# Epibenthic Schooling by Larvae of the Atherinid Fish *Leptatherina presbyteroides*: an Effective Mechanism for Position Maintenance

Aldo S. Steffe

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A common problem facing larvae in estuaries is how to maintain their position within an estuary and avoid being flushed out on the next ebb tide. Recently it has become increasingly apparent that fish larvae are often present in large numbers near the bottom (Weinstein et al., 1980; Melville-Smith et al., 1981; Schlotterbeck and Connally, 1982; Barnett et al., 1984; Norcross and Shaw, 1984; Robison, 1985; Brewer and Kleppel, 1986; Leis, 1986; Leis et al., 1989; Steffe, unpubl. data). The movement of larval fishes into and from the epibenthic layer, in response to changing environmental parameters, is often invoked to explain the dynamics of larval recruitment and retention within estuarine systems (Weinstein et al., 1980; Norcross and Shaw, 1984, and references therein; Robison, 1985). Despite the importance of the epibenthic layer to larval recruitment processes there are few published observations on the behaviour of fish larvae which inhabit the epibenthic layer (Leis, 1986).

Here I report observations on larval behaviour and distribution associated with the epibenthic schooling of the Australian atherinid *Leptatherina* (=*Atherinosoma*) *presbyteroides* (Richardson 1843), a small schooling fish which inhabits inshore marine waters and is known to enter the lower reaches of estuaries (Potter et al., 1986). This species is distributed across southern Australia (Potter et al., 1986). I argue that these observations are consistent with the hypothesis that epibenthic schooling is advantageous for position maintenance within a favoured area.

## Materials and methods

All larvae were collected from a marine dominated region of Port Hacking (34°5′S, 151°7′E), a temperate estuarine system on the east coast of Australia. The study area was located within, but near the outer seaward edge, of a large subtidal *Zostera capricorni* seagrass bed. The study area was characterized by the presence of many small 10–50 m² sand patch depressions. Depth ranged from 0.1–1.0 m at low tide and this area was subject to strong semi-diurnal tidal currents. Sand patches were typically deeper than the substrate of the surrounding seagrass by about 10–15 cm.

Larvae were observed and collected from sand patch areas in the two week period between 7–21 October 1984 using snorkel and dip net. All observations on larval behaviour were made during daylight (10.00–16.00 hrs). Larvae were preserved and stored in 5–10% seawater formalin. Using the size series method I identified these larvae as *Leptatherina presbyteroides* (fam. Atherinidae). This species can be easily distinguished by head and body pigmentation from other atherinid larvae found in this region (Steffe and Said, unpubl. data). Representative specimens of *L. presbyteroides* larvae from these collections are lodged in the Australian Museum, Sydney (AMS I. 26987–003).

To determine the size structure of larval schools I measured body length to the nearest 0.1 mm (i.e. notochord length in preflexion and flexion stages, and standard length in postflexion larvae) of 200 randomly chosen larvae with a dissecting microscope and ocular micrometer.

## Results

Larval schools which I visually estimated to contain $10^4$–$10^5$ fish, were present over most sand patches within the seagrass bed. I found only one fish species even though I collected several thousand larvae in total, from many separate schools. Thus, I confirmed these larval schools were monospecific aggregations of *Leptatherina presbyteroides*. Schools were always comprised of mixed size-class larvae and schools of uniform size-class individuals were never found. Larval size ranged from 7.9–14.9 mm with preflexion (9%), flexion (47%) and postflexion (44%) stages common in all schools (Fig. 1). This indicates that *L. presbyteroides* can school before any fins have formed. Even though the recorded range of larval size was large and all developmental stages were well represented it is possible that these parameters were underestimated due to the inherent net bias (i.e. extrusion of small larvae and avoid-

ance by larger larvae).

When not disturbed, larval schools were always orientated towards the direction of the prevailing current. Tightly packed larval schools were commonly found 1–10 cm above the sand substratum. Periodically, schools were observed to move vertically into the midwater above the level of the surrounding seagrass blades. At these times the distance between individual fish increased markedly and larvae apparently began to feed. They were ingesting particles which drifted past. Schools remained in the midwater for relatively short periods (5–10 min) after which they returned to the epibenthic layer and schooled tightly again. When a midwater school was threatened, e.g. by swimming towards them, larvae would quickly move to the epibenthic layer and school tightly. Larval schools were very reluctant to swim over seagrass or to move away from the sand patch areas. Even when continually threatened, a school would, on most occasions, split and swim back past the diver, regrouping at the opposite end of the sand patch. This behaviour is similar to that described by Leis (1986) for the larvae of *Spratelloides gracilis*.

Although larval schools were present over sand patches throughout the two weeks of observation they were never seen over the subtidal sand flats adjacent to the seagrass bed, nor over seagrass.

