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ABSTRACT

Worldwide, estuaries have been recognized as critical habitats for nearshore fish productivity through their capacity as nursery grounds and nutrient sources. The purpose of this study was to demonstrate the importance of the habitat characteristics of estuaries to commercial fish catch in Queensland, Australia, with particular focus on the role of mangrove, saltmarsh, and seagrass habitats, and their connectivity. Traditionally, such analyses have taken the single-habitat approach, i.e., assessing the value of individual habitat types. Combined occurrence of these habitats and their collective accessibility may better explain the importance of estuaries to nekton. A literature review identifies the role of estuaries as integrated systems for fisheries. **Our study provides strong supportive evidence for habitat-based, not species-based**, management of fisheries in Queensland. Outcomes from preliminary analyses in Queensland suggest that collective spatial characteristics of estuarine habitats such as size and structural connectivity significantly correlate with fish catch data with r^2 values > 0.7 for 17 commercial species groups. The catch of one quarter of the investigated species was best explained by the presence of mud- and sandflats. An exploration of currently available data on habitat distribution and fisheries catch shows the need to scrutinise their spatial and temporal accuracy, and how best to use them to understand estuarine-fisheries links. We conclude that structural connectivity of estuarine habitats is fundamental to the size of fish stocks and to optimizing the sustainable yield for commercial and recreational fishers.

Estuaries play an important, often essential, role in the life histories of many aquatic organisms (Blaber, 2000), including fish species of importance to indigenous, commercial, and recreational fishers (Dunning et al., 2001). In Australia, estuarine ecosystems comprising mangroves, seagrasses, and shallow-water areas provide critical habitats to about 70%–75% of fish and crustacean species in the fisheries of Queensland (Quinn, 1993) and New South Wales (Pollard, 1981). This value is lower for south-western Australia (20%) and Australia as a whole (32%), which are less dominated by estuary-dependent species (Lenanton and Potter, 1987). Australia's total annual economic value of the fishery industry in 2002 was AUD$7.4 billion (Williams, 2002) including the gross value of production (GVP) of AUD$2.3 billion (ABARE, 2005). The fisheries production from some coastal estuaries and lagoons is estimated at up to 3.3 t km^{-2} yr^{-1} (Pollard, 1994).

The importance of estuarine habitats rests not only with their extent, but also their combined occurrence and relation to each other. Attributes of the estuarine "seascape" may also be critical for sustaining productivity of coastal fisheries. We expect that estuary-dependent species catch would increase with the size of connected estuarine habitats. Previous studies have found positive correlations between mangrove extent and fisheries catch (Baran et al., 1999; Manson et al., 2005b) only a few have examined multiple habitats (Saintilan, 2004; Lee, 2005). Most estuary-dependent species use a wide range of habitats during their life history. Not all habitats contribute equally as nurseries (Beck et al., 2001), but comparison of their values has rarely been rigorously undertaken.

The purpose of this study is to demonstrate the importance of estuarine habitat characteristics to commercial fish catch, with particular focus on the role of mangroves, saltmarsh, seagrass, and mud- and sandflats as connected habitats driving observed fluctuations in fish catch. The connectivity of habitats can be a key factor in fish production by allowing exchange of energy and organisms (Merriam, 1984) among estuarine habitats. This also includes "edge effects", which reflect changes in ecological factors at the boundary between habitats, thus supporting the "chain of habitats" concept as a useful management system for Australian and worldwide species (e.g., Nagelkerken et al., 2001). Here we: (a) briefly analyze current knowledge and literature in regard to the importance and role of estuaries for fisheries; (b) examine deficiencies of studies that address the relationship between estuarine habitats and fish catch; (c) present information available for assessing the linkage between estuaries and commercially important fish species; (d) provide a case study relating combined occurrence of Queensland estuarine habitats with fish catch data using multiple regression models and non-metric multidimensional scaling (nMDS); and (e) discuss ways of assessing the data and benefits for fisheries management.

An Overview of Studies Linking Estuarine Characteristics and Fisheries Using Fish Catch Data.—The importance of biotic and abiotic characteristics of estuaries to fish assemblages has been demonstrated in a number of studies (Horn and Allen, 1976; Monaco et al., 1992; Pease, 1999; Blaber, 2000). More specifically, estuary size characteristics have been demonstrated to be correlated with fish assemblages, e.g., mouth width (Horn and Allen, 1976); mouth depth (Monaco et al., 1992), and water area (Pease, 1999).

Pollard (1994) attempted to collate and contrast the historical data for the south coast estuaries of New South Wales, Australia. He found that only rank abundance could be derived from this information for comparative purposes. The outcomes were affirmed in analyses undertaken by Pease (1999) and Saintilan (2004). These studies used similar multivariate techniques to Stergiou and Pollard (1994) and were based on commercial fisheries data for New South Wales. Interactions between abiotic and biotic estuarine characteristics and fish assemblages have been widely investigated in temperate estuaries (Perkins, 1974; Barnes, 1980; Day et al., 1989; Pease, 1999). A number of studies comparing commercial fish catch with estuarine habitats, in particular, mangroves and prawns in tropical and subtropical zones, have been completed in the last few decades. Most of these studies showed positive relationships, assuming that the area of tidal wetland habitat translates to the secondary production and catch of commercial fisheries (Baran and Hambrey, 1998; Baran et al., 1999; Manson et al., 2005a). Rönnbäck (1999), for example, listed the proportion of mangrove-related species in fisheries around the world giving a figure of 67% for eastern Australia. In Malaysia, it was estimated that 32% of the biomass (total fish catch) of the 1981 fish harvest could be linked to mangroves; while in the Philippines, about 72% of the catch between 1982 and 1986 was associated with mangroves (Paw and Chua, 1991).

Analyses of estuaries and fish catch data have demonstrated the potential of data sets available for Australia (Pease, 1999; Duffy et al., 2003; Saintilan, 2004; Manson et al., 2005b). Several studies have found correlations between the extent of mangroves and the catch in nearby fisheries (Staples et al., 1985; Manson et al., 2005b; Table 1).

