

Characteristics of the fish assemblages of soft substrata and reefs in north-western Australia and their relationships with latitude and various factors

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I declare that this thesis is my own account of my research and contains, as its main content, work which has not previously been submitted for a degree at any tertiary education institution.

(Michael Julian Travers)

Abstract

The overarching aim of this thesis was to provide the first quantitative account of the characteristics of the ichthyofaunas over the soft substrata and reefs of inshore waters along a continuous tropical coastline, which covers a substantial latitudinal range and three diverse marine bioregions, and to elucidate the factors that influence those characteristics. Fishes were thus sampled over both habitat types in deep ($\bar{x} = 22$ m) and shallow ($\bar{x} = 12$ m) inshore waters during both the dry and wet seasons at seven regularly-spaced locations along the ~1,500 km coastline of tropical north-western Australia (NWA). The fishes over soft substrata were sampled by otter trawling during the day, while those over adjacent reefs were sampled using traps during both the day and night.

The 110,521 fishes sampled represented 361 species, 197 genera and 85 families. 229 species were caught exclusively over soft substrata and 76 solely over reefs, with only 56 species recorded in both habitat types. The Leiognathidae, Carangidae, Terapontidae and Mullidae collectively contributed 69% to catches over soft substrata, while the Lethrinidae and Lutjanidae dominated catches over reefs (82%). Most species had an affinity with the faunas of the Pacific Ocean, reflecting the connective influence of the polewards-flowing Indonesian Throughflow current (ITF) to the NWA coast.

Species composition over soft substrata and reefs were both influenced more by location than by season and water depth and also than by day vs night in the case of reefs. While ichthyofaunal compositions over both habitat types change progressively with decreasing latitude/water temperature, they differ among the three bioregions, reflecting marked differences in environmental characteristics. Tidal range and turbidity decline

markedly with latitude. Rivers and mangrove forests are numerous in the Kimberley Bioregion in the north, but restricted in the Pilbara Bioregion in the south and, to an even greater extent, in the intermediate Canning Bioregion. The fish fauna of the Kimberley is particularly distinctive, containing several species belonging to families adapted for visual acuity and recognition in turbid waters, e.g. Leiognathidae and Lutjanidae.

Species richness and abundance of fishes over soft substrata in deep and shallow waters in the environmentally ‘stable’ dry season peaked at the northern and southern locations (Kimberley and Pilbara), whereas they essentially declined with latitude during the wet season. In contrast, those biotic variables over reefs rose to a peak in the central locations (Canning Bioregion) and then declined. It is thus relevant that the waters in the central bioregion are relatively low in productivity, a characteristic associated with good reef development, but less so for sustaining the substantial benthic macroinvertebrate fauna that constitutes the prey of many of the fish species found over soft substrata.

Analyses of the composite dataset produced for the ichthyofaunas of the NWA coast during this thesis have led to a greater understanding of the ecology of this important, but relatively little studied, coastline. Furthermore, the thesis has produced the type of crucial baseline data that will enable, in the future, any faunal changes brought about by climate change, increases in fishing pressure and other anthropogenic effects to be detected.

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Journal Publications

Publications arising from this thesis

The following paper was published from Chapter 2 of this thesis.

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The following paper was published from Chapter 3 of this thesis.

Travers, M.J., Potter, I.C., Clarke, K.R., & Newman, S.J. (2012). Relationships between latitude and environmental conditions and the species richness, abundance and composition of tropical fish assemblages over soft substrata. *Marine Ecology Progress Series* **446**, 221-241

The following paper was published from Chapter 4 of this thesis.

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Table of Contents

Abstract	1
Acknowledgements	3
Journal Publications	4
Chapter 1. General Introduction	8
1.1 Relationships between ichthyofaunal characteristics and latitude and bioregion	8
1.2 Relationships between ichthyofaunal characteristics and depth and habitat	12
1.3 Relationships between ichthyofaunal characteristics and seasonal and diel effects	14
1.4 Statistical approaches	16
1.5 Characteristics of the tropical north-western Australian coast	16
1.6 Broad aims of thesis	22
Chapter 2. The species compositions of fish faunas over soft substrata and reefs along the tropical coast of north-western Australia differ and change with latitude and bioregion	23
2.1 Introduction	23
2.2 Materials and Methods	27
2.2.1 Study area	27
2.2.2 Sampling regime	30
2.2.3 Environmental variables	32
2.2.4 Treatment of fishes	34
2.2.5 Cluster and ordination analyses	35
2.2.6 ANOSIM and SIMPROF tests	36
2.2.7 RELATE test	38
2.3 Results	39
2.3.1 Water temperature	39
2.3.2 Main fish families and zoogeographical categorisations	40
2.3.3 Habitat comparisons	43
2.3.4 Main species and families over soft substrata	44
2.3.5 Main species and families over reefs	46
2.3.6 Relationship to latitude and water temperature	46
2.3.7 Bioregional comparisons	54
2.4 Discussion	60
2.4.1 Comparisons between ichthyofaunal compositions over soft substrata and reefs	60
2.4.2 Relationship of ichthyofaunal composition with latitude and water temperature	65
2.4.3 Relationship of ichthyofaunal composition and bioregion	71
Chapter 3. Species richness, density and composition of the fish faunas over soft substrata along the tropical coast of north-western Australian are related to latitude and certain environmental variables	75
3.1 Introduction	75
3.2 Materials and Methods	78
3.2.1 Sampling regime	78
3.2.2 Sampling regime and environmental data.	79
3.2.3 Statistical analyses	80
3.3 Results	84
3.3.1 Environmental variables	84
3.3.2 Dominant species and families	87
3.3.3 Species richness and density of fishes	91
	5

3.3.4 Relationships between species composition and season and water depth	94
3.3.5 Relationships between species composition and both season and water depth at each location	98
3.3.6 Relationship between fish assemblages and environmental variables	104
3.4 Discussion	106
3.4.1 Species richness and density of fishes	106
3.4.2 Relationships between species composition and bioregion	109
3.4.3 Relationships between species composition and season	109
3.4.4 Relationships between species composition and depth	112
Chapter 4 Species composition of the fish assemblages over reefs along the tropical coast of north-western Australia is related to latitude, water depth, day vs night and season	117
4.1 Introduction	117
4.2 Materials and Methods	120
4.2.1 Sampling regime and environmental data	120
4.2.2 Statistical analyses	121
4.3 Results	125
4.3.1 Environmental variables	125
4.3.2 Dominant species and families	129
4.3.3 Relationships between species composition and season, water depth and day vs night	133
4.3.4 Relationships between species composition and both water depth and day vs night at each location	143
4.3.5 Relationships between species composition and both season and day vs night	146
4.3.6 Relationship between fish assemblages and environmental variables	149
4.4 Discussion	150
4.4.1 Comparisons between water depths, day vs night and season for each location	157
4.4.2 Diel and seasonal comparisons	159
4.4.3 Conclusions	162
Chapter 5 To what extent are species richness and abundance of reef fish faunas along an extensive tropical coast related to latitude and depth, season and day vs night?	164
5.1 Introduction	164
5.2 Materials and Methods	167
5.2.1 Study area	167
5.2.2 Sampling regime and environmental data	169
5.2.3 Statistical analyses	172
5.3 Results	175
5.3.1 Environmental variables	175
5.3.2 Number of species and relative abundance over reefs during the day	178
5.3.3 Number of species and relative abundance over reefs during the night	180
5.3.4 Number of species and relative abundance over reefs during the day and night	183
5.4 Discussion	186
5.4.1 Latitudinal trends in species richness and abundance	186
5.4.2 Species richness and abundance of fishes at intermediate latitudes in the dry season	188
5.4.3 Species richness and abundance of fishes at intermediate latitudes in the wet season	190
5.4.4 Species richness and abundance in deep vs shallow water and day vs night	192
5.4.5 Conclusions	195

Chapter 6. General Discussion	197
6.1 Latitudinal (temperature) and bioregional trends in ichthyofaunal composition	198
6.2 Comparisons of the compositions of the fish faunas over soft substrata and reefs	201
6.3 Relationships between ichthyofaunal composition and season, water depth and day vs night	202
6.4 Species richness and abundance	203
6.5 Zoogeography of tropical north-western Australian fishes	208
6.6 Management implications and directions for future research	209
REFERENCES	213

Chapter 1. General Introduction

1.1 Relationships between ichthyofaunal characteristics and latitude and bioregion

The patterns of distribution of marine and terrestrial organisms are related to environmental factors, which operate at a number of spatial and temporal scales (Gaston, 2000; Whittaker et al., 2001; Kreft and Jetz, 2007; Gaston and Blackburn, 2008; Tittensor et al., 2010). At a broad spatial scale, the characteristics of faunal assemblages are generally related to latitude and thus implicitly to temperature (Allen et al., 2002; Hawkins et al., 2003a; Brown, 2014), recognising, however, that, at a finer spatial scale, certain biophysical factors can lead to modification of the distribution patterns within latitudinal gradients (Gaston, 2000; Gaston and Blackburn, 2000; Hawkins et al., 2003a; Currie et al., 2004; Hillebrand, 2004b; Gaston et al., 2008; Tittensor et al., 2010; MacNeil and Connolly, 2015). Temporal changes in faunal characteristics are usually related either to the cyclical environmental changes that take place gradually throughout the year, as typically occurs with temperature, or abruptly, such as during sudden extreme climatic changes, e.g. cyclones or storms (Cheal et al., 2002; Rousseau et al., 2010; Munks et al., 2015).

Early studies, which explored the relationships between the characteristics of faunas and latitude, were undertaken in terrestrial ecosystems and showed that, in these systems, species richness peaked near the equator and then declined in a polewards direction (e.g. von Humboldt, 1828; Darwin, 1859; Fischer, 1960; Pianka, 1966). This trend was later recorded for a wide range of terrestrial organisms, including mammals (Huston, 1994; Rosenzweig, 1995; Hawkins, 2001; Hawkins et al., 2012), plants (Perelman et al., 2001; Francis and Currie, 2003), reptiles (Pianka, 1966), birds (Blackburn and Gaston,

1996; Hawkins et al., 2003b) and a number of other taxa (Fischer, 1960; Schall and Pianka, 1978; Hillebrand and Azovsky, 2001; Willig et al., 2003; Hillebrand, 2004a; Hillebrand, 2004b; Mittelbach, 2012). The results of ongoing studies stimulated several authors to explore whether such latitudinal trends also applied to the faunas in marine ecosystems (Rohde and Heap, 1996; Roy et al., 1998; Gray, 2002; Hillebrand, 2004a; Rex et al., 2005; Jablonski et al., 2013; Huang et al., 2015), including fishes (Bellwood and Hughes, 2001; Bellwood et al., 2005; Floeter et al., 2005; Tittensor et al., 2010; Parravicini et al., 2013). A meta-analysis by Hillebrand (2004a) concluded that, as with terrestrial faunas, the species richness of marine faunas changes progressively with latitude. That study also demonstrated, however, that the strength of this gradient varies with the type of biota, being greater for pelagic than benthic organisms and thus greater for nekton and mobile epifauna than for sessile fauna and infauna.

Although there is an extensive body of literature on the patterns exhibited by species richness along latitudinal gradients, the relationship between the abundance (density) of species and latitude has not been studied as comprehensively (Bellwood and Hughes, 2001). From the studies on animal abundance-latitude relationships, it is evident, however, that both positive relationships (*i.e.* density least at equatorial latitudes) and negative relationships (*i.e.* density greatest at equatorial latitudes) are present at different taxonomic levels (Currie and Fritz, 1993; Gaston and Blackburn, 1996; Johnson, 1998; Symonds et al., 2006; Symonds and Johnson, 2006; Stuart-Smith et al., 2013). Negative relationships, *i.e.* density greatest in tropical regions, have been recorded for marine fishes (Floeter et al., 2005; Stuart-Smith et al., 2013). The tendency for density, and particularly species richness, to change progressively with latitude inevitably leads to

corresponding changes in species composition. Such latitudinal changes in composition have been described for the fish faunas in the Atlantic Ocean (Floeter et al., 2001; Bender et al., 2013; Navarrete et al., 2014) and the Pacific coasts of the United States (Jay, 1996) and New Zealand (Anderson et al., 2013) and for a variety of other taxa in different regions (see review of Tittensor et al., 2010).

The overall tendency for the species richness, density and species composition of aquatic faunas to change progressively with latitude reflects the influence of sequential changes in not only water temperature, but also other variables (Currie and Fritz, 1993; Hawkins and Diniz, 2004; Tittensor et al., 2010; Sutcliffe et al., 2014). Such variables include day length, the extent of primary productivity and type and availability of habitat (Huston, 1994; Rosenzweig, 1995; Roy et al., 2000; Bellwood and Hughes, 2001; Mittelbach et al., 2001; Willig et al., 2003; Hawkins and Diniz, 2004; Bellwood et al., 2005; Tittensor et al., 2010; Parravicini et al., 2013). In other words, no single factor can be used exclusively to explain the latitudinal changes that occur in the characteristics of ichthyofaunas (Currie et al., 1999; Willig et al., 2003; Hillebrand, 2004a; Hillebrand, 2004b; Tittensor et al., 2010). An examination of global patterns showed, however, that, on the basis of the species in 13 groups, ranging from zooplankton to marine mammals, species richness was only strongly related to sea surface temperature of those environmental variables examined (Tittensor et al., 2010).

The majority of studies that have explored the relationship between the characteristics of a fauna and latitude have tended to focus on species richness and/or diversity rather than species composition (Gaston, 2000; Gaston and Blackburn, 2008). Emphasis has been placed, however, on identifying the ways in which the species

compositions of marine faunas along coasts are related not only to latitude, but more particularly to factors such as water temperature, habitat type, bioregion, water depth and time of day or year. Knowledge of the roles played by all of these factors is required to understand the ways in which coastal ecosystems function and thus enable the impacts of, for example, climate change and anthropogenic activities, e.g. fishing, to be predicted and managed (Hooper et al., 2005; Hoegh-Guldberg and Bruno, 2010; Hobday and Lough, 2011; Mora et al., 2011; Doney et al., 2012; Poloczanska et al., 2013; Ban et al., 2014). It is important to be able to identify the species ‘driving’ latitudinal changes and also the ‘borders’ of the distributions of the main species, because, for example, increases in water temperature associated with climate change, will presumably lead to a poleward shift in the distribution of a number of those species (Walther et al., 2002; Holt and Keitt, 2005; Parmesan et al., 2005; Brooker et al., 2007; Cheung et al., 2009; Burrows et al., 2011; Hobday and Lough, 2011; Doney et al., 2012).

Extensive stretches of coast, which span a wide latitudinal range, sometimes contain two or more relatively discrete bioregions, whose different environmental characteristics are reflected in different faunal characteristics (Floeter et al., 2001; Ferreira et al., 2004; Navarrete et al., 2014). In other words, the continuity in the pattern of latitudinal change in faunal characteristics becomes partially disrupted in such circumstances. For example, the reef fish faunas in two zoogeographic provinces or regions along the Brazilian coast differed markedly in species composition, due to the strong influence of the faunal barrier created by the intervening Amazonian freshwater outflow (Floeter and Gasparini, 2000). In contrast, Mahon et al. (1998) showed that the compositions of the demersal fish assemblages of the east coast of North America did not

correspond to the biogeographical regions of that coast, which had been designated on the basis of data for a range of taxa.

1.2 Relationships between ichthyofaunal characteristics and depth and habitat

Although the characteristics of fish faunas in inshore environments frequently change along a latitudinal gradient and are sometimes influenced by bioregional differences within such gradients, the waters in such environments, at any latitude, range in depth and often contain two or more very different habitats. These depth and habitat differences are typically reflected in pronounced differences in the characteristics of the ichthyofauna (McManus, 1985; Bianchi, 1991; Friedlander and Parrish, 1998; Williams et al., 2001; Holbrook et al., 2002a; Khalaf and Kochzius, 2002a; Johnson et al., 2013; Jankowski et al., 2015a; Pearson and Stevens, 2015; Pittman and Olds, 2015).

The results of trawling in a large embayment on the west coast of Australia showed that the species richness and densities of fishes were greater in deeper than shallower waters over soft substrata, whereas the opposite was true when the substratum was vegetated (Travers and Potter, 2002). In another trawl study further south on that coast, the species richness and density of fishes over soft substrata showed no obvious depth-related trend (Hyndes et al., 1999).

Differences between the ichthyofaunal characteristics in different depths can be the result of, for example, the tendency for some species, and particularly their juveniles, to occupy shallow inshore waters, where food may be more plentiful and the likelihood of predation by piscivorous fish less than in more offshore and deeper waters, whereas other

species have a ‘preference’ for the particular characteristics found in deeper water (e.g. Williams, 1991; Blaber et al., 1995; Francour, 1997; Friedlander and Parrish, 1998; Gray et al., 1998; Hyndes et al., 1999; Williams et al., 2001). These types of differences are highlighted by the results of the trawl study carried out by Blaber et al. (1990) in a range of water depths in northern Australia. Those results demonstrated that, among the 31 abundant species studied, nine increased in abundance with depth and two increased in abundance towards the shore, while the other 12 were most common in intermediate depths. Thus, there is no overarching trend for the density of all species at a particular location to increase or decrease with water depth.

The species richness, density and species composition of fish assemblages also typically differ among habitat types, such as unvegetated sand, seagrass, mangroves and reefs (e.g. Jenkins and Wheatley, 1998; Guidetti, 2000; Nagelkerken et al., 2000b; Travers and Potter, 2002; Nagelkerken et al., 2015). Indeed, the results of a study of fish assemblages in different habitat types and depths along a latitudinal gradient in coastal waters of the West Indies demonstrated that variation in species composition was explained more by habitat type than by some factor associated with latitude (Bouchon-Navaro et al., 2005). The ichthyofaunal compositions in coastal Scandinavian waters are also strongly influenced by habitat type, namely soft and rocky substrata (Pihl et al., 1994; Pihl and Wennhage, 2002).

Differences in species composition among habitat types result in partitioning of spatial and food resources among species that are likely to be competing for resources at a location and thereby reduce the potential for competition among those species (Holbrook et al., 2002b). Thus, factors leading to differences in composition among

habitats at a point along a latitudinal gradient will reflect, *inter alia*, variations in such features as the amount and types of habitat and food available (Bouchon-Navaro, 1986), and in the extent to which shelter is provided from predators (Luckhurst and Luckhurst, 1978; Stoner, 1983; Nagelkerken et al., 2000b; Nagelkerken and van der Velde, 2004).

Several studies have explored the extent of differences in the ichthyofaunal characteristics of soft substrata and coral reefs, which frequently constitute the two main habitat types in subtidal tropical marine waters (Longhurst and Pauly, 1987). There have been few statistically rigorous attempts, however, to determine whether the species compositions of the ichthyofaunas in these two habitat types differ in a consistent manner along an extensive latitudinal gradient.

1.3 Relationships between ichthyofaunal characteristics and seasonal and diel effects

Although the characteristics of ichthyofaunas vary spatially, e.g. with latitude and water depth, and with habitat type, they are also influenced by factors that change with time of year (e.g. Aburto-Oropeza and Balart, 2001; Chittaro and Sale, 2003; Biswas et al., 2014) and between day and night (e.g. Harmelin-Vivien, 1982; Galzin, 1987; Newman and Williams, 2001; Harvey et al., 2012a; Aguzzi et al., 2013). Changes in the temperature of inshore marine waters during the year influences a number of crucial trends, including peaks in productivity and the timing of reproduction and thus recruitment of fish species (Johannes, 1978; Robertson and Duke, 1990b). However, in certain tropical regions, heavy rainfall and cyclonic events also influence the level of productivity of inshore waters by leading to a marked increase in freshwater discharge and thus of the amount of nutrients flushed from estuaries into those waters (Nixon et al., 1986; Robertson and Blaber, 1992).

Such heavy freshwater discharge also greatly increases turbidity, which makes juvenile fish less visible to potential predators (Blaber and Blaber, 1980; Cyrus and Blaber, 1987a; Blaber, 2000; de la Moriniere et al., 2004).

The species richness, density and composition of fishes at a particular location in marine waters frequently change during the year (Watson and Goeden, 1989; Blaber et al., 1990; Wantiez et al., 1996; Castillo-Rivera et al., 2002; Mendoza et al., 2009; Shimadzu et al., 2013). Those cyclical changes are often related to consistent inter-annual variations in the timing of recruitment, the movements of certain species to different water depths in response to changes in water temperature and productivity, an increase in body size and/or the timing of the attainment of maturity (e.g. Rainer, 1984; Watson et al., 1990; Blaber et al., 1995). However, Tonks et al. (2008) were unable to identify any particular factor that would account for the changes in the compositions of the fish bycatch of prawn trawlers in a region in north-western Australia (NWA). While the species compositions of fish communities over reefs sometimes change seasonally, such changes do not occur as frequently as over soft substrata (e.g. Thomson and Gilligan, 1983; Aburto-Oropeza and Balart, 2001; Newman and Williams, 2001). The ichthyofaunal compositions over reefs can, however, change conspicuously and abruptly following extreme cyclonic events (Cheal et al., 2002; Rousseau et al., 2010).

The characteristics of ichthyofaunas have been shown to undergo diel changes in a range of environments (Starck and Davis, 1966; Hobson, 1968; Parrish, 1987; Nagelkerken et al., 2000a; Newman and Williams, 2001; Travers and Potter, 2002; Harvey et al., 2012b; Azzurro et al., 2013). Such changes are frequently associated with the timing of feeding

activity, which, in many species, occurs at night and thus reduces the risk of predation by visual piscivores (Sogard et al., 1989; Gray et al., 1998; Linke et al., 2001).

1.4 Statistical approaches

The development, during the last three decades, of a suite of sophisticated multivariate statistical methods for analysing data on faunal communities have been of great value in elucidating an understanding of the factors that influence the structure of faunal communities (Clarke and Green, 1988; Clarke, 1993; Clarke and Ainsworth, 1993; Anderson, 2001a; Clarke and Gorley, 2006; Anderson et al., 2008; Anderson et al., 2011). These techniques have thus provided the tools for rigorously analysing the species compositions of *a priori* groups (non-metric multidimensional scaling ordination, Analysis of Similarities, PERMANOVA), the relationships between species composition and environmental factors (e.g. BioEnv, RELATE and LINKTREE), and the identification of species that typify *a priori* groups and those which distinguish between such groups (Similarity of Percentages; SIMPER). These analytical methods have been used very effectively by various workers to explore the extent to which ichthyofaunal composition varies along a latitudinal gradient and with habitat and/or water depth. (e.g. Bianchi, 1991; Bianchi, 1992a; Bianchi, 1992b; Floeter et al., 2001; Williams et al., 2001; Floeter et al., 2004; Ellingsen et al., 2005; Gaertner et al., 2005; Anderson et al., 2013).

1.5 Characteristics of the tropical north-western Australian coast

The studies for this thesis were undertaken along the ~ 1,500 km coast of tropical north-western Australia (NWA) between Cape Voltaire at 14°S and Locker Point at 21°S

(Fig. 1.1). The NWA coast, and particularly the most northern bioregion, is characterised by extreme environmental conditions, reflecting, in part, the presence of large tides, which are the greatest of any tropical coastline in the world and lead to very strong tidal currents (8 to 22 km h⁻¹) and very high turbidity (Semeniuk, 1993; Wilson, 2013). Furthermore, the most northern bioregion is defined by a distinct monsoonal climate with a summer wet season occurring between November and April and a winter dry season between May and October, and, during the former, is subjected to more periodic cyclones than any other region of the world (Hall et al., 2001). The extreme wet and dry seasons are accompanied by marked differences in water temperature, productivity and turbulence (Thompson and Bonham, 2011; McKinnon et al., 2015b; McKinnon et al., 2015c).

Since the Australian Plate moved progressively northwards during the Caenozoic (Davies et al., 1987), the tropical coast of NWA has been located immediately south of the waters surrounding the Indo-Australian Archipelago (IAA), in which species richness is the greatest of all marine waters (Myers et al., 2000; Hughes et al., 2002b; Connolly et al., 2003). The NWA coast lies within the broader Indo-Pacific biogeographic realm that extends from the eastern shores of Africa to the small islands of the eastern Pacific Ocean. The major surface currents are derived from the South Java Current and the polewards-flowing Indonesian Throughflow (ITF) (Cresswell et al., 1993; Meyers et al., 1995; Domingues et al., 2007). These currents carry water of equatorial Indian and Pacific Ocean origin south-westwards off the NWA coast (Gordon, 2005; Domingues et al., 2007; Condie and Andrewartha, 2008), with the seasonally reversing Holloway Current running closer to

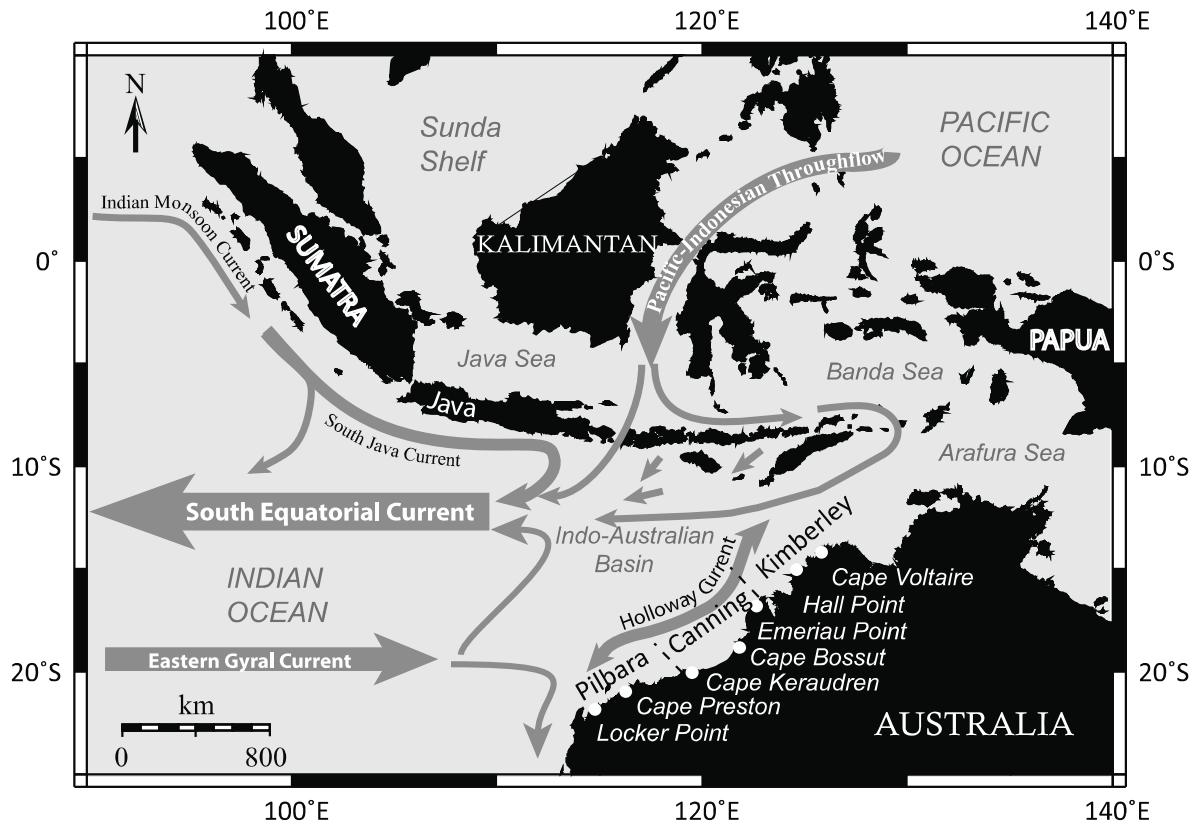


Figure 1.1 Map showing the seven locations sampled over soft substrata and reefs in tropical north-western Australia and the major surface currents in the region.

the coast (Fig. 1.1 Holloway and Nye, 1985; Condie and Andrewartha, 2008; D'Adamo et al., 2009). The ITF has been identified as making an important contribution to the northern headwaters of the Leeuwin Current (Domingues et al. 2007), which, unlike other eastern boundary currents in the Atlantic and Pacific Oceans, flows in a polewards direction (Smith et al., 1991; Ridgway and Godfrey, 2015).

The NWA coastline contains three marine bioregions, which differ in their geological and hydrological characteristics (Fig. 1.1; Semeniuk, 1993; Thackway and Cresswell, 1998; Brocx and Semeniuk, 2010; Wilson, 2013). These bioregions comprise the

sub-humid Kimberley in the north, the semi-arid Canning in the centre and the arid Pilbara bioregion in the south (Gentilli, 1972; Semeniuk, 1983; Brocx and Semeniuk, 2010). The Kimberley coast is subjected to particularly large tides (> 11 m) and highly seasonal discharges of freshwater from rivers, whereas the Canning coast is exposed to moderate tidal action and contains several small tidal creeks but no large rivers. The Pilbara coast, in which the tides are far smaller than along either the Kimberley or Canning coasts, contains a few large rivers and several tidal creeks (Fig. 2.1; Semeniuk, 1993; Wilson, 2013).

The inner shelf waters, which range from 5 to 30 m in depth, contain large areas of soft and hard substrata with reef types include fringing, patch and also true coral reefs in the strict sense (Fairbridge, 1953; Veron and Marsh, 1988; Hatcher, 1991; Wilson, 2013). The patch reefs along this coast consist mainly of a living veneer of scleractinian coral and encrusting coralline red algae, overlying inundated limestone pavement or igneous rock (Simpson, 1988; Hatcher, 1991; Brooke, 1995; Brooke, 1997; Wilson, 2013).

Despite the extent of the tropical north-western Australian coastline, the characteristics of the marine fish faunas of the Kimberley, Canning and Pilbara bioregions have been the subject of relatively few comparative studies. This is mainly due to the high research costs associated with working in one of the most remote and under-populated coasts of Australia. Checklists have been developed, however, for the fish faunas in areas within NWA (Allen, 1992; Hutchins, 1995; Allen, 1996; Morrison and Hutchins, 1997; Hutchins, 1999; Hutchins, 2001b; Hutchins, 2003; Moore et al., 2014) and as part of overall broad studies of the marine fish fauna. The analyses of Hutchins (2001a) and Fox and Beckley (2005) demonstrated that the ichthyofaunal composition of particularly the Kimberley bioregion was discrete from those of other regions on the west coast of

Australia. The characteristics of the fish faunas at two locations along the NWA coast have been related to differences in habitat types, such as mangroves, reefs and unvegetated sand (Blaber et al., 1985; Fitzpatrick et al., 2012). Trawling in offshore waters along the NWA coast, and thus outside those of the present study, demonstrated that the composition of the ichthyofaunas in these waters varied with depth and changed with latitude (e.g. Sainsbury, 1987; Sainsbury et al., 1993; Williams et al., 2001).

Although there is evidence that finfish trawl fisheries have influenced the composition of the fish fauna in NWA (Thresher et al., 1986; Sainsbury, 1987; Sainsbury, 1991), those fisheries are located in deeper waters well outside our study area. Furthermore, commercial and recreational fishing is minimal in the broad band of water along the NWA coast in which our sampling was conducted. Thus, the compositions of the fish faunas in our samples are unlikely to have been influenced markedly by anthropogenic factors.

The inshore shallow waters (< 30 m deep) along the NWA coast are mainly fished by recreational and charter boat anglers as the commercial trawl and trap fishers that operate on this coast are restricted to fishing in water depths greater than 50 and 30 m, respectively (Fletcher and Santoro, 2015). Commercial fishing of finfish occurs in these waters as part of the Kimberley Gillnet and Barramundi Managed Fishery (KGBMF) and the Mackerel Managed Fishery (MMF). The KGBF operates in the nearshore and estuarine zones of the NWA coast and predominantly targets Barramundi (*Lates calcarifer*), King Threadfin (*Polydactylus macrochir*) and Blue Threadfin (*Eleutheronema tetradactylum*) while the MMF targets Spanish Mackerel (*Scomberomorus commerson*). Although sharks have been fished commercially in these waters, fishing has been prohibited in the

northern shark fisheries since 2008/09 due to concerns for stock levels of the main species, e.g. Sandbar Shark (*Carcharhinus plumbeus*), Blacktip sharks (at least two species of *Carcharhinus*) and Tiger Shark (*Galeocerdo cuvier*) (Molony et al., 2013). The main finfish species targeted by recreational and charter fishers along this coast are Stripey Snapper (*Lutjanus carponotatus*), Grass Emperor (*Lethrinus laticaudis*), Spangled Emperor (*Lethrinus nebulosus*), Spanish Mackerel (*Scomberomorus commerson*), King Threadfin (*Polydactylus macrochir*) and Blue Threadfin (*Eleutheronema tetradactylum*) (Williamson et al., 2006; Ryan et al., 2015). Although recreational fishing can be reasonably intense in locations adjacent to highly populated areas, relatively little recreational fishing occurs in more remote locations, such as those to the north of Broome in the Kimberley Bioregion, however, charter fishing operators regularly cruise the Kimberley coast (Williamson et al., 2006). Fishes along the inshore NWA coast also suffer some mortality through being taken as bycatch by prawn trawlers in several prawn fisheries such as the Kimberley, Broome, Onslow and Nickol Bay Prawn Managed Fisheries (Fletcher and Santoro, 2015).

In their review of the data required for effective management of the coastal waters of NWA, Heyward et al. (2000) emphasised that there were major gaps in our knowledge of the ecology of fishes in this remote area. Furthermore, when reviewing the biophysical resources of the Canning Bioregion, Stewart et al. (2005) highlighted the limited amount of available information on the marine fauna of sub-tidal habitats along this coast. The paucity of information on the fish faunas of the reefs and soft substrata in inshore waters of NWA between 14 and 22°S contrasts starkly with the large amount of data accumulated for the ecology of fishes at comparable latitudes on the north-eastern coast of Australia (e.g. Russ, 1984a; Russ, 1984b; Sale, 1991; Meekan and Choat, 1997;

Syms and Jones, 2000; Syms and Jones, 2001; Cappo et al., 2004; Cappo et al., 2007; Cheal et al., 2008; Cheal et al., 2012; Cheal et al., 2013).

1.6 Broad aims of thesis

The first aim of this thesis was to establish a rigorous and carefully designed sampling regime that would enable the collection of representative samples of the fish faunas over soft substrata and reefs in inshore and more offshore and slightly deeper waters at regularly-spaced intervals along the full length of the tropical NWA coast. The resultant data could then be used to determine the characteristics of the ichthyofaunal assemblages in these waters and how those characteristics vary with latitude, bioregion, habitat type, time of year (season), water depth and, in the case of reefs, also between day and night. The various hypotheses to be tested regarding the relationships between the species richness, density and species composition of fishes and the environmental and other factors are given in detail in the aims in the four chapters describing the results.

Chapter 2. The species compositions of fish faunas over soft substrata and reefs along the tropical coast of north-western Australia differ and change with latitude and bioregion

2.1 Introduction

The vast majority of the numerous studies that have explored the relationship between faunal characteristics and latitude have focused on species richness rather than species composition (Chapter 1, Gaston, 2000; Willig et al., 2003). The ways in which the species compositions of fish faunas along a coast are related to factors associated with latitude, bioregion and habitat, together with the identification of the species mainly responsible for any ichthyofaunal differences associated with those three variables, are crucial for understanding coastal ecosystem function and predicting the impact on those faunas of such factors as climate change and anthropogenic activities, e.g. fishing (Chapin et al., 2000; Bellwood and Hughes, 2001; Hooper et al., 2005). The identification of such latitudinal patterns, and the borders of the distributions of species, are becoming particularly important as increases in water temperatures associated with global climate change causes shifts in the distribution of tropical species in a polewards direction (Walther et al., 2002; Holt and Keitt, 2005; Parmesan et al., 2005; Brooker et al., 2007; Cheung et al., 2009; Hobday and Lough, 2011; Cheung et al., 2012; Fernandes et al., 2013).

Statistical techniques, such as cluster analysis and multidimensional scaling ordination, provide biologists with the tools to explore visually whether the species composition of a given fauna changes with latitude and/or bioregion (e.g. Engle and Summers, 1999; Floeter and Gasparini, 2000; Williams et al., 2001; Kulbicki et al., 2013;

Navarrete et al., 2014). Such techniques, allied with associated tests (Clarke, 1993; Clarke and Warwick, 2001; Clarke et al., 2008), enable biologists to determine whether the species composition of faunal assemblages at different latitudes and/or in different regions are significantly different and, if so, to what extent and which species are mainly responsible for any such differences (e.g. Edgar et al., 2004). Furthermore, the development of other statistical procedures (e.g. Clarke, 1993; Clarke and Warwick, 2001; Clarke et al., 2008) makes it possible to ascertain whether latitudinal changes in composition are related to selected environmental variables (e.g. Engle and Summers, 1999; Vorwerk et al., 2003; Bender et al., 2013).

Although soft substrata and coral reefs frequently constitute the two main habitat types in sub-tidal tropical marine waters (Longhurst and Pauly, 1987), there have been no statistically rigorous attempts to determine whether the species compositions of the ichthyofaunas in these two habitat types differ in a consistent manner along an extensive latitudinal gradient. However, canonical redundancy analysis of presence-absence data for fishes in different habitat types in coastal waters of the West Indies, which included sand, seagrass and reef areas, demonstrated that, while the species composition in these waters reflected latitudinal and hydrological gradients, it was related mainly to habitat type (Bouchon-Navaro et al., 2005). Multivariate analyses, employing matrices constructed from the densities of the various species, also demonstrated that ichthyofaunal composition in coastal Scandinavian waters was related to habitat type, *i.e.* soft vs rocky bottom substrata (Pihl et al., 1994; Pihl and Wennhage, 2002).

As a result of the progressive northwards movement of the Australian plate during the Caenozoic (Davies et al., 1987), the tropical coast of north-western Australia (NWA)

now lies immediately south of the waters surrounding the Indo-Australian Archipelago (IAA), in which species richness is the greatest of any marine waters (Chapter 1, Myers et al., 2000; Hughes et al., 2002b; Connolly et al., 2003). While the distribution maps in Carpenter and Niem (1998-2001) show that the distributions of numerous tropical marine fish species extend southwards from the IAA into NWA, the degree of this extension varies among those species. The distribution data collated by Hoese et al. (2007) emphasise, however, that the NWA coast contains some endemic fish species.

As described in Chapter 1, the coastline of NWA comprises three distinct bioregions that differ markedly in terms of tidal regime, substrate composition and the amount of riverine input and presence of mangrove forest (Semeniuk, 1993; Thackway and Cresswell, 1998; Wilson, 2013). Multivariate analysis of broad relative abundance categories for reef fish faunas and presence/absence data for marine neritic fish species indicated that the tropical coast of NWA comprises two main biogeographic regions, *i.e.* the Kimberley and north-west coast (Hutchins, 2001a; Fox and Beckley, 2005). Note, however, that Hutchins (2001a) did not include data for the Canning Bioregion and that the data used by Fox and Beckley (2005) for that bioregion were limited. In contrast to the situation with fishes, no such bioregional distinctions were found following subjective assessments of the species compositions of cardiid bivalves (Wilson and Stephenson, 1977), seagrasses (Walker and Prince, 1987) and prosobranch molluscs (Wells and Threlfall, 1980).

A preliminary examination of the distributions of fishes in Carpenter and Niem (1998-2001), showed that the southern limits of the distributions of various fish species along the NWA coast varies considerably, and this will inevitably be reflected in changes in

composition with latitude. The continuity and substantial latitudinal range of the 1,500 km of this coast provides an ideal opportunity to explore the extents to which the species and familial compositions of fish assemblages change with latitude. The results acquired by an appropriate sampling regime can then be used to broadly explore the ways in which environmental factors, such as water temperature, are likely to influence changes in ichthyofaunal composition. However, any interpretations regarding latitudinal changes in such compositions need to recognise that the tropical NWA coast comprises three bioregions with their own distinct physico-chemical and biotic characteristics and that there will thus be an underlying bioregional influence. The presence of soft substrata and reefs along the full stretch of the NWA coastline (Fairbridge, 1967; Veron and Marsh, 1988; Wilson, 2013) also provides the opportunity of examining whether any latitudinal and bioregional trends in the ichthyofaunal compositions of these two very different habitat types are similar.

During the present study, fishes were sampled over soft substrata and reefs of inshore waters at regularly-spaced locations along the entire tropical coastline of NWA (Fig. 2.1). The main families and species caught over these two habitat types have been enumerated, thus enabling their contributions to the fish faunas over their respective habitats to be calculated and the contributions made by the number of species and the number of individuals in each zoogeographical category *sensu* Hoese et al. (2007) to be determined. The data on the contributions of the various species in the two habitat types at the various latitudes were subjected to a range of contemporary multivariate techniques to test the following hypotheses. (1) The species compositions of fishes caught by trawling over soft substrata and by trapping over reefs at each location differ markedly.

(2) The species compositions of soft substrata and reefs change in a broadly sequential and similar manner southwards along the NWA coast. (3) Latitudinal changes in the ichthyofaunal compositions of the two habitat types largely parallel those of water temperature. (4) The ichthyofaunal compositions of both soft substrata and reefs in the three bioregions differ, with that in the bioregion with the most discrete characteristics, *i.e.* Kimberley, being the most distinct. Particular focus has been placed on elucidating which species are especially responsible for contributing to any latitudinal trends and bioregional differences in ichthyofaunal composition in the two habitat types.

2.2 Materials and Methods

2.2.1 Study area

The characteristics of the NWA coast, in which sampling was conducted, are described in full in Chapter 1. The following account is thus restricted to summarising the broad details of this area that are directly related to the aims of this chapter.

The inshore waters (5 to 30 m deep) along the 1,500 km coast of tropical NWA contain large areas of both soft substrata and coral reefs (Fairbridge, 1967; Veron and Marsh, 1988; Wilson, 2013). The coastline extends from the warm and humid to sub-humid Kimberley Bioregion in the north, through the semi-arid Canning Bioregion in the centre to the cooler and arid Pilbara Bioregion in the south (Fig. 2.1 Gentilli, 1972; Semeniuk, 1983; Thackway and Cresswell, 1998; Brocx and Semeniuk, 2010). Tidal range declines markedly in a southwards direction from macrotidal in the Kimberley to mesotidal in the Canning and microtidal in most of the Pilbara (Semeniuk, 1993; Cresswell

and Badcock, 2000; Wilson, 2013). The strong tidal currents (8 to 22 km h⁻¹) and, to a lesser extent, the highly seasonal discharge from large rivers produced by alternating wet and dry seasons of the year, accounts for turbidity being far greater in the waters of the Kimberley coast than of the Canning coast, where tidal influence is not as strong and there are no large rivers. The small tidal range and presence of only a few large and highly seasonal rivers along the Pilbara coast results in the waters along this coast being far less turbid than the Kimberley coast and thus facilitate the development of extensive seagrass meadows in some areas. The embayments and tidal creeks and rivers of the Kimberley coast, and to a lesser extent small sections of the Pilbara and Canning coasts, contain substantial mangrove forests (Semeniuk, 1993; Brocx and Semeniuk, 2010; Wilson, 2013).

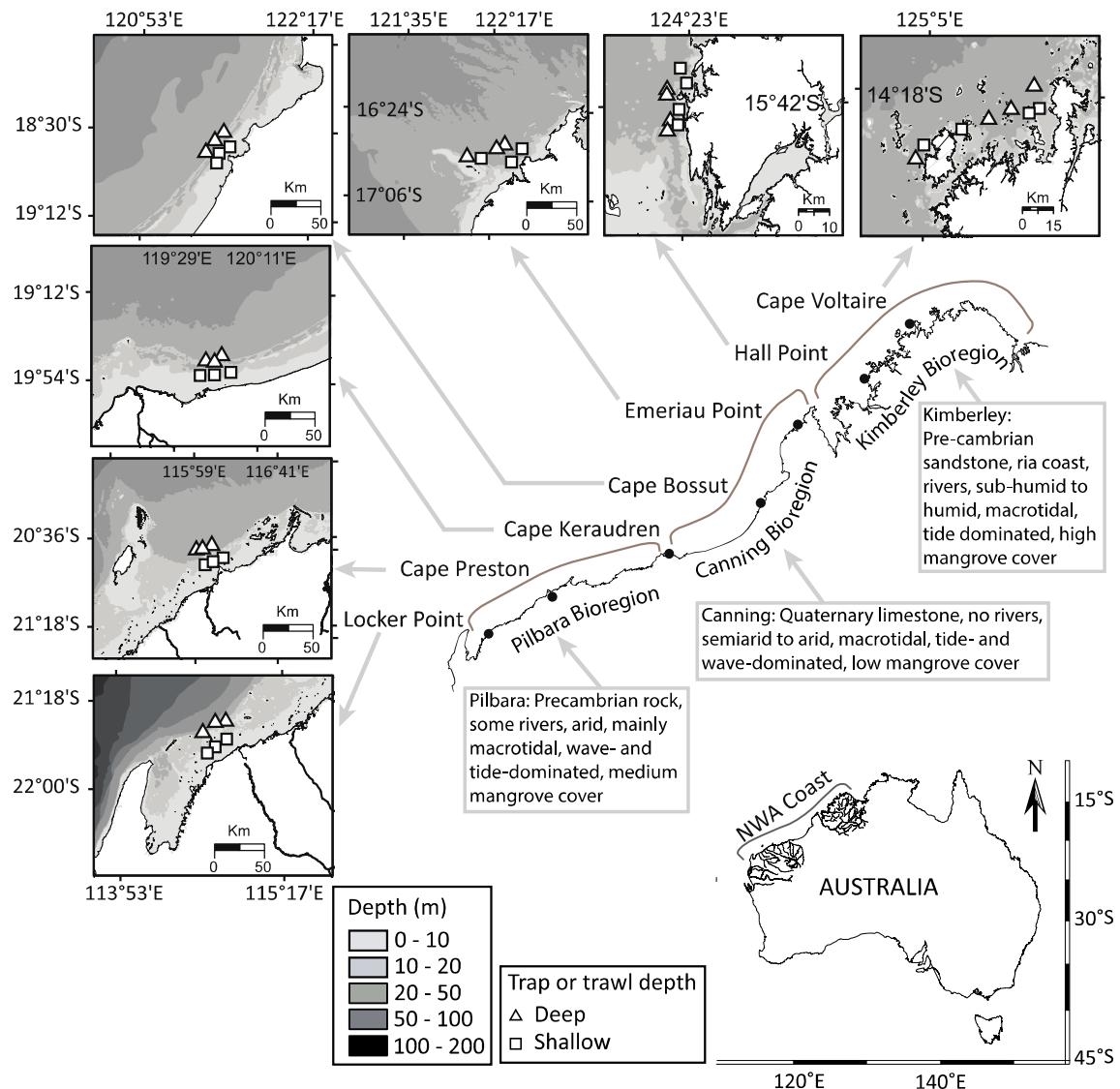


Figure 2.1 Study area where fishes over soft substrata and reefs were sampled by trawls and traps in both deep ($\bar{x} = 22$ m) and shallow ($\bar{x} = 12$ m) waters at each of the seven locations within three bioregions along the tropical north-western Australian coast in 2000, 2001 and 2002. Details of the key characteristics of each bioregion are provided *sensu* Brocx & Semeniuk (2010).

2.2.2 Sampling regime

Fishes were sampled over soft substrata by otter trawling and over nearby patch reefs by trapping at seven regularly-spaced locations along the Kimberley (Cape Voltaire and Hall Point), Canning (Emeriau Point, Cape Bossut and Cape Keraudren) and Pilbara coasts (Cape Preston and Locker Point). The deep ($\bar{x} = 22$ m) and shallow ($\bar{x} = 12$ m) waters over soft substrata and reefs were sampled by both methods at each of the seven locations (Fig. 2.1; Table 2.1). Trawling and trapping were both undertaken in early June to early September (dry season), of 2001, and in late February to late April (wet season) of 2002, and trapping was also conducted in mid June to mid August (dry season) of 2000 (Table 2.1a). All sampling was undertaken from the live-aboard vessels *RV Flinders* and *RV Naturaliste* operated by the Department of Fisheries, Western Australia.

The trawl comprised port and starboard nets, each having a foot-rope length of 30.5 m, with 50 and 45 mm stretched mesh in the wings and cod-end, respectively. When in operation, the mouth of the net was 8 m wide and 1 m high. On each occasion that a location was sampled, four replicate trawls were carried out during the day for 15 min in deep ($\bar{x} = 22$ m) and shallow ($\bar{x} = 12$ m) water depths at a boat speed of $\sim 3\text{-}4 \text{ km h}^{-1}$, each covering a distance of 1.1 to 1.7 km, and separated by a distance of at least 500m from that covered by each of the other trawls (Table 2.1b). The area swept during each trawl was calculated from the width of the net's mouth and the distance trawled, the latter determined from the latitudes and longitudes at the start and finish of each trawl.

The fish traps, which were specifically designed for the Pilbara and Kimberley trap fisheries, were rectangular and made of steel. They measured 600 mm in height, 1,500 mm in length and 1,200 mm in width and were covered with 50 mm square steel mesh.

They had a single 600 x 200 mm entrance on one side, which tapered to 600 x 100 mm internally. The traps were baited using 1kg of mulched fresh Australian Pilchard (*Sardinops sagax*) in each of two meshed bags. This bait had been shown to yield significantly higher catches than those of other baits tested in a trap study conducted in offshore waters of north-western Australia (Whitelaw et al., 1991). Bait was still present in all traps when retrieved at the end of sampling.

Trapping was undertaken in deep and shallow water depths during the dry season, *i.e.* early June to early September, of both 2000 and 2001, and during the wet season, *i.e.* late February to late April, of 2002 (Table 2.1a). In both 2000 and 2001, the deep and shallow waters at each location were sampled during the day using a group of ten traps set twice for ~4 h on each of three days and during the night by employing two groups of five traps set for ~10 h on two successive nights and occasionally a third night (Table 2.1b). The 4 h period of sampling during the day was selected to accommodate the requirements of concomitant studies on the biology of selected fish species, while the 10 h period of nocturnal sampling was employed because, for logistical and safety reasons, traps could only be set and retrieved once on any given night (Table 2.1b). It proved possible, however, in the wet season of 2002 to increase the soak time during the day to 10 h, using two sets of five traps, and thus employ the same sampling regime as during the night (Table 2.1b).

Traps were always set apart at distances of 50-200 m to reduce the likelihood of the “field of capture” of any trap overlapping that of any other trap (Eggers et al., 1982). The number of individual fishes of each species in each group of five or ten traps were

pooled and expressed as fishes (4 h^{-1} or fishes (10 h^{-1}), which was then considered a replicate for use in analyses of catch rates (abundance).

From the above, it follows that, in each wet and dry season, there were six replicates for the day and four to six replicates for the night for both deep and shallow waters at each of the seven main sampling locations (Table 2.1b). Note that, in studies carried out previously on fish trapping in north-western Australia, neither the catch rates nor species compositions of fishes differed within the range of the 4 to 10 h soak time employed during the present study (Whitelaw et al., 1991). Daytime sampling did not commence until 1 h after sunrise and was completed at least 1 h before sunset (Koslow et al., 1997).

2.2.3 Environmental variables

Water temperature and Secchi disc depth (depth of water clarity) in both deep and shallow waters at each location were recorded at four intervals throughout the first day of sampling both of those depths at each location in each of the three years of sampling. The distance from mainland shore was recorded immediately prior to collecting each replicate sample from over soft substrata and reefs and the water depth (to tidal datum) of each replicate trap or trawl sample was also recorded. Water temperature was recorded using a YSI 6600 Temperature probe and water depth by the ship's echo sounder.

Table 2.1 Details of (a) the timing of sampling at each of the seven locations in the three bioregions along the north-western Australian coast in 2000, 2001 and 2002 and (b) years (seasons), time (daylight or night), duration of each trawl or trap set, replication and frequency of sampling in both deep ($\bar{x} = 22$ m) and shallow ($\bar{x} = 12$ m) waters at each location.

(a)

	Dry season 2000	Dry season 2001	Wet season 2002
Kimberley Bioregion			
Cape Voltaire	29 Jul-3 Aug	14-20 Aug	10-16 April
Hall Point	3-8 Aug	20-25 Aug	17-22 April
Canning Bioregion			
Emeriau Point	11-17 Aug	26 Aug-4 Sep	23-28 April
Cape Bossut	3-8 July	20-25 June	11-15 March
Cape Keraudren	27 June- 2 July	14-19 June	5-10 March
Pilbara Bioregion			
Cape Preston	19-24 June	6-11 June	26 Feb-3 March
Locker Point	15-19 June	2-6 June	22-25 Feb

(b)

Year	Time of sampling	Trawl/set duration	No. of replicates per day or night	No. of days or nights	Total replicates
2000 (Dry)	Day	4 h	2 Sets of 10 Traps	3	6
	Night	10 h	2 Sets of 5 Traps	2 or 3	4-6
2001 (Dry)	Day	4 h	2 Sets of 10 Traps	3	6
	Day	15 min	4 Trawls	1	4
	Night	10 h	2 Sets of 5 Traps	2 or 3	4-6
2002 (Wet)	Day	10 h	2 Sets of 5 Traps	3	6
	Day	15 min	4 Trawls	1	4
	Night	10 h	2 Sets of 5 Traps	2 or 3	4-6

The tidal range at a location on each day of sampling that location was recorded as the difference between the maximum and minimum water heights. Precipitation was recorded as the total rainfall during sampling and in the preceding two weeks. Tidal range and precipitation data were obtained from the Australian Government Bureau of Meteorology. Average estimates of remotely-sensed chlorophyll *a* concentrations during the six months comprising the dry (May to October 2001) and wet seasons (November 2001 to April 2002) were calculated with the Giovanni online data system, developed and maintained by the NASA GES DISC (Acker and Leptoukh, 2007). Surface chlorophyll *a* concentration are used as proxy for phytoplankton concentration and thus of productivity (Lee et al., 2015).

Substratum hardness and complexity were estimated by a combination of visual assessment of the ship's echo-sounder signal, video footage from a drop camera as the ship passed along the trawl track and inspection of the biota retained in the trawl codend. The substratum covered during each trawl was categorised as either soft mud, soft sand, soft sand with sparse sponges, hard sand, hard sand with sparse sponges or hard sand with sponge and live gorgonian fragments.

2.2.4 Treatment of fishes

The fishes caught by each trawl were separated into species on the boat deck and the total number of each species recorded, while those taken in each trap were transferred to a tank with running seawater, from which they were subsequently removed, identified to species and then released live back into the ocean. Fish were

identified using the descriptions in Gloerfelt-Tarp and Kailola (1984), Sainsbury et al. (1985), Last and Stevens (1994), Allen (1997) and Carpenter and Niem (1998-2001). In the case of trawl samples, the number and wet weight of each species in each sample were recorded and expressed as the number and biomass of fishes 0.01 km^{-2} , respectively. As in the trawl study of Williams et al. (2001), catchability (q) was regarded as 1 because no information was available on the selectivity of the gear. Note, however, that the vast majority of species belong to the small and medium-sized categories, which, in the trawling study of Blaber et al. (1990) did not differ markedly in their values for q .

2.2.5 Cluster and ordination analyses

As the catches taken over soft substrata and reefs were obtained using very different methods, the number of each fish species in each replicate sample from each of those habitat types at each of the seven locations on each sampling occasion was expressed as a percentage of the total number of fish in that sample. Although this enabled the species composition in the two habitats to be compared directly, it is recognised that the compositions of particularly traps will be biased due to the selectivity of the sampling method. For cluster and ordination analyses, the percentage contribution of each species to each replicate sample obtained by both trawling and trapping was fourth-root transformed to appropriately take into account the numerous rare species collected by both sampling methods and to down-weight the contribution of the most dominant species with consistently high values (Clarke and Warwick, 2001). The means of the transformed values for each habitat type in each site were then calculated and used to construct a Bray-Curtis similarity matrix. This matrix was subjected both to hierarchical

agglomerative clustering (CLUSTER), employing complete linkage, and to non-metric multidimensional scaling (nMDS) ordination (Clarke and Gorley, 2006). The ordination also included the means (on transformed scales) for all samples in each habitat and the grand mean for all samples in both habitat types. This allowed the compositions of the different assemblages in each habitat to be correctly displayed in relation to each other, thereby enabling the relative magnitude of latitudinal change among sites in the two habitats to be compared.

