Influence of site, season and year on contributions made by marine, estuarine, diadromous and freshwater species to the fish fauna of a temperate Australian estuary

Article *in* Marine Biology · December 1989

DOI: 10.1007/BF00399578

3 authors:

N. R. Loneragan

Murdoch University

Ian Ceasar Potter

Murdoch University

R.C. Lenanton

Marine Biology 103, 461–479 (1989)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

Influence of site, season and year on contributions made by marine, estuarine, diadromous and freshwater species to the fish fauna of a temperate Australian estuary

N. R. Loneragan[1], **I. C. Potter**[1] and **R. C. J. Lenanton**[2]

[1] School of Biological and Environmental Sciences, Murdoch University, South Street, Murdoch, Western Australia 6150, Australia
[2] Western Australian Marine Research Laboratories, P.O. Box 20, North Beach, Western Australia 6020, Australia

Abstract

Catches obtained at regular intervals by beach seining, gill netting and otter trawling at ten, four and six sites, respectively, have been used to determine the contribution of the different species and life-cycle categories of fish to the ichthyofauna of the large Swan Estuary in temperate southwestern Australia between February 1977 and December 1981. These data were also examined to investigate the influence of site, season and year on the densities of the more abundant species. A total of 630 803 fish, representing 36 families and 71 species, were caught in the shallows using beach seines during this 5 yr study. Although the majority of these species were marine teleosts that were caught infrequently (marine stragglers), representatives of 7 of the 15 most abundant species were marine teleosts which entered the estuary regularly, and in large numbers (marine estuarine-opportunists). Of the remaining 8 most abundant species in the shallows, 7 completed their life cycle within the estuary (estuarine species) and 1 (*Nematalosa vlaminghi*) was anadromous, feeding for a period at sea and spawning in the upper reaches of the estuary. The contribution of individuals of the marine estuarine-opportunist category to catches in the shallows declined from nearly 95% in the lower estuary, to 17% in the middle estuary and 6% in the upper estuary. The estuarine and anadromous groups made a considerable contribution to the catches in both the middle and upper estuaries. By contrast, the contribution of freshwater species was small and even in the upper estuary accounted for only 0.2% of the catch. Site within the estuary generally influenced the catches of individual species to a greater extent than either season or year, or the interactions between these three factors. When seasonal effects were strong, they could be related to summer spawning migrations into the upper estuary (*Nematalosa vlaminghi, Amniataba caudavittatus*), spring immigrations into the lower estuary (*Mugil cephalus*), or winter movements into deeper and more saline waters (*Apogon rueppellii*). Annual variations in the density of *Torquigener pleurogramma* were related to marked annual differences in the recruitment of the 0+ age class.

Introduction

Large numbers of fish are found in the estuaries of temperate regions of both the northern and southern hemispheres (Cronin and Mansueti 1971, Day et al. 1981, Dando 1984, Potter et al. in press). The ways in which the different species of fish use these estuaries has been categorised by a number of workers, including McHugh (1967), Dando (1984), Wallace et al. (1984) and Lenanton and Potter (1987). Marine teleosts are typically the most abundant group of fish represented in estuaries (e.g. Day et al. 1981, Haedrich 1983, Claridge et al. 1986). Since the 0+ is generally by far the most abundant age class of such species in these systems, estuaries have frequently been referred to as fish nursery areas (Cronin and Mansueti 1971, Blaber 1980, Haedrich 1983). Although those marine fish species which enter estuaries regularly and in relatively large numbers have often been included in a category termed "estuarine-dependent" (e.g. McHugh 1976, Claridge et al. 1986), the observation that the juveniles of many of these species are also frequently abundant in protected inshore marine waters suggests that they would be more appropriately called "estuarine-opportunists" (Hedgpeth 1982, Lenanton and Potter 1987, Potter et al. in press). There are also several marine species which occur irregularly and only in small numbers in estuaries. The members of this group, which are often assumed to be stenohaline, have been referred to as "marine stragglers" (Claridge et al. 1986, Lenanton and Potter 1987). The remaining categories of teleosts which are found in estuaries include a few species which can complete the whole of their life cycle in estuaries, the catadromous and anadromous migrants which pass through estuaries on their way to and from spawning and feeding grounds, and the freshwater teleosts (Cronin and Mansueti 1971, Day et al. 1981, Haedrich 1983, Dando 1984, Blaber 1985, 1987). Members of the last group are rarely found in abundance in estuaries (Day et al. 1981, Haedrich 1983, Dando 1984).

Despite the fact that the above different categories of life cycles for those fish which utilize estuaries are widely accepted, there has apparently never been an attempt to quantify the relative contribution made by the numbers of individual fish within each category to the ichthyofauna of any estuary or to the major regions within an estuary. The absence of such information probably reflects in part the relative paucity of detailed data on the life cycles of many of these species (Haedrich 1983).

During the last 12 yr, the fish communities and populations of two large estuaries in south-western Australia have been studied in detail. These investigations have yielded information on the composition and structure of the fish community of the Peel-Harvey system (Potter et al. 1983, Lenanton et al. 1984, Loneragan et al. 1986, 1987). They have also provided extensive data on the biology of several of the more abundant species in this system and to an even greater extent of those in the nearby Swan Estuary. Information is thus now available on the life cycles of representatives of the dominant families in these systems, namely the Mugilidae, Atherinidae, Clupeidae, Gobiidae, Apogonidae, Plotosidae and Tetraodontidae (e.g. Chubb et al. 1981, Prince et al. 1982a, b, Prince and Potter 1983, Potter et al. 1983, 1988, Chubb and Potter 1984, 1986, Lenanton et al. 1984, Chrystal et al. 1985, Nel et al. 1985, Gill and Miller in press, also Gill, Murdoch University, Western Australia, unpublished data).

The aim of the present study was to use the data obtained by regular sampling over five consecutive years by beach seining and for more restricted periods by gill netting (1 yr) and otter trawling (4 yr) to quantify the contributions made to the fish fauna of the large Swan Estuary in temperate south-western Australia by both the individual species and the various life-cycle categories. Emphasis has also been placed on establishing whether these contributions differ between regions of the estuary and if the abundance of the dominant species within the shallows of this system varies with season and year. Wherever possible, comparisons are made with the ichthyofaunas of estuaries in temperate regions of southern Africa, which lie at similar latitudes, and with those of the northern hemisphere.

Materials and methods

Sampling regime

The Swan Estuary, which covers a surface area of approximately 53 km^2, comprises a long, narrow entrance channel that opens into extensive wide basins, which in turn lead into tidal, saline riverine areas (Hodgkin and Lenanton 1981, and present Fig. 1). Chalmer et al. (1976) have termed these three regions the lower, middle and upper estuary, respectively.

Beach seines were used between February 1977 and December 1981 to sample fish at ten sites in the shallow waters of the Swan Estuary (Fig. 1). Sampling at five of these sites (2, 3, 4, 5, 6) commenced in February 1977, but did not begin at Sites 1 and 8 on the main axis of the Swan until January 1978 and at Sites 9, 10 and 11 in the Canning River until April 1978 (Fig. 1). Sites on the main axis of the Swan (1–6, 8) were sampled every two weeks in 1977 and 1978, monthly in 1979, and usually bimonthly in 1980 and 1981. Sites in the Canning River (9, 10, 11) were sampled monthly in 1978 and 1979 and then bimonthly until the end of the study (see Chubb et al. 1981 for full details of the sampling regime).

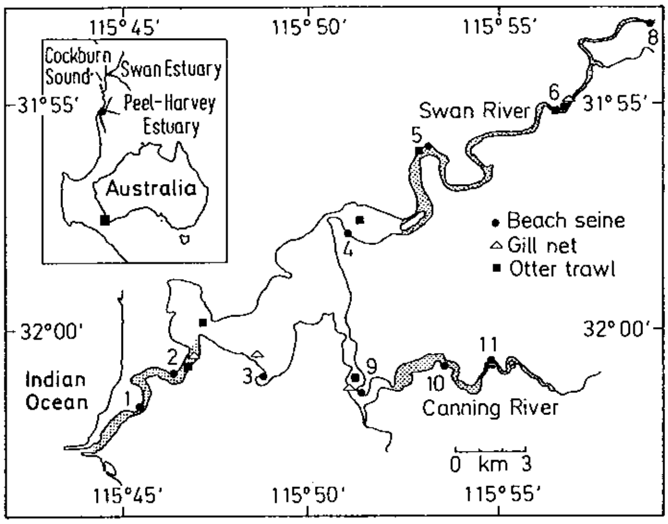

Fig. 1. Map showing location of beach seine, gill-net and otter-trawl sites in Swan Estuary. Lower and upper parts of estuary are shaded. Inset: location of Swan Estuary, south-western Australia

The beach seine used for sampling fish during 1977 was 102.5 m long, fished to a maximum depth of 2 m and swept a semi-circular area of 1 670 m^2. The stretch-mesh size of the wings and pocket of this net were 25.4 and 15.9 mm, respectively. While the seine used after January 1978 had the same mesh size and depth, it was longer (133 m) and therefore swept a greater area (2 815 m^2). Since various factors prevented the use of the full seine at Sites 1, 8 and 11, only half of this latter net was used at these sites, thus reducing the area swept to 704 m^2. Seining was carried out during the day, generally between 09.00 and 13.00 hrs.

Two composite gill nets, one sunken and one floating, were used to collect fish bimonthly between May 1978 and March 1979 from the more offshore waters of the Swan Estuary. Each gill net consisted of ten 20 m long panels of netting, ranging in stretch-mesh size from 38 to 102 mm in approximately 7 mm increments. Gill nets were set for 3 h, just after sunset, near Beach Seine Sites 2, 3, 6 and 9 (Fig. 1). The water depths at these four gill net sites were 16, 10, 3 and 3 m respectively.

An otter trawl was used to sample fish at monthly intervals from the deeper waters of the Swan Estuary between August 1977 and October 1980. This net was 5 m long and consisted of 51 and 25 mm mesh in the wings and pocket, respectively. When extended, the mouth of the trawl had a width of 2.6 m and a depth of 0.5 m. The warp and bridle lengths were 50 and 13 m, respectively. The trawl was towed by a 5.5 m boat at a speed of between 3 and 4 km h^{-1}. Two trawls of 5 min duration, covering a distance of approximately 250 to 300 m, were carried out during daylight close to Beach Seine Sites 2, 3, 4, 5, 6 and 9 (Fig. 1), where the water depths were 16, 13, 2, 3, 3 and 2 m, respectively.

It should be noted that as a result of net-selectivity, some species would have been under-represented in the samples obtained using the above three methods. For example, in gill nets (minimum mesh size = 38 mm), species which grow to a small maximum size (e.g. *Engraulis australis, Apogon rueppellii* and the atherinids) would not be caught as effectively as those which attain a larger size.

Biotic and environmental measurements

The total number of each species caught in each sample was recorded. The catches obtained by beach seines were expressed as numbers per 1 000 m^2 (subsequently referred to as density), whereas those taken in gill nets and otter trawls were calculated as numbers per 3 h and 5 min, respectively. The adjusted numbers (i.e., numbers per 1 000 m^2 in beach seines, or catch rates per 3 h and 5 min in gill nets and otter trawls, respectively) were used to calculate the percentage contribution of each species to the total catch in the system and each region of the Swan Estuary. The total length of all fish in each sample was measured to the nearest 1 mm, except when fish were damaged and when their numbers were large, in which case measurements were restricted to random subsample.

During the present study, it became clear that the Atherinidae and Gobiidae each contained an abundant and hitherto undescribed species (Prince et al. 1982a, Gill and Miller in press). The new species of atherinid, *Atherinosoma wallacei,* was initially grouped with *A. elongata, A. presbyteroides* and *Craterocephalus mugiloides,* whereas the new species of goby, *Papillogobius punctatus,* was included under *Favonigobius lateralis* (Prince et al. 1982b, Gill and Miller in press). [N.B. Two of the above atherinids, *A. wallacei* and *A. presbyteroides,* have now been placed in the genus *Leptatherina* (Pavlov et al. 1988)]. Since the numbers of *L. presbyteroides, L. wallacei, A. elongata* and *C. mugiloides* were not recorded separately until January 1979 (Prince et al. 1982b, Prince and Potter 1983), the proportions of each of these species taken in catches between January 1979 and December 1981 have been used to provide an approximate value for their abundance during the first two years of the study. The fact that *P. punctatus* occurs almost exclusively in the upper estuary, whereas *F. lateralis* is almost entirely confined to the lower estuary (Gill and Miller in press), has been used to estimate the numbers of these two species in the different regions of the estuary during the present study. Since *Pseudocaranx dentex* and *P. wrighti* have both been identified from the Swan, but were not recognized as distinct species during this study, they are referred to as *Pseudocaranx* spp.