Table 1. Overview of studies investigating relationships between estuarine habitat distribution and fisheries production for prawn (+) or fish (++) or both if not indicated in the last three decades (Baran, 1999; Manson et al., 2005a). Not reported is shown as "nr". The r^2 value indicates goodness of fit of a linear model between habitat and catch.

r^2 (n)	Region	Variable	Reference
Positive	Malaysia	Mangrove area	Macnae, 1974
0.54 (27)+; 0.64 (14)+	World, tropical	Intertidal area	Turner, 1977
0.89 (nr)+	Indonesia	Mangrove area	Martosubroto and Naamin, 1977
0.58 (6)+	Gulf of Carpentaria, Australia	Linear extent of mangroves	Staples et al., 1985
0.48 (10)++	Gulf of Mexico	Coastal vegetation area	Yáñez-Arancibia, 1985
0.53 (nr)++	World, tropical	Mangrove area	Pauly and Ingles, 1986
Positive	Philippines	Mangrove area	Camacho and Bagarinao, 1987
0.89 (10)+	Peninsular Malaysia	Mangrove area	Sasekumar and Chong, 1987
0.32 (nr)+	U.S.A	Salt marsh length interface	Browder et al, 1989
0.61 (18)+; 0.66 (18)+; 0.34 (15)++; 0.88 (5)++ 0.53 (18); 0.40 (20); 0.66 (12); 0.40 (18); 0.4 (34); 0.45 (39); 0.95 (nr)	Philippines	Mangrove area	Paw and Chua, 1991
0.95 (nr); 0.88 (5)++	Vietnam	Mangrove area	de Graaf and Xuan, 1998
Positive++	Philippines	Mangrove area	Gilbert and Janssen, 1998
0.38 (37)++	World, tropical	Coastline length, mangrove area, tidal amplitude	Lee, 2004
0.32–0.75 (49)	NewSouthWales Australia	Total area of mangrove, saltmarsh, seagrass	Saintilan, 2004
0.46–0.63 (8)	Malaysia	Mangrove area	Loneragan et al, 2005
0.37–0.70 (36)+; 0.57–0.77 (36)++	East coast Queensland, Australia	Mangrove perimeter, area shallow water, mangrove area/length coast line	Manson et al., 2005b

Lee (2004) suggested that the amount of intertidal habitats and energy available for material exchange, as indicated by tidal amplitude, rather than just the area of mangroves functions as a major driver for prawn production. The correlation of mangrove, saltmarsh, seagrass distribution as well as channels and flats in estuaries supports the idea of a link between these habitats. A study by Saintilan (2004) found a strong correlation between mangroves and saltmarsh distribution (correlation coefficient 0.79) for estuaries in New South Wales. Although studies have documented greater abundances of juvenile species in mangroves compared to other estuarine and inshore habitats (e.g., in Australia; Laegdsgaard and Johnson, 2001), other estuarine habitats and the strong links between them have been neglected (Sheridan and Hays, 2003). However, the continuity and interdependence of riverine, estuarine, and marine environments is an ecological reality for coastal fish resources (Baran et al., 1999). To maintain fisheries production, the combination of estuarine habitats that are utilized by different species and their various life history stages must be taken into account to ensure the inclusion of all resources required by these species (Lee, 2004). It is essential to determine the dependency of fish resources on estuarine environments by addressing the following questions regarding the capacity of any given species in completing its life cycle: (1) is the estuarine zone essential?, (2) how strong is the dependency on habitat?, and (3) which habitat characteristics are critical?

Methods

Data Collection.—Data on catch, effort (number of days and boats), and gross value of production for estuary-dependent species or species groups were provided by the Department of Primary Industries and Fisheries, Queensland (DPI&F) Assessment and Monitoring Unit (Table 2). This data set is based on daily logbook records reported by commercial fishers providing details of their catch and effort, covering the years 1988–2004, and recorded in half-degree grids (30-nmi) for the entire coast of Queensland. Data from each of the four fisheries (trawl, line, net, and pot) can be distinguished. The trawl fishery for prawns has two components: a within-estuary (river) beam-trawl fishery, and an offshore (and coastal foreshore) otter-trawl fishery. However, the Gulf of Carpentaria has only an offshore trawl fishery (Staunton-Smith et al., 2004). The fish catch data have an estimated error of 10% due to the type of recording, market fluctuations, policies, and management changes (L. Olyott, DPI and F, pers. comm.).

Data on Queensland coastal wetland vegetation were obtained from DPI&F Assessment and Monitoring Unit. The 1:100,000 coastal wetland vegetation map includes information on mangrove communities, saltmarsh and open water based on Landsat TM images and ground truthing (1987–1999). Data on channels, intertidal flats, and sandflats for estuaries were taken from Geoscience Australia (Geoscience Australia, 2004). This information was primarily sourced from the 1:100,000 scale National Topographic Map series produced by Geoscience Australia.

Fish Catch Data.—The coast of Queensland was divided into 13 separate sections for the purpose of this study. These sections were selected because of their importance to the commercial fisheries (L. Olyott, DPI and F, pers. comm.), likely independence between the catches, and their value which represented two thirds of Queensland's total fish catch [or 65% of the total fish catch in 2004 (DPI and F, 2005)]. Selection criteria for species were that they should be/have (1) relatively constant and high market values, (2) well known, (3) estuary-dependent, and (4) widespread throughout Queensland [based on Yearsley et al. (1999); L. Williams, DPI and F, pers. comm.].

Annual summaries of the fish catch data were calculated together with the following variables: latitudinal section, species or species group, fishery type, total catch (tonnes) and catch-per-unit-effort (CPUE, kg day^{-1}). Daily catch data recorded from compulsory commercial fishing logbooks were standardized for fishing effort by dividing the catch of each species by the number of days fished in each section (Tanner and Liggins, 2000). We separated the four fisheries (trawl, net, pot, line) but also used total CPUE, as the majority of the techniques are considered passive and their effort is measured in days with one technique dominating the fish catch for a species group. We compared total fish catch with the habitat parameters and did the same for CPUE for all fisheries and for individual fisheries to see whether different combinations would give similar outcomes. Yearly catch values for a total of 31 species or species groups were used. The fish species were selected according to their estuary dependence (Table 2). These species are mainly "marine-estuarine species" [see also Whitfield (1999) for a detailed classification], which use inshore areas and estuaries for significant periods of time, often (but not limited to) during their juvenile phase. Several marine-estuarine species have juveniles that are only found within estuarine habitats (e.g., *Penaeus merguiensis* De Man, 1898) (Staples et al., 1985; Vance et al., 1996). Some catadromous species travelling between freshwater and marine habitats use estuarine habitats at certain life-stages, e.g., *Lates calcarifer* (Bloch, 1790; Russell and Garrett, 1983). The fish species groups have been divided into dif-

Table 2. Selected species for the analyses with the total catch of 13 selected geographical areas along the coast of Queensland from 1988–2004 and suggested habitat dependence as described in Williams (2002). Channels and saltmarsh are not included. FL–Mud- and Sandflats, SG–Seagrass, MG–Mangrove, CH–Channels, SM–Saltmarsh.