2.2.6 ANOSIM and SIMPROF tests

Using data for the replicate samples obtained from over both soft substrata and reefs at each location, and again computing Bray-Curtis similarities on the transformed percentage contributions of each species, one-way Analysis of Similarities (ANOSIM) were employed to determine whether the compositions of the fish faunas in the two habitat types and in the same habitat type at the seven locations were significantly different. For each ANOSIM test, the null hypothesis that there were no significant differences among groups was rejected when the significance level (P) was $< 5\%$. The extent of any significant differences produced by this test was determined using the R -statistic value (Clarke, 1993), which can range from 1, *i.e.* all samples within each group are more similar to each other than to any of the samples from other groups, down to approximately zero, when the similarities within and between groups are the same. When pairwise ANOSIM comparisons detected that the fish composition differed significantly between habitat types and/or among locations, Similarity Percentages (SIMPER) were used to identify which species typified such *a priori* groups and distinguished each *a priori* group from the

other groups (Clarke, 1993). However, evidence for bioregional differences can be adduced without *a priori* distinctions by the following alternative style of test, namely SIMPROF.

The construction of similarity profiles, the SIMPROF test, was used to answer the general question of whether there were any overall structural differences among the fish communities at the seven locations, or whether the data from these locations behave as if drawn from a single, common community type. This test employed the multivariate structure of a species data matrix to test for the presence of significant multivariate structure (e.g. group structure) in an *a priori* unstructured set of samples and provides a means for preventing any further unwarranted analysis of the sub-structure of a group of samples (Clarke et al., 2008). Larger values of the test statistic π than expected provide evidence that significant group structure is present among the samples tested. This SIMPROF procedure is carried out hierarchically, proceeding downwards through the nodes of the dendrogram. Groups of samples that cannot be distinguished (*i.e.* appear to have a common community structure) are identified in the dendrogram by dashed lines (see Clarke et al. (2008) for further details of SIMPROF).

The question of whether the ichthyofaunas of the tropical coast of NWA belong either to two main bioregions *sensu* Fox and Beckley (2005), *i.e.* Kimberley and north-west shelf, or to three main bioregions *sensu* Semeniuk (1993) and Thackway and Cresswell (1998), *i.e.* Kimberley, Canning and Pilbara, requires a more directed test, since it specifically concerns the validity of an *a priori* defined structure. ANOSIM was thus employed to test for differences at a coarser spatial level than locations, namely whether the compositions of the fish fauna in the Kimberley, Canning and Pilbara bioregions are

distinguishable. The alternative hypothesis is that those of the Canning and Pilbara bioregions are indistinguishable, leaving two main bioregions *sensu* Fox and Beckley (2005). This test uses the locations within each bioregion as the ‘replicates’, rather than the samples within a location, which would be an inappropriate replication level for this hypothesis. Data were therefore averaged to location level, as described at the start of this section, and subjected to two-way crossed ANOSIM (Clarke, 1993), with factors being habitat (2 levels: soft substratum and reef) and bioregion (3 levels: Kimberley, Canning and Pilbara). Pairwise ANOSIM tests between bioregions, removing the effects of habitat, provide the required tests for discriminating between two and three bioregions.

2.2.7 RELATE test

The RELATE procedure (Clarke and Gorley, 2006) was used to quantify, for the ichthyofaunas in each habitat type, the extent to which the pattern of rank orders between the various pairs of locations in the biotic similarity matrix, paralleled those in distance matrices constructed from the latitudinal co-ordinates and from mean water temperatures at those locations. The pairwise R -statistic values from tests of differences in species composition between locations, employing the replicates within a location, are used to construct a community ‘similarity’ matrix (large R implying high similarity) to compare with the environmental distance matrices. This approach has the advantage of capturing differences in both average community structure at a site and variability around that average, both of which may depend on environmental differences. The correlation between a biotic and environmental matrix was considered significant if the associated P

value was < 5%. The Spearman rank correlation (ρ statistic) was used to assess the extent to which the multivariate structure of the two matrices agrees.

The PRIMER v6 statistical package (PRIMER-E, Plymouth, UK) was used for cluster analysis, ordination and associated tests.

2.3 Results

2.3.1 Water temperature

Mean water temperatures decreased sequentially from their maxima of $\sim 27.7^{\circ}\text{C}$ at the two most northern locations in the Kimberley Bioregion to 24.6°C at Cape Keraudren, and remained at about that level at the three most southern locations (Fig. 2.2).

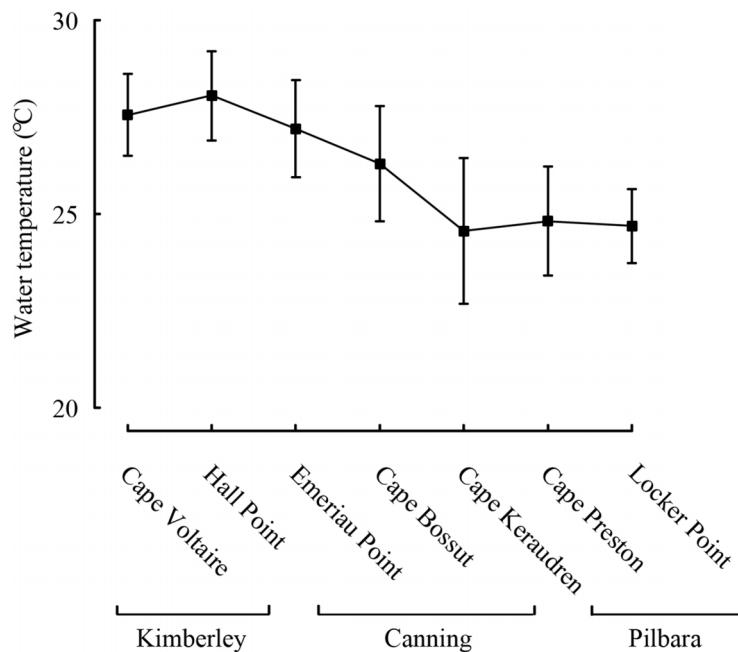


Figure 2.2 Mean water temperatures \pm 95% confidence intervals at each of the seven sampling locations along the north-western Australian coast. Means at each location were derived across deep and shallow waters in the two dry seasons of 2000 and 2001 and one wet season of 2002.

2.3.2 Main fish families and zoogeographical categorisations

Trawling over soft substrata and trapping over reefs at the seven sampling locations along the tropical coastline of NWA during 2000, 2001 and 2002 yielded 110,521 fishes, representing 85 families, 197 genera and 361 species (for lists of species and their nomenclature see Appendices 1 and 2). The most speciose families overall were the Carangidae, Epinephelidae (Epinepheline serranids *sensu* Craig and Hastings, 2007), Labridae, Lutjanidae and Tetraodontidae, which were represented by 29, 19, 16, 14 and 13 species, respectively, in the overall catch from both habitat types (Table 2.2). Twenty eight (35.0%) of the remaining families were represented by a single species. The 80 families recorded over soft substrata represented 176 genera and 285 species, while the 37 families recorded over reefs comprised 68 genera and 132 species. Thirty two of the 85 families (37.6%), 43 of the 197 genera (21.8%) and 56 of the 361 species (15.5%) were found over both soft substrata and reefs. Although both sampling methods were inevitably biased to some extent, and thus, in the case of reefs for example, did not contain a few labrid and pomacentrid species known to occur over such habitats in NWA (Hutchins, 2001a), they each caught a wide range of species and families of fishes.

The Carangidae contributed far more to the catches over soft substrata than reefs, whereas the reverse was particularly true for the Lethrinidae and Lutjanidae (Table 2.2). Some families were represented by relatively large numbers in the samples from one habitat type, but were either rare or not found in those from the other habitat type. For example, the Leiognathidae, Terapontidae and Synodontidae ranked first, third and fifth, respectively, in terms of the relative abundance of their individuals over soft substrata, but were not represented in samples from over reefs. In contrast, lutjanids comprised

nearly a third of the catches and ranked second in terms of abundance over reefs, whereas this family constituted less than 1% of the fishes obtained from over soft substrata and ranked only 19 in terms of relative abundance in that habitat type (Table 2.2).

Three hundred and forty nine (96.7%) of the 361 species recorded in the samples collected over both soft substrata and reefs were tropical (Appendices 1 and 2). Of the remainder, nine were sub-tropical, two were distributed from tropical through to temperate waters and one was temperate. One hundred and nine of the species (30.2%) have an Indo-west Pacific (IWP) distribution and 57 (15.8%) are Australian endemics, with a further 51 (14.1%) and 45 (12.5%) occurring in the Indo-west central Pacific and East Indo-west Pacific, respectively (Table 2.3). The only other two distribution categories to be represented by more than eight species were the West Pacific with 34 (9.4%) species and New Guinea/Australia with 30 species (8.3%). The above six categories constituted the main distribution categories for both the soft substrata and reef faunas, with the IWP ranking first in both habitat types, *i.e.* 31.2 and 22.7%, respectively (Table 2.3). The 57 Australian endemic species recorded overall included 18 that are confined to the west coast of Australia (Appendices 1 and 2).

Table 2.2 The most abundant families recorded over inshore soft substrata and reefs along ~1,500 km of the north-western Australian coastline, derived from samples collected from both habitat types at seven regularly-spaced locations. The percentage contributions of their individuals to the total catch of all individuals and of their ranking by abundance in each of those habitat types are shown.

Family	Number of species	Common name	Soft substrata	Reef
			%	%
Leiognathidae ¹⁰		Ponyfishes	38.1 ¹	-
Carangidae ²⁹		Jacks, Trevallies	13.5 ²	3.7 ³
Terapontidae ²		Grunters, Trumpeters	10.6 ³	-
Mullidae ¹²		Mullet	6.5 ⁴	<1.0
Synodontidae ⁶		Lizardfishes	5.2 ⁵	-
Pomacentridae ⁵		Damselfishes	3.7 ⁶	<1.0
Monacanthidae ¹⁰		Leatherjackets	3.3 ⁷	<1.0
Lethrinidae ¹²		Emperors, Emperor breams	1.9 ⁸	52.0 ¹
Tetraodontidae ¹³		Pufferfishes, Blowfishes	1.6 ⁹	<1.0
Apogonidae ¹⁰		Cardinalfishes	1.5 ¹⁰	-
Lutjanidae ¹⁴		Snappers	<1.0 ¹⁹	29.9 ²
Epinephelidae ¹⁹		Groupers	<1.0 ³¹	2.8 ⁴
Balistidae ²		Triggerfishes	<0.1 ⁵¹	2.1 ⁵
Nemipteridae ¹⁰		Threadfin breams	1.4 ¹¹	2.0 ⁶
Siganidae ³		Rabbitfishes	<1.0 ¹⁸	1.7 ⁷
Haemulidae ⁸		Grunts, Sweetlips, Javelinfishes	1.3 ¹³	1.7 ⁸
Labridae ¹⁶		Wrasses	1.0 ¹⁴	1.6 ⁹
Glaucosomatidae ¹		Pearl perches	<0.1 ⁴⁰	<1.0 ¹⁰
Total number of individuals			84 781	25 740

Table 2.3 Number of fish species representing each zoogeographical category in catches obtained over soft substrata and reefs collectively and separately along the north-western Australian coast, and the corresponding percentage contributions made to their respective totals by the number of species (n) and number of individuals (Ind.) of each zoogeographical category *sensu* Hoese et al. (2007).

Zoogeographical category	Soft substrata & reef			Soft substrata			Reef		
	Species		Ind.	Species		Ind.	Species		Ind.
	n	%	%	n	%	%	n	%	%
Indo-West Pacific	109	30.2	57.9	89	31.2	72.5	30	22.7	9.7
Australian endemics	57	15.8	11.5	52	18.2	3.0	16	12.1	39.4
Indo-West Central Pacific	51	14.1	2.6	30	10.5	2.9	26	19.7	1.4
East Indo-West Pacific	45	12.5	12.9	36	12.6	9.0	21	15.9	25.8
West Pacific	34	9.4	6.5	24	8.4	6.2	16	12.1	7.5
New Guinea/Australia	30	8.3	4.3	29	10.2	5.4	6	4.5	0.5
Circumglobal	8	2.2	0.2	7	2.5	0.2	4	3.0	<0.1
Indo-Pacific	7	1.9	0.7	3	1.1	<0.1	5	3.8	3.0
West Central Pacific	6	1.7	<0.1	3	1.1	<0.1	4	3.0	1.1
Atlantic Indo-West	3	0.8	0.2	3	1.1	0.2	-	-	-
Central Pacific									
Others	11	3.0	3.2	9	3.2	0.5	3	2.3	11.5
Total	361			285			132		

2.3.3 Habitat comparisons

Following cluster analysis of the mean percentage contributions of each fish species to the total catches obtained by trawling over soft substrata and by trapping over reefs at each location, the samples from these two different gear types formed very discrete clusters, with the division on the dendrogram occurring at a similarity level of only 0.4% (Fig. 2.3). One-way ANOSIM demonstrated that the composition of the fauna caught by trawling over soft substrata differed significantly from that by trapping over reefs ($P < 0.1\%$; $R = 0.90$). The fish assemblages over soft substrata were distinguished, in particular, from those over reefs by relatively far greater contributions of species such as *Saurida undosquamis*, *Pristotis obtusirostris*, *Torquigener pallimaculatus* and

Paramonacanthus choirocephalus, whereas the reverse was true for *Lutjanus carponotatus*, *Lethrinus punctulatus*, *Lethrinus laticaudis* and *Lutjanus lemniscatus*. Indeed, the last two species were not even caught over soft substrata.

2.3.4 Main species and families over soft substrata

Of the 285 species recorded over soft substrata, 274 (96.1%) are tropical, nine (3.1%) are subtropical and two (0.5%) are distributed from tropical through to temperate waters (Appendix 1). A large percentage of these species are distributed throughout the Indo-west Pacific (31.2%) and, of the remainder, 18.2% were endemic to Australia and 12.6% have an East-Indo-west Pacific distribution (Table 2.3). The number of Australian endemic species was greatest at Emeriau Point and Locker Point, *i.e.* 27, and made the greatest contribution to the total number of species at the first of those locations, *i.e.* 31.0% (Appendix 1).

The dominant families over soft substrata, *i.e.* Leiognathidae, Carangidae, Terapontidae and Mullidae, contributed 38.1, 13.5, 10.6 and 6.5%, respectively, to the total catch of fishes in this habitat (Table 2.2). The most abundant leiognathids were *Leiognathus splendens*, *Secutor insidiator* and *Leiognathus leuciscus*, with contributions of 19.3, 9.8, and 5.3%, respectively (Table 2.4). The two most abundant carangids were *Selaroides leptolepis* (6.0%) and *Carangooides malabaricus* (3.2%), and the only terapontid to make a substantial contribution to the catches was *Terapon theraps* (10.4%). The only mullid to contribute more than 5.0% to the total number of individuals was *Upeneus sulphureus* (5.2%).

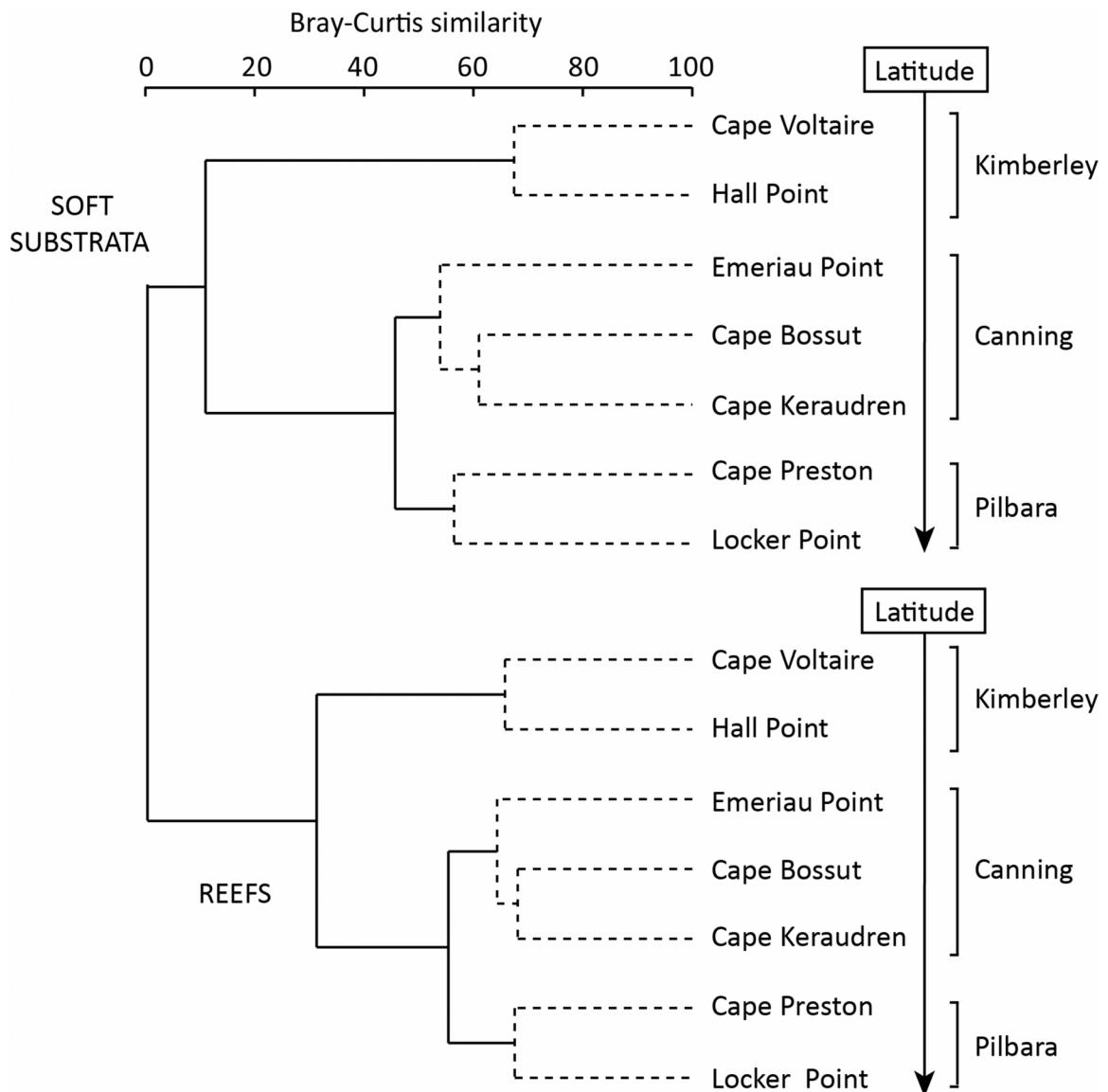


Figure 2.3 CLUSTER analysis, derived from the percentage contribution of each fish species collected over soft substrata and reefs at each of the seven sampling locations along the north-western Australian coast between 2000 and 2002. Solid lines indicate groups that the SIMPROF procedure determined were significantly different from each other.

2.3.5 Main species and families over reefs

Of the 132 fish species recorded over reefs, 131 are tropical and one, *i.e.* *Chrysophrys auratus*, has a temperate distribution (Appendix 2). The most speciose categories over reefs were the Indo-west Pacific, Indo-west-central Pacific and east-Indo-west Pacific with 30, 26 and 21 species, respectively. Sixteen of the species (12.1%) were Australian endemics, of which three were endemic to Western Australia (2.3%). The number of Australian endemics ranged from 5 at Cape Preston to 11 at Cape Bossut (Table 2.3).

In terms of abundance, the faunas over reefs were numerically dominated by species belonging to the Lethrinidae, Lutjanidae, Carangidae and Epinephelidae, which contributed 52.0, 29.9, 3.7 and 2.8%, respectively, to the total number of fishes in this habitat type (Table 2.2). The most abundant lethrinids were the NWA endemic *Lethrinus punctulatus*, which was previously referred to as *Lethrinus* sp. 3 by Carpenter and Niem (1998-2001), followed by *Lethrinus laticaudis* and *Lethrinus genivittatus*, with these three species contributing 36.3, 11.2 and 1.4%, respectively (Table 2.4). Lutjanids were largely represented by *Lutjanus carponotatus* (20.3%), *Lutjanus bitaeniatus* (3.6%) and *Lutjanus johnii* (1.6%). The only carangid to contribute more than 1.0% to the overall catch over reefs was *Gnathanodon speciosus* (2.8%).

2.3.6 Relationship to latitude and water temperature

On the dendrogram shown in Fig. 2.3, the samples from the three bioregions over both soft substrata and reefs are arranged in the same sequential order from north to south, *i.e.* progressing according to latitude from the most northern bioregion (Kimberley)

Table 2.4 The most abundant fish species caught over soft substrata and reefs along the north-western Australian coast, derived from samples collected at seven regularly-spaced locations. Percentage contributions to the total catch of all individuals and of their ranking (superscript) by abundance in both habitat types are shown.

Species	Common name Reef	Soft substrata	
		%	%
<i>Leiognathus splendens</i>	Blacktip Ponyfish	19.3 ¹	-
<i>Terapon theraps</i>	Largescale Grunter	10.4 ²	-
<i>Secutor insidiator</i>	Pugnose Ponyfish	9.8 ³	-
<i>Selaroides leptolepis</i>	Yellowstripe Scad	6.0 ⁴	-
<i>Leiognathus leuciscus</i>	Whipfin Ponyfish	5.3 ⁵	-
<i>Upeneus sulphureus</i>	Sunrise Goatfish	5.2 ⁶	-
<i>Saurida undosquamis</i>	Largescale Saury	3.6 ⁷	-
<i>Pristotis obtusirostris</i>	Gulf Damsel	3.6 ⁸	-
<i>Carangoides malabaricus</i>	Malabar Trevally	3.2 ⁹	-
<i>Paramonacanthus choirocephalus</i>	Pigface Leatherjacket	3.0 ¹⁰	-
<i>Lethrinus genivittatus</i>	Threadfin Emperor	3.5 ¹²	1.4 ¹⁰
<i>Lethrinus punctulatus</i>	Blue-spotted Emperor	<0.1 ²⁶¹	36.3 ¹
<i>Lutjanus carponotatus</i>	Stripey Snapper	<0.1 ¹⁰⁷	20.3 ²
<i>Lethrinus laticaudis</i>	Grass Emperor	-	11.2 ³
<i>Lutjanus bitaeniatus</i>	Indonesian Snapper	-	3.6 ⁴
<i>Gnathanodon speciosus</i>	Golden Trevally	<0.1 ¹¹⁹	2.8 ⁵
<i>Abalistes stellatus</i>	Starry Triggerfish	<0.1 ¹⁶³	2.1 ⁶
<i>Siganus fuscescens</i>	Black Rabbitfish	1.0 ²³	1.6 ⁷
<i>Lutjanus johnii</i>	Golden Snapper	-	1.6 ⁸
<i>Pentapodus emeryii</i>	Purple Threadfin Bream	-	1.4 ⁹

at the top to the most southern bioregion (Pilbara) at the bottom. In the case of the ordination plot derived from the same data, the samples from over soft substrata and reefs likewise have Cape Voltaire and Hall Point at one extreme and Cape Preston and Locker Point at the other (Fig. 2.4). Although the progressions between the samples for each sequential location are not strictly linear for the fauna in either habitat, the lines

connecting the samples from those sequential locations did not cross at any point on the ordination plot.

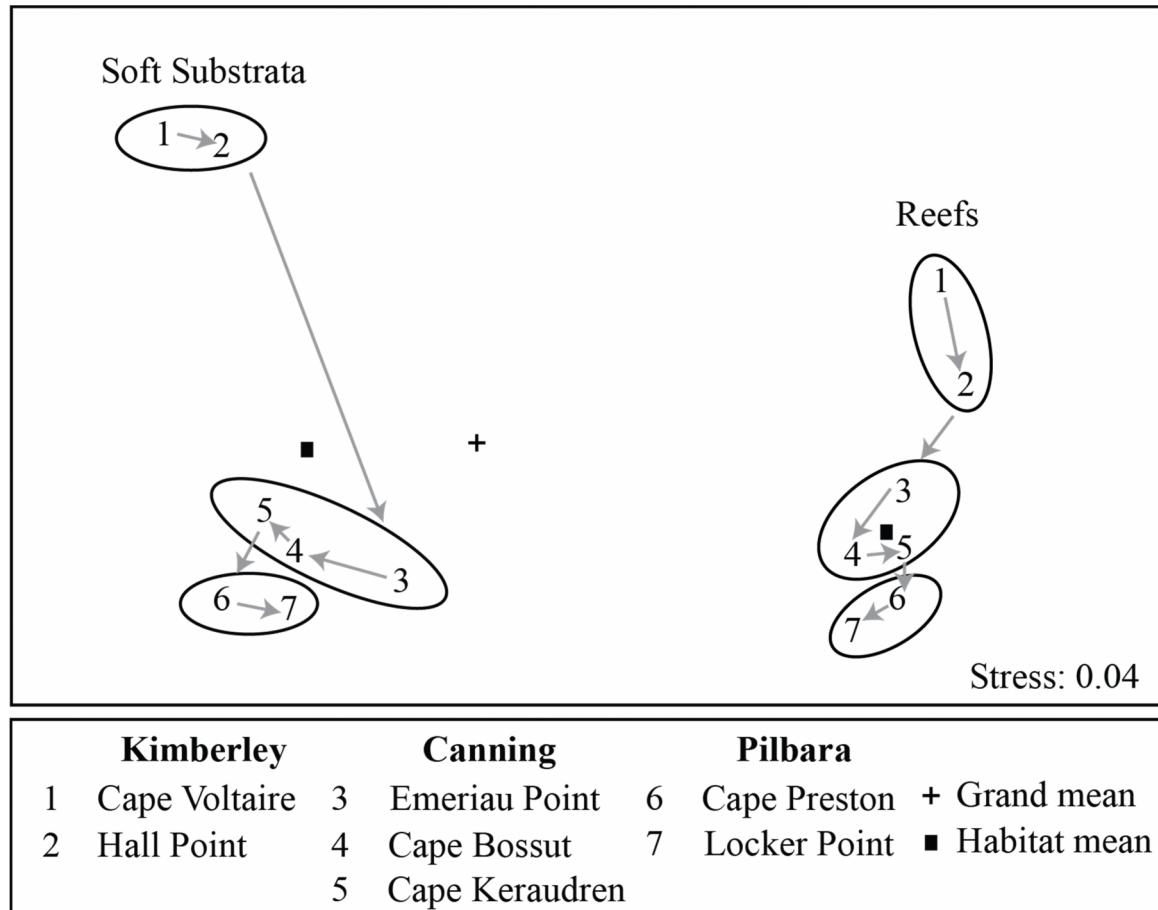


Figure 2.4. Non-metric two-dimensional (nMDS) ordination derived from the percentage contribution of each species collected over soft substrata and reefs at each of the seven sampling locations sampled along the north-western Australian coast between 2000 and 2002. Points in the ordination are grouped according to those determined by SIMPROF in Fig. 2.3.

One-way ANOSIM tests demonstrated that, overall, the species compositions over both soft substrata and reefs differed significantly among locations (both $P = 0.1\%$), with

the Global *R*-statistic being greater for soft substrata (0.615) than reefs (0.423). Pairwise ANOSIM comparisons showed that, over both soft substrata and reefs, the species composition of the fish fauna at each location differed significantly from that at each of the other locations ($P = 0.1$ to 1.1%). However, the *R*-statistic values for pairwise comparisons between the samples at the different locations in a habitat type varied greatly (Table 2.5a,b). Over soft substrata, the *R*-statistic for each comparison between samples was least when distances between locations were closest, ranging from 0.16 for Cape Preston vs Locker Point to 0.31 for Cape Bossut vs Cape Keraudren (Table 2.5a). In contrast, the *R*-statistic for comparisons between the faunas over soft substrata at widely separated locations exceeded 0.9, for example, in the case of the samples from both Cape Voltaire and Hall Point vs those at each of the other five locations.

The same trends were exhibited by the *R*-statistic values for pairwise comparisons between the samples from over reefs (Table 2.5b). Thus, in general, they were least for comparisons between closely-situated locations, with values ranging from ~ 0.1 to 0.2, and were greater for those between samples from both Cape Voltaire and Hall Point and each of the more southern locations, where they typically ranged from ~ 0.7 to 0.8.

SIMPER demonstrated that, over soft substrata, *T. theraps*, *L. leuciscus* and *Saurida tumbil* were important typifying species at each of the two most northern locations, whereas species such as *Saurida undosquamis* typified that fauna at each of the five southern-most locations (Table 2.6). The fauna at the most northern location, i.e. Cape Voltaire, was distinguished from that at each of the more southern locations by greater contributions and frequencies of occurrence of *L. splendens* and *C. malabaricus*, whereas

P. choirocephalus and *L. genivittatus* distinguished the fauna at Cape Preston and Locker Point, respectively, from those at all other locations.

SIMPER demonstrated that *L. carponotatus* was a very important species for typifying the fish faunas over reefs at all seven locations (Table 2.7). The same was true for *L. laticaudis* at all but the southern-most locations, i.e. Locker Point, and *L. punctulatus* was an important typifying species at the five most southern locations. The fish faunas at Cape Voltaire and Hall Point in the north were distinguished from those at all other locations by greater contributions and frequencies of occurrence of the lutjanids *L. johnii* and *L. bitaeniatus*, respectively, whereas that at Locker Point in the south was distinguished from that at each other location by greater contributions of *Lethrinus nebulosus* (Table 2.7). The fish faunas at Cape Preston and Cape Bossut were both distinguished from that at each other location by a greater contribution of *Abalistes stellatus*.

The RELATE procedure demonstrated that ichthyofaunal composition was related to latitude in the case of both soft substrata ($\rho = 0.66; P < 0.7\%$) and reefs ($\rho = 0.76; P < 0.1\%$) and also to water temperature over both soft substrata ($\rho = 0.41; P < 4.1\%$) and reefs ($\rho = 0.53; P < 1.3\%$).

Table 2.5 Global *R*-statistic values and significance levels for pairwise comparisons in one-way ANOSIM tests carried out on the percentage contribution of each fish species, derived from data collected at seven locations in tropical north-western Australia from (a) trawls over soft substrata in 2001 and 2002 and (b) fish traps over reefs in 2000, 2001 and 2002. * = 5%; ** = 1%; *** = 0.1%.

(a) Location	Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Keraudren	Cape Preston
Hall Point	0.27***					
Emeriau Point	0.91***	0.91***				
Cape Bossut	0.99***	0.98***	0.25***			
Cape Keraudren	0.89***	0.88***	0.32***	0.31***		
Cape Preston	1.00***	0.99***	0.40***	0.24**	0.32***	
Locker Point	0.93***	0.93***	0.33***	0.23***	0.16**	0.16**

(b) Location	Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Keraudren	Cape Preston
Hall Point	0.21***					
Emeriau Point	0.49***	0.36***				
Cape Bossut	0.65***	0.64***	0.07***			
Cape Keraudren	0.66***	0.67***	0.15***	0.17***		
Cape Preston	0.74***	0.82***	0.22***	0.20***	0.16***	
Locker Point	0.70***	0.71***	0.32***	0.28***	0.23***	0.20***

Table 2.6 Species identified by SIMPER which typified the fish assemblages of soft substrata at the seven locations in tropical north-western Australia (shaded boxes) and distinguished between the fish assemblages at each pair of those locations (non-shaded boxes). For each pairwise comparison between locations, the species that distinguish between the fauna at one location from another location are indicated by the initials of that location.

Location	Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Keraudren	Cape Preston	Locker Point
Cape Voltaire	<i>Leiognathus splendens</i> <i>Terapon theraps</i> <i>Leiognathus leuciscus</i> <i>Saurida tumbil</i> <i>Carangooides malabaricus</i>						
Hall Point	<i>Leiognathus splendens</i> ^{CV} <i>Carangooides malabaricus</i> ^s ^{CV} <i>Upeneus sulphureus</i> ^{CV} <i>Leiognathus equulus</i> ^{CV} <i>Caranx bucculentus</i> ^{HP}	<i>Terapon theraps</i> <i>Caranx bucculentus</i> <i>Leiognathus leuciscus</i> <i>Saurida tumbil</i> <i>Pseudorhombus arius</i>					
Emeriau Point	<i>Leiognathus splendens</i> ^{CV} <i>Terapon theraps</i> ^{CV} <i>Leiognathus leuciscus</i> ^{CV} <i>Carangooides malabaricus</i> ^{CV} <i>Leiognathus bindus</i> ^{HP}	<i>Terapon theraps</i> ^{HP} <i>Caranx bucculentus</i> ^{HP} <i>Leiognathus leuciscus</i> ^{HP} <i>Pristotis obtusirostris</i> ^{EP} <i>Leiognathus bindus</i> ^{HP}	<i>Pristotis obtusirostris</i> <i>Saurida undosquamis</i> <i>Tragulichthys jaculiferus</i> <i>Parapercis nebulosa</i>				
Cape Bossut	<i>Leiognathus splendens</i> ^{CV} <i>Terapon theraps</i> ^{CV} <i>Leiognathus leuciscus</i> ^{CV} <i>Pristotis obtusirostris</i> ^{CB} <i>Carangooides malabaricus</i> ^{CV} <i>Saurida tumbil</i> ^{CV}	<i>Terapon theraps</i> ^{HP} <i>Caranx bucculentus</i> ^{HP} <i>Pristotis obtusirostris</i> ^{CB} <i>Leiognathus leuciscus</i> ^{HP} <i>Leiognathus bindus</i> ^{HP}	<i>Pristotis obtusirostris</i> ^{CB} <i>T. pallimaculatus</i> ^{CB} <i>Saurida undosquamis</i> ^{CB} <i>Choerodon cephalotes</i> ^{EP}	<i>Saurida undosquamis</i> <i>Pristotis obtusirostris</i> <i>Torquigener pallimaculatus</i> <i>Parapercis nebulosa</i>			
Cape Keraudren	<i>Leiognathus splendens</i> ^{CV} <i>Terapon theraps</i> ^{CV} <i>Selaroides leptolepis</i> ^{CK} <i>Upeneus asymmetricus</i> ^{CK} <i>Carangooides malabaricus</i> ^{CV}	<i>Terapon theraps</i> ^{HP} <i>Selaroides leptolepis</i> ^{CK} <i>Upeneus asymmetricus</i> ^{CK} <i>Caranx bucculentus</i> ^{HP}	<i>Selaroides leptolepis</i> ^{CK} <i>Upeneus asymmetricus</i> ^{CK} <i>Pristotis obtusirostris</i> ^{CK} <i>T. pallimaculatus</i> ^{CK} <i>P. choirocephalus</i> ^{CK}	<i>Selaroides leptolepis</i> ^{CK} <i>Pristotis obtusirostris</i> ^{CB} <i>Upeneus asymmetricus</i> ^{CK}	<i>Saurida undosquamis</i> <i>Upeneus asymmetricus</i> <i>Torquigener pallimaculatus</i> <i>Paramonacanthus choirocephalus</i>		
Cape Preston	<i>Leiognathus splendens</i> ^{CV} <i>Terapon theraps</i> ^{CV} <i>Leiognathus leuciscus</i> ^{CV} <i>Carangooides malabaricus</i> ^{CV} <i>Paramonacanthus choirocephalus</i> ^{CP}	<i>Terapon theraps</i> ^{HP} <i>Caranx bucculentus</i> ^{HP} <i>Paramonacanthus choirocephalus</i> ^{CP} <i>Leiognathus leuciscus</i> ^{HP} <i>Parapercis nebulosa</i> ^{CP}	<i>Paramonacanthus choirocephalus</i> ^{CP} <i>T. pallimaculatus</i> ^{CP} <i>Saurida undosquamis</i> ^{CP} <i>Siganus fuscescens</i> ^{CP} <i>Engyprosopon grandisquamum</i> ^{CB}	<i>Paramonacanthus choirocephalus</i> ^{CP} <i>Pristotis obtusirostris</i> ^{CB} <i>Siganus fuscescens</i> ^{CP} <i>Engyprosopon grandisquamum</i> ^{CB}	<i>Selaroides leptolepis</i> ^{CK} <i>Pristotis obtusirostris</i> ^{CK} <i>Paramonacanthus choirocephalus</i> ^{CP} <i>Upeneus asymmetricus</i> ^{CK}	<i>Saurida undosquamis</i> <i>Parapercis nebulosa</i> <i>Torquigener pallimaculatus</i> <i>P. choirocephalus</i>	
Locker Point	<i>Leiognathus splendens</i> ^{CV} <i>Terapon theraps</i> ^{CV} <i>Leiognathus leuciscus</i> ^{CV} <i>Carangooides malabaricus</i> ^{CV} <i>Saurida tumbil</i> ^{CV} <i>Lethrinus genivittatus</i> ^{LP}	<i>Terapon theraps</i> ^{HP} <i>Caranx bucculentus</i> ^{HP} <i>Leiognathus leuciscus</i> ^{HP} <i>Lethrinus genivittatus</i> ^{LP} <i>Pristotis obtusirostris</i> ^{LP}	<i>Lethrinus genivittatus</i> ^{LP} <i>Pristotis obtusirostris</i> ^{LP} <i>Saurida undosquamis</i> ^{LP}	<i>Lethrinus genivittatus</i> ^{LP} <i>Pristotis obtusirostris</i> ^{CB} <i>Upeneus asymmetricus</i> ^{LP} <i>Torquigener pallimaculatus</i> ^{CB}	<i>Selaroides leptolepis</i> ^{CK} <i>Pristotis obtusirostris</i> ^{CK} <i>Lethrinus genivittatus</i> ^{LP}	<i>Lethrinus genivittatus</i> ^{LP} <i>P. choirocephalus</i> ^{CP} <i>Pristotis obtusirostris</i> ^{LP} <i>Siganus fuscescens</i> ^{CP} <i>Parapercis nebulosa</i> ^{CP}	<i>Saurida undosquamis</i> <i>Pristotis obtusirostris</i> <i>Paramonacanthus choirocephalus</i>

Table 2.7 Species identified by SIMPER as typifying the fish assemblages of reefs at the seven locations in tropical north-western Australia (shaded boxes) and distinguished between the fish assemblages at each pair of those locations (non-shaded boxes). For each pairwise comparison between locations, the species that distinguish between the fauna at one location from that at another location are indicated by the initials of that location.

Location	Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Keraudren	Cape Preston	Locker Point
Cape Voltaire	<i>Lutjanus carponotatus</i> <i>Lutjanus johnii</i> <i>Lethrinus laticaudis</i>						
Hall Point	<i>Lutjanus bitaeniatus</i> ^{HP} <i>Lutjanus johnii</i> ^{CV} <i>Lutjanus carponotatus</i> ^{HP} <i>Lutjanus lemniscatus</i> ^{CV}	<i>Lutjanus carponotatus</i> <i>Lethrinus laticaudis</i> <i>Diagramma labiosum</i>					
Emeriau Point	<i>Lethrinus punctulatus</i> ^{EP} <i>Lutjanus johnii</i> ^{CV} <i>Lethrinus laticaudis</i> ^{EP} <i>Epinephelus coioides</i> ^{CV}	<i>Lethrinus punctulatus</i> ^{EP} <i>Lutjanus bitaeniatus</i> ^{HP} <i>Diagramma labiosum</i> ^{HP}	<i>Lutjanus carponotatus</i> <i>Lethrinus laticaudis</i> <i>Lethrinus punctulatus</i>				
Cape Bossut	<i>Lethrinus punctulatus</i> ^{CB} <i>Lutjanus johnii</i> ^{CV} <i>Abalistes stellatus</i> ^{CB} <i>Pentapodus emeryii</i> ^{CB}	<i>Lethrinus punctulatus</i> ^{CB} <i>Abalistes stellatus</i> ^{CB} <i>Lutjanus bitaeniatus</i> ^{HP} <i>Pentapodus emeryii</i> ^{CB}	<i>Lethrinus punctulatus</i> ^{CB} <i>Abalistes stellatus</i> ^{CB} <i>Pentapodus emeryii</i> ^{CB}	<i>Lutjanus carponotatus</i> <i>Lethrinus punctulatus</i> <i>Lethrinus laticaudis</i>			
Cape Keraudren	<i>Lethrinus punctulatus</i> ^{CK} <i>Lutjanus johnii</i> ^{CV} <i>Lethrinus laticaudis</i> ^{CK} <i>Lutjanus lemniscatus</i> ^{CV}	<i>Lethrinus punctulatus</i> ^{CK} <i>Lutjanus bitaeniatus</i> ^{HP} <i>Lethrinus laticaudis</i> ^{HP} <i>Diagramma labiosum</i> ^{HP}	<i>Lethrinus laticaudis</i> ^{EP} <i>Lethrinus punctulatus</i> ^{CK} <i>Lutjanus carponotatus</i> ^{EP}	<i>Lethrinus punctulatus</i> ^{CB} <i>Abalistes stellatus</i> ^{CB} <i>Lutjanus carponotatus</i> ^{CB} <i>Pentapodus emeryii</i> ^{CB}	<i>Lethrinus punctulatus</i> <i>Lutjanus carponotatus</i> <i>Lethrinus laticaudis</i> <i>Epinephelus coioides</i>		
Cape Preston	<i>Lethrinus punctulatus</i> ^{CP} <i>Lutjanus johnii</i> ^{CV} <i>Abalistes stellatus</i> ^{CP}	<i>Lethrinus punctulatus</i> ^{CP} <i>Lutjanus bitaeniatus</i> ^{HP} <i>Abalistes stellatus</i> ^{CP} <i>Diagramma labiosum</i> ^{HP}	<i>Lethrinus laticaudis</i> ^{CP} <i>Abalistes stellatus</i> ^{CP} <i>Lutjanus carponotatus</i> ^{EP}	<i>Lethrinus punctulatus</i> ^{CB} <i>Abalistes stellatus</i> ^{CB} <i>Lutjanus carponotatus</i> ^{CB} <i>Pentapodus emeryii</i> ^{CB}	<i>Abalistes stellatus</i> ^{CP} <i>Lethrinus laticaudis</i> ^{CK} <i>Lethrinus punctulatus</i> ^{CP}	<i>Lethrinus punctulatus</i> <i>Lutjanus carponotatus</i> <i>Lethrinus laticaudis</i> <i>Abalistes stellatus</i>	
Locker Point	<i>Lethrinus punctulatus</i> ^{LP} <i>Lutjanus johnii</i> ^{CV} <i>Lethrinus laticaudis</i> ^{CV} <i>Lethrinus nebulosus</i> ^{LP}	<i>Lethrinus punctulatus</i> ^{LP} <i>Lethrinus laticaudis</i> ^{HP} <i>Lutjanus carponotatus</i> ^{HP} <i>Lutjanus bitaeniatus</i> ^{HP} <i>Lethrinus nebulosus</i> ^{LP} <i>Diagramma labiosum</i> ^{HP}	<i>Lethrinus laticaudis</i> ^{EP} <i>Lutjanus carponotatus</i> ^{EP} <i>Lethrinus nebulosus</i> ^{LP}	<i>Lethrinus punctulatus</i> ^{CB} <i>Lutjanus carponotatus</i> ^{CB} <i>Lethrinus laticaudis</i> ^{CB} <i>Lethrinus nebulosus</i> ^{LP} <i>Abalistes stellatus</i> ^{CB} <i>Pentapodus emeryii</i> ^{CB}	<i>Lethrinus punctulatus</i> ^{CK} <i>Lethrinus nebulosus</i> ^{LP} <i>Lethrinus laticaudis</i> ^{CK} <i>Lethrinus nebulosus</i> ^{LP} <i>Lutjanus carponotatus</i> ^{CK}	<i>Lethrinus laticaudis</i> ^{CP} <i>Abalistes stellatus</i> ^{CP} <i>Lethrinus laticaudis</i> ^{LP} <i>Lutjanus carponotatus</i> ^{CP}	<i>Lethrinus punctulatus</i> <i>Lutjanus carponotatus</i> <i>Lethrinus nebulosus</i> <i>Lethrinus atkinsoni</i>

2.3.7 Bioregional comparisons

In both of the main branches of the dendrogram, which corresponded to the samples from soft substrata and reefs, the samples from the two locations in the Kimberley Bioregion in the north, *i.e.* Cape Voltaire and Hall Point, formed a group that was well separated from that comprising the samples from locations further south in the Canning and Pilbara bioregions, with the divisions occurring at similarity levels of only 11 and 31%, respectively (Fig. 2.3). Within the cluster containing the samples from locations in the Canning and Pilbara bioregions, and irrespective of habitat type, the samples from Emeriau Point, Cape Bossut and Cape Keraudren in the Canning formed a group that was distinct from that comprising those for Cape Preston and Locker Point in the Pilbara. These divisions occurred at similarity levels of 46% with soft substrata and 55% with reefs (Fig. 2.3).

There is close agreement between the two types of hypothesis test described earlier (SIMPROF and ANOSIM), when assessing the distinctions between bioregions using the averaged data for each location. Two-way crossed ANOSIM employs *a priori* defined factors of ‘habitat’ (two levels: soft substrata and reef) and ‘bioregion’ (three levels: Kimberley, Canning and Pilbara), there being either two or three locations for each bioregion/habitat combination. Global tests for habitat and bioregion give $R = 1.0$ ($P < 1.0\%$) and $R = 0.86$ ($P < 0.1\%$), respectively. The pairwise R values for Kimberley vs Canning and Kimberley vs Pilbara are both 1 and the two closer bioregions in the cluster analysis, Canning and Pilbara, are likewise significantly separated in a pairwise test, with $R = 0.58$ ($P < 1.0\%$). Results of the *a priori* unstructured SIMPROF tests can be seen on the cluster dendrogram (Fig. 2.3), with all hierarchical divisions in both habitats down to the level of

bioregion being substantiated by the sequence of tests. Thus, the overall test for homogeneity of community structure in all 14 samples leads to rejection at $\pi = 16.0$ ($P < 0.1\%$). The splits between the Kimberley and other two bioregions give $\pi = 16.2$ ($P < 0.1\%$) and $\pi = 5.9$ ($P < 0.1\%$) for soft substrata and reefs, respectively. The faunas in the Canning and Pilbara are separated at $\pi = 2.1$ ($P < 0.5\%$) and $\pi = 1.8$ ($P < 1.6\%$), respectively. Although the SIMPROF test is unable to separate two samples into separate groups (the similarity profile consisting of only a single value!), it is relevant that neither the ichthyofaunal compositions of the soft substrata nor reef faunas at the three locations within the Canning Bioregion are separated by this test, $\pi = 0.8$ ($P = 62.4\%$) and $\pi = 0.7$ ($P = 73.1\%$), respectively.

On the ordination plot for both soft substrata and reefs, the points representing the samples from the two locations in the Kimberley Bioregion formed very discrete groups, lying clearly above those from the Canning and Pilbara bioregions (Fig. 2.4). Furthermore, in the case of reefs, the Canning Bioregion samples lay above those from the Pilbara Bioregion.

The soft substrata fauna of the Kimberley Bioregion was distinguished from those at all other bioregions by consistently greater contributions of *T. theraps*, *L. splendens*, *L. leuciscus* and *Caranx bucculentus*, whereas that in the Pilbara Bioregion was distinguished from that in each other bioregion by consistently greater contributions of *P. choirocephalus* and *Siganus fuscescens* (Table 2.8). The faunal composition in the Canning Bioregion was distinguished from that in the Kimberley Bioregion by greater contributions of *P. obtusirostris*, *P. choirocephalus* and *Saurida undosquamis* and from the

Pilbara Bioregion by greater contributions of *P. obtusirostris*, *S. leptolepis* and *Pentapodus porosus* (Table 2.8).

In the case of reefs, the fauna of the Kimberley Bioregion in the north was distinguished from those at all other bioregions by consistently greater contributions of *L. johnii*, *L. bitaeniatus*, *L. lemniscatus* and *Epinephelus coioides*, whereas that in the Pilbara Bioregion in the south was distinguished from that at each other bioregion by greater contributions of *L. punctulatus*, *L. nebulosus* and *Lutjanus russelli* (Table 2.9). The fauna of the Canning Bioregion was distinguished from that in the other bioregions by greater contributions of *L. laticaudis* and *P. emeryii*.

In terms of abundance, the Leiognathidae and Terapontidae were the top ranked families over soft substrata in the Kimberley Bioregion (Table 2.10a). The Terapontidae did not rank amongst the top ten families in either the Canning or Pilbara bioregions and the Leiognathidae only attained such ranking in the Canning Bioregion and even then it ranked only ninth. Conversely, the Pomacentridae, Monacanthidae and Tetraodontidae ranked in the top ten in both the Canning and Pilbara bioregions, but not in the Kimberley Bioregion.

In marked contrast to the situation over soft substrata, the same two families, *i.e.* Lethrinidae and Lutjanidae, dominated the fish faunas over reefs in each of the three bioregions, collectively contributing as much as 87, 79 and 84% to the individuals caught in the Kimberley, Canning and Pilbara bioregions, respectively (Table 2.10b). Furthermore, the Epinephelidae, Haemulidae, Carangidae, Labridae, Siganidae and Nemipteridae each ranked in the top ten in each of the three bioregions.

The Carangidae was the only family whose contributions to total numbers ranked it in the top ten families in both soft substrata and reefs in each bioregion, due to species

such as *Carangoides fulvoguttatus*, *Caranx bucculentus* and particularly *Gnathanodon speciosus* being abundant in both habitat types (Tables 2.1 and 2.3).

Table 2.8 Species identified by SIMPER as those which typified the fish assemblages over soft substrata at the three bioregions (shaded boxes) and distinguished between the fish assemblages at each pair of those bioregions (non-shaded boxes). For each pairwise comparison between bioregions, the species that distinguish between the fauna at one bioregion from another bioregion are indicated by the first letter of that bioregion.

Bioregion	Kimberley	Canning	Pilbara
Kimberley	<i>Terapon theraps</i> <i>Leiognathus leuciscus</i> <i>Saurida tumbil</i> <i>Leiognathus splendens</i> <i>Caranx bucculentus</i>		
Canning	<i>Terapon theraps</i> ^K <i>Leiognathus splendens</i> ^K <i>Leiognathus leuciscus</i> ^K <i>Caranx bucculentus</i> ^K <i>Pristotis obtusirostris</i> ^C <i>Carangoides malabaricus</i> ^K <i>Upeneus sulphureus</i> ^K <i>Saurida tumbil</i> ^K <i>Paramonacanthus choirocephalus</i> ^C <i>Saurida undosquamis</i> ^C <i>Torquigener pallimaculatus</i> ^C	<i>Saurida undosquamis</i> <i>Pristotis obtusirostris</i> <i>Paramonacanthus choirocephalus</i> <i>Parapercis nebulosa</i> <i>Torquigener pallimaculatus</i> <i>Pentapodus porosus</i>	
Pilbara	<i>Terapon theraps</i> ^K <i>Leiognathus splendens</i> ^K <i>Leiognathus leuciscus</i> ^K <i>Caranx bucculentus</i> ^K <i>Paramonacanthus choirocephalus</i> ^P <i>Carangoides malabaricus</i> ^K <i>Pristotis obtusirostris</i> ^P <i>Upeneus sulphureus</i> ^K <i>Saurida tumbil</i> ^K <i>Saurida undosquamis</i> ^P <i>Siganus fuscescens</i> ^P	<i>Pristotis obtusirostris</i> ^C <i>Selaroides leptolepis</i> ^C <i>Paramonacanthus choirocephalus</i> ^P <i>Upeneus asymmetricus</i> ^P <i>Siganus fuscescens</i> ^P <i>Torquigener pallimaculatus</i> ^P <i>Engyprosopon grandisquama</i> ^P <i>Nemipterus furcosus</i> ^P <i>Pentapodus porosus</i> ^C <i>Trachinocephalus myops</i> ^P <i>Parapercis nebulosa</i> ^P	<i>Saurida undosquamis</i> <i>Pristotis obtusirostris</i> <i>Torquigener pallimaculatus</i> <i>Paramonacanthus choirocephalus</i> <i>Parapercis nebulosa</i> <i>Nemipterus furcosus</i> <i>Siganus fuscescens</i>

Table 2.9 Species identified by SIMPER as those which typified the fish assemblages over reefs at the three bioregions (shaded boxes) and distinguished between the fish assemblages at each pair of those bioregions (non-shaded boxes). For each pairwise comparison between bioregions, the species that distinguish between the fauna at one bioregion from that at another bioregion are indicated by the first letter of that bioregion.

Bioregion	Kimberley	Canning	Pilbara
Kimberley	<i>Lutjanus carponotatus</i> <i>Lethrinus laticaudis</i> <i>Lutjanus johnii</i> <i>Lutjanus bitaeniatus</i> <i>Lutjanus lemniscatus</i> <i>Epinephelus coioides</i>		
Canning	<i>Lethrinus punctulatus</i> ^C <i>Lutjanus johnii</i> ^K <i>Lutjanus bitaeniatus</i> ^K <i>Lethrinus laticaudis</i> ^C <i>Lutjanus lemniscatus</i> ^K <i>Epinephelus coioides</i> ^K <i>Pentapodus emeryii</i> ^C <i>Lutjanus sebae</i> ^C	<i>Lutjanus carponotatus</i> <i>Lethrinus punctulatus</i> <i>Lethrinus laticaudis</i> <i>Diagramma labiosum</i>	
Pilbara	<i>Lethrinus punctulatus</i> ^P <i>Lutjanus johnii</i> ^K <i>Lethrinus laticaudis</i> ^K <i>Lutjanus carponotatus</i> ^K <i>Lutjanus bitaeniatus</i> ^K <i>Lethrinus nebulosus</i> ^P <i>Lutjanus lemniscatus</i> ^K <i>Epinephelus coioides</i> ^K <i>Lutjanus russelli</i> ^P <i>Lethrinus atkinsoni</i> ^P	<i>Lethrinus laticaudis</i> ^C <i>Lethrinus punctulatus</i> ^P <i>Lutjanus carponotatus</i> ^C <i>Lethrinus nebulosus</i> ^P <i>Abalistes stellatus</i> ^P <i>Lutjanus russelli</i> ^P <i>Pentapodus emeryii</i> ^C	<i>Lethrinus punctulatus</i> <i>Lutjanus carponotatus</i> <i>Lethrinus laticaudis</i> <i>Lethrinus nebulosus</i> <i>Lutjanus russelli</i>

Table 2.10 Ranking by abundance of the ten most abundant teleost families over (a) soft substrata and (b) reefs at each of the three bioregions in north-western Australia, and the percentage contribution of their individuals to the total catch.

