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Linking fish assemblages and attributes of mangrove estuaries in tropical Australia: criteria for regional marine reserves

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ABSTRACT: Quantifying natural features important in structuring fish assemblages is an essential pre-requisite to implementation of measures to conserve regionally representative whole ecosystems. Tropical estuaries are high in priority for protection, but fish-ecosystem relationships have rarely been analysed at multiple scales. Fishery-independent surveys (gill nets 19 to 152 mm mesh) were replicated seasonally (wet, dry) in 11 large estuaries along 1400 km of coast adjacent to the Great Barrier Reef. Fundamental differences in physical forces (river, wave, tidal) apparently generated variation in abiotic attributes, which distinguished Tide- from Wave-dominated systems. These trends correlated with patterns observed among estuarine fish assemblages, mediated by ecological and biological processes. Tide-dominated systems (n = 7), located in drier catchments, had greater mangrove area, wide deltaic mouths, and muddy substrate; in these systems, diversity was high with Ariidae, Belonidae and Haemulidae characterising the fish assemblages. Wave-dominated systems (n = 4), located in higher rainfall catchments, had constricted mouths, less mangrove area, and sandy substrate. For Wave-dominated systems, deltas (n = 2), had high diversity with Megalopidae characterising the fish assemblages, while true estuaries (n = 2) were relatively depauperate. Notably, none of the estuarine attributes explained the greater catch rates of Carangidae and Carcharhinidae observed in east Cape York. This trend may be attributed to negligible fishing pressure in the remote Cape York region. Overall, a substantial amount of the variation in fish assemblages (42.9%) was related to catchment hydrology, configuration of the estuary mouth, substrate and mangrove area. The results here support management programs incorporating a surrogate approach aimed at conserving the biodiversity of estuarine fish assemblages by combining regional and estuary scales in defining networks of reserve systems.

KEY WORDS: Marine reserves · Mangroves · Fish assemblages · Multivariate analysis · Estuaries · Habitat · Great Barrier Reef · Ecosystems

INTRODUCTION

Aquatic reserve networks can serve biodiversity conservation objectives by protecting regionally representative habitats at large spatial scales (from 100s to 1000s of km) (Sala et al. 2002). Such networks may also serve fisheries management objectives by conserving populations of target species within refugia and by providing sources of replenishment through spillover and recruitment (Russ 2002). Ideally, both sets of objectives can be addressed when designating aquatic reserves by applying a rigorous selection process. Protecting habitat surrogates is widely accepted as a strategic means for selecting high priority reserve areas (Ward et al. 1999). A pre-requisite to applying the surrogate approach is knowledge about the relationships between fish assemblages and habitat conditions. For tropical estuaries, implementing a systematic reserve selection process under the surrogate approach has been hampered because information about the under-

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lying relationships between rich faunal assemblages and essential habitat conditions is limited (Robertson & Blaber 1992). One reason for this knowledge gap is that, although many single estuaries have been well studied, few investigations have systematically examined relationships between habitat attributes and a broad ecological range of fishes in several discrete tropical estuaries across a heterogeneous region.

A broad-scale, replicated design is required to identify essential habitat factors influencing estuarine fish assemblages (Robertson & Duke 1987). For 28 temperate estuaries on the USA west coast, Monaco et al. (1992) found that 62 % of the variation in the number of taxa present in an estuary (based on available species lists) was explained by a single habitat variable: depth of the estuary entrance. For 53 estuaries, spanning sub-tropical to temperate latitudes in southeastern Australia, commercial fisheries databases were analysed by Pease (1999). The presence of a semi-permanent barrier at the estuary entrance strongly influenced the fish assemblages in the smaller (<4 km^2), mainly temperate estuaries. Re-analysis of the 30 larger estuaries revealed that latitude and sea water area explained 58 % of the variation in the fish assemblage data set. Thus, latitude, attributes of the estuary entrance, and sea-water area are apparently among the key variables important in structuring estuarine fish assemblages in a coastal region.

Reliance on species lists and fishery-dependent data has drawbacks for comparing fish assemblages of different estuaries, due to bias introduced by using non-standardised methods (Nagelkerken & van der Velde 2004). Therefore, uniform fishery-independent methods were used to investigate habitat attributes influencing estuarine fish assemblages in 2 island-wide studies. In 39 estuaries distributed around the temperate island state of Tasmania, Australia (22 500 km^2), beach seine sampling revealed that configuration of the estuary mouth explained the greatest amount of variation (34 %) in fish assemblage patterns (Edgar et al. 1999, 2000). At a smaller scale, on the Caribbean island of Curaçao (600 km^2), no discernible distinctions were found among 13 tropical embayments despite differences in bay surface area (<0.1 to 2.3 km^2) and wind exposure (Nagelkerken & van der Velde 2004). The investigators hypothesised that the homogeneity in the fish assemblages among the bays may have been due to island-wide similarities in tidal regime, geomorphology, geographical setting and occurrence of coral reefs offshore. Thus, the design of investigations seeking to establish essential habitat/fish assemblage relationships should encompass a variety of physical settings.

Surprisingly, only one comparable investigation has been conducted in multiple tropical estuaries along an extensive (400 linear km) continental coast (Ley & Halliday 2003). Fish assemblage/habitat relationships were analysed for 6 mangrove-dominated estuaries in northeastern Australia, using fishery-independent sampling (i.e. research gill-nets) and data for 6 habitat variables (commercial fishing, position in the estuary, water temperature, salinity, channel length, mangrove area). Based on canonical correlation analysis (CCA), mangrove area was the most influential variable relative to the overall fish assemblages. However, the magnitude of variation in fish assemblages explained by the habitat variables was low (14 %). Short-comings of that investigation may have included: (1) a limited geographic range, (2) linearity of CCA and (3) restriction of the habitat variables to within-estuary attributes only. For purposes of the current study, it was hypothesised that a greater number of tropical systems spanning a wide, heterogeneous geographic range, together with the inclusion of broader-scale attributes, and a more appropriate statistical analysis method, would reveal underlying habitat features of importance in structuring estuarine fish assemblages.

The current investigation draws upon ecological studies of singular and multiple estuaries in selecting attributes most likely to reveal patterns in fish assemblage/habitat relationships in tropical estuaries along an extensive (>1000 km) and diverse continental coast. The ecological bases for selection of attributes are briefly described below (see Table 1). Variability in salinity may lead to differences in the occurrence of fishes such as stenohaline predators, euryhaline residents and transients (Gunter 1961). Substrate and turbidity conditions may lead to variation in food webs (Blaber 1997, Thayer & Chester 1989). Greater area of mangroves may influence the abundance and composition of fish assemblages (Thayer et al. 1989, Ley et al. 1999, Nagelkerken et al. 2001). Morphology (depth, width, shape) of the estuary entrance may control exchange with offshore populations and influence habitat conditions within the estuary (Monaco et al. 1992, Edgar et al. 1999, Pease 1999). At the catchment scale, natural and anthropogenic inputs of detritus may vary with the size and condition of the basin, influencing this important part of the estuarine food base (Day et al. 1989). Furthermore, freshwater inflow (rainfall, topography) and tides control the position of aquatic conditions relative to stationary features such as mangrove shorelines, generating variability in spatially and temporally dynamic habitats in estuaries (Browder & Moore 1981, McIvor et al. 1994). Other attributes of ecological significance such as seagrass beds (Nagelkerken et al. 2001) were rare in the study area, with one exception (Nobbies, see 'Discussion').

The aim of the current study was to use fishery-independent methods to explore the potential in-

Table 1. Attributes of the estuaries indicating sources, units and values used in the analysis

Factors & variables	Estuary: No. from north to south:	Jacky Jacky 1. JJ	Escape 2. Es	Pascoe 3. Pa	Lockhart 4. Lo	McIvor 5. Mc	Russell 6. Ru	Hull 7. Hu	Haughton 8. Ha	Barrattas 9. Ba	Yellow Gin 10. Yg	Nobbies 11. No
Bioregion*	See Fig. 1	ECY	ECY	ECY	ECY	ECY	WTC	WTC	LMC	LMC	LMC	LMC
Classification*	Influence at entrance[a]	T	T	W	T	W	W	W	T	T	T	T
Sub-classification*	Geomorphology[b]	E	E	D	E	D	E	E	D	D	C	C
Exploitation*	Type of fishing[c]	Remote	Remote	Remote	Remote	Remote	Rec	Com	Rec	Com	Rec	Com
Latitude	Degrees and fractional minutes South[d]	10.9	11.0	12.5	12.9	15.2	17.2	18.0	19.3	19.4	19.8	19.8
Outfall	Direction, receiving waters	NE Newcastle Bay	NE Newcastle Bay	E Coral Sea	N Lloyd Bay	E Coral Sea	E Coral Sea	E Coral Sea	N Bowling Green Bay	N Bowling Green Bay	N Upstart Bay	N Upstart Bay
Tidal range	Meters: mean high to mean low tide[h]	2.6	2.7	2.2	2.1	2.1	1.9	2.1	2.4	2.4	2.3	2.3
Water depth	Meters at mouth, mid-tide range[e]	<5.0	<5.0	<1.0	<5.0	<1.0	<5.0	<1.0	<1.0	<1.0	<1.0	<1.0
Salinity**	Mean (parts per thousand)[f]	28.2	27.6	13.3	19.8	17.6	14.7	16.8	19.8	24.2	25.1	32.7
Temperature**	Water mean degrees (°C)[f]	28.5	28.3	28.1	27.5	27.0	24.6	24.4	26.6	26.9	26.2	26.6
Mudindex**	Composition estuary substrate[g]	4	2	1	4	3	2	2	5	5	4	2
Open water**	Area (km^2)[h]	66.18	18.11	3.03	15.9	2.9	3.80	2.44	7.74	7.25	3.0	5.29
Mangkm2**	Total area mangrove (km^2)[h]	80.0	44.0	2.3	48.0	2.0	6.0	12.0	32.0	18.0	19.0	14.0
EntWdkm**	Width estuary mouth[d,e]	5.0	2.7	0.2	3.0	0.5	0.2	0.1	3.0	3.0	0.8	2.5
Basinkm2**	Catchment (km^2)[h]	721	236	2077	900	516	1393	155	2111	1466	250	285
Condition**	Index[i]	1	1	1	1	1	2	2	2	3	2	1
Elevation**	Maximum 10 m contour[d]	100	100	450	500	500	1700	1400	100	100	100	100
Rainfall**	Annual average (mm)[j]	1467	1467	2139	1225	1939	3016	2855	888	888	1045	1045

