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DEFINING KEY FACTORS RELATING FISH POPULATIONS IN ESTUARIES AND THEIR HABITATS

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Summary
Some of the recent literature is reviewed and results of detailed studies of fish and crustacean populations in temperate estuaries of south-western Australia and New South Wales are synthesised and the approaches to these studies discussed. Studies on the west coast of Australia have concentrated on defining seasonal, annual and spatial patterns of change in the fish fauna of the Swan and Peel-Harvey estuaries. The emphasis has been on obtaining detailed knowledge of the life history strategies of fish in estuaries and interpreting the main factors affecting the fish populations and community structure in light of this information. On the east coast, more effort has been directed towards evaluating the importance of various habitats to fish in estuaries, particularly seagrass habitats in several different estuarine and inshore coastal systems. Conventional sampling techniques (i.e. beach seines, gill nets, otter and beam trawls) have been used to study fish populations in estuaries of both regions. In addition, in Western Australia, commercial catch data in the Peel-Harvey and Swan estuaries have been used to assess how fish populations have responded to the marked eutrophication in the former system. Artificial seagrass has also been used in NSW to test hypotheses about the importance of seagrass to larval and juvenile fish.

Introduction
Estuaries are complex ecosystems in which environmental conditions are influenced by water derived from both riverine and marine sources. Furthermore, a wide variety of species of fish, representing different life cycle categories, is found in estuaries (Loneragan et al. 1989; Potter et al. 1990). The influence of environmental factors can vary greatly among the different life cycle categories of fish. For example, marine species are generally influenced to a greater extent by changes in salinity than estuarine or anadromous species.

In this paper, I outline some of the environmental variation found in estuaries, discuss the fish fauna found with estuarine systems and examine approaches to the study of key factors which influence the fish fauna. Most of the discussion will focus on temperate estuarine systems in Australia, particularly those in south-western and south-eastern Australia. In reviewing studies of estuarine fish populations, it is important to consider details of the spatial and temporal scales that were used, as these can greatly influence the results and interpretation of the important factors influencing the fish populations.
The estuarine environment

Pritchard (1967) proposed the first widely accepted definition of an estuary, namely that an estuary is a semi-enclosed body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage. However, this definition does not cover the types of environment found in many estuaries in southern Africa and parts of Australia (particularly the south-west) where sand bars may form at the mouths of estuaries and the water within the estuary can become markedly hypersaline. In order to include these systems, Day (1980; 1981) proposed that an estuary is a partially enclosed coastal body of water which is either permanently or periodically open to the sea and within which there is a measurable variation of salinity due to the mixture of sea water with fresh water derived from land drainage.

Since estuaries are regions where there is a mixing of water derived from both oceanic and riverine sources, they are typically environments where characteristics of the water column can undergo pronounced fluctuations (Day et al. 1981; Haedrich 1983). In addition to a salinity gradient along the estuary, there may be abrupt and large changes in salinity, temperature, dissolved oxygen, turbidity, flow and nutrient levels (Haedrich 1983; Cloern and Nichols 1985). The amount of fresh water flowing into estuarine systems varies greatly according to latitude, the seasonal pattern and quantity of rainfall, and characteristics of the catchment (e.g. amount of clearing, soil type and gradient of slope into the tributary rivers) (Day 1981). An example of the variation in patterns of annual rainfall is provided below. In the temperate lowlands of Europe, the annual rainfall is approximately 650-760 mm and it rains throughout the year. Relatively continuous rainfall also occurs in Melbourne, south-eastern Australia and Christchurch, New Zealand (Day 1981). By contrast, both Cape Town in South Africa and Perth in south-western Australia have a similar total annual rainfall, but most rain falls in winter (Day 1981; McComb et al. 1981). In tropical regions of Australia, virtually all the rainfall is in summer and early autumn, and the total annual rainfall can be at least twice that of the above temperate regions (e.g. Davis 1988). The pattern of rainfall influences the timing of changes in hydrological conditions within estuarine systems and hence the times when these environments are suitable for colonisation by marine flora and fauna.

The influence of marine waters on the hydrology of an estuary can also vary greatly between systems. Thus, in funnel shaped estuaries, i.e. estuaries with a broad mouth and a channel width which decreases progressively with distance upstream, the influence of tides can be greatly accentuated (Day 1981). Contrasting with this pattern of tidal accentuation, is the situation in many estuaries, particularly those in southern Australia, where the tidal energy and the resulting change in water level, diminishes with distance from the estuary mouth (Day 1981).