(a) Soft substrata			Bioregion			
Rank	Kimberley	%	Canning	%	Pilbara	%
1	Leiognathidae	52.5	Carangidae	29.4	Synodontidae	16.8
2	Terapontidae	14.8	Pomacentridae	16.8	Monacanthidae	15.0
3	Carangidae	11.5	Synodontidae	8.2	Lethrinidae	14.3
4	Mullidae	7.2	Monacanthidae	7.6	Bothidae	9.7
5	Synodontidae	2.6	Tetraodontidae	5.2	Pomacentridae	8.3
6	Apogonidae	1.8	Labridae	4.3	Mullidae	6.0
7	Haemulidae	1.7	Nemipteridae	3.8	Carangidae	4.7
8	Gerreidae	1.1	Mullidae	3.7	Tetraodontidae	4.0
9	Sciaenidae	0.6	Leiognathidae	3.5	Siganidae	3.9
10	Pristigasteridae	0.6	Sillaginidae	3.2	Nemipteridae	3.8
	Total	94.4		85.9		86.4
(b) Reefs			Bioregion			
Rank	Kimberley	%	Canning	%	Pilbara	%
1	Lutjanidae	64.8	Lethrinidae	55.7	Lethrinidae	65.5
2	Lethrinidae	22.3	Lutjanidae	23.5	Lutjanidae	19.1
3	Epinephelidae	3.6	Carangidae	5.4	Epinephelidae	3.6
4	Haemulidae	3.0	Nemipteridae	2.4	Balistidae	3.4
5	Carangidae	2.5	Siganidae	2.3	Nemipteridae	2.5
6	Labridae	0.9	Balistidae	2.3	Labridae	1.5
7	Pomacanthidae	0.4	Epinephelidae	2.1	Siganidae	1.2
8	Siganidae	0.4	Labridae	1.8	Carangidae	0.5
9	Nemipteridae	0.2	Haemulidae	1.7	Haemulidae	0.5
10	Latidae	0.2	Glaucosomatidae	0.8	Pomacanthidae	0.5
	Total	98.4		98.0		98.3

2.4 Discussion

2.4.1 Comparisons between ichthyofaunal compositions over soft substrata and reefs

This study demonstrated that the species compositions of the ichthyofaunas sampled by trawling over soft substrata at regularly-spaced locations along the 1,500 km of the tropical NWA coast differed markedly from those sampled by trapping over adjacent reefs at the same locations. While some of these differences are attributable to differences in the selectivity of the two types of sampling gear, they also reflect variations in the ‘preference’ of certain species for one or other of the two habitat types. The pronounced differences in faunal composition in the catches taken over soft substrata and reefs are emphasised by comparing the contributions made by the most abundant families in the two habitats. Thus, whereas the three most abundant families over soft substrata were the Leiognathidae, Carangidae and Terapontidae, which collectively contributed nearly two thirds to the total number of fishes caught in that habitat, the two most abundant families over reefs were the Lethrinidae and Lutjanidae, which alone contained over 80% of all fishes obtained from that habitat. Furthermore, the Leiognathidae and Terapontidae were not caught over reefs and the contribution of the Lethrinidae and Lutjanidae over soft substrata was small. The differences between the compositions over soft substrata and reefs is further emphasised by the fact that the fourth to seventh ranked families over soft substrata were very poorly represented over reefs and that the Carangidae was the only family to rank amongst the seven most abundant families in both habitats.

As along the NWA coast, the Leiognathidae was very abundant in samples collected by trawling over soft substrata in other regions of the IWP and in the Bay of

Bengal (e.g. Ochavillo et al., 1989; Blaber et al., 1990; Federizon, 1992; Bianchi et al., 1996; Wantiez et al., 1996; Stobutzki et al., 2001; Alias, 2003; Garces et al., 2006). The success of leiognathids over soft substrata is attributable to their possession of a highly protrusible and downward-pointing mouth, which forms a tube ideally adapted for extracting, from soft substrata, the benthic macroinvertebrates that constitute the main prey of their larger individuals (Jaybalan, 1991; Woodland et al., 2001; Hajisamae et al., 2003).

The Carangidae, which is closely related to the Leiognathidae, but more widely distributed, was variably abundant in samples collected by trawling in areas to the north of the NWA coast (e.g. Ochavillo et al., 1989; Bianchi et al., 1996; Stobutzki et al., 2001). Although the Carangidae was the most speciose of all families over soft substrata in NWA (25 species), it was dominated by *Selaroides leptolepis*, *Caranx bucculentus* and *Carangoides malabaricus*. The first two of those species are also abundant in the Gulf area of northern Australia (Rainer and Munro, 1982; Ramm et al., 1990) and the first is also abundant in Malaysian coastal waters on the Sunda Shelf (Alias, 2003) and in the Phillipines (Federizon, 1992). In the Gulf of Carpentaria, *C. bucculentus* consumes substantial amounts of teleosts, with leiognathids contributing nearly 10% to its stomach contents, and epibenthic crustaceans, comprising mainly penaeid prawns and brachyuran crabs (Brewer et al., 1989; Brewer et al., 1994).

The third most abundant family over soft substrata, the Terapontidae, is, like the Leiognathidae, restricted to the Indo-West Pacific and lives in marine coastal, brackish and freshwater habitats (Nelson, 2006). The abundance of this family is almost exclusively due to the large numbers of *Terapon theraps* caught. This family did not rank highly in terms of abundance in the trawl catches obtained in most Indo-Pacific waters, ranking only ninth in

the catches taken from northern Australian waters by Stobutzki et al. (2001) and contributing even less to the faunas over soft substrata in other areas of the Indo-West Pacific (e.g. Jones and Derbyshire, 1988; Bianchi et al., 1996; Alias, 2003). However, Terapontidae are abundant in mangrove creeks in several Indo-Pacific locations (Blaber and Blaber, 1980; Laroche et al., 1997). The terapontid *Terapon jarbua* is an efficient predator of penaeid prawns, capable of changing from relying on visual cues when in clear water to ambush predation when in very turbid water (Macia et al., 2003). Furthermore, the fish scales removed from the posterior region of larger fishes represent the most abundant dietary item of this species in estuaries of the western Indian Ocean (Whitfield and Blaber, 1978).

The Mullidae, the fourth most abundant family over soft substrata in NWA, occurs in the Indian, Pacific and Atlantic Oceans (Nelson, 2006). The catches of this family were overwhelmingly dominated by *Upeneus sulphureus*, largely paralleling the situation in the waters of northern Australia, Bangladesh and New Caledonia (Ramm et al., 1990; Wantiez et al., 1996; Garces et al., 2006). The possession by mullids of a large downward-pointing mouth and chemosensory hyoid barbels enable the members of this family to forage effectively for the tanaeids, cumaceans and crabs that lie partly buried in soft substrata and are diagnostic of the diet of the members of this family (Gosline, 1984; Platell et al., 1998a; Platell and Potter, 2001).

The Synodontidae, the fifth and only other family that contributed > 5% to the total number of individuals caught over soft substrata, is widely distributed, occurring in the Indian, Pacific and Atlantic Oceans (Nelson, 2006). The species in this family have large mouths and are voracious predators, feeding mainly on other small fishes and crustaceans

(Sweatman, 1984), and their large contribution to the fauna in NWA parallels the situation in comparable inshore waters along the northern coast of Australia (Rainer and Munro, 1982; Ramm et al., 1990; Watson et al., 1990; Blaber et al., 1994a) and the Gulf of Thailand (Hajisamae, 2009). Amongst the five most abundant families on the north-western coast of Australia, the Synodontidae and Leiognathidae were considered by Longhurst and Pauly (1987) to be characteristic of the ichthyofaunas of the continental shelves in tropical areas in general.

In a study of demersal trawl fishing effects on the fish assemblages in more offshore waters than the present study in NWA, Thresher et al. (1986) showed an increased number of *Saurida* spp. (Synodontidae) in the catch during a 5 year period (1978- 1983). It is noteworthy that increases in population size of *Saurida* in NWA have been hypothesised to be the result of commercial trawl fishing either reducing the number of competitors and/or predators, or increasing the area of open sand habitat favored by synodontids (Sainsbury, 1987; Sainsbury, 1991; Sainsbury et al., 1997).

The Sciaenidae was found only in the Kimberley Bioregion during the present study, and even there the two species in this family contributed only 0.6% to the total number of fish caught. The members of this family make important contributions to the fish faunas of estuaries and immediately surrounding coastal waters of all tropical regions except those not located close to the equator in the Indo-West Pacific (Blaber, 2002). The single species of Sciaenidae recorded from the rockpools and embayments of mangrove creeks in north-western Australia was represented by only a few individuals (Pember, 2006). The very limited importance of the Sciaenidae to the fish faunas of the north-

western coastline of Australia may thus reflect the limited amount of rainfall and shortage of estuarine conditions that are so important to the members of this family (Blaber, 2002).

The dominance of the Lethrinidae in samples collected by traps in reefs in NWA parallels the situation recorded using baited traps over reefs in more offshore waters in the Pilbara bioregion (Whitelaw et al., 1991) and employing baited methods for capture elsewhere in the IWP (see references in Dalzell et al., 1996). Moreover, lethrinid larvae were very abundant among the larval fishes caught over a large fringing reef system in the vicinity of the most southern sampling location (McIlwain, 2003). The lethrinids caught over reefs were overwhelmingly dominated by *L. punctulatus* and *L. laticaudis*, which belong to a group of *Lethrinus* species that possess a high body and molariform and submolariform dentition (Lo Galbo et al., 2002). This type of dentition enable these species to process a wide range of the benthic invertebrates that are associated with reefs, such as sea urchins and certain molluscs and crustaceans. Although lethrinids were generally far more abundant in samples from over reefs than soft substrata, one species in this family, *L. genivittatus*, was numerous in both habitats.

Lutjanids, which are common on reef and rock habitats in the Indian, Pacific and Atlantic Oceans (Anderson and Allen, 2001), were represented by 14 species over reefs in NWA, with *L. carponotatus* contributing over two thirds of their number of individuals. This schooling species is also abundant on reefs at similar latitudes in north-eastern Australia, where it feeds on fishes, crustaceans and cephalopods (Connell, 1998; Newman and Williams, 2001; Cappo et al., 2007).

2.4.2 Relationship of ichthyofaunal composition with latitude and water temperature

The distribution of the ichthyofaunal samples from over soft substrata and reefs on the ordination plot, derived from the matrix constructed from the contributions of the various fish species to the samples collected from each of those habitat types at seven regularly-spaced sampling locations, facilitates a visual exploration of whether ichthyofaunal composition in one or both of those habitat types is related to latitude on the NWA coast and, if so, provides an idea of the extent of that relationship (Fig. 2.4). The presence of the samples from the most northern locations, *i.e.* Cape Voltaire and Hall Point, at the top of the plots for both soft substrata and reef ichthyofaunas and of those from these habitats at the two most southern locations, *i.e.* Cape Preston and Locker Point, at the bottom of their respective plots, with those from intervening locations occupying an intermediate position, clearly indicate that ichthyofaunal composition is related to latitude. ANOSIM tests demonstrated that the compositions of the faunas in each pair of locations were significantly different and that the differences were greater between the faunas at widely separated than adjacent locations. The RELATE procedure confirmed statistically that the ichthyofaunal composition of both soft substrata and reefs was significantly related to latitude.

As hypothesised, the ichthyofaunal compositions over soft substrata and reefs were both significantly related to water temperature. This relationship is hardly surprising as species composition and latitude are strongly related and increasing latitude is broadly accompanied by a decline in water temperature. The water flow along the NWA coast is warm and predominately poleward in direction due to the strong influence of the Indonesian Through Flow (ITF) and of the more inshore Holloway Current (Fig. 1.1;

D'Adamo et al., 2009). This accounts for water temperatures at each sampling location averaging 24°C and reaching maxima of 31°C and, even in winter, never declining below 21°C, but showing an overall decline from north to south. The presence of strong and warm poleward currents thus accounts for the vast majority (96%) of the 361 fish species caught over soft substrata and reefs in nearshore waters of NWA being tropical and to the nine subtropical species only being recorded in appreciable numbers at the southern three locations where temperatures were least.

On the basis of the zoogeographical categories to which each species caught during the present study had been assigned by Hoese et al. (2007), the distribution of most of those species also includes the Pacific Ocean, although the extent of their distributions in that ocean varies (see distribution maps in Carpenter and Niem, 1998-2001). The very substantial contributions made by species with a Pacific component to their distribution presumably reflects the strong connection provided by the southwards-flowing ITF for linking the western waters of the Pacific Ocean with the region of the Indian Ocean bordering the NWA coast (Gordon, 2005; Domingues et al., 2007). This connection would have developed since the time when, approximately 20 Ma, the Australian plate had progressed so far northwards that it collided with those of south-east Asia (Davies et al., 1987; Hall, 1996). While species could be transported as larvae from the Pacific Ocean towards the Indian Ocean through the ITF, the successful establishment of those species in a more southerly locality would rely on the presence of suitable habitats for their larvae, juveniles and adults during that movement (Leis, 1986; Palumbi, 1997; Bellwood and Wainwright, 2002). Such habitats are available throughout the Indo-Australian Archipelago (IAA) (Wolanski et al., 1988; Bellwood and Wainwright, 2002;

Hughes et al., 2002b). The implication that extensive gene flow has occurred between the faunas of regions in the Pacific and Indian Oceans, including that of NWA, is supported by the results of genetic studies of the population structure of a range of marine organisms, including coral reef fishes (Klanten et al., 2007), starfish (Williams and Benzie, 1996), corals (Pandolfi, 1992) and mud crabs (Gopurenko et al., 1999). The great importance of the IWP region to the origin of much of the fauna in NWA has been emphasised previously for reef fishes (Hutchins, 2001a; Hutchins, 2001b), molluscs (Wells, 1990), echinoderms (Marsh and Marshall, 1983) and corals (Hughes et al., 2002b).

Although the ITF, in particular, currently provides a continuous route for gene exchange between tropical organisms in the Indian and Pacific Oceans, sea levels are thought to have been substantially lower in the past and thus restricted the ITF and produced a landbridge between New Guinea and Australia (Williams et al., 2002). This would have greatly reduced the opportunities for genetic exchange between organisms in the Pacific and Indian Oceans. The multiple glaciations that occurred during the Pleistocene resulted in periods of repeated isolation of tropical marine faunas in the Pacific and Indian Oceans, which thus provided an important mechanism for population differentiation and incipient speciation (Williams et al., 2002). This could account for the evolution of some of the Australian endemics now found along the NWA coast. However, the potential role of other and earlier processes, such as tectonics and ocean circulation, in the evolution of the fauna of the IAA, should be taken into account (Barber and Bellwood, 2005). The endemic species contain several with the types of characteristics that would limit their ability to disperse widely (Randall, 1998) and would thus explain their limited distributions (Hughes et al., 2002b; Jones et al., 2002). For example, some of

these species exhibit parental care, such as the oral brooders *Apogon unitaeniatus* and *Siphamia cuniceps*, and others deposit and guard their eggs in burrows, such as *Halophyrne ocellatus*.

The correlation between species composition and latitude, now demonstrated for the ichthyofaunas of both soft substrata and reefs along the extensive stretch of the tropical NWA coastline, parallels that recorded over reefs on the Great Barrier Reef (Williams, 1991; Cappo et al., 2007) and in Brazil (Floeter et al., 2001) and over soft substrata on the west coast of North America (Jay, 1996). Likewise, the significant relationship between species composition and water temperature on the NWA coast over both habitats parallels those found with reef fish faunas along the Brazilian coast (Floeter et al., 2001) and in other tropical waters (Kuo et al., 2001).

Although the ichthyofaunal compositions over both soft substrata and reefs are clearly related to latitude, the dendrogram shown in Fig. 2.3 emphasises that while, over both habitat types, the ichthyofaunal composition of the Kimberley Bioregion is the most discrete, those of the Canning and Pilbara bioregions each have some highly distinctive features. The use of SIMPROF and ANOSIM confirmed that, irrespective of habitat type, the ichthyofaunal compositions of the Kimberley is significantly different from those of the Canning and Pilbara bioregions and that those of the latter two bioregions were also significantly different from each other. The remarkable similarity between the patterns of distributions of the clusters for the faunas over soft substrata and reefs on the dendrogram shown in Fig. 2.3 demonstrate that, in the case of both habitat types, the broad latitudinal changes that occur in ichthyofaunal composition along the NWA coastline encompass the same strong types of bioregional influence on composition.

The sequential change that occurs in the species compositions of fish assemblages over soft substrata and reefs along a north to south latitudinal axis in NWA is a consequence of site-staggered differences in the relative abundances of the various species along that axis (see e.g. Fig. 2.5). Some of the most abundant of the species that contributed to that latitudinal change were largely or entirely confined, however, to one or two bioregions and thus help account for the underlying bioregional influence on ichthyofaunal composition. This point is very well illustrated by comparing the relative contributions to the ichthyofaunas of the seven locations by certain species, which were shown by SIMPER to play an important role in distinguishing between the faunas at the different locations. Thus, for example, although *L. splendens* and *T. theraps* contributed as much as 30% to the total number of fishes caught over soft substrata at all locations, they were only found at the two most northern locations, *i.e.* Cape Voltaire and Hall Point in the Kimberley (Fig. 3.6). Likewise, *L. bitaeniatus* and *L. johnii*, which ranked fourth and seventh over reefs, respectively, in terms of numbers, were not caught south of Hall Point and were thus not represented in samples from either the Canning or the Pilbara bioregions. In contrast, *L. genivittatus* over soft substrata and *L. nebulosus* over reefs were largely restricted to one or two of the locations in the most southern bioregion, *i.e.* the Pilbara. While other species such as *C. cephalotes* and *P. obtusirostris* over soft substrata and *P. emeryii* and *L. punctulatus* over reefs were more widely distributed, they were largely or entirely confined to locations in the Canning and Pilbara bioregions. The above types of differences in the distributions of numerous species account for the major differences between the faunas of the Kimberly and Canning/Pilbara and the substantial differences that exist between those of the Canning and Pilbara bioregions.

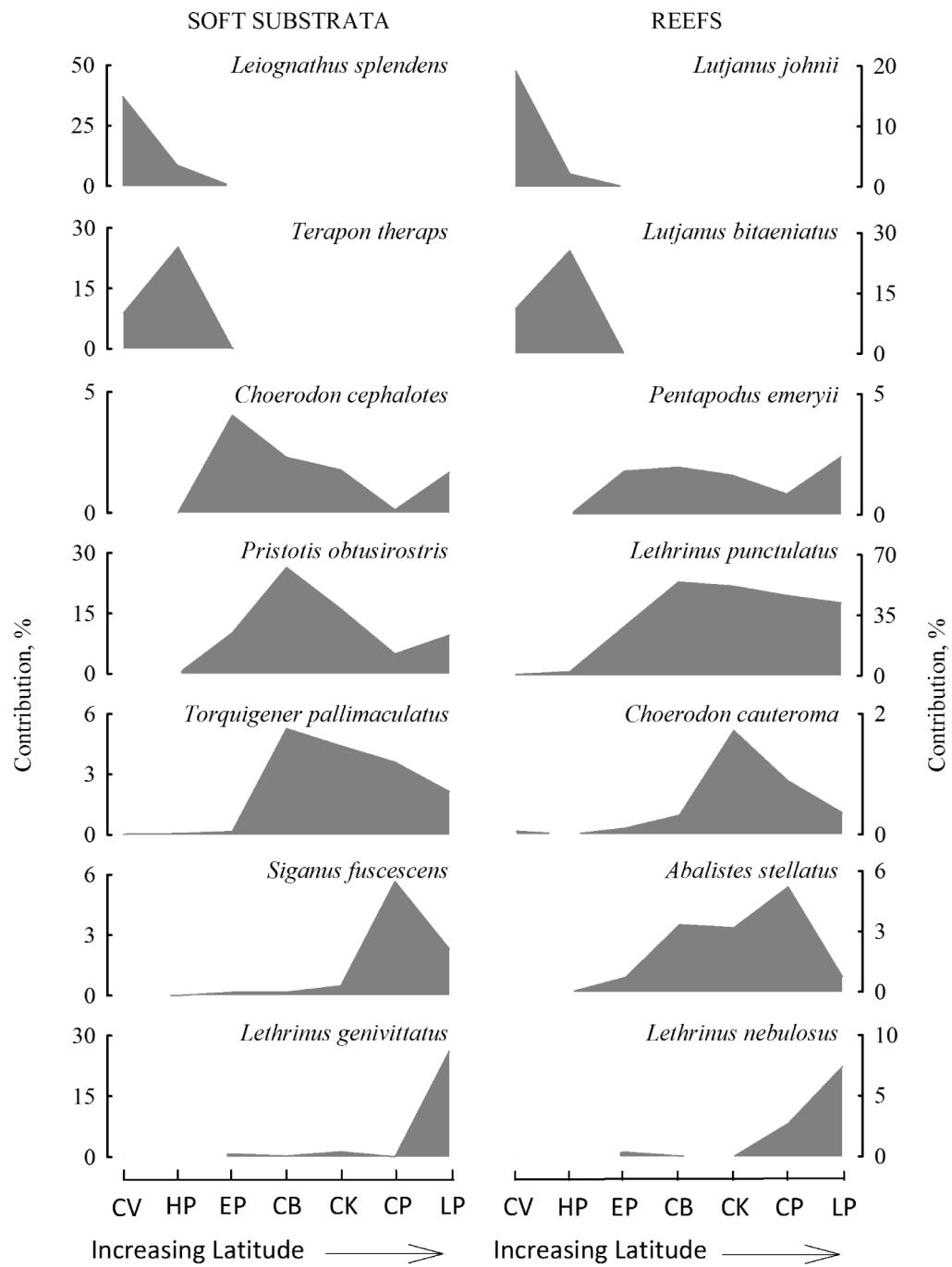


Figure 2.5 Percentage contributions of abundant fish species to the catches of fishes over soft substrata and reefs at each of the seven sampling locations along the north-western Australian coast. CV, Cape Voltaire; HP, Hall Point; EP, Emeriau Point; CB, Cape Bossut; CK, Cape Keraudren; CP, Cape Preston; LP, Locker Point.

2.4.3 Relationship of ichthyofaunal composition and bioregion

Although the same clear regional ichthyofaunal differences in composition were present over both soft substrata and reefs, the distinctions between the compositions of the Kimberley *vs* the Canning/Pilbara and less markedly Canning *vs* Pilbara bioregions were more pronounced with the former habitat type, reflecting, in part, greater bioregional differences at the family level. Thus, over soft substrata, the two most abundant families in the three bioregions differed, with this role being played by the Leiognathidae and Terapontidae in the Kimberley, the Carangidae and the Pomacentridae in the Canning and the Synodontidae and Monacanthidae in the Pilbara. In contrast, the Lethrinidae and Lutjanidae were the two most abundant families over reefs in each of the three bioregions. The contributions of their species varied markedly, however, among bioregions and the Haemulidae was relatively more abundant in the Kimberley than in either the Canning or Pilbara bioregions and the reverse was true for the Nemipteridae and Balistidae.

At the species level, seven of the ten species of the Leiognathidae found over soft substrata in the Kimberley were not caught in this habitat type in either the Canning or Pilbara. Furthermore, only one of the other three species, *L. leuciscus*, was collected in appreciable numbers outside the Kimberley, and even then it was very largely restricted to the Canning Bioregion and far less abundant there than in the Kimberley. As *L. splendens* and the terapontid *T. theraps* were particularly abundant in the Kimberley, it is relevant that these species, like certain other leiognathids and terapontids, use mangroves as nursery areas (Robertson and Duke, 1987; Blaber and Milton, 1990; Kimani et al., 1996; Ikejima et al., 2003) and that such vegetation was particularly abundant along

the coastline and around islands in the Kimberley (Semeniuk, 1993; Cresswell and Semeniuk, 2011). Leiognathids also possess adaptations, such as a bioluminescent system, which are highly advantageous for life in highly turbid and thus poorly-lit waters (McFall-Ngai and Morin, 1991; Woodland et al., 2002; Sparks et al., 2005) and therefore in conditions that characterize the Kimberley bioregion (Semeniuk, 1993). The fact that mangrove forests constitute important habitats for juvenile carangids (Blaber, 1986) would help account for the success of numerous species of this family in the Kimberley Bioregion and, apart from *Selaroides leptolepis*, their absence or low numbers in the Canning and Pilbara bioregions, where mangrove stands are, at best, sparse. The moderate to substantial numbers of *S. leptolepis* caught over soft substrata at all locations sampled along the NWA coast is highly atypical for a species of the Carangidae in this region, indicating that it does not have a strong preference for particular conditions over or near soft substratum. In contrast to the above species, *P. obtusirostris* was not found in the Kimberley, but was caught in large numbers at each location in the Canning and Pilbara, which indicates that this pomacentrid is not well adapted for life in the turbulent and turbid waters of the Kimberley.

Although the Synodontidae was the most abundant family over soft substrata in the Pilbara, this was very largely due to the substantial numbers of *Saurida undosquamis* in the samples from Cape Preston and Locker Point. The wide distribution of *S. undosquamis*, contrasts with the restriction of *Saurida tumbil*, the only other abundant synodontid, largely to Cape Voltaire and Hall Point in the Kimberley. As with the Synodontidae, the Monacanthidae is well represented in the ichthyofauna of the Pilbara due to large numbers of a single species, *P. choirocephalus*, but that species is also

moderately abundant in the Canning. The restriction of each of the five lethrinid species recorded over soft substrata entirely to the Pilbara Bioregion in all cases except for *L. genivittatus*, and even then 91% of the numbers of this latter species were restricted to the Pilbara, also contributes to the distinctness of the ichthyofaunal composition of this habitat in the most southern of the three bioregions.

The distinction between the species compositions of the reef fish faunas of the Kimberley and the Canning and Pilbara bioregions collectively, reflected, in particular, marked variations in the contributions of certain lutjanids and lethrinids. Thus, for example, among lutjanids, *L. bitaeniatus* and *L. johnii* were caught only in the Kimberley, whereas *Lutjanus sebae* was almost exclusively restricted to the Canning and Pilbara and, among lethrinids, *L. genivittatus* was caught only in the Canning and Pilbara and the vast majority of the very substantial numbers of *L. punctulatus* came from these two bioregions. In the case of *L. johnii* it is thus relevant that its juveniles are frequently found in mangroves (Blaber, 2000; Kiso and Mahyam, 2003; Nagelkerken, 2009; Igulu et al., 2014) and that these are abundant on the Kimberley coast. The restriction of species such as *L. johnii* to the Kimberley Bioregion was also suggested by Hutchins (1999) to be related to the environmental conditions of the bioregion. The restriction of *L. atkinsoni* and *L. nebulosus* largely or entirely to the Pilbara can be explained by their use of seagrass as nursery areas (Wilson, 1998; Nakamura and Sano, 2004) and that large meadows of these macrophytes are present in the vicinity of the reefs of this bioregion but not of those in the Canning Bioregion to the north (D. Walker pers. comm.). In contrast to all other abundant lutjanids and lethrinids, *L. carponotatus* and *L. laticaudis* were relatively

abundant over reefs throughout the study area and are thus adapted to the range of environmental conditions found over reefs along the full extent of the NWA coast.

In summary, this study has demonstrated that the ichthyofaunal compositions over both soft substrata and reefs along the extensive tropical NWA coast change in a largely progressive and similar manner according to latitude and that such changes are related to water temperature. These changes are attributable to site-staggered changes in the contributions of certain species along that latitudinal axis. However, the latitudinal changes in ichthyofaunal composition encompass strong bioregional differences and particularly between those of locations in the Kimberley vs those in the Canning and Pilbara further south, recognising that the compositions in the latter two bioregions are also distinct. Bioregional differences presumably reflect the influence of the very different environmental characteristics in the three bioregions, which included marked variations in tidal regime, turbidity and the extent to which mangrove stands or seagrass meadows are present nearby and could thus provide nursery habitats for certain key species. As most species caught along the tropical NWA coast are also found in the Western and West-Central regions of the Pacific Ocean to the north of Indonesia, it seems likely that many of those species are ‘connected’ to the NWA coast by the polewards-flowing Indonesian Throughflow (ITF) after the Australian plate had moved progressively northwards and collided with those of south-east Asia. If the trend in the last few decades towards an increase in water temperature along the NWA coast continues (Lough, 2008; Lough and Hobday, 2011), the presence of a significant relationship between species composition over soft substrata and reefs with temperature along this coast implies that the distribution of at least some species are likely to extend further south.

Chapter 3. Species richness, density and composition of the fish faunas over soft substrata along the tropical coast of north-western Australian are related to latitude and certain environmental variables

3.1 Introduction

The species richness, density and composition of faunal communities, including those of marine fishes, typically change with latitude, reflecting, in part, progressive changes in water temperature (Chapter 2, Bellwood and Hughes, 2001; Connolly et al., 2003; Hawkins and Diniz, 2004; Kulbicki et al., 2013) and often also productivity (Robertson and Blaber, 1992; Manson et al., 2005a; Manson et al., 2005b; Parravicini et al., 2013). These biotic variables also vary with distance from shore, due to certain species tending to occupy either shallow or deeper waters and/or moving into and out of areas at different stages in their life cycle (e.g. Bianchi, 1992a; Blaber et al., 1994b; Blaber et al., 1995; Connell and Lincoln-Smith, 1999; Gaertner et al., 1999; Hyndes et al., 1999; Jankowski et al., 2015a).

Although the species compositions of fish assemblages often change cyclically during the year (e.g. Hyndes et al., 1999; Kuo et al., 2001; Travers and Potter, 2002), they can also alter abruptly, e.g. when waters become turbid during cyclones (Jones and Syms, 1998; Cheal et al., 2002). Species composition and richness and density also differ among habitats, e.g. between soft substrata and reefs and between unvegetated substrata and seagrass meadows (e.g. Heck et al., 1989; Guidetti, 2000; Travers and Potter, 2002; Becker et al., 2012), and even when differences are more subtle, such as those resulting from

variations in the characteristics of the soft substrata (Harris and Poiner, 1991; Blaber et al., 1994b; Blaber et al., 1995).

The remote and extensive coastline of tropical NWA, undergoes extreme climatic changes during the year, with the dry winter season, which extends from May to October, leading into a very wet cyclonic summer season between November and April (Gentilli, 1972; Lough, 2008; Ng et al., 2015). During the warm wet season, the large volume of freshwater discharged from the large rivers along the Kimberley coast flushes substantial amounts of nutrients into inshore waters (Holloway et al., 1985; Condie and Dunn, 2006), leading to an increase in plankton density (McKinnon et al., 2015a; McKinnon et al., 2015b) and ultimately the amount of food for fishes.

The NWA coast comprises three main bioregions, *i.e.* the Kimberley, Canning and Pilbara, which differ markedly in such features as tidal range, turbidity, rainfall and the prevalence of rivers (Chapter 2; Semeniuk, 1993; Thackway and Cresswell, 1998; Brocx and Semeniuk, 2010; Wilson, 2013). Furthermore, the waters along the Kimberley and Pilbara coasts are more productive than those along the Canning coast (Condie and Dunn, 2006; Thompson and Bonham, 2011; McKinnon et al., 2015b) and, particularly in the Kimberley, they contain extensive mangrove forests (Cresswell and Semeniuk, 2011), which provide protection for fishes (Blaber and Blaber, 1980; Robertson and Duke, 1990a; Blaber et al., 1995; Nagelkerken et al., 2001; Mumby et al., 2004; Creighton et al., 2015). The results presented in Chapter 2 emphasise that the NWA coast contains a diverse and abundant fish fauna, which is consistent with the results of previous workers (Blaber et al., 1985; Hutchins, 1995; Hutchins et al., 1996; Morrison and Hutchins, 1997; Hutchins, 1999; Hutchins, 2001a; Hutchins, 2001b; Williams et al., 2001; Hutchins, 2003).

The data presented in Chapter 2, derived from sampling fishes by trawling and trapping in inshore waters along the 1,500 km coastline of tropical NWA, demonstrated that the composition of the fish assemblages over soft substrata and reefs and of the three bioregions of that coast differ markedly. The results also showed that species composition changed progressively with latitude, presumably reflecting, at least in part, the influence of water temperature. The ichthyofaunal data for dry and wet seasons and both water depths at each location were pooled for this broad overarching study, which therefore made no attempt to explore how the species richness, density and species composition of fishes over soft substrata along the NWA coast are related to season, water depth and a range of other environmental variables, such as temperature, productivity and freshwater input. That initial study also did not attempt to elucidate how the species richness and density of fishes over soft substrata were related to season and other factors.

Large scale studies are crucial for teasing out the most important factors in determining the characteristics of faunal assemblages, such as species richness, density and composition (Mahon et al., 1998; Gaertner et al., 2005; Selkoe et al., 2015), and for providing the data required to develop strategies for protecting tropical coastal ecosystems. Thus, in the present study, data derived from trawling at regular intervals along the NWA coastline were collated to quantify the species richness and densities of each fish species over soft substrata in deep and shallow inshore waters in the dry and wet seasons at the seven locations sampled along that tropical coast. The data for the fish faunas over soft substrata in the Kimberley, Canning and Pilbara bioregions were then subjected to univariate and multivariate analyses to address the following hypotheses. 1)

Species richness and densities of fishes are greatest in the Kimberley and Pilbara bioregions, where the productivity of inshore waters is greatest, and the nearshore waters of particularly the Kimberley contain extensive mangrove forests. 2) Species richness and density of fishes in the Kimberley are far greater in the wet season than in the less productive dry season. 3) Ichthyofaunal composition differs between seasons and water depths at each location. The species that contribute most to any differences between the ichthyofaunal compositions of the three bioregions and between those in the two seasons and depths at each location are determined. Finally, a matrix derived from the densities of the fish species caught over soft substrata in both water depths in the wet and dry seasons is subjected to a multivariate regression tree procedure to ascertain which members of a suite of environmental variables are most important in helping to explain any divisive clustering of ichthyofaunal compositions among locations and bioregions along the length of the tropical NWA coast.

3.2 Materials and Methods

3.2.1 Sampling regime

Full details of the complete regime for sampling the soft substrata along the NWA coast for fishes by trawling were provided in Chapter 2. As outlined in Table 2.1, soft substrata in deep and shallow waters at each of the seven sampling locations along the tropical NWA coast (Fig. 2.1) were sampled during daylight in the dry season of 2001 and in the wet season of 2002. For convenience, the numbers of replicates for each year and depth combination have been extracted from Table 2.1 and shown below in Table 3.1.

3.2.2 Sampling regime and environmental data.

Water temperature and depth, depth of water clarity and distance from mainland shore, were recorded immediately prior to undertaking each replicate trawl (For details see Chapter 2). The hardness and complexity of the substrata were estimated by a combination of visual assessment of the ship's sonar signal, video footage from a drop camera as the ship passed along the trawl track and inspection of the biota retained in the trawl codend. The substrata covered during each trawl was categorised as either soft mud, soft sand, soft sand with sparse sponges, hard sand, hard sand with sparse sponges or hard sand with sponge and live gorgonian fragments. On sampling each location, the tidal range was recorded as the difference between the maximum and minimum water heights, while precipitation was recorded as the total rainfall during sampling and in the preceding two weeks. Tidal range and precipitation data were obtained from the Australian Government Bureau of Meteorology (Chapter 2).

Table 3.1. Years (seasons), duration of each trawl, replication and frequency of sampling in both deep ($\bar{x} = 20$ m) and shallow ($\bar{x} = 10$ m) waters over soft substrata at each of the seven sampling locations in north-western Australia in 2001 and 2002.

Year (Season)	Time of sampling	Water depth	Trawl duration	Number of sampling days	Number of replicate trawls
2001 (Dry)	Day	Deep	15 min	1	4
		Shallow	15 min	1	4
2002 (Wet)	Day	Deep	15 min	1	4
		Shallow	15 min	1	4

3.2.3 Statistical analyses

Three-way Permutational Multivariate Analysis of Variance (PERMANOVAs) (Anderson et al., 2008) were used to determine whether water temperature, depth of water clarity and the species richness and total density of fishes differed among locations and between dry and wet seasons and water depths. When used on a single variable, PERMANOVA based on the derived Euclidean distance matrix returns classic ANOVA tables, with the pseudo-*F* statistics reducing to real *F* values (Anderson, 2001b; Anderson and Millar, 2004). The significance levels (*P*) are, however, determined by permutation rather than by appealing to any distributional assumptions, thus making the tests more robust. Note that PERMANOVAs were not carried out on other environmental variables because, unlike temperature and water depth, only single values were computed for those variables for each combination of site, season and depth. Prior to PERMANOVA, and separately for each of the variables, the relationship between the mean and standard deviation for each location, depth and season combination determined the choice of transformation to satisfy homoscedasticity (Clarke & Warwick 2001). Examination of the values for these variables demonstrated that, prior to PERMANOVA, water temperature and water clarity required a square root transformation, species richness a 4th root transformation and density a log_e transformation to meet the test assumption of homogenous dispersion (variance, here) among *a priori* groups (Anderson, 2001a).

The log_e densities of each fish species were used to calculate a Bray-Curtis similarity matrix. The data were considered to represent a three-way fully-crossed design that comprised location (7 levels) x season (2 levels, *i.e.* wet and dry) x water depth (2 levels, *i.e.* deep and shallow), with each factor being fixed. The effect of location was

considered fixed rather than random as the locations were selected to be distributed at regularly-spaced intervals along the coast, with inference requiring to be drawn about these specific locations and, by implication, the latitudinal gradient they represent, making a fully fixed-effect model appropriate. This matrix was subjected to PERMANOVA (Anderson, 2001a; Anderson et al., 2008) to test whether there were significant interactions between the above three factors. The results of these formal tests were then interpreted in the following two ways. (1) Examination of plots of non-metric multi-dimensional scaling (nMDS) ordinations based on Bray-Curtis similarities, which were carried out using either the original replicate data, sub-divided by location in this case, or the averaged data matrix over replicates of the log-transformed densities (Clarke and Gorley, 2006), plotted for all locations. (2) By determining the average influence of the location, season and depth effects, using three two-way crossed ANOSIM analyses (Clarke, 1993) for (i) location (latitude) *vs* the combined effects of season and depth (*i.e.* including their interaction), (ii) season *vs* the combined effects of location and depth and (iii) depth *vs* the combined effects of location and season. This was achieved by combining the values for the two removed factors in each case to a single factor representing all combinations of their levels. The resulting two-way ANOSIM statistic \bar{R} for example in case (i), is the average of the seven one-way ANOSIM R statistics for testing among locations separately for each of the four combinations of depth and season (R captures the difference between ‘among location’ and ‘within location’ rank dissimilarities). The \bar{R} value is therefore instructive as a measure of the overall magnitude of the location effect (whether this comes from main effects, interaction terms or both), which can then be compared with the similar two-way \bar{R} statistics for season and depth from cases (ii) and

(iii). However, \bar{R} of itself does not differentiate between situations where its constituent R values are consistent (main effect) or inconsistent (interactions), so it is useful, where PERMANOVA indicates the likely presence of interactions, to subdivide the ANOSIM analyses accordingly.

ANOSIM analyses are the preferred approach at this interpretational stage for three main reasons:

(1) the robustness of a fully non-parametric procedure (note that PERMANOVA is not fully non-parametric, since it depends on the measurement scale of the similarities rather than their ranks); (2) the exact match between rank-based ANOSIM tests and the most effective of the ordination techniques for displaying complex high-dimensional data in low-dimensional space, namely nMDS; and (3) the direct interpretability of the ANOSIM R and \bar{R} statistics as universally scaled measures of group separation. Whatever the chosen similarity measure, or its scaling, the value of R ranges from near 0, for little or no separation of the groups being compared, up to R near 1, for ‘complete’ separation, meaning that no two replicates from different groups are closer in community structure than any pair of replicates taken from the same group.

When testing showed the presence of non-negligible differences, two-way crossed Similarity Percentage analyses (SIMPER; Clarke and Gorley, 2006) were used to identify the fish species that typified the species composition of each *a priori* group and those responsible for distinguishing between the compositions in each pair of groups. Utilising the full replicate data, the RELATE procedure (Clarke and Gorley, 2006) was used to quantify the extent to which the pattern of rank orders between the ichthyofaunal compositions of the various samples in the biotic similarity matrix, derived from the

density data used in the nMDS ordination analyses, paralleled those in distance matrices constructed at higher taxonomic levels, *i.e.* genus, family, sub-order, order and super-order (Somerfield and Clarke, 1995). The Spearman rank correlation (ρ) was used to assess the extent to which the multivariate structure of the two matrices agreed.

The following application of the Linkage Tree (LINKTREE; Clarke et al., 2008) routine was used to examine which thresholds of the eight environmental variables (water temperature and depth, mean spring tidal range, depth of water clarity, chlorophyll *a*, rainfall, distance to shore and substratum type), were indicative of the successive separation of sites into subgroups from a constrained divisive cluster analysis. LINKTREE is a non-metric modification of the multivariate regression tree approach of De'ath (2002). Thus, a binary "linkage tree" is constructed that reflects how samples from an underlying (biotic) resemblance matrix are most naturally split into successively smaller groups, based on maximising the ANOSIM R -statistic (Clarke, 1993) for a binary split of each group, allowable divisions being constrained to those for which at least one of the environmental variables takes larger values for all samples in one of the subgroups than those in the other subgroup. At each branching node of the tree, quantitative thresholds are therefore provided of the variables from explanatory data, e.g. environmental values that mirror the division in the biological samples. In theory, the terminal group to which any new multivariate sample could be assigned is thus determined by ascertaining whether its values for the variables specified at each successive node of the tree are less than or greater than the given thresholds.

The LINKTREE procedure was applied to the Bray-Curtis similarity matrix calculated from the data averaged over replicates, the explanatory variables being the

untransformed measurements for the seven environmental variables, also averaged for each combination of location, season and depth. A Similarity Profile permutation test (SIMPROF; Clarke et al., 2008) was used in conjunction with LINKTREE to provide stopping rules for the successive subdivisions at those nodes at which no significant multivariate structure was considered to be present among the remaining biological samples, using $P > 0.05$ as the significance criterion. The LINKTREE and SIMPROF routines thus produce a constrained divisive clustering in which terminal nodes comprise groups of sites with high internal similarity, together with a sequence of inequalities on the environmental variables that 'explain' each biotic group. It is recognised that no inference of causality is possible with such an observational study.

All of the preceding multivariate analyses were carried out using the PRIMER v6 multivariate statistics package (Clarke and Gorley, 2006), together with the PERMANOVA+ add-on module where appropriate (Anderson et al., 2008).

3.3 Results

3.3.1 Environmental variables

PERMANOVA demonstrated that water temperature differed significantly between dry and wet seasons and among locations (both $P < 0.001$) and between water depths ($P < 0.05$), with significant interactions for location \times depth, location \times season and depth \times season. The values for the mean squares emphasised that temperature was more strongly related to season (9.8) than to either location (0.32) or water depth (0.005), with those for season and location far greater than for the interactions. At each location, water temperatures in both depths were far greater during the wet than dry seasons (Fig. 3.1a).

While water temperatures at the more northern locations were similar in deep and shallow waters in both the wet and dry seasons, they increasingly diverged with depth in a southwards direction during both seasons, but with those for shallow water becoming greater than deep in the wet and those for deep water becoming greater than shallow water in the dry season (Fig. 3.1a).

Mean depth of water clarity differed significantly among locations ($P < 0.001$) and between seasons ($P < 0.05$), but not between water depths ($P > 0.05$), and there were no significant interactions between these variables ($P > 0.05$). Mean square values emphasised that water clarity was related more to location (1.10) than season (0.09). Water clarity was least in both the dry and wet seasons at Cape Voltaire and Hall Point in the north (~ 1.7 m) and greatest in the dry and wet seasons at Locker Point in the south, with respective values of 4.3 and 3.8 m, with secondary peaks at Emeriau Point (Fig. 3.1b).

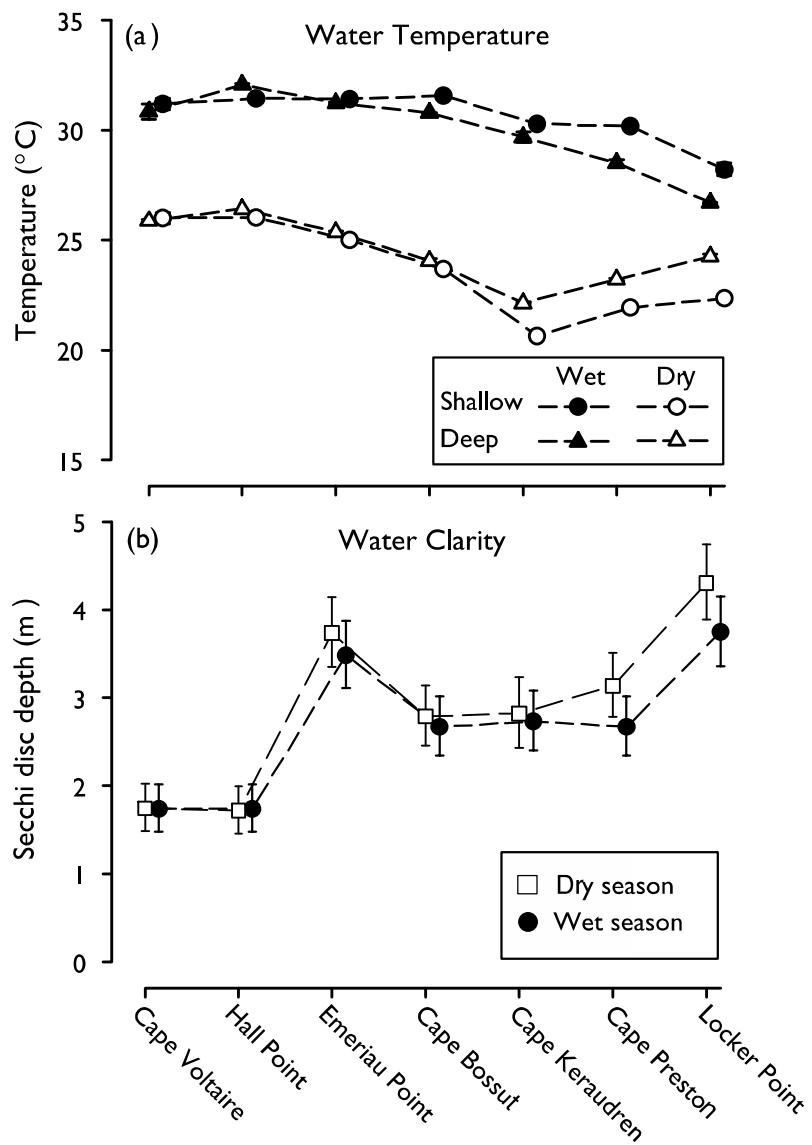


Figure 3.1. Mean values $\pm 95\%$ confidence intervals for (a) water temperatures and (b) water clarity depths at each of the seven sampling locations in tropical north-western Australia. Note error bars are often too small to be illustrated on the plot.

Although water clarity was very similar in the wet and dry seasons at the two most northern locations (Cape Voltaire and Hall Point), it was greater during the dry at the other five locations and particularly at the two most southern locations (Cape Preston and Locker Point).

3.3.2 Dominant species and families

Trawling in deep and shallow inshore waters at the seven locations along the NWA coast in 2001 and 2002 yielded 84,781 fishes, which represented 272 species of teleost belonging to 167 genera and 74 families (Table 3.2). None of the 13 elasmobranch species, representing nine genera and six families, was abundant or regularly caught, which was likely to reflect the reduced ability of these particular nets to catch the faster moving species of elasmobranch.

Certain species showed a pronounced tendency to occur either exclusively or predominantly in certain locations, seasons and/or water depths. For example, *Leiognathus splendens*, *Secutor insidiator* and *Terapon theraps* were all very abundant at Cape Voltaire and Hall Point in the Kimberley Bioregion, whereas they were caught at only one of the five locations in the Canning and Pilbara bioregions further south and even then were represented by only three individuals of a single species (Table 3.2). In contrast, the reverse trend was exhibited by *Pristotis obtusirostris* and *Paramonacanthus choirocephalus*, while species such as *Selaroides leptolepis* and *Saurida undosquamis* were regularly present in samples collected from throughout the length of the NWA coast.

Table 3.2. List of the most abundant fish species, and their numbers, biomass and percentage contributions in catches, obtained by daytime trawling over soft substrata in deep (D) and shallow (S) inshore waters at seven locations in NWA in the dry and wet seasons of 2001 and 2002, respectively. The mean densities of each species in each depth and season at each of the seven sampling locations and the total numbers and total biomasses of all species and the overall means in terms of density and biomass are also provided.

Species	Numbers		Cape Voltaire				Hall Point				Emeriau Point				Cape Bossut				Cape Keraudren				Cape Preston				Locker Point										
	N	(%)	B	(%)	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S									
<i>Leiognathus splendens</i>	16354	19.3	168	8.2	177	193	1270	1532	12	32	75																										
<i>Terapon theraps</i>	9041	10.7	201	9.8	150	40	379	182	28	97	140	784																		3							
<i>Secutor insidiator</i>	8284	9.8	65	3.2	<1		65	1419			419	2																									
<i>Selaroides leptolepis</i>	5070	6.0	119	5.8	21	4	5	1	28		122		1		4	20			90	1			461	230			36		70	<1							
<i>Leiognathus leuciscus</i>	4484	5.3	60	2.9	27	144	18	155	13	13	2	469							27			2	73			<1											
<i>Upeneus sulphureus</i>	4380	5.2	76	3.7	7	16	258	190	<1		14	406																	11								
<i>Saurida undosquamis</i>	3079	3.6	161	7.9	9	3	35	30	2	1	4	21	1	12	1	55	15	9	46	7	4	27	27	25	28	37	142	14	33	4	41	35					
<i>Pristotis obtusirostris</i>	3068	3.6	34	1.7									6	21	3	26	6	86	7	44	157	1	186		24	6	9	12	16	27	8	72					
<i>Carangooides malabaricus</i>	2705	3.2	31	1.5	67	52	337	46	1	1	3	53									1																
<i>Paramonacanthus choirocephalus</i>	2505	3.0	33	1.6									1	<1	1	119	4	2	5		2	41	21	38	46	252	2	1	6	41	1	3					
<i>Caranx bucculentus</i>	2411	2.8	96	4.7	12	12	27	45	<1	105	21	263					3	<1	1	119	4	2	5		2	41	21	38	46	252	2	1	6	41	1	3	
<i>Lethrinus genivittatus</i>	1586	1.9	39	1.9									<1	3	<1		1	<1			<1	33	2							1	12	91	13	223			
<i>Saurida tumbil</i>	1074	1.3	82	4.0	17	10	58	96	2	13	2	28					<1			<1				2	<1							<1					
<i>Pomadasys maculatum</i>	998	1.2	38	1.8	3	10	2	183			1	15																									
<i>Torquigenes pallimaculatus</i>	877	1.0	12	0.6					2				1	10	<1	<1	<1			1	3	17	7	1	8	70	7	15	12	8	4	6	20	2			
<i>Upeneus asymmetricus</i>	768	0.9	16	0.8																																	
<i>Leiognathus equulus</i>	728	0.9	19	0.9	91	17	8	11	2		6	2																									
<i>Secutor interruptus</i>	726	0.9	2	0.1	<1	2	1	135	<1		27																										
<i>Leiognathus fasciatus</i>	613	0.7	13	0.6					134				<1	1																							
<i>Enyprosopon grandisquama</i>	527	0.6	6	0.3					1		<1						2	1	<1		8	2	<1		1	17		<1	12	43	1	29	6	1			
<i>Leiognathus bindus</i>	473	0.6	2	0.1	<1	16	47		16	9	10	4																									
<i>Enyprosopon maldiviensis</i>	465	0.5	9	0.4																																	
<i>Siganus fuscescens</i>	445	0.5	14	0.7					0				<1	1			<1				2	4	5	<1	5	39		16	1	5	1	24					
<i>Gerres filamentosus</i>	423	0.5	12	0.6	18	4	3	31		1	<1	34																									
<i>Choerodon cephalotes</i>	418	0.5	47	2.3					1				7	13	2		9	4	<1	<1	15	23	7														
<i>Johnius borneensis</i>	388	0.5	8	0.4	2				3	8	46	19					1	2	1	2	1	2	1	3	27	17	2	6	4	7	1	<1					
<i>Parapercis nebulosa</i>	386	0.5	17	0.9					1																												
<i>Pentapodus porosus</i>	384	0.5	21	1.0									5	1	13	3	7	2	8	<1	2	4	17		1	<1	1	4	7	4	4	2					
<i>Sillago ingenua</i>	376	0.4	14	0.7					2	5	1									1	9			47	7			1	2								
<i>Apogon unitaeniatus</i>	373	0.4	3	0.1	2				21	16	5	<1	7	28							3		1	16	1	1	4	1	9	3	<1	38	<1				
<i>Nemipterus furcosus</i>	372	0.4	15	0.7																																	
<i>Leiognathus decorus</i>	350	0.4	5	0.3									38	1	40																						
<i>Apogon fasciatus</i>	319	0.4	3	0.1	1	1			52	11	2	3	9																								
Total numbers	84781		3036	2472	13055	20463	1068	1891	6804	12080	424	254	621	1225	372	601	1088	334	683	1141	4549	2398	869	2118	852	857	1695	1288	962	1581							
Total biomass (kg)		2047	85	55	209	341	21	62	107	316	35	10	41	27	25	28	26	6	19	53	120	40	46	155	36	16	53	35	53	29							
Mean overall density, no. 0.01 km ⁻²	298		661	544	2793	4606	211	388	962	2476	90	52	134	266	87	135	237	76	214	353	954	520	205	502	181	169	378	281	232	383							
Mean overall biomass, kg 0.01 km ⁻²		19	21	14	52	85	5	15	27	79	9	2	10	7	6	7	7	1	6	18	30	10	11	39	9	4	13	9	13	7							
Number of species	285		50	51	62	76	44	45	72	53	50	28	42	43	47	35	33	23	33	58	44	45	36	44	26	33	95	57	52	37							

Leiognathus splendens, *Secutor insidiator*, *Selaroides leptolepis* and *Leiognathus leuciscus*, ranked first, second, fourth and fifth, respectively, in terms of overall abundance, but with the densities of each of these species greater during the wet season, whereas the reverse was true for *Engyprosopon grandisquama* (Table 3.2). At locations where they were recorded, *L. leuciscus*, *Paramonacanthus choirocephalus*, *Caranx bucculentus* and *Saurida tumbil* tended to be more abundant in shallow waters, while the opposite was true for *Leiognathus equulus* and *Pentapodus porosus*.

The Leiognathidae contributed nearly 40% to the total number of fish caught, with only the Carangidae and Terapontidae otherwise contributing more than 10% (Table 3.3). The Leiognathidae at Cape Voltaire and Hall Point, the locations to which this family was largely confined, contributed more in the wet than dry seasons (Table 3.3). When the Monacanthidae was abundant at a location, it tended to contribute more to the numbers in shallow than deeper waters, whereas the reverse was almost invariably the case with the Labridae (Table 3.3). In terms of their percentage contributions to the catches, the Leiognathidae, Carangidae and Terapontidae ranked first, second and third, respectively, in both deep and shallow waters, and the Leiognathidae likewise ranked first in the dry and wet seasons and the Carangidae ranked second in the wet season and third in the dry season (Table 3.3). While the Monacanthidae ranked second in the dry season, it ranked only seventh in the wet season and fifth in shallow water and did not rank amongst the top ten in deep water. Although the Leiognathidae ranked first in both water depths and both seasons, its total number in shallow water exceeded that in deep water by 1.9 times and that in the wet season exceeded that in the dry season by as much as 8.0 times.

Table 3.3. List of the most abundant families of teleosts, and their numbers and percentage contributions in catches, obtained by daytime trawling over soft substrata in deep (D) and shallow (S) inshore waters at seven locations in NWA in the dry and wet seasons of 2001 and 2002, respectively. The percentage contribution of each family in terms of numbers in each depth and season at each of the seven sampling locations are also provided.