*Included as factors in the multivariate analysis

**Included as variables in the multivariate analysis

[a] T: Tide-dominated; W: Wave-dominated

[b] D: Delta; E: Estuary; C: Creek

[c] Com: commercial netfishing permitted; Rec: recreation fishing only; Remote: inaccessible by road

[d] Estimated from topographic sheets at the estuary mouth

[e] Estimated from navigation charts at the estuary mouth

[f] Average of data recorded every 5 min by 1 or 2 DataSonde Hydrolab units while nets were fishing

[g] Substrate categories: High mud content = 5; Mud/Sand = 4: White sand = 3; Rock/Shell/Sand = 2; Rock = 1

[h] Australian Estuarine Database (AED; www.ozestuaries.org); Line drawings of all 11 estuaries can be viewed on this website

[i] Based on percent of catchment cleared (AED); 1 = nearly pristine; 2 = 15–30 % cleared for crops/pasture; 3 = 30–70 % cleared for crops/pasture. Note: no estuaries studied had urbanisation in the catchment

[j] From Furnas (2003). Rain gauges averaged for the catchment. Pascoe River values from Australian Bureau of Meteorology station at the community near the entrance to the estuary

fluence of these abiotic factors on the use of tropical estuaries by fish. To allow comparability of the results, the current approach employs multivariate analyses similar to those used in recent temperate and sub-tropical studies (Edgar et al. 1999, Pease 1999).

MATERIALS AND METHODS

Study area. The study area extends from the northeastern tip of Australia (10° 42′ S, 142° 32′ E) 1400 km southeast to Cape Upstart (19° 50′ S, 147° 46′ E) (Fig. 1). The Great Barrier Reef lies adjacent to the study area on the east. The Great Dividing Range (maximum elevation 1700 m) extends the length of the study area, with the main ridge of mountains varying in proximity to the shoreline. Semi-diurnal tidal cycles prevail, ranging from <2 m on neap to >4 m on spring tides, with little variation in range across the study area (Table 1). Regional and estuarine classification frameworks were applied as grouping factors in the analysis. At the regional scale, 27 drainage basins in the study area comprise 3 bioregions based on geology, soils, terrestrial vegetational communities, and marine conditions (Australian Department of Environment & Heritage 1999, Sattler & Williams 1999). The estuaries themselves were classified using a 2-tiered, process-based classification framework for coastal waterways, which synthesizes river, wave and tide power (Dalrymple et al. 1992, Harris et al. 2002). Firstly, at the broadest level, a general estuarine classification was applied based on the relative influence of tide (Tide-dominated, T) or wave action (Wave-dominated, W) at the entrance to the estuary. Secondly, a sub-classification was applied, depending on geological maturity (infilling) and riverine flow, generally defined as: (1) well infilled systems with strong riverine inflow (deltas, D); (2) more moderately infilled systems with a more equal balance between riverine inflow and tides (true estuaries, E); and (3) low riverine inflow (creeks, C) (Harris et al. 2002). Thus, for example, Haughton is a Tide-dominated Delta, TD (Table 1).

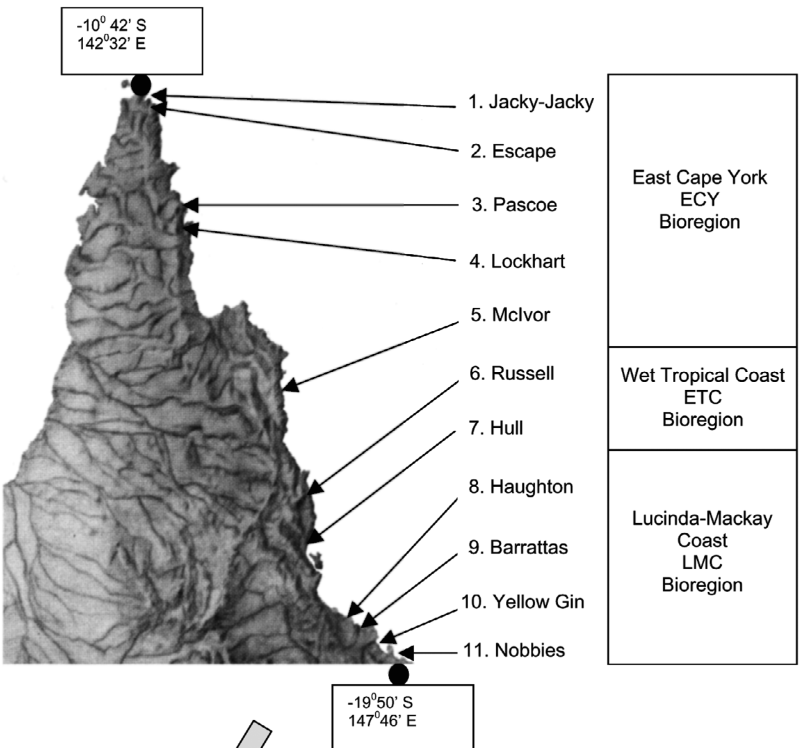

Fig. 1. Study area showing the locations of the 11 estuaries along the northeastern coast of Australia. Also shown are the 3 bioregions designated by the Australian Department of Environment and Heritage (1999)

Abiotic data and analysis. Of the 110 estuaries situated in the study area, 11 large (catchment >150 km^2, mangrove/water area >4 km^2) estuaries were selected (Fig. 1). The estuaries themselves are in relatively pristine condition with no development along the continuous mangrove shorelines (*Avicennia marina*, *Rhizophora stylosa*, *Ceriops* spp.), no wastewater input, and limited agricultural runoff. Regulated commercial gill-net fishing is permitted in Nobbies, Barrattas and Hull (Ley et al. 2002), while recreational line-fishing is permitted in all 11 estuaries. However, only subsistence indigenous and limited adventure tour fishing occur in the 5 estuaries located in the remote ECY (beyond road access). Exploitation (i.e. commercial, recreational, remote) was examined as the 4th grouping factor in the analysis.

For the 11 estuaries, abiotic data and relevant sources are summarised in Table 1. Relationships among regional, catchment, estuary and sample scale attributes are conceptually illustrated in Fig. 2. Salinity and water temperature were recorded for each sample. Each estuary was assigned an ordinal Mudindex rating (1 to 5) representing a progression of increasing substrate muddiness (Afifi & Clark

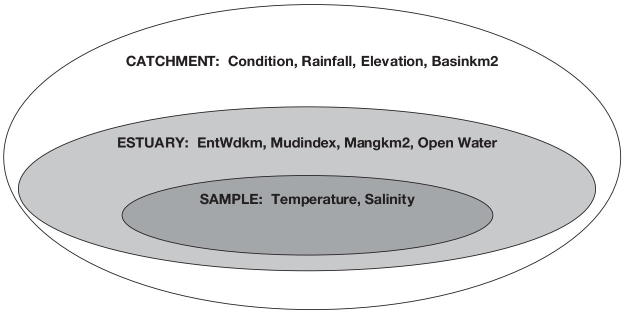

Fig. 2. Conceptual illustration of relationships among the 10 abiotic attributes arranged by scale. See Table 1 for attribute definitions

1984). Four attributes (Open water, Mangkm2, Basinkm2, Condition) were extracted from the Australian Estuarine Database (AED; www.ozestuaries.org) (Bucher & Saenger 1991, Harris et al. 2002). Long-term averages were extracted for annual rainfall by catchment from Furnas (2003). Maximum elevation in the catchment, estuary entrance width (EntWdkm), and latitude of the estuary mouth were estimated from topographic maps and nautical charts. A final table was constructed comprised of the 11 attributes quantified for each sample (n = 34). Latitude was eliminated from the analysis to 'allow the variables to speak for themselves' (Clarke & Ainsworth 1993). If 2 variables were highly correlated ($r > 0.90$), only one was retained for further analysis. Following graphical inspection, values were transformed ($\ln(x + 1)$) to reduce skewness (Clarke & Warwick 2001). A similarity matrix was derived based on normalised Euclidean distances (not standardised). From this matrix, a cluster analysis was conducted based on group-average clustering and plotted as a dendrogram. In addition, the table of abiotic attributes was normalised and ordinated using principal components analysis (PCA).

Fish data and analysis. Upstream (2 to 10 km from the mouth) and downstream sites (within 1 km of the mouth) were sampled with groups of monofilament gillnets, each 33 m long by 4.5 m deep, with stretched mesh sizes of 152, 102 and 51 mm. Multi-panel nets, 30 m long by 2 m deep, with stretched mesh sizes of 19, 25 and 32 mm were also deployed. Although the wide range of net mesh sizes was intended to capture fish in a variety of size classes and morphologies, not all species were effectively sampled in these diverse tropical systems (see 'Discussion'). Sampling trips were conducted in 2 phases: (1) February and June 1996 in east Cape York on the Australian Institute of Marine Science vessel, 'Harry Messel', and (2) March and July 1998 and 1999 in the remainder of the study area. In each estuary, samples taken in February and March represent the 'wet' season, while the samples taken in June and July represent the 'dry' season. Season was applied as the 5th grouping factor in the analysis. Nets were set for up to 11 daylight hours. Catch was recorded on each hourly check by species, size and abundance. Most fish that were alive when removed from the nets were measured and released. On rare occasions, net marks indicated that an individual was re-captured from an earlier check and data were therefore not recorded for that individual. Dead fish and unknown species were frozen and retained for identification and gut contents analysis. Food items were identified to general taxa and summarised by frequency of occurrence, i.e. percentage of all fish in a taxa having consumed a particular food item (Bowen 1996).