Salinities and temperatures at the water surface, and in the case of gill netting and otter trawling also at the bottom of the water column, were recorded at the time of sampling. Monthly rainfall values were obtained from the Western Australian Bureau of Meteorology.

Life-cycle designations

Each species has been categorised as marine or estuarine (E) or anadromous (A) or freshwater (F). It should be noted, however, that some species in the estuarine category can also complete their life cycle in marine environments (Chubb et al. 1979, Prince et al. 1982b, Chrystal et al. 1985, Potter et al. 1986). The marine category was subdivided into marine stragglers (S), i.e., species which occur irregularly and in small numbers in the Swan Estuary, and marine estuarine-opportunists, i.e., species which are regularly found in numbers in the Swan estuary at some stage of their life cycle. The results of a detailed study of the ichthyoplankton of the Swan Estuary (Neira 1989, also Neira, Murdoch University, Western Australia personal communication) helped clarify which of the less well studied species spawned in the estuary. This work has shown that *Arenigobius bifrenatus* breeds in the estuary and should not therefore have been placed in the marine estuarine-opportunist category as it was in Potter et al. (in press). The relative contributions made by the number of individuals (after adjustment to a constant area swept for beach seines and duration of sampling for gill netting and otter trawling) in each life-cycle category to the ichthyofauna of the whole estuary and each of its three main component regions have been calculated.

Analysis of abundance data

Three-way analyses of variance (ANOVA) were used to ascertain whether the densities of each of the 15 most abundant species caught in beach seines differed amongst sites, seasons (autumn, winter, spring and summer) and years (autumn of one year to summer of the next). Like season and year, site was also considered as a fixed factor because sites were chosen as representative of different regions of the estuary. An unequal number of samples were present in each cell of the ANOVA. Because the distributions of the catch data were frequently skewed, the numerical data were log-transformed ($\log_{10}[N+1]$). Since Cochran's C test showed that the variance was still often heterogeneous, conclusions from the results of ANOVAs have concentrated on those cases where significance levels were less than 0.01. Where ANOVA showed a significant difference, an *a posteriori* Student-Newman-Keuls (SNK) test was used to determine which means were significantly different at the 0.05 level of probability (Underwood 1981). A similar approach was used to investigate whether the catch rates of the 10 most abundant species in gill nets varied with site and season, and likewise if the 5 most abundant species in otter trawls varied amongst site, season and year.

Results

Rainfall

Although there are no long-term historical data for salinity in the Swan Estuary, the seasonal and annual trends will obviously follow those of rainfall. The mean annual rainfall for the years between 1876 and 1986 was 871 mm. Based on the 111 yr mean values for each month, the wettest months

Table 1. Summary of data on surface salinity and temperature recorded at times when beach seining was carried out in Swan Estuary between February 1977 and December 1981. Distance: distance from estuary mouth; CV: coefficient of variation

Site and distance	Salinity (‰)			Temperature (°C)		
	mean	range	CV (%)	mean	range	CV (%)
Lower estuary						
1 (3 km)	32.1	4.9–38.0	19.4	20.3	13.8–26.5	17.0
2 (6 km)	29.8	3.0–38.0	25.6	20.2	13.5–27.2	19.3
Middle estuary						
3 (15 km)	28.4	3.2–39.6	30.6	20.4	11.8–30.0	24.7
9 (22 km)	19.5	0.7–36.7	63.2	18.7	11.3–27.0	25.6
4 (23 km)	24.0	2.2–35.7	44.4	20.9	11.7–30.0	20.7
Upper estuary						
10 (26 km)	14.3	0.3–33.4	78.8	19.3	11.2–30.1	28.2
5 (29 km)	18.4	0.8–34.1	56.3	21.3	11.7–30.5	23.2
11 (30 km)	5.5	0.3–30.3	145.9	19.4	11.0–30.0	29.0
6 (38 km)	11.6	0.8–28.2	65.8	20.5	13.2–30.0	24.4
8 (44 km)	8.6	0.6–24.4	72.7	19.9	12.3–28.0	24.8

were June, July and August (winter) and the driest were December, January and February (summer), the two periods contributing 56 and 4% to the total annual rainfall, respectively. The minimum and maximum annual rainfall in the years between 1940 and 1986 were 509 mm in 1940 and 1 340 mm in 1945. During the current study, the driest and wettest years were 1979 (560 mm) and 1978 (971 mm), respectively.

Salinity and temperature

The mean surface salinities between February 1977 and December 1981 decreased with increasing distance from the estuary mouth, the values ranging from 32.1‰ at Site 1 to 8.6 and 5.5‰ at Sites 8 and 11, respectively (Table 1). Mean salinities exceeded 19‰ at Sites 1–4 and 9, which were each located in either the lower or middle estuary and within 24 km of the estuary mouth. The highest individual salinity recorded in the system was the 39.6‰ measured at Site 3 in May 1978. Individual salinities less than 1‰ were recorded at Sites 5 and 6 and 8–11 during July and August of some years (Table 1). The coefficient of variation (CV) for surface salinity, which provides a measure of the seasonal fluctuations in salinity, increased markedly from the lower to upper estuary. Thus, the CVs for salinity at Sites 1 and 2 in the lower estuary were 19.4 and 25.6%, compared with values of between 56.3 and 145.9% at Sites 5 and 11 in the upper estuary (Table 1).

Mean temperatures in the Swan were relatively constant throughout the estuary, ranging from 18.7 °C at Site 9 to 21.3 °C at Site 5 (Table 1). The CVs showed much less variation among sites for temperature (range 17.0 to 29.0%) than for salinity. The lowest and highest individual temperatures were the 11.0 °C recorded at Site 11 in July 1981 and the 30.5 °C at Site 5 in January 1980. The seasonal trends shown by the monthly surface salinities and temperatures at the different sites during 1979 and 1980 are shown in Prince et al. (1982b).

Beach-seine catches

A total of 630 803 fish, representing 36 families and 71 species, were caught by beach seines in the shallows of the Swan Estuary between February 1977 and December 1981 (Table 2). After adjusting the numbers in each sample to a constant area (1 000 m^2), those of each of the 15 most abundant species contributed between 0.9 and 47.3% to the adjusted total catch and collectively accounted for >98% of that total (Table 2).

The clupeid *Nematalosa vlaminghi* was the most numerous species caught in beach seines, contributing 47.3% to the adjusted total number of fish (Table 2). Since adult *N. vlaminghi* feed in marine environments, and then migrate into the upper reaches of estuaries to spawn, this species has been termed semi-anadromous (Chubb and Potter 1984, 1986). For convenience, *N. vlaminghi* is referred to as anadromous in the present study. Five species of atherinids, comprising two marine species which utilize estuaries opportunistically (*Leptatherina presbyteroides* and *Atherinomorus ogilbyi*), and three species which in south-western Australia are largely or entirely confined to estuaries (*L. wallacei, Atherinosoma elongata* and *Craterocephalus mugiloides*), each ranked in the top 15 species (Prince et al. 1982b, Prince and Potter 1983, and present Table 2). The Terapontidae was represented by two abundant species, namely *Pelates sexlineatus* and *Amniataba caudavittatus*, which ranked fifth and eighth, respectively (Table 2). The former is a marine estuarine-opportunist, whereas the latter is rarely found outside estuaries in south-western Australia (Chubb et al. 1979, Potter et al. 1983, also Wallace and Potter, Murdoch University, Western Australia, unpublished data).

Although the mugilids *Mugil cephalus* (6th) and *Aldrichetta forsteri* (11th) are both marine estuarine-opportunists, juveniles of *M. cephalus* measuring 40 to 100 mm in length are rarely found in marine waters in south-western Australia and thus have a particularly strong preference for estuarine environments in this region (Chubb et al. 1981). The seventh most abundant species was the tetraodontid *Torquigener pleurogramma*, which in some years is found in very large numbers in the Swan Estuary (Potter et al. 1988). Although the Apogonidae is mainly a tropical/subtropical family (Lachner 1953), one of its species (*Apogon rueppellii*) ranked ninth. This species is capable of completing its life cycle within both estuaries and the protected inshore marine environments of south-western Australia (Chrystal et al. 1985). Two species of Gobiidae, namely *Favonigobius lateralis*, a marine estuarine-opportunist, and *Pseudogobius olorum*, which is confined to estuaries in south-western Australia (Gill and Miller in press, also Gill, Murdoch University, Western Australia, unpublished data), ranked 10th and 13th respectively. *Engraulis australis*, the 12th species by relative abundance, can spawn in both estuaries and protected inshore marine waters (Blackburn 1950, Arnott and McKinnon 1985).

The data in Table 2 show that the contribution made by each of the more abundant species to the catches taken in each of the three main regions of the estuary varies greatly. This feature, which reflects differences in the relative abundance of the various species at sites in the different regions of the estuary, and also the influence of season and years on density, is explored in greater detail in a subsequent section ("Site, seasonal and annual variation in catches").

The mean lengths of all but three of the 15 most abundant species caught in beach seines were less than 100 mm (Table 2). In the case of seven of these teleosts, this reflects the small maximum size attained by these species. Data on the growth of the three species with mean lengths exceeding 100 mm show that the relatively high mean length of *Nematalosa vlaminghi* (190 mm), *Torquigener pleurogramma* (160 mm) and *Amniataba caudavittatus* (126 mm) is in each case attributable to a relatively rapid growth rate and the presence of a number of age classes in the estuary (Chubb and Potter 1986, Potter et al. 1988, also Wallace and Potter, Murdoch University, Western Australia, unpublished data). The largest fish taken in beach seines was the sciaenid *Argyrosomus hololepidotus*, which measured 848 mm.

Gill-net catches

Gill nets set in the more offshore regions of the Swan Estuary between May 1978 and March 1979 yielded 2 651 fish, representing 18 families and 22 species (Table 3). The top ten species accounted for 94.2% of the adjusted total catch (Table 3). As with beach seines, the anadromous *Nematalosa vlaminghi* ranked first in gill nets, contributing 61.1% to the adjusted total. This teleost was also the most numerous species in each region of the estuary, accounting for 28.8% of the adjusted catches in the lower estuary, 33.5% in the middle and 86.7% in the upper estuary (Table 3). *Pelates sexlineatus*, *Mugil cephalus*, *Engraulis australis* and *Amniataba caudavittatus* also ranked in the top ten species in gill nets and were amongst the most numerous species caught in beach seines (Tables 2, 3).

Five of the 10 most abundant species caught in gill nets did not rank amongst the 15 most numerous species in beach seines (cf. Tables 2, 3). This group included the marine estuarine-opportunists *Cnidoglanis macrocephalus* and *Pomatomus saltatrix*, and the estuarine species *Plactycephalus endrachtensis* (Chubb et al. 1979, Potter et al. 1983, 1986, Nel et al. 1985, and present Table 3). It also included *Sardinella lemuru*, a species which is abundant in marine waters near the Swan (Hutchins and Swainston 1986), but was only numerous on isolated occasions in the Swan, and the *Pseudocaranx* complex. Until more is known of the respecitve contribution and biology of the two species of *Pseudocaranx*, they are also placed in the straggler category. This categorisation is consistent with the fact that fewer than 20 individuals of either *S. lemuru* or the *Pseudocaranx* complex were counted amongst the very large total catch of fish obtained by beach seines in the shallows (Table 2).

The mean lengths of all species caught in gill nets, except *Engraulis australis*, exceeded 100 mm. The smallest fish caught was a 65 mm *E. australis*, while the largest was a 1 210 mm *Argyrosomus hololepidotus*. The longest mean length recorded was the 604 mm for *A. hololepidotus* (Table 3).

The influence of site on catch rates in gill nets, which accounts for differences in the contributions of the different species to the catches in each region of the estuary (Table 3) is considered in detail together with the influence of season, in a later section ("Site, seasonal and annual variation in catches").