Family	Cape Voltaire				Hall Point				Emeriau Point				Cape Bossut				Cape Keraudren				Cape Preston				Locker Point													
	Numbers		Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet												
	N	(%)	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S												
Leiognathidae	32461	38.2	44.9	65.9	49.9	75.7	23.0	14.2	62.6	19.8	0.9	0.4	3.3	9.3	2.0	39.9	1.4	0.3	0.5	49.5	51.2	0.3	0.2	22.5	0.1	0.1	0.3	30.4	0.2									
Carangidae	11495	13.5	17.1	13.8	14.3	2.3	0.9	48.0	2.7	22.2	0.9	0.4	0.2	0.2	2.0	11.5	0.5	14.3	0.1	0.2	0.2	0.1	0.2	0.1	8.4	11.6	10.2	1.4										
Terapontidae	9047	10.6	22.7	7.3	13.6	4.0	13.0	24.9	14.6	31.7	1.2	3.4	9.2	4.1	0.3	0.3	1.5	16.4	0.8	9.0	0.9	1.8	4.0	2.2	9.5	2.0	7.2	0.6	1.9	15.2	13.0	4.4	18.2	9.1				
Mullidae	5482	6.5	1.2	3.4	9.2	4.1	0.3	0.3	1.5	16.4	2.0	27.9	0.8	21.0	2.0	27.9	1.4	24.7	10.6	19.6	10.5	1.9	8.8	2.9	5.2	19.6	8.8	79.1	8.4	11.7	1.2	5.2	7.2	9.0	9.5	3.6	18.8	
Synodontidae	4433	5.2	4.0	2.4	3.3	2.7	1.8	3.5	0.6	2.0	6.2	39.8	2.1	9.8	6.2	63.9	2.7	58.6	73.5	0.5	19.5	11.7	2.3	7.2	22.7	50.3	1.3	1.3	2.6	15.9	0.7	0.9						
Pomacentridae	3154	3.7									2.1	0.8	2.9	45.1	2.1	0.8	2.9	45.1	5.2	1.5	2.0	0.3	0.9	11.7	2.3	7.2	0.6	1.9	15.2	8.4	11.6	10.2	1.4					
Monacanthidae	2828	3.3			1.2	0.4	1.2		0.1		0.5		2.4	0.1	0.5	0.2	2.4	0.1	1.2	0.3	0.1	0.9	0.2	0.1	0.3	0.3	3.6	32.7	6.4	58.3								
Lethrinidae	1603	1.9									0.5		0.2	0.1	0.5	0.2	0.3	0.1	1.1	2.6	8.6	12.4	0.3	2.7	8.2	6.2	7.4	2.4	4.7	7.4	3.6	7.4	3.7	0.8				
Tetraodontidae	1389	1.6	0.6	0.8	0.6	0.2		0.5	0.3	0.6	0.2	1.5	0.3	0.7	1.2	0.4	0.2	0.8	0.3	0.5	0.5	0.1	0.2	0.1	0.1	0.3	1.5	0.1	0.1	0.1	0.1							
Apogonidae	1269	1.5	0.6	0.1	3.5	0.5	8.4	0.7	5.8	1.6	1.2	0.4			1.2	0.4	1.4	0.8	0.3	0.5	0.5	0.1	0.2	0.1	0.1	0.3	1.5	0.1	0.1	0.1	0.1							
Nemipteridae	1207	1.4	2.0	0.7	0.6	0.1	0.1	0.9	0.3	0.3	6.7	4.7	10.2	2.4	6.7	4.7	10.2	2.4	9.2	1.4	4.8	0.5	2.9	6.5	3.6	1.3	1.1	1.5	1.3	7.2	3.5	1.5	18.2	0.6				
Bothidae	1147	1.3					0.3	0.1			1.7	5.8	0.2	0.7	1.7	5.8	0.2	0.7	10.2	1.8	0.1	0.5	4.9	0.1	10.3	8.9	1.4	39.4	2.2	1.8	0.1	0.1						
Haemulidae	1082	1.3	0.6	1.8	0.1	4.2			0.1	0.6	0.2		1.3		0.2	1.3	1.8	0.1					0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1					
Labridae	836	1.0					0.4		0.2		26.3	0.7	26.9	1.5	26.3	0.7	26.9	1.5	17.8	4.0	0.2	0.3	8.6	7.8	1.2	4.6	0.3	1.1	0.2	2.3	4.0	0.1	1.5					
Gerreidae	708	0.8	3.2	0.8	0.3	1.3		3.0	<0.1	1.7					0.8	0.6	0.2	0.4	11.4		8.9	5.0	2.6	0.5	9.4		0.2	0.1	0.2	1.8	0.1	0.2	0.1					
Sillaginidae	620	0.7	0.1	0.2	0.1	0.1	2.0		0.1						0.3	0.5	0.2	0.4	11.4	0.2	0.4	11.4	8.9	5.0	2.6	0.5	9.4	0.2	0.1	0.2	0.1							
Paralichthyidae	614	0.7	0.3	0.5	0.2	0.1	4.2	1.1	0.1	0.9	3.1	5.0	0.7	0.5	7.4	3.7	1.5	0.3	2.1	3.5	0.1	1.2	2.8	1.8	2.6	2.5	2.3	0.7	1.1	0.6								
Siganidae	445	0.5					0.1				0.3		0.5		0.5	0.2	0.2	0.7	1.2	0.5	<0.1	0.7	1.2	0.5	0.2	0.4	7.7	9.3	0.3	1.6	0.3	6.3						
Lutjanidae	410	0.5		0.1		0.3	0.1	<0.1	0.4	4.6	17.8	2.9	1.8	0.2	0.6	1.8	0.2	0.6	0.1	0.8	0.1	0.2	2.6	0.1	0.2	0.1	0.1	0.2	0.1	0.1	0.1	0.1						
Priacanthidae	409	0.5		0.1	0.2	0.1	0.3	0.2	0.2	0.5	2.1	0.2	0.6	0.6	1.1	0.1	0.8	2.2	1.2	0.2	0.4	4.5	0.2	2.6	0.2	0.6	0.2	0.6	0.1	0.1	0.2	0.1						
Sciaenidae	389	0.5	0.3	<0.1	0.1	0.2	21.5		2.0		0.5		2.1	0.2	0.6	1.1	0.1	0.8	2.2	1.2	0.2	4.5	0.2	2.6	0.2	0.6	0.2	0.6	0.1	0.1	0.2	0.1						
Pinguipedidae	386	0.5				<0.1					1.6	3.1	1.0	0.8	1.7	1.6	2.3	0.9	0.1	0.5	0.1	0.5	13.0	3.3	1.3	3.5	1.0	2.5	0.5	0.1	0.1	0.1						
Pristigasteridae	342	0.4				0.8	0.2	7.9		1.8					1.6	3.1	1.0	0.8	1.7	1.6	2.3	0.9	0.1	0.5	0.1	0.5	13.0	3.3	1.3	3.5	1.0	2.5	0.5	0.1	0.1	0.1		
Engraulidae	295	0.3		<0.1	0.2	0.3	4.7		3.4																													
Chaetodontidae	280	0.3							0.1		16.2		3.8	0.2	0.5	0.2	0.2	0.1	4.6	0.5	0.5	0.5	0.1	0.3	0.2	0.2	3.6	0.5	0.2	0.8	0.2	0.2	0.2					
Pomacanthidae	264	0.3							<0.1		13.0		10.8	0.2	2.4	3.1	1.5	3.0	3.2	0.7	0.1																	
Clupeidae	257	0.3			0.1	0.1	1.1		<0.1	0.1																												
Polynemidae	248	0.3	0.2	0.3	0.4	0.6	0.4		0.9																													
Platycephalidae	210	0.2	0.3	0.2	0.2	0.1	2.5	0.4	0.1	0.2	0.7	0.4	0.2	0.6	0.6	0.2	0.1	0.3	1.3	0.1	0.1	0.5	0.1	0.5	0.1	0.6	0.9	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1		
Diodontidae	208	0.2			0.1	<0.1			<0.1		4.4	3.1	0.7	0.8	0.6	1.7	0.2	0.3	0.2	10.7	0.1	0.1	0.1	0.4	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1

In contrast, differences in the abundances of the Carangidae in deep and shallow water and between the Pomacentridae in the dry and wet seasons were small. This emphasises the importance of taking into account both the percentage contributions and abundances when comparing data for species in different water depths and seasons.

3.3.3 Species richness and density of fishes

The species richness and density of fishes over soft substrata were both significantly related to location and the density was also significantly related to season (Table 3.4). There were, however, significant interactions between location and season for both biotic variables, a marginally significant location \times depth interaction for number of species and an interaction between location, season and depth for density. The mean square values (Table 3.4) emphasise that species richness was strongly related to location, which had a strong interaction with both season and depth, and that density was strongly related to both location and season.

In the dry season, the mean species richness and density in deep water declined from high values at the two most northern locations to their minimum at geographically-intermediate locations, and then rose at the most southern locations (Fig. 3.2a,c). While the species richness and density in shallow water during the dry season followed similar trends, they tended to decline in the most southern part of the Pilbara (Fig. 3.2a,c). The mean species richness and density in deep and shallow waters in the wet season likewise initially declined in a southwards direction, but subsequently peaked sharply at Cape Keraudren and then declined to lower levels at the two locations in the Pilbara (Fig. 3.2b,d).

Table 3.4 Mean squares (MS), F values and significance levels (*P*) for PERMANOVAs of the number of fish species and density of fishes in deep and shallow waters at seven locations along the coast of north-western Australia in the dry season of 2001 and wet season of 2002. *df*, degrees of freedom.

	df	Number of species			Density		
		MS	F	P	MS	F	P
Location (L)	6	5.52	12.3	<0.001	2.50	37.7	<0.001
Season (S)	1	0.19	0.4	0.512	2.64	39.8	<0.001
Depth (D)	1	0.82	1.8	0.178	0.23	3.5	0.066
L × S	6	2.45	5.5	<0.001	0.58	8.9	<0.001
L × D	6	1.28	2.9	0.013	0.09	1.4	0.230
S × D	1	0.03	0.1	0.784	0.00	0.1	0.838
L × S × D	6	0.95	2.1	0.058	0.31	4.7	<0.001
Residual	82	0.44			0.06		

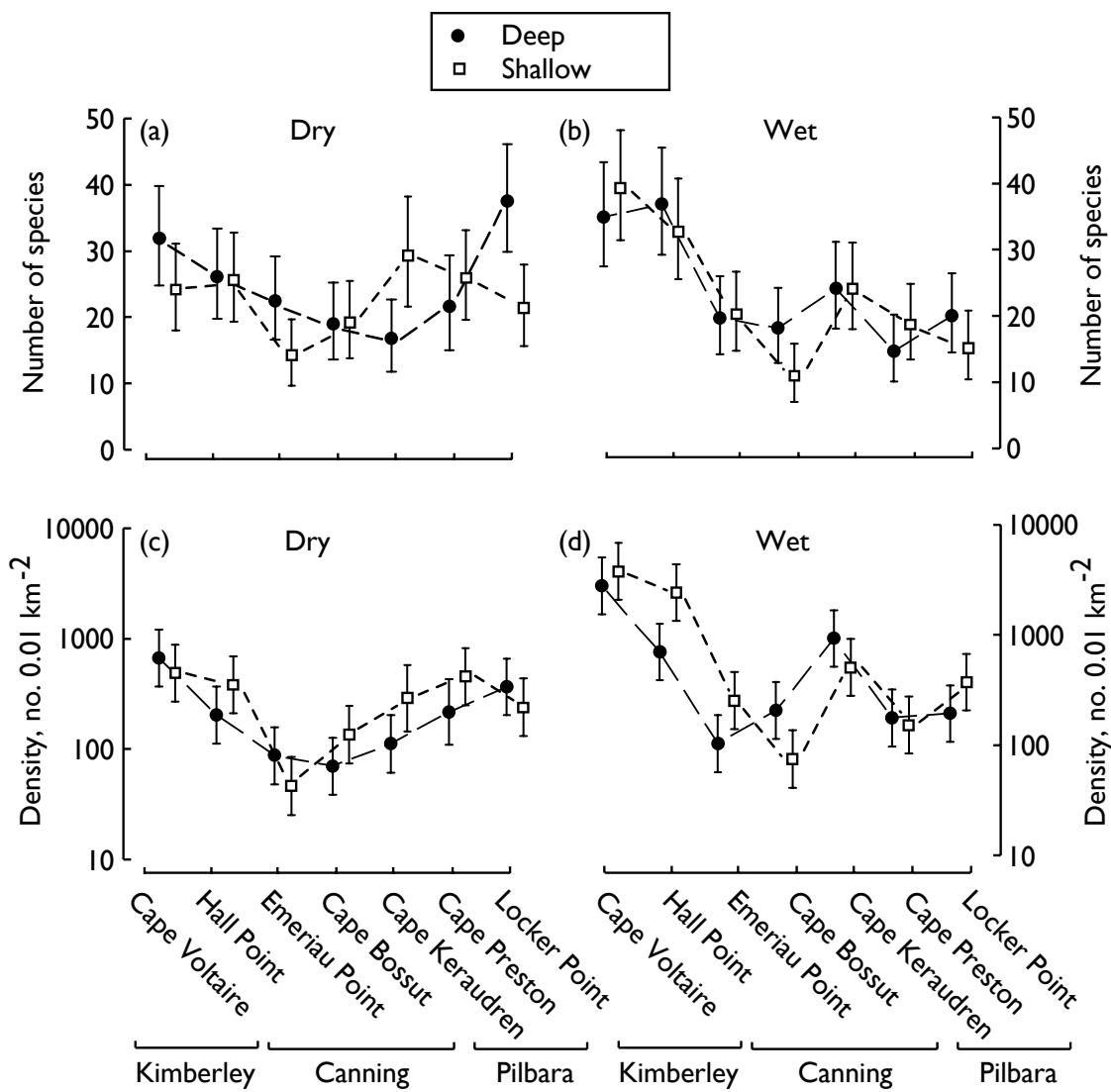


Figure 3.2. Mean values $\pm 95\%$ confidence intervals for the numbers of fish species in deep and shallow waters in (a) the dry and (b) wet seasons and for the mean densities of fish in deep and shallow waters in the (c) dry and (d) wet seasons. Data were derived from samples collected by trawling over soft substrata in deep and shallow waters at seven locations in north-western Australia in the dry season of 2001 and the wet season in 2002.

3.3.4 Relationships between species composition and season and water depth

While species composition over soft substrata was shown by PERMANOVA to be significantly related to location, season and depth, there were significant interactions between location and both season and depth, and between each of these three factors (Table 3.5). The two-way crossed ANOSIM test, using location and a combined season-by-depth factor, thus removing any confounding influence of season and/or depth individually, gave a \bar{R} statistic of 0.85 for location, while the \bar{R} statistic for season, removing the combined effects of location and depth, was 0.72, and that for depth, removing the combined effects of location and season, was 0.68 (all at $P < 0.001$). However, these tests of strong averaged effects did contain some significant interactions (see above).

Two-way ANOSIM comparisons between the ichthyofaunal compositions over soft substrata at pairs of locations (again removing depth and season effects) showed that the species composition at each location differed significantly from that at each other location ($P = 0.1\text{-}0.6\%$), with \bar{R} statistic values ranging from 0.17 for Cape Preston vs Locker Point to 1.0 for Cape Voltaire vs Cape Preston (Table 3.6). In general, the \bar{R} statistic values for comparisons between the faunal compositions in adjacent locations were far less than those between widely-separated locations. Species that made major contributions to the differences in the ichthyofaunal compositions among locations included *Terapon theraps*, *Leiognathus leuciscus* and *Leiognathus splendens*, which were in far greater densities and more regularly caught at Cape Voltaire and/or Hall Point than at any of the southern locations (Table 3.6). In contrast, greater contributions of *Paramonacanthus choirocephalus* distinguished the fauna at Cape Preston from all other locations.

Table 3.5. Mean squares (MS), *F* values and significance levels (*P*) for location × season × depth PERMANOVA for the Bray-Curtis matrix derived from density data for the various fish species collected over soft substrates by trawling at seven locations along the tropical NWA coast in deep and shallow waters during the dry season of 2001 and wet season of 2002. df, degrees of freedom.

	df	MS	<i>F</i>	<i>P</i>
Location (L)	6	23237	19.6	<0.001
Season (S)	1	12999	10.9	<0.001
Depth (D)	1	9585	8.1	<0.001
L x S	6	4839	4.1	<0.001
L x D	6	7944	6.7	<0.001
D x S	1	1487	1.2	0.2
L x S x D	6	2606	2.2	<0.001
Residuals	82	1186		

Table 3.6. Global *R*-statistic values and significance levels for pairwise comparisons in one-way ANOSIM tests carried out on the percentage contribution of each fish species derived from data collected at seven locations in trawls over soft substrata in 2001 and 2002. * = 5%; ** = 1%; *** = 0.1%.

Location	Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Keraudren	Cape Preston
Hall Point	0.21***					
Emeriau Point	0.91***	0.91***				
Cape Bossut	0.99***	0.98***	0.27***			
Cape Keraudren	0.89***	0.88***	0.31***	0.28***		
Cape Preston	1.0***	0.99***	0.43***	0.22**	0.31***	
Locker Point	0.93***	0.93***	0.33***	0.23***	0.18**	0.17**

The demonstration by PERMANOVA and ANOSIM tests that the ichthyofaunal composition over soft substrata is influenced by location, season and water depth is borne out by the nMDS ordination plot shown in Fig. 3.3, in which the samples from Cape Voltaire and Hall Point in the Kimberley Bioregion form a group at the top that is discrete from all of those at the other five locations at the bottom of the plot. However, unlike the situation at Cape Voltaire, the samples from Hall Point are separated more on the basis of depth than season, which accounts, in part, for the interaction between location, season and depth. In the five most southern locations, the samples from the dry season lie to the left and/or below all but one of those from the wet season. The samples from the dry and wet seasons in deepwater at Emeriau Point are closely apposed and relatively discrete from those in shallow water at this location, which are more widely dispersed, and thus together contribute to the interaction between season and depth.

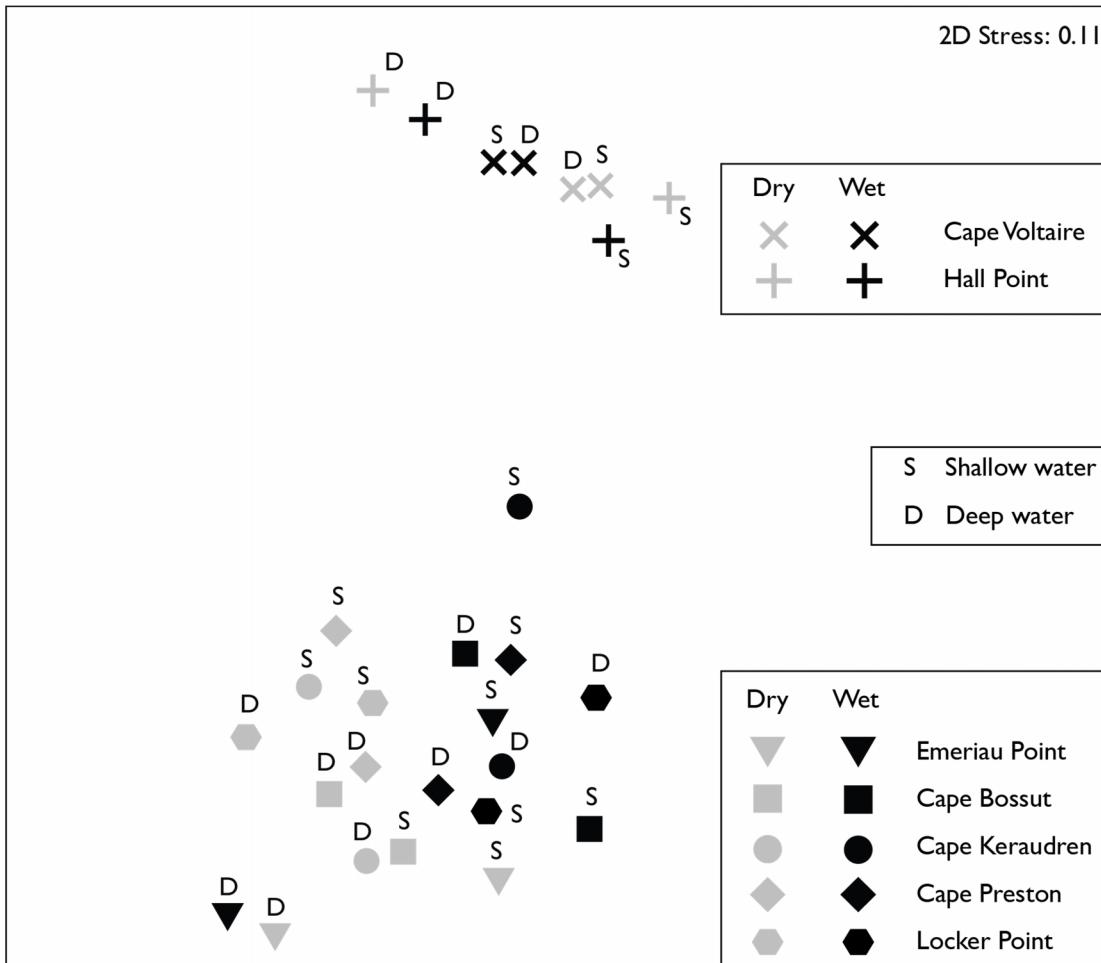


Figure 3.3. Non-metric multidimensional scaling (nMDS) ordination derived from matrix constructed from the densities of each fish species over soft substrata in deep and shallower waters at each of the seven locations in north-western Australia during the dry season of 2001 and wet season of 2002.

The RELATE test demonstrated that the similarity matrix used to produce the ordination plot in Fig. 3.3 was correlated with the distance matrices constructed at higher taxonomic levels, *i.e.* genus ($\rho = 0.96$), family ($\rho = 0.93$), sub-order ($\rho = 0.85$) and order ($\rho = 0.60$). Thus, the pattern of distribution of points shown in the nMDS ordination derived

using species data (Fig. 3.3) was strongly retained when the multivariate analyses were conducted at higher taxonomic levels and particularly up to sub-order.

3.3.5 Relationships between species composition and both season and water depth at each location

On the ordination plots derived from ichthyofaunal data for the various locations, the samples from deep and shallow waters in the dry season lie entirely or very largely above those from deep and shallow waters in the wet season at all locations except Emeriau Point, where only the samples from shallow waters were separated on the basis of season (Fig. 3.4a-g). The samples from deep and shallow waters at each location also typically showed limited overlap, with those from shallow water lying entirely or very largely to the right of those from deep water at all locations except Cape Voltaire (Fig. 3.4a).

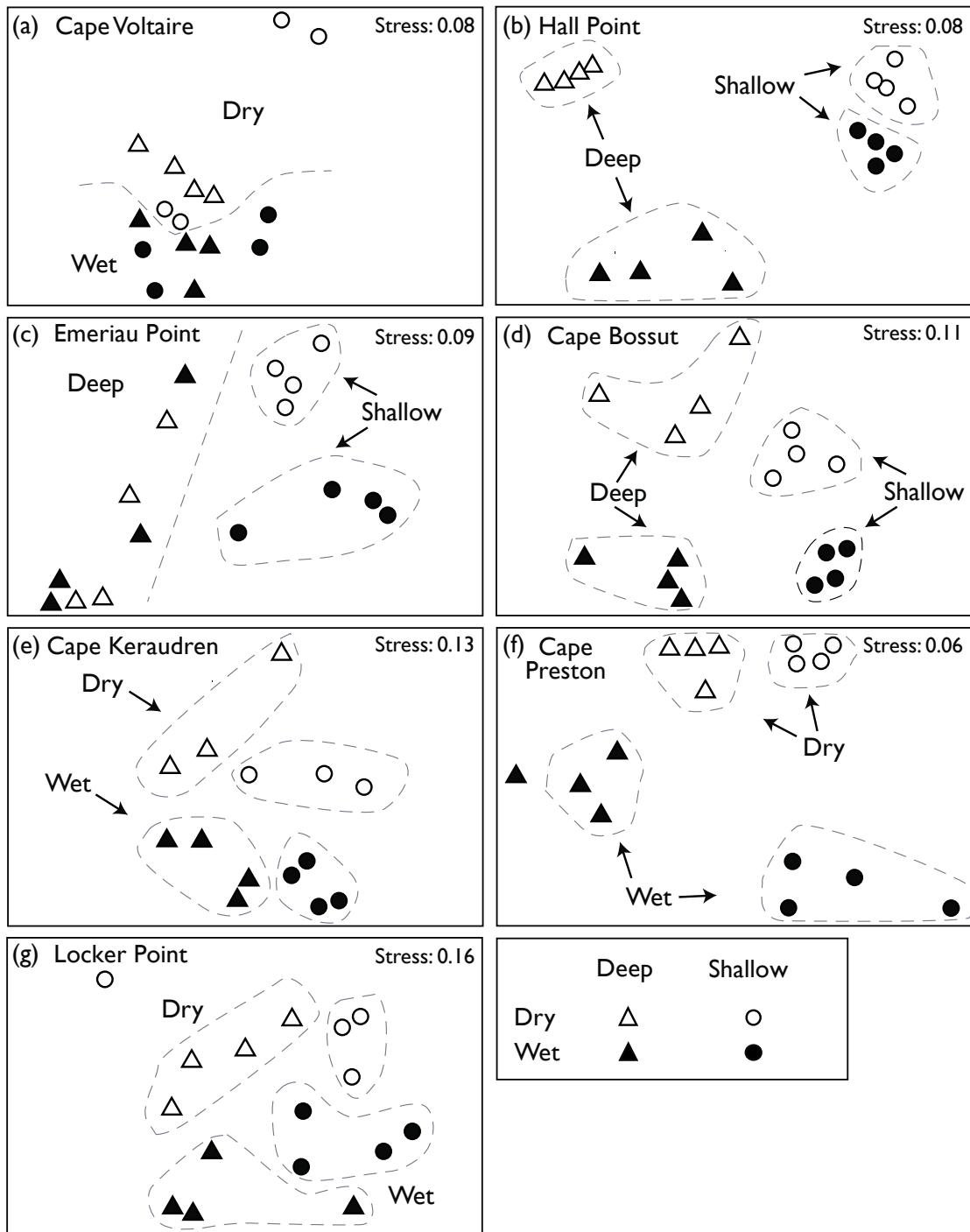


Figure 3.4. Non-metric multidimensional scaling (nMDS) ordinations of the densities of the various fish species caught by trawling over soft substrata in deep and shallow waters at (a) Cape Voltaire, (b) Hall Point, (c) Emeriau Point, (d) Cape Bossut, (e) Cape Keraudren, (f) Cape Preston and (g) Locker Point in the dry season of 2001 and wet season of 2002.

Two-way crossed ANOSIM tests, involving season vs depth, confirmed that species composition differed significantly between both dry and wet seasons and deep and shallow waters at every location except Cape Voltaire, where the composition differed significantly only between seasons (Table 3.7). The \bar{R} statistic values emphasised that the magnitude of the differences in ichthyofaunal composition between both seasons and water depths were greatest at Hall Point and Cape Preston and least at Cape Voltaire and Locker Point.

Two-way crossed SIMPER emphasised that, at Cape Voltaire and Hall Point, the mullid *Upeneus sulphureus* was present in such far greater densities in the wet than dry seasons that it was the most important species for distinguishing between the faunas in those two seasons (Table 3.8). There was also a strong tendency for the densities of leiognathid species and the carangid *Carangoides malabaricus* to be consistently greater at those two northern locations. Far greater densities of the carangid *Selaroides leptolepis* and far lower densities of the flounder *Engyprosopon grandisquama* distinguished the fauna in the wet from dry seasons at the southernmost locations. At Cape Bossut, Cape Preston and Locker Point, the ichthyofaunas in deep waters were distinguished from those in shallow waters by relatively greater densities of *Pseudorhombus argus* (Table 3.9). Greater densities of the mullid *Upeneus assymetricus* and the siganid *Siganus fuscescens* distinguished the faunas of shallow from deep waters at three and two of the most southern locations, respectively.

Table 3.7. Global *R*-statistic values and significance levels for season × depth two-way crossed ANOSIM tests, carried out separately for each location, using data for samples collected over soft substrata in the dry and wet seasons. Significance level: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Location	Season	Depth
Cape Voltaire	0.69**	0.14
Hall Point	0.90***	1.00***
Emeriau Point	0.38*	0.76**
Cape Bossut	0.83**	0.70**
Cape Keraudren	0.78**	0.64**
Cape Preston	0.97***	0.98**
Locker Point	0.48**	0.59***

Table 3.8. Species detected by SIMPER as distinguishing the fish assemblage in the dry season (2001) from that in the wet season (2002) at each of seven locations in north-western Australia, listed in decreasing order of their contribution to the average dissimilarity between the two seasons. High (>1.5) ratios of dissimilarity to standard deviation (Diss/SD) have been highlighted in bold face for relevant species, *i.e.* indicating consistent discriminators. Asterisk denotes species ‘favouring’ the dry over wet season.

	Distinguishing species	Mean density		Diss/SD
		Dry	Wet	
Cape Voltaire	<i>Upeneus sulphureus</i>	11.2	223.8	2.1
	<i>Leiognathus splendens</i>	185.1	1401.1	1.2
	<i>Secutor insidiator</i>	0.2	741.8	1.3
	<i>Leiognathus bindus</i>	0.1	31.7	2.0
	<i>Terapon theraps</i>	95.0	280.5	1.3
	<i>Leiognathus equulus*</i>	54.2	9.3	1.9
	<i>Carangoides malabaricus</i>	59.1	191.4	1.7
Hall Point	<i>Upeneus sulphureus</i>	0.2	210.4	2.5
	<i>Leiognathus leuciscus</i>	12.8	235.6	2.2
	<i>Terapon theraps</i>	62.2	462.1	2.0
	<i>Carangoides malabaricus</i>	1.1	27.8	1.6
	<i>Caranx bucculentus</i>	52.8	142.1	1.4
	<i>Pseudorhombus arsius</i>	6.5	10.9	2.0
	<i>Leiognathus moretoniensis</i>	2.7	13.8	2.1
Emeriau Point	<i>Paramonacanthus choirocephalus</i>	0.5	60.0	1.1
	<i>Selaroides leptolepis</i>	0.4	11.9	1.3
	<i>Pentapodus porosus</i>	2.7	8.3	1.4
	<i>Tragulichthys jaculiferus*</i>	1.3	0.3	1.2
	<i>Synodus sageneus*</i>	2.8	1.5	1.2
Cape Bossut	<i>Selaroides leptolepis</i>	< 0.1	45.1	0.9
	<i>Torquigener pallimaculatus</i>	1.7	12.3	1.8
	<i>Engyprosopon grandisquama*</i>	5.2	0.1	1.5
	<i>Choerodon cephalotes*</i>	6.3	0.2	1.3
	<i>Synodus dermatogenys*</i>	2.9	< 0.1	2.0
	<i>Pseudorhombus spinosus*</i>	2.3	< 0.1	1.5
Cape Keraudren	<i>Selaroides leptolepis</i>	< 0.1	345.3	2.4
	<i>Paramonacanthus choirocephalus</i>	21.1	29.4	1.5
	<i>Lagocephalus scleratus</i>	0.7	16.7	1.5
	<i>Chaetodontoplus duboulayi*</i>	8.4	3.3	1.4
	<i>Engyprosopon grandisquama*</i>	9.0	0.2	1.3
	<i>Pentapodus vitta</i>	1.6	9.9	1.8
Cape Preston	<i>Paramonacanthus choirocephalus*</i>	149.3	1.8	3.5
	<i>Engyprosopon grandisquama*</i>	27.6	0.3	3.3
	<i>Siganus fuscescens*</i>	21.7	7.9	1.8
	<i>Trachinocephalus myops*</i>	6.8	0.7	2.8
	<i>Saurida undosquamis</i>	32.5	78.0	1.6
	<i>Selaroides leptolepis</i>	< 0.1	18.0	1.0
Locker Point	<i>Paramonacanthus choirocephalus*</i>	24.0	1.7	1.2
	<i>Torquigener pallimaculatus*</i>	13.0	0.9	1.5
	<i>Trachinocephalus myops*</i>	8.8	0.2	1.3
	<i>Engyprosopon grandisquama*</i>	17.4	0.3	1.3
	<i>Selaroides leptolepis</i>	< 0.1	35.1	1.0
	<i>Nemipterus furcosus</i>	1.8	19.2	1.0

Table 3.9. Species detected by SIMPER as distinguishing the fish assemblage in deep water from that in shallower water at each of six locations in north-western Australia, listed in decreasing order of their contributions. High (>1.5) ratios of dissimilarity to standard deviation (Diss/SD) have been highlighted in bold face, indicating especially consistent discriminators. Asterisk indicates species ‘favouring’ deep over shallow waters.

	Distinguishing species	Mean density		
		Deep	Shallow	Diss/SD
Cape Voltaire		Not significant		
Hall Point	<i>Selaroides leptolepis</i>	-	22.7	2.6
	<i>Caranx bucculentus</i>	16.6	72.2	1.3
	<i>Leiognathus splendens*</i>	43.3	16.2	2.3
	<i>Carangoides humerosus</i>	< 0.1	15.4	1.9
	<i>Johnius borneensis*</i>	25.4	-	1.5
	<i>Ulua aurochs</i>	-	15.2	2.9
	<i>Thryssa setirostris*</i>	9.2	-	2.2
	<i>Leiognathus leuciscus</i>	6.7	44.2	1.6
Emeriau Point	<i>Saurida undosquamis</i>	0.6	33.9	2.8
	<i>Chaetodontoplus duboulayi*</i>	13.0	0.2	2.2
	<i>Paramonacanthus choirocephalus</i>	0.7	59.8	1.1
	<i>Choerodon vitta*</i>	14.3	1.0	1.7
	<i>Choerodon cephalotes*</i>	10.1	0.8	2.4
	<i>Coradion chrysozonus*</i>	5.3	0.2	1.4
Cape Bossut	<i>Pristotis obtusirostris</i>	6.2	65.3	1.6
	<i>Pentapodus porosus*</i>	7.8	1.2	1.7
	<i>Saurida undosquamis *</i>	30.8	7.9	1.6
	<i>Paramonacanthus choirocephalus *</i>	4.2	1.0	1.9
	<i>Parapercis nebulosa*</i>	3.4	1.4	1.5
	<i>Pseudorhombus argus*</i>	2.6	0.8	1.8
Cape Keraudren	<i>Pristotis obtusirostris*</i>	171.6	0.6	2.1
	<i>Leiognathus leuciscus</i>	-	37.3	1.4
	<i>Torquigener pallimaculatus*</i>	35.2	7.5	2.2
	<i>Pentapodus porosus*</i>	9.5	1.9	1.8
	<i>Paramonacanthus choirocephalus</i>	11.4	39.1	1.3
	<i>Upeneus asymmetricus</i>	10.7	33.6	1.4
	<i>Nemipterus furcosus*</i>	9.9	0.8	1.3
	<i>Chaetodontoplus duboulayi*</i>	6.1	4.9	1.5
	<i>Pseudorhombus arsius</i>	0.3	3.1	1.6
Cape Preston	<i>Upeneus asymmetricus</i>	0.4	17.6	1.3
	<i>Siganus fuscescens</i>	2.4	27.1	1.3
	<i>Priacanthus tayenus</i>	0.1	13.6	1.4
	<i>Pseudorhombus arsius</i>	0.2	4.7	2.3
	<i>Crossorhombus azureus*</i>	4.6	0.1	2.1
	<i>Pseudorhombus argus*</i>	3.2	0.2	1.4
	<i>Paramonacanthus choirocephalus</i>	24.4	126.7	1.7
Locker Point	<i>Lethrinus genivittatus</i>	12.7	157.0	1.0
	<i>Pristotis obtusirostris</i>	12.0	49.3	1.2
	<i>Nemipterus furcosus*</i>	20.6	0.3	1.1
	<i>Engyprosopon maldiviensis*</i>	53.7	-	1.1
	<i>Siganus fuscescens</i>	1.0	14.3	1.1
	<i>Choerodon cephalotes</i>	2.5	7.9	2.0
	<i>Saurida undosquamis*</i>	36.9	19.2	1.3
	<i>Upeneus asymmetricus</i>	9.1	11.5	1.3
	<i>Pseudorhombus argus*</i>	3.6	0.2	1.3
	<i>Paramonacanthus choirocephalus</i>	3.6	22.1	1.3

3.3.6 Relationship between fish assemblages and environmental variables

The LINKTREE analysis in Fig. 3.5 represents the separation of the 28 combinations of location, depth and season into groups identified by a divisive cluster analysis of the species composition of the fish faunas, together with 'explanations' of those bifurcations in terms of thresholds on individual environmental variables. The separations of the faunas at the two locations in the Kimberley from those in the five locations in the Canning and Pilbara further south were explicable by a combination of greater tidal ranges and reduced water clarity. Greater chlorophyll *a* concentrations, *i.e.* greater primary productivity, water temperatures and rainfall were important in explaining the difference between the faunas in the wet and dry seasons in the Kimberley, and higher water temperatures were also important for explaining the differences between the faunas in the wet and dry seasons in both the Canning and Pilbara (Fig. 3.5). The distinction between the faunas in the Canning and Pilbara during the dry season was related to a greater tidal range and lower productivity in the former bioregion. The split between the samples from the deeper water in both dry and wet seasons at Emeriau Point from those of all other samples from the Canning and Pilbara were associated with the unique substratum type (hard sand with sponge and gorgonian corals) in the deep waters at that Canning location.

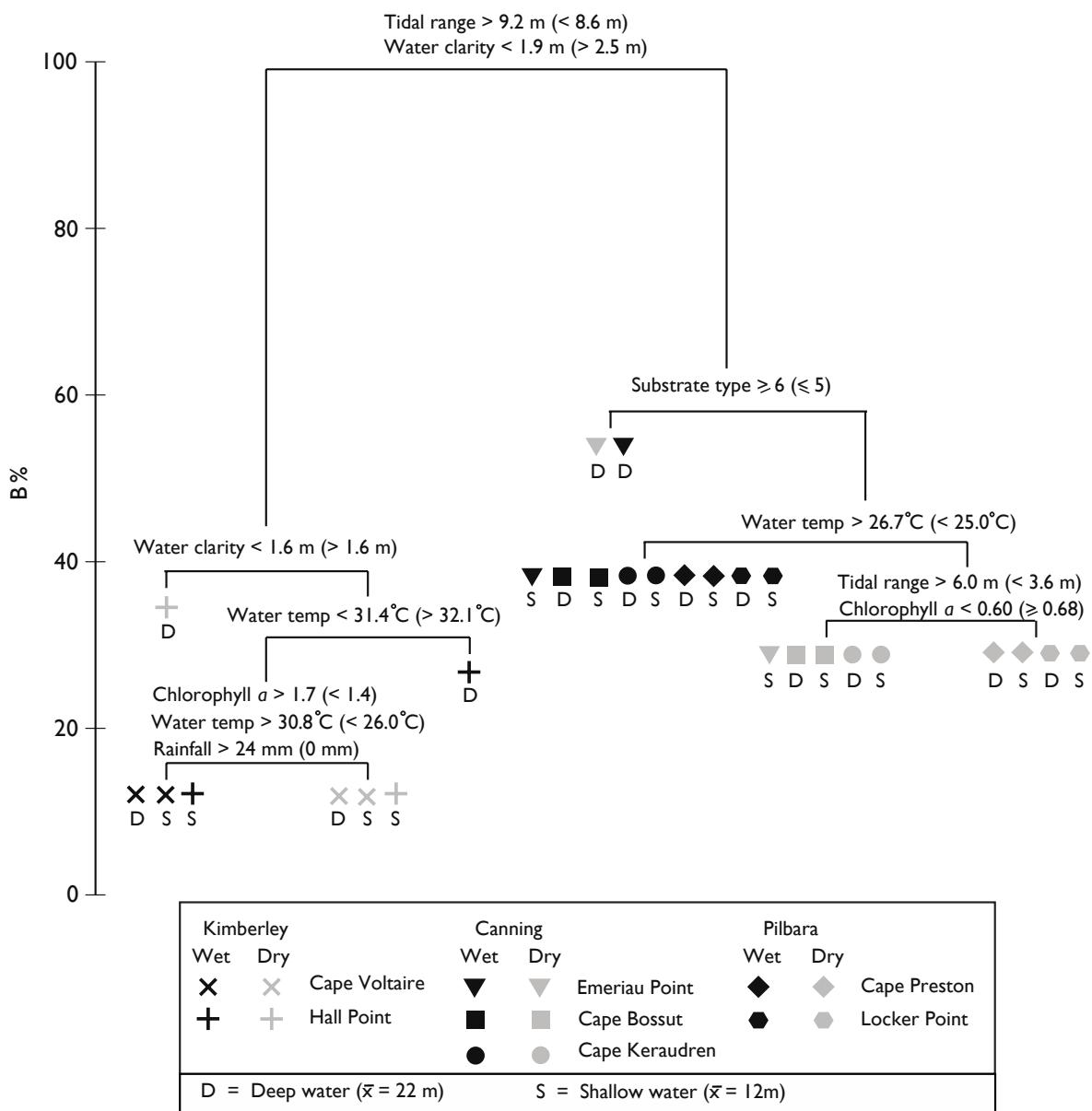


Figure 3.5. Linkage tree and associated physical and environmental variable thresholds that relate to the separation of the soft substratum fish communities of inshore waters in north-western Australia. Unbracketed and bracketed thresholds given at each branching node indicate that a left and right path, respectively, should be followed through the tree. Chlorophyll *a* concentrations are expressed as mg m^{-3} .

3.4 Discussion

3.4.1 Species richness and density of fishes

This study demonstrated that, in the dry season in NWA, the species richness and density of fishes over soft substrata in deep water both underwent the same remarkably consistent “concave” pattern of change in a southwards direction along this extensive tropical coast, and that this trend was also largely followed by density in shallow waters. Thus, both of these variables declined progressively from high levels in the Kimberley to their lowest levels in the Canning and then rose in the Pilbara. Furthermore, species richness in shallow water in the dry season was also least in the first two of the Canning locations, *i.e.* Emeriau Point and Cape Bossut. The above trends imply that, in the dry season, the Kimberley and Pilbara bioregions provide an environment, which, in terms of productivity and other factors, is more beneficial for a range of demersal fish species than the intervening Canning Bioregion. It is thus relevant that chlorophyll *a* concentrations, and thus primary productivity, in the dry season are greater in the Kimberley and Pilbara bioregions than in the Canning Bioregion (Condie and Dunn, 2006). Furthermore, very substantial mangrove forests are present in nearshore waters along the coast and in the mouths of creeks and rivers of the Kimberley Bioregion and, to a lesser extent, in certain parts of the Pilbara, whereas such forests are not found in the Canning Bioregion. Mangrove forests are typically very productive ecosystems, supporting the abundant suite of benthic invertebrates that constitute the prey of many bottom-dwelling fish species and providing protection from predation for the juveniles of fish species that move further from the shore as they increase in size and/or become mature (Robertson and Duke, 1987; Robertson and Blaber, 1992; Blaber et al., 1995; Alongi, 1998; Mumby et al., 2004;

Manson et al., 2005a; Igulu et al., 2014; Serafy et al., 2015; Sheaves et al., 2015). Indeed, teleosts such as *Siganus fuscescens*, *Arius* spp. and *Saurida undosquamis*, which are abundant as juveniles in mangroves along the Pilbara coast (Blaber et al., 1985), were numerous as adults at Cape Preston and Locker Point in the Pilbara (Table 3.2).

As the species richness and density of fishes in deep and shallow waters in the wet season followed the same overall sequential downward trend between Cape Voltaire in the north and Cape Bossut in the middle of the Canning as in the dry season, the greater productivity in the Kimberley than Canning, and the benefits derived from the mangrove forests found in that bioregion, presumably likewise played a major role in driving that trend. The species richness and density in both deep and shallow waters at the two Kimberley locations were far greater, however, during the wet than dry seasons. It is thus relevant that the amount of nutrients discharged by rivers and creeks into the inshore waters in the Kimberley increases markedly during the wet and warmer season (Condie and Dunn, 2006; McKinnon et al., 2015a) and thus leads to a rise in primary productivity and consequently sequential increases upwards in the trophic levels within the food chain. Furthermore, turbidity was far greater in the two Kimberley locations than at all other locations, particularly during the wet season, and thus, as elsewhere, would have reduced the likelihood of predation (Blaber and Blaber, 1980; Cyrus and Blaber, 1987b).

As species richness in the shallow and particularly deeper waters at Locker Point, and also density in deeper waters, were greater in the dry than wet seasons, it is particularly noteworthy that this location was atypical in that productivity peaked during the dry rather than wet season (Acker and Leptoukh, 2007). Density in shallow water was slightly greater, however, in the wet than dry season.

Species richness in shallow water during the dry season declined between Cape Keraudren and Locker Point, whereas the converse trend was exhibited by those two biotic variables in deep water and by density between Cape Preston and Locker Point. This suggests that, during this season, some species tend to move from shallow to deep water at the more southern locations. It thus appears relevant that water temperature at the most southern locations was greater in the deeper than shallow waters in the dry season, whereas the reverse applied in the wet season (Fig. 3.1a). As species richness and density in both depths in the wet season at Cape Keraudren were far greater than those at each of the neighbouring locations, it appears pertinent that the major cyclone, which crossed the coast at Cape Keraudren three weeks prior to sampling in the wet season, would have led to local mixing of shelf sediments and increases in chlorophyll *a* (McKinnon et al., 2003) and thus to the provision of a rich source of food for fish species. The pronounced peaks in species richness and abundance of fishes at Cape Keraudren during the wet season could thus reflect an immigration of fishes into that productive location from waters to the north and south.

The concave decrease and then increase in species richness over soft substrata with increasing latitude during the dry season along the NWA coast contrasts with the progressive north-south decline in this biotic variable over a similar latitudinal range along the tropical north-eastern Australian (NEA) coast, based on predominantly fishes observed using underwater video in a range of lagoonal and inter-reef habitats at various times of the year (Cappo et al. 2007). The trend observed on the NWA coast in the wet season followed more closely that on the NEA coast in that species richness was likewise greatest at the most northern locations for reasons discussed above.

3.4.2 Relationships between species composition and bioregion

Analyses, using LINKTREE, emphasise that, irrespective of season and water depth, there is a trenchant separation between the compositions of the ichthyofaunas of the Kimberley Bioregion and those of the Canning and Pilbara bioregions. This technique showed that these pronounced inter-regional differences, which reflect, in particular, far higher densities of two species of both leiognathid and carangid and one species of terapontid and mullid at the northern locations, is best explained by the effects of the greater turbidity and tidal ranges of the coastal waters of the Kimberley Bioregion. Leiognathids possess adaptations, such as a bioluminescent system, that would be particularly advantageous for life in these turbid waters (Woodland et al., 2002; Sparks et al., 2005; Borsa et al., 2007). Furthermore, leiognathids and the other above species use mangroves as nursery areas (Robertson and Duke, 1987; Blaber and Milton, 1990; Kimani et al., 1996; Ikejima et al., 2003), which are particularly abundant in the Kimberley Bioregion. The above species are also abundant over soft substrata in turbid inshore waters of northern Australia (Ramm et al., 1990; Blaber et al., 1994a; Blaber et al., 1995; Blaber, 2000) and of Indonesia, Malaysia and Thailand (Pauly and Matosbroto, 1996; Nurhakim, 2003), and thus form part of the species rich shallow turbid-water fish fauna that extends northwards and eastwards from NWA (Blaber, 2000).

3.4.3 Relationships between species composition and season

My analyses also emphasised that, overall, the ichthyofaunal composition over soft substrata along the extensive NWA coast is influenced markedly by season (wet vs dry) and water depth (Figs. 3.3 & 3.4). Indeed, ichthyofaunal composition differed significantly

between seasons at all seven locations and between water depths at all of those locations except Cape Voltaire. The extent of these differences are emphasised by the \bar{R} statistic for both season and depth in two-way crossed ANOSIM tests always exceeding ~ 0.5 at all locations, except in the case of depth at Cape Voltaire and season at Emeriau Point, and being as high as 0.9 to 1.0 for both factors at Hall Point and Cape Preston. The substantial differences between the compositions in each season and in both water depths at all locations except Cape Voltaire and Emeriau Point are also emphasised by the discreteness of the samples for those four groups on the ordination plots for all but the last two locations (Fig. 3.4b,d-g). The samples for the dry and wet seasons at Cape Voltaire and for shallow water in the dry and wet seasons at Emeriau Point, however, also formed distinct groups.

The use of LINKTREE emphasised that greater concentrations of chlorophyll *a*, *i.e.* productivity, and higher rainfall (and thus freshwater discharge) and water temperatures were important environmental variables for explaining the separation of the ichthyofaunal compositions in the wet and dry seasons in the Kimberley Bioregion and particularly at Cape Voltaire. This is presumably related to differences in the extents of the effects on the reproduction and recruitment of the various fish species in the wet and dry seasons in the Kimberley that would be brought about by the very different levels of productivity and temperature. The rise in productivity and temperature in the wet season would enhance the reproduction and growth of many fish species and the invertebrates that constitute their prey (McKinnon et al., 2015c).

The leiognathids, whose far greater densities in the wet than dry season were important for distinguishing between the faunas in those seasons at locations within the

Kimberley, included *Leiognathus splendens*, *L. bindus*, *L. leuciscus*, *L. moretoniensis* and *Secutor insidiator* (Table 3.8). As these schooling teleosts are recruited into waters along the NWA coast during the wet season (Staunton-Smith et al., 1999) and feed on copepods and ostracods early in their life cycle (Woodland et al., 2001), their juveniles would be able to capitalise on the abundant source of planktivorous food that becomes available during that productive season (Blaber and Blaber, 1980; Blaber et al., 1990; Thorrold and McKinnon, 1995; McKinnon et al., 2003; McKinnon et al., 2015a). The large numbers of these small teleosts provide, in turn, a rich source of food for fish species such as *Carangoides malabaricus*, *Terapon theraps*, *Caranx bucculentus*, *Pomadasys maculatus* and *Pseudorhombus arsius*, and would thus account for the marked rise in the densities of those piscivorous species in the wet season (Table 3.8; Blaber et al., 1989). Furthermore, as the mullid *Upeneus sulphureus* and the adults of leiognathid species feed on benthic macroinvertebrates (Platell et al., 1998b; Lukoschek and McCormick, 2001; Hajisamae, 2009), the pronounced increases that occur in their densities during the wet season presumably reflect the increases that have been shown to occur in those types of prey during that season (Ward and Rainer, 1988).

The results of LINKTREE emphasise that, except with deep waters at Emeriau Point, higher water temperatures were important in explaining the marked distinction between the compositions in the wet season in the Canning and Pilbara bioregions from those in the dry season in those bioregions. Thus the marked differences in temperature, of up to 10°C, between those seasons at these regions apparently led to the immigration of some fish species and/or to the emigration of others. The only species that consistently played a role in distinguishing between the ichthyofaunas in the wet and dry seasons in the

Canning and Pilbara bioregions was *Selaroides leptolepis*, which is a schooling planktivore that is recruited into inshore waters during the wet season through the action of wind-driven easterly movements of water (Shuntov, 1971).

LINKTREE also demonstrated that a lower tidal range and greater productivity best explained the differences between the compositions of the Pilbara and Canning bioregions during the dry season. As discussed, this suggests that, particularly during the dry season, the Pilbara Bioregion provides an environment, which, in terms of productivity and other factors, is more beneficial for a range of demersal fish species than the Canning Bioregion immediately to its north. It is thus relevant that nitrates are transported from offshore deeper waters towards the Pilbara coast in the early dry season as a result of a weakening in the poleward flow of the Leeuwin Current (Holloway et al., 1985; Furnas, 2007; Thompson et al., 2011). The results of LINKTREE also emphasised that the unique characteristics of the deep water habitat at Emeriau Point, *i.e.* the presence of substantial amounts of sponges, sea whips and gorgonian corals, were crucial in helping to explain the distinction between the fauna in those waters from those at all other locations.

3.4.4 Relationships between species composition and depth

The results demonstrate that, at all locations except Cape Voltaire, the compositions of the fish faunas in the deep and shallow water sites were conspicuously different, even though the mean depths differed by only 10 to 14 m. This parallels the situation recorded over soft substrata in the Gulf of Carpentaria in tropical northern Australia, where the compositions of the fish faunas changed progressively in successive water depths of 2.9 – 4.2, 5.0 – 10.6 and 15.6 – 21.9 m (Rainer and Munro, 1982; Rainer,

1984). Relatively small differences in water depth have also been shown to be accompanied by changes in ichthyofaunal composition in temperate waters on the south-east and south-west coasts of Australia (Connell and Lincoln-Smith, 1999; Hyndes et al., 1999). Although ichthyofaunal composition tended neither to be related more to water depth than season or *vice versa* across the locations sampled, it was shown to be consistently related more to water depth than to season over soft substrata along the continental slopes of Angola (Bianchi, 1992a) and the west coast of Australia (Williams et al., 2001). The differences between the mean depths in the deep and shallow water sites were far less, however, than the 24 - 460 and 200 - 1,500 m differences in the latter two studies. The lack of a significant difference between the species composition in deep and shallow waters at Cape Voltaire is almost certainly related to the fact that the numerous islands present at this Kimberley location have a disruptive effect on the relationships between ichthyofaunal compositions in different water depths (Fig. 2.1).

The results of SIMPER demonstrated that no species was consistently important in distinguishing between the fish faunas in deep and shallow water depths at more than three locations along the length of the NWA coast. Indeed, the only species that distinguished between the compositions in deep and shallow waters at even three locations were the mullid *Upeneus assymetricus* and the bothid *Pseudorhombus argus*, with the densities of the former consistently greater in deeper than shallow waters at Cape Keraudren, Cape Preston and Locker Point, whereas the reverse was true for the latter species at Cape Bossut, Cape Preston and Locker Point. However, unlike *P. argus*, the densities of its congener *P. arsius* were greater in shallow than deeper waters at Cape Preston. Such 'partitioning' by depth is consistent with the report that the former species

lives more offshore and in water depths of 13 to 60 m and that the latter species is typically found in river mouths and along the coast (Amaoka and Hensley, 2001).

The presence of far greater densities of *Caranx bucculentus* in shallow than deeper waters at Hall Point is consistent with the results of other studies, which showed that this small carangid is also abundant in similar turbid shallow waters elsewhere in northern Australia and, within which it feeds predominantly on small fishes and crustaceans (Rainer and Munro, 1982; Brewer et al., 1989; Ramm et al., 1990; Brewer et al., 1994). The pomacanthid *Chaetodontoplus duboulayi* and chaetodontid *Coradion chrysozonus* are unusual in that they feed extensively on sponges (Allen, 1981; Lieske and Myers, 1994), thus it is not surprising that this angelfish and butterflyfish were particularly important in distinguishing the fauna in the deep water habitat at Emeriau Point, as that habitat was unique among the sampling sites in containing substantial amounts of poriferans. The finding that the lethrinid *Lethrinus genivittatus* and labrid *Choerodon cephalotes* distinguished the faunas in shallow from deep waters at Locker Point can be explained by the fact that seagrass meadows, which are typically used by the juveniles of these species (Fairclough et al., 2008), are abundant in nearshore waters close to Locker Point (Walker and Prince, 1987).

In contrast to the above species, many others are abundant in both deep and shallow waters, which is hardly surprising in view of the relatively small differences in water depth. These include certain leiognathid species, such as *Leiognathus bindus* and *L. equulus*, which are known to spawn in both deep and shallow waters (Staunton-Smith et al., 1999).

In summary, this study emphasises that the species richness, density and composition of fishes over soft substrata in inshore waters along a very extensive tropical coastline vary with latitude and among bioregions. These differences are related to a number of factors, including marked variations in productivity and whether substantial mangrove forests are present and thus provide important nursery areas for fish that subsequently move further from shore. A divisive clustering technique demonstrated that the major difference between the ichthyofaunal compositions of the bioregions/locations along this coast is explained by the presence of a greater tidal range and turbidity in the most northern bioregion. Ichthyofaunal composition is also influenced by factors such as atypical substratum characteristics, e.g. the presence of large amounts of sponges and gorgonian corals. Although species composition was related more to latitude than to either season (wet vs dry) or water depth, the composition at each sampling location was almost invariably strongly related to both of these latter factors. Differences in composition between wet and dry seasons in the most northern of the three bioregions, *i.e.* Kimberley, are associated with the higher water temperatures and greater fluvial discharge and productivity that characterise the monsoonal wet season in that bioregion. Greater water temperatures also help explain the differences between the ichthyofaunal compositions in the wet season in the Canning and Pilbara bioregions from those in the dry season at those bioregions. The species that typified the ichthyofaunas in different bioregions/locations and distinguished between the ichthyofaunas in wet vs dry seasons and deep vs shallow waters have been identified and the ways in which such differences may be related to variations in the timing of recruitment and pattern of movements are discussed. The provision of sound quantitative data on the distributions of fish species and

elucidation of the factors that influence ichthyofaunal composition along the NWA coast, which is already experiencing increases in water temperatures (Lough, 2008; Lough and Hobday, 2011), provides invaluable baseline information for the processes involved in developing marine protected areas and assessing the impact of climate change and nearshore developments on marine resources along this coast.