Catch per hour of net deployment was calculated for each net set, standardised by unit of effort, and combined for all nets by estuary (n = 11) and trip (n = 2 Cape York, n = 4 elsewhere), resulting in 34 catch per unit effort (CPUE) samples. Fish were aggregated by family (see 'Discussion') and standardised by sample size for analysis. Because the occurrence of rare taxa was of interest, data were 4th-root-transformed for analysis. Multivariate analyses were facilitated by use of PRIMER V6 (Primer-E). Due to the dominance of zero-counts, the Bray-Curtis index of similarity was used to derive a matrix of similarity values between pairs of samples (Clarke 1993). Relationships among groups were ascertained using cluster analysis and non-metric multidimensional scaling (MDS). The relative multivariate variability within groups defined in the ordinations was analysed by calculation of the index of multivariate dispersion (IMD, MVDISP routine) (Warwick & Clarke 1993). Significance of the influence of grouping factors was tested using 1-way analysis of similarities (ANOSIM), a test based on ranks of the values in the similarity matrix. As indicated above, 5 grouping variables were tested: estuarine classification, subclassification, season, exploitation and bioregion. Between each pair of samples, ANOSIM calculated an R-statistic indicating how separated they were, with $R > 75\%$ very different in composition; $75\% > R > 25\%$ different but with some scatter in the data; when $R < 25\%$, the data were too scattered to provide a measure of difference between 2 groups. The significance level of each R-statistic was also determined based on how many times a given value appeared in the permutation tests (Clarke 1993). SIMPER analyses identified which families were responsible for distinguishing spatial groups. For each family, SIMPER calculated a discrimination index, defined as the ratio of the average contribution to similarity between groups (numerator) to the standard deviation of similarity between groups (denominator). The higher the value of the discrimination index, the more informative the species was for discriminating between groups (Clarke & Warwick

2001). A second index indicated the degree to which a family typified a group, termed the typifying index. This index was based on the contribution a family made to the average similarity within a group (numerator) divided by the standard deviation of similarity among the group samples (denominator) (Clarke & Warwick 2001). In either case, the index value depended on both the magnitude and the consistency of the family's contribution.

Analysis of inter-relationships between the fish and abiotic datasets. The BIO-ENV routine was used to analyse the correlation between spatial patterns associated with abiotic variables and the spatial patterns associated with CPUE by family. For the fish data, input for the BIO-ENV procedure was the similarity matrix of standardised, 4th-root-transformed CPUE by sample (fish similarity matrix). For the abiotic data, input was a similarity matrix derived from a table of natural log-transformed values ($\ln(x + 1)$), ordinated by normalised Euclidean distances (not standardised) (abiotic similarity index). BIO-ENV generated subsets of abiotic variables which maximised the Spearman rank correlations between abiotic and fish similarity matrices. The best combinations of abiotic variables were ranked and listed as output from the procedure.

Univariate analyses. Number of families, Margalef species richness index (d), Shannon Diversity Index (H') and CPUE were calculated by sample. For these community attributes, and for selected CPUE and abiotic data, F-tests evaluated homogeneity of variances and, if necessary, data were transformed (Clarke & Warwick 2001). One-way analyses of variance (ANOVA) and Fisher's LSD tests were applied to determine if means differed significantly between groups (Statistica 6 StatSoft).

RESULTS

Analysis of abiotic attributes

Ten variables were initially included in the analysis of abiotic attributes (Table 1). Two catchment scale variables, rainfall and elevation, were well correlated (r = 0.96), and thus only one (elevation) was retained for derivation of the similarity matrix. Similarly, 2 estuary scale variables, open water and Mangkm2, were well correlated (r = 0.90), and only Mangkm2 was retained. Cluster analysis using the remaining 8 abiotic variables led to the distinction of 2 major groups at the Euclidean distance of 4. These 2 groups corresponded with the estuarine classifications, i.e. all samples from Wave-dominated separated from Tide-dominated estuaries (Fig. 3a). The 2 major groups were comprised of subgroups corresponding with the estuarine sub-classifications as indicated, i.e. creeks (TC), true estuaries (TE, WE) and deltas (TD, WD).

The first 3 principal components (PC) explained 77.7 % of the variation in the abiotic data set (Table 2). PC1 explained 36.6 % of the variation and was most highly correlated with 4 variables, 3 at the estuary scale (Mangkm2, Mudindex, EntWdkm) and 1 at the catchment scale (elevation). PC2 explained 22 % of the variation and was most highly correlated with 2 catchment scale variables (Condition, Basinkm2). PC3 explained a

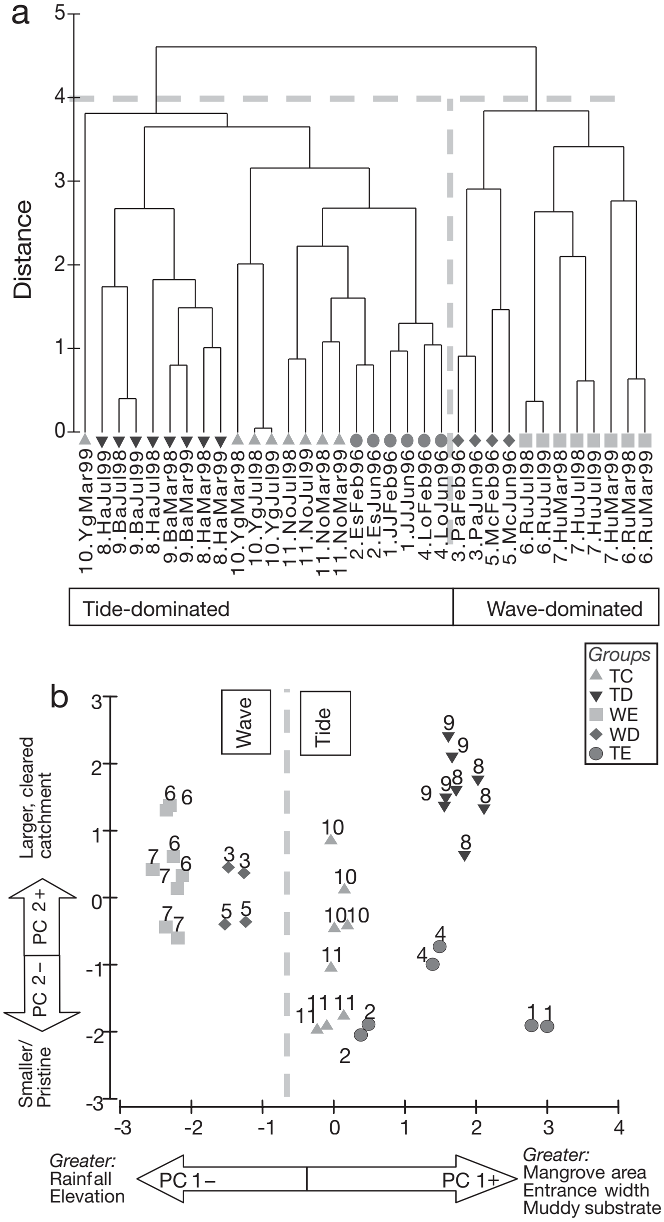

Fig. 3. (a) Dendrogram showing group average clustering of 34 samples based on 8 abiotic variables. Dashed line shows the division between Wave-dominated (W) and Tide-dominated (T) systems. (b) Ordination of 34 samples by principle components analysis (PCA) based on 8 abiotic attributes. See Table 1 for group definitions

Table 2. Coefficients for linear combinations of abiotic attributes making up the principal components (PCs). Also shown are the values of the percentage variation explained by the first 3 PCs. Values in bold type were correlated with the principal component at greater than 0.40

Variable	PC1	PC2	PC3
Salinity	0.18	–0.36	**–0.61**
Temperature	0.18	0.07	**0.70**
Mangkm2 [a]	**0.46**	–0.20	0.09
Mudindex	**0.43**	0.40	–0.18
Condition	–0.01	**0.61**	–0.32
Elevation [b]	**–0.47**	0.10	–0.02
EntWdkm	**0.55**	–0.06	0.01
Basinkm2	0.11	**0.53**	0.04
%Variation	36.6	22.0	19.1
Cum. %Variation	36.6	58.6	77.7

[a] Mangkm2 and open water area were correlated at r = 0.90
[b] Rainfall and elevation were correlated at r = 0.96

further 19.1 % of the variation and was well correlated with 2 sample scale variables (Salinity, Temperature). Samples on the right side of the principal components plot (PC1 vs PC2) were from Tide-dominated systems, with wide deltaic entrances, muddy substrate and greater mangrove area, occurring within lower elevation, drier catchments (Fig. 3b, Table 2). Samples on the left side of the PC plot were from Wave-dominated systems, with narrow entrances, sandy or rocky substrate, and relatively reduced area of mangrove coverage, occurring within higher elevation catchments with more rainfall. Along the PC2 ordination axis, 2 pristine systems with small catchment size, Nobbies (11) and Escape (2), contrasted with the large, agriculturally-developed catchments of the Barrattas (8) and Haughton (9). Surprisingly, Nobbies was similar to Escape, despite their locations at opposite extremes of the latitudinal gradient (see Fig. 1). Thus, the 8 abiotic variables explained the underlying bases for group memberships identified in the cluster and PC analyses.