Common name and fish catch class	Taxa	Habitat	Catch (t)
Barramundi	*Lates calcarifer* (Bloch, 1790)	MG	8,212
Bream	*Monodactylus argenteus* (Linnaeus, 1758), *Pomadasys maculatum* (Bloch ,1793), *Acanthopagrus australis* (Akazaki, 1984), *Acanthopagrus berda* (Forsskål, 1775), *Plectorhinchus gibbosus* (Lacépède, 1802), Sparidae spp.	MG, FL, SG	10,870
Bugs	*Thenus indicus* (Leach, 1815), *Thenus orientalis* (Lund, 1793)	FL	2,921
Blue Swimmer Crab	*Portunus pelagicus* (Fox, 1924)	FL	5,277
Mud Crab	*Scylla serrata* (de Haan, 1833)	MG	513
Dart	*Trachinotus anak* (Ogilby, 1909), *Trachinotus blochii* (Lacépède, 1801), *Trachinotus botla* (Shaw, 1803), *Trachinotus* spp.	FL	1,025
Flathead	*Platycephalus fuscus* (Cuvier, 1829), *Platycephalus* spp.	SG, FL	6
Flounder	*Pseudorhombus jenynsii* (Bleeker, 1855), *Pseudorhombus arsius* (Amaoka, 1969), *Pseudorhombus spinosus* (McCulloch, 1914)	FL	465
Grunter	*Hephaestus fuliginosus* (Macleay, 1883), *Pomadasys* spp.	FL	14
Milkfish	*Chanos chanos* (Forsskål, 1775)	MG	7,954
Mullet	*Liza vaigiensis* (Quoy and Gaimard, 1825), *Liza subviridis* (Valenciennes, 1836), *Liza argentea* (Quoy and Gaimard, 1825), *Valamugil georgii* (Bleeker, 1858), *Valamugil seheli* (Forsskål, 1775), *Mugil cephalus* (Linnaeus, 1758), *Parupenaeus* spp. *Trachystoma petardi* (Castelnau, 1875), Mugilidae spp.	FL	28,447
Prawns-bait	Family Penaeidae	–	152
Prawns-banana	*Fenneropenaeus indicus* (Milne-Edwards, 1837), *Fenneropenaeus merguiensis* (de Man, 1888)	MG, FL	7,801
Prawns-bay	*Metapenaeus macleayi* (Haswell, 1879), *Metapenaeus insolitus* (Racek and Dall, 1965)	–	5,906
Prawns-endeavour	*Metapenaeus endeavouri* (Schmitt, 1926), *Metapenaeus ensis* (De Haan, 1844)	SG	11,803
Prawns-greasy	*Metapenaeus bennettae* (Racek and Dall, 1965)	MG, FL	1,415
Prawns-king	*Penaeus monodon* (Fabricius, 1798), *Penaeus semisulcatus* (De Haan, 1844)	SG	27,389
Prawns-school	*Metapenaeus macleayi* (Haswell, 1879)	SG	654
Prawns-tiger	*Penaeus esculentus* (Haswell, 1879)	SG	23,438
Prawns-unspecified	Penaeidae spp.	–	69

Table 2. Continued.

Common name and fish catch class	Taxa	Habitat	Catch (t)
Rays	*Gymnura australis* (Ramsay and Ogilby, 1886), *Himantura toshi* (Whitley, 1939), *Myliobatis australis* (Macleay, 1881), *Urolophus paucimaculatus* (Dixon, 1969), *Rhynchobatus djiddensis* (Forsskål, 1775), *Dasyatis kuhlii* (Müller and Henle, 1841), *Aetobatus narinari* (Euphrasen, 1790, *Trygonorrhina* sp. Dasyatidae spp.	FL	142
Sawfish-unspecified	*Pristis zijsron* (Bleeker, 1851), Pristidae spp.	FL	13
Sea Perch-mixed	Lutjanidae spp.	MG	27
Sea Perch-mangrove jack	*Lutjanus argentimaculatus* (Forsskål, 1775)	MG	1,046
Snapper	*Pagrus auratus* (Foster, 1801), *Etelis carbunculus* (Cuvier, 1828), Caesionidae spp., Lutjanidae spp.	SG, FL	726
Tailor	*Pomatomus saltatrix* (Linneo, 1766)	FL	2,599
Tarwhine	*Rhabdosargus sarba* (Forsskål, 1775)	–	10
Threadfin-blue	*Eleutheronema tetradactylum* (Shaw, 1804)	FL	33
Threadfin-king	*Polydactylus macrochir sheridani* (Macleay, 1884)	MG	2,045
Threadfin-unspecified	Polynemidae spp.	–	5,226
Whiting	*Sillago ciliata* (Cuvier, 1829), *Sillago analis* (Whitley, 1943), *Sillago maculata* (Quoy and Gaimard, 1824), *Sillago burrus* (Richardson, 1842), *Sillago ingenuua* (McKay, 1985), *Sillago sihama* (Forsskål, 1775), *Sillago robusta* (Stead, 1908), Sillaginidae spp.	MG, FL	17,739

ferent categories according to their known or suggested habitat requirements. These groups were then tested for their dependence using forward stepwise regression with the respective fish species as the dependent variable to identify any relationship between the geomorphic variables and fisheries catches.

Geomorphic Data.—The GIS software ArcGis v. 9.0 was used to access and visualize the estuarine habitat data and to produce raster maps of the habitats with a 10 × 10 m grid size. The DPI and F 1:100,000 vector data of the coastal wetland vegetation were combined with intertidal vector data from Geoscience Australia. The resulting vector data layer was converted to a 10 × 10 m grid for each for the 13 regions applying the assigned GDA 94 projection for each section using ArcGis v. 9.0. Each grid layer was analyzed with the spatial metrics analysis package Fragstats 3.3 (McGarigal et al., 2002) to calculate the total area (CA), perimeter (Peri), mean perimeter to area ratio (PARA), number of patches (NP) and a connectivity index (CONNECT), giving a value for the distances between patches (threshold 100 m) within the 13 separate sections.

The connectivity index (CONNECT) is defined as:

$$\text{CONNECT} = \left[\frac{\sum_{j=k}^{n} c_{ijk}}{\frac{n_i(n_i - 1)}{2}} \right] \times 100$$

The index is equal to the number of functional connections between all patches of a particular patch type ($\Sigma c_{ijk,}$ where c_{ijk} = 0 if patches j and k are not within the specified distance of 100 m of each other and c_{ijk} = 1 if patch j and k are within the specified distance of 100 m), divided by the total number of possible connections between all patches of the corresponding patch type, and converted to a percentage (Clarke and Warwick, 2001). We used the lowest possible threshold to avoid the inclusion of habitat patches that were divided by a barrier (e.g., terrestrial vegetation). The perimeter to area ratio was measured for each habitat as a mean which equals the sum, across all patches of the corresponding patch type and patch metric values, divided by the number of patches (McGarigal et al., 2002). Over 140 estuaries from > 300 recognized Queensland estuaries were covered, ranging from the Gulf of Carpentaria (17°S, 141°E) to Coolangatta (28°S, 153°E). The following classes were used: channels, mangroves, saltmarsh, seagrass, combined mud- and sandflats, total number of estuaries, and latitude per section. Mangroves, saltmarsh, channel, mud- and sandflats were calculated separately for total wetland parameters to look at the overall effect of the wetland on fish catch data. Seagrass was not included due to its overlapping with the channel habitats on the digital map, which did not allow its separate calculation. The habitat parameter of each geographical area was assigned the corresponding grid code from the DPI and F fishery grid (Fig. 1).

