



Contrasting patterns of energy metabolism in northern vs southern peripheral European flounder populations exposed to temperature rising and hypoxia

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ABSTRACT

A two months common garden experiment was carried out to explore the potential differences of energy metabolism in northern core (France, 50°N and 47°N) vs southern peripheral (Portugal, 41°N) populations of European flounder *Platichthys flesus*, submitted to cold condition (CC: water temperature = 10 °C) and to warm and hypoxic condition (WHC: water temperature = 22 °C, and moderate hypoxia with O₂ saturation = 40% during the last 6 days). Convergent growth rates (in length) were observed in the different populations and conditions, when the southern peripheral population of Portugal did not grow under cold conditions. A general reduction in liver lipid storage was observed in all populations subjected to WHC when compared to CC, whereas muscle lipid storage was unaffected. The thermal and hypoxia treatment induced changes in muscle phospholipids (PL) ratios: phosphatidylserine/PL, phosphatidylinositol/PL, between northern and southern populations. Fish from northern estuaries displayed marked anaerobiosis in WHC (increased liver LDH activity) vs marked aerobiosis under CC (higher muscle CS and CCO activities). Contrariwise, fish from the southern estuary displayed equilibrium between anaerobiosis and aerobiosis activities in WHC. Flounders from the southern population exhibited generally lower G6PDH activity (proxy for anabolism and for defense against oxidative damage), tissue-specific anaerobiosis response (muscle LDH activity) and lower CS and CCO muscle activities (aerobiosis markers) when compared to northern populations. Globally, these inter-population differences in bioenergetics suggest that southern peripheral vs northern core populations have developed differential capacity to cope with interacting stressors and that much of this variation is more likely due to local adaptation.

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1. Introduction

The effect of ongoing global warming on aquatic ectotherms has been widely described in the literature, considering its possible impacts on bioenergetics and individual performances (Pörtner, 2002; Pörtner and Knust, 2007; Pörtner and Peck, 2010), disease tolerance (Macnab and Barber, 2012) and life-history traits (Ito

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et al., 2008; Neuheimer et al., 2011; Otero et al., 2012). Furthermore, studies on marine fishes and invertebrates suggest that adaptive divergence among populations does occur in response to contrasted selection forces related to the thermal gradient over the distribution area of species, considering gene expression (Oleksiak et al., 2005; Whitehead and Crawford, 2006; Larsen et al., 2011), energetic metabolism (Sylvestre et al., 2007; Fanguet et al., 2009; Schulte, 2014) and life history traits (Conover et al., 2006; Haraal et al., 2010a, b; Sanford and Kelly, 2011).

Natural populations are increasingly subjected to interacting and cumulative effects of multiple environmental and human

stressors in aquatic systems; paradoxically, research examining the effects of multiple stressors is somehow uncommon (Gunderson et al., 2016). Numerous coastal systems are now submitted to global warming as well as periodical eutrophication-related decrease in oxygen availability (Breitburg et al., 2009; Greenwood et al., 2010; Gillanders et al., 2011). A recent study suggested that both thermal and hypoxia tolerance are functionally associated in *Salmo salar* families, which displayed a substantial genetic variation in thermal and hypoxia tolerance, and thus could respond to selection linked to global climate change (Anttila et al., 2013). Plasticity and adaptive evolution may allow salmon populations to cope with high temperature and hypoxia, at least on the acute time scales associated with extreme exposures (McBryan et al., 2013).

Estuarine fish have developed substantial capacity to cope with different stressors (changing temperature, oxygenation and salinity) at various time scales. Within its life time the organism could compensate through phenotypic plasticity, whilst across a few generations epigenetic changes may allow lineages to adjust their physiology to a stressor. Evolutionary adaptation may result in genetic changes at the population level that modify the species' sensitivity to a stressor across many generations; hence, inter-population variation detected in the sensitivity of estuarine fish populations to environmental stressors suggests that local adaptation can shape the stress response even in organisms that are broadly tolerant and plastic (Schulte, 2014).

In the present study, our fish model is the European flounder *Platichthys flesus* which displays an extensive geographic distribution along the north-east Atlantic, from Portugal to Norway, including the Baltic Sea (Martinho et al., 2013). This species is commonly found in estuaries and brackish waters (Dando, 2011; Morais et al., 2011), and has been used to investigate the adaptation/vulnerability of populations facing stressors in coastal systems (Hemmer-Hansen et al., 2007; Larsen et al., 2007, 2013; Dupuy et al., 2015; Lavergne et al., 2015). From 1987 to 2006, the abundance of northern temperate species such as *P. flesus* decreased in the Bay of Biscay, their abundance being negatively correlated to mean water temperature during year of birth (Hermant et al., 2010). The Portuguese coast is the southern distribution limit of this species which is nowadays very rare at the latitude of Lisbon, where it was abundant a few decades ago (Cabral et al., 2001).