Chapter 4 Species composition of the fish assemblages over reefs along the tropical coast of north-western Australia is related to latitude, water depth, day vs night and season

4.1 Introduction

The waters along the north-western Australian (NWA) coast contain an extensive series of reefs and span three bioregions, *i.e.* the Kimberley, Canning and Pilbara (Chapters 1, 2; Fig. 2.1 Simpson, 1988; Semeniuk, 1993; Thackway and Cresswell, 1998; Brocx and Semeniuk, 2010; Wilson, 2013). The Kimberley coast in the north is characterised by very high tides and highly seasonal discharge from large rivers, both of which are far greater than along the Pilbara coast in the south (Cresswell and Badcock, 2000; Wilson, 2013). The Canning coast, which is located between that of the Kimberley and Pilbara, is subjected to moderate to high tidal action and contains no major rivers (Fig. 2.1). Rainfall in north-western Australia is very high between mid-spring and late summer and minimal during most of the rest of the year (Lough, 2008; Ng et al., 2015).

Although the reef fish faunas of the tropical NWA coastline have been the subject of few ecological studies, several species lists have been developed for the fish faunas of much of this coast (Allen, 1992; Hutchins, 1995; Allen, 1996; Hutchins, 1996; Morrison and Hutchins, 1997; Hutchins, 1999; Hutchins, 2001b; Hutchins, 2003; Moore et al., 2014). These have been augmented by those reported in Chapters 2 and 3. The paucity of quantitative ecological information on the fish fauna of the extensive reefs found in north-western Australia between 14° and 22°S contrasts starkly with the large amount of quantitative data on fish communities on the Great Barrier Reef at comparable latitudes

on the north-eastern coast of Australia (e.g. Russ, 1984a; Russ, 1984b; Sale, 1991; Meekan and Choat, 1997; Syms and Jones, 2000; Syms and Jones, 2001; Cappo et al., 2007; McCook et al., 2010).

Several studies have compared the diversity, densities and/or compositions of the reef fish faunas in different tropical regions, based on their own data (e.g. Williams, 1983; Roberts et al., 1992; Caley, 1995; Meekan and Choat, 1997; Munday, 2002; DeMartini and Friedlander, 2004; Bouchon-Navaro et al., 2005; Cappo et al., 2007) or on those collated from various studies (e.g. Floeter and Gasparini, 2000; Bellwood and Hughes, 2001; Floeter et al., 2001; Harmelin-Vivien, 2002; Ferreira et al., 2004; Floeter et al., 2004; Connolly et al., 2005; Mellin et al., 2006; Mellin et al., 2010; Kulbicki et al., 2013; Parravicini et al., 2013; Sutcliffe et al., 2014). Most of those studies focused on comparing the diversity and density of the fish faunas on different reefs or have only used presence/absence or broad relative abundance data for species when comparing the community structures of those assemblages (Floeter and Gasparini, 2000; Hutchins, 2001a; Ferreira et al., 2004). The studies of Floeter et al. (2001) and Cappo et al. (2007), which are two of the few to quantitatively examine aspects of community structure of reef fish faunas in regions along an extensive coastline, distinguished faunal groups and related those to characteristics of the physical environment (e.g. gradients of water depth and oceanographic processes).

From the combined results of previous individual studies, it is evident that the community structure of the fish faunas over reefs can vary not only with latitude, but also with water depth (e.g. Russ, 1984a; Friedlander and Parrish, 1998; Holbrook et al., 2002a; Khalaf and Kochzius, 2002b; Brokovich et al., 2008; Pearson and Stevens, 2015), day vs

night (e.g. Galzin, 1987; Newman and Williams, 2001; Rickel and Genin, 2005; Azzurro et al., 2007; Harvey et al., 2012a; Harvey et al., 2012b; Myers et al., 2016) and time of year (e.g. Aburto-Oropeza and Balart, 2001; Chittaro and Sale, 2003; Letourneau et al., 2008; López-Pérez et al., 2013). No study has investigated in an integrated manner, however, the ways in which the species compositions of the fish faunas over reefs vary with water depth, season and day vs night, at intervals along an extensive and continuous tropical coastline that encompasses a wide latitudinal range.

The data in Chapter 2, derived from sampling fishes by trawling over soft substrata and by trapping over reefs in deep and shallow inshore waters along the 1,500 km coastline of tropical NWA, demonstrated that fish assemblages differed markedly between these two habitat types and among the bioregions of that coast and changed progressively with latitude, presumably reflecting, in part, the influence of water temperature. The data produced for dry and wet seasons in both water depths and in deep and shallow water at each location were pooled for that broad overarching study. The trap data for reefs have not been subjected to higher level analyses, involving separate factors, and no attempt has been made to elucidate how the species composition of fishes over reefs along the NWA coast are related to season, water depth and day vs night and how changes in species composition are related to a range of other environmental variables.

This chapter provides quantitative data on the species composition of reef faunas, at intervals, along the approximately 1,500 km coastline of tropical NWA, which, although very remote, contains commercial and recreational fisheries (Fletcher and Santoro, 2015). The results are used to employ, for the first time, an integrated, multivariate statistical

approach to explore the ways in which a number of variables influence the species compositions of the tropical fish faunas of reefs along an extensive and continuous coastline. The sampling regime, which employed traps and thus caught predominantly carnivorous fish, was designed to test the following hypotheses regarding reef fish faunas along this extensive stretch of coastline. 1) The species composition will differ with latitude because, from their reported distributions (e.g. Carpenter and Niem, 1998-2001; Hutchins, 2001a; Hoese et al., 2007), many of the main species expected to be found in the study area extend to varying degrees southwards into tropical NWA and the coastline encompasses three bioregions that vary markedly in their hydrological characteristics. 2) Because of the effects of extremes in climatic conditions at different times of the year, the composition will differ between wet and dry seasons. 3) The composition of fishes will also vary with water depth and day *vs* night. Emphasis will be placed on elucidating which of the above variables has the greatest influence.

4.2 Materials and Methods

4.2.1 Sampling regime and environmental data

Full details of the complete regime for collection of environmental data and trapping fishes over reefs along the NWA coast are provided in Chapter 2. As outlined in Table 2.1, reefs in deep and shallow waters at each of the seven sampling locations along the tropical NWA coast (Fig. 2.1) were sampled during both day and night in the dry season of 2000 and 2001 and in the wet season of 2002. For the convenience of the reader, the numbers of replicates for each year, depth and day or night combination have been extracted from Table 2.1 and shown below in Table 4.1.

Note that the data from deep water at Cape Keraudren (Canning Bioregion) were not included in analyses because, in contrast to the situation with shallow waters, the reefs in these waters were sparse. The data for shallow water at Cape Keraudren were thus also not included in analyses because, unlike the situation at other locations, comparable data were not available for both water depths. Some comparisons have been made, however, between the abundant species over reefs in shallow waters at Cape Keraudren and those at the other six locations.

4.2.2 Statistical analyses

Three-way PERMANOVA was used to determine whether water temperature and water clarity differed between locations, seasons and water depths. The number of each species caught in each group of five or 10 traps set in both water depths on each sampling occasion were pooled and expressed as an average catch rate for the traps in that group, *i.e.* number of fish per trap per 5 h. Each group of traps set on any single occasion in a location was regarded as a replicate. Thus, for each of the six locations on each sampling occasion, there were four or six replicates for both deeper and shallow water during both day and night (Table 4.1). Note that, in studies carried out previously on fish trapping in NWA, neither the catch rates nor the species compositions of fishes differed within the range of 4–10 h soak time employed during the present study (Whitelaw et al., 1991).

Examination of the values for these variables demonstrated that, prior to statistical analysis, water temperature and water clarity required square-root transformation and catch rates of each species a fourth-root transformation, to meet the

test assumption of homogenous dispersion (variance, here) among *a priori* groups (Anderson, 2001a).

Table 4.1. Years (seasons), time (daylight or night), duration of each set, replication and frequency of sampling in both deep ($\bar{x} = 22$ m) and shallow ($\bar{x} = 12$ m) waters at each of the six sampling locations in north-western Australia in 2000, 2001 and 2002.

Year	Time of sampling	Set duration	Number of replicates per day or night	Number of sampling days or nights	Total number of replicates
2000 (Dry)	Day	4 h	2 sets of 10 traps	3	6
	Night	10 h	2 sets of 5 traps	2 or 3	4-6
2001 (Dry)	Day	4 h	2 set of 10 traps	3	6
	Night	10 h	2 sets of 5 traps	2 or 3	4-6
2002 (Wet)	Day	10 h	2 sets of 5 traps	3	6
	Night	10 h	2 sets of 5 traps	2 or 3	4-6

The following statistical analyses of the fish data derived from samples collected with fish traps were used to ascertain the extent of any significant differences in the species compositions of the ichthyofauna between locations, years (seasons), water depth (deep vs shallow) and day vs night.

The transformed catch rate for each species in each group of traps in each water depth during both the day and night and in each of the three years at each of the six main sampling locations were used to construct a Bray-Curtis similarity matrix. This matrix was subjected to PERMANOVA (Anderson, 2001a; Anderson et al., 2008), with the focus being on determining whether there were significant interactions between the above four factors. The interpretation of these formal test results followed the rationale

set out in Chapter 3 section 3.2.3. The data were considered to represent a four-way fully-crossed design that comprised location (6 levels) \times year (3 levels, 2000, 2001 and 2002) \times water depth (2 levels, *i.e.* deep and shallow) \times diel (2 levels, *i.e.* day and night), with each factor fixed.

The same procedure above was then repeated to produce a second similarity matrix using the mean transformed catch rate for each group of replicates, rather than the catch rate for the replicates themselves. The second matrix was used for cluster analyses and, for visual clarity, also for the non-metric multidimensional scaling (nMDS) ordinations which displayed the data for all variables, *i.e.* location, water depth, year (season) and day *vs* night and for those for the night and day-time samples in each water depth \times season combination. nMDS ordination was used to interpret interactions (or lack of interactions) between factors that resulted from the PERMANOVA tests. The first matrix was used for the two other ordinations, which explore the influence of water depth, season and time of day at each location individually, and all ANOSIM and SIMPER tests (Clarke and Warwick, 2001). When the stress level of a two dimensional ordination approached 0.2, the data were plotted as a three dimensional solution (Clarke and Warwick, 2001). One-way and two-way crossed ANOSIM tests were employed to explore whether the compositions of the fish faunas differed significantly among locations, deep *vs* shallow waters, dry *vs* wet seasons and day *vs* night. For each ANOSIM test, the null hypothesis that there were no significant differences among groups was rejected when the significance level (P) was $< 5.0\%$. The extent of any significant differences between *a priori* groups was determined from the R -statistic value (Clarke and Green, 1988; Clarke, 1993), which can range from 1, *i.e.* all samples

within each of the groups are more similar to each other than to any of the samples from other groups, to approximately 0, when average similarities within and between groups are the same. SIMPER was used to identify which species best typify faunal assemblages and contribute most to any differences between samples.

The following application of the Linkage Tree (LINKTREE; Clarke et al., 2008) routine was used to elucidate which thresholds of the seven environmental variables (water temperature and depth, mean spring tidal range, depth of water clarity, chlorophyll *a*, rainfall and distance to shore), were indicative of the successive separation of sites into subgroups from a constrained divisive cluster analysis. As described in Chapter 3, LINKTREE is a non-metric modification of the multivariate regression tree approach of De'Ath (2002). Thus, a binary “linkage tree” is constructed that reflects how samples from an underlying (biotic) resemblance matrix are most naturally split into successively smaller groups, based on maximising the ANOSIM *R*-statistic (Clarke, 1993) for a binary split of each group, allowable divisions being constrained to those for which at least one of the environmental variables takes larger values for all samples in one of the subgroups than those in the other subgroup. At each branching node of the tree, quantitative thresholds are therefore provided of the variables from explanatory data, e.g. environmental values that mirror the division in the biological samples. In theory, the terminal group to which any new multivariate sample could be assigned is thus determined by ascertaining whether its values for the variables specified at each successive node of the tree are less than or greater than the given thresholds.

The LINKTREE procedure was applied to the Bray-Curtis similarity matrix calculated from the data averaged over replicates, the explanatory variables being the untransformed measurements for the seven environmental variables, also averaged for each combination of location, season, depth and day vs night. A Similarity Profile permutation test (SIMPROF; Clarke et al., 2008) was used in conjunction with LINKTREE to provide stopping rules for the successive subdivisions at those nodes at which no significant multivariate structure was considered to be present among the remaining biological samples, using $P > 0.05$ as the significance criterion. The LINKTREE and SIMPROF routines thus produce a constrained divisive clustering in which terminal nodes comprise groups of sites with high internal similarity, together with a sequence of inequalities on the environmental variables that 'explain' each biotic group. It is recognised that no inference of causality is possible with such an observational study.

All of the preceding analyses were carried out using the PRIMER v6 multivariate statistics package (Clarke and Gorley, 2006), together with the PERMANOVA+ add-on module where appropriate (Anderson et al., 2008).

4.3 Results

4.3.1 Environmental variables

PERMANOVA demonstrated that water temperatures over reefs differed significantly between locations, years (comprising the dry seasons of 2000 and 2001 and wet season of 2002), locations and water depths and all two and three-way interactions were significant (Table 4.2). At each location, the mean water temperatures in both deep

and shallow water were far greater during the wet than dry seasons (Fig. 4.1a,b). In the wet season, the mean water temperatures in both deep and shallow waters declined progressively in a southerly direction from their maxima at the four most northern locations to their minima at Locker Point, the most southern location (Fig. 4.1a,b). During the dry season, mean water temperatures in both depths declined southwards from their maxima at the two most northern locations, with the trend more pronounced in 2000 than 2001 (Fig. 4.1a,b).

Mean Secchi disc depth differed significantly among locations, years and depths and there was a significant interaction between location and year (Table 4.2). Water clarity was greater in deep than shallow water (Fig. 4.1c). Mean water clarity in the dry seasons of 2000 and 2001 and wet season of 2002 rose from their lowest levels at Cape Voltaire and Hall Point in the north to Emeriau Point, after which it declined to lower levels at Cape Bossut, and ultimately rose to high levels at Locker Point, the most southern sampling location. The highest levels recorded at Cape Preston in the dry season of 2000 are clearly the main contribution to the significant interaction between location and year (Fig. 4.1d).

Mean chlorophyll *a* values at each location were almost invariably greater in the wet season than in either of the two dry seasons (Fig. 4.1e). The lowest chlorophyll *a* concentrations were recorded in the dry season at Cape Voltaire and Cape Bossut and were highest at Locker Point in each of the three years.

Table 4.2. Mean squares (MS), *F* values and significance levels (*P*) for PERMANOVAs of water temperature and water clarity in deep and shallow waters during the day at 6 locations along the north-western Australian coast in 2000 and 2001 (dry seasons) and 2002 (wet season). df, degrees of freedom.

	df	Water temperature			Water clarity		
		MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
Location (L)	5	74.315	926.3	<0.001	25.2	111.4	<0.001
Year (Y)	2	6.728	8327.3	<0.001	3.8	16.6	<0.001
Depth (D)	1	0.005	6.7	0.014	3.0	13.3	0.002
L × Y	10	0.063	78.4	<0.001	1.3	5.7	<0.001
L × D	5	0.002	2.5	0.030	0.4	2.0	0.095
Y × D	2	0.053	66.2	<0.001	0.3	1.1	0.354
L × Y × D	10	0.012	14.6	<0.001	0.3	1.5	0.145
Residual	108	0.001	926.3		0.2		

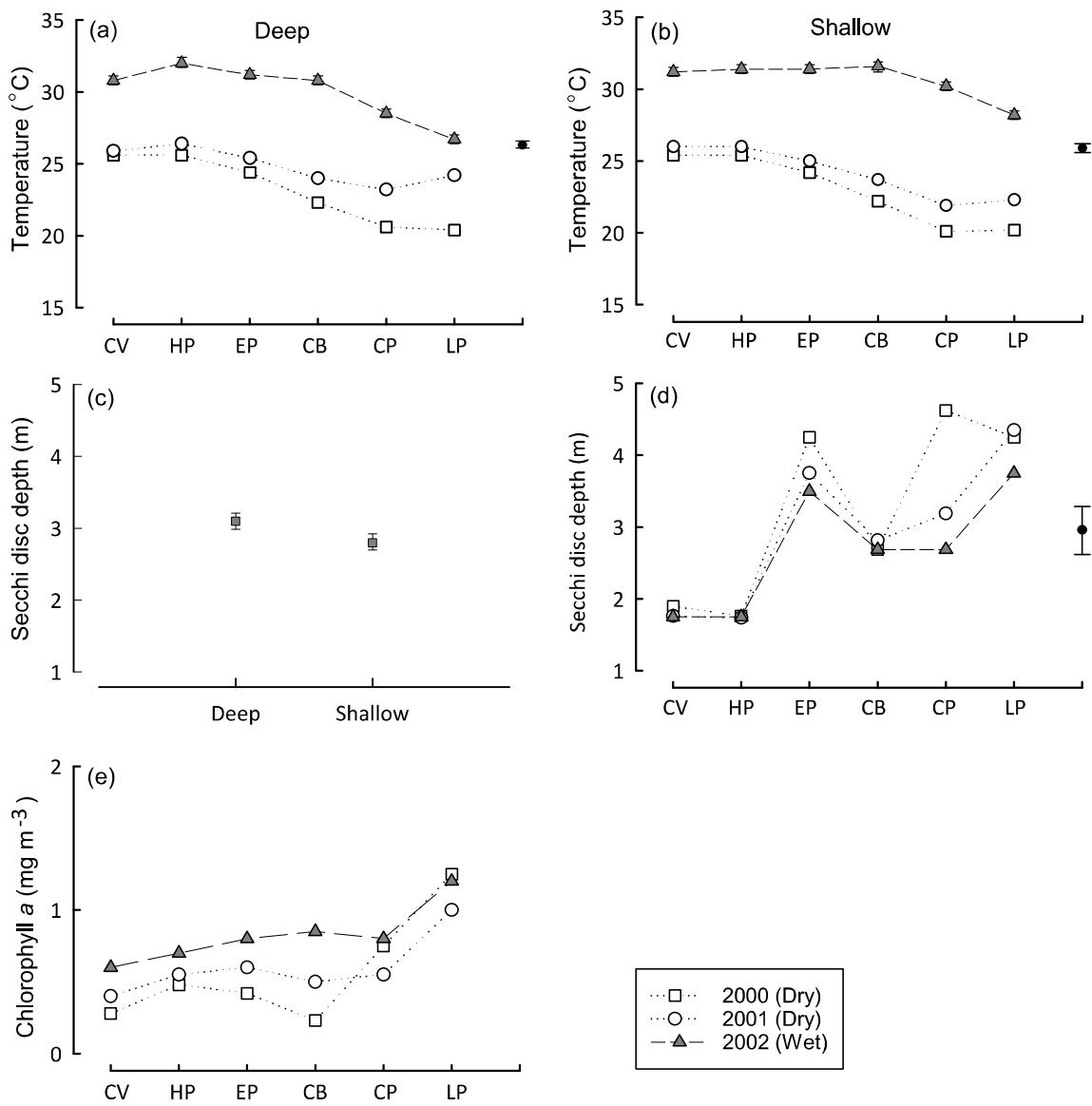


Fig. 4.1. Mean values for water temperature in a) deep water and b) shallow water and for d) Secchi disc depth (water clarity) and e) chlorophyll *a* at the six sampling locations along the north-western Australian coast in the dry seasons of 2000 and 2001 and wet season of 2002. c) Mean Secchi disc depth $\pm 95\%$ confidence intervals in deep and shallow waters. Overall mean and indicative 95% confidence intervals are presented in a), b) and d). All values have been back transformed.

4.3.2 Dominant species and families

Fish trapping in deep and shallow waters in each of the six main sampling locations in NWA during the day and night in 2000, 2001 and 2002 yielded a total of 23, 377 individuals of teleosts (Table 4.3). The samples contained 119 species of teleost, representing 58 genera and 32 families. Each of the 13 species of elasmobranch, representing five families (Table 4.3), was caught only very occasionally. The Epinephelidae, Lutjanidae, Lethrinidae and Carangidae were represented by 16, 14, 9 and 9 species, respectively (Table 4.4), and collectively contributed 88.9% to the total catch.

The north-western Australian endemic Blue-spotted Emperor *Lethrinus punctulatus* was the most abundant species and contributed 34.8% to the overall catch. The Stripey Snapper *Lutjanus carponotatus* and the Grass Emperor *Lethrinus laticaudis* were the next most abundant species, with respective contributions of 20.8 and 11.6% (Table 4.3). The above three species thus collectively accounted for more than 67.0% of the fish taken in traps. The next most abundant species were the Indonesian Snapper *Lutjanus bitaeniatus*, the Golden Trevally *Gnathanodon speciosus* and the Starry Triggerfish *Abalistes stellatus* and were the only other species to contribute more than 2.0% to the total catch (Table 4.3).

The contributions of *Lethrinus punctulatus*, *L. carponotatus* and *L. laticaudis* to the catches varied among locations and between water depths. Thus, although *Lethrinus punctulatus* contributed $\geq 20.7\%$ to the catches in deep and shallow waters at the four most southern locations, it was either not recorded or contributed $\leq 5.1\%$ to those in deep and shallow waters at the two most northern locations, i.e. Cape Voltaire and Hall Point. In contrast, the contributions made by *L. carponotatus* and *L. laticaudis* to

the catches in both water depths were greatest at the three and two most northern locations, respectively (Table 4.3). The Golden Snapper *Lutjanus johnii* and *L. bitaeniatus* were caught only at Cape Voltaire and Hall Point, whereas *A. stellatus*, the Purple Threadfin Bream *Pentapodus emeryii* and the Spangled Emperor *Lethrinus nebulosus* were not caught at either of these locations, but were abundant in samples from the four more southern locations (Table 4.3). The data for shallow waters at Cape Keraudren, which were not included in the multivariate analysis (see Materials and Methods for rationale), showed that *Lethrinus punctulatus*, *L. carponotatus* and *L. laticaudis* were the most abundant species at this Pilbara location, with contributions of 69.5, 9.5 and 5.6%, respectively.

At the two most northern locations, *L. bitaeniatus* contributed substantially to the catches in deep waters, *i.e.* 19.2 and 49.4%, but was either absent or made only a small contribution to those in shallow waters. Furthermore, *A. stellatus* was always relatively more abundant in catches from deep than shallow water and sometimes markedly so.

Table 4.3 List of fish species that contributed $\geq 0.3\%$ of the total catch taken by trapping over reefs in deep (D) and shallow (S) waters at six locations in north-western Australia during the day and night between 2000 and 2002. The ranking by abundance and percentage contribution of each species overall and the percentage contributions of each species to the catches in each depth at each location are provided.

Family	Species	Rank	n	(%)	Kimberley Bioregion				Canning Bioregion				Pilbara Bioregion			
					Overall		Cape Voltaire		Hall Point		Emeriau Point		Cape Bossut		Cape Preston	
					D	S	D	%	D	%	D	%	D	%	D	S
Lethrinidae	<i>Lethrinus punctulatus</i>	1	8143	34.8	1.4	-	-	5.1	20.7	41.9	52.1	57.2	45.7	47.5	31.1	51.8
Lutjanidae	<i>Lutjanus carponotatus</i>	2	4858	20.8	19.3	31.3	24.7	50.4	35.8	15.6	20.5	11.9	9.0	14.9	2.7	11.1
Lethrinidae	<i>Lethrinus laticaudis</i>	3	2701	11.6	16.2	23.6	15.4	25.0	25.5	7.5	2.0	6.9	4.3	9.2	-	11.5
Lutjanidae	<i>Lutjanus bitaeniatus</i>	4	927	4.0	19.2	1.9	49.4	-	-	-	-	-	-	-	-	-
Carangidae	<i>Gnathanodon speciosus</i>	5	707	3.0	0.1	1.4	-	3.0	1.4	15.1	4.6	2.8	0.2	-	1.0	0.6
Balistidae	<i>Abalistes stellatus</i>	6	465	2.0	-	-	-	-	0.8	0.6	5.1	1.2	8.3	1.7	1.4	0.2
Lutjanidae	<i>Lutjanus johnii</i>	7	420	1.8	22.6	15.4	3.9	0.3	-	-	-	-	-	-	-	-
Siganidae	<i>Siganus fuscescens</i>	8	382	1.6	0.1	1.5	-	0.2	1.4	1.5	0.9	6.0	0.5	2.1	0.4	1.5
Lethrinidae	<i>Lethrinus genivittatus</i>	9	350	1.5	-	-	-	-	-	-	3.0	1.3	2.0	0.5	9.3	2.3
Lutjanidae	<i>Lutjanus lemniscatus</i>	10	343	1.5	4.4	7.0	0.5	2.5	1.9	1.0	0.0	0.3	2.2	2.0	0.7	0.9
Nemipteridae	<i>Pentapodus emeryii</i>	11	333	1.4	-	-	-	-	1.6	2.1	2.5	1.3	1.6	-	5.1	0.1
Lethrinidae	<i>Lethrinus nebulosus</i>	12	322	1.4	-	-	-	-	0.1	0.7	-	0.1	4.4	0.7	13.8	1.9
Labridae	<i>Choerodon cyanodus</i>	13	282	1.2	0.2	1.2	-	2.3	0.8	5.4	0.1	1.6	0.2	1.5	-	1.0
Lethrinidae	<i>Lethrinus atkinsoni</i>	14	278	1.2	-	-	-	-	-	-	-	-	4.0	-	15.8	0.1
Lutjanidae	<i>Lutjanus sebae</i>	15	246	1.1	-	-	-	-	0.8	0.2	1.0	1.7	5.6	0.1	1.1	0.3
Haemulidae	<i>Diagramma labiosum</i>	16	233	1.0	1.5	1.6	2.4	2.9	1.4	0.1	0.9	0.4	1.3	0.2	0.2	0.1
Epinephelidae	<i>Epinephelus coioides</i>	17	230	1.0	4.5	5.8	1.4	2.0	0.1	0.1	0.3	0.8	-	1.5	-	1.7
Lutjanidae	<i>Lutjanus russelli</i>	18	220	0.9	-	0.1	0.1	-	-	-	0.6	0.1	1.1	6.1	1.8	3.5
Epinephelidae	<i>Epinephelus bilobatus</i>	19	182	0.8	-	-	-	-	0.4	2.7	0.1	0.2	1.8	1.0	2.1	1.5
Lethrinidae	<i>Lethrinus lentjan</i>	20	180	0.8	0.6	1.1	-	1.9	0.3	0.6	-	0.2	0.8	5.2	-	0.7
Lutjanidae	<i>Lutjanus malabaricus</i>	21	104	0.4	2.8	0.5	-	-	0.2	-	-	0.2	0.1	1.6	-	2.1
Glaukosomatidae	<i>Glaukosoma magnificum</i>	22	103	0.4	-	-	0.4	-	1.0	0.2	0.8	0.7	-	-	-	0.4
Epinephelidae	<i>Plectropomus maculatus</i>	23	86	0.4	0.4	1.1	0.1	0.2	0.6	0.1	0.8	0.0	0.4	0.2	0.1	0.1
Carangidae	<i>Carangooides fulvoguttatus</i>	24	85	0.4	-	-	-	-	1.0	0.6	0.1	0.9	-	-	0.4	-
Monacanthidae	<i>Monacanthus chinensis</i>	25	73	0.3	-	-	0.2	0.4	0.0	0.4	0.6	0.5	-	0.7	0.4	0.2
Total number of fish			23377		1009	857	1451	1329	3688	2167	3627	2962	1854	1639	1287	1507
Total number of species			119		30	32	23	33	51	40	46	46	46	32	50	52

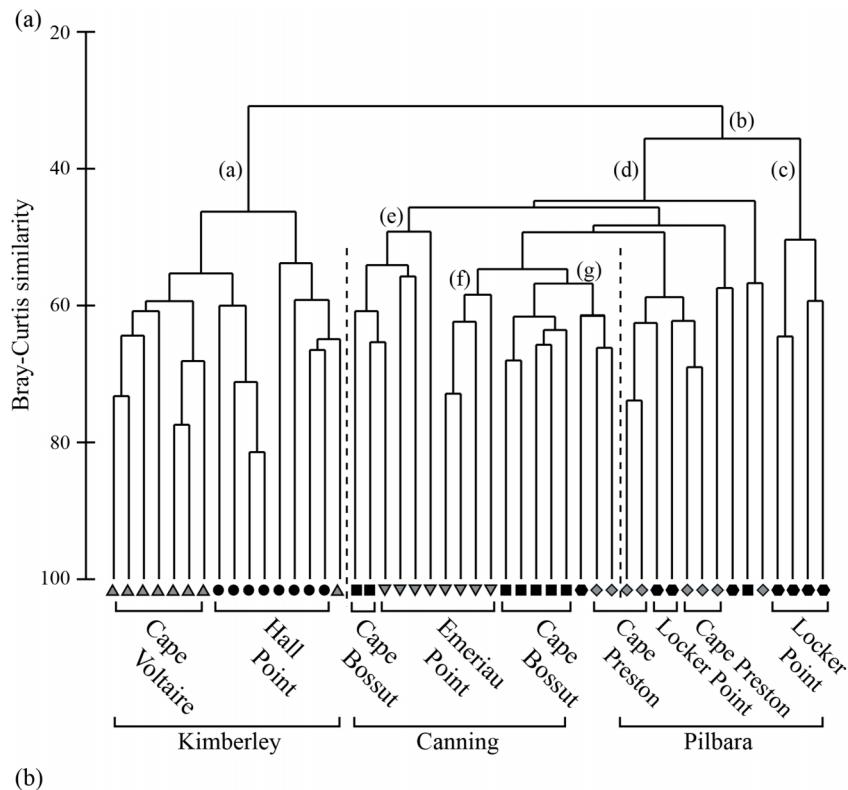
Table 4.4. List of fish families and their common names and the number of species of each family recorded in traps in north-western Australia between 2000 and 2002.

Family	Common name	No. of species
Epinephelidae	Groupers	16
Lutjanidae	Snappers	14
Lethrinidae	Emperors	9
Carangidae	Jacks	9
Carcharhinidae	Requiem sharks	7
Chaetodontidae	Butterflyfishes	7
Haemulidae	Grunts	6
Labridae	Wrasses	6
Mullidae	Goatfishes	5
Nemipteridae	Butterfly breams	5
Pomacanthidae	Angelfishes	4
Ephippidae	Batfishes	3
Monacanthidae	Leatherjackets	3
Siganidae	Rabbitfishes	3
Tetraodontidae	Toadfishes	3
Acanthuridae	Surgeonfishes	2
Balistidae	Triggerfishes	2
Batrachoididae	Frogfishes	2
Dasyatidae	Stingrays	2
Diodontidae	Porcupinefishes	2
Echeneidae	Diskfishes	2
Hemiscyllidae	Long-tail carpetsharks	2
Ostraciidae	Cowfishes	2
Pomacentridae	Damselfishes	2
Sphyraenidae	Barracudas	2
Ariidae	Fork tailed catfishes	1
Caesionidae	Fusiliers	1
Ginglymostomatidae	Nurse sharks	1
Glaucosomatidae	Pearl perches	1
Holocentridae	Squirrelfishes	1
Latidae	Giant perches	1
Muraenidae	Moray eels	1
Orectolobidae	Carpetsharks	1
Platycephalidae	Flatheads	1
Scaridae	Parrotfishes	1
Sciaenidae	Croakers	1
Scorpaenidae	Scorpionfishes	1
Sparidae	Seabreams	1

4.3.3 Relationships between species composition and season, water depth and day vs night

When the mean catch rates of fishes over reefs in deep and shallow waters during the day and night and in dry and wet seasons were subjected to classification, one of the two first subdivisions (a) on the dendrogram comprised two clusters that consisted exclusively of all samples from Cape Voltaire and Hall Point in the Kimberley Bioregion (Fig. 4.2a). Furthermore, within that subdivision, all but one of the samples from Cape Voltaire formed a cluster that was discrete from the two clusters comprising samples from Hall Point. The second subdivision (b) on the dendrogram contained all samples from locations in the Canning and Pilbara bioregions and a small cluster (c) with four of the samples from Locker Point and a large cluster (d) containing the other samples from Locker Point and all of those from Cape Preston, Cape Bossut and Emeriau Point (Fig. 4.2a). Within the subdivision (d), two clusters comprised exclusively or almost exclusively samples from either Emeriau Point (e,f) or Cape Bossut (g). All but three of the samples from locations in the Pilbara Bioregion formed clusters to the right of the second dotted line on the dendrogram and all samples between the two dotted lines came predominantly from the Canning Bioregion (Fig. 4.2a).

When these same data were subjected to nMDS ordination, the samples showed a very marked tendency to form groups on the basis of latitudinal position and therefore also of bioregion (Fig. 4.2b). Thus, samples from the two most northern locations, *i.e.* Cape Voltaire and Hall Point (Kimberley Bioregion) formed a group in the upper part of the plot and above those from the two most southern latitudes, *i.e.* Cape Preston and Locker Point



(b)

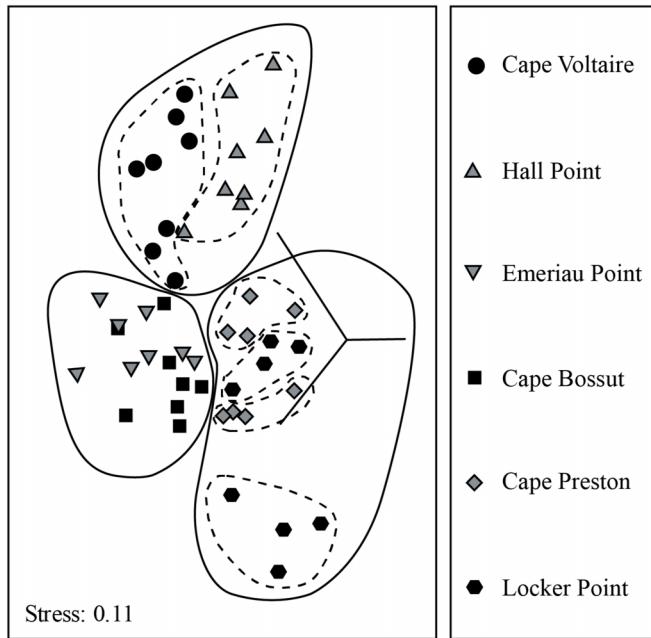


Figure 4.2. Results of (a) cluster analysis and (b) two-dimensional nMDS ordination of mean catch rates of each fish species in samples collected over reefs at each of the six locations in deep and shallow waters during the day and night between 2000 and 2002.

(Pilbara Bioregion) on the right and those from the two intermediate locations, *i.e.* Emeriau Point and Cape Bossut (Canning Bioregion) on the left (Fig. 4.2b).

While species composition was shown by PERMANOVA to be significantly related to location, year, depth and day *vs* night, all two-way interactions were significant except for that between depth and day *vs* night (Table 4.5). There were also significant three-way interactions for location and year and both depth and day *vs* night and for location, depth and day *vs* night.

Table 4.5. Mean squares (MS), F values and significance levels (*P*) for location \times Year \times depth \times diel (day *vs* night) PERMANOVA for the various fish species collected over reefs by trapping at six locations along the tropical north-western Australian coast in deep and shallow waters during the dry season of 2000 and 2001 and wet season of 2002. df = degrees of freedom.

Source	df	MS	F	<i>P</i>
Location (L)	5	36558	27.7	< 0.001
Year (Y)	2	9437	7.1	< 0.001
Depth (D)	1	24415	18.5	< 0.001
Diel (N)	1	24648	18.7	< 0.001
L \times Y	10	3182	2.4	< 0.001
L \times D	5	9114	6.9	< 0.001
L \times N	5	3255	2.5	< 0.001
Y \times D	2	2431	1.8	0.009
Y \times N	2	2208	1.7	0.019
D \times N	1	572	0.4	0.937
L \times Y \times D	10	2307	1.7	0.001
L \times Y \times N	10	1635	1.2	0.056
L \times D \times N	5	1972	1.5	0.011
Y \times D \times N	2	1042	0.8	0.768
L \times Y \times D \times N	10	1195	0.9	0.741
Residuals	239	1321		

One-way ANOSIM showed that, overall, the species compositions differed significantly among locations and between water depths, seasons and day vs night (all $P = 0.1\%$). However, the Global R statistic was far greater for location (0.462) than for day vs night (0.100), depth (0.093) and season (0.079), which were all similarly low. Pair-wise ANOSIM comparisons showed that the species composition of the fish fauna at each location differed significantly from that at each other location (all $P = 0.1\%$), with R -statistic values ranging from 0.144 for Cape Bossut vs Emeriau Point to 0.788 for Cape Voltaire vs Cape Bossut (Table 4.6). In general, the R -statistic values for comparisons between the faunas in adjacent locations were far less than those between widely-separated locations.

Table 4.6. Global significance levels (%) and R -statistic values (brackets) for pairwise comparisons in a one-way ANOSIM test carried out on data for fish samples collected in fish traps over reefs between 2000 and 2002.

Location	Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Preston
Hall Point	0.1 (0.224)				
Emeriau Point	0.1 (0.592)	0.1 (0.403)			
Cape Bossut	0.1 (0.788)	0.1 (0.657)	0.1 (0.144)		
Cape Preston	0.1 (0.776)	0.1 (0.707)	0.1 (0.203)	0.1 (0.226)	
Locker Point	0.1 (0.719)	0.1 (0.623)	0.1 (0.339)	0.1 (0.297)	0.1 (0.199)

SIMPER demonstrated that *L. carponotatus* was an important typifying species at all six locations and that the same was true for *L. laticaudis* at all but the most southern location, *i.e.* Locker Point, and that *Lethrinus punctulatus* was an important typifying species at the four most southern locations (Table 4.7). The fauna at Cape Voltaire in the north was distinguished from those at all other locations by greater catch rates and frequencies of occurrence of *L. johnii* and the Darktail Snapper *Lutjanus lemniscatus*, whereas that at Locker Point in the south was distinguished from that at each other location by a greater catch rate and frequency of occurrence of *L. nebulosus* (Table 4.7). The fauna at Hall Point was distinguished from those at all other locations by relatively greater contributions of *L. bitaeniatus* and the Painted Sweetlip *Diagramma labiosum*. The fish fauna at both Cape Preston and Cape Bossut were distinguished from that at each other location by a greater contribution of *A. stellatus*, and that at Cape Bossut was distinguished from that at Cape Preston by greater contributions of *Lethrinus punctulatus*, *L. carponotatus* and *P. emeryii*. *Lethrinus punctulatus* was one of the main species that distinguished the fauna at each location in the Canning and Pilbara bioregions from that at each location in the Kimberley (Table 4.7). The fauna in shallow water at Cape Keraudren was also typified by the same three main species as those at the other six main locations, *i.e.* *L. carponotatus*, *L. laticaudis* and *Lethrinus punctulatus*.

Since the Global *R*-statistic value was far greater for location than for any of the other three variables, attention was next focused on comparing the compositions of the fish faunas among the six locations in the context of each water depth × season

Table 4.7. Species identified by SIMPER as those which typified the fish assemblages of reefs at the six locations (shaded boxes) and distinguished between the fish assemblages at each pair of those locations (non-shaded boxes). Samples collected in each diel period (day and night), depth and season have been pooled in this analysis. Species that distinguish the fauna at one location from another are indicated by the initials of that location.

Location	Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Preston	Locker Point
Cape Voltaire	<i>Lutjanus carponotatus</i> <i>Lutjanus johnii</i> <i>Lethrinus laticaudis</i>					
Hall Point	<i>Lutjanus btaeniatus</i> ^{HP} <i>Lutjanus johnii</i> ^{CV} <i>Lutjanus carponotatus</i> ^{HP} <i>Lutjanus lemniscatus</i> ^{CV}	<i>Lutjanus carponotatus</i> <i>Lethrinus laticaudis</i> <i>Diagramma labiosum</i>				
Emeriau Point	<i>Lethrinus punctulatus</i> ^{EP} <i>Lutjanus johnii</i> ^{CV} <i>Lethrinus laticaudis</i> ^{EP} <i>Lutjanus carponotatus</i> ^{EP} <i>Epinephelus coioides</i> ^{CV} <i>Lutjanus lemniscatus</i> ^{CV}	<i>Lethrinus punctulatus</i> ^{EP} <i>Lutjanus btaeniatus</i> ^{HP} <i>Diagramma labiosum</i> ^{HP}	<i>Lutjanus carponotatus</i> <i>Lethrinus laticaudis</i> <i>Lethrinus punctulatus</i>			
Cape Bossut	<i>Lethrinus punctulatus</i> ^{CB} <i>Lutjanus johnii</i> ^{CV} <i>Abalistes stellatus</i> ^{CB} <i>Lutjanus carponotatus</i> ^{CB} <i>Lutjanus lemniscatus</i> ^{CV} <i>Pentapodus emeryii</i> ^{CB}	<i>Lethrinus punctulatus</i> ^{CB} <i>Lutjanus btaeniatus</i> ^{HP} <i>Abalistes stellatus</i> ^{CB} <i>Pentapodus emeryii</i> ^{CB}	<i>Lethrinus punctulatus</i> ^{CB} <i>Abalistes stellatus</i> ^{CB} <i>Pentapodus emeryii</i> ^{CB}	<i>Lutjanus carponotatus</i> <i>Lethrinus punctulatus</i> <i>Lethrinus laticaudis</i>		
Cape Preston	<i>Lethrinus punctulatus</i> ^{CP} <i>Lutjanus johnii</i> ^{CV} <i>Abalistes stellatus</i> ^{CP} <i>Lutjanus lemniscatus</i> ^{CV} <i>Epinephelus coioides</i> ^{CV}	<i>Lethrinus punctulatus</i> ^{CP} <i>Lutjanus btaeniatus</i> ^{HP} <i>Abalistes stellatus</i> ^{CP} <i>Lutjanus carponotatus</i> ^{EP}	<i>Lethrinus laticaudis</i> ^{CP} <i>Abalistes stellatus</i> ^{CP} <i>Lutjanus carponotatus</i> ^{CB} <i>Pentapodus emeryii</i> ^{CB}	<i>Lethrinus punctulatus</i> ^{CB} <i>Abalistes stellatus</i> ^{CB} <i>Lutjanus carponotatus</i> ^{CB} <i>Pentapodus emeryii</i> ^{CB}	<i>Lethrinus punctulatus</i> <i>Lutjanus carponotatus</i> <i>Lethrinus laticaudis</i> <i>Abalistes stellatus</i>	
Locker Point	<i>Lethrinus punctulatus</i> ^{LP} <i>Lutjanus johnii</i> ^{CV} <i>Lethrinus laticaudis</i> ^{CV} <i>Lethrinus nebulosus</i> ^{LP} <i>Lutjanus lemniscatus</i> ^{CV} <i>Lutjanus carponotatus</i> ^{CV} <i>Epinephelus coioides</i> ^{CV}	<i>Lethrinus punctulatus</i> ^{LP} <i>Lethrinus laticaudis</i> ^{HP} <i>Lutjanus carponotatus</i> ^{HP} <i>Lutjanus btaeniatus</i> ^{HP} <i>Lethrinus nebulosus</i> ^{LP} <i>Diagramma labiosum</i> ^{HP}	<i>Lethrinus laticaudis</i> ^{EP} <i>Lutjanus carponotatus</i> ^{EP} <i>Lethrinus nebulosus</i> ^{LP}	<i>Lethrinus punctulatus</i> ^{CB} <i>Lutjanus carponotatus</i> ^{CB} <i>Lethrinus laticaudis</i> ^{CB} <i>Lethrinus nebulosus</i> ^{LP} <i>Abalistes stellatus</i> ^{CB} <i>Pentapodus emeryii</i> ^{CB}	<i>Lethrinus laticaudis</i> ^{CP} <i>Abalistes stellatus</i> ^{CP} <i>Lethrinus nebulosus</i> ^{LP} <i>Lutjanus carponotatus</i> ^{CP}	<i>Lethrinus punctulatus</i> <i>Lutjanus carponotatus</i> <i>Lethrinus nebulosus</i>

combination (Fig. 4.3). The data for day and night, which overall were marginally more influential than those for either depth or season, were kept separate. On the ordination plots for deep water \times dry season and for deep water \times wet season, the day and night samples for each location were closely apposed and progressed downwards from those for Cape Voltaire and Hall Point at the top to those for Locker Point in the south (Fig. 4.3a,c). The samples for the six locations in both the shallow water \times dry season and shallow water \times wet season combinations followed the same trends, but with those for day at each location lying to the left of that for night (Fig. 4.3b,d).

Two-way crossed ANOSIM, using replicates for deep water during both dry and wet seasons, demonstrated that species composition differed significantly among locations and between day and night (all $P = 0.1\%$). Global R -statistic values for location during both dry and wet seasons, *i.e.* 0.669 and 0.881, respectively, were far greater than for day vs night, *i.e.* 0.335 and 0.420, respectively. Pair-wise tests showed that the species compositions at each location differed significantly from that at each other location, with R statistic values ranging from 0.225 to 1.000 during the dry season and from 0.486 to 1.000 during the wet season. The R -statistic values for these comparisons followed the same trends as seen in Table 4.6, *i.e.* they were far less for comparisons between faunas in adjacent locations than between those in widely-separated locations.

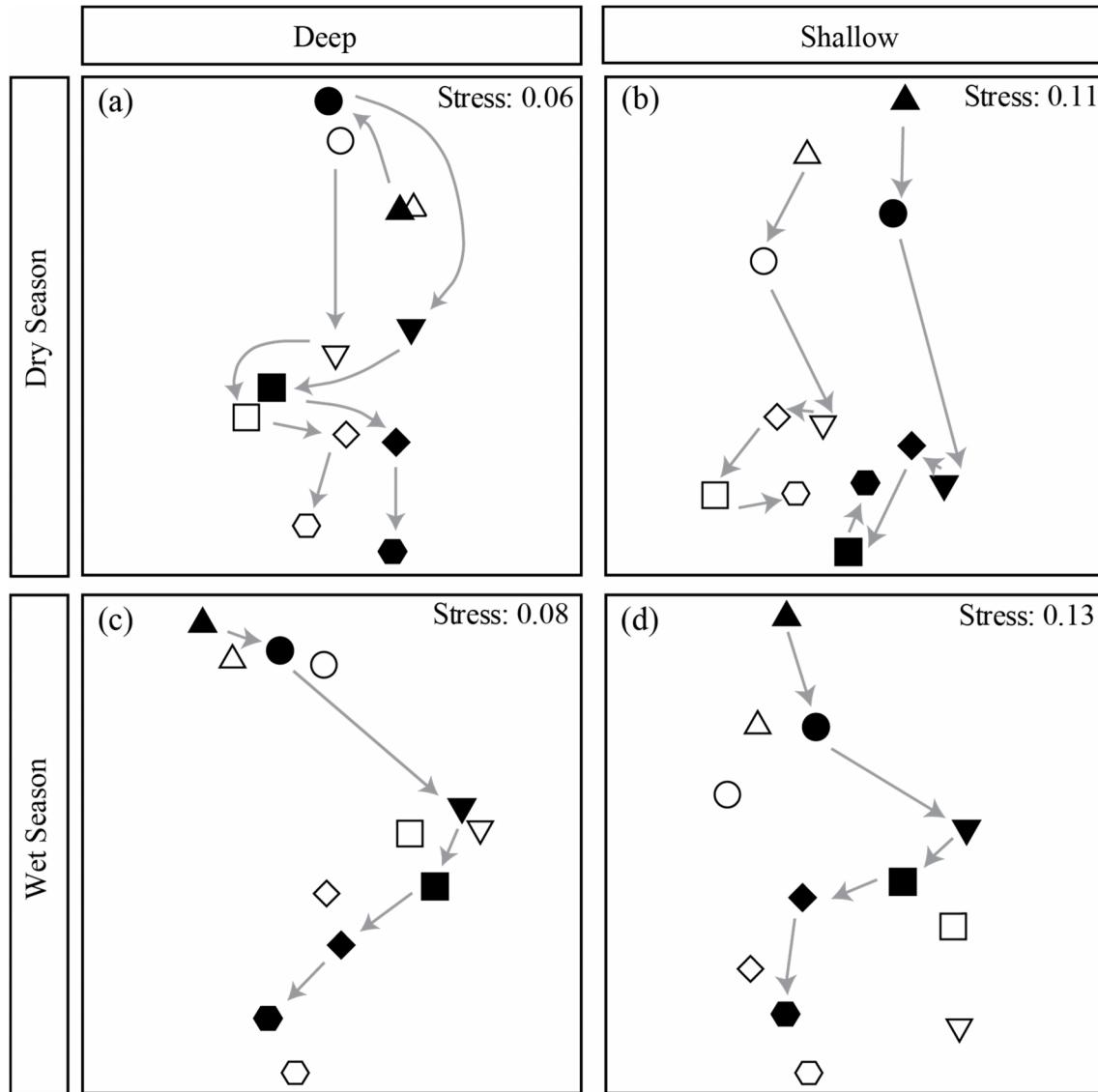


Figure 4.3. Two-dimensional nMDS ordinations of mean catch rates of each fish species in samples collected over reefs at each of the six locations during the dry season in (a) deep and (b) shallow waters and during the wet season in (c) deep and (d) shallow waters during the day and night between 2000 and 2002. Cape Voltaire (\triangle , day \blacktriangle , night); Hall Point (\circ , day \bullet , night); Emeriau Point (∇ , day and \blacktriangledown , night); Cape Bossut (\square , day and \blacksquare , night); Cape Preston (\diamond , day and \blacklozenge , night); Locker Point (\lozenge day and \blacklozenge , night).

The species compositions in shallow water during the dry and wet seasons also differed significantly among locations and between day and night ($P = 0.1\text{--}1.0\%$). R -statistic values in the dry and wet seasons were greater for location, *i.e.* 0.517 and 0.563, respectively, than those for day vs night, *i.e.* 0.307 and 0.180, respectively. Pair-wise tests demonstrated that the species compositions at each location were significantly different from that at each other location, except in four cases during the wet season, *i.e.* for Emeriau Point vs Cape Bossut, Cape Preston and Locker Point and for Cape Preston vs Locker Point, with R statistic values for the significant comparisons ranging from 0.186 to 0.827 during the dry season and from 0.339 to 0.858 during the wet season. SIMPER emphasised that the main typifying species for each location in the cases of each water depth \times season combination are often the same as those given earlier for the overall data for location, *i.e.* which did not differentiate between depth, season and day vs night (Table 4.7). However, unlike the situation with the combined data, *L. bitaeniatus*, *A. stellatus*, Red Emperor *Lutjanus sebae* and Yellowtail Emperor *Lethrinus atkinsoni* were major typifying species in deep water in both dry and wet seasons at Hall Point, Cape Bossut, Cape Preston and Locker Point, respectively. Moreover, in deep water in the dry season, *L. johnii* and *P. emeryii* were major typifying species at Hall Point and Cape Bossut, respectively, and the same was true of *L. nebulosus* at Cape Preston and Locker Point. In contrast, *L. laticaudis* typified the shallow water ichthyofauna during both dry and wet seasons at Locker Point.

Table 4.8. Species identified by SIMPER as those which typified the fish assemblages over reefs in shallow and deep waters at each of the six locations a-f (shaded boxes) and distinguished between the fish assemblages at each pair of those water depths (non-shaded boxes). Samples collected during both the day and night in each season have been pooled in this analysis. For each location ^s and ^d refer to the species that distinguish between the fauna in shallow from deep waters and in deep from shallow waters, respectively.

Cape Voltaire		Hall Point		
Shallow	Deep	(b)	Shallow	Deep
<i>Lutjanus carponotatus</i>		Shallow	<i>Lutjanus carponotatus</i> <i>Lethrinus laticaudis</i>	
<i>Lethrinus laticaudis</i>		Deep	<i>Lutjanus bitaenaitus</i> ^d <i>Lutjanus johnii</i> ^d <i>Lutjanus carponotatus</i> ^s <i>Diagramma labiosum</i> ^d <i>Lutjanus lemniscatus</i> ^s <i>Epinephelus coioides</i> ^s	<i>Lutjanus bitaenaitus</i> <i>Lutjanus carponotatus</i> <i>Lethrinus laticaudis</i>
<i>Lutjanus johnii</i>				
<i>Lutjanus lemniscatus</i>				
<i>Lutjanus bitaenaitus</i> ^d				
<i>Lethrinus laticaudis</i> ^s				
<i>Lutjanus carponotatus</i> ^s				
<i>Lutjanus johnii</i> ^d				
<i>Epinephelus coioides</i> ^s				

Emeriau Point		Cape Bossut		
Shallow	Deep	(d)	Shallow	Deep
<i>Lutjanus carponotatus</i>		Shallow	<i>Lutjanus carponotatus</i> <i>Lethrinus punctulatus</i> <i>Lethrinus laticaudis</i>	
<i>Lethrinus punctulatus</i> ^s	<i>Lutjanus carponotatus</i>	Deep	<i>Lethrinus punctulatus</i> ^d <i>Abalistes stellatus</i> ^d <i>Gnathanodon speciosus</i> ^d <i>Siganus fuscescens</i> ^s <i>Pentapodus emeryii</i> ^d <i>Lethrinus laticaudis</i> ^s <i>Lutjanus sebae</i> ^d	<i>Lutjanus carponotatus</i> <i>Lethrinus punctulatus</i> <i>Abalistes stellatus</i> <i>Pentapodus emeryii</i>
<i>Lethrinus laticaudis</i>				
<i>Lutjanus carponotatus</i> ^d				
<i>Choerodon cyanodus</i> ^s				

Cape Preston		Locker Point		
Shallow	Deep	(f)	Shallow	Deep
<i>Lethrinus punctulatus</i>		Shallow	<i>Lethrinus punctulatus</i> <i>Lutjanus carponotatus</i> <i>Lethrinus laticaudis</i>	
<i>Lutjanus carponotatus</i>		Deep	<i>Lethrinus laticaudis</i> ^s <i>Lethrinus atkinsoni</i> ^d <i>Lutjanus carponotatus</i> ^s <i>Lethrinus nebulosus</i> ^d <i>Pentapodus emeryii</i> ^d	<i>Lethrinus atkinsoni</i> <i>Lethrinus punctulatus</i> <i>Lethrinus nebulosus</i>
<i>Lethrinus laticaudis</i>				
<i>Lutjanus sebae</i> ^d				
<i>Abalistes stellatus</i> ^d				
<i>Lethrinus lentjan</i> ^s				
<i>Lethrinus laticaudis</i> ^s				
<i>Lethrinus nebulosus</i> ^d				

4.3.4 Relationships between species composition and both water depth and day vs night at each location

Two-way crossed ANOSIM between location and each of water depth, day vs night and seasons were all significant ($P = 0.1\%$), yielding R -statistic values of 0.307, 0.177 and 0.122, respectively. The influence of water depth and day vs night on the compositions of the fish assemblages at each location were thus explored in the dry and wet seasons, separately. On the ordination plots for each location during both the dry and wet seasons, the samples for deep waters lay entirely or very largely to the left of those for shallow water in all cases except for Cape Voltaire during the dry and wet seasons and for Cape Bossut during the dry season (Fig. 4.4). The samples collected during the day and night also sometimes showed limited overlap. This applied in particular to Cape Bossut during the dry season, Cape Preston in both dry and wet seasons and Emeriau Point in the wet season.

