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Recruitment of fish larvae and juveniles into two estuarine nursery areas with evidence of ebb tide use

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A B S T R A C T

Recruitment of larvae and early juveniles, against the ebb tide in the shallower, slower-flowing marginal areas of two permanently open estuaries in the Eastern Cape, South Africa was observed. To determine tidal, diel and seasonal variations of larval and juvenile fish recruitment, fyke nets were used during a 24-hour cycle over two years from December 2010 to October 2012. On either side of each estuary bank, two fyke nets with mouth openings facing opposite directions (i.e. one net facing the incoming or outgoing tide and the other facing the opposing direction) were used to sample fishes. The aims of this study were to determine if 1) on the flood tide, were the nets facing the incoming tide collecting more larvae and early juveniles recruiting into the estuarine nursery area, than the nets facing the opposing direction and 2) on the ebb tide, were the nets facing the sea, and hence the opposing direction of the outgoing ebb tide, collecting more fishes recruiting into the nursery against the ebb tide, than the nets facing the outgoing ebb tide? Larval and juvenile fish CPUE, species diversity and richness varied seasonally between estuarine systems and between diel and tidal conditions. Highest catches were recorded on the flood tide, which coincided with sunrise in the Swartkops Estuary. Greatest catches of larvae and early juveniles were observed during the ebb tide at night in the Sundays Estuary. On the ebb tide, higher catches of several dominant species and several commercially important fishery species, occurred in the fyke nets which faced the sea, indicating the early developmental stages of these fish species are not necessarily being lost from the nursery. These larvae and juveniles are actively swimming against the ebb tide in the shallower, slower-flowing marginal areas facilitating recruitment against ebb flow.

1. Introduction

The importance of estuaries as nursery areas for fishes is well documented, both in South Africa (Harris and Cyrus, 1995; Whitfield, 1998; Strydom and Whitfield, 2000; Strydom et al., 2003) and internationally (Elliott et al., 1990; Potter and Hyndes, 1999; Nordlie, 2003; Able, 2005). Several coastal marine fish species are estuarine-dependent and are known to spawn at sea. Their early developmental stages including postflexion larvae, enter estuarine nursery areas that are characteristically sheltered and rich in food resources (Clark et al., 1969; Wallace and van der Elst, 1975; Strydom and Whitfield, 2000). The recruitment of larvae through an estuarine mouth and subsequent transport up an estuary are critical for successful completion of the life cycle. Recruitment into estuarine nursery areas is challenging as there is a net flow of water from the estuary to the ocean, and often current speeds exceed larval swimming speeds. Larvae and early juveniles recruiting into estuaries must therefore adopt strategies for successful ingress into estuarine nursery grounds (Islam et al., 2007).

The actual process of recruitment into estuaries may either be active via swimming, or passive via drift with tidal currents (Rijnsdorp et al., 1985). Larvae may use either large-scale displacement by major currents or selective tidal stream transport (STST) to enter estuaries (Norcross and Shaw, 1984; Boehlert and Mundy, 1994; Jenkins et al., 1997; Forward et al., 1999; Jenkins et al., 1999). Vertical movement of the very early stages of fish larvae and circadian and tidal rhythms also play an important role in controlling drift, allowing larvae to remain in favourable areas (Melville-Smith et al., 1981; Boehlert and Mundy, 1988; Joyeux, 1999). Selective tidal stream transport, is the process whereby larvae ascend actively in the water column during the flood tide and return to the bottom during the ebb tide (Rijnsdorp et al., 1985; Boehlert and Mundy, 1988; Schultz et al., 2003; Miller and Shanks, 2004; Islam et al., 2007). Larvae can therefore be

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advected upstream during flood tides, and during the ebb tide, larvae can avoid seaward-moving water layers, thereby facilitating retention within the estuary (Jager, 1999; DiBacco et al., 2001). There appears to be an energetic advantage to selectively occupy tidal currents during recruitment (Metcalfe et al., 1990) although utilizing tidal flow as a mechanism for retention occurs exclusively in stratified estuaries. Stimuli including salinity, olfactory cues, electric field and pressure changes all serve as possible cues that would allow for preferred current directions to be selected (Miller, 1988; Sulkin, 1990). Diurnal changes in tidal transport have also been observed with increases in abundance of fishes during the night (Forward Jr. and Tankersley, 2001; Islam et al., 2007). This appears to be related to the light level behavioural cue (Luo, 1993). In temperate regions, recruitment is related to water temperature, photoperiod and the seasonal production cycles of zooplankton and phytoplankton. The diel and tidal cycle is also known to influence recruitment (Lyczkowski-Shultz et al., 1990; Doherty and McIlwain, 1996; Power, 1997; Young et al., 1997). Evidence suggests that greater recruitment success and enhanced maintenance within estuarine nursery habitats occurs when larval and juvenile fishes utilize diel and tidal cycles (Melville-Smith et al., 1981; Beckley, 1985; Boehlert and Mundy, 1988).