Otter-trawl catches

A total of 6 805 fish, representing 22 families and 33 species, were caught in otter trawls between August 1977 and October 1980 (Table 4). The estuarine-breeding *Apogon rueppellii* comprised 75.3% of the adjusted total catch and dominated the samples taken in both the lower (85.5%) and middle (78.9%) estuary (Table 4). Even in the upper estuary this species made a greater contribution (39.4%) than any other species. Only two other species, *Torquigener pleurogramma* and *Amniataba caudavittatus*, contributed more than 5% to the adjusted total catch obtained for the whole estuary.

The top five species in trawls accounted for 94.5% of the adjusted catch (Table 4). In contrast to the situation with the samples obtained by beach seines and gill nets, the anadromous *Nematalosa vlaminghi* made a relatively minor contribution (1.2%) to the adjusted total catch in otter trawls. The mean length of all but *Apogon rueppellii* of the five most abundant species exceeded 100 mm (Table 4).

Life-cycle categories

Although the number of beach-seine samples from the lower estuary (119) was less than those taken in either the middle (188) or upper estuary (267), the number of species recorded in this region (57) was greater than in either the middle (44) or upper estuary (33) (Tables 2, 5).

Samples collected by beach-seining throughout the Swan Estuary contained a high proportion (73.2%) of marine species (Table 5). Approximately 70% of the 52 marine species were stragglers from local coastal waters, the remaining 15 species being marine estuarine-opportunists. Although all but one of the estuarine-opportunistic species penetrated the middle estuary, most marine stragglers were confined to the lower estuary (Table 5). While all of the 14 species which complete their life cycles within the Swan were recorded in both the middle and upper regions of this system, three were never found in the lower estuary. The single anadromous species, *Nematalosa vlaminghi*, was caught in all three regions of the estuary. Three of the four freshwater species were collected only from the upper estuary.

Table 2. Numbers, total length and life-cycle category (S: marine stragglers; O: marine estuarine-opportunists; E: estuarine; A: anadromous; F: freshwater) of species caught in beach seines throughout Swan Estuary, and relative contribution of these species to the adjusted numbers in the whole estuary and its lower, middle and upper regions. Data are based on catches obtained between February 1977 and December 1981. The relative contributions were calculated from numbers in each sample after these had been adjusted to a constant area of 1 000 m^2. Dash indicates species not caught in that region

Rank	Species	Total catch		Percent (>0.1%)			Mean length (mm)	Length range (mm)	Life cycle
		no	%	lower	middle	upper			
1	*Nematalosa vlaminghi*	215 656	47.3	0.1	43.9	75.7	190	26–323	A
2	*Leptatherina presbyteroides*	65 605	14.4	47.1	1.0	<0.1	49	20– 80	O
3	*Leptatherina wallacei*	31 432	6.9	–	9.6	10.0	47	17– 87	E
4	*Atherinomorus ogilbyi*	24476	5.4	15.7	3.0	0.3	74	25–140	O
5	*Pelates sexlineatus*	19 797	4.3	13.6	0.9	0.2	62	12–225	O
6	*Mugil cephalus*	15 091	3.3	1.1	4.5	4.2	80	21–495	O
7	*Torquigener pleurogramma*	12 549	2.8	8.9	0.3	<0.1	160	30–230	O
8	*Amniataba caudavittatus*	11 783	2.6	0.1	10.6	1.4	126	15–288	E
9	*Apogon rueppellii*	10 950	2.4	2.4	5.9	1.2	45	12–101	E
10	*Favonigobius lateralis*	8 527	1.9	4.5	3.0	–	43	18– 75	O
11	*Aldrichetta forsteri*	7 766	1.7	3.5	2.4	0.4	99	22–380	O
12	*Engraulis australis*	7 086	1.6	<0.1	2.5	2.1	62	31–140	E
13	*Pseudogobius olorum*	6 077	1.3	0.1	2.1	1.8	36	15– 64	E
14	*Atherinosoma elongata*	6 046	1.3	0.9	6.0	<0.1	48	26– 79	E
15	*Craterocephalus mugiloides*	3 897	0.9	0.4	2.6	0.5	51	25– 66	E
16	*Acanthopagrus butcheri*	1 836	0.4	<0.1	0.1	0.7	170	23–490	E
17	*Papillogobius punctatus*	1 370	0.3	–	0.4	0.4	41	20– 72	E
18	*Arenigobius bifrenatus*	988	0.2	<0.1	0.7	0.2	77	23–150	E
19	*Hyperlophus vittatus*	986	0.2	0.3	0.5	0.1	50	33– 75	O
20	*Sillago maculata*	951	0.2	0.1	1.0	<0.1	96	29–180	O
21	*Spratelloides robustus*	859	0.2	0.6	–	–	56	52– 63	O
22	*Pomatomus saltatrix*	838	0.2	<0.1	0.1	0.3	111	47–256	O
23	*Gerres subfasciatus*	624	0.1	<0.1	0.6	0.1	85	18–193	O
24	*Gambusia affinis*	520	0.1	–	<0.1	0.2	32	13– 52	F
25	*Favonigobius suppositus*	392	<0.1	–	<0.1	0.2	45	18– 93	E
26	*Haletta semifasciata*	194	<0.1	0.1	<0.1	–	96	58–176	S
27	*Platycephalus endrachtensis*	117	<0.1	<0.1	0.1	<0.1	272	40–593	E
28	*Cnidoglanis macrocephalus*	64	<0.1	<0.1	0.1	<0.1	309	36–630	O
29	*Trachurus novaezelandiae*	63	<0.1	–	<0.1	<0.1	153	130–165	S
30	*Sillago schomburgkii*	62	<0.1	<0.1	<0.1	–	149	56–312	S
31	*Rhabdosargus sarba*	56	<0.1	<0.1	<0.1	<0.1	77	23–323	S
32	*Hyporhamphus regularis*	51	<0.1	<0.1	<0.1	<0.1	111	12–209	E
	Galaxias occidentalis	51	<0.1	–	–	<0.1	67	50– 93	F
34	*Meuschenia freycineti*	47	<0.1	<0.1	–	<0.1	47	20–146	S
35	*Gymnapistes marmoratus*	46	<0.1	<0.1	–	–	59	29– 96	S
36	*Scobinichthys granulatus*	31	<0.1	<0.1	–	–	40	22– 71	S
37	*Urocampus carinirostris*	29	<0.1	<0.1	<0.1	<0.1	66	53– 77	E
38	*Scorpis aequepinnis*	28	<0.1	<0.1	<0.1	–	49		S
39	*Pseudorhombus jenynsii*	23	<0.1	<0.1	<0.1	–	295	43–381	O
40	*Acanthaluteres brownii*	20	<0.1	<0.1	–	–	67	43– 82	S
41	*Sardinella lemuru*	19	<0.1	–	<0.1	–			S
42	*Contusus brevicaudus*	17	<0.1	<0.1	<0.1	–	111	66–202	S
43	*Sillaginodes punctatus*	13	<0.1	<0.1	<0.1	–	121	32–190	S
44	*Monacanthus chinensis*	12	<0.1	<0.1	–	–	83		S
45	*Pseudocaranx* spp.	10	<0.1	<0.1	<0.1	–	70	41–113	S
46	*Stigmatopora argus*	6	<0.1	<0.1	<0.1	–			S
47	*Enoplosus armartus*	5	<0.1	<0.1	–	–	44	32– 67	S
	Neoodax balteatus	5	<0.1	<0.1	–	–			S
49	*Ammotretis elongatus*	4	<0.1	<0.1	–	–	82	77– 87	S
50	*Parupeneus signatus*	3	<0.1	<0.1	–	–			S
	Carassius auratus	3	<0.1	–	–	<0.1			F
	Edelia vittata	3	<0.1	–	–	<0.1			F
53	*Pelsartia humeralis*	2	<0.1	<0.1	–	–	52	44– 65	S
	Eocallionymus papilio	2	<0.1	<0.1	–	–	68	63– 73	S
	Siphamia cephalotes	2	<0.1	<0.1	–	–	38	33– 42	S
	Sphyraena obtusata	2	<0.1	<0.1	–	–	108		S
	Cristiceps australis	2	<0.1	<0.1	–	–	95	95	S
	Tridentiger trigonocephalus	2	<0.1	<0.1	–	–	53		S
	Diodon nichthemerus	2	<0.1	<0.1	–	–	58	33– 85	S
	Callogobius mucosus	2	<0.1	–	<0.1	–	62		S
	Argyrosomus hololepidotus	2	<0.1	–	<0.1	–	631	330–848	O

Table 2 (continued)

Rank	Species	Total catch no	Total catch %	Percent (>0.1%) lower	Percent (>0.1%) middle	Percent (>0.1%) upper	Mean length (mm)	Length range (mm)	Life cycle
62	*Hippocampus angustus*	1	<0.1	<0.1	–	–			S
	Leviprora inops	1	<0.1	<0.1	–	–	155		S
	Histiogamphelus gallinaceus	1	<0.1	<0.1	–	–			S
	Lissocampus runa	1	<0.1	<0.1	–	–			S
	Leviprora laevigatus	1	<0.1	<0.1	–	–			S
	Arripes georgianus	1	<0.1	<0.1	–	–			S
	Neatypus obliquus	1	<0.1	<0.1	–	–	32		S
	Cynoglossus broadhursti	1	<0.1	–	<0.1	–	34		S
	Brachaluteres jacksonianus	1	<0.1	–	<0.1	–	57		S
	Eubalichthys mosaicus	1	<0.1	–	<0.1	–			S
Total									
	adjusted no. of fish	455 723		137 398	80 154	238 171			
	actual no. of fish	630 803		138 906	205 861	286 036			
	No. of species	71		57	44	33			
	No. of samples	574		119	188	267			

Table 3. Numbers, total length and life-cycle category of species caught in gill nets throughout Swan Estuary and relative contribution of these species to the adjusted numbers in the whole estuary and its lower, middle and upper regions. Data are based on catches obtained between May 1978 and March 1979. The relative contributions were calculated from numbers in each sample after these had been adjusted to a constant sampling time of 3 h. Abbreviations as in Table 2

Rank	Species	Total catch *N*	Total catch %	Percent (>0.1%) lower	Percent (>0.1%) middle	Percent (>0.1%) upper	Mean length (mm)	Length range (mm)	Life cycle
1	*Nematalosa vlaminghi*	1 287	61.1	28.8	33.5	86.7	203	89– 361	A
2	*Sardinella lemuru*	142	6.7	10.5	17.6	–	168	133– 199	S
3	*Pelates sexlineatus*	103	4.9	11.2	10.0	–	174	129– 257	O
4	*Cnidoglanis macrocephalus*	86	4.1	18.7	0.7	0.2	322	147– 580	O
5	*Mugil cephalus*	79	3.7	0.5	8.5	2.7	301	144– 543	O
6	*Pomatomus saltatrix*	63	3.0	5.6	6.0	0.6	248	126– 415	O
7	*Platycephalus endrachtensis*	62	2.9	9.1	3.8	0.1	348	93– 580	E
8	*Engraulis australis*	60	2.8	0.5	8.2	1.1	85	65– 97	E
9	*Amniataba caudavittatus*	59	2.8	–	1.3	4.6	209	123– 285	E
10	*Pseudocaranx* spp.	45	2.1	8.2	1.8	–	195	131– 246	S
11	*Aldrichetta forsteri*	28	1.1	0.2	3.3	0.8	246	168– 372	O
12	*Acanthopagrus butcheri*	25	1.2	–	0.4	2.1	290	102– 408	E
13	*Argyrosomus hololepidotus*	21	1.0	0.2	1.3	1.2	604	200–1210	O
14	*Trachurus novaezelandiae*	19	0.9	3.0	1.1	–	153	130– 179	S
15	*Torquigener pleurogramma*	16	0.8	1.9	1.6	–	160	81– 170	O
16	*Apogon rueppellii*	4	0.2	0.5	0.5	–	102	97– 108	E
17	*Gerres subfasciatus*	3	0.1	–	0.5	–	184	150– 208	O
18	*Pseudorhombus jenynsii*	2	0.1	0.5	–	–	232	178– 333	O
19	*Sillago maculata*	1	<0.1	0.2	–	–	158		O
	Scobinichthys granulatus	1	<0.1	–	0.2	–			S
	Chelidonichthys kumu	1	<0.1	0.2	–	–			S
	Atherinomorus ogilbyi	1	<0.1	–	0.2	–	149		O
Total									
	adjusted no. of fish	2 108		427	552	1 129			
	actual no. of fish	2 651		518	656	1 477			
	no. of species	22		17	19	11			
	no. of samples	27		7	13	7			