Data Analysis.—Statistical analyses were carried out using the PRIMER 5.0 (Clarke and Ainsworth, 1993) and SPSS 12.01 software packages. Correlation analyses and non-metric multidimensional scaling (nMDS) were used to explore dependency and similarity between perimeter, area, mean perimeter to area ratio, and connectivity of mangroves, saltmarsh, seagrass, mud- and sandflats, using Bray Curtis similarity and Euclidean distance. Data were square root transformed prior to analysis to normalize the variances. CPUE variables were not transformed whereas other variables were square root, fourth root or $\log_{10}$ transformed to reduce the right-skewness of the data. nMDS was used to represent the similarity of estuaries on the basis of habitats using Euclidean distance as a common method for modeling habitat distances (Conner et al., 2002). The extent to which habitat variables explained the variability in fish catch and CPUE was determined using the BIO-ENV procedure (Clarke and Ainsworth, 1993). This procedure generated various similarity matrices from subsets of the environmental variables and displayed the best of these various correlations (Mantel's tests). In addition, multiple regression models were used to investigate which of the estuarine habitats accounted for the variation in fisheries production throughout the region. For this approach the CPUE for each fishery as well as an averaged CPUE for all fisheries was applied. In order to exclude auto-correlation within the data (Pyper and Peterman, 1998), results from correlation analysis were reviewed for consistency with the theoretical mechanisms proposed before the analysis, with the expectation that high correlation exists between habitats themselves and estuarine fish catch. Further considerations were given to "outliers", where species groups had less than 100 t catch in more than half of the investigated sections. These groups were excluded from the later analysis.

Results

Fisheries and Environmental Data.—The total estuarine fish catch from all 13 geographical areas between 1988 and 2004 was 174,000 t compared to 255,000 t for the whole coast of Queensland (Fig. 2). There was little overlap in the species caught in the four fisheries, except for blue swimmer crabs *Portunus pelagicus* (Linnaeus, 1758), which were caught in both the pot (> 60% of the catch) and trawl fisheries, and whiting (*Sillago* spp.) which were caught in the trawl (> 50% of the catch) specifically directed towards stout whiting (*Sillago robusta* Stead, 1908) and net fisheries. There have been differences in catches throughout the regions with the highest catch in Moreton Bay and Fraser Island, which also had the highest effort. The highest CPUE for all fisheries (pot, line, net, and trawl) was in the Moreton Bay and Fraser region,

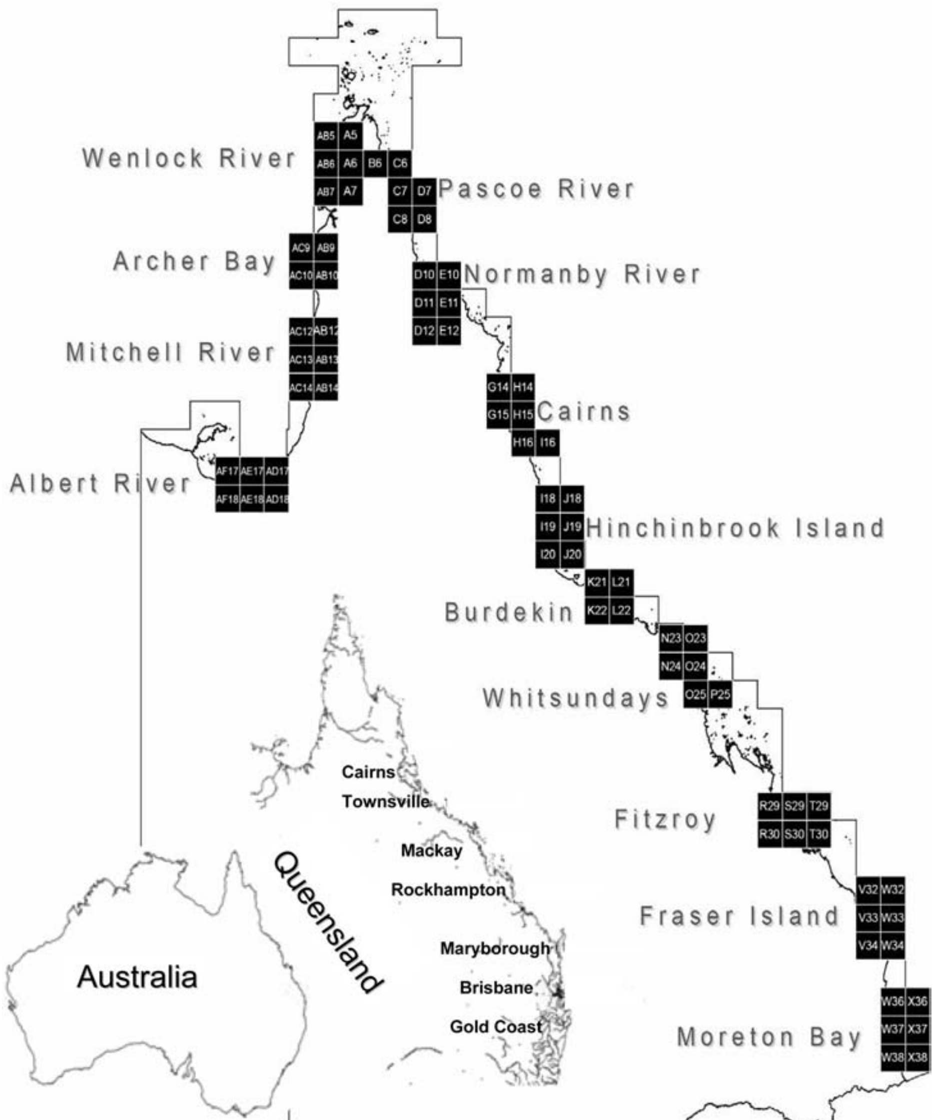

Figure 1. Location of investigated area showing major cities and river systems in Queensland and selected geographical areas with fish catch grids for preliminary analyses of the study (modified from Geoscience Australia, 2004).

where mullet (e.g., *Mugil cephalus* Linnaeus, 1758) contributed 28% and whiting (*Sillago* spp.) 12% towards the total catch. The CPUE in the line fishery was high in the central region (e.g., Hinchinbrook) and also in the north where effort was in general low and for some species (e.g., *Platycephalus* spp.), too low to provide a meaningful CPUE. The net fishery dominated in the Gulf regions where the total catch and effort are low. The prawn fishery is not included within inshore grids as the trawl fishery in the Gulf of Carpentaria is undertaken only offshore. Barramundi (*L. calcarifer*) and mud crab *Scylla serrata* (Forskål, 1775) catches accounted for more than half of the total catch in these regions.

