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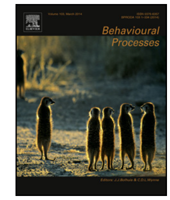

An experimental test of in-season homing mechanisms used by nest-guarding male Largemouth Bass following displacement

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ABSTRACT

Through manipulations of sensory functions, researchers have evaluated the various mechanisms by which migratory fish, particularly in lotic systems, locate natal spawning grounds. Comparatively less work has occurred on the ways by which fish in lentic systems locate spawning sites, and more specifically, the ways by which displaced fish in these systems locate their broods post spawning. The primary goal of this research was to determine the sensory mechanisms used by nesting, male Largemouth Bass to navigate back to their brood following displacement. This was accomplished by comparing the ability of visually impaired, olfactory impaired and geomagnetically impaired individuals to return to their nests after a 200 m displacement, relative to control males. All treatments were designed to be temporary and harmless. We analyzed the data using a generalized linear mixed model, and found that the probability of an olfactory impaired individual returning to his nest within a given time interval was significantly lower than the probability of a geomagnetically impaired individual returning. Overall, it appears as though olfaction is the most important sensory mechanism used for homing in Largemouth Bass.

1. Introduction

Largemouth Bass, *Micropterus salmoides*, are the most popular sportfish in North America (Quinn and Paukert, 2009). In early spring, males are particularly susceptible to angling due to their parental care strategies (Jennings, 1997; Philipp et al., 1997; Suski and Philipp, 2004). When water temperatures rise to approximately 14 °C, male Largemouth Bass move to shallow waters, where they build a nest and attract a female for spawning (Kramer and Smith, 1962). The nest-building process typically takes place in a sandy or muddy substrate, and involves sweeping a 60–90 cm circular region clean of vegetation and debris. Largemouth Bass eggs can also simply be deposited on a log or a patch of vegetation (Kramer and Smith, 1962). After the deposition and fertilization of the eggs, the female departs, but the male remains, sometimes for over a month after the eggs hatch, in order to provide parental care. He does so by fanning his tail over the nest to prevent sediment from smothering eggs and fry, and by actively and aggressively defending the nest against predators (Kramer and Smith, 1962). This period of parental care is key to the survival of offspring and thus to the persistence of the species. However, these aggressive males readily attack fishing lures that land in their nest, making them more vulnerable to angling during the parental care period (Jennings, 1997; Philipp et al., 1997; Suski and Philipp, 2004).

If a fish is caught, and returned to the water, it is not uncommon for the fishing boat to drift away from the initial location as the fish is removed from the hook. This means that fish are often not returned exactly at their capture location. Competitive angling events exacerbate this problem, since fish are not released immediately after capture; they can be temporarily held and transported in livewell confinements, and then released great distances (even greater than a kilometer) away from their capture site (Wilde, 2003). For a male, nest-guarding Largemouth Bass, both scenarios result in the fish not being returned to the water exactly above his nest. However, many studies have reported that male Largemouth Bass are capable of finding and returning to their nest location, even after being displaced by as much as 1 km (e.g.: Hanson et al., 2007; Hanson et al., 2007). Moreover, the bass' return, assuming that they are not exhausted from the capture event, is relatively rapid, suggesting that there is some level of directed swimming as opposed to fish encountering the nests by chance alone (Hanson et al., 2007). This journey back to the nest is vital for the success of the brood,

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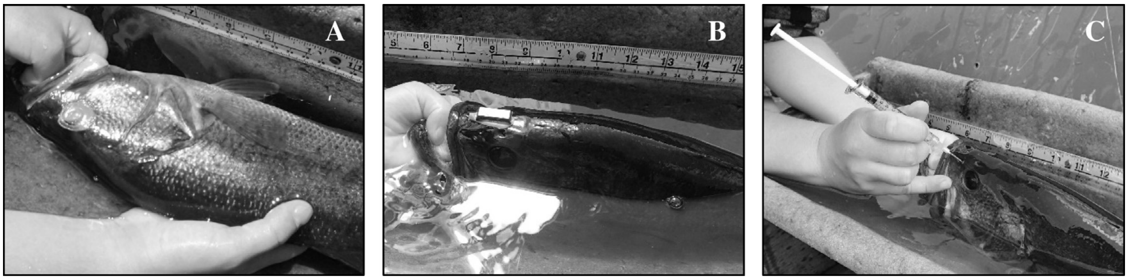

Fig. 1. Nesting, male Largemouth Bass subjected to A) visual impairment, B) geomagnetic impairment and C) olfactory impairment.

since any time spent away from the nest increases the exposure of eggs and fry to predation, which in turn increases the likelihood of a male abandoning his nest (Philipp et al., 1997). However, in spite of the importance of this return to the nest, the mechanisms behind the phenomenon have not previously been studied.