Marine estuarine-opportunists contributed 34.5% to the adjusted total numbers of individuals caught in the shallows of the Swan Estuary, compared with only 0.3% by the marine stragglers (Table 5). The contribution of the marine estuarine-opportunists to the adjusted total catches in the different regions declined progressively from 94.8% in the lower estuary to 17.2 and 5.6% in the middle and upper estuary respectively. The anadromous category (*Nematalosa vlaminghi*) exhibited the reverse trend, with as much as 75.7% of the adjusted total catch in the upper estuary being

Table 4. Numbers, total length and life-cycle category of species caught in otter trawls throughout Swan Estuary, and relative contribution of these species to the adjusted numbers in the whole estuary and its lower, middle and upper regions. Data are based on catches obtained between August 1977 and October 1980. The relative contributions were calculated from numbers in each sample after these had been adjusted to a constant sampling time of 5 min. Abbreviations as in Table 2

Rank	Species	Total catch		Percent (>0.1%)			Mean length (mm)	Length range (mm)	Life cycle
		N	%	lower	middle	upper			
1	*Apogon rueppellii*	7 202	75.3	85.5	78.9	39.4	65	24–106	E
2	*Torquigener pleurogramma*	784	8.2	2.0	11.7	0.1	168	132–214	O
3	*Amniataba caudavittatus*	498	5.2	–	1.2	35.0	179	69–270	E
4	*Platycephalus endrachtensis*	287	3.0	5.2	2.0	4.8	289	142–560	E
5	*Cnidoglanis macrocephalus*	266	2.8	<0.1	3.1	5.5	329	97–720	O
6	*Pseudorhombus jenynsii*	120	1.3	3.8	0.7	–	197	87–350	O
7	*Nematalosa vlaminghi*	118	1.2	–	0.1	9.1	122	68–264	A
8	*Pelates sexlineatus*	57	0.6	–	0.7	1.0	134	77–264	O
9	*Pseudogobius olorum*	44	0.5	–	0.6	0.8	43	22– 60	E
10	*Acanthopagrus butcheri*	39	0.4	–	0.1	2.9	143	86–311	E
11	*Monacanthus chinensis*	23	0.2	1.1	–	–	133	65–223	S
	Gerres subfasciatus	23	0.2	–	0.3	0.4	76	42–176	O
13	*Callionymus goodladi*	19	0.2	0.9	<0.1	–	122	84–162	O
14	*Argyrosomus hololepidotus*	18	0.2	<0.1	0.2	0.6	203	61–308	O
15	*Pseudocaranx* spp.	16	0.2	0.3	0.1	–	92	48–231	S
16	*Sillago maculata*	9	0.1	0.1	0.1	–	123	110–139	O
17	*Scobinichthys granulatus*	5	0.1	0.2	<0.1	–	99	89–114	S
18	*Cynoglossus broadhursti*	4	<0.1	0.2	–	–	142	133–155	S
19	*Gymnapistes marmoratus*	3	<0.1	0.1	–	–	95	83–130	S
	Favonigobius lateralis	3	<0.1	–	<0.1	–	40	36– 48	O
	Arenigobius bifrenatus	3	<0.1	–	<0.1	0.1	106	86–128	E
22	*Mugil cephalus*	2	<0.1	–	<0.1	<0.1	200	192–208	O
	Brachaluteres jacksonianus	2	<0.1	<0.1	–	–	81	52–110	S
	Hyperlophus vittatus	2	<0.1	–	<0.1	–	40	38– 42	O
	Engraulis australis	2	<0.1	–	<0.1	–	50	49– 51	E
	Trachurus novaezelandiae	2	<0.1	–	<0.1	–	204	145–263	S
	Aldrichetta forsteri	2	<0.1	–	<0.1	–			O
28	*Eucallionymus papilio*	1	<0.1	<0.1	–	–	101		S
	Eubalichthys mosaicus	1	<0.1	<0.1	–	–	100		S
	Pomatomus saltatrix	1	<0.1	–	–	0.1			O
	Leviprora laevigatus	1	<0.1	<0.1	–	–	161		S
	Leptatherina presbyteroides	1	<0.1	–	<0.1	–			O
	Leptatherina wallacei	1	<0.1	–	–	<0.1	48		E
Total									
	adjusted no. of fish	9 562		2 015	6 350	1 197			
	actual no. of fish	6 805		1 980	2 938	1 167			
	no. of species	33		19	25	16			
	no. of samples	488		48	234	156			

attributable to this species. Those fish species which complete their life cycle in the estuary (estuarine) contributed a far higher proportion to the total catches in the middle (38.9%) and upper estuary (18.5%) than to the total catch in the lower estuary (4.0%). The relative contribution by numbers of freshwater species, even in the upper estuary, was only 0.2%.

Although the proportion of species caught in gill nets which came from marine waters (72.7%) was similar to that in beach seines, the contribution of marine estuarine-opportunists (50.0%) was far higher (Table 6). The contribution of estuarine species to the total number of species in the whole system (22.7%) and each of the regions (17.6 to 40.0%) was similar to that recorded in beach seines (cf. Tables 5, 6).

Marine stragglers, as well as marine estuarine-opportunists, contributed between 20.6 and 39.0% to the adjusted total gill-net catch in the lower and middle estuary (Table 6). The single anadromous species accounted for 61.1% of the adjusted total catch in the whole system and dominated catches in the upper estuary (86.7%). The contributions of individuals in the estuarine category ranged from 7.8% in the upper to 14.1% in the middle estuary.

The trends shown by the number of species in the various life-cycle categories caught in otter trawls throughout the estuary and within its three main regions were similar in many respects to those obtained with beach seines (cf. Tables 5, 7). Thus, marine species were the dominant group, and of these the estuarine-opportunists tended to penetrate further upstream than the stragglers. Likewise, the number of estuarine species recorded in both the middle and upper estuary (7 in each case) was greater than in the lower estuary (3).

The numbers of individuals of the estuarine category caught in otter trawls contributed over 82% to the adjusted catches in all three regions of the estuary (Table 7).

Table 5. Numbers of species and individuals and percentage contribution of each life-cycle category to total numbers recorded in beach seines in Swan Estuary between February 1977 and December 1981. The relative contributions were calculated from numbers in each sample after these had been adjusted to a constant sampling area of 1 000 m^2

Life-cycle category	Whole estuary		Region of estuary					
			lower		middle		upper	
	N	%	*N*	%	*N*	%	*N*	%
Species								
stragglers	37	52.1	31	54.4	14	31.8	3	9.1
opportunists	15	21.1	14	24.6	14	31.8	11	33.3
estuarine	14	19.7	11	19.3	14	31.8	14	42.4
anadromous	1	1.4	1	1.8	1	2.3	1	3.0
freshwater	4	5.6	0	0.0	1	2.3	4	12.1
total	71		57		44		33	
Individuals								
stragglers	1 526	0.3	1 397	1.0	65	0.1	64	<0.1
opportunists	157 296	34.5	130 317	94.8	13 747	17.2	13 228	5.6
estuarine	80 668	17.7	5 535	4.0	31 152	38.9	43 980	18.5
anadromous	215 656	47.3	149	0.1	35 189	43.9	180 323	75.7
freshwater	577	<0.1	0	0.0	1	<0.1	576	0.2
adjusted total	455 723		137 398		80 154		238 171	

Table 6. Numbers of species and individuals and percentage contribution of each life-cycle category to total numbers recorded in gill nets in Swan Estuary between May 1978 and March 1979. The relative contributions were calculated from numbers in each sample after these had been adjusted to a constant sampling time of 3 h

Life-cycle category	Whole estuary		Region of estuary					
			lower		middle		upper	
	N	%	*N*	%	*N*	%	*N*	%
Species								
stragglers	5	22.7	4	23.5	4	21.1	0	0.0
opportunists	11	50.0	9	52.9	9	47.4	5	50.0
estuarine	5	22.7	3	17.6	5	26.3	4	40.0
anadromous	1	4.5	1	58.8	1	5.3	1	10.0
total	22		17		19		10	
Individuals								
stragglers	208	9.9	94	22.1	114	20.6	1	0.1
opportunists	403	19.1	166	39.0	176	31.8	61	5.4
estuarine	210	10.0	43	10.1	78	14.1	88	7.8
anadromous	1 287	61.1	123	28.9	185	33.5	979	86.7
adjusted total	2 108		426		553		1 129	

Site, seasonal and annual variation in catch rates

Beach seines

Three-way ANOVAs showed that the mean density of each of the 15 most numerous species in beach seines differed significantly amongst sites ($P<0.001$, Table 8). Furthermore, for 11 of the species, the mean square for site in these ANOVAs was greater than those for season and year (Table 8). At the 99% level, the density of each species, except those of *Leptatherina presbyteroides*, *L. wallacei*, *Engraulis australis* and *Atherinosoma elongata*, also differed significantly amongst seasons. Year was a significant factor at $P<0.01$ for all species, except *L. presbyteroides*, *Favonigobius lateralis*, *Aldrichetta forsteri*, *L. wallacei* and *Atherinosoma elongata*. The site × season, site × year and season × year interaction terms were significant at $P<0.01$ for 11, 8 and 5 species, respectively, whereas the site × season × year interaction term was significant at $P<0.01$ for only *Torquigener pleurogramma*. The mean squares for the interaction terms were always much lower than those for the most highly significant main effect (Table 8). When the sums of squares for each term in the ANOVA was expressed as a percentage of the total variation, the contribution of the main effects was greater than that due to the interactions in the case of all species except *E. australis* and *Craterocephalus mugiloides*.

Table 7. Numbers of species and individuals and percentage contribution of each life-cycle category to total numbers recorded in otter trawls in Swan Estuary between August 1977 and October 1980. The relative contributions were calculated from numbers in each sample after these had been adjusted to a constant sampling time of 5 min

Life-cycle category	Whole estuary		Region of estuary					
			lower		middle		upper	
	N	%	*N*	%	*N*	%	*N*	%
Species								
stragglers	10	30.3	9	50.0	4	16.0	0	0.0
opportunists	14	42.4	6	33.3	13	52.0	8	50.0
estuarine	8	24.2	3	16.7	7	28.0	7	43.8
anadromous	1	3.0	0	0.0	1	4.0	1	6.3
total	33		18		25		16	
Individuals								
stragglers	79	0.8	65	3.2	14	0.2	0	0.0
opportunists	1 291	13.5	122	6.1	1 075	16.9	95	7.9
estuarine	8 074	84.4	1 826	90.7	5 253	82.7	993	83.0
anadromous	118	1.2	0	0.0	8	0.1	109	9.1
adjusted total	9 562		2 013		6 350		1 197	

Table 8. Mean squares and significance levels for three-way ANOVAs of densities of 15 most abundant species caught in beach seines in Swan Estuary between February 1977 and December 1981. N. B.: Taxonomic difficulties early in the study (see "Materials and methods – Biotic and environmental measurements") restricted analysis of all atherinid data (×), except those for *Atherinomorus ogilbyi*, to the period between March 1979 and November 1981. DF: degrees of freedom