Two-way crossed ANOSIM tests demonstrated that, during both the dry and wet seasons at each location, the species composition differed significantly between water depths, except at Cape Voltaire during the wet season ($P = 0.1\text{--}5.0\%$). The R -statistic values emphasised that the differences were greatest at Hall Point, Cape Preston and Locker Point during both seasons and at Emeriau Point during the wet season (Table 4.9). The species compositions also differed significantly between day and night at each location, except at Cape Bossut and Locker Point during the wet season and even in these two instances the P values were very close to significant (Table 4.9). The differences between the distribution of night-time and day-time samples on the ordination plots for

Cape Bossut and Cape Preston during the dry season and for Emeriau Point and Cape Preston during the wet season are reflected in substantial *R*-statistic values (Table 4.9). The *R*-statistics demonstrate that, during the dry and wet seasons at any given location, ichthyofaunal composition was almost invariably influenced more by depth than day vs night.

Lethrinus laticaudis was a major typifying species of shallow water at all six locations and was one of the main species whose relative abundance and frequency of occurrence distinguished the fish communities of shallow from deep water at four of those locations (Table 4.8). *Lutjanus carponotatus* was a typifying species of the fauna in shallow water at all six locations and of those of deep water at all but one of those locations, and distinguished the fauna of shallow from deeper waters at three locations. Greater contributions of *L. johnii* and *L. bitaeniatus* distinguished the deep water from shallow water fauna at Cape Voltaire and Hall Point in the Kimberley, whereas the reverse pertained with the Gold-spotted Rockcod *Epinephelus coioides* and Stripey Snapper *L. carponotatus*. At the more southern locations, *i.e.* Cape Bossut and Cape Preston, the species compositions in deep water were distinguished from those in shallow water by relatively greater numbers of *L. sebae* and *A. stellatus*, whereas the reverse was true for the Black Rabbitfish *Siganus fuscescens* and the Redspot Emperor *Lethrinus lentjan*. At the most southern location, the fauna in deep water was distinguished from that in shallow water by relatively greater numbers of *L. atkinsoni* and *L. nebulosus*, whereas greater numbers of *L. laticaudis* and *L. carponotatus* distinguished the shallow water (Table 4.8).

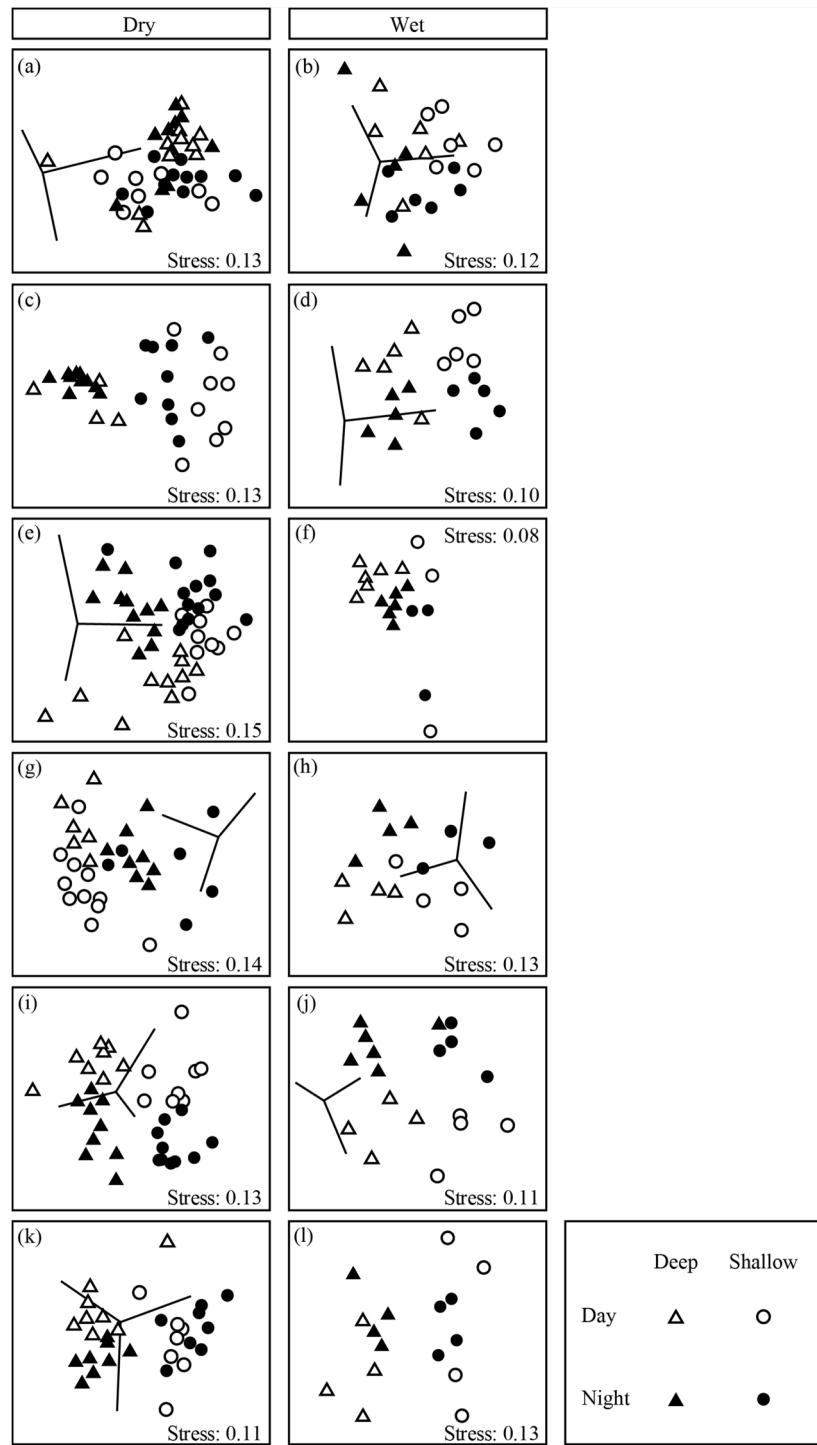


Fig. 4.4. Two or three-dimensional MDS ordinations of the catch rates of each fish species in each replicate sample collected over reefs in deep (Δ day, \blacktriangle night) and shallow (\circ day, \bullet night) waters during the dry and wet seasons at each of the six locations, namely (a,b) Cape Voltaire; (c,d) Hall Point; (e,f) Emeriau Point; (g,h) Cape Bossut; (i,j) Cape Preston and (k,l) Locker Point, between 2000 and 2002.

Table 4.9. Global significance levels (%) and *R*-statistic values (brackets) for diel × season two-way crossed ANOSIM tests for both deep and shallow waters, carried out on data for fish samples collected in fish traps over reefs between 2000 and 2002. Values in boldface represent those that are significant.

Location	Deep		Shallow	
	Season	Diel	Season	Diel
Cape Voltaire	1.0 (0.208)	26.7	1.8 (0.200)	0.3 (0.210)
Hall Point	5.7	1.0 (0.647)	0.9 (0.233)	0.5 (0.262)
Emeriau Point	31.0	0.1 (0.379)	3.1 (0.279)	2.5 (0.154)
Cape Bossut	0.1 (0.563)	0.1 (0.571)	0.1 (0.545)	0.1 (0.460)
Cape Preston	0.1 (0.394)	0.1 (0.373)	0.1 (0.528)	0.1 (0.454)
Locker Point	0.1 (0.376)	0.4 (0.339)	2.5 (0.252)	0.4 (0.242)

4.3.5 Relationships between species composition and both season and day vs night

When the catch rates of fish over reefs were ordinated separately for deep and shallow water at each location, most samples from the dry season formed a relative discrete group to the left of those from the wet season, except in deep water at Hall Point and Emeriau Point (Fig. 4.5). Furthermore, in both deep and shallow water at each location, most of the daytime samples tended to lay to the left or below those collected during the night (Fig. 4.5). Two-way crossed ANOSIM tests showed that the compositions of the fish fauna at each location differed significantly between dry and wet seasons in each water depth, except in deep water at Hall Point and Emeriau Point, and between day and night in both water depths at all locations except in deep water at Cape Voltaire

(Table 4.9). R -statistic values for season were greatest for both deep and shallow water at Cape Bossut and Cape Preston ($R = 0.563$ and 0.394). The R -statistic values for season and day vs night did not differ markedly in shallow waters at any location or in deep waters at Cape Bossut, Cape Preston and Locker Point (Table 4.9). However, they did differ markedly in deeper water at Cape Voltaire, Hall Point and Emeriau Point, and demonstrated that the seasonal effect was greater than day vs night at the first of those locations, whereas the reverse was true at the other two locations.

Lethrinus laticaudis was a major typifying and distinguishing species for the dry season in deep water at Cape Voltaire and Cape Preston and the same was true for *P. emeryii* at Cape Bossut and *L. nebulosus* at Locker Point. In shallow water, the most distinctive point of comparison between dry and wet seasons is provided by *Lethrinus punctulatus*, which was a major typifying and distinguishing species for the dry season at Emeriau Point, Cape Bossut, Cape Preston and Locker Point and a distinguishing species for the dry vs wet seasons at Hall Point. *Lutjanus sebae* was a typifying and distinguishing species for the dry season at Cape Bossut, and *L. laticaudis* was a distinguishing species for the dry season at the three most southern locations, i.e. Cape Bossut, Cape Preston and Locker Point. *Epinephelus coioides* helped distinguish the species compositions in the wet from dry seasons at Hall Point and Locker Point.

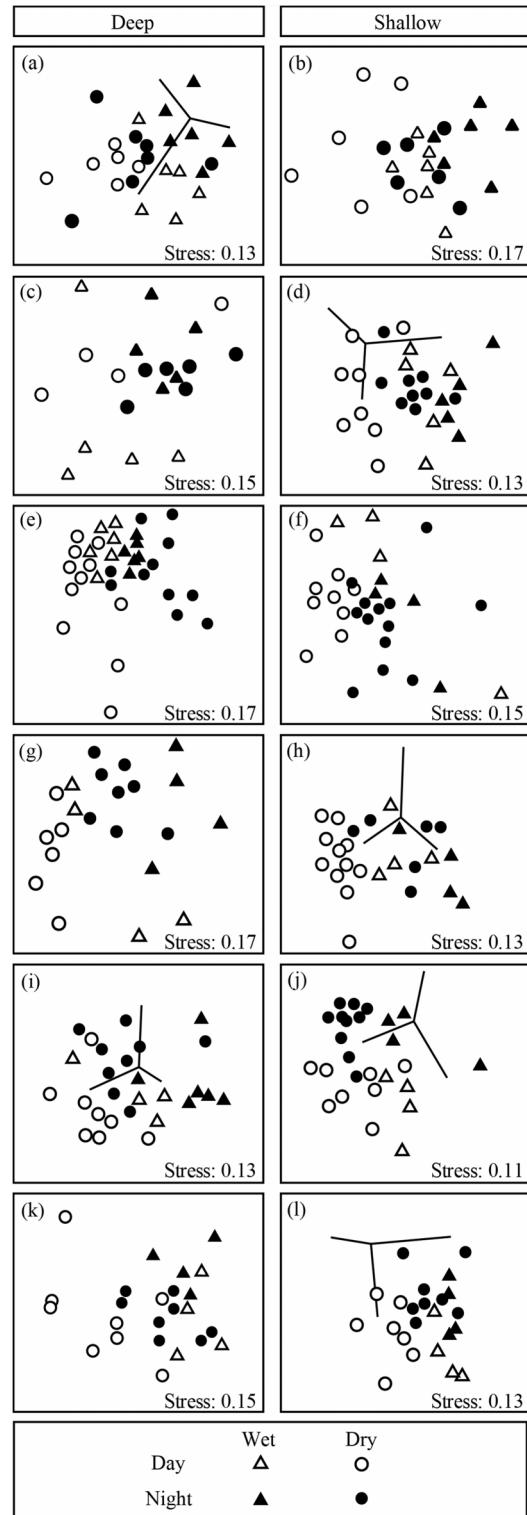


Figure 4.5. Two or three-dimensional MDS ordinations of the catch rates of each fish species in each replicate sample collected over reefs during the dry (\circ day, \bullet night) and wet (\triangle day, \blacktriangle night) seasons in deep and shallow waters at each of the six locations, namely (a,b) Cape Voltaire; (c,d) Hall Point; (e,f) Emeriau Point; (g,h) Cape Bossut; (i,j) Cape Preston; and (k,l) Locker Point between 2000 and 2002.

In deep water, *Lethrinus punctulatus* and *P. emeryii* typified and distinguished the day from night-time samples at Emeriau Point, and the same was true for *E. coioides* at Hall Point. In contrast, the night-time samples were typified by and distinguished from day-time samples by *L. johnii* at Hall Point and by *L. atkinsoni* at Locker Point. The species compositions in shallow waters during the day were distinguished from those at night by greater contributions of *L. lemniscatus* at Hall Point, Emeriau Point and Cape Preston, whereas *L. laticaudis* distinguished the day-time samples at the remaining three locations, *i.e.* Cape Voltaire, Cape Bossut and Locker Point. Greater contributions of *Lethrinus punctulatus*, *G. speciosus*, *S. fuscescens* and the Blue Tuskfish *Choerodon cyanodus* distinguished day from night-time samples in shallow waters at Cape Bossut. In shallow water, *C. cyanodus* was a typifying and distinguishing species for the day-time samples at Hall Point, Emeriau Point and Cape Bossut. However, no other species acted as both a typifying and distinguishing species for either the day or night-time samples at more than one location. *Epinephelus coioides*, *L. sebae* and *L. nebulosus* acted as both typifying and distinguishing species for the day-time samples at Cape Voltaire, Cape Bossut and Locker Point, respectively, whereas the reverse pertained with *L. johnii* at Cape Voltaire.

4.3.6 Relationship between fish assemblages and environmental variables

The linkage tree, representing the separation of the 48 combinations of location, time of day, water depth and season into groups identified by a divisive cluster analysis of the species composition of the fish faunas, together with 'explanations' of those bifurcations in terms of thresholds on individual environmental variables, are provided in Fig. 4.6. The separations of the faunas in the two locations in the Kimberley Bioregion

from the other four and more southern locations in the Canning and Pilbara bioregions were explainable by greater tidal ranges and less water clarity. Greater levels of chlorophyll α and higher water temperatures appeared important in explaining the difference between the faunas in the wet and dry seasons in the Kimberley Bioregion and also the Canning Bioregion. The split between the samples from the deeper water in both dry and wet seasons at Emeriau Point from those of all other samples from the Canning and Pilbara were identified with the unique substrate type (hard sand with sponge and gorgonian corals) in the deep waters at that Canning location.

4.4 Discussion

This study has yielded the first quantitative data aimed at elucidating how the compositions of the teleost faunas associated with inshore reefs at different locations along the approximately 1,500 km of coastline of tropical north-western Australia vary according to a range of influential ecological factors. Thus, the compositions of the fish faunas over reefs at intervals along that coast were able to be compared statistically and thereby facilitate an examination of the relative extents to which the ichthyofaunal composition of these habitats are influenced by location (latitude), water depth, season (wet vs dry) and time of day (day vs night). However, it is recognised that, as the samples were collected using baited traps, the results are derived from data principally for carnivorous fish.

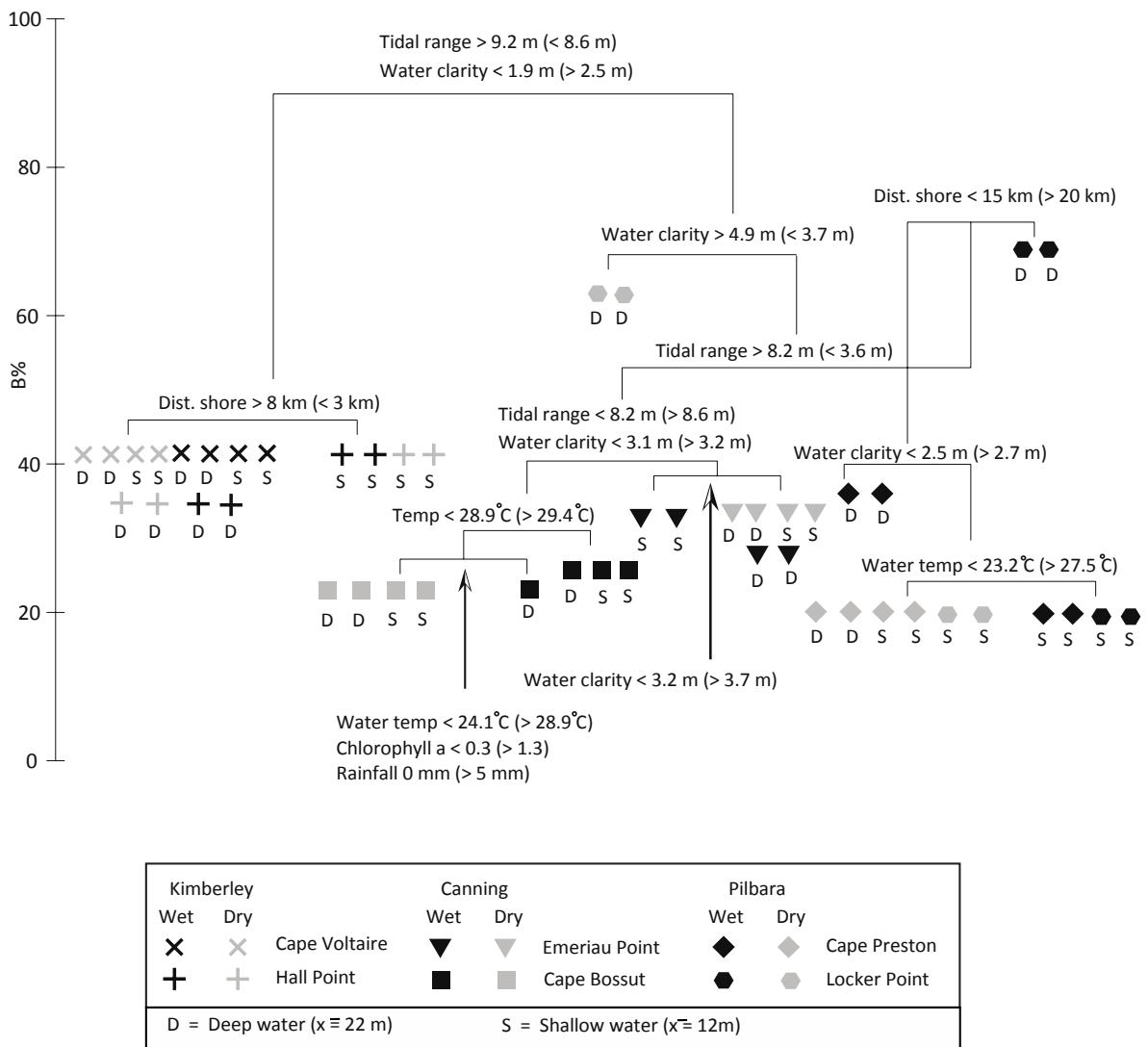


Figure 4.6. Linkage tree and associated physical and environmental variable thresholds that relate to the separation of the reef fish communities of inshore waters in north-western Australia. Unbracketed and bracketed thresholds given at each branching node indicate that a left and right path, respectively, should be followed through the tree. Chlorophyll *a* concentrations are expressed as mg m^{-3} .

The most speciose families were the Epinephelidae, Lutjanidae and Lethrinidae, which parallels the situation that was recorded likewise using baited traps on the Great Barrier Reef at similar latitudes in north-eastern Australia (Newman and Williams, 2001). These three families each ranked in the top eight of the most speciose of the 18 families recorded by Hutchins (2001a) over reefs in a comparable region in north-western Australia. However, unlike the present study, the Labridae and Pomacentridae ranked very high in terms of number of species in Hutchins' study, reflecting his use of a rapid visual census technique rather than baited traps and thus an ability to detect herbivores as well as carnivores. Epinephelids and lutjanids are also particularly well represented over reefs in tropical and sub-tropical waters elsewhere in the world (e.g. Thresher, 1991; Rooker et al., 1997; Rocha and Rosa, 2001), whereas lethrinids are almost exclusively restricted to the Indo-West Pacific (Carpenter, 2001). The dominance of the above three families is consistent with these species being carnivores (Anderson and Allen, 2001; Carpenter, 2001; Heemstra and Randall, 2001). Indeed, dietary analyses strongly indicate that over 60% of the fish community of coral reefs are carnivorous (Jones et al., 1991). The Lethrinidae and Lutjanidae were the two most abundant families and the Epinephelidae the third to fifth most abundant family in three different surveys of the demersal trawl fishery on the continental shelf of NWA (Sainsbury, 1987).

Lethrinus punctulatus, *L. laticaudis* and *Lutjanus carponotatus* were by far the most abundant species, collectively contributing approximately two thirds of the total catch of the 119 species collected along the Kimberley, Canning and Pilbara coastlines. The overwhelming contribution of these three species to the total number of fish caught is consistent with the fact that *Lethrinus punctulatus*, *L. carponotatus* and *L. laticaudis* were

among the top three typifying species at four, six and five sampling locations, respectively. The fact that *Lethrinus punctulatus* is endemic to NWA and a highly targeted commercial species in the region has obvious implications for management and conservation, particularly as there is currently no published information on the biological attributes or stock status of this species. Hutchins (2001a) found that *L. carponotatus* was one of the most abundant species during his study of reefs at sites comparable to the present study, but that, unlike the present study, *Lethrinus punctulatus* was only rarely or occasionally encountered and that the same was true of *L. laticaudis* except at a sampling site near Cape Voltaire, where it was frequently caught.

The use of classification, MDS ordination and ANOSIM tests demonstrated that the species compositions of the inshore reef fish faunas of NWA were related far more to location along the coastline than to water depth, season and time of day. Furthermore, the results demonstrate statistically that the species compositions of the fish faunas over inshore reefs along the NWA coast showed a pronounced tendency to change progressively from north to south, irrespective of water depth, season and time of day. Moreover, on the ordination plot, derived using mean catch rates for day and night in each water depth in each season, the samples from each bioregion formed groups in which the samples for the different bioregions did not intermingle (Fig. 4.3). Although both Williams (1991) and (Cappo et al., 2007) found that, on the Great Barrier Reef, the compositions of fish communities also varied with latitude, that variation was far less than that recorded across the shelf. The tendency for the fish fauna of each bioregion to form separate groups compliments the findings of Hutchins (2001a), which, on the basis of classification of relative abundance estimates of reef fish species distinguished four reef

fish assemblages along the Western Australian coastline, *i.e.* Kimberley, offshore atoll, north-west and south-west assemblages. Anderson and Millar (2004) also found spatial differences in the compositions in the reef fish faunas along the east coast of the north island of New Zealand, *i.e.* in temperate waters, and over a far shorter distance than where the present study was conducted.

Among the three species which dominated the reef fish faunas of tropical NWA, *L. carponotatus* and *L. laticaudis* made relatively greater contributions at the northern than southern locations, but to differing extents, whereas *Lethrinus punctulatus* was rarely found north of Emeriau Point, which is consistent with the results of visual surveys conducted by Hutchins (1999). The differences in the relative importance of these species to the faunas in different locations contributes, to some extent, to the progressive changes that occur in community composition with increasing latitude. However, they were augmented by differences among the ‘latitudinal’ trends exhibited by other species. For example, while *L. johnii* was the major typifying and distinguishing species in the most northern location, *i.e.* Cape Voltaire, it was otherwise found only at the next most northern location, *i.e.* Hall Point, and *L. bitaeniatus* was an important species for distinguishing the fauna at Hall Point from those at other locations and was only caught elsewhere at Cape Voltaire. In contrast, *A. stellatus*, the Threadfin Emperor *Lethrinus genivittatus*, *P. emeryii* and *L. nebulosus* were always caught at the two most southern locations and never at the two most northern locations. Moreover, *A. stellatus* and *L. nebulosus* were very important distinguishing species at Cape Preston and Locker Point, respectively.

Differences in the locations at which the main species were caught was often largely consistent with the geographical ranges recorded for those species (Carpenter and Niem, 1998-2001; Hoese et al., 2007). *Lutjanus johnii* is widespread in the Indo-west Pacific from the Fiji Islands to the east coast of Africa, but, in Western Australia, only extends southwards into the northernmost part of the state (Anderson and Allen, 2001). Although the present study has extended slightly the southernmost recorded distribution of the Golden Snapper to about 16°S, the data show that the distribution cuts out sharply above this latitude. As this species is very abundant at 14°S, it is relevant that its juveniles occupy mangroves (Blaber, 2000; Kiso and Mahyam, 2003), which are common in nearshore waters at this latitude. Anderson & Allen (2001) show *L. bitaeniatus* as having a similar distribution in NWA to *L. johnii*, but recognise that this distribution is based on only a few specimens collected in Indonesia and the NWA coast. These results demonstrate that, even though the Indonesian Snapper is not found in the four most southern locations, its abundance was so great at Cape Voltaire and Hall Point in the Kimberley Bioregion that this species ranked number four overall among species caught throughout the whole study area.

The distribution map of Carpenter (2001) shows *L. nebulosus* as occurring along much of the western and eastern coasts of Australia and to be widely distributed in the Indo-Pacific to the north of Australia. However, this species was only abundant in the two most southern of my sampling locations and was not found in the two northernmost locations. This apparent anomaly suggests that *L. nebulosus* is not well adapted to living in the particularly turbid waters that characterise the Kimberley Bioregion (Semeniuk, 1993).

Abalistes stellatus is also shown by Matsuura (2001) as having a wide Indo-Pacific

distribution that extends southwards throughout northern Western Australia and, yet like *L. nebulosus*, was absent from catches in the two sampling locations in the Kimberley Bioregion. Hutchins (1999) has made the point that the fish species that occupy the waters of the Kimberley coast must be particularly well adapted to coping with turbidity.

In contrast to the above four species (*L. johnii*, *L. bitaeniatus*, *L. nebulosus* and *A. stellatus*), *Lethrinus punctulatus* is confined to waters extending northwards from Shark Bay in Western Australia and eastwards possibly to as far as Darwin in northern Australia (J.B. Hutchins pers. comm. Carpenter, 2001; Hoese et al., 2007). However, my data demonstrate that, in Western Australia, this species is far more abundant in the Canning and Pilbara bioregions in the south than in the Kimberley Bioregion in the north. Thus, as with *L. nebulosus*, the greater abundance of *Lethrinus punctulatus* at Cape Preston and Locker Point in the south than at locations further north probably reflects a ‘preference’ of this species for clearer water. It is also relevant that juvenile *L. punctulatus* are abundant over macroalgal covered reefs in the Canning and Pilbara bioregions (C.B. Wakefield pers. comm.) and this habitat type is not common in the inshore waters at the two Kimberley locations sampled in this study (Huisman and Sampey, 2014).

Pentapodus emeryii is shown by Russell (2001) as occupying the tropical west Pacific and to occur along the Western Australian coast only between 19 and 21°S. Although the data obtained during the present study are consistent with the above distribution in that *P. emeryii* was not found in the Kimberley Bioregion in the north, it was caught at Emeriau Point and Cape Bossut at latitudes of 15 and 17°S in the Canning Bioregion and thus to the north of that recorded by Russell (2001).

From the above comparisons, it is evident that the latitudes to which some Indo-Pacific species extend southwards into Western Australian waters vary, and that some species, which are widely distributed to the north of Australia, were caught in the Pilbara and Canning Bioregions, but not in the Kimberley Bioregion further north. The absence of the latter species from the samples taken from Cape Voltaire and Hall Point probably reflects the more extreme environmental conditions at locations within the Kimberley Bioregion.

4.4.1 Comparisons between water depths, day vs night and season for each location

In general, the ichthyofaunal composition at each location was related to a greater extent to water depth than to either day vs night or season. This contrasts with the results for fish on the Great Barrier Reef, based on studies of the Lethrinidae, Lutjanidae and Epinephelidae, in which the compositions differed more between day and night than with water depth (Newman and Williams, 2001). Water depth has been shown to influence the compositions of fish communities of many reefs (McGehee, 1994; Lara and Gonzalez, 1998; Khalaf and Kochzius, 2002b; Friedlander et al., 2010; Jankowski et al., 2015a). Furthermore, the compositions of the fish faunas in the deep and shallow waters of a large subtropical marine embayment and in temperate coastal waters further south in Western Australia also differ significantly (Hyndes et al., 1999; Travers and Potter, 2002). The important influence of water depth in the present study is emphasised by the fact that, during both dry and wet seasons, the compositions of the fish faunas in deep and shallow waters at each location were significantly different. These differences were most

pronounced at Hall Point in the Kimberley Bioregion and at Cape Preston and Locker Point in the Pilbara. The differences at Hall Point are probably attributable to the marked differences in the depth of the deep and shallow sites at this location, while those at Cape Preston and Locker Point are more likely to reflect the fact that the distances between the deep and shallow sites and differences in their water temperatures were greatest at these two locations. Differences between the ichthyofaunal compositions of reefs in deep and shallow waters have also been found in other regions of the world (e.g. Friedlander and Parrish, 1998; Newman and Williams, 2001; Khalaf and Kochzius, 2002b). Furthermore, a cross-shelf effect was found with fish faunas on the Great Barrier Reef (Williams, 1991; Newman and Williams, 1996; Cappo et al., 2007). The differences in the species compositions between the reefs in deep and shallow waters in north-western Australia may also be related to certain aspects of the physical environment along this coastline. For example at Hall Point, the shallow reef sites were restricted to relatively shorter distances from shore, i.e. < 1 km, than those at locations, such as Cape Bossut, where shallow reefs extended distances up to 10 km from shore (see Fig. 2.1).

The most important species in distinguishing the deep from shallow waters at both Cape Voltaire and Hall Point was *L. bitaeniatus*. A greater abundance of the Indonesian Snapper in deeper water is consistent with this species being recorded as occurring in deeper reef areas (Anderson and Allen, 2001). However, the present data does demonstrate that, in north-western Australia, this species can still be abundant in water depths less than 30 m, which contrasts with the observations of the above workers that this species occurs solitarily or in small groups and in water depths of 40-65 m.

Lutjanus sebae and *A. stellatus* were important in distinguishing the fish faunas of the deep from shallow waters at both Cape Bossut and Cape Preston. The former species, which is highly valued by commercial and recreational fishers, occurs in water depths up to at least 150 m (Newman and Dunk, 2002) and thus far beyond the maximum depths sampled during the present study. This species, and also *A. stellatus*, were more abundant in samples collected from deep than shallow waters on the Great Barrier Reef (Newman and Williams, 2001).

Lethrinus laticaudis was a major typifying species of shallow waters at all six locations and one of the main species that distinguished the fish communities of shallow from deep water at five of those locations. It is thus relevant that this species spends its early life in seagrass beds and mangroves and moves offshore as it becomes an adult (Carpenter, 2001). *Lutjanus carponotatus*, which typified the fauna of the shallow water at all locations and distinguished the fauna in shallow from deep water at three of those locations, was more abundant over reefs located in shallow nearshore than deeper offshore waters on the Great Barrier Reef (Newman and Williams, 1996).

4.4.2 Diel and seasonal comparisons

Galzin (1987) demonstrated that, in Polynesian reefs, the compositions of the fish communities differed between day and night and between dry and wet seasons, but did not explore which of those variables had the greatest influence. The results of the present study showed that, particularly in shallow waters, the influence of the season and diel effects at the various locations did not differ markedly. The fact that *L. carponotatus* and

L. laticaudis were among the top two or three typifying species for both day and night at each location emphasises that the diel differences in faunal composition were often relatively subtle, with only a few species being relatively more numerous in the catches taken during either the day or night in either deep or shallow water at two or more locations. However, the three main lethrinid species, *Lethrinus punctulatus*, *L. laticaudis* and *L. nebulosus*, did tend to be more abundant in trap catches during the day than night, which is consistent with the results of previous trapping studies in north-western and north-eastern Australia (Whitelaw et al., 1991; Newman and Williams, 2001) and video based studies in waters off the west coast of Australia (Harvey et al., 2012b). Although these results clearly imply that these lethrinids forage during the day, Carpenter and Allen (1989) state that most species of lethrinids feed at night, but recognise that many species “forage coincidentally or purposefully during the day”.

The relatively greater catches and the increased frequency of capture of *E. coioides* during the day than night at four locations, is consistent with another epinephelid, *Serranus atricauda*, typically feeding during the day (Morato et al., 2000). However, in his review, Parrish (1987) considers that most groupers feed at all times of the day, but that those that forage in the water column may feed more actively in daylight, whereas those that rely heavily on benthic invertebrates may be more active at night. The fact that *A. stellatus* of the family Balistidae also made relatively greater contributions during the day in both the deep and shallow waters at the same two locations, parallels the results of Newman and Williams (1995) on the Great Barrier Reef. Furthermore, the relatively greater contributions of *L. johnii* to night-time catches is consistent with lutjanids typically feeding at night (Randall and Brock, 1960; Hobson, 1965; Starck and Davis, 1966; Hobson,

1968; Hobson, 1974; Parrish, 1987). However, another lutjanid, *L. lemniscatus*, played a major role in distinguishing day-time from night-time samples at three locations.

The use of LINKTREE emphasised that greater concentrations of chlorophyll *a*, *i.e.* productivity, rainfall (and thus freshwater discharge) and higher water temperatures were important environmental variables for explaining the separation of the ichthyofaunal compositions in the wet and dry seasons in the Kimberley Bioregion and particularly at Cape Voltaire. As pointed out earlier, productivity increases markedly during the wet season in the Kimberley, presumably due to substantial increases in nutrient input as a result of marked increases in freshwater discharge from the productive catchment of this bioregion (McKinnon et al., 2015a). The rise in productivity and temperature in the wet season would improve the ‘environment’ for reproduction and growth of many fish species and the invertebrates that constitute their prey. However, such increases during the wet season would be unlikely to have the same direct influence on all species, which would account for the differences between the ichthyofaunal compositions in the wet and dry seasons.

Although environmental conditions, and in particular water temperature, differed markedly between seasons, differences in the relative abundances of only four species distinguished between the faunas in dry and wet seasons in either the deep or shallow waters at more than one location. However, *Lethrinus punctulatus* is a particularly good example of a distinguishing species for the dry season in that it performs this role in shallow waters at five of the six locations and in deep waters at two of those locations. In addition, *L. laticaudis* played an important role in distinguishing the dry from wet seasons in shallow waters at four locations and in deep waters at two locations. It is noteworthy

that only one species, *E. coioides*, distinguished the fauna in the wet season from that in the dry season at more than one location.

4.4.3 Conclusions

The results of this study demonstrate that the ichthyofaunal compositions over reefs of the Kimberley, Canning and Pilbara bioregions were relatively discrete. Species composition was influenced far more by location (latitude) than by water depth, season and time of day, and underwent a gradational change southwards. The latter change reflected differences in the trends exhibited by the relative abundances of certain species with increasing latitude and the confinement of other species largely to particular bioregions.

Lethrinus punctulatus was rarely recorded in the two most northern locations and was abundant in the four most southern locations, whereas *Lutjanus carponotatus* and *Lethrinus laticaudis* were relatively more abundant in northern than in southern locations. *Lutjanus bitaeniatus* and *Lutjanus johnii* were found exclusively at the two locations in the Kimberley bioregion where tidal range was greatest and water clarity least, whereas *Abalistes stellatus*, *Pentapodus emeryii* and *Lethrinus nebulosus* were not caught in this region but were found in both locations of the Canning and Pilbara bioregions.

The species composition in deep and shallow waters at each location almost invariably differed significantly between day and night and between dry and wet seasons, with species such as *L. bitaeniatus*, *L. johnii*, *Lutjanus sebae* and *A. stellatus* being more abundant over deep reefs, whereas *L. carponotatus*, *L. laticaudis*, *Siganus fuscescens* and *Lethrinus lentjan* were more numerous over shallow reefs. Higher productivity levels

(chlorophyll *a*) during the wet season was an important environmental variable underlying seasonal changes in species composition. Species such as *L. johnii* and *Lethrinus atkinsoni* were relatively more important in night-time than daytime catches, whereas the reverse applied to *Lethrinus lentjan*, *L. laticaudis* and *Choerodon cyanodus*, *Lethrinus punctulatus* and *L. laticaudis* were relatively more important in catches during the dry than wet season.

Chapter 5 To what extent are species richness and abundance of reef fish faunas along an extensive tropical coast related to latitude and depth, season and day vs night?

5.1 Introduction

Numerous studies, often using a collation of the extensive data in museum records, have demonstrated that the number of species of various fauna in marine environments typically decline in a poleward direction, *i.e.* from tropical to temperate waters (e.g. Rex et al., 2005; Jablonski et al., 2006; Tittensor et al., 2010). Some of these studies have shown that the relative abundance of a given fauna also declines along that latitudinal gradient (Floeter et al., 2005; Arakaki et al., 2014). In the case of fishes, declines in these two biotic variables along a latitudinal range reflect, *inter alia*, such factors as changes in water temperature, habitat availability and productivity (e.g. Bellwood and Hughes, 2001; Floeter et al., 2004; Bellwood et al., 2005; Floeter et al., 2005; Mellin et al., 2010; Tittensor et al., 2010; Parravicini et al., 2013). Such latitudinal changes are reflected in progressive changes in species composition (e.g. Chapter 2; Bellwood and Hughes, 2001; Floeter et al., 2004; Cappo et al., 2007; Anderson et al., 2013; Kulbicki et al., 2013). Any examination of the extent to which the species richness and abundance of fishes, and thus also species composition, are related to latitude should take into account that these biotic variables are influenced by factors associated with, *inter alia*, season, water depth and time of day and the extent to which there are, for these variables, interactions among locations and those factors.

The numerous studies, which have explored whether the species richness and abundance of fishes in coastal marine environments differ among one or more of the

above three factors, have frequently employed data derived from samples collected at just one or two locations (e.g. Harvey et al., 2012a; Azzurro et al., 2013; Schultz et al., 2014). They have generally shown that these two biotic variables are greater in the wet than dry ‘seasons’ in tropical regions, where environmental differences between those seasons are marked and species typically spawn in the warmer and more productive former season (Blaber et al., 1995; López-Pérez et al., 2013; Biswas et al., 2014). Depth-related studies show that the species richness and abundance of fishes are typically greater in shallow than deeper waters, particularly in the case of reefs, with those in shallow water tending to be more complex (Hyndes et al., 1999; Brokovich et al., 2008; Mellin et al., 2010; Anderson et al., 2013; Schultz et al., 2014; Jankowski et al., 2015a; Jankowski et al., 2015b). It is important to recognise, however, that the degree of these depth-related differences can vary with the extent of the difference in water depth and that significant differences may occur for one biotic variable and not the other (Hyndes et al., 1999; Brokovich et al., 2008; Pearson and Stevens, 2015).

In terms of diel effect, the species richness and abundance of fishes over open soft substrata tend to be greater during the night than day, reflecting a nocturnal movement of the dominant fish species in coastal waters from more protected environments to those where they are less susceptible to predation and where they feed mainly on benthic macro-invertebrates (Gray et al., 1998; Travers and Potter, 2002). Such nocturnal movements account, in part, for species richness and abundance over reefs being greater during the day than night (Nagelkerken et al., 2000a; Harvey et al., 2012a).

The results of Chapter 3 demonstrated that the species richness and abundance of fishes, located over soft substrata along the extensive tropical NWA coastline in the

'stable' dry season, each declined and then rose in a concave manner with increasing latitude, rather than declining progressively as is typical along a latitudinal gradient. Those two biotic variables were also shown to differ between seasons and for the extent and direction of differences between deep and shallow water to vary among locations. There has been no comparable integrated statistical study on fish faunas over reefs.

Analysis of distribution data for fish species, derived mainly from museum and other records, demonstrate that the ichthyofaunal composition of marine waters along the continuous western Australian coastline from 13°S in tropical waters in the north to 35°S in temperate waters on the south coast changes progressively with latitude (Fox and Beckley, 2005). Multivariate analyses, using the densities and catch rates of fish species, derived from trawling and trapping, respectively, showed that the ichthyofaunal composition over both soft substrata and reefs within the ~1,500 km of the tropical NWA component of that coastline change in a progressive manner from north to south (Chapter 2). Those analyses also revealed, however, that the species composition in those two habitats varied among bioregions along that coastline, with that in the Kimberley Bioregion in the north being particularly distinct from those in the Canning Bioregion in the centre and Pilbara Bioregion in the south. These bioregional differences are related to differences in environmental conditions. Thus, the monsoonal Kimberley Bioregion is characterised by the presence of particularly high tidal ranges, turbidity and numerous mangrove-lined rivers and creeks, whereas the Canning and especially the Pilbara bioregions are far more arid and the former of these contains no substantial rivers (see Materials and Methods for further details).

In the present study, data on species richness and abundance of fishes over reefs on the NWA coast, derived from trapping at well-spaced locations, provided an excellent opportunity to determine statistically, and in an integrated manner, how those two biotic variables change with latitude along an extensive coastline and are related to season, water depth and time of day. Emphasis has been placed on elucidating whether those two variables change from north to south in the manner of the fish fauna over soft substrata (Chapter 3), *i.e.* in an essentially concave manner during the dry season and less markedly during the less stable wet season, and on accounting for any changes along the latitudinal axis. Finally, the data are used to determine whether the extent and direction of the values for species richness and abundance of fishes remain essentially consistent between wet and dry seasons, deep and shallow water and day *vs* night along the full stretch of the NWA coast.

5.2 Materials and Methods

5.2.1 Study area

The inner shelf waters of tropical NWA (Fig. 5.1) contain reefs comprising a veneer of scleractinian coral and encrusting coralline red algae overlying hard limestone pavement or igneous rock (Simpson, 1988; Hatcher, 1991; Brooke, 1995; Brooke, 1997; Wilson, 2013). They thus differ from the fringing, patch and platform reefs found in shallower waters along that coast (Wilson, 2013). The tidal range declines southwards from a maximum of ~12 m in the Kimberley to a minimum of ~3 m in the Pilbara (Cresswell and Badcock, 2000; Wilson, 2013).

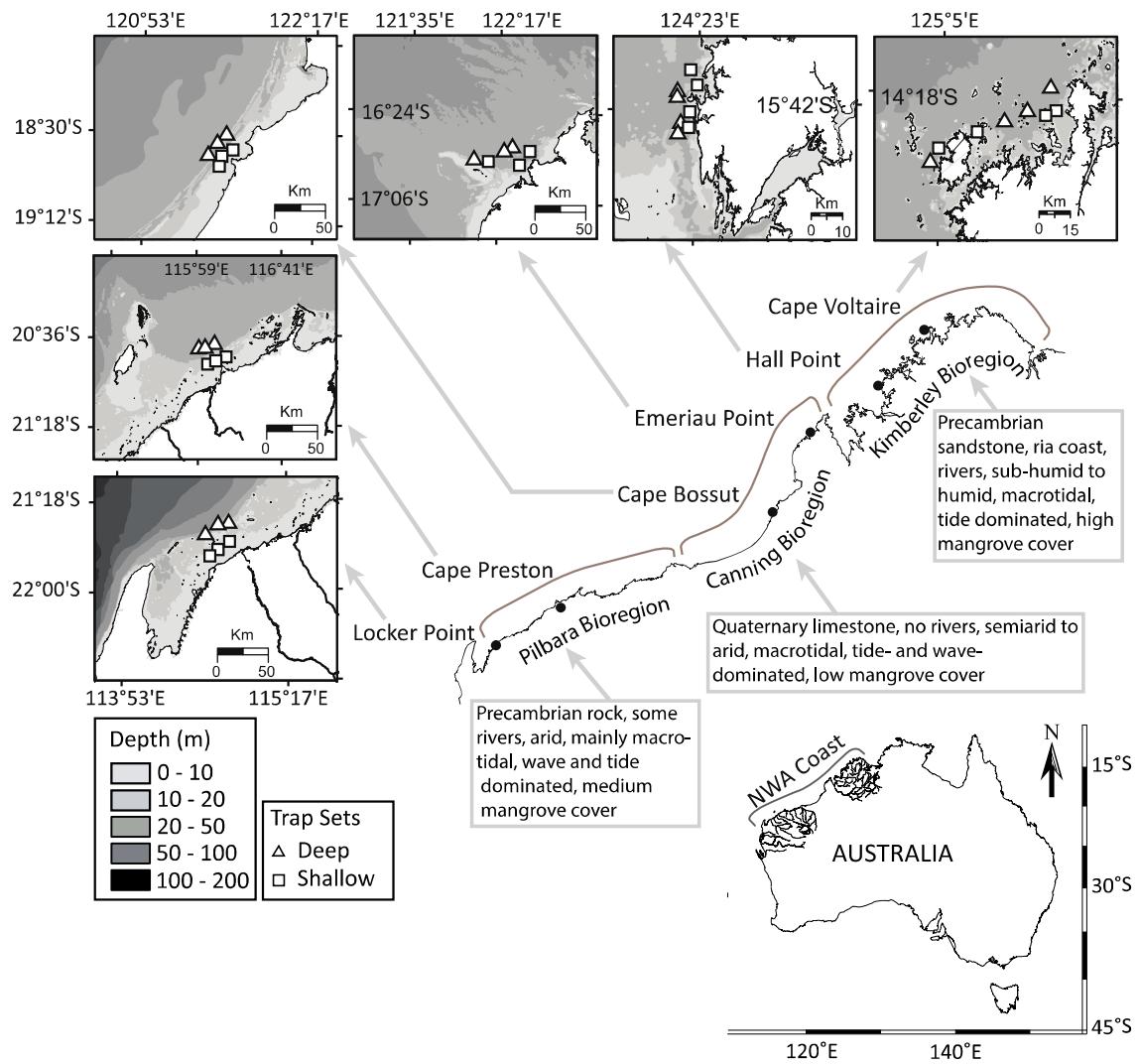


Fig. 5.1. Study area where fishes over reefs were sampled by traps in both deep ($\bar{x} = 22$ m) and shallow ($\bar{x} = 12$ m) waters at each of the six locations at three bioregions along the north-western Australian (NWA) coast in 2000, 2001 and 2002. Details of the key characteristics of each bioregion *sensu* Brocx & Semeniuk (2010) are provided.

The NWA coast is subjected to the highest frequency and severity of annual cyclones of any coast in Australia (Hassim and Walsh, 2008), and is thus characterised by distinct wet and dry seasons each year (Lough, 2008; Hobday and McDonald, 2014; Ng et al., 2015). The resultant large seasonal discharges of freshwater from rivers along the Kimberley coast and strong tidal currents (8 to 22 km h⁻¹) result in the turbidity of its inshore waters, and especially in the wet season, being far greater than along the Canning coast and even more particularly the Pilbara coast (Harris and Heap, 2003; McKinnon et al., 2015a). These strong discharges and tidal mixing (Holloway et al., 1985; Furnas, 2007) also lead to increased productivity, particularly in the Kimberley Bioregion, where zooplankton production is 7-fold higher than at comparable latitudes on the north-east coast of Australia (McKinnon et al., 2015b). Furthermore, chlorophyll *a* values along the NWA coast are the highest that have been recorded along any coastline in Australia (Condie and Dunn, 2006; McKinnon et al., 2015b). Numerous mangrove forests, which, together with adjacent areas, act as nursery areas for some coastal fish species (Blaber, 1980; Robertson and Duke, 1987; Blaber, 2000; Nagelkerken et al., 2001; Nagelkerken et al., 2002; Mumby et al., 2004; Nagelkerken et al., 2008; Nagelkerken, 2009), are present in the rivers, creeks and small bays of the Kimberley Bioregion and, to a lesser extent, of the creeks and embayments in the Canning and Pilbara bioregions (Semeniuk, 1993; Brocx and Semeniuk, 2010; Wilson, 2013).

5.2.2 Sampling regime and environmental data

For the convenience of the reader, and because of the complexity of the sampling regime, details of the sampling regime and environmental measurements previously

provided in Chapter 2 are essentially repeated below at this later stage in the thesis. The fishes over reefs in deep (15-30 m, $\bar{x} = 22$ m) and shallow (5-15 m, $\bar{x} = 12$ m) inshore waters were sampled by trapping at six well-spaced locations along the NWA coast, with two locations in each of the Kimberley (Cape Voltaire and Hall Point), Canning (Emeriau Point and Cape Bossut) and Pilbara, Cape Preston and Locker Point, bioregions (Fig. 5.1; Table 5.1). Trapping was undertaken during the day and night in deep and shallow waters during the dry season (early June to early September) of both 2000 and 2001 and during the wet season (late February to late April) of 2002 (Table 5.1). The fish traps, which were 600 mm high, 1,500 mm long and 1,200 mm wide were covered throughout with 50 mm square steel mesh, except in their 600 \times 200 mm entrance. The bait comprised 2kg of mulched fresh Australian Pilchard (*Sardinops sagax*), which a trap study in offshore waters of north-western Australia had shown to yield significantly greater catches than the other baits tested (Whitelaw et al., 1991). Bait was still present in all traps when retrieved at the end of sampling. Each fish was identified to species using descriptions in Gloerfelt-Tarp and Kailola (1984), Sainsbury et al. (1985), Last and Stevens (1994), Allen (1997) and Carpenter and Niem (1998-2001).

In both 2000 and 2001, the deep and shallow waters at each location were sampled during the day using a group of 10 traps set twice for ~ 4 h on each of three days and during the night by employing two groups of five traps set for ~ 10 h on two successive nights and occasionally a third night (Table 5.1). The 4 h period of sampling during the day was selected to accommodate the requirements of concomitant studies on the biology of selected fish species, while the 10 h period of nocturnal sampling was employed because, for logistical and safety reasons, traps could only be set and retrieved once on any given

night (Table 5.1). It proved possible, however, in the wet season of 2002 to increase the soak time during the day to 10 h, using 2 sets of 5 traps, and thus employ the same sampling regime as during the night (Table 5.1). Traps were always set apart at distances of 50-200 m to reduce the likelihood of the ‘field of capture’ of any trap overlapping that of any other trap (Eggers et al., 1982). The total number of fish species recorded in each group of five or 10 traps was expressed as number of species per 4 or 10 h and considered a replicate for use in analyses of species richness. The number of fishes in each group of five or 10 traps were pooled and expressed as fishes $(4\text{ h})^{-1}$ or fishes $(10\text{ h})^{-1}$, which was then considered a replicate for use in analyses of catch rates (abundance).

Water temperature and Secchi disc depth (depth of water clarity) in both deep and shallow waters at each location were recorded at four intervals throughout the first day of sampling both of those depths at each location in each of the three years of sampling. The tidal range at a site on the day of sampling was recorded as the difference between the maximum and minimum water heights at that site on that day, while precipitation was recorded as the total rainfall that occurred during sampling and in the preceding two weeks. Tidal range and precipitation data were obtained from the Australian Government Bureau of Meteorology. Average estimates of remotely-sensed surface chlorophyll *a* concentrations during five months in the dry (May to September 2001) and wet (December 2001 to April 2002) seasons were calculated using the Giovanni online data system, developed and maintained by the NASA GES DISC (Acker & Leptoukh 2007). Surface chlorophyll *a* concentration are used as proxy for phytoplankton concentration and thus of productivity (Lee et al., 2015).

Table 5.1 Years (seasons), time (day or night), duration of trap set, replication and frequency of sampling in both deep ($\bar{x} = 22$ m) and shallow ($\bar{x} = 12$ m) waters at each of the six locations sampled along the north-western Australian coast in 2000, 2001 and 2002.

Year	Time of sampling	Set duration	No. of replicates per day or night	No. of days or nights	Total replicates
2000 (Dry)	Day	4 h	2 Sets of 10 Traps	3	6
	Night	10 h	2 Sets of 5 Traps	2 or 3	4-6
2001 (Dry)	Day	4 h	2 Sets of 10 Traps	3	6
	Night	10 h	2 Sets of 5 Traps	2 or 3	4-6
2002 (Wet)	Day	10 h	2 Sets of 5 Traps	3	6
	Night	10 h	2 Sets of 5 Traps	2 or 3	4-6

5.2.3 Statistical analyses

PERMANOVA (Anderson et al., 2008) was used to analyse the data on water temperature and clarity (Secchi disc depth) in each depth and year at each location. When used on a single variable, as throughout this paper, PERMANOVA returns classic ANOVA tables, with the pseudo-*F* statistics reducing to real *F* values. The significance levels (*P*) are, however, determined by permutation rather than by appealing to any distributional assumptions, thus making the tests more robust. PERMANOVA was also used to test whether the number of species and catch rates of fishes differed between locations, years (seasons), water depth and day vs night. A combination of three separate PERMANOVAs were required, however, to achieve these aims because of the differences in sampling time, particularly between day and night. It is important to note that, because of the well-known dependence of species richness on sampling effort, all tests on numbers of species are carried out on subsets of the full data for which the sampling units involved identical

trap times. Thus, the first, second and third of these PERMANOVAs tested the following hypotheses individually. Number of species and catch rates of fishes differed between: 1) locations, years and water depth, using the data from 4 h samples during the day in 2000 and 2001; 2) locations, years (seasons) and water depth, using the data from 10 h samples during the night in 2000, 2001 and 2002; and 3) locations, water depth and day vs night, using the data from 10 h samples during the day and night in 2002. Each of these three PERMANOVAs was considered to represent a three-way crossed design, with each factor fixed. The effect of location was considered fixed rather than random as the locations were selected to be distributed at well-spaced intervals along the coast, with inference requiring to be drawn about these specific locations and, by implication, the latitudinal gradient they represent, making a fully fixed-effect model appropriate. Examination of the values for these variables demonstrated that, prior to PERMANOVA, water temperature, water clarity and number of species required a square root transformation and catch rates a $\ln(x+1)$ transformation to meet the test assumption of homogenous dispersion (variance, here) among *a priori* groups (Anderson, 2001a).

On each sampling occasion at each of the six locations, there were six replicates for the day and four to six replicates for the night for both deep and shallow waters (Table 5.1). Each of these replicates represents total species richness over a *consistent* number of traps (10 or five, depending on the particular test), with a similar construction for each abundance replicate, expressed as an average catch rate of fish per trap. Pooling the information at this lowest level of repeated sampling is important, particularly for number of species, in obtaining enough information for a viable replicate and to estimate a meaningful concept of species richness (not the spot diversity in a single trap but richness

within the reef area which the deployed five or 10 traps represent). Each replicate is then expressed, in the three tests, as numbers or abundance: 1) per 4 h for each day sample in 2000 and 2001; 2) per 10 h for each night sample in 2000, 2001 and 2002; and 3) per 10 h for each daylight sample in 2002 (Table 5.1).

Although the above pooling of the lowest level variability reduces the apparent total number of replicates and thus residual degrees of freedom available for PERMANOVA, it provides a more meaningful definition of species richness and a less pseudo-replicated residual, whilst still giving sufficient degrees of freedom for effective tests. All replicates were considered independent.

Note that examination of the raw data revealed that trap catches were characterised by a number of extremely high catches and numerous zero catches. Thus, the cell variances tended to be functions of the cell means (the larger the mean the larger the variance), a common feature of abundance patterns. This is somewhat ameliorated by the pooling over sets of traps, as defined above, but was then effectively removed by transformation at the new replicate level (square root for richness and log for abundance).

When PERMANOVA detected a significant difference for an interaction term or a main effect that was not involved in any significant interaction, plots displaying the marginal means and 95% confidence intervals of each level of the relevant factor(s) were used to ascertain the source of those differences. The means and intervals in these plots were back-transformed to original scales to allow easier interpretation. Note also that, when the confidence intervals of two or more means overlapped markedly and thus obscured the trend exhibited by species richness and/or catch rates at a location, the

overall mean with an indicative 95% confidence interval for a group mean at that position is presented in the figures.

5.3 Results

5.3.1 Environmental variables

To allow the reader to be able readily to consider the results of the analysis of the biotic variables in the context of the environmental variables, the results of the environmental analyses given in Chapter 4 are repeated here. PERMANOVA demonstrated that water temperatures over reefs differed significantly between locations, years (comprising the dry seasons of 2000 and 2001 and wet season of 2002), locations and water depths and all two and three-way interactions were significant (Table 5.2). At each location, the mean water temperatures in both deep and shallow water were far greater during the wet than dry seasons (Fig. 5.2a,b). In the wet season, the mean water temperatures in both deep and shallow waters declined progressively in a southerly direction from their maxima at the four most northern locations to their minima at Locker Point, the most southern location (Fig. 5.2a,b). During the dry season, mean water temperatures in both depths declined southwards from their maxima at the two most northern locations, with the trend more pronounced in 2000 than 2001 (Fig. 5.2a,b).