## Discussion

As larvae of marine atherinids are primarily neustonic (Leis and Rennis, 1983; Schmitt, 1983; Steffe, pers. observ.) it was surprising to frequently find many large epibenthic schools of *L. presbyteroides* larvae. Larval *L. presbyteroides* of all developmental stages have also been collected from surface waters with conventional plankton nets in the Swan River estuary, Western Australia (F. J. Neira, pers. comm.). As there is no reason to suspect that larval *L. presbyteroides* in eastern Australia are obligate epibenthic dwellers one must ask what possible advantage(s) do they gain from epibenthic schooling?

A possible explanation is that these larvae might have been exploiting an epibenthic food resource located only in the sand patch areas, but this is unlikely. I did not observe or catch any invertebrates in the sand patch areas which could have been potential food items. Larvae were never
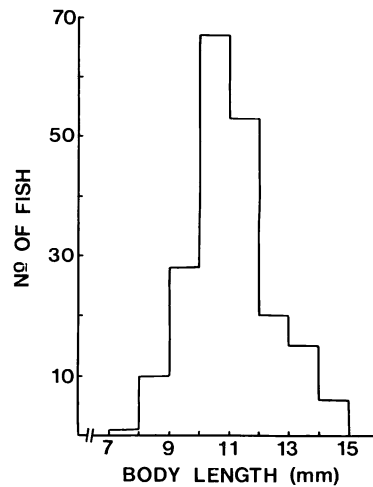


Fig. 1. Length frequency histogram for *Leptatherina presbyteroides* larvae from epibenthic schools (n = 200, x̄ = 11.0, SD = 1.3).

seen feeding when schooling in the epibenthic layer even though I often observed them feeding in the midwater immediately after a school had moved from the epibenthos. These observations are inconsistent with the feeding hypothesis.

I suggest that the main benefit obtained is position maintenance within a favoured area. Visual contact with a fixed reference point such as the seabed is required for larval fishes to detect current direction (Arnold, 1969, 1974; Blaxter, 1970). *L. presbyteroides* larvae appeared to be responding to the strong tidal currents in the study area. Larvae always faced into the direction of the current. Larval schools remained near the bottom most of the time, and episodic feeding forays by schools into the midwater were brief.

Changes in bottom contour and structure can be expected to alter the epibenthic current velocity. Thistle et al. (1984) found that small scale changes in flow associated with microtopographic structures such as individual seagrass shoots and polychaete tubes could enhance copepod abundances. It is likely that the epibenthic current flow inside the sand patch areas would also be reduced as a result of the uneven bottom topography and the baffling effects of nearby seagrass blades. More importantly, larvae occupying these low current refuges should be better able to avoid transportation by tidal currents relative to larvae swimming over bare flat substrates outside of seagrass beds,

Two observations on larval distribution support this argument. Firstly, epibenthic schools of *L. presbyteroides* were only found over sand patch areas within the seagrass bed. Larvae were never observed schooling over the adjacent flat sand bottom, or seagrass, at similar depth. Secondly, epibenthic larval schools persisted over the sand patch areas throughout the two week observation period.

Preflexion, flexion and postflexion stages were well represented in all larval schools. This was surprising given that it is usually fishes of similar sizes which school together (Bond 1979). The tendency for similar sized individuals to school together is linked to the differential swimming capabilities of different sized fishes (Bond 1979). Size segregation occurs because small individuals are unable to sustain the faster cruising speeds of large fish. Thus, the observed persistence of mixed size-class schools over sand patches suggests that school movement is limited and provides evidence that effective position maintenance occurs. The formation of these epibenthic larval schools in low current refuges could be explained by the passive recruitment of different sized larvae from the plankton, but the observed behaviour of larvae after settlement suggests that larvae actively maintain their location over sand patch areas. Such behaviour should enhance larval survival and therefore would be favoured by natural selection.

It is likely that a similar position maintenance mechanism is also used by the larval stages of other estuarine and nearshore fishes. Co-ordinated schooling by larvae in the epibenthic layer can create problems for quantitative sampling (Leis, 1986), particularly if epibenthic schooling is restricted to small but favoured areas as was found in *L. presbyteroides*. The use of specialized epibenthic sampling methods do not guarantee accurate estimates of larval abundance. For example, estimates of epibenthic larval abundances derived from surveys using randomly selected stations will be characterized by large variances. This problem may, in part, be overcome by selecting stations using criteria which influence near bottom larval distributions such as bottom topography and epibenthic current velocities.

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(School of Biological Sciences, Macquarie University, North Ryde, N.S.W. 2109, Australia)

トウゴロウイワシ科魚類 *Leptatherina presbyteroides* 仔魚における近底層群性の場所確保機構としての意義

Aldo S. Steffe

オーストラリア産トウゴロウイワシ科魚類 *Leptatherina*(=*Atherinosoma*) *presbyteroides* 仔魚が主に藻場内の砂質域の近底層部において群泳することを観察した. 群体は単一種で構成されているが, 体長組成は複数のモードを持っていた. 群性個体は近底層域では高密度に分布し, 摂餌を行う場合は上層に移行して分散する傾向が認められた. この近底層群性の意義は流れの弱い場所を確保することによって生残を高めることにあると推定された.