Species	Main effects			2-way interactions			3-way interaction	Residual
	Site (S) (9 DF) (9 DF ×)	Season (Se) (3) (3)	Year (Y) (4) (2)	S × Se (27) (27)	S × Y (32) (18)	Se × Y (11) (5)	S × Se × Y (83) (45)	(385) (146)
Opportunists								
Leptatherina presbyteroides (×)	9.68***	0.54	0.01	0.30	0.23	0.38	0.26	0.21
Atherinomorus ogilbyi	5.36***	1.36**	2.17***	0.71***	0.37	0.44	0.40*	0.28
Pelates sexlineatus	3.81***	3.59***	0.74**	0.80***	0.92***	0.24	0.19	0.21
Mugil cephalus	5.34***	8.54***	2.42***	0.58*	0.43	1.12***	0.32	0.33
Torquigener pleurogramma	17.42***	0.60***	1.50***	0.30***	0.76***	0.38***	0.22***	0.10
Favonigobius lateralis	18.26***	1.78***	0.12	0.31***	0.24***	0.16	0.14	0.11
Aldrichetta forsteri	4.50***	1.24**	0.77*	0.82***	0.44**	0.75***	0.30	0.23
Estuarine								
Leptatherina wallacei (×)	9.19***	0.87*	1.22*	0.51*	0.55**	0.56	0.33	0.27
Amniataba caudavittatus	1.86***	9.52***	1.21**	0.55***	0.35	0.22	0.21	0.24
Apogon rueppellii	8.47***	7.93***	1.80***	0.76***	0.76***	0.55**	0.31*	0.21
Engraulis australis	1.48***	0.63*	1.13***	0.57***	0.49***	0.19	0.20	0.21
Pseudogobius olorum	3.53***	6.28***	1.50***	0.46***	0.50***	0.52**	0.22	0.19
Atherinosoma elongata (×)	2.78***	0.23	0.15	0.29**	0.19	0.13	0.13	0.14
Craterocephalus mugiloides (×)	1.58***	1.50***	1.54**	0.33	0.45*	0.27	0.23	0.22
Anadromous								
Nematalosa vlaminghi	25.83***	39.63***	4.52***	2.97***	0.95*	1.28*	0.63	0.62

* $=P<0.05$; ** $=P<0.01$; *** $=P<0.001$

Since ANOVAs showed that the densities of most species were influenced to a greater degree by the main effects than by the interactions and that site was usually the most important of these effects, the trends shown by the geometric mean densities have been investigated at each site over the entire sampling period. The mean densities of six of the marine-estuarine opportunist species were greatest at either Site 1 or Site 2 in the lower estuary and declined with distance upstream from the estuary mouth (Fig. 2). *Mugil cephalus* was the only abundant estuarine-opportunist to differ from this pattern, with the highest mean densities of this species being recorded at Sites 8 and 11 in the upper estuary (Fig. 2). Maximum mean densities for the abundant estuarine-opportunists in beach seines ranged from 5.8 fish per 1 000 m^2 for *Pelates sexlineatus* at Site 2 to 57.3 fish per 1 000 m^2 for *Leptatherina presbyteroides* at Site 1 (Fig. 2). The greatest

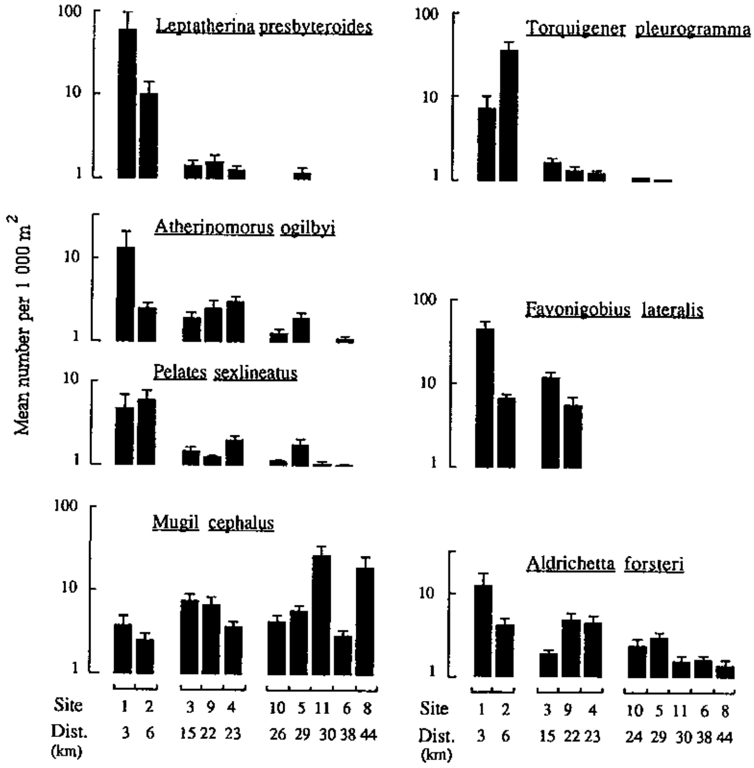

Fig. 2. Geometric mean densities (± 1 SE) of seven most abundant marine estuarine-opportunist species taken in beach seines at the ten sampling sites in Swan Estuary between February 1977 and December 1981. Dist.: distance from estuary mouth

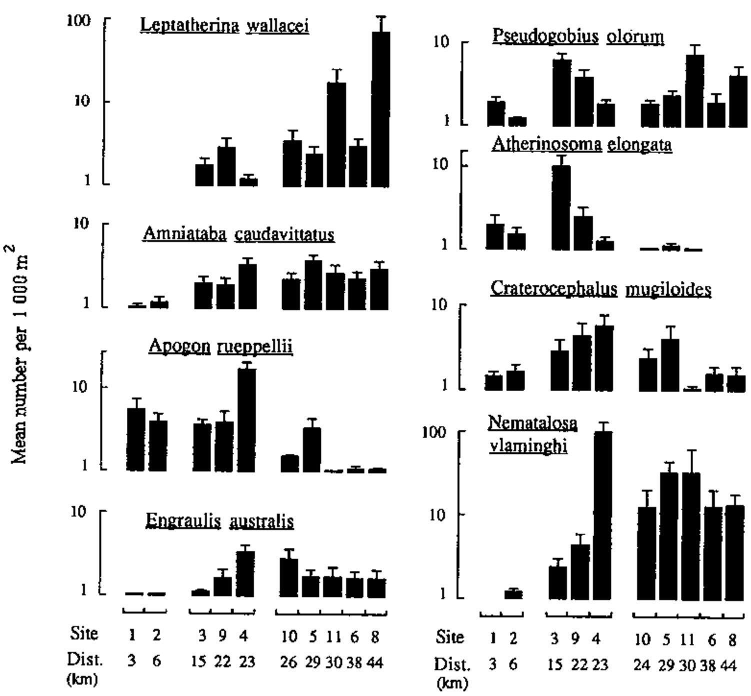

Fig. 3. Geometric mean densities (± 1 SE) of seven most abundant estuarine species and anadromous *Nematalosa vlaminghi* taken in beach seines at the ten sampling sites in Swan Estuary between February 1977 and December 1981. Dist.: distance from the estuary mouth

single density of an opportunist was the 6 250 fish per 1 000 m^2 recorded for *Atherinomorus ogilbyi* at Site 1 in June 1978.

In contrast to the trends shown by the geometric mean densities for the marine estuarine-opportunistic species, the highest mean densities for the abundant estuarine species and the anadromous *Nematalosa vlaminghi*, were recorded at sites in the middle and upper estuary (Fig. 3). Furthermore, the mean densities of all these species, except *Apogon rueppellii*, were low in the lower estuary. The highest individual density recorded for any of these species was the 36 244 fish per 1 000 m^2 of *N. vlaminghi* taken at Site 11 in May 1979. Maximum mean densities for the estuarine and anadromous species ranged from 3.3 fish per 1 000 m^2 for

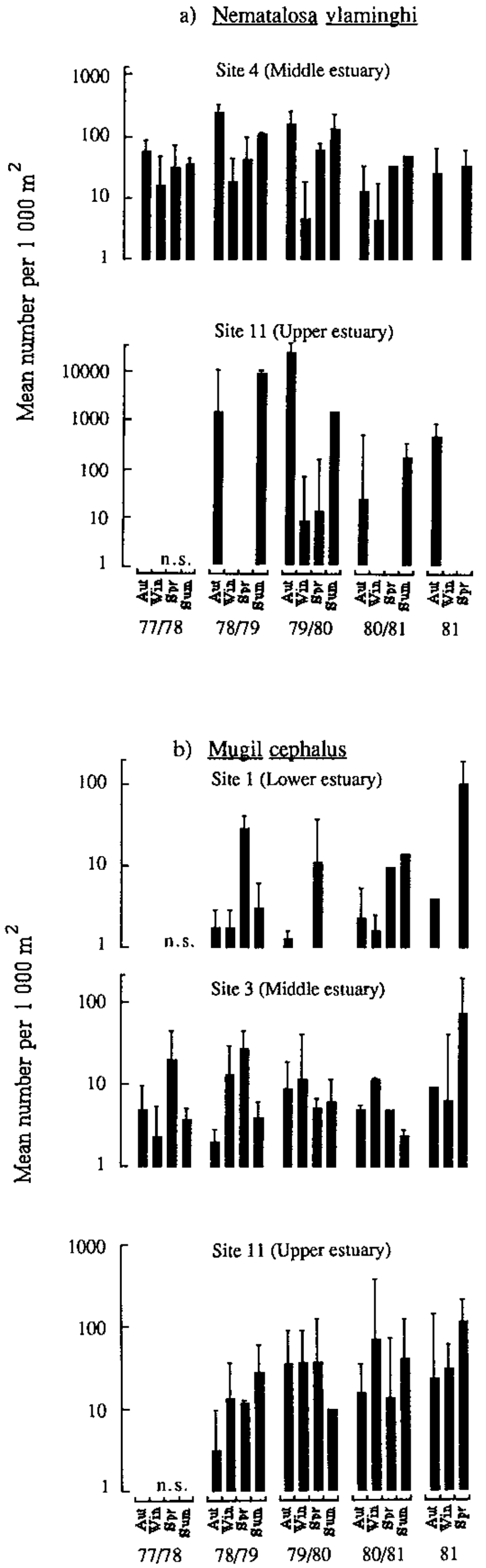

Fig. 4. *Nematalosa vlaminghi* (a) and *Mugil cephalus* (b). Geometric mean density (± 1 SE) in different seasons at Sites 4 and 11 (a) and 1, 3 and 11 (b) in Swan Estuary between March 1977 and November 1981. n.s.: not sampled (see "Materials and methods – Sampling Regime" for details

Engraulis australis at Site 4 to 97.1 fish per 1 000 m^2 for *N. vlaminghi* at the same site (Fig. 3).

The mean squares for season exceeded or were similar to those for site for only *Pelates sexlineatus, Mugil cephalus, Amniataba caudavittatus, Apogon rueppellii, Pseudogobius olorum, Craterocephalus mugiloides* and *Nematalosa vlaminghi* (Table 8). Seasonal changes were most pronounced for *N. vlaminghi* at Site 11 (Fig. 4a), where the SNK test showed that the densities in summer and autumn (overall means for these seasons = 1 126 and 925 fish per 1 000 m^2, respectively) were significantly greater than in spring and winter (overall means = 2.3 and 1.8 fish per 1 000 m^2, respectively). Similar seasonal changes were recorded for *N. vlaminghi* at the other sites in the upper estuary. Seasonal differences were less marked for this species at Site 4 in the middle estuary (Fig. 4a), but catches in autumn, spring and summer (range of means = 96.7 to 252 fish per 1 000 m^2, respectively) were significantly higher than in winter (overall mean = 17.1 fish per 1 000 m^2). The mean densities of *Pelates sexlineatus* at Sites 1 and 2, *Amniataba caudavittatus* at Sites 4, 5 and 10, and *Apogon rueppellii* at Sites 2, 3, 4 and 9, were also significantly greater in either summer or autumn than in winter or spring.

The SNK test showed that the mean density of *Mugil cephalus* at Site 1 in the lower estuary was significantly higher in spring (25.2 fish per 1 000 m^2) than in the other three seasons (range of means = 1.5 to 2.6 fish per 1 000 m^2) and at Site 3 was significantly greater in the spring (18.8 fish per 1 000 m^2) than in both summer and autumn (4.0 and 4.2 fish per 1 000 m^2) (Fig. 4b). The density of *M. cephalus* did not differ significantly, however, amongst Seasons at Site 11 in the upper estuary (Fig. 4b). The mean density of *Pseudogobius olorum* at Sites 3 and 11 was significantly greater in spring than in autumn and winter.

The mean square for year was always less than for either site or season and frequently for both (Table 8). It was the second most important main factor in the ANOVAs for *Atherinomorus ogilbyi, Torquigener pleurogramma, Leptatherina wallacei, Engraulis australis* and *Craterocephalus mugiloides*. However, year was not a significant factor for *L. wallacei* at $P < 0.01$. The density of *A. ogilbyi* at Site 1 was significantly lower in 1978/1979 than in other years, whereas densities of *T. pleurogramma* at Sites 1 and 2 were significantly greater in 1977/1978 and 1980/1981 than in other years (see also Potter et al. 1988). The densities of *C. mugiloides* at Sites 3, 4, and 9 were significantly lower in 1981 than in 1979/1980 and 1980/1981, while densities of *E. australis* at Sites 4, 5 and 10 were significantly lower in 1977/1978 than in other years.