The fish fauna of estuaries

Relatively large numbers of the juveniles of some marine teleosts regularly enter estuaries in the temperate regions of both the Northern and Southern hemispheres (e.g. Gunter 1938; Pearcy and Richards 1962; McHugh 1967; Cronin and Mansueti 1971; Day et al. 1981; Haedrich 1983; Claridge et al. 1986). It is for this reason that estuaries have often been referred to as fish nursery areas (Cronin and Mansueti 1971; Haedrich 1983; Blaber 1985; Potter et al. 1990). Many other marine species are found only in small numbers in estuaries and generally in the high salinity regions towards their mouths (Haedrich 1983; Claridge et al. 1986).

Estuaries are used by anadromous species as a route between feeding areas in marine waters and their spawning grounds in freshwater, whereas they allow the reverse migration in the case of catadromous species (Day et al. 1981; McComb et al. 1981). In tropical regions of Australia, virtually all the rainfall is in summer and early autumn, and the total annual rainfall can be at least twice that of the above temperate regions (e.g. Davis 1988). The pattern of rainfall influences the timing of changes in hydrological conditions within estuarine systems and hence the times when these environments are suitable for colonisation by marine flora and fauna.
1981; Haedrich 1983; Dando 1984). A few species of teleost, almost certainly of marine origin, have evolved the ability to complete the whole of their life cycle within estuarine environments (Ross and Epperley 1985; Potter et al. 1986a; 1990). Some of these 'estuarine' species are also represented by populations in marine environments (Lenanton 1977; Prince et al. 1982; Chrystal et al. 1985; Potter et al. 1986b). The upper reaches of estuaries are occasionally penetrated by a few of the more euryhaline freshwater teleosts (Cronin and Mansueti 1971; Day et al. 1981).

The very high numbers of the juveniles of some of the marine species of teleost found in estuaries have led to these species frequently being included with estuarine and diadromous species in a category termed estuarine-dependent (Clarke et al. 1969; Pollard 1976; 1981; Van den Broek 1979; Fourtier and Legget 1982; Haedrich 1983; Beckley 1984; Blaber 1987). Since several recent studies have shown that a number of these marine species which are found in abundance in estuaries also utilize marine environments extensively at the same stage of their life cycles (Lenanton 1982; Beckley 1984; Smale 1984; Lenanton and Potter 1987), it has been suggested that these species would be more appropriately termed 'estuarine-opportunists' (Hedgpeth 1982; Lenanton and Potter 1987). A number of the marine teleosts which utilize estuaries as nurseries contribute to important commercial and recreational fisheries in either or both marine and estuarine waters. There is thus a clear need to preserve estuarine environments for the successful management of a number of important fisheries (e.g. McHugh 1976; Beal 1980). The importance of estuaries to commercial fisheries is emphasised by the fact that the 'estuarine-dependent' species of fish and crustaceans comprised 69% of the total weight landed by the commercial fishery of the United States in 1970 (McHugh 1967). Estuarine-dependent species have been estimated as contributing a similarly high proportion (70%) to the commercial fisheries in New South Wales, eastern Australia (Pollard 1976; 1981). Although this value for estuarine-dependent species is lower for south-western Australia and for Australia as a whole (20 and 32%, respectively), this still represents a large catch (Newell and Barber 1975; Lenanton and Potter 1987). In addition to commercial fishing, recreational fishing is an important activity in estuaries in many regions of the world (Caputi 1976; Lenanton 1979; Day et al. 1981; Marais 1988).

Factors influencing fish in estuaries

Several hypotheses have been invoked to explain why estuaries are used so extensively by the juveniles of marine fishes. For example, it has been suggested that, because estuaries are among the most productive environments in the world (Whittaker 1975; Correll 1978; Mann 1982), they supply an abundance of food, thereby facilitating the growth of juvenile fish. Furthermore, the presence of higher temperatures in estuaries than in marine waters would facilitate increased growth rates of fish in estuarine environments. In addition to the higher growth rates in estuaries, predation rates are believed to be lower in estuaries than the ocean. This view is supported by the fact that the incidence of large teleost piscivores is generally lower in estuaries than in marine waters (Blaber 1980; Blaber and Blaber 1980; Haedrich 1983). The macrophyte beds and turbid waters which are often found in estuaries are likely to increase protection from predation in these systems (Blaber and Blaber 1980; Lenanton et al. 1984; Cyrus and Blaber 1987a; b).