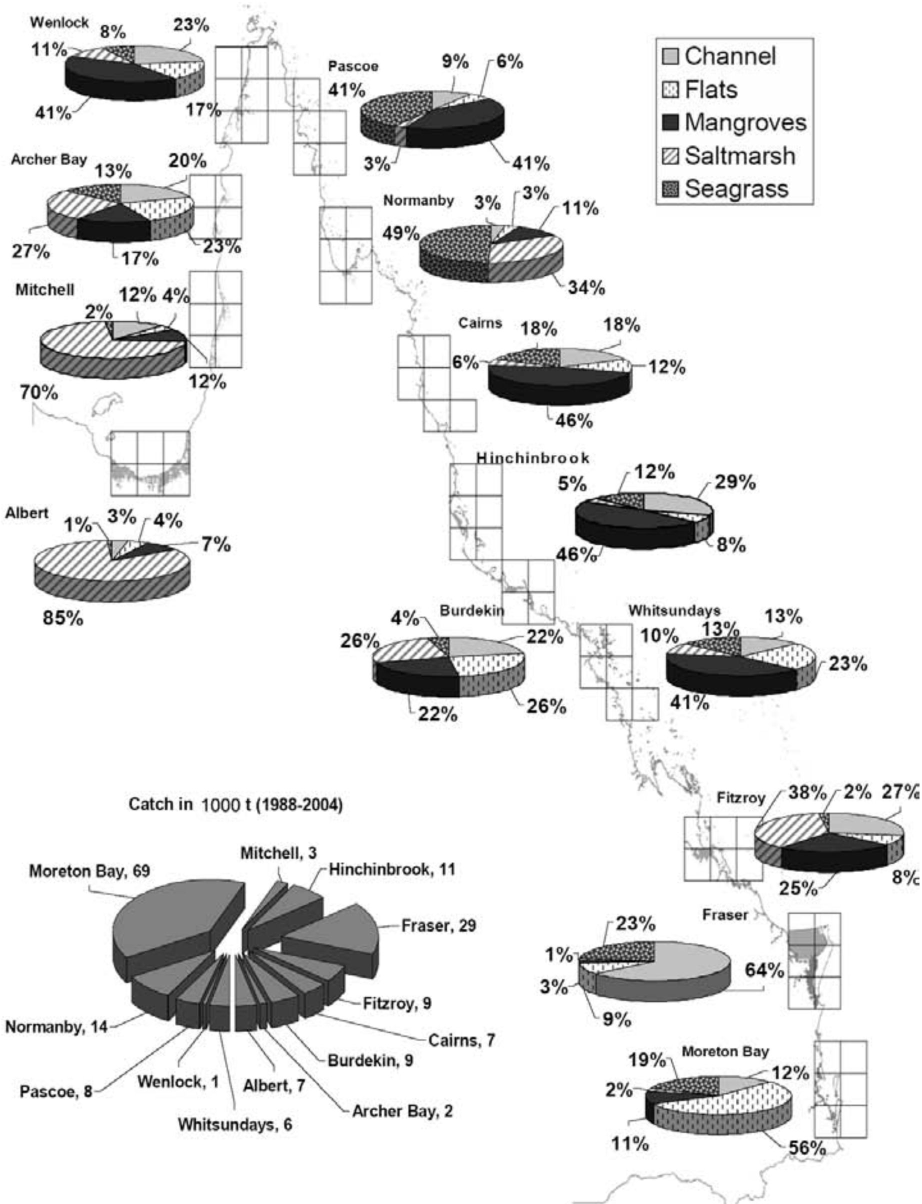

Figure 2. Total catch of 31 estuary-dependent species groups for 13 selected regions in Queensland, Australia, between 1988–2004 and their extent of estuarine habitats.

A large range of different estuarine habitat characteristics was covered by the selected geographical areas (Fig. 2). One extreme occurred in the north with the Albert River section having a large area of saltmarsh/saltpan and high number of mangrove patches and the other extreme at the southern end of Queensland with Moreton Bay providing large areas of flats, channel perimeter, and seagrass perimeter. Large areas of mangrove occurred in the Hinchinbrook region whereas the Burdekin region had a high number of channel and patches of flats. The Fraser region dominated in the

Table 3. Data on selected environmental variables for 13 locations for wetland components of: channels, flats (mud and sand), mangroves, saltmarsh, seagrass, and total wetlands. Variables include: area in km^2, perimeter in km, number of patches and estuaries, mean perimeter to area ration (Mn_P:A) in km, and connectivity in %. Locations include: Al–Albert River, Ar–Archer Bay, Bu–Burdekin River, Ca–Cairns, Fi–Fitzroy River, Fr–Fraser, Hi–Hinchinbrook, Mi–Mitchell River, Mo–Moreton Bay, No–Normanby, Pa–Pascoe, We–Wenlock, Wh–Whitsundays.

Parameters	Al	Ar	Bu	Ca	Fi	Fr
Latitude	18	14	20	16	24	25
Estuaries	7	5	11	13	12	6
Channel area	11	6	20	3	26	366
Perimeter	1,412	813	2,132	483	1,659	1,828
Patches	27	16	431	22	23	186
Mn_P:A	2,193	276	333	1,167	779	115
Connectivity	3.70	0.83	0.07	3.03	1.58	0.00
Flats area	15	7	23	2	8	51
Perimeter	400	888	2,409	231	629	2,737
Patches	33	104	486	58	117	138
Mn_P:A	321	262	355	719	503	443
Connectivity	0.57	0.15	0.07	0.36	0.22	0.30
Mangrove area	25	5	20	8	24	15
Perimeter	5,720	763	2,132	776	4,478	2,038
Patches	2,471	312	431	126	1,281	544
Mn_P:A	447	342	333	256	432	367
Connectivity	0.01	0.05	0.07	0.46	0.03	0.06
Saltmarsh area	280	8	23	1	35	6
Perimeter	11,760	1,221	2,409	132	4,081	1,421
Patches	1,016	458	486	75	1,032	726
Mn_P:A	463	331	355	334	404	411
Connectivity	0.07	0.08	0.07	0.14	0.03	0.03
Seagrass area	4	4	4	3	2	132
Perimeter	123	112	157	95	126	292
Patches	8	6	28	18	29	9
Mn_P:A	36	49	140	248	158	146
Connectivity	0	0	0	0	0	0
Wetlands area	358	27	66	13	92	434
Perimeter	5,622	2,175	3,320	954	3,841	2,623
Patches	514	368	328	70	210	113
Mn_P:A	461	344	382	323	443	433
Connectivity	0.09	0.12	0.08	0.54	0.29	0.51

channel category with Hervey Bay having large areas of seagrass. The Mitchell River section had the highest channel connectivity index and Normanby River, the highest flats connectivity index (Table 3).

Furthermore, we detected significant positive correlation between estuarine habitat variables. Out of 304 estuaries and their adjacent habitats in Queensland, we found significant positive correlation between mangroves and saltmarsh area ($r = 0.41$, $P < 0.01$, $n = 304$) and between seagrass and mangrove area ($r = 0.40$, $P < 0.01$, $n = 304$) (Table 4), suggesting that these habitats mostly occur together and may be regarded as a network of adjacent ecosystems.

Table 3. Continued.