Gill nets

Catch rates of the ten most numerous species caught at the four gill net sites between May 1978 and March 1979 are shown in Fig. 5. The relatively small number of occasions when site and season were significant for the catch rates of the marine estuarine-opportunists and estuarine species

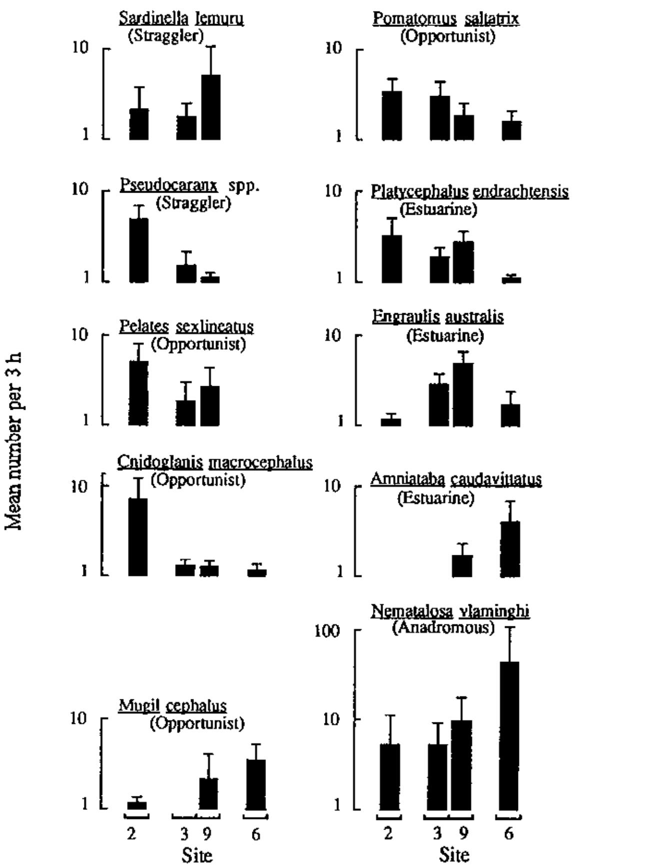

Fig. 5. Geometric mean catch rates (±1 SE) of ten most abundant species caught in gill nets at the four sampling sites in Swan Estuary between May 1978 and March 1979

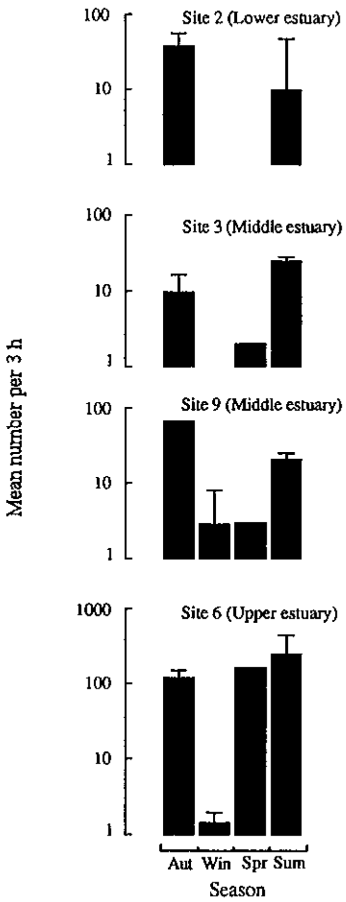

Fig. 6. *Nematalosa vlaminghi.* Geometric mean catch rates (±1 SE) in different seasons in gill nets at the four sampling sites in Swan Estuary between May 1978 and March 1979

(Table 9) may be related to a combination of the inherent variability in these catch rates and the relatively small number of samples collected using this method. However, the catch rates of the marine estuarine-opportunist *Cnidoglanis macrocephalus*, differed significantly amongst sites ($P<0.001$, Table 9), with higher mean catch rates being recorded in the lower estuary than at sites in either the middle or upper estuary (Fig. 5). Catch rates of the anadromous *Nematalosa vlaminghi* in gill nets also differed significantly amongst sites, with greater catch rates at Site 6 in the upper estuary (43.3 fish per 3 h) than at Sites 2, 3 and 4 further downstream, where the means ranged from 5.2 to 9.4 fish per 3 h (Table 9, Fig. 5). The mean square for season for *N. vlaminghi* was higher, however, than for sites (Table 9). The mean catch rates of this species at each site were higher in summer and autumn than in winter (Fig. 6). The significant effect of site and season and the significant site × season interaction on the catch rates of the marine straggler *Sardinella lemuru*, reflect the absence of this species from gill nets set in the upper estuary and the restriction of this species to the winter and spring in the lower estuary and the spring and summer in the middle estuary.

Table 9. Mean squares and significance levels for two-way ANOVAs of catch rates of ten most abundant species taken in gill nets between May 1978 and March 1979

Species	Main effects		2-way interaction	Residual
	Site (S) (3 DF)	Season (Se) (3)	S × Se (9)	(11)
Stragglers				
Sardinella lemuru	0.54**	0.30**	0.56***	0.04
Pseudocaranx spp.	0.67*	0.11	0.03	0.11
Opportunists				
Pelates sexlineatus	0.61*	0.21	0.28	0.16
Cnidoglanis macrocephalus	1.01***	0.30***	0.16**	0.02
Mugil cephalus	0.34	0.16	0.20	0.13
Pomatomus saltatrix	0.17	0.14	0.13	0.14
Estuarine				
Platycephalus endrachtensis	0.29	0.14	0.08	0.14
Engraulis australis	0.47*	0.08	0.08	0.11
Amniataba caudavittatus	0.56*	0.22	0.12	0.10
Anadromous				
Nematalosa vlaminghi	1.30**	3.51***	0.32	0.16

* $=P<0.05$; ** $=P<0.01$; *** $=P<0.001$

Table 10. Mean squares and significance levels for three-way ANOVAs of catch rates of five most abundant species taken in otter trawls between September 1977 and August 1980

Species	Main effects			2-way interactions			3-way interaction	Residual
	Site (S) (5 DF)	Season (Se) (3)	Year (Y) (3)	S × Se (15)	S × Y (15)	Se × Y (5)	S × Se × Y (25)	(314)
Opportunists								
Torquigener pleurogramma	0.44***	0.13	0.28**	0.08	0.07	0.16**	0.13***	0.05
Cnidoglanis macrocephalus	0.28***	0.15*	0.10	0.07	0.05	0.07	0.04	0.05
Estuarine								
Apogon rueppellii	9.56***	2.45***	1.38***	1.13***	0.36	1.20***	0.43*	0.24
Amniataba caudavittatus	0.78***	0.20**	0.05	0.08**	0.05	0.04	0.04	0.04
Platycephalus endrachtensis	0.56***	0.12*	0.36***	0.12***	0.06	0.11**	0.06*	0.04

* = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$

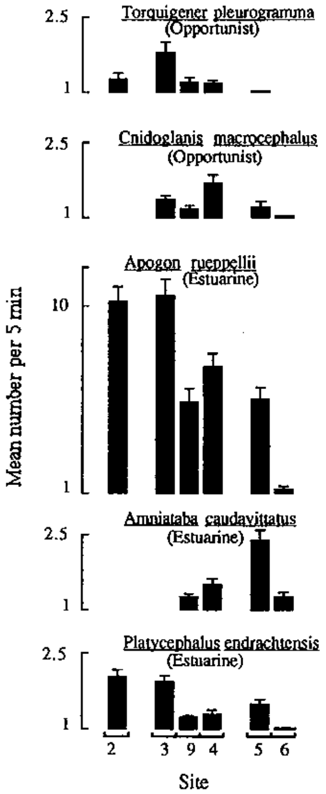

Fig. 7. Geometric mean catch rates (±1 SE) of the five most abundant species caught in other trawls at the six sampling sites in Swan Estuary between August 1977 and October 1980

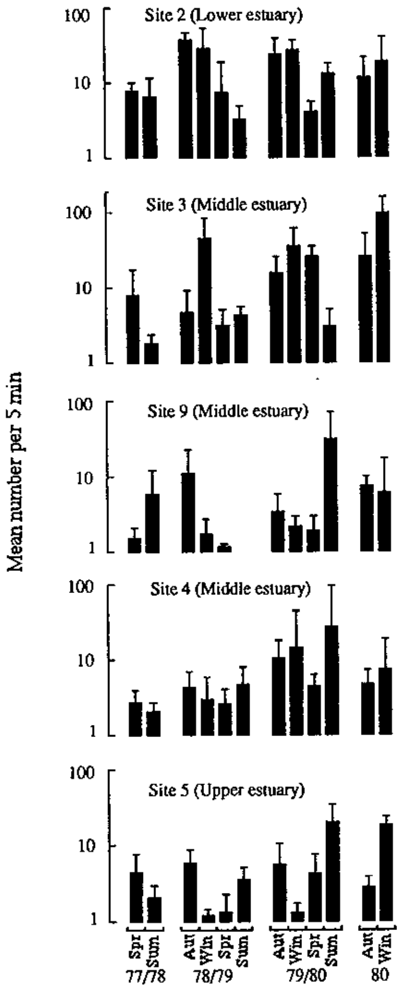

Fig. 8. *Apogon rueppellii*. Geometric mean catch rates (±1 SE) in different seasons at five otter trawl sampling sites in Swan Estuary between September 1977 and August 1980

Otter trawls

The catch rates of the five most abundant species caught in otter trawls differed significantly amongst sites ($P<0.001$, Table 10). While season and year were also significant at the 0.01 level for two and three species respectively, the mean square for these factors were always lower than for site. The highest mean catch rates for all species except *Amniataba caudavittatus* were recorded at sites in the middle or lower estuary (Fig. 7). Catch rates of by far the most abundant species in otter trawls, *Apogon rueppellii*, also differed amongst seasons, with higher catch rates being recorded at Sites 2 and 3 in the winter than in the summer (Fig. 8). No significant seasonal pattern of change was recorded at Sites 4, 5 and 9 (Fig. 8).

Discussion and conclusions

Contribution of marine species

The extensive data obtained by beach-seining at ten sites throughout the Swan Estuary at regular intervals over 5 yr show that large numbers of teleosts are present in the shallows of this large temperate system in south-western Australia. Although 73.2% of the 71 species came from marine waters, less than a third of these entered the estuary in sufficient regularity and numbers to be regarded as marine estuarine-opportunists. The marine straggler and marine estuarine-opportunist life cycle categories thus comprised 52.1 and 21.1%, respectively, of the total number of species caught in the shallows of the Swan Estuary. The above contribution of marine species to the total number of species caught in the Swan is very similar to that recorded for the ichthyofauna in the large Severn Estuary in the United Kingdom. Thus, on the basis of samples from three sites in the Severn Estuary, which were also collected regularly over a 5 yr period, the marine stragglers and marine estuarine-opportunists in that system comprised 52.8 and 18.0% of the 89 species caught, respectively (Claridge et al. 1986). From samples taken throughout temperate, subtropical and tropical South Africa (Wallace et al. 1984), 48.5% of the fish species found in the estuaries of that large region would be categorised as marine stragglers and a further 33.5% would be marine estuarine-opportunists. The above percentage contribution of stragglers is far lower, however, than the 71.4% recently estimated for estuaries in just the temperate regions of southern Africa (Potter et al. in press). The higher contribution of stragglers in the latter study can be attributed to the incorporation of extensive museum records for fish in estuaries, which increased the number of rare species but not opportunists. When a similar approach was adopted for estuaries throughout south-western Australia, a similar high value of 68.0% was obtained for the contribution of marine stragglers (Potter et al. in press). The increase in the number of marine stragglers provided by the use of museum and fisheries records accounts for the relatively low contribution of marine estuarine-opportunists estimated in the latter review of fish in the estuaries of temperate South Africa (12.2%) and south-western Australia (13.4%).