Table 3. Sample (n = 34) average catch per net hour (CPUE) netted during daylight hours aggregated by family

Family	Sample mean	Sample standard deviation	Percent occurrence
Ambassidae	1.57	3.56	29
Ariidae	5.18	11.13	62
Atherinidae	0.04	0.20	6
Batrachoididae	0.36	2.08	3
Belonidae	4.33	7.97	50
Bothidae	0.01	0.05	3
Carangidae	7.79	9.09	88
Carcharhinidae	1.72	6.27	44
Centropomidae	2.26	4.53	59
Chanidae	0.56	2.27	24
Chirocentridae	0.33	1.32	12
Clupeidae	16.06	21.36	74
Drepanidae	0.67	2.06	41
Echeneidae	0.04	0.16	6
Elopidae	0.12	0.47	9
Engraulidae	6.56	15.84	29
Ephippidae	0.01	0.05	3
Gerreidae	1.11	3.72	24
Gobiidae	0.03	0.18	3
Haemulidae	2.58	4.97	65
Hemiramphidae	3.31	11.24	38
Leiognathidae	3.59	8.81	56
Leptobramidae	1.64	6.48	18
Lutjanidae	0.22	0.53	24
Megalopidae	2.65	7.37	35
Monodactylidae	0.10	0.40	9
Mugilidae	31.70	24.88	94
Platycephalidae	0.37	1.40	12
Plotosidae	0.03	0.10	9
Polynemidae	0.74	1.36	38
Rhinobatidae	0.04	0.17	6
Scatophagidae	0.67	1.95	26
Sciaenidae	0.14	0.67	9
Scombridae	0.98	2.08	44
Serranidae	0.11	0.33	12
Siganidae	0.02	0.12	3
Sillaginidae	0.46	1.37	24
Sparidae	0.15	0.46	18
Sphyraenidae	0.58	1.44	29
Stromateidae	0.12	0.49	9
Terapontidae	0.02	0.13	3
Tetraodontidae	0.71	2.86	9
Toxotidae	0.36	0.84	24

Analysis of fish community trends

In the 34 samples taken by the research teams within the 11 estuaries, 4382 fish were netted, representing 43 families and 116 species (Appendix 1). With an average catch per unit effort (CPUE) of 31.7 fish per sample and a percent frequency of occurrence of 94 %, Mugillidae were the most common fish netted (Table 3). Clupeidae were also common (CPUE 16.06, 74 % of the samples). Carangidae were third most common (CPUE 7.79, 88 % of the samples).

For the fish assemblage data set, inspection of the cluster analysis dendrogram (not illustrated) did not reveal any trends based on the 5 grouping factors tested. The initial MDS plots depicting the arrangement of samples, based on the rank order of the Bray-Curtis similarity values, revealed that 4 sample outliers (YgMar99, BaJun99, NoJul99, HuJul99) led to the collapse of the 30 remaining samples to an apparent single point. Sequential removal (Clarke & Warwick 2001) of these 4 samples (see below) unveiled the structure of the remainder in a final plot having a moderate stress level of 0.22 (Fig. 4). Samples separated into 2 sectors of the diagram: Tide-dominated (Tide) systems in the lower right quadrant, and Wave-dominated (Wave) systems arranged in a relatively dispersed distribution pattern forming an arc from the lower left to upper right.

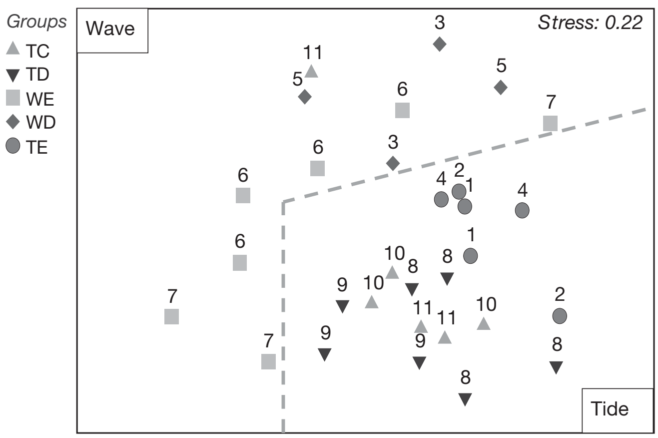

Fig. 4. Ordination of 30 samples by multidimensional scaling analysis (MDS) based on 43 families. Dashed line shows the division between Wave-dominated (Wave) and Tide-domi-nated (Tide) estuaries. See Table 1 for group definitions

differed significantly ($p < 0.05$) in 5 of the 6 possible cases; 1 pair (WE vs WD) did not separate significantly due to overlap and dispersion (Table 5). Thirdly, although replicate samples were taken in all estuaries during both wet and dry periods, season was not a systematic cause of variation. Fourthly, tests of the influence of exploitation on fish assemblage patterns revealed that although commercially and recreationally fished estuaries did not differ significantly from each other ($p = 0.315$), each differed from the remote and presumably lightly fished estuaries in east Cape York. Finally, each of the 3 bioregions differed significantly in fish assemblages. Given the analyses of these 5 factors, the estuarine sub-classifications most comprehensively accounted for the variation in the distributional patterns observed, and, thus, the composition of these 4 groups was examined in greater detail.

Within the Tide-dominated sector of the MDS diagram (Tide), 2 sub-groups were evident (Fig. 4). One sub-group, comprised of creeks and deltas, was moderately dispersed (IMD = 0.966), and included Haughton (8) and Barratas (9) (TDs), and Yellow Gin (10) and Nobbies (11) (TCs). Replicate samples from these 4 estuaries were well-mixed and will henceforth be referred to as the TCD sub-classification group. A second Tide-dominated sub-group, true estuaries, was relatively compact, and included Jacky Jacky (1), Escape (2) and Lockhart (4) (TEs).

Within the Wave-dominated sector of the MDS diagram (Wave), 2 sub-groups were also evident. One sub-group, comprised of deltas, was moderately dispersed, including Pascoe (3) and McIvor (5) (WDs). A second sub-group, comprised of true estuaries, was highly dispersed, including Russell (6) and Hull (7) (WEs); this group also included 1 replicate from Nobbies (11) (TC).

Five 1-way analyses of similarity (ANOSIM) were conducted based on the predefined ecological grouping factors (Table 4). Firstly, 2 broad estuarine classification groups (W vs T) were well separated (ANOSIM R = 47.4 %, $p < 0.001$). Secondly, the 4 sub-classification groups (TCD, TE, WE, WD) were also well separated (Global R = 41.7 %) and paired comparisons

Table 4. Summary of 1-way analyses of similarity (ANOSIM) comparisons between fish assemblages tested for 5 grouping factors. Data are CPUE by sample with 4 outliers removed

Grouping factor	No. of groups	Global relationship	Pairwise comparison	
Estuarine classification groups[a]	2	R = 47.4 % p < 0.001	W vs. T	
Estuarine sub-classification groups[b]	4	R = 41.7 % p < 0.001	TCD vs. WE	R = 45.7 %, p < 0.002
			TCD vs. WD	R = 65.1 %, p < 0.003
			TCD vs. TE	R = 25.2 %, p < 0.024
			WE vs. WD	R = 21.4 %, p < 0.112
			WE vs. TE	R = 47.5 %, p < 0.003
			WD vs. TE	R = 48.8 %, p < 0.005
Season[c]	2	R = –2.20 % p < 0.658		
Exploitation[d]	3	R = 21.3 %	Commercial vs. Recreational	R = 2.80 %, p = 0.315
		p < 0.001	Commercial vs. Remote	R = 37.9 %, p < 0.001
			Recreational vs. Remote	R = 24.9 %, p < 0.003
Bioregion[e]	3	R = 43.0 % p < 0.001	LMC vs. WTC	R = 45.7 %, p < 0.002
			LMC vs. ECY	R = 38.5 %, p < 0.001
			WTC vs. ECY	R = 51.3 %, p < 0.001

[a]W: Wave-dominated (Estuaries 3, 5, 6, 7 in Table 1); T: Tide-dominated (Estuaries 1, 2, 4, 8, 9, 10, 11)

[b]TCD (Estuaries 8, 9, 10, 11); TE (Estuaries 1, 2, 4); WE (Estuaries 6, 7); WD (Estuaries 3, 5)

[c]Dry season: Jun/Jul; Wet season: Feb/Mar

[d]Commercial: open to gill net fishing (Estuaries 7, 9, 11); Recreational: open only to recreational line-fishing (Estuaries 6, 8, 10); Remote: north of Cooktown, beyond coastal road access (Estuaries 1, 2, 3, 4, 5)

[e]LMC: TCD (Estuaries 8, 9, 10, 11); WTC: WE (Estuaries 6, 7); ECY: TE (Estuaries 1, 2, 4) and WD (Estuaries 3, 5)

Table 5. Mean values of diversity attributes based on unstandardised data for 4 estuarine sub-classification groups (see Table 4). One-way analysis of variance (ANOVA) was used to test for the significance of differences among the groups with post hoc multiple comparison tests (Fisher's LSD test, similar groups indicated by letters a and b). Total catch (N) was transformed ($\ln(x + 1)$) prior to analysis. Also shown is the index of multivariate dispersion based on standardised CPUE

Estuarine sub-classification groups[a]	Mean per sample: No. of families	Total catch N	Margalef family richness *d*	Shannon diversity *H'*	CPUE	Index of multivariate dispersion
	$p < 0.002$	$p < 0.030$	$p < 0.003$	$p < 0.050$	$p = 0.140$	IMD
TCD	14.4 a	343 a	2.5 a	1.57 a	47.3	0.966
WE	8.3 b	88 b	1.7 b	1.40 b	21.6	1.439
WD	14.0 a	246 a	2.4 a	1.61 a	5.8	0.972
TE	17.3 a	410 a	2.8 a	1.64 a	14.1	0.575
Mean of all samples	13	258	2.3	1.5	30.5	

[a]TCD (Estuaries 8, 9, 10, 11); TE (Estuaries 1, 2, 4); WE (Estuaries 6, 7); WD (Estuaries 3, 5)

Number of families, total catch, family richness, and diversity were each significantly lower for WE (Table 5). Highest indices occurred in TE for each measure. TCD had the greatest catch rate, while WD was much lower.