The number of species, density of individual species and the species composition of the fish community undergo seasonal changes in many estuaries (Gunter 1938; Dahlberg and Odum 1970; McErlean et al. 1973; Haedrich and Haedrich 1974; Livingston 1976; Quinn 1980; Bell et al. 1984; Claridge et al. 1986; Quinn and Kojis 1986). While these cycles have often been related to salinity and/or tempera-
ture, other variables, particularly in tropical or sub-tropical estuaries, may be more important in some cases. For example, in Moreton Bay in eastern Australia and the Lake St. Lucia estuarine system of South Africa, turbidity was important when spatial differences in salinity were relatively small (Blaber and Blaber 1980; Cyrus and Blaber 1987a; b). Similarly, in the absence of a strong salinity gradient, distance from estuary mouth had an important influence on the abundance and composition of juvenile fish associated with seagrass (Zostera capricorni) in the Hawkesbury River Estuary, eastern Australia (Bell et al. 1988). From the above, it can be seen that abiotic factors such as salinity, temperature, distance from estuary mouth and turbidity, and biotic variables such as aquatic vegetation, predation and competition, may affect the distribution and abundance of individual species and the structure of the fish communities of estuaries (see also Orth and Heck 1980; Young 1981; Orth et al. 1984; Pollard 1984).

**Estuarine fish studies**

Both the sampling methods used to investigate the fish fauna in estuaries and the range of estuarine environments sampled, have varied greatly among studies. For example, Thorman (1986) utilized a small beach seine to sample fish at sites along 60 km of the southern Bothnian Sea, whereas Little et al. (1988) used the same method of sampling at four sites in a tropical mangrove creek with no more than 5 km separating the most distant sites. In the former study, salinities were always less than 10‰, whereas they were very close to that of sea water in the mangrove creek (34-36‰). Differences in the scale of an investigation, such as those outlined above, can dramatically influence the results and hence the conclusions drawn from a study (Doherty and Williams 1988; Levin 1992). This point is often overlooked when comparisons are made between the findings from different studies.

In a review of estuarine fish studies, Haedrich (1983) made a plea for further work on the life history of fishes within estuaries, as well as highlighting the paucity of long term studies in these environments. Few studies of estuarine fish appear to have exceeded two years in duration (Haedrich 1983) and of those which have spanned a longer time period, most appear to have sampled only a limited number of sites or range of estuarine conditions. Thus, in a five year study of the fish fauna in a lagoon on the west coast of the United States, beach seines were used to catch fish at four sites, all with salinities very close to that of sea water, separated by distances of less than 2 km (Onuf and Quammen 1983). The six year investigation of Hillman et al. (1977) was also carried out at sites with salinities very similar to that of the ocean. Although significant seasonal variations in salinity were recorded during a five year study of the fish fauna in the Severn Estuary, United Kingdom, the major data source came from sampling at only one site (Claridge et al. 1986; Potter et al. 1986a). Very little is thus known of the relative importance of the influence of site within estuary, season and year on the abundance, and community structure of fish populations in estuaries.

**Approaches to studies of fish populations in Western Australian estuaries**

Work in the Swan Estuary of south-western Australia was undertaken over a five year period to gain a detailed understanding of the taxonomy and life histories of the fish found in this estuary; to investigate changes in the abundance of species and the composition of the fish fauna over the length of the system and with season and year; and to understand how different species were affected by changes in environmental variables, particularly salinity and temperature. These studies were jointly directed by Ian Potter of Murdoch University and Rod Lenanton of the Bernard Bowen Fisheries Research Institute,
with funding from the Western Australian Departments of Fisheries, and Conservation and Environment.

The Swan Estuary covers a surface area of approximately 53 km² and is the second largest estuarine system in south-western Australia. This estuary and that of the Peel-Harvey (c 80 km south) are two permanently open systems on the west coast, whose mouths are separated by a distance of about 55 km. They are the most important estuaries for commercial and recreational fishing in this region (Lenanton 1979; Lenanton 1984; Lenanton et al. 1984).

