al. 2013). These behaviours are associated with foraging, territorial defence, mate finding, and dispersal as well as habitat choice. For example, individuals with high activity increase both growth and the risk of mortality from predation, thus resulting in a similar fitness than low activity individuals (Stamps 2007). Réale et al. (2010) associated behaviour (*i.e.* activity, superficial exploration, boldness and aggressiveness) with physiology (*i.e.* immunity, metabolism and oxidative stress). This so-called "pace-of-life" syndrome emphasizes integration of behavioural variation within a slow-fast demographic and metabolic continuum. If we try to evaluate the impacts of GCC in this theoretical context of "pace-of-life" syndrome, alevins should be selected according to their probability to avoid starvation or their ability to withstand it during period of food scarcity (Figure 4). With a high prey production in late spring, alevins emerging later diminish their risk of starvation. Likewise, alevins with low metabolic rate and a high amount of reserves have a high ability to survive during starvation. Late emerging alevins have low metabolic rates, then it is possible that alevins exhibit these two traits simultaneously as they are probably correlated but these alevins usually have a low amount of reserves. According to the "pace-of-life" syndrome (Ricklefs & Wikelski 2002; Réale et al. 2010), shy alevins which are associated with low metabolic rate could be favoured.

This selection could have consequences on adult spawning strategies, on maternal investment and on the whole population functioning and dynamics. Despite this very speculative scenario, it is still difficult to predict which direction will take the selection with Global Climate Change and, for now, very few elements are available.

Effects of Global Climate Change on Emergence: **Ultimate mechanisms**

Under conditions of **Food scarcity**

Selection: ↘ Risk of starvation or ability to face it

| Late emergent | Low Metabolic Rate | ⟷ | More Reserves |

Selection on alevins according to
Pace of life syndrome

Ricklefs & Wikelski 2002
Réale et al. 2010

"Shy"?

Consequences on Life History strategies???
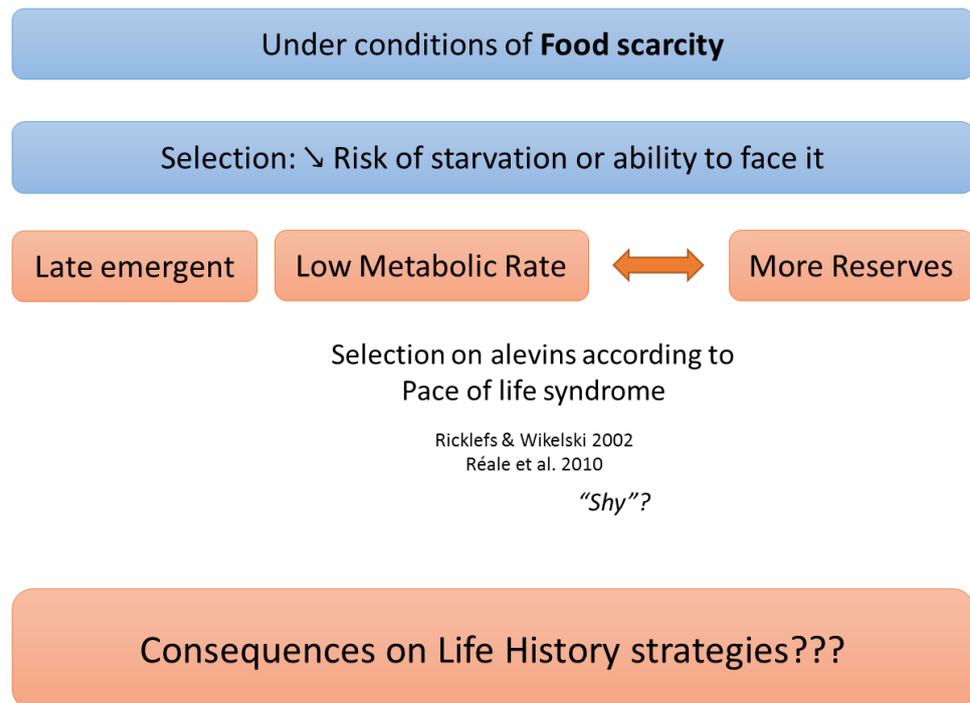
Figure 4 According to the environmental conditions (food scarcity), alevins could be selected depending on their ability to avoid or to face periods of starvation. This could have consequences on life history strategies and on the whole population functioning.

We did not succeed in increasing sufficiently the water velocities in our experimental facilities to approach flood velocities. However, the link between moderate water velocities and the invertebrate propensity to drift has been clarified for the three species we focused on. Even if results depended in part on the experimental conditions, we found three distinct patterns and we provided a precise quantification of the drift probability of the taxa studied. Laboratory experiment also allowed us to assess the ability of alevins to face starvation, the consequences of such stress on their metabolism and their ability to recover according to temperature. These two experiments could be reproduced with temperatures ranging from 4 to 14°C, which corresponds to the limits of the thermal tolerance of brown trout alevins (Elliott 1994) and temperature that alevins can face throughout their distributional range (Jonsson & Jonsson 2009). Consequently, according to thermal conditions, the drift propensity of invertebrates

would allow to evaluate the trophic availability for alevins (and more widely for drift-feeding fish) and the metabolic, survival and growth consequences of alevins facing periods of starvation would be nearly known. These data (those already acquired and those from future potential experiments) should be used as basis for calibrating and developing a global individual-based model (Grimm 1999) to simulate scenarios of GCC and to better understand the consequences on brown trout alevin survival and growth (Clark et al. 2001). Incrementing results from studies on the phenology and the productivity of systems could provide complementary elements for modelling climate change related scenarios and the consequences of rising temperature and occurrence of flood on a brown trout population.

It is forecasted that Global Climate Change should increase the intensity of hydrological events as well as their frequency. Connell (1978) proposed the Intermediate Disturbance Hypothesis (IDH), which states that in absence of disturbance, species richness is expected to be low with more competitive species dominating and outcompeting the others. Similarly, when disturbances are too frequent, few species are able to resist to the changes in their environment or to colonize during the brief periods between disturbances. Under a disturbance regime that is intermediate in frequency and intensity, both rapid colonizers and more competitive species co-occur and species richness is maximised (Townsend et al. 1997). The increase in flood frequency associated with GCC should diminish species diversity of invertebrates and this could potentially affect the quality of prey for brown trout. Chironomids are pioneer species, have short life cycle and quick turn-over rates. As they constitute the main part of brown trout diet, frequent floods could increase the production of Chironomids and make them more available for brown trout.

Lastly, in Southern and Mediterranean Europe, GCC should induce more droughts in spring. Droughts reduce the volume of water available for fish, impeding or preventing their migration and adversely affecting water quality, especially water temperature and dissolved oxygen (Elliott 2000). The aggregation of organisms (invertebrates and fish) could modify the intra-/inter-specific interactions, as well as the amount of prey and their availability for predators. Then, it should be interesting to study the consequences of drought on the invertebrate assemblage and on just-emerged alevins.

To conclude, this work highlighted the possible consequences of GCC on the invertebrate fauna and on young trout stages of brown trout. In a local management context, it is difficult to mitigate the effects of GCC on riverine ecosystems. The building of a flood control dam would limit the intensity of floods but would not reduce their occurrence. It would be necessary to

study the consequences of these facilities on the hydrological river regime and on the biota in order to evaluate their effectiveness. However, it appears necessary to limit other sources of disturbance to the biota (*i.e.* pollution or habitat fragmentation) in order to limit the stress induced by the interaction between GCC and others potential factors.

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