The tendency for Largemouth Bass to navigate back to their nests following displacement can be considered in-season homing, since the journeys are made within a given breeding season (Gerking, 1959). Aside from black bass (which includes Largemouth Bass and the closely-related Smallmouth Bass, *Micropterus dolomieu*), several other fish species, including Brook Trout (*Salvelinus fontinalis*; O'Connor and Power, 1973), Pink Salmon (*Oncorhynchus gorbuscha*; Helle, 1966), and Cutthroat Trout (*Oncorhynchus clarkia*; McCleave, 1967) are known to perform in-season homing. However, their journeys differ in the sense that displaced fish can return to a particular spawning region within a given lake or stream, but not necessarily to a designated nest containing eggs or fry. While the navigational mechanisms used by these fish are unclear in most cases, Cutthroat Trout have been found to use a combination of olfaction and vision (McCleave, 1967; Jahn, 1969; McCleave and Labar, 1972).

In some fish species, homing can also occur when adults return to their natal hatching location to spawn. This is referred to as reproductive homing (Gerking, 1959). Reproductive homing is common and well-studied in many anadromous salmonid species, who navigate to the sea as juveniles, and then return to their natal site as adults to reproduce. There is mounting evidence that the oceanic portion of the migrations is guided by the sun's position, polarized light patterns and the geomagnetic field (Quinn, 1980; Hawryshyn et al., 1990; Walker et al., 1988; Dittman and Quinn, 1996; Putman et al., 2013, 2014), while the freshwater portion of the journeys appears to be primarily guided by olfactory cues (see reviews by: Nevitt and Dittman, 1999; Hino et al., 2009; Ueda, 2011, 2012), with vision playing a secondary role in some cases (e.g.: Jahn, 1968; Groves et al., 1968; LaBar, 1971 Groves et al., 1968; LaBar, 1971).

The objective of this experiment was to determine how nest-guarding, male Largemouth Bass return to their nests after displacement. This was accomplished by assessing the homing ability of sensory-impaired fish (i.e., visual, olfactory and geomagnetic impairments) relative to appropriate controls. Some of the sensory impairment techniques in past studies have been quite invasive and sometimes even permanent. For example, olfactory occlusion has been accomplished by cutting the olfactory nerve (Bertmar and Toft, 1969), cauterizing the nasal rosettes (Lorz and Northcote, 1965), or suturing across the nares after packing them with cotton, wax, petroleum jelly or a combination of the three (Groves et al., 1968). Blinding has been accomplished by cutting the optic nerve (Bardach, 1958), by removing the optic lens and replacing it with petroleum jelly and carbon toner (Groves et al., 1968), by injecting formalin into the pupil (Lorz and Northcote, 1965) or by injecting aqueous benzethonium chloride into the eyeball (McCleave, 1967; Jahn, 1969; LaBar, 1971). A major requirement of our study was to design all treatments to be temporary and as harmless as possible given that animal welfare norms have changed considerably since the time when many of these sensory impairment strategies were first developed. Thus, we developed a novel visual impairment method, namely the application of dental adhesive. This experiment also represents one of the first tests of in-season homing mechanisms where displacement involves moving fish from a spe-

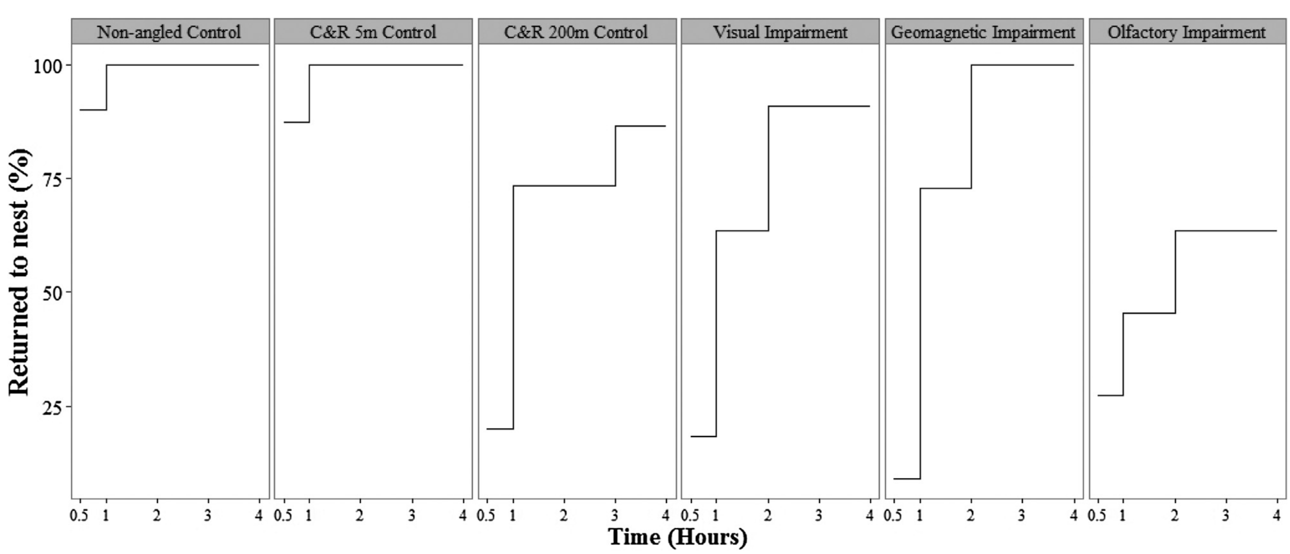

Fig. 2. The cumulative percentage of Largemouth Bass in each treatment group to return to their nests after 0.5 h, 1 h, 2 h, 3 h and 4 h.