Parameters	Hi	Mi	Mo	No	Pa	We	Wh
Latitude	19	16	27	15	12	12	21
Estuaries	21	4	21	6	6	8	22
Channel area	19	6	16	3	3	15	7
Perimeter	329	1,300	1,910	627	441	1,344	1,177
Patches	114	8	129	14	10	12	55
Mn_P:A	2,882	1,407	1,299	392	899	331	1,078
Connectivity	1.41	10.8	0.57	0.00	2.22	0.00	1.28
Flats area	5	2	73	3	2	11	12
Perimeter	70	314	3,290	175	154	645	1,109
Patches	133	64	344	20	42	82	240
Mn_P:A	527	555	680	250	540	337	445
Connectivity	0.21	0.25	0.15	1.05	0.46	0.39	0.24
Mangrove area	30	6	15	10	14	27	21
Perimeter	2,584	1,128	2,026	1,647	1,114	3,341	2,420
Patches	280	618	539	688	186	725	512
Mn_P:A	290	344	315	335	282	281	359
Connectivity	0.17	0.02	0.06	0.03	0.16	0.04	0.08
Saltmarsh area	3	37	3	32	1	7	5
Perimeter	520	4,842	632	3,315	350	1,526	1,040
Patches	251	1,157	447	833	196	838	601
Mn_P:A	360	310	422	336	339	347	425
Connectivity	0.05	0.03	0.04	0.04	0.14	0.03	0.03
Seagrass area	8	0	25	47	14	5	7
Perimeter	400	0	1,307	409	250	129	409
Patches	59	0	277	14	15	14	105
Mn_P:A	96	0	289	87	32	61	155
Connectivity	0	0	0.05	1.10	0	0	0.05
Wetlands area	56	53	208	51	20	61	44
Perimeter	2,660	5,810	2,664	3,432	1,194	4,369	2,575
Patches	108	914	73	755	125	626	242
Mn_P:A	355	337	504	343	293	342	385
Connectivity	0.33	0.04	0.76	0.04	0.19	0.07	0.11

Relationships Between Estuarine Habitats Total Fish Catch and Cpue Data.—We compared total catch with different variables of the data set and found the best fit between section data of total fish catch and the wetland connectivity index (r^2 = 0.62) (Fig. 3). Furthermore, total catch correlated with the wetland mean perimeter to area ratio (r^2 = 0.45) and averaged CPUE for all fisheries correlated with total wetland area (r^2 = 0.55).

An nMDS based on square root transformed total fish catch data using Bray Curtis similarity showed a clear grouping of three classes for combined CPUE: (1) South eastern Queensland; (2) Central and Northern Queensland; and (3) the Gulf of Carpentaria (Fig. 4A). The nMDS using standardized habitat parameters and applying Euclidean distance as a similarity measure resulted in some overlap with the nMDS based on standardized catch with the following groups: (1) Fraser and Moreton Bay (2) Whitsundays, Hinchinbrook, Cairns, Pascoe, and Wenlock (3) Albert, Mitchell, and Normanby. The Fitzroy, Archer Bay, and Burdekin sections did not show clear

Table 4. Pearson correlation of different estuarine habitat types in Queensland for 304 estuaries. $P < 0.05$*, $P < 0.01$**.

Habitats	Saltmarsh	Seagrass	Flats	Channels
Mangroves	.411**	.403**	.576**	.627**
	Saltmarsh	–	.120*	.180*
		Seagrass	.224**	.897**
			Flats	.499**

grouping. The distribution of wetland connectivity is an important factor separating the regions, with the Fraser and Moreton Bay region having the highest connectivity index (Fig. 4B).

The highest correlation was found in BIO-ENV (0.729) between CPUE for all fisheries and the wetland mean perimeter to area ratio, followed in rank order by the wetlands and flats connectivity index, and the total number of estuaries.

Stepwise Multiple Regression Analysis of Key Species.—The most important environmental parameter for nine out of 24 species or species groups for predicting CPUE with stepwise regression was the total area of mud- and sandflats as well as patches and their connectedness, followed by the wetlands parameters, which gave good CPUE prediction for another four species. The fitted model for flats, for example, accounted for 70%–90% of the variation in CPUE of mullet (e.g., *M. cephalus*), blue swimmer crab (*P. pelagicus*), and dart (*Trachinotus* spp.) (Table 5). Mangrove parameters were less important than expected for the mangrove related species such as barramundi (*L. calcarifer*) and mud crabs (*S. serrata*) [for comparison see Manson et al. (2005b)], for which total wetland and seagrass parameters gave the best fit, albeit weak. This fit was, however, rather weak. Prawn CPUE data were in general best explained by the presence of flats, channels and total wetland parameter. For the seagrass related group it was wetlands or other parameters. Seagrass parameters did not emerge as significant.

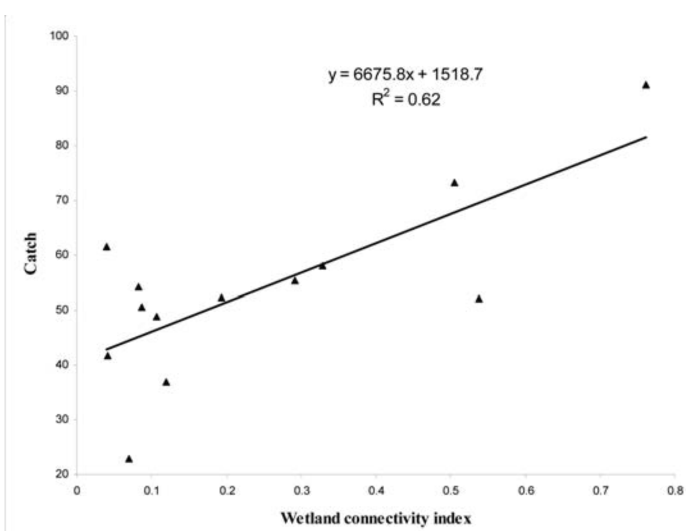

Figure 3. Relation between wetland connectivity and total catch from 13 geographical areas along the coast of Queensland (catch has been fourth root transformed).