Taxonomic composition

A summary of the SIMPER analyses showing families contributing most to the dissimilarity between the 4 estuarine sub-classification groups is presented in Table 6. TCD samples typically included Ariidae, Carangidae, Haemulidae and Mugillidae (Table 6, Part B). These 4 families also typified TE, joined by Belonidae and Carcharhinidae. Three families were typically netted in WD systems: Carangidae, Megalopidae and Mugillidae. In contrast, the only family that was identified as diagnostic of WE was Mugillidae, a family which also typified all 4 groups.

The role of these 6 key families in the distinction of the 4 sub-classification groups was quantified by the discrimination index (Table 6, Part C). Consistency and magnitude of distributional trends have been further clarified by circle plots overlaid on the fish assemblage MDS diagram (Fig. 4) and by univariate analyses of mean catch rates (Fig. 5).

Ariidae discriminated TCD from WD and WE, as well as TE from WD and WE (Table 6, Part C). Every sample from the Tide-dominated systems included Ariidae (Fig. 5a), with significantly greater catch rates in TE (Fig. 5b). Haemulidae showed similar trends (Fig. 5c) but average CPUE did not differ significantly among the groups (Fig. 5d). Belonidae discriminated WE from TE, and was consistently caught in most samples from Tide-dominated systems, with average CPUE significantly lower for WE (=0) (Table 6, Fig. 5e,f).

Carangidae discriminated TCD from WD and TE (Table 6, Part C), with average CPUE significantly

Table 6. Comparison of sub-classification groups by top discriminating families based on SIMPER analysis of CPUE data for 30 samples. The families listed in this summary table had a typifying index greater than 1.3 and a discrimination index greater than 1.5 for at least one comparison. The average similarity and average dissimilarity values for all families in the samples within the grouping are given (abbreviations for groups given in Table 4)

Family	A. Average CPUE by cluster[a]: TCD	TE	WE	WD	B. Typifying index >1.3[b]: TCD	TE	WE	WD	C. Discrimination index >1.5[b]: TCD vs. WE	TCD vs. WD	TCD vs. TE	WE vs. WD	WE vs. TE	WD vs. TE
Ariidae	4.49	12.98	3.28	0.00	2.18	3.60	na	*0*	2.60	2.65	*1.37*	*0.40*	2.26	2.9
Belonidae	6.89	4.11	0.00	3.06	*0.87*	3.56	*0*	*0.41*	*1.33*	*1.21*	*1.40*	*0.87*	3.43	*1.44*
Carangidae	4.02	17.86	2.78	17.77	3.27	10.40	*0.93*	7.10	*1.30*	2.08	2.28	*1.35*	*1.41*	*1.27*
Carcharhinidae	0.16	2.54	0.10	9.95	*0.29*	5.42	na	*0.84*	*0.77*	*1.07*	2.25	*1.04*	2.51	*1.33*
Haemulidae	3.66	2.97	0.88	1.09	1.47	1.32	*0.22*	*0.41*	1.65	1.76	*1.19*	*0.80*	*1.43*	*1.42*
Megalopidae	0.13	0.78	0.76	19.27	*0.11*	*0.78*	*0.22*	4.02	*0.72*	2.77	*1.34*	2.1	*1.27*	1.63
Mugillidae	32.99	34.8	32.74	19.8	3.87	3.87	1.30	6.06	*1.20*	*1.36*	*1.17*	*1.33*	*1.15*	*1.35*
Average similarity or dissimilarity					52.2	60.8	40.7	52.4	59.8	61.6	50.3	60.4	62.3	51.0

[a]Values given are untransformed means
[b]All index values are given for comparison purposes; indices <1.3 (typifying index) and <1.5 (discrimination index) are italicised
na = no results possible given the data

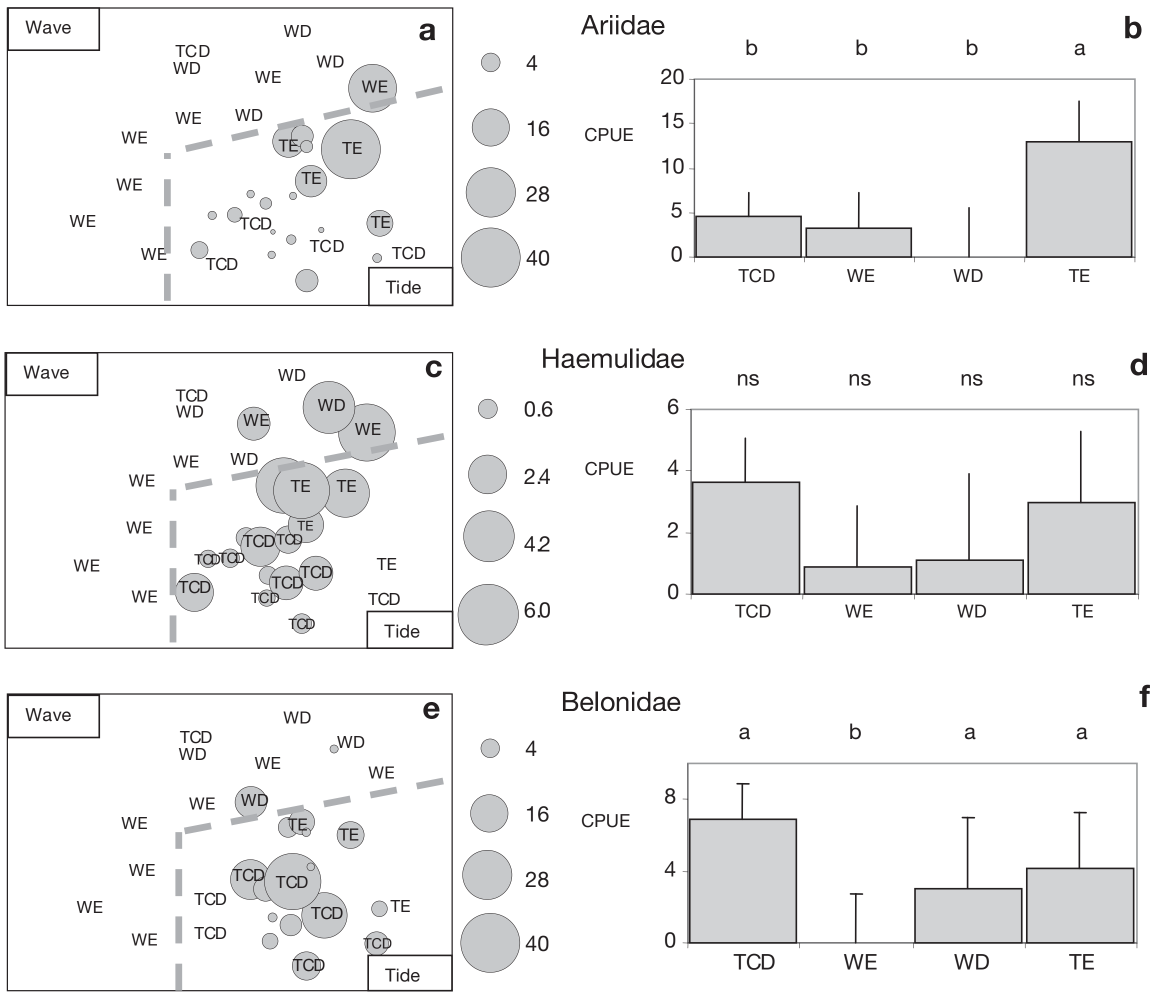

Fig. 5 (above and opposite page). Diagrams summarising multivariate and univariate analyses of standardized catch rates for key discriminating families (Table 6). See Table 1 for group definitions. Left panels: MDS ordination plots of 30 fish samples (Fig. 4) superimposed by circles sized in proportion to average catch per unit effort; dashed line shows the division between Wave-dominated (Wave) and Tide-dominated (Tide) estuaries. Right panels: average catch per unit effort (with error bars representing standard error) by sub-classification group. Letters above columns indicate membership in groups formed by Fisher's LSD test. ns: not significant. (a,b) Ariidae; (c,d) Haemulidae; (e,f) Belonidae; (g,h) Carangidae; (i,j) Carcharhinidae; (k,l) Megalopidae

greater in WD and TE (Fig. 5g,h). The 2 groups (WD, TE) having higher catch rates of Carangidae were, in fact, all of the East Cape York (ECY) systems surveyed in this study (i.e. Estuaries 1 to 5, Fig. 1). Likewise, Carcharhinidae, which discriminated TCD from TE, and WE from TE, were consistently caught in WD and TE, systems where average CPUE was significantly greater (Fig. 5i,j). Finally, Megalopidae, which discriminated WD from each of the other groups, was consistently caught in WD, with CPUE significantly greater in WD systems (Fig. 5k,l).

Thus, while each of the 6 key discriminating families had a somewhat unique distribution, overall trends emerged. Firstly, all Tide-dominated systems (TE, TDC) had high and/or consistent catch rates of Ariidae, Haemulidae and Belonidae (Fig. 5a–f). Secondly, catch in ECY sites (TE, WD) usually had high and/or consistent catch rates of Carangidae and Carcharhinidae (Fig. 5g–j). Finally, Megalopidae were always caught in high numbers in WD (Fig. 5k,l).

Of the 4 outlier samples, 3 had unusually high catch rates for a particular family (compare with averages, Table 3). Specifically, for HuJul99, 88.27 Clupeidae were caught per net hour and for BaJul99, 47.61 Ariidae were caught per net hour. For YgMar99, 18.2 Centropomidae were caught per net hour as a fish kill was observed due to oxygen levels as low as 1.76 mg l^{-1}. For 1 outlier, NoJul99, only 3 families were caught: Haemulidae, Mugillidae and Carangidae.