The Swan Estuary comprises a long, narrow Entrance Channel that opens into extensive wide basins, which in turn lead into tidal, saline riverine areas, termed the lower, middle and upper estuary, respectively. Over the five year study, mean salinity ranged from 30‰ to 8.6‰ in the lower and upper estuary respectively (Loneragan et al. 1989). By contrast, mean temperature during this period was relatively constant (c 20°C) throughout the estuary. Variation in salinity increased with distance from the estuary mouth, whereas the variation in temperature was relatively stable in the different regions of the estuary. Both salinity and temperature were lower in the winter and spring than the summer and autumn. In the upper estuary, salinities can increase to about 30‰ during the late summer and early autumn, only slightly lower than salinities in the middle and lower estuary at this time. Other environmental variables such as turbidity, freshwater flow and nutrient levels are likely to vary in a similar way to the variation with distance from estuary mouth and season shown by salinity.

Large beach seines (swept area = 1 670 m² and 2 815 m²) were used over a five year period to sample fish at ten sites in the shallow waters of the Swan Estuary (see Loneragan et al. 1989). Sampling for most of this study was at fortnightly or monthly intervals. In terms of distance from the estuary mouth, the sites were from 2 to 44 km upstream of the mouth.

The most abundant families of fish in the Swan were the Clupeidae, Terapontidae, Mugilidae, Apogonidae and Atherinidae. Of the 15 most abundant species in the shallows of the Swan Estuary, seven were marine teleosts which entered the estuary regularly and in large numbers (marine estuarine-opportunist), seven completed their life cycle within the estuary (estuarine) and one (Nematalosa vlaminghi) was anadromous. The contribution of individuals of the marine estuarine-opportunist category to catches in the shallows declined from nearly 95% in the lower estuary, to approximately 17% in the middle estuary and 6% in the upper estuary. The estuarine and anadromous groups together comprised 83 and 94% of the catches in the middle and upper estuaries, respectively.

The number of species and density of fish (measures of community structure) were influenced by distance from the estuary mouth, salinity and temperature; they declined with distance from estuary mouth and rose with increasing salinity and temperature. Classification and ordination distinguished the ichthyofauna of the saline reaches of the rivers from that of the lower reaches of the estuary. The faunal composition of the middle estuary of the Swan was also relatively distinct from those of the lower and upper estuary (Loneragan and Potter 1990). A secondary pattern of variation in the fish fauna, due to seasonal changes in composition, particularly in the upper estuary, was also detected using classification and ordination.

Site within the Swan Estuary generally influenced the densities of individual species to a greater extent than either Season or Year, or the interactions between these factors. When seasonal effects were important, they could be related to summer spawning migrations into the upper estuary (Nematalosa vlaminghi, Ammiantaba caudavittatus), spring recruitment of 0+ individuals into the lower estuary (Mugil cephalus) or winter movements into deeper and more saline waters (Apogon rueppelli). Marked
Annual variations in the density of *Torquigener pleurogramma* were related to large differences in the recruitment of the 0+ age class between years.

The studies within the Swan have helped to gain an understanding of the life histories and factors affecting fish populations over a broad spatial scale. More recent work has focussed on a finer spatial scale and has investigated the importance of macrophytes to fish in Wilson Inlet, a seasonally closed estuary on the south coast of Western Australia (Humphries et al. 1992).

**Approaches to studies of fish populations in New South Wales estuaries**

Much of the work in New South Wales has been carried out under the direction of Johann Bell and Dave Pollard of the NSW Fisheries Research Institute. Detailed studies of fish populations in estuaries have been completed in Botany Bay (e.g. Anon. 1981a; b) and in more recent years, concurrently in several estuaries along the coast of NSW (e.g. Ferrell and Bell 1991; McNeill et al. 1992; Worthington et al. 1992). Both these major studies were initiated in response to potential environmental impacts in coastal regions: extensions to Sydney airport in Botany Bay; and proposed development of port facilities in Jervis Bay for the Navy.

In general, the focus in these studies has been on establishing the importance of various habitats to fish and decapod populations, particularly seagrass compared with bare substrate. These studies have been carried out in regions of estuarine systems which appear to have a similar variation in salinity to that found in the lower Swan Estuary. The fish fauna is thus likely to be dominated by the juvenile stages of marine species. Estuarine and migratory (i.e. anadromous and catadromous) species are not likely to have been major contributors to the fish fauna in these studies.

