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Poor oxic conditions in a large estuary reduce connectivity from marine to freshwater habitats of a diadromous fish

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ABSTRACT

Connectivity in aquatic systems is often related to abundance and permeability of physical barriers, such as dams, which delay or impede movements of biota with important consequences for aquatic biodiversity. Water quality may, however, also control connectivity between essential habitats. In macrotidal estuaries, Estuarine Turbidity Maxima (ETM) have a strong impact on water quality because of the low oxygen concentration occurring as a response to the related high bacterial and low photosynthetic activities. In this study, we assess Allis shad estuarine spawning migration in 2011 and 2012 in the Loire River (France) where the ETM occurs at spring and summer. Using an acoustic telemetry array, we show that trans-estuarine migration is inhibited during hypoxic episodes in the middle part of the estuary. Shad tends to stay in downstream areas, and even at sea, where oxygen conditions are more suitable. Trans-estuarine migration occurs hastily during neap tide when the ETM decreases, both in terms of spatial extent and intensity, inducing a shift in a set of covariates including dissolved oxygen, which increases, and suspended matter, which decreases. In the context of climate warming, ETM are expected to increase with probable adverse implications for shad migration success and doubtless other diadromous populations.

1. Introduction

Disruption of connectivity along rivers is known to be a major cause of freshwater aquatic biodiversity loss, especially for fish (Lucas and Baras, 2001; Pringle et al., 2000), and among them diadromous species which decline throughout the world (Limburg and Waldman, 2009). At an individual level, connectivity alteration may prevent fish from reaching essential habitats, such as spawning habitats, and accomplishing their life cycle (Lucas et al., 2009). At a population level, it may impede (re-) colonization of habitats, reduce population dynamics and jeopardize viability (Morita and Yamamoto, 2002). Connectivity is usually considered from a physical point of view and its alteration is evaluated, for instance, by counting the number and characterizing the permeability of physical obstacles such as dams or other infrastructures (Bourne et al., 2011; Cote et al., 2009; Fullerton et al., 2010; Hall et al., 2011; Laffaille et al., 2009). Therefore, most management plans target these obvious obstacles to improve fish movements and restore populations: fish passage may be settled (Prato et al., 2011) or dams may be removed (Hart et al., 2002), for instance. Conversely, the absence of such barriers is generally assumed to allow fish to freely move between habitats and connectivity can be considered as good. Other factors may however control fish habitats connectivity. Among them, physico-chemical conditions, which are much more variable and difficult to assess, can also limit or even impede fish movements (Buysse et al., 2008; Lucas and Baras, 2001; Maes et al., 2008). Low dissolved oxygen level, high temperature or suspended matter level may act as real barriers to fish migration but their impact is rarely investigated.

Macrotidal estuaries of large rivers often develop an Estuarine Turbidity Maximum (ETM). The conjunction of tide and river flow results in the resuspension of fine particles. Moreover, two

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phenomena occur with increasing salinity: organic matter, resulting from the death of aquatic organisms experiencing fatal osmotic stress, increases and dissolved matter flocculates. Yet the high turbidity reduces the photosynthetic activity and the increase of bacterial activity resulting from this amount of dissolved matter available leads to high oxygen consumption. Therefore, ETM may be associated with hypoxic or even anoxic conditions, especially under high temperatures and low river flows (Abril et al., 1999; Talke et al., 2009). Although ETM are natural phenomena, anthropogenic activities can exacerbate its development in terms of intensity, duration, frequency and spatial extent. For instance, channelization or deepening of estuaries for navigation may severely impact mudflat functionality (i.e., reduced sediment trapping) and can also extend the ETM (Kerner, 2007; Talke et al., 2009). In the context of global change, water temperature increases and concurrent declines in discharge will favour the development of ETM and hypoxic, even anoxic, episodes (Lanoux et al., 2013). Although this phenomenon can be advantageous for larval and juvenile fish feeding and survival due to higher prey concentrations (Islam and Tanaka, 2006), some fish populations could be, and are probably already, negatively impacted by it (Marchand, 1993; Thouvenin et al., 1994). Therefore, this phenomenon deserves particular attention especially since the effect of restoring riverine physical continuity in the upstream parts of catchments would be unfruitful if migration is disturbed in the estuarine bottleneck. Indeed, it has been shown that, the further downstream the barriers to migration occur, the stronger the consequences on diadromous fish are (Cote et al., 2009; Lucas et al., 2009; Rolls, 2011).