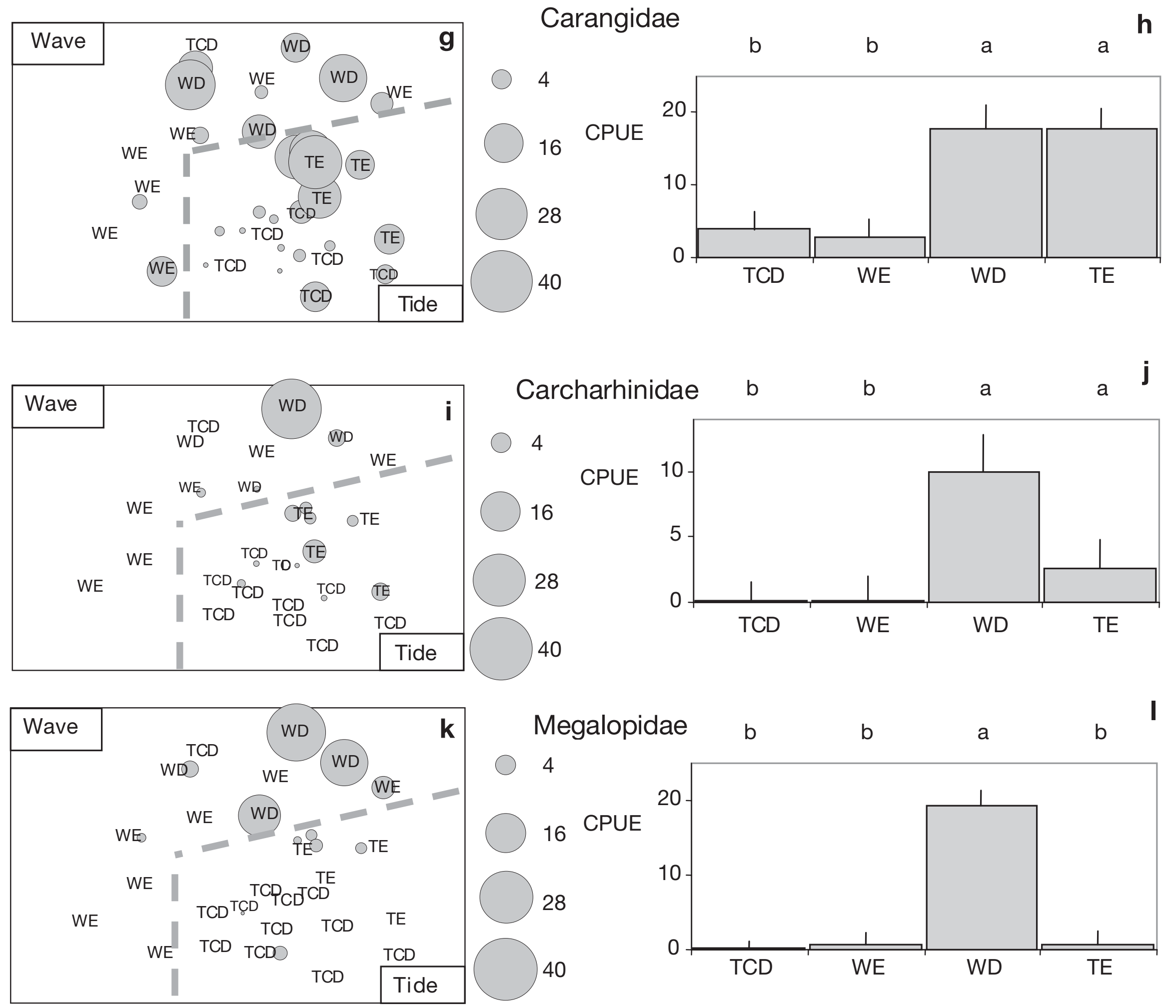

Fig. 5 (continued)

Fish assemblage and abiotic variable relationships

Each abiotic variable was individually tested for correlation with the fish assemblage matrix of similarity (4 outliers removed) using the BIO-ENV routine. The best correlations occurred for elevation, rainfall, Mangkm2 and EntWdkm (Table 7a). The relative influence of these abiotic variables upon the overall distribution pattern derived for the fish assemblage based on the MDS analysis has been illustrated in Fig. 6. One general pattern conveyed by this analysis was that samples which were similar in terms of fish assemblage patterns were also similar in terms of these abiotic attributes. For example, all the samples in the lower right quadrant of the fish MDS analysis (Fig. 3b) were in catchments with lower elevation/less rainfall, greater mangrove area, and greater estuary entrance width (Fig. 6a–c). ANOVA results further illustrate the differences among the 4 classifications in terms of these key attributes (Table 7b).

Correlation values for the combinations of abiotic variables were generated by BIO-ENV. The best combination of abiotic variables was found for a selection of 6 variables, yielding a correlation coefficient of 42.9% (Table 7c). The best combinations for each set of variables less than 6 are also presented in Table 7c.

DISCUSSION

The geomorphic process-based framework (Dalrymple et al. 1992, Harris et al. 2002) was an appropriate basis for classifying whole coastal water bodies in the study area. As illustrated conceptually in Fig. 7, the abiotic attributes varied systematically among the 11 estuaries apparently due to complex interactions among 3 main forces (river flow, tides and exposure to waves at the entrance) generating trends in habitat conditions. Not only were attributes of the estuaries themselves important discriminators, but catchment

Table 7. Comparison of abiotic attributes and fish assemblages based on BIO-ENV analysis. (a) Rank correlation for individual abiotic variables and the fish assemblage matrix; (b) One-way analysis of variance (ANOVA) was used to test for significant differences in means among the groups. Results of post hoc multiple comparison tests (Fisher's LSD test) are indicated by letters; (c) Summary of the best-correlated combinations of variables listed by Spearman rank correlation level. Data presented are the best combinations for the maximum number of variables shown in the first column

(a)

Variable number	Variable name	Correlation
1	Water area	0.039
2	Salinity	0.094
3	Temp	0.046
4	Latitude	0.099
5	Mangkm2	**0.284**
6	Mudindex	0.115
7	Condition	0.113
8	**Elevation**	**0.374**
9	**Rain**	**0.372**
10	**EntWdkm**	**0.234**
11	Basinkm2	0.070

(b)

Estuarine classification groups	Mean per sample Mangkm2	Elevation (m)	Rainfall (mm)	EntWdkm
	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$
TCD	21.62 b	100 d	960 c	2.38 b
WE	8.57 c	1571 a	2947 a	0.15 e
WD	1.15 d	400 b	1563 b	0.38 d
TE	57.33 a	233 c	1386 b	3.54 a

(c)

Number of variables	Correlation	Variable selections
6	0.429	2,5,7,8,9,11
5	0.420	2,5,7,8,9
4	0.415	2,5,8,9
3	0.413	2,8,9
2	0.393	2,9
1	0.374	8

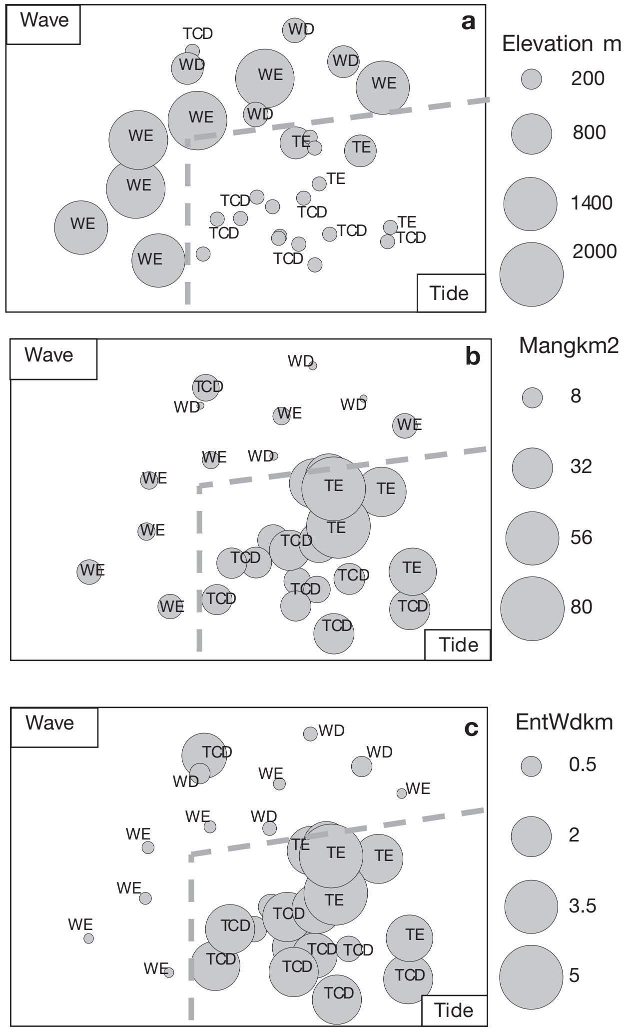

Fig. 6. MDS ordination of fish assemblages (Fig. 4) with key abiotic attributes (Table 7) superimposed by circles sized in proportion to the values for each sample. Dashed line shows the division between Wave-dominated (Wave) and Tide-dominated (Tide) estuaries. See Table 1 for group definitions. (a) Elevation (m); (b) Mangkm2; (c) EntWdkm

scale variables (i.e. encompassing attributes and processes at a scale broader than the estuary itself) added substantially to classifying these coastal water bodies. Results of the current study indicate that this classification framework also correlates substantially with variation in fish assemblages among the estuaries. Abiotic factors having the greatest correlation with fish community composition in these tropical estuaries were: (1) hydrology (rainfall, elevation); (2) configuration of the estuary mouth (EntWdkm); and (3) area of mangrove coverage (Mangkm2) (Table 7). These general features generate physico-chemical and biological processes fundamentally influencing habitat use by tropical estuarine fishes.