Mean Secchi disc depth differed significantly among locations, years and depths and there was a significant interaction between location and year (Table 5.2). Water clarity was greater in deep than shallow water (Fig. 5.2c). Mean water clarity in the dry seasons of 2000 and 2001 and wet season of 2002 rose from their lowest levels at Cape Voltaire and Hall Point in the north to Emeriau Point, after which it declined to lower

levels at Cape Bossut, and ultimately rose to high levels at Locker Point, the most southern sampling location. The highest levels recorded at Cape Preston in the dry season of 2000 are clearly the main contribution to the significant interaction between location and year (Fig. 5.2d).

Mean chlorophyll *a* values at each location were almost invariably greater in the wet season than in either of the two dry seasons (Fig. 5.2e). The lowest chlorophyll *a* concentrations were recorded in the dry season at Cape Voltaire and Cape Bossut and were highest at Locker Point in each of the three years.

Table 5.2. Mean squares (MS), *F* values and significance levels (*P*) for PERMANOVAs of water temperature and water clarity in deep and shallow waters during the day at six locations along the north-western Australian coast in 2000 and 2001 (dry seasons) and 2002 (wet season). df, degrees of freedom.

df	Water temperature			Water clarity			
	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	
Location (L)	5	74.315	926.3	<0.001	25.2	111.4	<0.001
Year (Y)	2	6.728	8327.3	<0.001	3.8	16.6	<0.001
Depth (D)	1	0.005	6.7	0.014	3.0	13.3	0.002
L × Y	10	0.063	78.4	<0.001	1.3	5.7	<0.001
L × D	5	0.002	2.5	0.030	0.4	2.0	0.095
Y × D	2	0.053	66.2	<0.001	0.3	1.1	0.354
L × Y × D	10	0.012	14.6	<0.001	0.3	1.5	0.145
Residual	108	0.001	926.3		0.2		

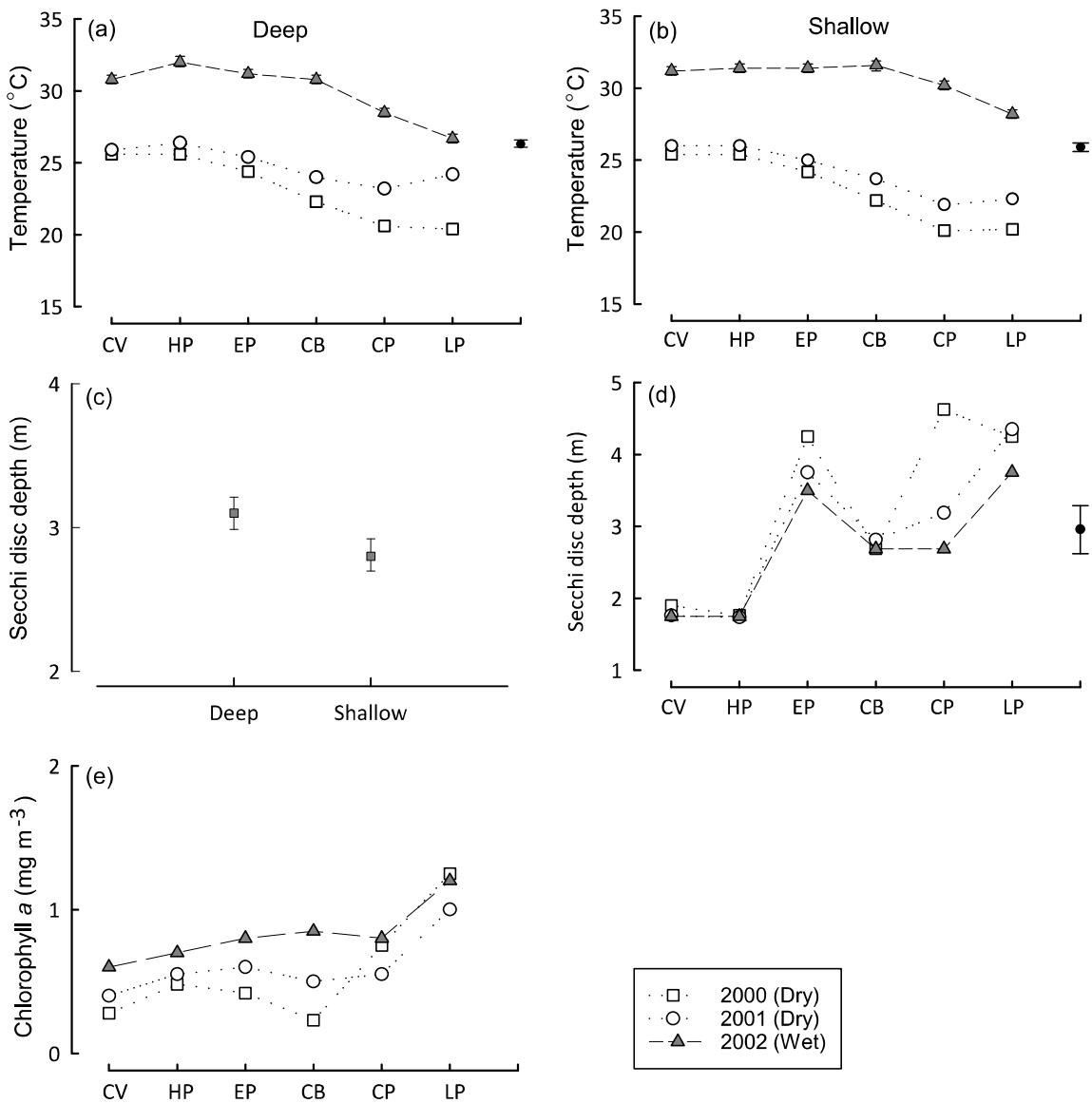


Fig. 5.2. Mean values for water temperature in a) deep water and b) shallow water and for d) Secchi disc depth (water clarity) and e) chlorophyll *a* at the six sampling locations along the north-western Australian coast in the dry seasons of 2000 and 2001 and wet season of 2002. c) Mean Secchi disc depth $\pm 95\%$ confidence intervals in deep and shallow waters. Overall mean and indicative 95% confidence intervals are presented in a), b) and d). All values have been back transformed.

5.3.2 Number of species and relative abundance over reefs during the day

The number of fish species in trap samples collected over reefs during the day in 2000 and 2001 differed significantly among locations and, more marginally, between years (Table 5.3). The mean number of species increased from a minimum at Cape Voltaire in the north to peak at Cape Bossut and then declined to Cape Preston and Locker Point in the south (Fig. 5.3a). The mean number of species was greater in 2001 than 2000 (Fig. 5.3b).

Table 5.3. Mean squares (MS), *F* values and significance levels (*P*) for PERMANOVAs of the numbers of species and catch rates of fishes over reefs in deep and shallow waters during the day at the six sampling locations along the north-western Australian coast in the dry season of 2000 and 2001. df, degrees of freedom.

	df	Number of species			Catch rate		
		MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
Location	5	3.224	7.8	<0.001	128.85	16.8	<0.001
Year (Y)	1	2.035	4.9	0.027	0.683	0.1	0.771
Depth (D)	1	0.786	1.9	0.178	25.996	3.4	0.067
L x Y	5	0.985	2.4	0.052	20.477	2.7	0.031
L x D	5	0.296	0.7	0.607	8.593	1.1	0.356
Y x D	1	0.149	0.3	0.554	1.324	0.2	0.675
L x Y x D	5	0.389	0.9	0.459	6.882	0.9	0.479
Residual	76	0.414			7.648		

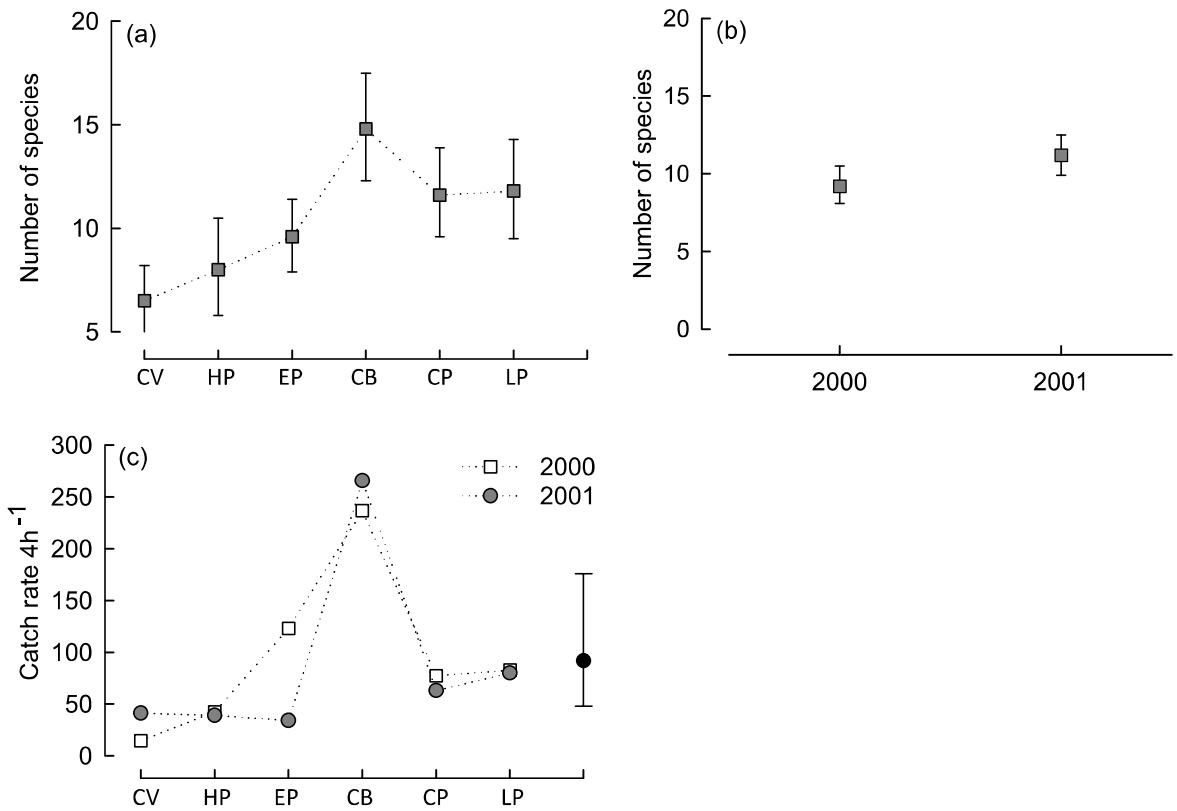


Fig. 5.3. Data for variables derived from sampling over reefs during the day in deep and shallow waters at the six sampling locations along the north-western Australian coast in the dry seasons of 2000 and 2001. Mean numbers of fish species \pm 95% confidence intervals are shown for each location in a) and for 2000 and 2001 in b). c) Mean catch rates of fishes for each location in 2000 and 2001, with overall mean and indicative 95% confidence interval at the right of the plot. All values have been back transformed.

Catch rates differed significantly among locations and there was a marginally significant interaction between location and year (Table 5.3). The trends exhibited by catch rates along the NWA coast in 2000 and 2001 were similar, and essentially parallel those of number of species (Fig. 5.3a), rising to a particularly sharp peak at Cape Bossut and then declining precipitously (Fig. 5.3c). The difference in catch rate between the two years at each of the six locations was small, with the marginal interaction clearly attributable to a somewhat higher value in 2000 at Emeriau Point.

5.3.3 Number of species and relative abundance over reefs during the night

On the basis of data for reef fishes in deep and shallow waters during the night in 2000 and 2001 (dry seasons) and 2002 (wet season), the mean number of fish species differed significantly among locations, years and water depths and there were significant two-way and three-way interactions (Table 5.4). The mean number of fish species in deep water in 2000 declined between Cape Voltaire and Hall Point and then rose progressively to Cape Preston after which they declined to Locker Point in the south (Fig. 5.4a). The trend in 2001 was similar, except that the increase occurred between Emeriau Point and Cape Bossut (Fig. 5.4a). The mean number of species in the wet season of 2002 rose progressively from Cape Voltaire in the north to Cape Bossut and then remained at slightly lower levels at Cape Preston and Locker Point in the south (Fig. 5.4a). In shallow waters at night, the mean number of species at all locations except Locker Point were greater in the two dry seasons than in the wet season and, at all locations except Cape Voltaire, were greater in the dry season of 2001 than in the dry season of 2000 (Fig. 5.4b).

Table 5.4. Mean squares (MS), *F* values and significance levels (*P*) for PERMANOVAs of the numbers of species and catch rates of fishes over reefs in deep and shallow waters during the night at the six sampling locations along the north-western Australian coast in 2000, 2001 (dry seasons) and 2002 (wet season). df, degrees of freedom.

	df	Number of species			Catch rate		
		MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
Location (L)	5	1.66	8.6	<0.001	0.249	2.9	0.015
Year (Y)	2	2.65	13.7	<0.001	0.719	8.4	<0.001
Depth (D)	1	1.48	7.6	0.006	0.217	2.5	0.112
L × Y	10	0.42	2.2	0.021	0.212	2.5	0.010
L × D	5	0.69	3.6	0.004	0.255	3.0	0.014
Y × D	2	0.26	1.3	0.253	0.130	1.5	0.230
L × Y × D	10	0.49	2.6	0.007	1.423	0.1	0.093
Residual	127	0.19			0.085		

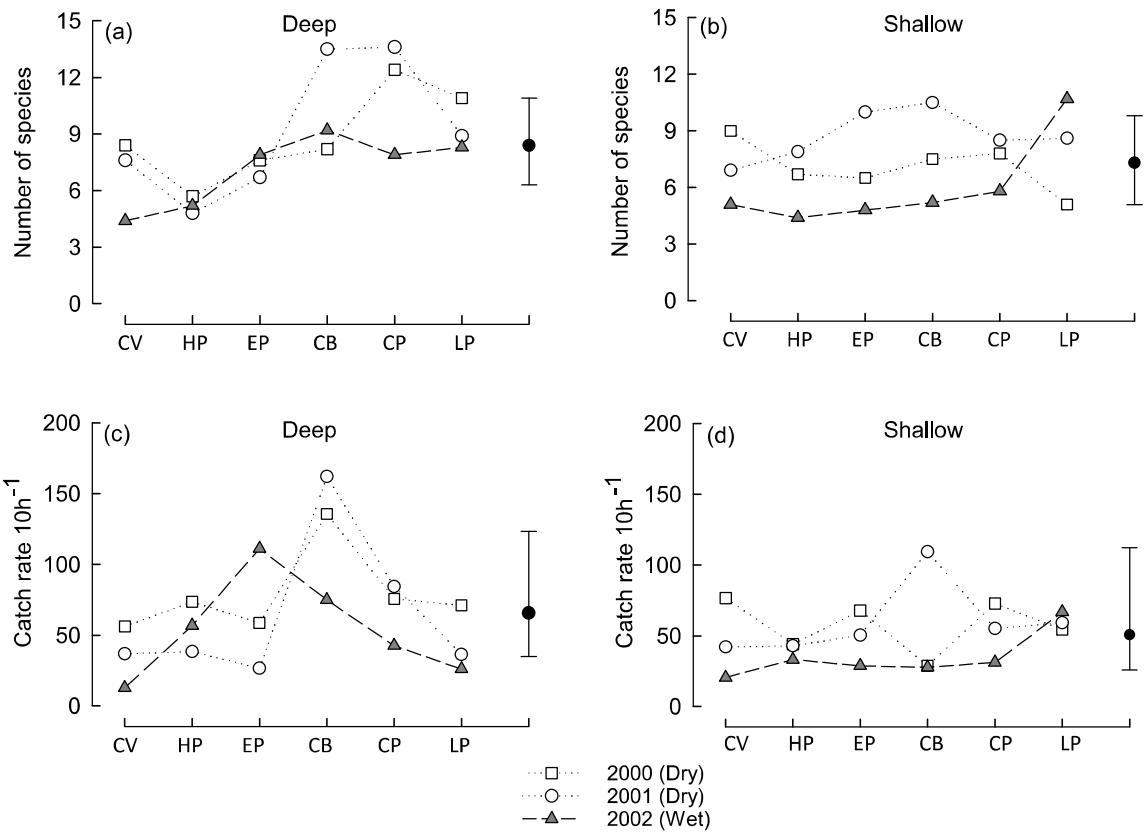


Fig. 5.4. Mean numbers of fish species recorded over reefs during the night in a) deep waters and b) shallow waters at the six sampling locations along the north-western Australian coast in 2000 and 2001 (dry seasons) and 2002 (wet season). a) and c) show the corresponding mean catch rates of fishes in deep and shallow waters. Overall mean and indicative 95% confidence intervals are presented in a) to d). All values have been back transformed.

Catch rates, likewise derived from data for reef fishes in deep and shallow waters at night during the two dry seasons and wet season, differed significantly among locations and years and there were significant interactions between location and both year and depth (Table 5.4). The mean catch rates in the two dry seasons followed similar trends, rising to maxima at Cape Bossut and then declining precipitously to those at Locker Point in the south (Fig. 5.4c). Although mean catch rates in the wet season of 2002 also rose to a peak, that maximum occurred at Emeriau Point, rather than at Cape Bossut.

The trend followed by mean catch rates in shallow water at night in 2001 closely parallels that for deep water in that year, thus likewise rising to a very well defined peak at Cape Bossut (Fig. 5.4d). In contrast, the catch rate in shallow water at that location in 2000 was the lowest recorded for that water depth at any location. The mean catch rate in shallow water at each location in the wet season was almost invariably less than the corresponding values for the two dry seasons and, unlike the situation in deep water, did not rise to a peak at Emeriau Point. Note, however, the larger degree of uncertainty in mean catch rates for all the combinations of location, year and depth, evident also from the relatively modest *F* values in the PERMANOVA analysis for catch rates (Table 5.4). The dominant term there is seen to be the year main effect, clearly attributable from the plot to differences between the wet and dry seasons (Fig. 5.4c,d).

5.3.4 Number of species and relative abundance over reefs during the day and night

For both the mean number of species and mean catch rate of fishes over reefs during the day and night in 2002 (wet season), the main effects of location, depth and day vs night were significant and there was a significant interaction between location and

depth (Table 5.5). The mean number of species and catch rates were both markedly greater during the day than night (Fig. 5.5a,c).

The mean number of species in deep water increased progressively from Cape Voltaire to Emeriau Point and then declined, whereas, in shallow water, it increased progressively in a southwards direction (Fig. 5.5b). The mean catch rates in deep water followed a similar pattern of change to that of number of species in that depth, except that it rose to a particularly sharp peak at Emeriau Point (Fig. 5.5d). The mean catch rates in shallow water were least at Cape Voltaire and greatest at Locker Point with those for the intermediate locations being similar.

Table 5.5. Mean squares (MS), *F* values and significance levels (*P*) for PERMANOVAs of the numbers of species and catch rates of fishes over reefs in deep and shallow waters during the day and night at the six sampling locations along the north-western Australian coast in the wet season of 2002. df, degrees of freedom.

	df	Number of species			Catch rate		
		MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
Location (L)	5	1.512	5.1	<0.001	0.814	8.1	<0.001
Depth (D)	1	1.372	4.6	0.033	0.511	5.1	0.027
Day/Night (N)	1	4.618	15.6	<0.001	0.632	6.3	0.013
L × D	5	0.946	3.2	0.009	0.355	3.5	0.005
L × N	5	0.473	1.6	0.163	0.092	0.9	0.477
D × N	1	0.001	<0.01	0.956	0.005	0.1	0.822
L × D × N	5	0.071	0.2	0.944	0.099	1.0	0.429
Residual	88	0.294			0.100		

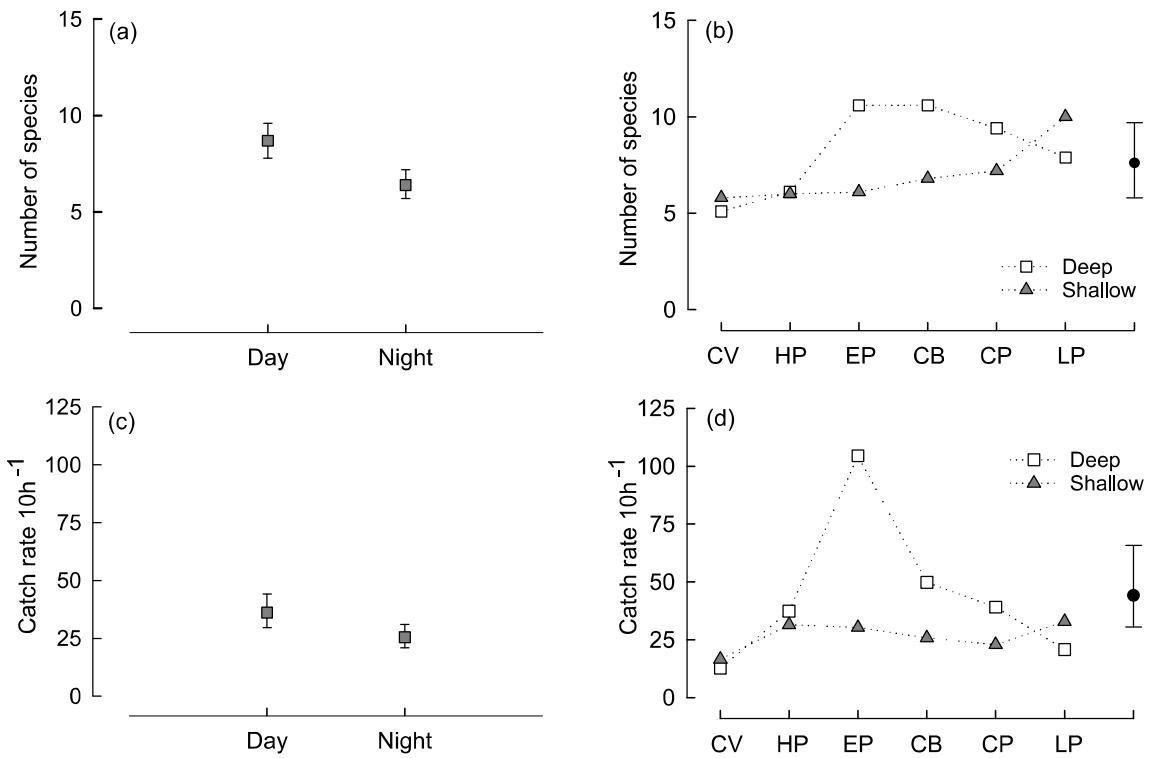


Fig. 5.5. (a) Mean number of species and c) mean catch rates of fishes during the day and night in the wet season of 2002 and b) mean numbers of species and d) mean catch rates of fishes in deep and shallow waters at the six sampling locations along the north-western Australian coast in the same wet season. Overall mean and indicative 95% confidence intervals are presented in b) and d). All values have been back transformed.

5.4 Discussion

This is the first study to use an integrated sampling and statistical approach to obtain and analyse data for fishes over inshore reefs at several widely-spaced locations, to determine how the numbers of species and abundances (catch rates) of reef fishes change with latitude along an extensive tropical coast and are related to water depth, season and day *vs* night. Emphasis was first placed on determining whether the number of species and abundance of fishes on that coast decreased with latitude, *i.e.* poleward, as typically occurs in marine waters in various parts of the world and particularly with number of species (e.g. Bellwood and Hughes, 2001; Connolly et al., 2003; Hillebrand, 2004b; Mellin et al., 2010; Tittensor et al., 2010; Parravicini et al., 2013; Stuart-Smith et al., 2013). As the trends exhibited by the number of species and catch rates of fishes did not follow the traditional paradigm, the potential reasons for such divergence were then explored. Such divergence could usually be related to marked differences between the environmental conditions in the three bioregions along that axis, *i.e.* Kimberley in the north, Canning in the centre and Pilbara in the south (Semeniuk, 1993; Cresswell et al., 2011; Cresswell and Semeniuk, 2011; Wilson, 2013). The data next facilitated an exploration of whether the direction of the difference between the number of species and/or the abundance of fishes over reefs remains the same in deep *vs* shallow waters, dry *vs* wet seasons and day *vs* night, along the full latitudinal range of the NWA coast.

5.4.1 Latitudinal trends in species richness and abundance

As the tropical NWA coast, sampled during the present study, extends for ~1,500 km in a south-westerly direction from Cape Voltaire in the north to Locker Point in the

south, it corresponds to a north-south distance of ~850 km. This represents a substantial latitudinal range of ~8°, which thus provided an appropriate basis for exploring the relationships between the trends exhibited by biotic variables and latitude. Although this coastline is of great biogeographical interest (Fox and Beckley, 2005; Wilson, 2013) and its resources subject to commercial and recreational fishing (Fletcher and Santoro, 2015; Ryan et al., 2015) and industrial developments and tourism (Smallwood et al., 2011; PDC, 2015), the present study provides the first combined quantitative data for the number of species and abundance of fishes over reefs at intervals along this important coast.

Although water temperature declines in a southwards direction along the NWA coast, neither the number of species nor catch rates of fishes followed that trend in either deep or shallow waters, wet or dry seasons or during the day or night. Indeed, the mean number of species and abundance of fishes over reefs were less in the more northern locations (Kimberley Bioregion) than southern locations (Pilbara Bioregion), which, in the case of species richness, parallels the earlier results of Hutchins (2001) and Fox & Beckley (2005), based on essentially presence/absence data for these two bioregions. As the development of coral reefs is typically inversely related to water clarity (Montaggioni, 2005), it appears relevant that the values for Secchi disc depth are greater at the two most southern locations than at the two most northern locations. It is thus hypothesised that the volume, structure and/or complexity of reefs is greater in the more southern than northern locations and thus provide a more optimal environment for reef fishes. Although there are no published data comparing the characteristics of the types of reefs along the NWA coast, on which this study was based, examination of extensive video footage of those reefs along that coast is consistent with this suggestion (Travers unpublished data),

with the data of Lyne et al. (2006) and McLean et al. (2017) emphasising that reef development in the Pilbara Bioregion is extensive.

5.4.2 Species richness and abundance of fishes at intermediate latitudes in the dry season

From the above, it follows that the ichthyofauna of the NWA coast does not follow the traditional paradigm that, on the basis of data from a range of taxa, including fishes, corals, marine gastropods and bivalves, the number of species and abundance decreases with latitude and thus with decreasing water temperature (Bellwood and Hughes, 2001; Connolly et al., 2003; Floeter et al., 2004; Connolly et al., 2005; Floeter et al., 2005; Rex et al., 2005; Jablonski et al., 2006; Arakaki et al., 2014). Although the numbers of species and abundances of fishes over reefs were both greater at the locations at higher than lower latitudes along the NWA coast, the maximum values for these two biotic variables were recorded at locations at intermediate latitudes. This strongly suggests that the pattern of latitudinal change exhibited by these biotic variables is influenced markedly by differences between the environmental characteristics at the various locations representing the three bioregions and that these over-ride any overall directional trend with latitude. This parallels the conclusion by Wilson (2013) that, in the case of molluscs and other marine invertebrates, strong regional environmental factors outweigh any latitudinal diversity gradient along the NWA coast.

It was striking that, during the day in the dry seasons of 2000 and 2001, the mean number of species and catch rates of fishes over reefs both reached a maximum at Cape Bossut in the Canning Bioregion, with the catch rates in both years producing a

particularly sharp peak at that location. Furthermore, during the night, the mean number of species, and especially catch rates, also peaked at Cape Bossut in deep water in those dry seasons and in shallow water in 2001. These pronounced peaks in species richness and abundance at Cape Bossut imply that, during both the day and night in the dry season, the reef environment at that location is particularly favorable for habitation by the reef fish species that live along the NWA coast.

The paucity of published data on the structure and complexity of the type of reefs, in which fishes were sampled in the Canning Bioregion in general and Cape Bossut in particular, make it difficult to establish why those reefs are so conducive to occupation by fishes. However, as corals flourish in waters of low productivity (Montaggioni, 2005), it appears relevant that, on the basis of remotely-sensed measurements made at 8 day intervals, chlorophyll *a* concentrations during the dry season are far less along the stretch of Canning coast in which Cape Bossut is located, than anywhere else along the full length of the NWA coast and thus including those of both the Kimberley and Pilbara bioregions (Condie & Dunn, 2006). The low chlorophyll *a* concentrations recorded at Cape Bossut at the time of sampling in the dry season in 2000 and 2001, and thus essentially representing one off measurements are consistent with those trends (Fig. 5.5e). The low primary productivity therefore suggests that conditions are optimal for reef development and thus for providing good habitat for fishes at Cape Bossut. The low productivity at Cape Bossut would also account for the species richness and abundance of fishes over soft substrata adjacent to reefs constituting the lowest recorded at any location along the NWA coast (Chapter 3).

The amount of cover available for fishes on the reefs in and around Cape Bossut would be enhanced by the presence, on those reefs, of extensive filter-feeding communities, comprising alcyonarian sea whips and gorgonians, a wide variety of sponges and ascidians (Lyne et al., 2006; Keesing et al., 2011), and therefore contribute to the particularly high species richness and abundance of fishes at this location. As the very high abundances of fishes over reefs at Cape Bossut during the dry season were due, in particular, to the presence of exceptionally large numbers of *Lethrinus punctulatus*, the characteristics of those reefs must provide a particularly suitable habitat for this lethrinid. The very large numbers of this species at Cape Bossut are illustrated by the overall mean catch rate of this lethrinid at this location in the dry seasons reaching a level as high as 87 fish $(10\text{ h})^{-1}$, which corresponds to 32% of the total catch. That mean catch rate exceeds by a factor of two times that recorded for *Lethrinus punctulatus* at Cape Preston, where this lethrinid was also the most abundant species.

5.4.3 Species richness and abundance of fishes at intermediate latitudes in the wet season

Although the mean values for species richness and abundance of fishes in deep water during the wet season at Cape Bossut in the Canning Bioregion were the highest and second highest among locations, respectively, those values were not appreciably greater than at other locations and, in the case of catch rate in particular, did not produce the very pronounced peak exhibited in both deep and shallow waters during the dry season. Furthermore, neither species richness nor abundance in shallow waters at Cape

Bossut during the wet season showed any tendency to be greater than those at other locations.

The shift in the wet season at Cape Bossut, from relatively very high catch rates in the dry season to far lower values in deep water and even more particularly shallow water in the wet season, was due mainly to a massive decline in the abundance of *L. punctulatus*. Thus, the overall mean catch rate of this lethrinid at Cape Bossut at night fell precipitously from 65 (10 h)⁻¹ in the dry season to 5 (10 h)⁻¹ during the wet season. Furthermore, the same pronounced downwards trend between dry and wet seasons was exhibited by the next five most abundant species, *i.e.* *Lutjanus carponotatus*, *Lethrinus laticaudis*, *Gnathanodon speciosus*, *Abalistes stellatus* and *Siganus fuscescens*. The above differences in the relative abundance of fishes in different water depths in the dry and wet seasons, strongly suggest that, during the wet season, the above six species exhibit a very strong tendency to move out of shallow waters and for some to move beyond the sampling sites, before returning to deep and shallow waters during the following dry season. Such movements would enable these species to avoid the effects of the turbulent water conditions present in inshore waters during the wet season.

Although both species richness and abundance of fishes typically peaked at Cape Bossut during the dry season, the catch rate in deep water during the wet season reached its maximum at Emeriau Point at the northern end of the Canning Bioregion (Fig. 5.4c), due, in particular, to substantial numbers of *L. carponotatus* and *L. laticaudius*. In contrast, the catch rates, and also species richness, in shallow water at Emeriau Point during the wet season were low and far less than in deep water. It is highly relevant that, at Emeriau Point, the catch rate (and also species richness) in shallow water were less in the wet

season than in both dry seasons, whereas the reverse was the case for catch rate in deep water. This clearly implies that, at Emeriau Point in the wet season, species tend to move out from shallow waters and to congregate in deeper waters, including those sampled in the current study.

The trends exhibited by catch rates in deep water in dry and wet seasons (Fig. 5.4c) provide a particularly good example of the ways in which there can be a strong interaction between location and season for such a biotic variable and thus the danger of using data from just one or two sampling occasions for generalising on the relationships between a biotic variable and other factors. Thus, as already discussed above, the catch rate in deep water was greater in the wet season than two dry seasons at Emeriau Point, whereas the reverse was true for Cape Bossut, the other sampling location in the Canning Bioregion, noting that the trends exhibited from Cape Voltaire in the North to Locker Point in the south were consistent in the dry seasons in two successive years.

5.4.4 Species richness and abundance in deep vs shallow water and day vs night

The results of this study demonstrated that, during the ‘stable’ dry season, neither the species richness nor the abundance of fishes over reefs along the NWA coast was related to depth. While the lack of such a distinction with these two biotic variables runs counter to the results of a number of other studies (e.g. Moranta et al., 1998; Leathwick et al., 2006; Zintzen et al., 2012; Anderson et al., 2013), it should be borne in mind that, in contrast to those particular studies, the means for the deep and shallow water depths in the current study differed by only ~10 m. While Friedlander et al. (2010) demonstrated that the number of species and density of fishes over reefs at an unexploited remote atoll

in the central North Pacific increased with water depth, that trend was based on visual observations using SCUBA and was largely driven by increases in the abundance of planktivores. On the basis of samples from water depths, similar to those in the current study, and in eight consecutive seasons, the species richness and density of fishes over soft substrata at locations along the lower west coast of Australia were not consistently related to water depth (Hyndes et al., 1999). Likewise, the mean number of species and total abundance over soft substrata varied inconsistently among depths, locations and sites along the lower east coast of Australia (Connell and Lincoln-Smith, 1999).

In contrast to the situation in the dry season, the species richness and catch rate of fishes in the wet season were both related to depth, with interactions with location. The values for both biotic variables were appreciably greater in deep than shallow waters at the two locations sampled in the Canning Bioregion, presumably reflecting movement of fishes into deeper and less turbulent waters (see previous section), whereas they were essentially the same at the two locations in the Kimberley Bioregion at which both deep and shallow waters are turbulent throughout the year.

On the basis of the samples collected over the same time interval, *i.e.* 10 h in the wet season of 2002, species richness and catch rate were greater during the day than night. As there was no interaction between either of those biotic variables and either location or water depth, those diel differences were maintained in both water depths along the full extent of the NWA coastline. The greater species richness and abundance during the day parallels the trend recorded for reefs elsewhere in tropical (Galzin, 1987; Rooker et al., 1997; Nagelkerken et al., 2000a) and temperate waters (Azzurro et al., 2007; Harvey et al., 2012a; Myers et al., 2016). The results contrast with those of a trap study

on the Great Barrier Reef which demonstrated greater abundance of fishes during the night than day (Newman and Williams, 1995), however, the two fish species that predominantly drove that trend were either not recorded in the present study (*Lutjanus adetii*) or in very low numbers (*Lutjanus quinquefasciatus*) at the two locations where they were recorded. The greater species richness and catch rate in baited traps during the day than night presumably reflects, in part, a greater tendency for the carnivorous fishes found over reefs on the NWA coast to feed during the day. A tracking study in north-eastern Australia of *Lethrinus miniatus* (Currey et al., 2015) also showed, however, that this lethrinid can move at night from reefs to over soft substrata and thereby also contribute to the abundances over reefs relatively greater during the day than night.

The multivariate methods employed in Chapter 4 demonstrated that diel differences in the compositions of fishes over reefs along the NWA coast were due to species, such as *Lethrinus laticaudis*, *Lethrinus punctulatus*, *Lethrinus nebulosus* and *Choerodon cyanodus*, being more abundant in traps set during the day. *Lethrinus nebulosus* was also more abundant in traps set during day than at night in deeper and more offshore waters beyond those sampled in the present study area (Anonymous, 1990) and *Choerodon rubescens*, a congener of *C. cyanodus*, was shown by baited underwater videos to be more abundant over reefs during the day at the Houtman Abrolhos Islands, further south on the west coast of Australia (Harvey et al., 2012b). In contrast to the trends exhibited by a number of species on the NWA coast, *Lutjanus johnii* was more abundant in the traps set during the night than day (Chapter 4), with the physiological features of its eyes adapted for vision in low light intensities (Lythgoe et al., 1994).

5.4.5 Conclusions

The results of this study clearly demonstrate that species richness and abundance of fishes over reefs along the NWA coast in the dry season do not follow the traditional trend of declining in a polewards direction. It is proposed that the greater values for these biotic variables at the more southern than northern latitudes are related to better developed reefs in the less turbid Pilbara Bioregion and thus to a better habitat for fishes. Species richness and abundance of fishes actually peaked sharply, however, at intermediate latitudes, *i.e.* in the central Canning Bioregion, due in particular to very large numbers of lethrinids such as *Lethrinus punctulatus*, which is endemic to north-western Australia and also one of the top five commercially targeted fish species in deeper offshore waters along the NWA coast (Fletcher and Santoro, 2015). This trend presumably reflects an over-riding influence of differences between the reefs in that bioregion and those in the northern Kimberley Bioregion and southern Pilbara Bioregion. It thus appears relevant that the well-developed reefs in the Canning Bioregion are structurally more complex through an abundance of filter-feeding fauna, comprising mainly sea whips, gorgonians, sponges and ascidians.

During the ‘stable’ dry season, the species richness and abundance of fishes did not differ with water depth. Both biotic variables were greater during the day than night, reflecting a greater tendency for species such as *Lethrinus laticaudis*, *Lethrinus punctulatus*, *Lethrinus nebulosus* and *Choerodon cyanodus* to be more abundant in traps set during the day.

The results of analyses of the catch rates of fishes in the dry and wet seasons, together with abundance data of individual species, imply that many individuals of certain

species move out of shallow water during the wet season when those waters are especially turbulent. They also suggested that, in the Canning Bioregion, there was a greater tendency for individuals to congregate over reefs in deeper waters at one location than the other location, possibly reflecting a greater movement of individuals at that other location to habitats beyond those reefs.

One of the most important findings of this study is that the number of species and abundance of fishes were greatest at the intermediate locations, *i.e.* in the Canning Bioregion as previous studies of fishes and other marine fauna along the NWA coast had focused on the Kimberley and Pilbara bioregions.

Chapter 6. General Discussion

The composite studies undertaken for this thesis have elucidated the ichthyofaunal characteristics of the fish faunas over soft substrata and reefs in inshore shallow and slightly deeper waters along the extensive (1,500km) and remote tropical coast of north-western Australia (NWA). These studies demonstrated that, in the case of both habitat types, the species composition of fishes changed progressively with increasing latitude (Chapters 2, 3 and 4), whereas the species richness and abundance of fishes did not follow the trend typically recorded elsewhere, *i.e.* to decline with latitude (Chapters 3 and 5). Multivariate analyses emphasised that the species composition over soft substrata and reefs were very different and demonstrated that composition differed between deep and shallow water, between wet and dry seasons and between day and night, and identified the species responsible for the main differences in each of those comparisons (Chapters 3 and 4). Focus was placed on elucidating, in the case of both multivariate and univariate measures, whether any differences are maintained along the full length of the NWA coast. The potential environmental factors that could account for latitudinal differences in the multivariate and univariate measures were explored.

Care was taken to design a sampling regime, which obtained for robust statistical analyses, an appropriate number of quantitative replicate samples of fishes from deep and shallow waters over both soft substrata and reefs at seven regularly-spaced intervals along the NWA coast during both dry and wet seasons. The resultant high quality data were thus able to be subjected with confidence to the range of multivariate and univariate statistical analyses required for testing various hypotheses. This involved, not only the use

of traditional PERMANOVA, ANOSIM and non-metric multi-dimensional scaling (nMDS) ordination, but also SIMPROF and LINKTREE (Clarke et al., 2008). The use of SIMPROF established, without any *a priori* assumptions, those samples that formed groups whose compositions were similar and statistically different from other such groups, while LINKTREE elucidated the environmental variables that explained variations in ichthyofaunal composition among locations, water depths and seasons (see Chapters 3, 4).

The following Discussion focuses on outlining and integrating the main results and conclusions of this thesis regarding the species composition, number of species and abundance of fishes over the two main habitats along a continuous and extensive tropical coastline and highlighting the crucial factors to which those characteristics are related. The results and implications of these data have greatly increased our knowledge of the ecology and zoogeographical relevance of the inshore waters of this important but relatively little studied geographical region. In addition, they provide the crucial baseline data that will be required, in the future, to detect any changes in the ichthyofaunas that occur as a result of fishing, climate change and other effects.

6.1 Latitudinal (temperature) and bioregional trends in ichthyofaunal composition

CLUSTER analysis and nMDS ordination, derived from percentage contributions of individual species to the samples obtained from regularly-spaced locations, clearly demonstrated visually that the species compositions of the ichthyofaunas over both soft substrata and reefs followed a similar progressive change with increasing latitude down the tropical NWA coast. Furthermore, the RELATE test emphasised that this sequential

latitudinal change in composition in both habitat types is associated with declining water temperature. The parallel sequential changes in composition in both habitat types reflect the progressive loss of some species between the northern and southern locations, and a concomitant introduction of new species. For example, over soft substrata, species such as *Leiognathus splendens* and *Secutor insidiator* were super-abundant at the two most northern locations and yet were not caught at any of the five locations further south, while the reverse trend was exhibited by *Pristotis obtusirostris*. Similarly, over reefs, *Lutjanus johnii* made a relatively large contribution to the catches at the two most northern locations, but was absent from those further south, whereas *Lethrinus atkinsoni* and its congener *L. genivittatus* were confined to more southern locations. The basis for these types of differences are clearly related, in part, to differences between the environmental characteristics of the Kimberley Bioregion in the north and the Canning and Pilbara bioregions in the south, which are discussed below. Similar sequential latitudinal (temperature) trends to those now recorded for NWA have been described for ichthyofaunas in other parts of the world, including over reefs in Brazil (Floeter et al., 2001) and the Great Barrier Reef in north-eastern Australia (Williams, 1991; Cappo et al., 2007) and over soft substrata on the west coast of North America (Jay 1996) and in the East Atlantic (Macpherson and Duarte, 1994).

The use of the SIMPROF routine, employing the same quantitative contribution data as used for the above multivariate analyses, emphasised that, in terms of composition, the ichthyofaunas of each of the three bioregions along this coast, *i.e.* Kimberley, Canning and Pilbara, are discrete. There is thus a partial disruption in the continuity of the progressive poleward change in ichthyofaunal composition over both

soft substrata and reefs along the NWA coast, with the composition of the Kimberley Bioregion the most discrete. The multivariate analyses of Hutchins (2001a) and Fox and Beckley (2005), which employed essentially the presence or absence of species at intervals along the entire western Australian coastline, also emphasised that the composition of the fish faunas of the Kimberley Bioregion was particularly distinct. The Canning Bioregion was scarcely represented, however, in the datasets used for those two studies. In the context of reefs, the results presented in this thesis have drawn attention to the hitherto unrecognised importance of this habitat as a reservoir of high species richness and abundance of fishes in this understudied bioregion (Chapter 5).

LINKTREE highlighted that, in both habitat types, the differences between the ichthyofaunal composition of the Kimberley Bioregion and those of both the Canning and Pilbara bioregions were explained by the influence of a far greater tidal range and turbidity in the Kimberley. It is thus not surprising that the most distinctive feature of the ichthyofauna of the Kimberley Bioregion was the very high abundances over soft substrata of several species of leiognathid and over reefs of certain lutjanids, and thus representing families that are particularly well adapted to living in waters in which visibility is limited. These adaptations include the possession of bioluminescence by leiognathids (Woodland et al., 2002; Sparks et al., 2005; Borsa et al., 2007) and very well developed eyes by lutjanids (Lythgoe et al., 1994; Anderson and Allen, 2001).

The distinctions between the ichthyofauna of the Canning and Pilbara bioregions, in the case of reefs during both the wet and dry seasons and of soft substrata during the dry season, was mainly explained by the effects of a greater tidal range in the Canning. The fact that ichthyofaunal compositions in the Canning and Pilbara bioregions were not

clearly discrete during the wet season accounts for LINKTREE not highlighting any environmental factor that differentially influenced the ichthyofaunas in those two bioregions during that season.

6.2 Comparisons of the compositions of the fish faunas over soft substrata and reefs

This thesis demonstrated statistically that the species composition of the fish faunas over soft substrata differed markedly from those over reefs at the seven locations sampled along the NWA coast. This point is emphasised by the discovery that, while as many as 285 and 132 species, respectively, were recorded over soft substrata and reefs along that coast, only 56 of these species were common to both habitat types and thus represented just 15.5% of the total number of species recorded across both habitat types. Furthermore, only 22% of the genera and 38% of the families of fishes were common to both soft substrata and reefs.

Comparisons of the tabulated data in Chapter 2 emphasise that the catches over soft substrata and reefs were both dominated by two (but different) families, which were each represented by several species. Thus, the Leiognathidae with 10 species and Carangidae with 29 species, contributed over 50% to the catches over soft substrata, while the Lethrinidae with 12 species and Lutjanidae with 14 species comprised over 80% of those taken over reefs. The trend for leiognathids to be particularly abundant over soft substrata parallels that found in this habitat type elsewhere in tropical waters of the Indo-Pacific, where the protrusible mouths of these species facilitates the extraction of their benthic macro-invertebrate prey from the substrata (Jaybalan, 1991; Woodland et al., 2001; Hajisamae et al., 2003). The presence over reefs of a large number of lethrinids and

lutjanids, which are carnivorous and adapted to feeding on such prey, is a characteristic of the fish faunas of this habitat type in all major oceans, apart from the Atlantic (Anderson and Allen, 2001; Carpenter, 2001).

6.3 Relationships between ichthyofaunal composition and season, water depth and day vs night

The use of two-way crossed ANOSIM emphasised that the ichthyofaunal composition, over both soft substrata and reefs, was related more to location (latitude) than to either season or water depth or to a diel effect in the case of reefs. However, comparisons of the R statistic values for those variables revealed that ichthyofaunal composition was more closely related to season and water depth in the case of soft substrata than with reefs.

The greater 'influence' of factors associated with season over soft substrata than reefs presumably reflects, in part, the fact that certain species in this open habitat will be particularly susceptible to the extreme environmental changes that occur in the wet season and particularly following cyclonic events, than would typically be the case around reefs which would provide a measure of protection.

Depth-related differences reflected a greater tendency for fish species to be more abundant in shallow than deep waters at locations where the habitat occupied by their juveniles is well represented, e.g. seagrass beds and mangrove forests. For example, *Lethrinus genivittatus* was relatively more abundant in shallow than deep water over soft substrata at Locker Point, where seagrass meadows are prevalent in nearshore waters, and the same trend was exhibited by *Lethrinus laticaudis* over reefs at that location.

In terms of the diel effect, for which data could only be recorded for reefs during the wet season, examples were provided by the greater abundances of *Choerodon cyanodus*, *Epinephelus coioides* and *Abalistes stellatus* during the day at three or four locations and the reverse trend for *Lutjanus johnii* at night.

6.4 Species richness and abundance

It was particularly striking that, during the dry season, the species richness and density of fishes over soft substrata, and particularly in deeper waters, both exhibited the same concave pattern of decline and then rise along this coast, with their minima in the central Canning Bioregion (Chapter 3). This trend was attributed to that bioregion having the lowest productivity of any of the three bioregions (Condie and Dunn, 2006). The fact that reefs flourish in less productive environments (Montaggioni, 2005) then accounts for the species richness and catch rates of fishes over reefs in the dry season exhibiting the reverse trend, *i.e.* a convex pattern of rise and then decline (Chapter 5).

Although the species richness and density of fishes over soft substrata in the wet season also declined southwards to low levels at Emeriau Point and Cape Bossut in the Canning Bioregion, they did not subsequently increase to the same extent as with Cape Preston and Locker Point in the Pilbara (Chapter 3). As with the dry season, species richness and densities over reefs in the wet season exhibited the inverse trend of that over soft substrata (Chapters 3,5). Thus, the trends exhibited by these two biotic variables with latitude were similar in both habitats during the dry and wet seasons.

The above similarity accounts for the fact that, even when the data for species richness over soft substrata and over reefs during the dry and wet seasons are combined,

there is still clearly an inverse and significant relationship between species richness in these two habitat types (Fig. 6.1a), and the same is true for the Shannon-Wiener diversity index (Fig. 6.1b). Since the ichthyofaunal compositions of these two habitats are so different, with only 56 of the 389 species recorded in both habitat types, and just two of these were abundant in both habitat types, it seems unlikely that the above inverse trends reflect the effects of predation on species in one or both of the habitats. Indeed, as the main species over each habitat are adapted to that particular habitat, the amount of interaction between species in the two habitats will be limited.

Although the inverse trends exhibited by species richness, and also relative abundance, over soft substrata and reefs, may reflect an inverse relationship between the areas and/or quality of these two habitats along the NWA coast, there are insufficient data on those habitat types at the locations sampled during this thesis to confirm whether or not this is the case. There is thus clearly a need to develop a better understanding of the extent and morphological characteristics of the two main habitat types along the NWA coast, before it is possible to determine the basis for the remarkable inverse relationship between the number of species and abundance of fishes over soft substrata and reefs.

The above concave trend exhibited by species richness and density of fishes over soft substrata and the reverse convex trend exhibited by species richness and catch rate of fishes over reefs, emphasise that neither of these biotic variables decline progressively with latitude along the NWA coast. This runs counter to the generalisation that species richness and abundance decline in a polewards direction (e.g. Jablonski et al., 2006; Tittensor et al., 2010; Arakaki et al., 2014). In the case of reefs, the high species richness and abundance of fishes in the central Canning Bioregion reiterate the need for the

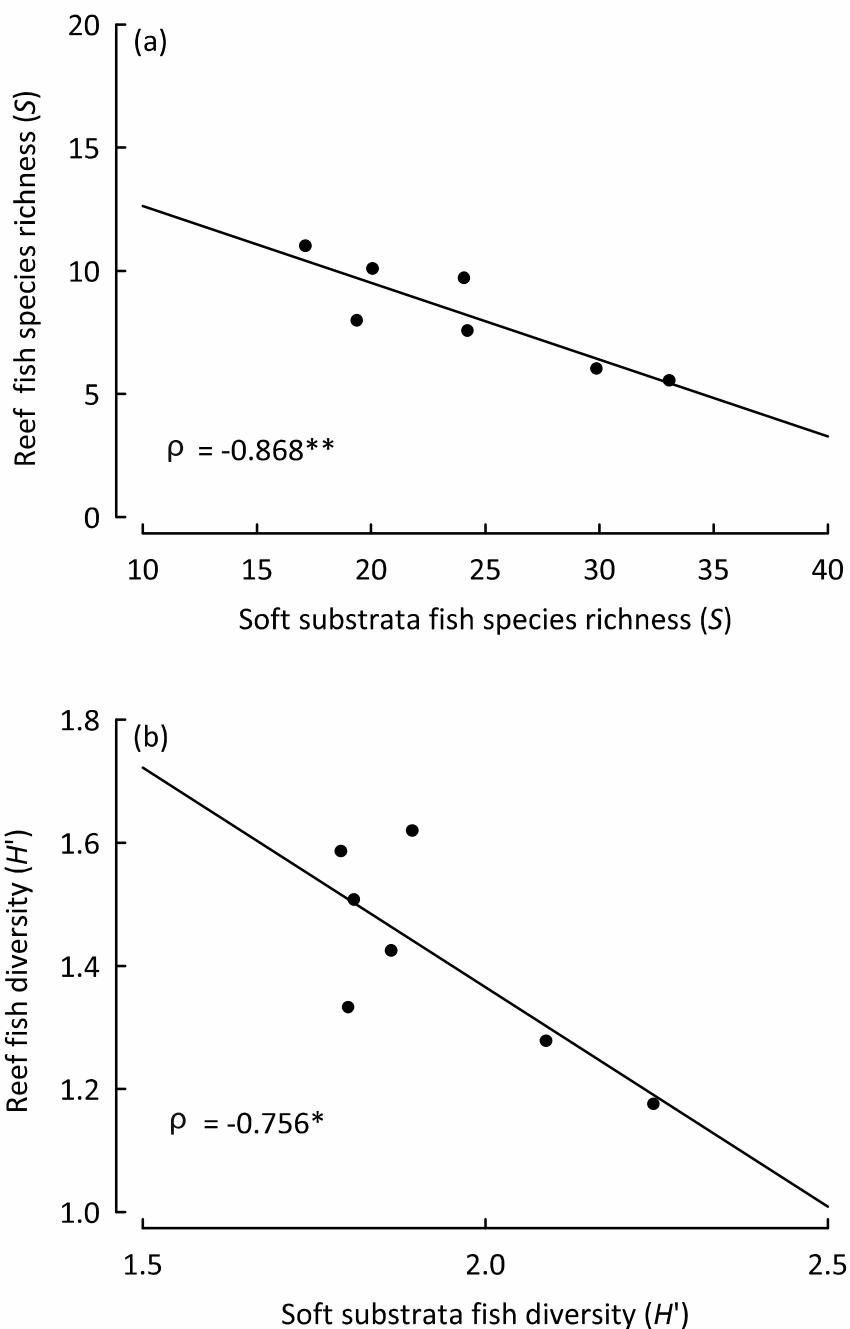


Fig. 6.1. Relationships between the diversity of fishes over soft substrata and reefs at each of the seven locations sampled along the north-western Australian coast expressed as a) mean number of fish species (S) and b) Shannon-Wiener diversity (H'). The Pearson correlation coefficient (ρ) and line of best linear fit are shown in each plot, together with significance level. *; $P < 0.05$, **; $P < 0.001$.

collection of more data on the neglected ichthyofauna and more particularly the extent and morphological characteristics of the reefs of this bioregion.

The plot shown in Fig. 3.2 in Chapter 3 demonstrates very clearly that, over soft substrata in both deep and shallow waters, the main difference between the univariate biotic measures in the wet and dry seasons resides in a greater species richness and more particularly density in the wet than dry season. As discussed earlier, this marked difference is presumably related, at least in part, to the increase in productivity brought about by a large input of nutrients and organic material in the massive discharge of freshwater that occurs from rivers in this season (McKinnon et al., 2015a). Such productivity would be particularly beneficial to the juveniles of a number of fish species that were caught in trawls in shallow waters in the different sampling locations during that season.

In the case of reefs, the number of species and catch rate of fishes in shallow waters were almost invariably greater in the dry than wet season (Chapter 5). It was suggested that this reflected a movement of substantial numbers of certain species from the more turbulent shallow waters to the more ‘stable’ deeper waters. The fact that, at Emeriau Point, the catch rate in deep water was far greater in the wet season than in either of the two dry seasons, suggests that there has been a particularly strong tendency for certain species to congregate more offshore during extreme weather conditions.

This thesis demonstrated that, on the basis of samples collected during the day from regularly-spaced locations along the extensive NWA coast, species richness and density over soft substrata were not consistently greater in one water depth than the other in either the dry or wet season (Chapter 3). Indeed, in the case of density over soft

substrata, there was a strong three-way interaction between location, season and depth. There was also a strong interaction between location and depth for both the number of species and catch rates over reefs. This reflected the contrast between markedly greater values for both species richness and abundance of fishes in deep than shallow water in the two locations in the Canning Bioregion, whereas they were typically similar in each of the two water depths at each of the other locations. The above findings demonstrate the importance of obtaining samples from a sufficiently wide distribution, when attempting to determine whether those two biotic variables are characteristically greater in shallow than deeper water or *vice versa*.

As it was not possible to trawl at night, exploration of whether there was a diel effect with either species richness or abundance was only possible with reefs in the wet season of 2002, during which trap samples were able to be obtained during 10 h of sampling during both the day and the night. The resultant data clearly showed that both of these biotic variables were greater during the day than night, reflecting the fact that most of the species over reefs feed during the day (Chapter 5). This diel effect parallels that recorded for fishes over reefs elsewhere (Nagelkerken et al., 2000a; Harvey et al., 2012b; Myers et al., 2016).