The dependence of approximately 72 fish species known to utilize South African estuaries as feeding grounds or nursery areas, has been categorized (Table 1) according to the extent juveniles depend on estuaries (Whitfield, 1998). Based on this classification, the import or export of larvae and juveniles to and from estuaries is likely to differ between estuarine association categories (Beckley, 1985). According to Beckley (1985), estuarine resident species that spawn in estuaries are likely to lose early development stages near the estuary mouth when they become entrained on the ebb-tide. Conversely, larvae and juveniles of marine species that spawn at sea are likely to enter the estuary on the flood tide while incidental marine species are likely to show irregular patterns in the export or import of larvae (Beckley, 1985). Strydom and Wooldridge (2005) reported peaks in density of larval fishes after the onset of darkness predominantly associated with the nocturnal ebb tide. High catches of larvae observed during the ebb tide does not necessarily imply that these larvae are lost from estuarine systems, but using hydrostatic pressure changes (Kingsford et al., 2002) associated with the ebb tide, larvae could be recruiting into estuaries against the ebb tide as was suggested by Strydom and Wooldridge (2005). Juvenile mugilid species have been observed to recruit into a subtropical estuary in South Africa by actively swimming against the strong ebb tide (Harrison and Cooper, 1991).

In light of these findings, the hypothesis was put forward that larvae could be recruiting into estuary nursery areas against the ebb tide as suggested by Strydom and Wooldridge (2005). In South Africa, isolated studies have assessed the rhythmic activity of larval fishes in estuaries and are linked to either the diel or the tidal cycle (Melville-Smith et al., 1981; Beckley, 1985; Whitfield, 1989a, b; Strydom and Wooldridge, 2005). These studies however, have not assessed the swimming direction of larvae and early juveniles when sampling a particular tidal state. The present study aimed to investigate the influence of the diel and tidal cycle on larval and juvenile fish directional movement using fyke nets over spring tides in two warm-temperate permanently open South African estuaries. Various movement patterns exhibited by different species could also be analysed as well as the mechanisms of transport resulting from these movements.

Table 1
Categories of fishes that utilise southern African estuaries (Whitfield, 1998).

Categories	Description of categories
Ib	Estuarine species that breed only in estuaries
Ib	Estuarine species that breed in estuaries and the marine environment
IIa	Euryhaline marine species that usually breed at sea, but the juveniles are dependent on estuaries as nursery areas
IIb	Euryhaline marine species that usually breed at sea, with the juveniles occurring in estuaries but also being found at sea
IIc	Euryhaline marine species that usually breed at sea, with the juveniles occurring in estuaries but being more abundant at sea
III	Marine stragglers not dependent on estuaries
IV	Freshwater species
V	Catadromous species

2. Materials and methods

2.1. Study site

Larval and juvenile fishes were collected from the permanently open Sundays (33°43′19″S; 25°50′57″E) and Swartkops (33°51′54″S; 25°38′00″E) estuaries in Algoa Bay, on the south east coast of South Africa (Fig. 1). The Sundays Estuary is ~21 km long, with a width of ~800 m at its widest point near the mouth, and ~20 m at the head with depths that range from 5 m in the lower reaches to 2 m in the upper reaches (Wooldridge and Erasmus, 1980; Marais, 1981; Whitfield and Harrison, 1996). The Swartkops Estuary is ~16 km long, with a width of ~350 m at its widest point near the mouth and ~90 m in the upper reaches with depths that vary from 2 m in the lower reaches to 3.5 m in the upper reaches (Baird et al., 1986, 1988). The Sundays drains a catchment area of 22 063 km^2 while the Swartkops only 1354 km^2 (Baird et al., 1986). The Sundays Estuary has continuous freshwater inflow (Jerling and Wooldridge, 1995) supplemented by an inter-basin water-transfer scheme (Pech et al., 1995) and displays a full salinity gradient linked to the inter-basin water-transfer scheme and return flows from the citrus farming practices above the estuary (Wooldridge and Bailey, 1982; MacKay and Schumann, 1990). Although the Swartkops River, which feeds the Swartkops Estuary, is dammed on the main course as well as at the tributaries, there is minimal effect on river flow (Baird et al., 1986, 1988). The lower reaches of the Swartkops Estuary is characterised by extensive intertidal mud flats, islands and saltmarshes (Baird et al., 1986, 1988) while there is an absence of salt marshes or large mud flats in the Sundays Estuary (Beckley, 1984). These estuaries are located in the warm-temperate climatic zone and experience a bimodal rainfall pattern (Lubke and de Moor, 1998). Tides in Algoa Bay are semi-diurnal with a mean spring amplitude of 1.6 m and a maximum of 2.1 m (Talbot and Bate, 1987). The Sundays and Swartkops estuaries are large systems considered in fair and good ecological condition respectively (Whitfield, 2000) and both are of high conservation importance (Turpie et al., 2002).

2.2. Field sampling and fish identification

Samples were collected on two occasions during each season, December and January, and March and April in summer and autumn respectively. Winter and spring sampling took place in June and July and in September and October respectively. Two years of sampling was undertaken, starting in December 2010 and culminating in October 2012 at fixed sampling stations on either bank, in the mouth region of each estuary. In total, 16 sampling trips were conducted and these were all standardized over the new moon period. Each estuary was sampled sequentially. At each estuary, four fyke nets were laid. On each bank, two, double-winged, 6 hooped, 1 mm mesh size fyke nets were set using an anchor