The estuaries

Variation among the catchments was largely a function of rainfall and elevation, attributes which were highly correlated ($r = 0.96$). This relationship probably occurred due to spatial variation in the orographic effect throughout the study area (Furnas 2003). The Great Dividing Range occurs directly adjacent to the shores of the Pacific Ocean in each of the Wave-dominated catchments (Russell, Hull, McIvor, Pascoe). In addition to coastal rainfall, storms high in the rainforest flush freshwater into the estuaries. The dual sources of rainfall (highland and local) apparently generate salinity conditions that are relatively lower and

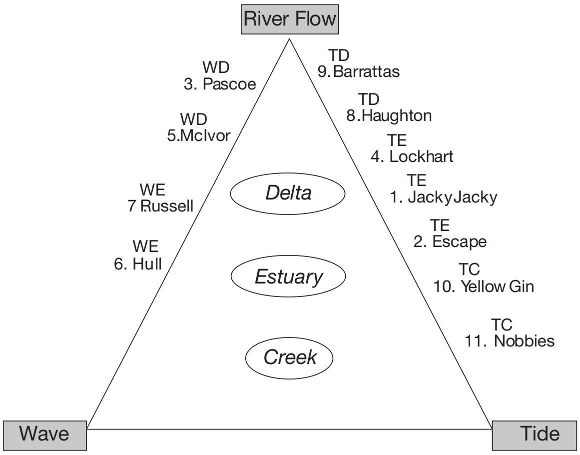

Fig. 7. Conceptual arrangement of study sites based on the perceived relative power of 3 forces, riverine, tide and waves (after Dalrymple et al. 1993)

more variable in these systems (Halliday et al. 2001). In contrast, Tide-dominated systems were located in catchments with lower elevations where the Great Dividing Range lies further inland. In these catchments, the orographic effect was not a dominant process, and thus they received less, more predictable, rainfall than the Wave-dominated systems.

Classification of the estuaries was also a function of influences at the estuary entrance. In higher elevation catchments, rivers reach the coast via a relatively narrow floodplain. The outfalls of the resultant Wave-dominated systems flow straight into the exposed open coast where high wave energy overrides the influence of tides at the mouth (Harris et al. 2002). As a result, one distinctive feature of Wave-dominated systems is a constricted mouth (see Table 7b) flanked by a sandy barrier. In contrast, the Tide-dominated systems occur along more protected sections of lower relief coasts, and in these systems tidal forces are a greater influence than offshore winds at the estuary entrance, thus generating a wide deltaic mouth.

In the process-based classification framework, Wave- and Tide-dominated systems differed in terms of habitat available to fishes. All Tide-dominated systems had organically rich, muddy substrate (Fig. 3b, Table 1). At the sub-classification level, Tide-dominated deltas (TD) and estuaries (TE) had elongate mud banks, aligned parallel to the direction of tidal flow, and separated from one another by deep channels. Mangrove forests partially covered the mud banks, often backed by freshwater wetlands and *Melaleuca* spp. swamps. Prior to data analysis, Yellow Gin and Nobbies were thought to be examples of the third sub-classification type, Tide-dominated creeks (TC). As expected, Yellow Gin had fine muddy substrate, observed high turbidity, and abundant mangroves (Table 1). However, Nobbies did not conform with expectations for TCs, in that the substrate was comprised of coarse sand and shells, water clarity was high, and an expansive seagrass bed occurred immediately offshore (a feature that was unique among all the estuaries in the current study). Freshwater springs are known to occur in the area, and thus Nobbies may receive groundwater seepage modifying the habitat conditions.

The forces generating habitat conditions in Wave-dominated systems differ from Tide-dominated systems because tidal influence and waves are attenuated by the sandbar at the narrow estuary mouth (Harris et al. 2002). As such, substrate in the Wave-dominated systems was mainly sand, shell and/or rock due to riverine flushing. Pascoe and McIvor were typical of Wave-dominated deltas (WD), in which the river connects to the sea with little or no interior basin (Harris et al. 2002). Mangroves were limited in area, mainly forming a fringe along the immediate shoreline (*Nypa fruticans* in McIvor; *Rhizophora* spp. in Pascoe). Hull and Russell true estuaries (WE) had broad central basins inside the mouth with moderately expansive mangrove areas, attributes which generally distinguish WE from WD (Table 7b).

Given these attributes, the availability of food and cover, as well as the nature of the aquatic conditions, differed greatly among the systems. These habitat differences strongly influenced the composition of the fish communities, as discussed below.

Fish/habitat relationships

Among the 4 estuarine sub-classification groups (TCD, TE, WE, WD) which most comprehensively accounted for the variation in fish assemblages, WE (Russell, Hull) had significantly lower diversity, family richness and greater dispersion (Table 5). The WE estuaries also had variable salinities (Halliday et al. 2001), a known stressor for biotic communities (Montague & Ley 1993, Sheaves 1998). In contrast, the greatest family richness and smallest dispersion index were found for TE (Jacky Jacky, Escape, Lockhart), where salinity may be more predictable.

Fish assemblages in Tide-dominated systems were separated from Wave-dominated systems due to higher catch rates of Ariidae, Belonidae and Haemulidae (Table 6). Common euryhaline residents and marine migrants in Indo-Pacific estuaries (Blaber 1997), these fishes were caught in adult and juvenile size classes (Table 8). High turbidity, a defining characteristic of Tide-dominated systems (Ryan et al. 2003), was consistently observed, possibly affording greater protection for small to mid-sized demersal fishes through reduced visual predator effectiveness (Blaber 1997). Expansive deltaic entrances, comprised of mud banks, mangroves and complex networks of narrow sinuous channels, may also provide protection from predation and enhance food

Table 8. Life history, food items consumed and estuary type in which catch rates were high and/or consistent (see Table 6). Maximum length is given for the most prevalent species comprising the catch by family (Appendix 1)

	Ariidae	Belonidae	Carangidae		Carcharhinidae	Haemulidae	Megalopidae
	various species	*Strongylura strongylura*	*Caranx ignobilis*	*Scomberoides commersonianus*	*Carcharhinus leucas*	*Pomadasys kaakan*	*Megalops cyprinoides*
Fraction of family total (%)		60	58	19	77	62	100
Life history stage							
Max. size (mm)[a]		500	1200	1700	3500	800	1500
Size caught (mm)	190–472	200–460	50–459	50–900	500–1100	57–620	210–515
Estuary type selected[b]	TCD, TE	TCD, TE	WD, TE (ECY)	WD, TE (ECY)	WD, TE (ECY)	TCD, TE	WD
Food items[c]							
Crabs: portunid			8 %				
Crabs: sesarmid/grapsid	65 %		8 %		10 %	33 %	17 %
Shrimps: penaeid	9 %		54 %	16 %	10 %	17 %	17 %
Shrimps: *Acetes* spp.	4 %		10 %	5 %			
Burrowing crustaceans	26 %		18 %		10 %	50 %	
Fish: benthic	13 %		6 %		20 %		
Fish: other	13 %	100 %	42 %	100 %	60 %	17 %	83 %
Fish: scales	4 %					17 %	
Insects							50 %
Molluscs	22 %				20 %	17 %	
Non-chitinous invertebrates	22 %					25 %	
Plants	9 %		4 %				
Number of gut specimens	23	10	50	44	10	12	6
Size of gut specimens (mm)	460–472	360–460	176–459	213–800	398–750	140–620	372–477

[a]Froese & Pauly (2005); [b]interpreted from Table 6 and Fig. 5; [c]percent frequency of occurrence

webs for demersal fishes such as Ariidae and Haemulidae. Stomach contents of Ariidae and Haemulidae contained a variety of foods typically associated with muddy substrate and mangrove detritus, including sesarmid and grapsid crabs, burrowing crustaceans and molluscs (Table 8) (Robertson & Blaber 1992, Ellison & Farnsworth 2001). Belonidae, predators which capture prey by diving from the surface in shallow waters (Blaber 1997), had consumed only small pelagic fishes. Thus, the fishes which distinguished the Tide-dominated estuaries from Wave-dominated systems (Ariidae, Haemulidae and Belonidae) were common euryhaline families, well-adapted to mangroves, mud flats and high turbidity.

East Cape York (ECY) systems (TE, WD), had higher catch rates of Carangidae and Carcharhinidae (Table 6). The abiotic attributes measured in this study varied among these systems, and did not explain this observed pattern. This unexplained source of variation in fish distribution indicates why the best combination of abiotic variables had a correlation with the fish data set of only 42.9 % (Table 7c). Limited food habits analyses identified these families as mainly piscivores, and size ranges suggested the catch was largely comprised of juveniles (Table 8). Thus, the ECY estuaries may primarily function as nursery/feeding grounds for these families. Given that ECY is the northern-most bioregion, latitude might explain these trends; i.e., Carangidae and Carcharhinidae may become increasingly prevalent in more tropical estuaries. However, latitude was very poorly correlated with fish assemblage patterns (Table 7). Variation in conditions on the oceanside of the region may also contribute to the pattern observed in ECY. For example, recruitment of reef fish may vary due to coral reef area, patch density and larval/juvenile hydrodynamic pathways. However, given the remoteness of ECY estuaries and the finding that exploitation was a significant factor in structuring the fish assemblages overall (Table 5), capture of Carangidae and Carcharhinidae by both commercial and recreational fishers in more populated areas (LMC and WTC) was very likely to have contributed to the observed pattern. Higher catch rates in ECY may be indicative of how designation of no-take reserves (i.e. closed to all exploitation) would influence populations of these families elsewhere in the study area. Indeed, the ECY estuaries may represent examples of unexploited fish assemblages typical of the region, if top level predators such as Carangidae and Carcharhinidae were not removed by fishing.