The studies of Wallace et al. (1984) in southern Africa indicated that the juveniles of 22 species of marine teleost were found only in the estuaries of this region and were thus concluded to be "dependent" on estuarine habitats as nursery areas. By contrast, in south-western Australia the juveniles of only one marine species (*Mugil cephalus*), which is abundant in estuaries and is not also found in local inshore coastal waters, could similarly be regarded as dependent on estuaries (Chubb et al. 1981, Lenanton and Potter 1987, Potter et al. in press). The considerable number of species which as juveniles are found only in estuaries in southern Africa has been attributed to the relative shortage of protected inshore marine areas in this region (Potter et al. in press). However, the coastal waters near the mouth of the Swan Estuary contain an abundance of detached macrophytes which provide extensive alternative nursery areas and these waters are also sheltered by a fringing limestone reef (Lenanton et al. 1982, Lenanton and Caputi 1989).

Although only 15 species were collected in sufficient numbers and regularity in the shallows of the Swan Estuary to be regarded as marine estuarine-opportunists, 7 of these ranked amongst the 15 most abundant species. Furthermore, they constituted 34.5% of the fish fauna in the shallows. Since many of those fish represented the 0+ age class (Chubb et al. 1981, Prince and Potter 1983, Potter et al. 1988, also Potter, Murdoch University, Western Australia, unpublished data), the shallows of the Swan Estuary play an important role as a nursery area for local marine teleosts. While this parallels the situation in estuaries in many other parts of the world (e.g. Pearcy and Richards 1962, Haedrich and Haedrich 1974, Blaber and Blaber 1980, Blaber 1985, Claridge et al. 1986, Whitfield in press), the present study apparently provides the first quantitative estimate of the contribution of the marine estuarine-opportunists to the catches made throughout any estuarine system.

While 11 of the 15 marine estuarine-opportunists caught in the shallows of the Swan Estuary penetrated the upper estuary, their contribution to the numbers within the different regions of the estuary declined markedly from nearly 95% in the lower estuary to approximately 6% in the upper estuary. By contrast, only 3 of the 37 species of marine stragglers were recorded in the upper estuary and the contribution of this group to the number of individuals in even the lower estuary was very low. The restriction of this group to the lower estuary, where for many months the salinities are close to full-strength sea water (present Table 1, and Prince et al. 1982b), suggests that at least some of these species are stenoholine.

Contribution of estuarine and anadromous species

Twelve of the 14 species of teleost which can pass through the whole of their life cycle in the Swan Estuary were either moderately or very abundant in the system. Moreover, only *Apogon rueppellii* and *Engraulis australis* are also represented by substantial populations in local inshore waters (Chrystal et al. 1985, Hutchins and Swainston 1986). The importance to the ichthyofauna of the Swan Estuary of species which can pass through the whole of their life cycle in estuarine environments is illustrated by the considerable contribution (38.9%) they made to the catch in the large wide basins of the middle estuary. Like the marine estuarine-opportunists, the estuarine category also included 7 species which ranked amongst the top 15 in terms of numbers. The number of these estuarine species and their contribution to the total numbers was greater, however, in the middle and upper estuary than in the lower estuary. The concentration of the estuarine teleosts in the middle and upper regions would appear to be of value to such species since it would almost certainly reduce the chances of their being flushed out to sea during periods of high freshwater discharge. Such a conclusion is based on the fact that the effects of flushing would be moderated in the wide basins that constitute the middle estuary of the Swan. Moreover, these basins contain areas of deep water which, even during heavy freshwater flushing, remain high in salinity and relatively unaffected by the strong movement of surface waters. Certainly, species such as *A. rueppellii* occupy deeper waters to a far greater extent in the winter, when surface salinities are lowest, than they do at other times of the year (Chrystal et al. 1985).

The importance of estuarine species to the fish fauna of the Swan Estuary contrasts with the situation in the Severn Estuary in the United Kingdom, where only one abundant species, the common goby *Pomatoschistus microps*, was regarded at typically estuarine (Claridge et al. 1986). It has been suggested that the presence of a relatively high number of species which pass through the whole of their life cycle in the Swan, and also other estuaries in south-western Australia, reflects adaptations to the problems posed by the landlocking to which these systems tend to be subjected as a result of sand bars forming at their mouths (Potter et al. 1986 and in press). The fact that selection pressures during periods of isolation from the sea would be greatest on species with short life cycles, helps to account for the fact that most of the estuarine species in the Swan typically live for only one or two years (Prince and Potter 1983, Chrystal et al. 1985, Potter et al. 1986). Three of the most abundant of these species belonged to the Atherinidae, a family which is common in the shallows of estuaries in many parts of the world (Day et al. 1981, Haedrich 1983, Chao et al. 1985, Potter et al. 1986). In temperate South Africa where, like south-western Australia, some estuaries also become closed due to sand bar formation at their mouths, the ichthyofaunas are often dominated by the atherinid *Atherina breviceps* and the clupeid *Gilchristella aestuaria*, both of which have short life cycles and can complete their life cycle within estuaries (Blaber et al. 1981, Beckley 1984, Bennett et al. 1985, Blaber 1985, Talbot and Baird 1985).

Although estuarine species were an important component of the fish fauna in the shallows of the middle and upper estuary, their contribution was exceeded by that of the anadromous category, represented only by the clupeid *Nematalosa vlaminghi*. This species constituted over 40 and 75% of the numbers in these regions, respectively. Like the Atherinidae, the Clupeidae is also an important component of the fish faunas of many estuarine systems in both the northern and southern hemispheres (Haedrich 1983, Beckley 1984, Ross and Epperly 1985, Claridge et al. 1986). The number of freshwater species caught in the estuary was small and made only a minor contribution to the catches of even the upper estuary.

Influence of site on catches

The data collected on fish densities at various sites throughout the Swan Estuary over five years, which is unusually detailed for estuarine fish populations (Haedrich 1983), have allowed us to investigate the influence of site, season and year on the densities of the most abundant species in the shallows of the Swan Estuary. In general, site within the estuary exerted a greater influence on the densities of these species in the shallows than either season or year. Differences in the densities at the various sites help explain differences in the contribution of the various species and life-cycle categories to the catches in the three main regions of the estuary (Table 2). Thus, for example, the greatest densities of all except one of the marine estuarine-opportunistic species were recorded at sites in the lower estuary, i.e., within 6 km of the estuary mouth, whereas those of the estuarine and anadromous species occurred at sites in the middle or upper estuary, i.e., at distances greater than 15 km from the estuary mouth. However, the degree to which the various marine estuarine-opportunists penetrated the estuary varied. Thus, *Leptatherina presbyteroides*, *Pelates sexlineatus* and *Torquigener pleurogramma* occurred mainly in the lower estuary, whereas *Atherinomorus ogilbyi* and *Aldrichetta forsteri* were also taken in numbers in the middle estuary. The trends shown by the mean catches of *P. sexlineatus* in gill nets followed a similar pattern to that obtained by beach seines in the shallow waters. The fact that the general trend for each of the above marine species to decrease in density with increasing distance upstream from the estuary mouth was not followed by *Mugil cephalus*, can be attributed to the relatively rapid movement of the 0+ recruits of this species through the estuary (Chubb et al. 1981). This rapid movement is consistent with the tendency for juvenile *M. cephalus* to move upstream towards areas of low salinity (Thomson 1957, Blaber 1987).

Although each of the various estuarine species were well represented in either or both of the middle and upper estuaries, the degree to which they extended downstream of these regions varied. For example, the densities of *Apogon rueppellii* at the two lower estuary sites matched those at two of the three sites in the middle estuary, whereas *Leptatherina wallacei* and *Engraulis australis* were absent or rare in the lower estuary. The fact that most estuarine species were recorded in numbers throughout the middle and upper estuary at most times of the year indicates that they must be relatively euryhaline. Since salinities in the shallows of these regions vary markedly with season, such a characteristic would be essential for the survival of these species. However, *A. rueppellii* does migrate into deeper waters in the lower and middle estuary during heavy freshwater flushing and thus avoids the low salinities found in the shallows at this time (Chrystal et al. 1985).

Seasonal changes in catches

The density of the anadromous species *Nematalosa vlaminghi* in the shallows showed pronounced seasonal changes. The similarity between seasonal changes in the abundance of this species at each of the five sites in the upper estuary can be related to the pattern of the migratory movements of this species. Thus, the high densities at sites in the upper estuary between late spring (November) and the end of autumn (May) occurred during the time when older and larger *N. vlaminghi* were moving into the region to spawn and the new 0+ fish were being recruited into the population (Chubb and Potter 1984). By contrast, *N. vlaminghi* was rarely caught in the upper estuary during winter and early spring, when freshwater discharge increased markedly and produced a sharp decline in surface salinity in this region. The seasonal trends shown by densities of *N. vlaminghi* in the shallows were paralleled by the catch rates of this species taken in deeper waters by gill nets. The seasonal changes in beach-seine catches of *Amniataba caudavittatus* in the upper estuary are also related to the immigration of this species into upstream spawning areas. Indeed, the estuarine *A. caudavittatus* spawns at a similar upstream locality and time, i.e., November to February, as the anadromous *N. vlaminghi* (Chubb and Potter 1984, also Wallace and Potter, Murdoch University, Western Australia, unpublished data).

The large seasonal changes in densities shown by the estuarine species *Apogon rueppellii* at sites in the shallows of both the lower and middle estuary can be related to the inshore and offshore movements of this species. Thus, sexually maturing *A. rueppellii* migrate into the shallows during the late spring and, as a result of their subsequent spawning, large numbers of small 0+ fish are found on the banks in the late summer and early autumn (Chrystal et al. 1985). Fish move away from the banks in the autumn, and few remain in the shallows during the heaviest periods of freshwater flushing in the winter. The highly reduced densities of *A. rueppellii* in the shallows between the late autumn and early spring corresponds with the time of greatly increased catches in otter trawls at Sites 2 and 3, where the water was deeper than 4 m (present Fig. 8, and Chrystal et al. 1985).

Densities of two of the abundant marine-estuarine opportunistic species, *Pelates sexlineatus* and *Mugil cephalus*, also changed with season. The seasonality of catches of *M. cephalus* in beach seines in the lower estuary reflects to a large degree the rapid movement of new 0+ recruits through this part of the system during the winter and spring (Chubb et al. 1981). By contrast, numbers of *P. sexlineatus* were higher in summer and autumn than in winter. From an examination of the length-frequency histograms for *P. sexlineatus* and, on the basis of work carried out in the nearby Peel-Harvey system (Potter et al. 1983), these seasonal changes in numbers of *P. sexlineatus* can also be attributed to an immigration of 0+ fish into the estuary in the summer.

Annual changes in catches

Catches of *Craterocephalus mugiloides* were significantly lower in 1981 than in the other years of the study, whereas those of another atherinid (*Atherinomorus ogilbyi*) and *Engraulis australis* were lowest in 1978/1979 and 1977/1978, respectively. Densities of *Torquigener pleurogramma* also showed significant annual changes in the shallows, with higher catches being recorded in 1977/1978 and 1980/1981 than in other years. High densities of *T. pleurogramma* in the Swan Estuary can be related to the large annual differences in the level of recruitment of this marine species, and particularly that of its 0+ age class. Densities of this species were high in 1977/1978, due to the retention of strong 1975 and 1976 year-classes (Potter et al. 1988). A decline in numbers of these year-classes in 1978 and 1979, combined with virtually no recruitment of new 0+ fish, led to a marked fall in the numbers during this period. Catches then rose sharply in mid-1980, when a vary large number of 0+ fish entered the estuary (Potter et al. 1988). Annual differences in the relative abundance of the above four species in the Swan Estuary and a lack of correspondence between the peak years of abundance for these species parallels the situation recorded for some of the most abundant teleosts in the Severn Estuary (Claridge et al. 1986).

In conclusion, this study has shown that in terms of number of individuals, all but one of the most abundant fish species in the shallows of the Swan Estuary are either marine teleosts which enter the estuary early in life or teleosts which spawn in the estuary. The one exception was an anadromous species, which was the most numerous species in catches made by both beach seine and gill net. The relative contribution of individuals in the marine estuarine-opportunist category was greatest in the lower estuary, whereas those of the estuarine and anadromous categories were highest in the middle and upper estuary. Although small numbers of many marine species were recorded in the lower estuary, thereby supplementing the marine estuarine-opportunists in this region, few species of freshwater teleosts were caught even in the upper estuary. During this study, site within the estuary generally had a more important influence on the density of the abundant species in the shallows than either season or year. Seasonal changes in abundance could generally be related to spawning activities, either through immigration of older individuals into spawning areas or the immigration of new 0+ recruits.