The results of much of the work on the importance of seagrass systems to fish populations in Australia have been summarised by Bell and Pollard (1989). In their introduction they summarise the findings of previous studies and reviews with the following (modified from Bell and Pollard 1989):

- the diversity and density of fish are usually higher in seagrass than nearby bare areas;
- fish and decapods are found in seagrass for different lengths of time and at different stages of the life history;
- many fish species settle into seagrass from the plankton;
- seagrass, seagrass detritus and infauna of the seagrass are an underutilised food source for most species of fish compared to planktonic and epifaunal crustaceans;
- different species of fish are found in different positions in the seagrass canopy;
- the composition of the fish community and the relative abundance of different species can be influenced by the position of the bed in relation to other habitats and on the time of day; and
- the species composition of different seagrass beds often differs, even when the beds are adjacent.

The importance of different habitats to fish populations has been investigated by field sampling in single estuarine systems and more recently through concurrent sampling of a number of estuaries over the 18 months. The abundances of different species has then been correlated with attributes of the habitat, such as the shoot density of seagrass (e.g. Worthington et al. 1992). The results of these studies have been enhanced through the use of experimental field studies to test hypotheses about the importance of seagrass to fishes. This has involved studying settlement of larvae in artificial seagrass and examining the effect of manipulating the height and density of naturally
From the general increase in abundance of fish and crustaceans with increased seagrass structure (i.e. higher shoot density, biomass) within a seagrass bed, it was proposed that predation and habitat selection were the main processes explaining these correlations (Heck and Orth 1980; Orth et al. 1984). More recently Bell and Westoby (1986) proposed an alternative hypothesis: that the distribution of fish and crustaceans among separate seagrass beds reflects the supply of larvae to those beds. They proposed that larvae settle to the first bed they encounter, regardless of the characteristics of the seagrass, and that individuals rarely leave the shelter of that bed during the following three to four months. Both the experimental field studies and the more descriptive work support the supply hypothesis. Worthington et al. (1992) conclude that the density of seagrass shoots explained little of the large scale variation in abundance of fish and decapods among separate seagrass beds and that their data support the supply model.

**Summary and future directions**

Work on the fish faunas found in estuaries is challenging due to the variability in both the types of species of fish found in these systems and in the environment itself. The approach of studying life histories has greatly improved our understanding of the dynamics of fish populations in estuaries of south-western Australia and the environmental factors which affect populations and the composition of the fauna. Over the relatively large spatial scales investigated in these studies, distance from estuary mouth and salinity (hence also the hydrology and characteristics of the catchment) have been identified as key factors affecting the composition of the fish fauna in the Swan Estuary.

Because of the detailed knowledge of fish populations in open estuaries and inshore waters of the west coast, it is timely to consider testing the generally held hypotheses about estuaries concerning their high productivity and refuge value for fish. Since the variation in the fish fauna is now well documented over a relatively large spatial scale, it is also appropriate to examine the importance of different habitat types in regions where environmental conditions are similar e.g. importance of seagrass in the lower and middle Swan system. Further work also needs to be undertaken to determine whether the factors affecting fish populations in open estuaries are the same in seasonally open and closed systems.

In the studies of fish populations of estuaries of New South Wales, most of the studies appear to have been undertaken at a smaller spatial scale within a particular system. At this level, variation in habitat type has an important influence on fish populations and community structure. Levin (1992) has suggested that the mechanisms affecting populations and communities vary according to the scale of the study and the hypotheses being investigated. This generality certainly seems to apply to studies of fish populations in estuaries on the east and west coasts of Australia. If we are interested in fish of the lower region of the estuary where salinity is relatively stable, then different habitat types and location of the habitats may determine the composition of the fish community and abundance of different species. However, if the hypothesis concerns the system as a whole, then distance from the estuary mouth and associated variables such as salinity are the key variables.

Bell and Pollard (1989) have discussed areas for new work on fish fauna in seagrass systems and suggested that the following areas were important:

- the effect of size, shape and location of the habitat within the estuary;
- the hypothesis that fish and decapods settle in the first bed they encounter and do not leave the bed; and
• differences in fish communities between different seagrass beds within the same estuary—are they due do the fact that the beds may be situated at different depths or to differences in the attributes of the seagrass? Does seagrass possess important attributes for fish populations or will different structures generate the same patterns in abundance?

In addition to these hypotheses, recent work by Underwood (1993) has challenged us to consider the design of studies on fish populations where the aim is to detect the effects of an impact. Can we apply his concept of multiple control estuaries when the catchment characteristics and morphology (hence hydrology and salinity regimes) of different systems vary greatly?

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