Wave-dominated deltas (WD), both located in ECY (Pascoe, McIvor), had higher catch rates of Megalopidae, all in larger juvenile size classes (Table 8). These systems had by far the lowest mangrove coverage and narrowest entrances of all the systems (Table 7b), as well as other unique habitat features discussed above. In addition, overall catch rates for all species combined were also relatively low in WD (Table 5). Insects (cicadas, coleopterans, odonata) were the dominant food items found in the stomachs of *Megalops cyprinoides* (Table 8). This species has the capacity to breathe air from the surface to supplement its oxygen supply and often occurs in waters with low dissolved oxygen (Allen et al. 2002). Wave-dominated deltas may become stratified as the estuary entrance becomes constricted, perhaps leading to oxygen depletion (Edgar et al. 1999). Thus, while these systems may be relatively low quality habitats for most estuarine fishes in terms of food, cover and aquatic conditions, juvenile *M. cyprinoides* apparently thrive in them with little competition and predation.

Limitations of the study

Although a range of mesh sizes was deployed, one limitation of the study was the selectivity of the research gill nets. Ancillary line-fishing data (unbaited lures) collected concurrently with ECY net sampling suggest that although abundances varied, most families in larger size classes were probably represented in the net samples, i.e. only 1 line-caught family was not represented in the net samples: Opistognathidae (n = 3). In terms of catch rates, Lutjanidae, Serranidae and Sparidae comprised 21, 18 and 5%, respectively of the line-caught fishes (n = 359), while these families comprised <1% of the total netted fishes (n = 1715). However, the influence of gear selectivity on abundance would have been reduced by applying a 4th-root-transformation to the catch data, thereby increasing differentiation between sites based on rare species (Clarke & Green 1988). Ideally, a combination of methods would improve the sampling regime in future studies. It should be noted that in pilot studies carried out for the current investigation, frequent sightings and interactions with estuarine crocodiles *Crocodylus porosus* in ECY led to the elimination of certain sampling techniques (e.g. visual census, trap nets) and procedures for safety reasons.

A further limitation of the study was the risk that analysis at the family level of taxonomic resolution biased the results. Taxonomic uncertainty was a problem in the current study because these comprehensive surveys of fish communities in the remote east Cape York estuaries were largely unprecedented and useful taxonomic keys have not yet been developed for several families in the region. However, comparing the effects of taxonomic aggregation in multivariate analyses, several investigators have generated the same patterns of similarities among sites regardless of whether taxa were analysed at the level of species, genus or family (Karakassis & Hatziyanni 2000, Clarke & Warwick 2001). Furthermore, of the 43 families identified, 22 were represented by a single species (Appendix 1); i.e., for these 22 taxa analysis at the family level resulted in the loss of no information. Finally, at the regional scale of the current study, the family level of taxonomic resolution may indeed be the most effective for discerning ecological patterns (Nagelkerken & van der Velde 2004).

Management implications

Estuaries are vulnerable to human activities which can reduce their value as fish habitats. Management actions to conserve estuarine values may include: (1) prevention of degradation of important processes and attributes through regulatory measures, and (2) fully protecting high value systems as aquatic reserves. Firstly, based on the results of the current study, essential underlying factors of prime importance in determining the fish assemblages were defined by an interaction of catchment hydrology, configuration of the estuary mouth, and mangrove area. Developments that significantly modify river flow (e.g. water diversions), interrupt natural processes at the mouth (e.g. stabilisation projects), or eliminate mangroves are likely to fundamentally alter the habitat and the fish assemblages supported by these systems. Finally, the results here support programs using a surrogate approach and generally available data to establish network of estuarine reserves for the conservation of fish biodiversity throughout broad coastal regions.

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Appendix 1. Catch by species and estuarine sub-classification group netted in 11 northeastern Australian estuaries

Family	Species	TCD[a]	TE[b]	WD[c]	WE[d]
Carcharhinidae	*Carcharhinus ambionensis*				2
	Carcharhinus leucas	8	16	9	
	Carcharhinus limbatus		1		
	Carcharhinus sp.	7	2		2
	Negaprion acutidens		6	4	
Rhinobatidae	*Aptychotrema rostrata*		1	1	
Elopidae	*Elops australis*	4			
Megalopidae	*Megalops cyprinoides*	4	12	85	3
Clupeidae	*Anodontostoma chacunda*	10	24	50	
	Clupeidae		40	4	
	Escualosa thoracata	36			6
	Herklotsichthys castelnaui	691	27		71
	Nematalosa come	53	17	22	1
	Nematalosa erebi				9
	Sardinella albella		18		
	Sardinella brachysoma	81	9		
	Sardinella sp.		40		
Engraulidae	*Stolephorus commersoni*	9			3
	Stolephorus nelsoni	18			
	Stolephorus sp.	13			2
	Thryssa hamiltoni	193			2
Chirocentridae	*Chirocentrus dorab*	3			1
Chanidae	*Chanos chanos*	3	3	2	
Ariidae	*Arius* spp.	95	101		5
Plotosidae	*Plotosidae*		1		
	Plotosus canius		3		
Batrachoididae	*Halophryne diemensis*	3			
Hemiramphidae	*Arrhamphus sclerolepis*	27	6		37
	Hyporhamphus quoyi	1			2
	Zenarchopterus buffonis	7	2		2
Belonidae	*Strongylura strongylura*	86	20		
	Strongylura urvilli		7	1	
	Tylosurus crocodilus		19	30	
	Tylosurus gavialoides		9		
Atherinidae	*Atherinidae*		5		
Platycephalidae	*Platycephalus fuscus*	4		1	
	Platycephalus sp.			2	
Centropomidae	*Lates calcarifer*	73	9	9	13
	Psammoperca waigiensis		1		
Ambassidae	*Ambassis gymnocephalus*	2	3		
	Ambassis nalua	1			
	Ambassis vachelli	32			4
Serranidae	*Epinephelus malabaricus*	2	1	1	
Terapontidae	*Amniataba caudavittatus*			2	
Echeneidae	*Echeneidae*		2		
	Echeneis naucrates			1	
Sillaginidae	*Sillaganidae*		1		
	Sillago analis	1			
	Sillago ciliata		2		
	Sillago sihama	9			1
Carangidae	*Carangidae*	1			
	Carangoides uii		1		
	Caranx bucculentus	1			
	Caranx ignobilis	8	48	22	4
	Caranx papuensis			1	
	Gnathanodon speciosus		5	5	
	Scomberoides commersonianus	40	166	35	6
	Scomberoides lysan	5	9	1	1
	Scomberoides sp.		1		
Carangidae (cont.)	*Scomberoides tala*	1	2	18	1
	Scomberoides tol		38	2	
	Trachinotus blochi		1	1	2
	Ulua mentalis		1		
Leiognathidae	*Gazza minuta*		6		
	Leiognathus brevirostrus	2	1		
	Leiognathus equulus	11	2	26	46
	Leiognathus fasciatus			3	
	Leiognathus sp.	1	2	2	
	Leiognathus splendens	8			
	Secutor ruconius	1			
Lutjanidae	*Lutjanus argentimaculatus*	2		1	2
	Lutjanus johnii	1	1		
	Lutjanus russelli			1	
Gerreidae	*Gerreidae*		2		
	Gerres abbreviatus		2	1	
	Gerres acinaces			13	
	Gerres argyreus			1	
	Gerres filamentosus	2		6	1
	Gerres macrosoma			2	
Haemulidae	*Plectorhynchus gibbosus*	]1	8		
	Pomadasys argenteus	32	2	1	1
	Pomadasys kaakan	39	29	5	1
Sparidae	*Acanthopagrus berda*	1	4	3	
Sciaenidae	*Nibea soldado*	11			
Monodactylidae	*Monodactylus argenteus*			3	3
Leptobramidae	*Leptobrama mulleri*	38			
Toxotidae	*Toxotes chatareus*	3	17	2	
	Toxotes jaculatrix		1		
Ephippidae	*Platax orbicularis*		1		
Drepanidae	*Drepane punctata*	11	11	3	12
Scatophagidae	*Scatophagus argus*	1	8	2	
	Scatophagus multifasciatus	6	7	1	
Mugilidae	*Liza subviridis*	171	170	47	3
	Liza vaigiensis	18	31	10	8
	Mugil cephalus	10			
	Mugilidae		102	11	
	Valamugil buchanani	35	48	6	11
	Valamugil cunnesius	248	8	13	85
	Valamugil seheli	11	1	1	2
	Valamugil sp.	11	39	9	3
Sphyraenidae	*Sphyraena barracuda*		2	6	1
	Sphyraena jello	1	16		1
	Sphyraena sp.	1			2
Polynemidae	*Eleutheronema tetradactylum*	48	5		
	Polydactylus macrochir	16	3		
	Polynemidae		1		
	Polynemus heptadactylus	1			
Gobiidae	*Glossogobius biocellatus*	1			
Siganidae	*Siganus lineatus*		3		
Scombridae	*Scomberomorus semifasciatus*	17	7	1	5
Stromateidae	*Parastromateus niger*	1	5		
Bothidae	*Pseudorhombus arsius*		1		
Tetraodontidae	*Arothron hispidus*	2			
	Arothron reticularis	1			
	Chelonodon patoca	2			
	Marilyna pleurosticta	2			
Grand total	**Abundance (n = 4382)**	**2300**	**1226**	**489**	**367**
	Count (n = 116)	**72**	**74**	**51**	**40**

[a]TCD: Tide-dominated Creek/Delta (from Table 2; Estuaries 8, 9, 10, 11). [b]TE: Tide-dominated Estuary (Estuaries 1, 2, 4).
[c]WD: Wave-dominated Delta (Estuaries 3, 5). [d]WE: Wave-dominated Estuary (Estuaries 6, 7).

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