Acknowledgements. We thank C. Chubb, J. Wallace, P. Chrystal, P. Yewers and all other colleagues and friends who assisted with the extensive field work in this project. The designation of life-cycle categories was facilitated through discussions with F. Neira, who also assisted with the preparation of one of the figures. H. Gill gave further information about the distribution of gobies within the Swan Estuary. Statistical advice was provided by N. Caputi, and helpful comments on the manuscript came from N. Caputi, C. Chubb, P. Humphries and G. Hyndes. This project was funded by the Western Australian Department of Fisheries.

Literature cited

Arnott, G. H., McKinnon, A. D. (1985). The distribution and abundance of eggs and larvae of the anchovy, *Engraulis australis antipodum* Günther, in relation to temperature and salinity in the Gippsland Lakes. Aust. J. mar. Freshwat. Res. 36: 433–439

Beckley, L. E. (1984). The ichthyofauna of the Sundays Estuary, South Africa, with particular reference to the juvenile marine component. Estuaries 7: 248–258

Bennett, B. A., Hamman, K. C. D., Branch G. M., Thorne, S. C. (1985). Changes in the fish fauna of the Bot River estuary in relation to opening and closure of the estuary mouth. Trans. R. Soc. S. Afr. 45: 449–464

Blaber, S. J. M. (1980). Fish of the Trinity Inlet system of north Queensland with notes on the ecology of fish faunas of tropical Indo-Pacific estuaries. Aust. J. mar. Freshwat. Res. 31: 137–146

Blaber, S. J. M. (1985). The ecology of fishes of estuaries and lagoons of the Indo-Pacific with particular reference to southeast Africa. In: Yanez-Arancibia, A. (ed.) Fish community ecology in estuaries and coastal lagoons: towards an ecosystem integration. Universidad Nacional Automoma de Mexico, Mexico City, p. 247–266 (ISBN 968-837-618-3)

Blaber, S. J. M. (1987). Factors affecting recruitment and survival of mugilids in estuaries and coastal waters of southeastern Africa. Am. Fish. Soc. Symp. 1: 507–518

Blaber, S. J. M., Blaber, T. G. (1980). Factors affecting the distribution of juvenile estuarine and inshore fish. J. Fish Biol. 17: 143–162

Blaber, S. J. M., Cyrus, D. P., Whitfield, A. K. (1981). The influence of zooplankton food resources on the morphology of the estuarine clupeid *Gilchristella aestuarius* (Gilchrist, 1914), Envir. Biol. Fish. 6: 351–355

Blackburn, M. (1950). A biological study of the Australian anchovy *Engraulis australis* (White), in Australian waters. Aust. J. mar. Freshwat. Res. 1: 3–84

Chalmer, P. N., Hodgkin, E. P., Kendrick, G. W. (1976). Benthic faunal changes in a seasonal estuary of south-western Australia. Rec. West. Aust. Mus. 4: 383–410

Chao, L. H., Pereira, L. E., Vieira, J. P. (1985). Estuarine fish community of the dos Patos Lagoon, Brazil. A baseline study. In: Yanez-Arancibia, A. (ed.) Fish community ecology in estuaries and coastal lagoons: towards an ecosystem integration. Universidad Nacional Automoma de Mexico. Mexico City, p. 429–450 (ISBN 968-837-618-3)

Chrystal, P. J., Potter, I. C., Loneragan, N. R., Holt, C. P. (1985). Age structure, growth rates, movement patterns and feeding in an estuarine population of the cardinalfish *Apogon rueppellii*. Mar. Biol. 85: 185–197

Chubb, C. F. Hutchins, J. B., Lenanton, R. C. J., Potter, I. C. (1979). An annotated checklist of the fishes of the Swan-Avon river system, Western Australia. Rec. West. Aust. Mus. 8: 1–55

Chubb, C. F., Potter, I. C. (1984). The reproductive biology and estuarine movements of the gizzard shad, *Nematalosa vlaminghi* (Munro). J. Fish Biol. 25: 527–543

Chubb, C. F., Potter, I. C. (1986). Age, growth and condition of the Perth herring, *Nematalosa vlaminghi* (Munro) (Dorosomatinae) in the Swan Estuary, south-western Australia. Aust. J. mar. Freshwat. Res. 37: 105–112

Chubb, C. F., Potter, I. C., Grant, C. J., Lenanton, R. C., Wallace, J. (1981). The age structure, growth rates and movements of sea mullet, *Mugil cephalus* L., and yellow-eye mullet, *Aldrichetta forsteri* (Valenciennes), in the Swan-Avon river system. Aust J. mar. Freshwat. Res. 32: 605–628

Claridge, P. N., Potter, I. C., Hardisty, M. W. (1986). Seasonal changes in movements, abundance, size composition and diversity of the fish fauna of the Severn Estuary. J. mar. biol. Ass. U. K. 66: 229–258

Cronin, L. E., Mansueti, A. J. (1971). The biology of the estuary. In: Douglas, P. A., Stroud, R. H. (eds.) A symposium on the biological significance of estuaries. Sport Fishing Institute, Washington, D. C., p. 14–39

Dando, P. R. (1984). Reproduction in estuarine fish. In: Potts, G. W., Wootton, R. J. (eds.) Fish reproduction strategies and tactics. Academic Press, London, p. 155–170

Day, J. H., Blaber, S. J. M., Wallace, J. H. (1981). Estuarine fishes. In: Day, J. H. (ed.) Estuarine ecology with particular reference to Southern Africa. Balkema, Rotterdam, p. 197–221

Gill, H. S., Miller, P. J. (in press). A new genus and species of goby from the Swan Estuary, Western Australia, with a redescription of the genus *Favonigobius* Whitley, 1930. Rec. West. Aust. Mus.

Haedrich, R. L. (1983). Estuarine fishes. In: Ketchum, B. H. (ed.) Ecosystems of the world. Vol. 26: Estuaries and enclosed seas. Elsevier Scientific Publishing Co., Oxford, p. 183–207

Haedrich, R. L., Haedrich, S. O. (1974). A seasonal survey of the fishes in the Mystic River, a polluted estuary in downtown Boston, Massachusetts. Estuar. cstl mar. Sci. 2: 59–73

Hedgpeth, J. W. (1982). Estuarine dependence and colonisation. Atlantica 5: 57–58

Hodgkin, E. P., Lenanton, R. C. (1981). Estuaries and coastal lagoons of south-western Australia. In: Neilson, B. J., Cronin, L. E. (eds.) Nutrient enrichment in estuaries. Humana Press, New Jersey, p. 307–321

Hutchins, B., Swainston, R. (1986). Sea fishes of southern Australia. Swainston Publishing, Perth, Western Australia

Lachner, E. A. (1953). Family Apogonidae: cardinalfishes. Bull. U.S. natn. Mus. 202: 412–498

Lenanton, R. C. J., Caputi, N. (1989). The roles of food supply and shelter in the relationship between fishes (in particular *Cnidoglanis macrocephalus* (Valenciennes)) and detached macrophytes in the surf zone of sandy beaches. J. exp. mar. Biol. Ecol. 128: 165–176

Lenanton, R. C. J., Potter, I. C. (1987). Contribution of estuaries to commercial fisheries in temperate Western Australia and the concept of estuarine dependence. Estuaries 10: 28–35

Lenanton, R. C. J., Potter, I. C., Loneragan, N. R. Chrystal, P. J. (1984). Age structure and changes in abundance of three important teleosts in a eutrophic estuary. J. Zool., Lond. 203: 311–327

Lenanton, R. C. J., Robertson, A. I., Hansen, J. A. (1982). Nearshore accumulations of detached macrophytes as nursery areas for fish. Mar. Ecol. Prog. Ser. 9: 51–57

Loneragan, N. R., Potter, I. C., Lenanton, R. C. J., Caputi, N. (1986). Spatial and seasonal differences in the fish fauna in the shallows of a large Australian estuary. Mar. Biol. 92: 575–586

Loneragan, N. R., Potter, I. C., Lenanton, R. C. J., Caputi, N. (1987). Influence of environmental variables on the fish fauna of the deeper waters of a large Australian estuary. Mar. Biol 94: 631–641

McHugh, J. L. (1967). Estuarine nekton. In: Lauff, G. H. (ed.) Estuaries. American Association for the Advancement of Science, Washington, D. C., p. 581–620

McHugh, J. L. (1976). Estuarine fisheries: are they doomed? In: Wiley, M. (ed.) Estuarine processes. Vol. 1. Academic Press, New York, p. 15–27

Neira, F. J. (1989). Systematics and ecology of larval lampreys and fishes. Phd thesis, Murdoch University, Western Australia

Nel, S. A., Potter, I. C., Loneragan, N. R. (1985). The biology of the catfish *Cnidoglanis macrocephalus* (Plotosidae), in an Australian estuary. Estuar., cstl Shelf Sci. *21*, 895–909.

Pavlov, A., Ivantsoff, W., Last, P. R., Crowley, L. E. L. M. (1988). *Kestratherina brevirostris*, a new genus and species of silverside (Pisces: Atherinidae) with a review of atherinid marine and estuarine genera of southern Australia. Aust. J. mar. Freshwat. Res. 39: 385–397

Pearcy, W. G., Richards, S. W. (1962). Distribution and ecology of fishes of the Mystic River Estuary, Connecticut. Ecology 43: 248–259

Potter, I. C., Beckley, L. E., Whitfield, A. K., Lenanton, R. C. J. (in press). The roles played by estuaries in the life cycles of fishes in temperate western Australia and southern Africa. In: Bruton, M. N. (ed.) Alternative life history styles of fishes. Kluwer Academic Press, Dordrecht

Potter, I. C., Cheal, A. J., Loneragan, N. R. (1988). Protracted estuarine phase in the life cycle of the marine pufferfish *Torquigener pleurogramma*. Mar. Biol. 98: 317–329

Potter, I. C., Ivantsoff, W., Cameron, R., Minnard, J. (1986). Life cycles and distribution of atherinids in the marine and estuarine waters of southern Australia. Hydrobiologia 139: 23–40

Potter, I. C., Loneragan, N. R., Lenanton, R. C. J. Chrystal, P. J., Grant, C. J. (1983). Abundance, distribution and age structure of fish populations in a Western Australian estuary. J. Zool., Lond. 200: 21–50

Prince, J. D., Ivantsoff, W., Potter, I. C. (1982a). *Atherinosoma wallacei* (Teleostei: Atherinidae), a new species of estuarine and inland water silverside from the Swan-Avon and Murray rivers, Western Australia. Aust. Zool. 21: 63–74

Prince, J. D., Potter, I. C. (1983). Life cycle duration, growth and spawning times in five species of Atherinidae (Teleostei) in a

Western Australian estuary. Aust. J. mar. Freshwat. Res. 34: 287–301
Prince, J. D., Potter, I. C., Lenanton, R. C. J., Loneragan, N. R. (1982b). Segregation and feeding of atherinid species (Teleostei) in south-western Australian estuaries. Aust. J. mar. Freshwat. Res. 33: 865–880
Ross, S. W., Epperly, S. P. (1985). Utilization of shallow estuarine nursery areas by fishes in Pamlico Sound and adjacent tributaries, North Carolina. In: Yanez-Arancibia, A. (ed.) Fish community ecology in estuaries and coastal lagoons: towards an ecosystem integration. Universidad Nacional Automoma de Mexico, Mexico City, p. 207–232 ISBN 968-837-618-3
Talbot, M. M. J., Baird, D. (1985). Feeding of the estuarine round herring *Gilchristella aestuarius* (G&T) (Stolephoridae). J. exp. mar. Biol. Ecol. 87: 199–214
Thomson, J. M. (1957). The penetration of estuarine fish into freshwater in the Albert River. Proc. R. Soc. Qd 68: 17–20
Underwood, A. J. (1981). Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr. mar. Biol. A. Rev. 19: 513–605
Wallace, J. H., Kok, H. M., Beckley, L. E., Bennett, B. A., Blaber, S. J. M., Whitfield, A. K. (1984). South African estuaries and their importance to fishes. S. Afr. J. Sci. 80: 203–207
Whitfield, A. K. (in press). Life history styles of fishes in south African estuaries. In: Bruton, M. N. (ed.) Alternative life history styles of fishes. Kluwer Academic Press, Dordrecht

Date of final manuscript acceptance: August 11, 1989.
Communicated by G. F. Humphrey, Sydney