A population genetics study highlighted a significant genetic differentiation among flounder populations distributed between the English Channel and Portugal, and the particular genetic status of a southern peripheral population in Portugal, located in the Mondego estuary (Calvès et al., 2013). Furthermore, a field survey conducted on flounders underlined a general reduction of energetic metabolism and protein synthesis in the Mondego population vs two northern populations located in the Bay of Biscay and in the English Channel (Borcier et al., 2016). Thus, the previous studies suggest that peripheral flounder populations of Portugal could be isolated from French populations and could experience different abiotic conditions.

It remains to determine whether the genetic differentiation between peripheral and central populations, is reflected by phenotypic variation underlying the adaptive potential of populations across the geographical range (Eckert et al., 2008). In this context, we have implemented a Common Garden (CG) experiment to explore the genetic contribution to the variability in phenotypic traits. We examined bioenergetic biomarkers to identify potential patterns of local adaptation of populations along a latitudinal gradient. Juvenile flounders were sampled in one southern peripheral population (from the Lima estuary in Portugal) vs two northern core populations (from the Vilaine and Canche estuaries in France), and acclimated to common laboratory conditions during several weeks, before starting CG experiments.

Individuals from the three populations were challenged in two contrasted treatments over two months: i) “cold temperature/high oxygen” treatment and ii) “warm temperature” treatment, for sixty days, coupled with a “mild hypoxia” during the last 6 days. The major aim of this study was to mimic a summer event, with rising temperature followed by an hypoxia event, and to decipher possible differences in the bio-energetic response of populations faced with multistress.

2. Materials and methods

2.1. Fish collection, sampling sites and experimental design

European flounder juveniles (estimated age of 8 months; total length = 8–15 cm) were collected with a beam trawl in October 2013 in three estuaries (120 young of the year per estuary): the Canche and the Vilaine in France and the Lima estuary in Portugal (Fig. 1). The Canche estuary is considered as a pristine system, displaying a limited level of contamination by pollutants (Amara et al., 2007, 2009). The Vilaine estuary shows moderate levels of pollutants (Laroche et al., 2013), and exhibits periodically hypoxic conditions during summertime, mainly induced by eutrophication and by the retention/leak of waters by a dam in the upper part of the estuary favoring water stratification (Menesguen et al., 2001). The moderately polluted Lima estuary is located 200 km north of the southern limit of the flounder distribution area (the Mondego estuary); this system is considered as a functional nursery area for several flatfish species, exhibiting a typical spring estuarine recruitment for *P. flesus*, without inter-annual variations (Ramos et al., 2010).

Fish were transported by road in a 500 L tank filled with sea water from the field, to IFREMER fish rearing facilities in Plouzané (France). Individuals were then acclimated to local sea temperature and salinity (9 °C, 35 PSU) for two months, and fed with food pellets with a daily ration corresponding to 3% of their biomass. After the acclimation period, fish were pit-tagged and randomly assigned to a “cold condition” (CC) tank or a “warm and hypoxic condition” (WHC) tank. Both 1.2 m³ tanks contained 150 fish (50 fish from each population). Depth was maintained to 50 cm, and water was renewed at a rate of 50 L per hour. Tanks were cleaned from waste

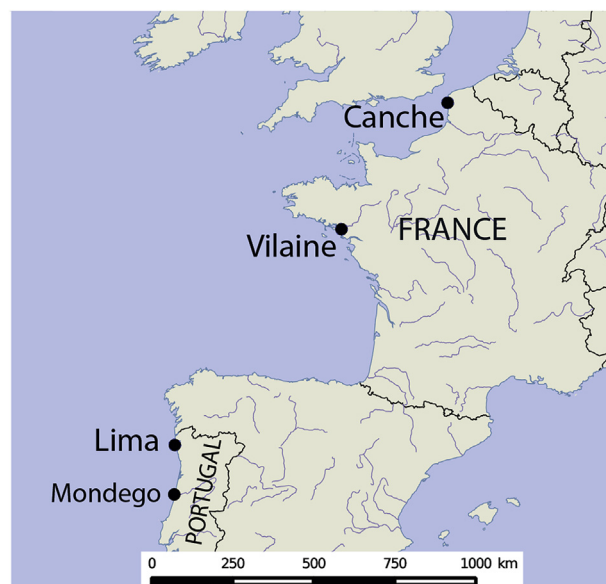


Fig. 1. Map of the sampling locations.

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