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Assessing connectivity of estuarine fishes based on stable isotope ratio analysis

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Abstract

Assessing connectivity is fundamental to understanding the population dynamics of fishes. I propose that isotopic analyses can greatly contribute to studies of connectivity in estuarine fishes due to the high diversity of isotopic signatures found among estuarine habitats and the fact that variations in isotopic composition at the base of a food web are reflected in the tissues of consumers. Isotopic analysis can be used for identifying nursery habitats and estimating their contribution to adult populations. If movement to a new habitat is accompanied by a shift to foods of distinct isotopic composition, recent immigrants and residents can be distinguished based on their isotopic ratios. Movement patterns thus can be reconstructed based on information obtained from individuals. A key consideration is the rate of isotopic turnover, which determines the length of time that an immigrant to a given habitat will be distinguishable from a longtime resident. A literature survey indicated that few studies have measured turnover rates in fishes and that these have focused on larvae and juveniles. These studies reveal that biomass gain is the primary process driving turnover rates, while metabolic turnover is either minimal or undetectable. Using a simple dilution model and biomass-specific growth rates, I estimated that young fishes with fast growth rates will reflect the isotopic composition of a new diet within days or weeks. Older or slower-growing individuals may take years or never fully equilibrate. Future studies should evaluate the factors that influence turnover rates in fishes during various stages of the life cycle and in different tissues, as well as explore the potential for combining stable isotope and otolith microstructure analyses to examine the relationship between demographic parameters, movement and connectivity.

Keywords: connectivity; stable isotopes; estuarine fishes; migration; movement; nursery habitat

1. Introduction

Connectivity can be defined as the rate of exchange of individuals of the same species among spatial units (Polis et al., 1997). Assessing the degree of connectivity among fish populations can include studies at the landscape level (Talley, 2000), among different stages of the life cycle (Gillanders et al., 1993), or among individuals of the same species with different patterns of habitat utilization and migration histories (Secor, 1999; McCarthy and Waldron, 2000; Zlokovitz et al., 2003). Documenting movement patterns among different habitats, relating these to specific underlying processes and examining the relationship between exchange rates and population dynamics are integral to understating connectivity (Polis et al., 1997; Able and Fahay, 1998; Secor, 1999).

Beck et al. (2001) recently proposed that estuarine nurseries are those habitats that contribute disproportionately more individuals to spatially separate adult populations on an areal basis. This implies that the level

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of connectivity between specific nursery habitats and adult populations must be assessed. This is particularly critical considering that the connectivity of estuarine fishes may be threatened due to the extensive habitat loss and degradation of that has plagued estuaries during the last decades (Chambers, 1992; Kennish, 2002).

The spatial and temporal pattern of occupancy of specific habitats within estuarine systems and their adjacent coastal areas may vary as a function of life history strategy or among cohorts of a given species (Able and Fahay, 1998). While resident species complete their entire life cycle in one or several habitat types, transients spend a specific part of their life cycle within estuaries. Facultative estuarine occupants are those in which only a fraction of a population utilizes estuaries. Movement among habitats may be obligatory, as in species that must recruit to estuaries to survive, or facultative, involving the active selection of a specific habitat type (Polis et al., 1996).

Within an estuary, the selection of a specific habitat may be related to its availability and structural complexity, the prey and predator fields, physical transport processes and local environmental conditions (Blaber and Blaber, 1980; Bell and Westoby, 1986a,b; Jenkins et al., 1997; Levin et al., 1997). Marked temporal trends in abundance also can result from seasonal patterns of migration into, from or within estuaries, as well as from variable survival (Weinstein et al., 1980; Boehlert and Mundy, 1988; Rooker et al., 1998, 1999). Habitat utilization by individuals of a given species may be associated with size- or age-specific habitat preferences and the spatial availability of suitable habitats (Able and Fahay, 1998).

The movement of estuarine fishes has been inferred predominantly from temporal and spatial abundance estimates coupled with analysis of size-frequency distributions, various tagging methods and the examination of otolith marks (Gillanders et al., 2003). More recently, natural chemical tracers have been used. The chemical composition of otoliths has been used to identify source estuaries for coastal populations of adults, infer natal origin of estuarine-dependent species, examine the migration patterns of anadromous and catadromous species and differentiate between estuarine and coastal habitat utilization (Thorrold et al., 2001; Forrester and Swearer, 2002; Gillanders, 2002; Gillanders and Kingsford, 2003). Although differences in otolith chemistry have been documented among fishes captured in different areas of the same estuarine system (Gillanders and Kingsford, 2000; Sánchez-Jerez et al., 2002a), the use of this approach for tracing movement among habitats over relatively small spatial scales or weak environmental gradients is still in its infancy.

Stable isotope ratios (SIR) of carbon, nitrogen and sulfur ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) of soft tissues have been used to examine movement to, from and within estuaries (Fry, 1981, 1983; Deegan et al., 1990; Fantle et al., 1999; Fry et al., 1999; Herzka et al., 2002a) as well as in other systems and taxa (Hobson, 1999; Rubenstein and Hobson, 2004). This approach is based on the premise that specific primary producer groups tend to exhibit distinctive isotopic signatures that are propagated through a local food web (Michener and Schell, 1994). Tracing the movement of fishes in estuarine systems using stable isotopes requires an individual to experience a shift to foods of distinct isotopic composition following movement to a new habitat. If the isotopic composition of available foods differs following movement of a new habitat, it will be gradually reflected in an organism's tissues (Fry and Arnold, 1982; Hesslein et al., 1993, Fig. 1). Stable isotope ratios thus serve as natural tags for distinguishing recent immigrants from those that have partially or fully equilibrated to the isotopic composition of the prey consumed in a new habitat (Hesslein et al., 1991; Fry et al., 1999; Herzka et al., 2002a).

I review the use of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ for addressing questions pertaining specifically to the movement and connectivity of fishes in estuarine systems. I briefly identify the characteristics of estuaries that make these systems amenable to tracing the movement of fishes among habitats using stable isotope ratios, and evaluate the role of growth and metabolic turnover in driving the rate at which isotopic equilibrium will be reached following a shift to isotopically distinct prey. The various types of information that can be obtained using this technique are examined, including the potential for estimating the contribution of specific habitat types to the production of adults and the reconstruction of movement patterns.

2. Estuarine habitat, fishes and stable isotope ratios

One of the hallmark characteristics of estuarine systems is spatial and temporal variation in the types of habitats available to fishes, such as seagrass meadows, macroalgal mats, marshes (including micro-algal-dominated tidal creeks), unvegetated areas and

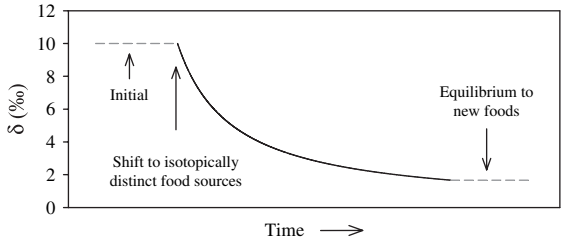

Fig. 1. Expected pattern of isotopic change exhibited by a fish that undergoes a shift to isotopically distinct foods. Isotopic values were arbitrarily selected.