Whereas they have severely declined, and some species have already disappeared in various large and medium Western European systems (Limburg and Waldman, 2009), the Loire River (France) is considered as one of the last bastions for diadromous fish. Indeed, most of them are still present e.g., Atlantic salmon *Salmo salar* (Linnaeus 1758), European eel *Anguilla anguilla* (L. 1758), sea lamprey *Petromyzon marinus* (L. 1758), river lamprey *Lampetra fluviatilis* (L. 1758), Allis shad *Alosa alosa* (L. 1758) and Twaite shad *Alosa fallax* (Lacépède, 1803). It is suspected that this diversity results from a reasonably good connectivity level along the main axes i.e., the Loire and Allier rivers (Lasne and Laffaille, 2008). Nonetheless, various factors such as pollution and obstructions in tributaries contributed to population declines (Steinbach, 2001). In addition to these upstream pressures, it is likely that an ETM developing in the Loire Estuary and causing episodic hypoxic or even anoxic conditions could be problematic for diadromous fish (Etcheber et al., 2007; Marchand, 1993; Thouvenin et al., 1994) or other amphihaline, such as grey mullet (Sauriau et al., 1994), and may be the main factor affecting population within the catchment (Steinbach, 2001).

In this study, the impacts of the ETM and associated hypoxic conditions on a diadromous fish, the Allis shad, is addressed. Dissolved oxygen concentrations (DO) < 3 mg l^{-1} are known to be stressful for migrating spawners in other alosine species (Chittenden, 1973; Maes et al., 2008) and thus, may be stressful for Allis shad too. Unfortunately, such low concentrations have been observed in the Loire River estuary at spring during the migratory period of shads (Thouvenin et al., 1994). In order to evaluate Allis shad behaviour facing such supposedly stressful conditions and the impact on the onset and patterns of the spawning migration, we used an acoustic telemetry array deployed in the Loire River estuary in 2011 and 2012. Migratory patterns were investigated in medium to late migratory periods when hypoxic and anoxic episodes were likely to occur. We tested the hypothesis that migratory behaviour is disrupted during hypoxic or anoxic conditions, which could therefore delay estuarine migration with probable consequences on spawning success.

2. Materials and methods

2.1. Study area

The Loire River catchment is the largest one in France with a drainage area of 117 000 km^2. On average, the discharge at the catchment mouth is about 850 m^3 s^{-1} with significant inter- and intra-annual fluctuations. Indeed, the Loire River is subject to very intense flash floods from autumn to spring and to severe drought from spring to autumn. The Loire itself is 1012 km long and has relatively good connectivity for fish in a large downstream part (<500 km from the tidal limit). The main tributary, the Allier River, is almost free of impassable barriers and might be colonized by a well-known relict Atlantic salmon population (Perrier et al., 2011). The Vienne River has been restored (Maison Rouge dam dismantled in 1999) and recolonization by diadromous species is expected. Conversely, most of the other tributaries have been largely regulated by dams whose impact on diadromous fish distribution is severe, for instance in the Maine catchment (Laffaille et al., 2009; Lasne and Laffaille, 2008). In terms of water quality, the Loire River has very high nitrates and ammonia levels due to farming activities i.e., livestock and fertilizers (Moatar and Meybeck, 2005). Conversely, the impact of industrial activity on water quality is relatively low (Moatar and Meybeck, 2007). The fluvial part of the Loire River itself (e.g., upstream of the estuary) seems to be rarely or locally affected by hypoxic conditions (Moatar et al., 1999). Considering the limit of tidal influence as the upstream boundary at Varades, the Loire River estuary is about 80 km (Fig. 1). Its width varies from 4000 next to the outlet to 200 m upstream. It has been largely modified for navigation purposes, and more precisely, it has been deepened. As a result, the influence of tide has moved upstream and mudflats do not play their role of sediment trapping anymore, contributing to the reinforcement of the ETM.

In the Loire River, Allis shad spawn 550–750 km from the sea (Boisneau et al., 1990). After 3–6 months in freshwaters, juveniles leave the river to the sea, where growth lasts for 4–5 years. Adults penetrate the estuaries from April to May/early June (Baglinière and Elie, 2000; Rochard, 2001). Most individuals are semelparous but a fraction (<10%) may reproduce twice (Baglinière and Elie, 2000). Although very little information is available on Loire's population status, it is suspected to decline (Bach et al., 2015) and, in the Gironde system (the other large and close river historically supporting large populations), the population collapsed in the recent decades (Rougier et al., 2012).

2.2. Environmental data

Since 2007, a number of physico-chemical phenomena are being monitored in the estuary by GIP Loire Estuaire (www.loire-estuaire.org): maximum turbidity zone, hypoxia and salinity. The ETM corresponds to the area where the concentration of suspended matter exceeds 1 g l^{-1} and is mainly located in the lower part of the estuary (Etcheber et al., 2007). In 2011 it moved up in the upper estuary (GIP Loire Estuaire, comm. pers.). ETM may be associated with areas characterised by a dissolved oxygen concentration lower than 5 mg l^{-1} and even down to 1 mg l^{-1} (Thouvenin et al., 1994) (see Abril et al. (1999) for details on the underlying processes). Environmental data were provided by GIP Loire-Estuaire (www.loire-estuaire.org) and came from Paimboeuf (dissolved oxygen, measured every 10 min), Cordemais (salinity and suspended matter, hourly obtained) and Le Pellerin (temperature, measured every 10 min) (Fig. 1). Using different stations was necessary to provide complete data series for each variable since some stations had long periods of non-available data due to sensor problems. Small time shifts due to tide influence between these near sites were negligible