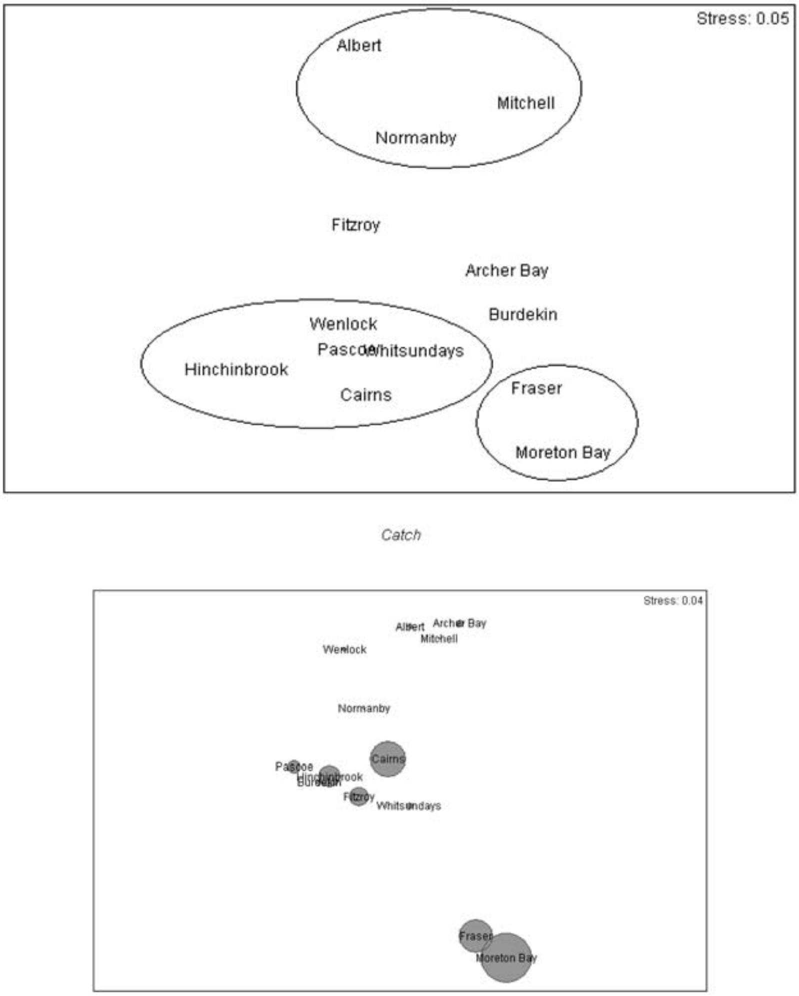

Figure 4. nMDS for 13 selected geographical areas (A) (based on untransformed standardized habitat parameters and latitude using Euclidean distance) showing the three groups: Southern Queensland, Central, and Northern Queensland, and the Gulf of Carpentaria; and (B) (based on square root transformed catch data and Bray Curtis similarity) in Queensland, Australia. The value of the wetland connectivity index is indicated by the size of circles.

The models identified mangrove parameters (connectivity) as being important in predicting CPUE for whiting (*Sillago* spp.) and greasy prawns (*Metapenaeus bennettae* Racek and Dall, 1965). Latitude was the only parameter fitted to the model for king prawns (*Penaeus monodon* Fabricius, 1798, *Penaeus semisulcatus* de Haan, 1844) that explained the variation in CPUE of this species group, accounting for 56% of variation (Table 5). The total number of estuaries per geographical area was only important as a predictor for CPUE for banana prawns, e.g., *Fenneropenaeus indicus* (H. Milne Edwards, 1837). Some species groups did not show any significant relationship with any of the variables [grunter, *Pomadasys* spp.; snapper, *Pagrus auratus* (Forster in Bloch and Schneider, 1801) or had no significant r^2 value (flathead, *Platycephalus* spp.; flounder, *Pseudorhombus* spp.; rays, e.g., *Gymnura australis* (Ramsay and Ogilby, 1886); threadfin unspecified, Polynemidae; sawfish, Pristidae]. Their to-

Table 5. Significant r^2 values for the two most important variables in stepwise multiple regressions predicting CPUE for 24 species groups showing: A CPUE–all fisheries, N CPUE–net, T CPUE–trawl, C CPUE–pot, L CPUE–line. P < 0.05*, P < 0.01**.

Habitat	Species	Parameters	Type	Adjusted r^2	Df
MG	Barramundi	Seagrass NP, Wetlands NP	A CPUE	0.684*	12
		Seagrass Peri, Saltmarsh Peri	L CPUE	0.648*	10
FL	Blue Swimmer crab	Flats CA, Channel CA	A CPUE	0.896**	12
		Channel CA, Seagrass NP	C CPUE	0.935**	11
		Wetlands CA, Saltmarsh PARA	T CPUE	0.817*	8
MG, FL, SG	Bream	Flats CA, Channel NP	A CPUE	0.861**	12
		Flats CA, Channel connect	N CPUE	0.900**	12
FL	Bugs	Flats NP	A CPUE	0.535*	12
		Flats NP, Seagrass Peri	T CPUE	0.734*	8
FL	Dart	Flats CA, Wetlands CA	A CPUE	0.944**	12
		Flats CA, Wetlands CA	N CPUE	0.913**	12
MG	Milkfish	Flats connect, Seagrass PARA,	A CPUE	0.649*	12
MG	Mud Crabs	Flats connect, Mangrove CA, Wetlands NP	A CPUE	0.543*	12
		Wetlands NP, Mangrove CA, Flats connect	C CPUE	0.546*	12
FL	Mullet	Flats CA	A CPUE	0.743**	12
		Flats CA	N CPUE	0.789**	12
–	Prawns, Bait	Flats connect, Saltmarsh PERI	A CPUE	0.553*	12
		Flats connect	T CPUE	0.658*	8
MG, FL	Prawns, Banana	Flats PARA, number of estuaries	A CPUE	0.653*	11
		Flats PARA	T CPUE	0.522	8
–	Prawns, Bay	Flats NP	A CPUE	0.634*	12
		Flats NP	T CPUE	0.915**	8
SG	Prawns, Endeavour	Wetlands Peri, Flats connect	A CPUE	0.578*	12
		Latitude	T CPUE	0.591	8
MG, SG, FL	Prawns, Greasy	Mangrove connect, Saltmarsh connect	A CPUE	0.701**	12
		Channel Peri, Saltmarsh Peri	T CPUE	0.958**	6
SG	Prawns, King	Latitude	A CPUE	0.563*	12
		Latitude	T CPUE	0.492	8
SG	Prawns, School	Channel CA, Wetlands connect	A CPUE	0.880**	12
		Wetlands all CA, Saltmarsh connect	T CPUE	0.956**	8
SG	Prawns, Tiger	Wetlands Peri	A CPUE	0.293	12
		Wetlands PARA, Saltmarsh CA	T CPUE	0.938**	8
–	Prawns unsp.	Channel NP, Flats NP	A CPUE	0.867**	12
		Channel NP, Flats NP	T CPUE	0.844*	8
MG	Sea perch	Wetlands NP	A CPUE	0.750**	12
		Channel CA, Channel PARA	L CPUE	0.924**	12
MG	Mangrove Jack	Channel connect, Wetlands NP	A CPUE	0.849**	12
		Channel connect, Wetlands NP	N CPUE	0.854**	12
FL	Tailor	Channel connect, Saltmarsh connect	A CPUE	0.858**	12
		Channel connect, Saltmarsh connect	N CPUE	0.898**	12
–	Tarwhine	Flats CA	A CPUE	0.622*	12
FL	Threadfin Blue	Seagrass NP	A CPUE	0.885**	12
		Channel Peri	N CPUE	0.566*	12
MG	Threadfin King	Saltmarsh CA	A CPUE	0.828**	12
		Saltmarsh CA	N CPUE	0.935**	12
MG, FL	Whiting	Wetlands all CA, Mangrove connect	A CPUE	0.959**	10
		Wetlands PARA, Seagrass CA	N CPUE	0.773**	12
		Channel CA, Wetlands connect	T CPUE	0.995**	8

tal catch throughout the 13 geographical areas was generally low. When leaving out areas with no catch, we found fewer differences between CPUE for all fisheries and CPUE for the most important individual fisheries. The habitat to CPUE relation was relatively consistent throughout the different data sets.

Discussion and Conclusion

This study has shown an empirical link between estuarine habitat and fishery production for estuary-dependent species. Intertidal flats were one of the most important variables explaining fish catch variation in Queensland according to regression analyses for single species. These outcomes are similar to findings by Saintilan (2004) for New South Wales, Australia. The BIO-ENV results with CPUE for all fisheries further demonstrated that flats were one of the most important variables. This suggests that the significance of mud- and sandflats has been greatly underestimated in broad scale analyses to date. Mud- and sandflats are often in proximity to mangroves, salt marshes, and seagrass beds, suggesting connectivity. Larger fish of the same species use the flats and unvegetated areas in inshore and open waters of estuaries as feeding grounds (Chong et al., 2001; Laegdsgaard and Johnson, 2001). These ecosystems are an important habitat for larger fish species, have high microbial activity and large quantities of MPB (microphytobenthos). Mullet (Mugilidae spp.) for example feed on detritus, diatoms, algae, and small invertebrates that they filter from mud and sand (Williams, 2002). According to our results, their catch is best explained by the size of mud- and sandflats. Mudflats are common in tropical Australia with extensive occurrence in northern Australia due to large tidal ranges. However, defining just one habitat as the major driver of CPUE from the data is misleading. Our results support the model that fish species depend on a number of habitats with the overall catch and CPUE being dependent on the whole estuarine wetland habitat suite rather than any single habitat. For example, mangrove jack *Lutjanus argentimaculatus* (Forsskål, 1775) is known to utilize all types of tidal wetlands as juveniles (Williams, 2002) and prefers sheltered areas in channels. Therefore, areas with high channel connectivity and relatively large wetland patch perimeter are likely to promote higher mangrove jack catches.

Although mangroves were well represented in the 13 geographical areas they were not the only important habitat. One reason is that many fish and crustaceans only use mangrove forests for a part of the tidal cycle (Vance et al., 2002). Noting that mangroves are flooded < 50% of the time (Duke, 2006), the availability of adjacent habitats must be important as well. Some estuarine species move and migrate between habitat types, localities, and regions, (e.g., sea mullet *M. cephalus*) (Cappo et al., 1998). This implies that it is difficult and possibly misleading to separate the value of each habitat type from the broader estuarine values when looking at fish catch data.

The connectivity index calculated with the program “Fragstats” appears to be a useful parameter that did not strongly correlate with other habitat parameters but combines their values in biologically meaningful ways. The index was positively related to total catch and combined CPUE of all fisheries. One explanation for this relationship may be the importance of easily accessible estuarine habitats to fish for the provision of food and shelter. The connectivity index reflects the proximity of habitat patches and therefore their potential accessibility. The differences between CPUE in the north and the south may also be related to a reduction in habitat connectivity in the northern habitats. Studies of habitat connectivity are important; as connectivity influences other ecological processes such as species distribution, food availability, and population dynamics.

Extraneous Influences.—Associated with the habitats are a number of abiotic factors such as rainfall, which may influence fish catch (Meynecke et al., 2006) but have not been considered in this study. Data on environmental factors could be useful in regression analyses to explain more of the variation in catch and it is essential to better understand how the interactions of such factors affect the distribution of fish within various estuary types and broad geographic areas (Blaber, 2000). Other factors such as stock-recruitment relationships, habitat changes, pollution impacts, competition and predation, management plans, fuel prices, and market forces also influence the fish catch data and may be considered in future analyses.

The analyses are limited by the resolution of the data set, the type of fish selected and spatial classification of habitats. An a priori classification of the data is essential as unclassified aggregation can lead to misinterpretation. Assessments may be improved by: (1) refining parameters; (2) including species that are not estuary-dependent; and (3) conducting analyses over a range of spatial and temporal scales since the spatial scale of data collection can affect covariance and correlation statistics (Dungan et al., 2002). Analyses, for example, between the fish catch data and small areas of estuarine habitats are not meaningful, as the spatial resolution of fish catch data does not support such a spatial scale. Some data in Queensland are now collected at the 6 nmi scale, which can significantly improve the usefulness of the data. The spatial scale problem may also be overcome by newly available spatial analysis techniques (Campbell et al., 2006). Additional limitations in fish catch data include the recording of fish by common names, which can often result in confusion of specific identity. In order to refine the fish catch data, harvest by recreational anglers and charter operators should be included in analyses as well (Hancock, 1995).

The correlations in our study were generally strong, with r^2 values usually above 0.7, however, this cannot be used to assume causality because of possible non-linearity of linking mechanisms (Baumann, 1998) and the small size of the data sets. In general, we found that species or species groups with an overall low catch record had weak or non-significant results when nMDS and stepwise regression analyses were used. Significance test for most of the adjusted r^2 values resulted in significance at 0.01 probability levels. A standard experiment wise error test showed a 0.26 probability that the significance tests resulted in a Type I error. The actual experiment wise error rate will range between the computed experiment wise error rate (0.26) and the test wise error rate (0.01). The computed experiment wise error rate can be reduced further by reducing the size of the allowable error (significance level) for each comparison but may fail to identify an unnecessarily high percentage of actual significant differences in the data (Olejnik et al., 1997). Another way of assessing such correlated parameters can be achieved with the application of multivariate decision trees (Breiman et al., 1984; De'ath and Fabricius, 2000).

Unfortunately, there is a lack of essential life-history information for most of the major fishery species in Australia. There is a need for additional information on "critical" habitat requirements and processes such as recruitment, post-recruitment mortality and competition, spawning, and species interactions: information that is important in assessing the value of habitats for fishery species (Beck et al., 2001) and modelling. Beck et al. (2001) argued that the importance of a habitat as a nursery site depended not only on whether it supported more juvenile fish, but more importantly, its actual contribution to the adult (breeding) population. This juvenile-adult link is almost non-existent in analyses conducted to date. It is important therefore to include different life history stages in future analyses.

In conclusion, healthy and functional estuarine wetlands are fundamental to the health of fish stocks and for optimizing sustainable yield for commercial and recreational fishers. The protection of one habitat type will only benefit a minority of commercially important fish species. To optimize habitat and fisheries management, a combination of estuarine habitats should be considered in fisheries management, supporting the move from conventional single-species or single-habitat management to ecosystem-based management (NRC, 1999). Fishery systems are complex, and the management systems needed to optimize the benefits accruing from fisheries require institutions and knowledge systems that are able to cope with the multi-disciplinary requirements of the fisheries management function. Fisheries managers need to broaden their knowledge base in order to make informed decisions. The controversy over estuarine outwelling has benefited from recent tracer techniques, such as stable isotope analyses, which enable the tracking of food sources for individual species (Lee, 2005). In many cases, the results question the extent of the outwelling hypothesis (Odum, 1968), suggesting the need for further studies and refinement of current knowledge. Deficiencies of studies that address the relationship between estuarine habitats and fish catch are mainly due to their single-habitat approach. The present data on fish catch and estuarine habitat distribution allowed for modelling but has its spatial limitations. The analyses showed a strong dependency by 24 estuarine species or species groups or different estuarine wetland habitats, with mud- and sandflats being most important for 25% of the species. Overall, the results show that a broad diversity of coastal habitats, other than those receiving the most attention, are essential to the completion of fish life cycles. Our investigation contributes to the broader knowledge of coastal habitats and how they influence fisheries catch and productivity. Future studies concerning fish catch and estuarine habitats could benefit from: (1) refined collection of fisheries-dependent data; (2) considerations of linked processes between estuarine and coastal habitat types; and (3) enhanced knowledge of life history stages of estuarine dependent fish species.

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