6.5 Zoogeography of tropical north-western Australian fishes

The vast majority of fish species recorded for the NWA coast during this study have a wide-ranging tropical distribution with a strong Indo-Pacific affinity, which reflects the direct connection to the Pacific Ocean provided by the Indonesian Throughflow current that flows southwards from the wider Pacific Ocean towards the NWA coast (Gordon, 2005; Domingues et al., 2007). This transport mechanism also accounts for the dominance of Indo-west Pacific species among several other faunal taxa in NWA marine waters (Wilson, 2013), such as molluscs (Wells, 1990), echinoderms (Marsh and Marshall, 1983), corals (Hughes et al., 2002b) and crustaceans (Jones, 2003).

It is also noteworthy, however, that the distributions of several species found on the NWA coast were restricted to Australian waters and even to just north-west Australian waters. Thus, Australian endemics accounted for 12% of all species recorded over reefs and as much as 18% of those over soft substrata. Endemism values greater than 10% within a region are considered by Briggs and Bowen (2012) to be indicative of marine biogeographic provincial status. Furthermore, the Blue-spotted Emperor *Lethrinus punctulatus*, which only occurs in north-western Australia, accounted for 35% of the total catch of fishes over reefs. The relatively high levels of endemism contrast with the lower values recorded by Hutchins (1999) along the Kimberley coast where only 8% of the 469 species recorded were restricted to Australia.

The endemic species contained several with characteristics that would limit their ability to disperse widely (Randall, 1998) and would thus help explain their limited distributions (Hughes et al., 2002a; Jones et al., 2002). For example, some of these species exhibit parental care, such as the oral brooders *Apogon unitaeniatus* and *Siphamia*

cuniciceps and those which deposit and guard their eggs in burrows such as *Halophyrne ocellatus*.

6.6 Management implications and directions for future research

The development in this thesis of robust quantitative data on the composition and ecology of the fish faunas along the tropical coast of NWA provides crucial information for predicting the changes likely to occur in the ichthyofauna due to changes in the environment. The types of changes that are likely to be particularly relevant include those associated with climate change and increased fishing pressure as human population size increases along this coast.

There is strong evidence that water temperatures along the NWA coast have been increasing during recent years (Lough, 2008; Hobday and Lough, 2011), and thus account for the rise in the prevalence of coral bleaching (Hobday and Lough, 2011; Pratchett et al., 2014). Thus, as species composition over both soft substrata and reefs in this region have now been shown to be related to temperature, the distribution of at least some of the species, which are now largely or entirely restricted to the Kimberley Bioregion, would be expected to extend further south (Cheung et al., 2012). However, such extensions would presumably be largely restricted to species not specifically adapted for living in the particularly turbid conditions that characterise the Kimberley coast. Such species potentially include *Leiognathus splendens*, *L. leuciscus*, *Caranx bucculentus* and *Terapon theraps*, which live over soft substrata and *Lutjanus bitaeniatus* and *Lutjanus johnii*, which live over reefs. Conversely, species such as *Siganus fuscescens*, *Parupeneus chrysopileuron* and *Chromis fumea*, which were essentially found only at Cape Preston and Locker Point

at the southern end of the NWA coast, would be predicted to become at least greatly reduced in numbers or to disappear entirely from that region of the western Australian coast.

The seven sampling locations include three (Hall Point, Cape Keraudren and Cape Preston) that are considered representative of areas of the coast, whose biodiversity and other characteristics potentially made them candidates for marine parks (Wilson, 1994). Thus, the data now acquired for the characteristics of the ichthyofaunas at these three locations will be invaluable for ongoing discussions regarding where marine parks should be located along the NWA coast (Heyward, et al 2000). Moreover, should these areas be thus designated, the data provide a baseline for effective subsequent monitoring aimed at determining whether any changes were occurring in the fish faunas, particularly with regard to the size distribution of key targeted species (Taylor et al., 2015). Furthermore, there is a need to identify the essential fish habitat (EFH) of indicator species along the NWA coast, including studies aimed at elucidating the movement patterns of fish species between habitats and sites important for key aspects of the life-cycles of fishes such as spawning and recruitment (Babcock et al., 2005; Valavanis et al., 2008; Taylor and Mills, 2013).

Although the NWA coast is extremely remote and underpopulated, its rich inshore fish resources are still targeted by commercial and recreational fishers (Fletcher and Santoro, 2015). Thus, the baseline data now acquired for the fish faunas of regularly-spaced locations along the NWA coast will be invaluable to managers when they are assessing the impact of fishing on the stocks in the inshore waters of this coast. This crucial baseline data and quantitative checklists of species can also be utilised to explore

more extensive latitudinal patterns of species richness and composition, particularly as the NWA coast lies immediately to the south of the Indo-Australian Archipelago (IAA), where species richness is the greatest of all marine waters (Myers et al., 2000; Hughes et al., 2002b).

The fact that the most abundant species over the reefs in this study (*Lethrinus punctulatus*) is endemic to NWA and also a highly targeted commercial species along the NWA coast (Fletcher and Santoro, 2015), has obvious implications for management and conservation, particularly as there is no published information on the biological attributes or stock status of this species, and strongly suggests that relevant biological studies are required in the future. Repeating the sampling regime used in this study following a fifteen-year period would provide a dataset from which the potential effects of fishing and other factors could be examined, particularly for lethrinids, lutjanids and epinephelids.

As this study has highlighted that the ichthyofaunas of soft substrata and reefs along the NWA coast are related to the environmental conditions experienced by fishes along that coast, it would be beneficial to conduct fine-scale experimental studies that explore the direct influence of tidal range and turbidity (or other environmental variables) on fish faunas in the Kimberley Bioregion. The contrasting result regarding the importance of diel influences on reef fish faunas between NWA and the GBR (Newman and Williams, 1995) suggest that the greater turbidity in NWA than the GBR, and thus lower available light, may be partly responsible for the diel effects not being as great in NWA.

The development of a greater understanding of the role of estuaries in NWA, particularly the importance of mangroves, is an important task for future research.

Estuaries provide juvenile nursery habitat for many species of fish that inhabit marine environments as adults as well as providing suitable habitat for the wide range of macroinvertebrate and planktonic prey that form the diet of the juveniles of many species of fish (Blaber, 2013). *Caranx ignobilis*, an important recreational species along the NWA coast (Williamson et al., 2006; Ryan et al., 2015), has been shown to utilise mangroves as nursery areas in northern Australia (Blaber, 1986) and Hawaii (Smith and Parrish, 2002), where they consume crustaceans, especially small penaeids (Blaber and Blaber, 1980). The higher turbidity of the estuarine waters provides additional refuge from predation. The juveniles of a number of marine fish species have been shown to ‘prefer’ turbid estuarine conditions (Blaber and Blaber, 1980; Cyrus and Blaber, 1987a; Cyrus and Blaber, 1987b) and to avoid clear water.

The strong and significant inverse relationship between soft substrata and reef fish diversity indices along the NWA coast (Fig. 6.1) provides an ideal opportunity to test hypotheses aimed at detecting the underlying link that leads to species richness declining in one habitat and increasing in the other main habitat.

It should also be recognised that, on the NWA coast, mangrove forests are most abundant by far in the Kimberley Bioregion and that, on the basis of modelling, it is predicted that increased warming of waters in a poleward direction will be accompanied by a corresponding poleward extension in the distribution of mangrove forests. Thus, species such as *Lutjanus johnii*, *Lutjanus argentimaculatus* and *Epinephelus coioides* which utilise, as nursery areas, the extensive mangrove forests in the nearshore and estuarine waters of the Kimberley, may undergo population expansion southwards along that coast.

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Appendix 1. Check list of fishes collected by otter trawling over soft substrata in inshore waters (< 30 m depth) at seven locations along the north-western Australian coast between 14 and 22°S. Geographical distribution categories are: T, tropical; S, subtropical; Te, temperate; A, Australian endemic; (W), Western Australian endemic; 1, Indo-West Pacific; 2, Indo-West central Pacific; 3, New Guinea-northern Australia; 4, East-Indo-West Pacific; 5, West Pacific; 6, Circumglobal; 7, East Atlantic Indo-West Pacific; 8, Atlantic Indo-West central Pacific; 9, West central Pacific; 10, East Indian; 11, Indian; 12, Indo Pacific; 13, South-West Pacific; 14, Atlantic Indo-West Pacific; 15, East Indo-West-central Pacific. ‡, indicates specimen was retained; * and + indicates family or species was recorded in the Gulf of Carpentaria (G), respectively, by Blaber *et al.* (1994).

	Category	Total	Kimberley		Canning			Pilbara			G			
			Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Keraudren	Cape Preston	Locker Point					
Class CHONDRICHTHYES														
Subclass ELASMOBRANCHII														
Order ORECTOLOBIFORMES														
Family STEGOSTOMATIDAE (Leopard shark) *														
<i>Stegostoma fasciatum</i> (Hermann, 1783)	T,1	1								1	+			
Order CARCHARHINIFORMES														
Family CARCHARHINIDAE (Whaler sharks) *														
<i>Carcharhinus dussumieri</i> (Valenciennes, 1839)	T,1	14		14							+			
<i>Carcharhinus limbatus</i> (Valenciennes, 1839)	T,6	6		6							+			
<i>Carcharhinus obscurus</i> (Lesueur, 1818)	T,6	6		6										
<i>Rhizoprionodon acutus</i> (Rüppell, 1837)	T,7	1		1							+			
Order RAJIFORMES														
Family RHINIDAE (Sharkfin guitarfishes) *														
<i>Rhina australis</i> Bloch & Schneider, 1801	T,1	1							1					
<i>Rhynchobatus australiae</i> Whitley, 1939	T,4	9	6						1	2	+			
Family DASYATIDAE (Stingrays) *														
<i>Dasyatis annodata</i> Last, 1987	T,A	20	16	4							+			
<i>Dasyatis kuhlii</i> (Müller & Henle, 1841)	T,1	2				1					+			
<i>Dasyatis leylandi</i> Last, 1987	T,3	20			16					2	+			
<i>Himantura toshi</i> Whitley, 1939	T,3	26	11	15										
Family GYMNURIDAE (Butterfly rays) *														
<i>Gymnura australis</i> (Ramsay & Ogilby, 1886)	T,3	30	20	8							2			
Family MYLIOBATIDAE (Eagle rays) *														
<i>Aetomylaeus nichofii</i> (Schneider, 1801)	T,1	3	3								+			
Class ACTINOPTERYGII														
Division TELEOSTEI														
Order ANGUILLIFORMES														
Family MURAENIDAE (Moray eels) *														
<i>Gymnothorax undulatus</i> (Lacepède, 1803)	T,2	1								1				
Family MURAENESOCIDAE (Pike eels) *														
<i>Muraenesox cinereus</i> (Forsskål, 1775)	T,1	6	6								+			

Appendix 1 continued.

	Category	Total	Kimberley		Canning			Pilbara			G
			Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Keraudren	Cape Preston	Locker Point		
Order AULOPIFORMES											
Family SYNODONTIDAE (Lizardfishes) *											
<i>Saurida tumbil</i> (Bloch, 1795)	T,1	1074	819	227	1	4	14	4	5		
<i>Synodus dermatogenys</i> (Fowler, 1912)	T,2	39				25	2		12	+	
<i>Synodus indicus</i> (Day, 1873)	T,1	15							15		
<i>Synodus sageneus</i> Waite, 1905	T,4	45			16	2		20	7	+	
<i>Saurida undosquamis</i> ‡	T,5	3079	348	198	324	357	344	1015	493	+	
<i>Trachinocephalus myops</i> (Forster, 1801)	T,S,Te,8	181			4	24	11	64	78	+	
Order LAMPTRIDIFORMES											
Family VELIFERIDAE (Veilfins) *											
<i>Velifer hypselopterus</i> Bleeker, 1879	T,1	10					6	1		3	+
Order BATRACHOIDIFORMES											
Family BATRACHOIDIDAE (Toadfishes)											
<i>Batrachomoeus dahli</i> (Rendahl, 1922)	T,W	6			6						
<i>Batrachomoeus occidentalis</i> Hutchins, 1976	T,W	1								1	
<i>Halophryne ocellatus</i> Hutchins, 1974	T,W	1				1					
Order LOPHIFORMES											
Family ANTENNARIIDAE (Frogfishes) *											
<i>Antennarius striatus</i> (Shaw, 1794) ‡	T,8	1		1							
Order MUGILIFORMES											
Family MUGILIDAE (Mullets)											
<i>Mugil cephalus</i> Linnaeus, 1758	T,S,Te,6	6			6						
Order CLUPEIFORMES											
Family PRISTIGASTERIDAE (Longfin herrings) *											
<i>Pellona ditchela</i> Valenciennes, 1847	T,1	342	136	206						+	
Family ENGRAULIDAE (Anchoovies) *											
<i>Setipinna tenuifilis</i> (Valenciennes, 1848)	T,4	12		12							
<i>Stolephorus indicus</i> (van Hasselt, 1823)	T,2	22	10	12						+	
<i>Thryssa hamiltonii</i> (Gray, 1835)	T,1	109	55	54						+	
<i>Thryssa setirostris</i> (Broussonet, 1782)	T,1	153	18	135						+	
Family CLUPEIDAE (Herrings, Sardines, Sprats) *											
<i>Anodontostoma chacunda</i> (Hamilton-Buchanan, 1822)	T,2	94	93	1							
<i>Herklotisichthys collettei</i> Wongratana, 1987 ‡	T,W	19	19								
<i>Herklotisichthys lippa</i> (Whitley, 1931) ‡	T,A	50	42	8						+	
<i>Sardinella albella</i> (Valenciennes, 1847) ‡	T,1	77	77							+	
<i>Sardinella brachysoma</i> Bleeker, 1852	T,1	15	15								
<i>Sardinella gibbosa</i> (Bleeker, 1849)	T,1	2	1				1			+	
Order SILURIFORMES											
Family ARIIDAE (Sea catfishes) *											
<i>Arius thalassinus</i> (Rüppell, 1837) ‡	T,1	49		49						+	
Family PLOTOSIDAE (Eeltail catfishes) *											
<i>Euristhmus microceps</i> (Richardson, 1845)	T,W	15	3	12						+	

Appendix 1 continued.

	Category	Total	Kimberley		Canning			Pilbara		G
			Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Keraudren	Cape Preston	Locker Point	
<i>Euristhmus nudiceps</i> (Günther, 1880) ‡	T,3	2		2						+
Order GASTEROSTEIFORMES										
Family SYNGNATHIDAE (Pipefishes, Seahorses)										
<i>Filicampus tigris</i> (Castelnau, 1879)	S,A	1				1				
<i>Hippocampus alatus</i> Kuiter, 2001 ‡	T,3	1								1
<i>Hippocampus angustus</i> Günther, 1870	S,W	1								1
<i>Hippocampus multispinus</i> Kuiter, 2001 ‡	T,3	9			4	2	2			1
Family FISTULARIIDAE (Cornetfishes) *										
<i>Fistularia commersonii</i> Rüppell, 1838	T,6	132	80	17		1	19		15	+
<i>Fistularia petimba</i> Lacepède, 1803	T,8	2				1		1	1	+
Family CENTRISCIDAE (Shrimpfishes) *										
<i>Aeoliscus strigatus</i> (Günther, 1861)	T,2	21								21
<i>Centriscus scutatus</i> Linnaeus, 1758	T,2	11	4			2	1		4	+
Order SCORPAENIFORMES										
Family DACTYLOPERIDAE (Flying gurnards) *										
<i>Dactyloptena papilio</i> Ogilby, 1910 ‡	T,A	1						1		+
Family SCORPAENIDAE (Scorpaenfishes) *										
<i>Apistus carinatus</i> (Bloch & Schneider, 1801)	T,4	18	16	2						+
<i>Dendrochirus zebra</i> (Cuvier, 1829)	T,2	1							1	+
<i>Inimicus sinensis</i> (Valenciennes, 1833)	T,4	1						1		+
<i>Minous versicolor</i> Ogilby, 1910	T,A	1						1		+
<i>Pterois volitans</i> (Linnaeus, 1758)	T,9	4			2				2	
<i>Scorpaenopsis venosa</i> (Cuvier, 1829)	T,4	6	6							
Family TETRAROGIDAE (Waspfishes)										
<i>Liocranium praepositum</i> Ogilby, 1903	T,5	4			1	1	2			
<i>Paracentropogon longispinus</i> (Cuvier, 1829)	T,4	1					1			
<i>Paracentropogon vespa</i> Ogilby, 1910	T,A	11					2	4	5	
Family APLOACTINIDAE (Velvetfishes) *										
<i>Paraploactis pulvinus</i> Poss & Eschmeyer, 1978 ‡	T,A	1								1
Family TRIGLIDAЕ (Searobins) *										
<i>Lepidotrigla cf japonica</i>	T,5	10				1		1		8
<i>Lepidotrigla russelli</i> Cerro & Lloris, 1995	T,A	1		1						
Family PLATYCEPHALIDAE (Flatheads) *										
<i>Elates ransonnetii</i> (Steindachner, 1877)	T,4	54	28	26						+
<i>Inegocia harrisii</i> (McCulloch, 1914) ‡	T,A	4	1	2	1					
<i>Inegocia japonica</i> (Tilesius, 1812) ‡	T,4	124	27	33	2	3	15	25	19	+
<i>Platycephalus arenarius</i> Ramsay & Ogilby, 1886	T,3	3					3			
<i>Platycephalus endrachtensis</i> Quoy & Gaimard, 1825	T,3	19	9	8	1				1	+
<i>Sorsogona tuberculata</i> (Cuvier, 1829)	T,1	7			1	1	2		3	+
Order PERCIFORMES										
Family LATIDAE (Giant perches)										
<i>Hypopterus macropterus</i> (Günther, 1859)	S,W	1							1	

Appendix 1 continued.

	Category	Total	Kimberley		Canning			Pilbara		G
			Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Keraudren	Cape Preston	Locker Point	
Family EPINEPHELIDAE										
(Coral cods, Groupers, Rock cods) *										
<i>Cephalopholis boenak</i> (Bloch, 1790)	T,1	3				1		1	1	+
<i>Epinephelus bilobatus</i> Randall & Allen, 1987	T,W	5			4		1			
<i>Epinephelus multinotatus</i> (Peters, 1877)	T,11	3					3			
<i>Epinephelus rivulatus</i> (Valenciennes, 1830)	T,1	3							3	
<i>Epinephelus sexfasciatus</i> (Kuhl & van Hasselt, 1828)	T,4	172	55	116			1			+
<i>Plectropomus maculatus</i> (Bloch, 1790)	T,5	4			4					+
<i>Sacura parva</i> Heemstra & Randall, 1979	T,10	2							2	
Family CENTROGENIIDAE										
(False Scorpionfish)										
<i>Centrogenys vaigiensis</i> (Quoy & Gaimard, 1824)	T,1	1					1			
Family PSEUDOCHROMIDAE (Dottybacks, Eel blennies) *										
<i>Congrogadus spinifer</i> (Borodin, 1933)	T,A	5			4		1			
<i>Labracinus lineatus</i> (Castelnau, 1875)	T,W	5						2	3	
Family PRIACANTHIDAE (Bigeyes) *										
<i>Priacanthus hamrur</i> (Forsskål, 1775) ‡	T,2	22		7	2		1	1	11	+
<i>Priacanthus macracanthus</i> Cuvier, 1829	T,4	132		9	13		109		1	+
<i>Priacanthus tayenus</i> Richardson, 1846	T,1	256	54	27	3	15	38	119		+
Family APOGONIDAE (Cardinalfishes) *										
<i>Apogon albimaculosus</i> Kailola, 1976	T,3	84		84						+
<i>Apogon brevicaudata</i> Weber, 1909 ‡	T,3	12			2	4	5		1	
<i>Apogon cavittensis</i> (Jordan & Seale, 1907) ‡	T,5	14			3	3			8	
<i>Apogon fasciatus</i> (White, 1790)	T,1	319	261	58						+
<i>Apogon monospilus</i> Fraser, Randell & Allen, 2002 ‡	T,9	1							1	
<i>Apogon nigripinnis</i> Cuvier, 1828	T,1	7				3			4	+
<i>Apogon poecilopterus</i> Cuvier, 1828	T,5	307	124	180		3				+
<i>Apogon rueppellii</i> Günther, 1859	T,3	5							5	
<i>Apogon unitaeniatus</i> Allen, 1995	T,A	373	142	223					8	
<i>Siphamia cf cuniceps</i> Whitley, 1941	S,A	1				1				
Family SILLAGINIDAE (Whitings) *										
<i>Sillago burrus</i> Richardson, 1842	T,5	140	3		3		63	71		+
<i>Sillago ingenuua</i> McKay, 1985 ‡	T,5	376	36	26	4	42	251	14	3	+
<i>Sillago lutea</i> McKay, 1985	T,10	78	6	21	2	1	48			+
<i>Sillago vittata</i> McKay, 1985 ‡	S,W	26					26			
Family LACTARIIDAE (False trevallies) *										
<i>Lactarius lactarius</i> (Bloch & Schneider, 1801)	T,1	3	3							+
Family ECHENEIDAE (Remoras, Sharksuckers) *										
<i>Echeneis naucrates</i> Linnaeus, 1758	T,6	5			1		2	1	1	+
Family RACHYCENTRIDAE (Cobia) *										
<i>Rachycentron canadum</i> (Linnaeus, 1766)	T,14	6	2	2		1		1		+

Appendix 1 continued.

	Category	Total	Kimberley		Canning			Pilbara		
			Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Keraudren	Cape Preston	Locker Point	G
Family CARANGIDAE (Jacks, Trevallies) *										
<i>Alectis indica</i> (Rüppell, 1830)	T,1	33	6	27						
<i>Alepes apercna</i> Grant, 1978 ‡	T,A	25	8	1	2	6	8			
<i>Atule mate</i> (Cuvier, 1833)	T,2	103	4	88		2	6	6	3	+
<i>Carangoides caeruleopinnatus</i> (Rüppell, 1830)	T,1	2		2						+
<i>Carangoides chrysophrys</i> (Cuvier, 1833) ‡	T,1	2		1		1				+
<i>Carangoides equula</i> (Temminck & Schlegel, 1844) ‡	T,2	1							1	
<i>Carangoides fulvoguttatus</i> (Forsskål, 1775)	T,1	47					43	1	3	+
<i>Carangoides hedlandensis</i> (Whitley, 1934)	T,1	103	4	65			34			+
<i>Carangoides humerosus</i> (McCulloch, 1915)	T,3	279	56	223						+
<i>Carangoides malabaricus</i> (Bloch & Schneider, 1801)	T,1	2705	2328	284		5	88			+
<i>Carangoides talamparoides</i> Bleeker, 1852 ‡	T,1	66	15	50			1			+
<i>Caranx bucculentus</i> Alleyne & Macleay, 1877	T,3	2411	441	1925	12		33			+
<i>Caranx heberi</i> (Bennett, 1830)	T,1	6	5	1						
<i>Caranx kleinii</i> (Bloch, 1793)	T,1	110	110							+
<i>Decapterus macarellus</i> (Cuvier, 1833)	T,6	19	19							
<i>Gnathanodon speciosus</i> (Forsskål, 1775)	T,12	22	10		8			3	1	+
<i>Megalaspis cordyla</i> (Linnaeus, 1758) ‡	T,1	65	9	56						+
<i>Pantolabus radiatus</i> (Macleay, 1881)	T,3	168	43	125						+
<i>Parastromateus niger</i> (Bloch, 1795)	T,1	38	3	29		1	4		1	+
<i>Scomberoides tol</i> (Cuvier, 1832)	T,1	1		1						+
<i>Selar boops</i> (Cuvier, 1833)	T,2	16	16							+
<i>Selaroides leptolepis</i> (Kuhl & van Hasselt, 1833)	T,1	5070	145	731	113	399	3229	182	271	
<i>Seriolina nigrofasciata</i> (Rüppell, 1829) ‡	T,1	28		16	4	1	6	1		+
<i>Ulua aurochs</i> (Ogilby, 1915)	T,5	177		148		16	3	10		+
<i>Ulua mentalis</i> (Cuvier, 1833)	T,1	2							2	
Family LEIOPNATHIDAE (Ponyfishes) *										
<i>Gazza minuta</i> (Bloch, 1797)	T,2	204	69	135						+
<i>Leiognathus bindus</i> (Valenciennes, 1835)	T,1	473	282	191						+
<i>Leiognathus decorus</i> (De Vis, 1884)	T,1	350	169	174			7			+
<i>Leiognathus equulus</i> (Forsskål, 1775)	T,2	729	582	146					1	+
<i>Leiognathus fasciatus</i> (Lacepède, 1803) ‡	T,1	613	609	4						+
<i>Leiognathus leuciscus</i> (Günther, 1860) ‡	T,1	4484	1578	2427		133	344	1	1	+
<i>Leiognathus moretoniensis</i> Ogilby, 1912 ‡	T,3	245	91	154						+
<i>Leiognathus splendens</i> (Cuvier, 1829)	T,1	16354	14463	1891						+
<i>Secutor insidiator</i> (Bloch, 1787)	T,1	8284	6455	1829						+
<i>Secutor interruptus</i> (Valenciennes, 1835)	T,4	725	602	123						
Family LUTJANIDAE (Snappers) *										
<i>Lutjanus carponotatus</i> (Richardson, 1842) ‡	T,4	27		13	12	1	1			
<i>Lutjanus erythropterus</i> Bloch, 1790	T,1	5				5				+
<i>Lutjanus malabaricus</i> (Schneider, 1801) ‡	T,1	186	64	51	11		2	56	2	+
<i>Lutjanus sebae</i> (Cuvier, 1828) ‡	T,1	2						2	2	+

Appendix 1 continued.

	Category	Total	Kimberley		Canning			Pilbara			G
			Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Keraudren	Cape Preston	Locker Point		
<i>Lutjanus vitta</i> (Quoy & Gaimard, 1824)	T,15	191			142	4	42			3	+
Family CAESONIDAE (Fusiliers) *											
<i>Caesio cuning</i> (Bloch, 1791)	T,4	2									2
<i>Pterocaesio digramma</i> (Bleeker, 1865)	T,5	1									1
<i>Pterocaesio marri</i> Schultz, 1953	T,2	1									1
Family GERREIDAE (Mojarras, Silverbiddies) *											
<i>Gerres filamentosus</i> Cuvier, 1829 ‡	T,1	423	255	168							+
<i>Gerres subfuscatus</i> Cuvier, 1830 ‡	T,A	1									1
<i>Pentaprion longimanus</i> (Cantor, 1850)	T,4	284	180	88						14	2
Family HAEMULIDAE (Grunts, Sweetlips, Javelinfishes) *											
<i>Diagramma labiosum</i> Macleay, 1883 ‡	T,5	26			17	6		1	2		
<i>Pomadasys argenteus</i> (Forsskål, 1775)	T,1	58	58								+
<i>Pomadasys maculatus</i> (Bloch, 1797)	T,1	998	922	75		1					+
Family SPARIDAE (Breams, Snappers, Porgies) *											
<i>Argyrops spinifer</i> (Forsskål, 1775)	T,1	11						1	10		+
Family LETHRINIDAE (Emperors, Emperor breams) *											
<i>Gymnocranius elongatus</i> Senta, 1973	T,1	7									7
<i>Gymnocranius griseus</i> (Schlegel, 1844)	T,4	5									5
<i>Lethrinus genivittatus</i> Valenciennes, 1830 ‡	T,4	1586			18	6	113	3	1446		+
<i>Lethrinus punctulatus</i> (Macleay, 1878)	T,A	1									1
<i>Lethrinus variegatus</i> Valenciennes, 1830	T,1	4									4
Family NEMIPTERIDAE (Threadfin breams) *											
<i>Nemipterus celebicus</i> (Bleeker, 1854) ‡	T,5	15								15	+
<i>Nemipterus furcosus</i> (Valenciennes, 1830)	T,4	372								187	+
<i>Nemipterus hexodon</i> (Quoy & Gaimard, 1824)	T,4	241	184	57	12	13	87	73	187		
<i>Nemipterus peronii</i> (Valenciennes, 1830) ‡	T,1	25									+
<i>Pentapodus porosus</i> (Valenciennes, 1830)	T,3	384			103	81	101	26	73		
<i>Pentapodus vitta</i> Quoy & Gaimard, 1824	S,W	92			16		76				
<i>Scolopsis margaritifer</i> (Cuvier, 1830)	T,5	1		1							
<i>Scolopsis monogramma</i> (Kuhl & van Hasselt, 1830)	T,4	17			2	2	1	11	1		+
<i>Scolopsis taeniopterus</i> (Kuhl & van Hasselt, 1830)	T,5	60		59				1			+
Family POLYNEMIDAE (Threadfins) *											
<i>Polydactylus multiradiatus</i> (Günther, 1860)	T,5	248	185	63							+
Family SCIAENIDAE (Croakers) *											
<i>Johnius amblycephalus</i> (Bleeker, 1855)	T,4	1	1								+
<i>Johnius borneensis</i> (Bleeker, 1850)	T,1	388	57	331							+
Family MULLIDAE (Goatfishes) *											
<i>Parupeneus barberinoides</i> (Bleeker, 1852)	T,9	16								16	
<i>Parupeneus chrysopleuron</i> (Temminck & Schlegel, 1843)	T,4	56								56	
<i>Parupeneus heptacanthus</i> (Lacepède, 1801)	T,2	2								1	1
<i>Upeneus asymmetricus</i> Lachner, 1954	T,2	768			46	368		176	178		+
<i>Upeneus luzonius</i> (Jordan & Seale, 1907)	T,5	25			1	14				10	+
<i>Upeneus</i> sp. 1 (Sainsbury <i>et al</i> , 1985)	T, W	36	4							32	+

Appendix 1 continued.

	Category	Total	Kimberley		Canning			Pilbara		G
			Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Keraudren	Cape Preston	Locker Point	
<i>Upeneus sulphureus</i> Cuvier, 1829	T,1	4380	2152	2171					57	+
<i>Upeneus sundaicus</i> (Bleeker, 1855)	T,1	100	20	18					62	+
<i>Upeneus tragula</i> Richardson, 1846 ‡	T,1	99			57	12	10	1	19	+
Family GLAUCOSOMATIDAE (Pearl perches)										
<i>Glaukosoma magnificum</i> (Ogilby, 1915)	T,A	39				16		23		
Family CHAETODONTIDAE (Butterflyfishes) *										
<i>Chaetodon assarius</i> Waite, 1905	S,W	51							51	
<i>Chelmon marginalis</i> Richardson, 1842	T,A	68				39		24	5	+
<i>Chelmon muelleri</i> (Klunzinger, 1880)	T,A	19		19						+
<i>Coradion chrysozonus</i> (Cuvier, 1831)	T,4	105			51	3	47		4	+
<i>Heniochus acuminatus</i> (Linnaeus, 1758)	T,2	10							10	
<i>Parachaetodon ocellatus</i> (Cuvier, 1831)	T,4	27			2		20	4	1	+
Family POMACANTHIDAE (Angelfishes) *										
<i>Chaetodontoplus duboulayi</i> (Günther, 1867)	T,5	250		6	124	32	85		3	+
<i>Chaetodontoplus personifer</i> (McCulloch, 1914)	T,A	14			1		3		10	
Family TERAPONTIDAE (Grunters, Trumpeters) *										
<i>Pelates quadrilineatus</i> (Bloch, 1790)	T,1	6		4				2		+
<i>Terapon theraps</i> (Cuvier, 1829)	T,1	9042	3491	5532		2			17	+
Family CIRRHITIDAE (Hawkfishes)										
<i>Cirrhitichthys aprinus</i> (Cuvier, 1829)	T,4	4							4	
<i>Cirrhitichthys oxycephalus</i> (Bleeker, 1855)	T,12	14							14	
<i>Cyprinocirrhites polyactis</i> (Bleeker, 1875) ‡	T,1	3							3	
Family CEPOLIDAE (Bandfishes)										
<i>Acanthocepola abbreviata</i> (Valenciennes, 1835)	T,1	1						1		
Family POMACENTRIDAE (Damselfishes) *										
<i>Amphiprion clarkii</i> (Bennett, 1830)	T,1	2					2			
<i>Chromis fumea</i> (Tanaka, 1917)	T,5	84							84	
<i>Pristotis obtusirostris</i> (Günther, 1862)	T,1	3068			257	633	1415	233	530	+
Family LABRIDAE (Wrasses) *										
<i>Anampsese lennardi</i> Scott, 1959	T,A	22			7	3	8	4		+
<i>Choerodon anchorago</i> (Bloch, 1791)	T,4	1			1					
<i>Choerodon cauteroma</i> Gomon & Allen, 1987	T,A	14			4	5	1		4	
<i>Choerodon cephalotes</i> (Castelnau, 1875)	T,5	418	6		102	55	156	6	93	+
<i>Choerodon monostigma</i> Ogilby, 1910	T,3	100		67	32				1	+
<i>Choerodon sugillatum</i> Gomon, 1987	T,A	5			3			1	1	+
<i>Choerodon vitta</i> Ogilby, 1910	T,3	197			143	16	32	5	1	
<i>Halichoeres nebulosus</i> (Valenciennes, 1839)	T,1	1							1	
<i>Oxycheilinus orientalis</i> Gunther, 1862 ‡	T,1	7							7	
<i>Stethojulis interrupta</i> (Bleeker, 1851) ‡	T,1	3							3	
<i>Suezichthys soelae</i> Russell, 1985	T,W	1							1	
<i>Iniistius</i> sp. undescribed species	T,W	68			8	14	2	41	3	
Family SCARIDAE (Parrotfishes) *										
<i>Scarus ghobban</i> Forsskål, 1775 ‡	T,12	1			1				+	

Appendix 1 continued.

	Category	Total	Kimberley		Canning			Pilbara			G
			Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Keraudren	Cape Preston	Locker Point		
Family PINGUIPEDIDAE (Grubfishes, Sandperches)											
<i>Parapercis nebulosa</i> (Quoy & Gaimard, 1825)	T,A	386	4		31	43	23	230	55		
Family BLENNIIDAE (Blennies) *											
<i>Xiphiasia setifer</i> Swainston, 1839	T,1	1					1				+
Family CALLIONYMIDAE (Dragonets, Stinkfishes) *											
<i>Calliurichthys qfilum</i> Fricke, 2000 ‡	T,3	2								2	+
<i>Calliurichthys grossi</i> Ogilby, 1910	T,A	21		6	1	1	2	10	1	1	+
<i>Dactylopus dactylopus</i> (Valenciennes, 1837)	T,4	2		1						1	+
<i>Orbonyx rameus</i> (McCulloch, 1926)	T,13	5								3	+
<i>Pseudocalliurichthys goodladi</i> (Whitley, 1944) ‡	S,W	97		1	27	1		66	2		
<i>Repomucenus meridionalis</i> Suwardji, 1965 ‡	T,5	1				1					
<i>Repomucenus sublaevis</i> McCulloch, 1926	T,A	16	4	2			2	7	1	+	
Family GOBIIDAE (Gobies) *											
<i>Yongeichthys nebulosus</i> (Forsskål, 1775) ‡	T,1	6							6		
Family EPHIPPIDAE (Batfishes, Spadefishes) *											
<i>Platax teira</i> (Forsskål, 1775) ‡	T,1	1								1	+
<i>Zabidius novemaculeatus</i> (McCulloch, 1916)	T,3	7	5	2							+
Family SIGANIDAE (Rabbitfishes) *											
<i>Siganus fuscescens</i> (Houttuyn, 1782)	T,4	445			1	4	42	266	128	+	
Family SPHYRAENIDAE (Barracudas) *											
<i>Sphyraena forsteri</i> Cuvier, 1829	T,2	1							1	+	
<i>Sphyraena putnamae</i> Jordan & Seale, 1907	T,2	35	35								+
Family TRICHIURIDAE (Cutlassfishes, Hairtails) *											
<i>Tentoriceps cristatus</i> (Kunzinger, 1884)	T,1	1	1								
<i>Trichiurus lepturus</i> Linnaeus, 1758	T,6	18	17	1							+
Family SCOMBRIDAE (Mackerels, Tunas) *											
<i>Rastrelliger kanagurta</i> (Cuvier, 1816) ‡	T,1	1							1	+	
<i>Scomberomorus muroi</i> Collette & Russo, 1980	T,3	1					1				+
<i>Scomberomorus queenslandicus</i> Munro, 1943	T,3	41	6	32			3				+
Family CENTROLOPHIDAE (Trevallas, Medusafishes) *											
<i>Psenopsis humerosa</i> Munro, 1958	T,3	13	13								+
Order PLEURONECTIFORMES											
Family PSETTODIDAE (Psettodids) *											
<i>Psettodes erumei</i> (Bloch & Schneider, 1801) ‡	T,1	180	119	58			1	1	1	1	+
Family BOTHIDAE (Lefteye flounders) *											
<i>Asterorhombus intermedius</i> (Bleeker, 1866)	T,2	1									+
<i>Asterorhombus osculus</i> Arai, 1998	T,W	25			18	1		7			
<i>Bothus myriaster</i> Temminck & Schlegel, 1846	T,1	1								1	
<i>Bothus pantherinus</i> (Rüppell, 1830)	T,2	15				3		5	7		
<i>Crossorhombus azureus</i> (Alcock, 1889)	T,4	104						41	63		
<i>Engyprosopon grandisquama</i> (Temminck & Schlegel, 1846)	T,1	527	6	1	14	46	62	236	162	+	
<i>Engyprosopon maldivensis</i> (Regan, 1908) ‡	T,4	465							465	+	
<i>Grammatobothus polyophthalmus</i> (Bleeker, 1866) ‡	T,4	6					1		5	+	

Appendix 1 continued.

	Category	Total	Kimberley		Canning			Pilbara		G
			Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Keraudren	Cape Preston	Locker Point	
<i>Laeops parviceps</i> Günther, 1880 ‡	T,5	3		3						
Family PARALICHTHYIDAE (Sand flounders) *										
<i>Pseudorhombus argus</i> Weber, 1913	T,3	157			21	30	41	31	34	+
<i>Pseudorhombus arsius</i> (Hamilton, 1822)	T,1	343	71	173	1	16	27	45	10	
<i>Pseudorhombus elevatus</i> Ogilby, 1912	T,1	1							1	+
<i>Pseudorhombus jenynsii</i> (Bleeker, 1855)	T,A	37			8	1	5	11	12	
<i>Pseudorhombus spinosus</i> McCulloch, 1914	T,A	76		1	7	21	16	19	12	+
Family PLEURONECTIDAE (Righteye flounders) *										
<i>Psammodiscus ocellatus</i> Günther, 1862	T,W	1				1				
Family SOLEIDAE (Soles) *										
<i>Aseraggodes melanospilos</i> (Bleeker, 1854)	T,5	1						1		
<i>Dexillus muelleri</i> (Steindachner, 1879)	T,4	2		1		1				
<i>Zebrias cancellatus</i> (McCulloch, 1916) ‡	S,W	1				1				
<i>Zebrias quagga</i> (Kaup, 1858)	T,1	2		2						+
Family CYNOGLOSSIDAE										
<i>Cynoglossus macropthalmus</i> Norman, 1926	T,A	2		1					1	
<i>Paraplagusia bilineata</i> (Bloch, 1787) ‡	T,1	14	7	1			6			
<i>Paraplagusia longirostris</i> Chapleau, Renaud & Kailola, 1991	T,3	75	1	74						
Order TETRAODONTIFORMES										
Family TRIACANTHIDAE (Triplespines) *										
<i>Triacanthus biaculeatus</i> (Bloch, 1786)	T,1	6	6							
<i>Trixiphichthys weberi</i> (Chaudhuri, 1910)	T,4	78	20	54			4			+
Family BALISTIDAE (Triggerfishes) *										
<i>Abalistes stellatus</i> (Anonymous, 1798)	T,1	9			1	1	4	1	2	+
<i>Sufflamen fraenatus</i> (Latrelle, 1804)	T,2	7							7	
Family MONACANTHIDAE (Leatherjackets, Filefishes) *										
<i>Anacanthus barbatus</i> Gray, 1831	T,4	15			5	3			7	
<i>Cantherhines fronticinctus</i> (Günther, 1866)	T,1	7							7	
<i>Chaetodermis penicilligera</i> (Cuvier, 1817)	T,5	14			2		1	1	10	
<i>Monacanthus chinensis</i> (Osbeck, 1765)	T,5	8			2	1		2	3	
<i>Paramonacanthus choirocephalus</i> (Bleeker, 1852) ‡	T,4	2505			558	47	409	1272	219	
<i>Paramonacanthus filicauda</i> (Günther, 1880)	T,3	247	229	18						
<i>Paramonacanthus pusillus</i> (Rüppell, 1828)	T,1	6						3	3	
<i>Pseudomonacanthus elongatus</i> Fraser-Brunner, 1940	T,A	15			11		2		2	
<i>Pseudomonacanthus peroni</i> (Holland, 1854) ‡	T,3	9		1			3		5	+
<i>Thamnaconus tessellatus</i> (Günther, 1880)	T,5	3			3					
Family OSTRACIIDAE (Boxfishes, Cowfishes) *										
<i>Lactoria cornuta</i> (Linnaeus, 1758)	T,2	2							2	
<i>Lactoria diaphana</i> (Bloch & Schneider, 1801)	T,2	5			4		1			
<i>Lactoria fornasini</i> (Bianconi, 1846) ‡	T,2	2							2	
<i>Ostracion cubicus</i> Linnaeus, 1758	T,2	2							2	
<i>Rhynchostracion nasus</i> (Bloch, 1785)	T,4	16		6	3	1	4	2	+	

Appendix 1 continued.

	Category	Total	Kimberley		Canning			Pilbara		G
			Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Keraudren	Cape Preston	Locker Point	
Family TETRAODONTIDAE (Pufferfishes, Blowfishes) *										
<i>Arothron stellatus</i> (Bloch & Schneider, 1801)	T,2	1		1						+
<i>Canthigaster coronata</i> (Vaillant & Sauvage, 1875)	T,2	23								23
<i>Canthigaster rivulatus</i> (Temminck & Schlegel, 1850)	T,2	39								39
<i>Chelonodon patoca</i> (Hamilton-Buchanan, 1822)	T,1	13		4	9					
<i>Feroxodon multistriatus</i> (Richardson, 1854)	T,A	8				5	3			+
<i>Lagocephalus lunaris</i> (Bloch & Schneider, 1801)	T,1	24		13	11					+
<i>Lagocephalus sceleratus</i> (Gmelin, 1789)	T,2	312		54	8	5	26	161	44	14
<i>Lagocephalus spadiceus</i> (Richardson, 1845) ‡	T,1	81		74	6	1				+
<i>Torquigener hicksi</i> Hardy, 1983	T,A	4		4						
<i>Torquigener pallimaculatus</i> Hardy, 1983 ‡	T,A	827		11	12	4	126	387	169	118
<i>Torquigener whitleyi</i> (Paradice, 1927)	T,A	9		4	4					1
<i>Tylerius spinosissimus</i> (Regan, 1908)	T,1	1								+
Family DIODONTIDAE (Porcupinefishes) *										
<i>Cyclichthys hardenbergi</i> de Beaufort, 1939	T,3	10		10						
<i>Cyclichthys orbicularis</i> (Bloch, 1785)	T,1	118				5	113			
<i>Diodon holocanthus</i> Linnaeus, 1758	T,6	1								1
<i>Tragulichthys jaculiferus</i> (Cuvier, 1818)	T,A	79		7	41	10	16	3	2	+
Total number of individuals		84781	38970	21897	2524	2394	8774	4696	5526	
Total number of species		285	103	115	87	73	99	77	144	
Total number of Australian endemic species		52	11	16	27	12	20	17	27	
Total number of Western Australian endemic species		19	2	3	7	1	3	3	9	

Appendix 2. Check list of fishes collected by fish trapping over reefs in inshore waters (< 30 m depth) at seven locations along the north-western Australian coast between 14°S and 22°S. Geographical distribution categories are: T, tropical; S, subtropical; Te, temperate; A, Australian endemic; (W), Western Australian endemic; 1, Indo-west Pacific; 2, Indo-west central Pacific; 3, New Guinea-northern Australia; 4, East-Indo-west Pacific; 5, West Pacific; 6, Circumglobal; 7, East Atlantic Indo-west Pacific; 8, Atlantic Indo-west central Pacific; 9, West central Pacific; 10, East Indian; 11, Indian; 12, Indo Pacific; 13, South-west Pacific; 14, Atlantic Indo-west Pacific; 15, East Indo-west-central Pacific. ‡, specimen retained.

	Category	Total	Kimberley		Canning			Pilbara			
			Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Keraudren	Cape Preston	Locker Point		
Class CHONDRICHTHYES											
Subclass ELASMOBRANCHII											
Order ORECTOLOBIFORMES											
Family ORECTOLOBIDAE (Wobbegongs)											
<i>Orectolobus wardi</i> Whitley, 1939	T,A	4		3		1					
Family HEMISCYLLIDAE (Longtail carpet sharks)											
<i>Chiloscyllium punctatum</i> Muller & Henle, 1838	T,4	9	1	4	2	2					
<i>Hemiscyllium trispiculare</i> Richardson, 1843	T,5	1			1						
Family GINGLYOSTOMATIDAE (Nurse sharks)											
<i>Nebrius ferrugineus</i> (Lesson, 1830)	T,2	17	2	2	5		5	2	1		
Order CARCHARHINIFORMES											
Family CARCHARHINIDAE (Whaler sharks)											
<i>Carcharhinus amblyrhynchos</i> (Bleeker, 1856)	T,1	4	2	2							
<i>Carcharhinus limbatus</i> (Valenciennes, 1839)	T,6	1	1								
<i>Carcharhinus melanopterus</i> (Quoy & Gaimard, 1824)	T,2	2	1	1							
<i>Carcharhinus sorrah</i> (Valenciennes, 1839)	T,1	1	1								
<i>Loxodon macrorhinus</i> Muller & Henle, 1839	T,1	1							1		
<i>Negaprion acutidens</i> (Rüppell, 1837)	T,2	3				1	1	2			
<i>Triakodon obesus</i> (Rüppell, 1837)	T,12	5		2	1			2			
Order RAJIFORMES											
Family DASYATIDAE (Stingrays)											
<i>Dasyatis kuhlii</i> (Müller & Henle, 1841)	T,1	2				1		1			
<i>Taeniura lymma</i> (Forsskål, 1775)	T,1	1	1								
Class ACTINOPTERYGII											
Division TELEOSTEI											
Order SILURIFORMES											
Family ARIIDAE (Sea catfishes)											
<i>Arius thalassinus</i> (Rüppell, 1837) ‡	T,1	6		1	5						
Order BATRACHOIDIFORMES											
Family BATRACHOIDIDAE (Toadfishes)											
<i>Halophryne diemensis</i> (Lesueur, 1824)	T,5	1		1							
<i>Halophryne ocellatus</i> Hutchins, 1974	T,W	1					1				

Appendix 2 continued.

	Category	Total	Kimberley		Canning		Pilbara	
			Cape Voltaire	Hall Point	Emerau Point	Cape Bossut	Cape Keraudren	Cape Preston
Order BERYCIFORMES								
Family HOLOCENTRIDAE (Squirrelfishes)								
<i>Myripristis hexagona</i> (Lacepède, 1802)	T,1	1						1
Order SCORPAENIFORMES								
Family SCORPAENIDAE (Scorpionfishes)								
<i>Pterois volitans</i> (Linnaeus, 1758)	T,9	1			1			
Family PLATYCEPHALIDAE (Flatheads)								
<i>Levirpora inops</i> (Jenyns, 1840)	T,A	1		1				
<i>Platycephalus endrachtensis</i> Quoy & Gaimard, 1825	T,3	1				1		
Order PERCIFORMES								
Family LATIDAE (Giant perches)								
<i>Psammoperca waigiensis</i> (Cuvier, 1828)	T,4	20	8	2		7	1	1
Family EPINEPHELIDAE (Coral cods, Groupers, Rock cods)								
<i>Cephalopholis miniata</i> (Forsskål, 1775)	T,1	3						3
<i>Cromileptes altivelis</i> (Valenciennes, 1828)	T,4	3		1	2			
<i>Diplopriion bifasciatum</i> Cuvier, 1828	T,4	1				1		
<i>Epinephelus areolatus</i> (Forsskål, 1775)	T,1	2	1					1
<i>Epinephelus bilobatus</i> Randall & Allen, 1987	T,W	194	3		72	9	12	49
<i>Epinephelus bleekeri</i> (Vaillant, 1877)	T,1	18		1				17
<i>Epinephelus coioides</i> (Hamilton, 1822)	T,1	278	95	47	5	34	48	24
<i>Epinephelus cyanopodus</i> (Richardson, 1846)	T,9	1		1				
<i>Epinephelus fasciatus</i> (Forsskål, 1775)	T,1	39				19	4	5
<i>Epinephelus fuscoguttatus</i> (Forsskål, 1775)	T,2	1						1
<i>Epinephelus malabaricus</i> (Bloch & Schneider, 1801)	T,2	7		2	2		2	1
<i>Epinephelus multinotatus</i> (Peters, 1877)	T,11	27				9	14	1
<i>Epinephelus polyphekadion</i> (Bleeker, 1849)	T,2	9						1
<i>Epinephelus quoyanus</i> (Valenciennes, 1830)	T,1	10			1	6	2	1
<i>Epinephelus rivulatus</i> (Valenciennes, 1830)	T,1	12						12
<i>Plectropomus maculatus</i> (Bloch, 1790)	T,5	103	13	4	24	31	17	12
Family ECHENEIDAE (Remoras, Sharksuckers)								
<i>Echeneis naucrates</i> Linnaeus, 1758	T,6	4			1	2		1
<i>Remora remora</i> (Linnaeus, 1758)	T,6	1					1	
Family CARANGIDAE (Jacks, Trevallies)								
<i>Alepes aperca</i> Grant, 1978 ‡	T,A	1						1
<i>Carangoides fulvoguttatus</i> (Forsskål, 1775)	T,1	87			50	30	2	5
<i>Carangoides gymnostethus</i> (Cuvier, 1833)	T,1	37			14	21		1
<i>Carangoides talamparoides</i> Bleeker, 1852 ‡	T,1	1	1					
<i>Caranx bucculentus</i> Alleyne & Macleay, 1877	T,3	53	36	9	7			1
<i>Caranx ignobilis</i> (Forsskål, 1775)	T,2	17	7	8	2			
<i>Caranx sexfasciatus</i> Quoy & Gaimard, 1825	T,12	15				15		
<i>Caranx tille</i> Cuvier, 1833	T,1	8	5			3		
<i>Gnathanodon speciosus</i> (Forsskål, 1775)	T,12	730	13	40	380	249	23	3
								22

Appendix 2 continued.

	Category	Total	Kimberley		Canning			Pilbara	
			Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Keraudren	Cape Preston	Locker Point
Family LUTJANIDAE (Snappers)									
<i>Lutjanus argentimaculatus</i> (Forsskål, 1775) ‡	T,2	2	1	1					
<i>Lutjanus bitaeniatus</i> (Valenciennes, 1830) ‡	T,5	927	210	717					
<i>Lutjanus carponotatus</i> (Richardson, 1842) ‡	T,4	5217	463	1028	1657	1096	359	412	202
<i>Lutjanus erythropterus</i> Bloch, 1790	T,1	17	3			6		7	1
<i>Lutjanus fulviflamma</i> (Forsskål, 1775)	T,2	9						1	8
<i>Lutjanus johnii</i> (Bloch, 1792) ‡	T,1	420	360	60					
<i>Lutjanus lemniscatus</i> (Valenciennes, 1828)	T,4	346	104	40	93	9	3	74	23
<i>Lutjanus malabaricus</i> (Schneider, 1801) ‡	T,1	104	32		7	6		28	31
<i>Lutjanus quinquefasciatus</i> (Bloch, 1790)	T,1	54				2		29	23
<i>Lutjanus rivulatus</i> (Cuvier, 1828)	T,2	2			1		1		
<i>Lutjanus russelli</i> (Bleeker, 1849) ‡	T,1	245	1	1		23	25	120	75
<i>Lutjanus sebae</i> (Cuvier, 1828) ‡	T,1	267	2		34	87	21	105	18
<i>Lutjanus vitta</i> (Quoy & Gaimard, 1824)	T,15	65				18	6	14	27
<i>Syphorus nematophorus</i> (Bleeker, 1860) ‡	T,5	25			4		16	3	2
Family CAESONIDAE (Fusiliers)									
<i>Caesio cuning</i> (Bloch, 1791)	T,4	17	2	7	2			5	1
Family HAEMULIDAE (Grunts, Sweetlips, Javelinfishes)									
<i>Diagramma labiosum</i> Macleay, 1883 ‡	T,5	334	29	73	53	46	101	27	5
<i>Plectrohinchus gibbosus</i> Lacepède, 1802	T,4	9	2	2	3		2		
<i>Plectrohinchus multivittatus</i> (Macleay, 1878)	T,A	17		1	4	9	3		
<i>Plectrohinchus polytaenia</i> (Bleeker, 1852)	T,4	33			28	3	2		
<i>Plectrohinchus vittatus</i> (Linnaeus, 1758)	T,2	1					1		
<i>Pomadasys kaakan</i> (Cuvier, 1830)	T,4	33	33						
Family SPARIDAE (Breams, Snappers, Porgies)									
<i>Chrysophris auratus</i> (Bloch & Schneider, 1801)	Te,13	1						1	
Family LETHRINIDAE (Emperors, Emperor breams)									
<i>Lethrinus atkinsoni</i> Seale, 1910	T,9	278						74	204
<i>Lethrinus genivittatus</i> Valenciennes, 1830 ‡	T,4	359					9	46	155
<i>Lethrinus laticaudis</i> Alleyne & Macleay, 1877 ‡	T,13	2875	365	556	1103	275	174	229	173
<i>Lethrinus lentjan</i> (Lacepède, 1802)	T,2	180	15	25	23	6		101	10
<i>Lethrinus miniatus</i> (Bloch & Schneider, 1801)	T,5	10				2			8
<i>Lethrinus nebulosus</i> (Forsskål, 1775) ‡	T,1	322			20	2		94	206
<i>Lethrinus olivaceus</i> Valenciennes, 1830	T,2	18			7		1	1	9
<i>Lethrinus punctulatus</i> (Macleay, 1878)	T,A	9353	14	68	1672	3582	1210	1627	1180
<i>Lethrinus ravus</i> Carpenter & Randall, 2003	T,5	2							2
Family NEMIPTERIDAE (Threadfin breams)									
<i>Nemipterus furcosus</i> (Valenciennes, 1830)	T,4	22			1	7			14
<i>Nemipterus hexodon</i> (Quoy & Gaimard, 1824)	T,4	2	2						
<i>Pentapodus emeryii</i> (Richardson, 1843)	T,5	371			106	130	38	30	67
<i>Pentapodus porosus</i> (Valenciennes, 1830)	T,3	54	1	2		14	7	3	27
<i>Scolopsis monogramma</i> (Kuhl & van Hasselt, 1830)	T,4	74	3	2	15	32	8	4	10

Appendix 2 continued.

	Category	Total	Kimberley		Canning		Pilbara	
			Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Keraudren	Cape Preston
Family LUTJANIDAE (Snappers)								
<i>Lutjanus argentimaculatus</i> (Forsskål, 1775) ‡	T,2	2	1	1				
<i>Lutjanus bitaeniatus</i> (Valenciennes, 1830) ‡	T,5	927	210	717				
<i>Lutjanus carponotatus</i> (Richardson, 1842) ‡	T,4	5217	463	1028	1657	1096	359	412
<i>Lutjanus erythropterus</i> Bloch, 1790	T,1	17	3			6		7
<i>Lutjanus fulviflamma</i> (Forsskål, 1775)	T,2	9						1
<i>Lutjanus johnii</i> (Bloch, 1792) ‡	T,1	420	360	60				8
<i>Lutjanus lemniscatus</i> (Valenciennes, 1828)	T,4	346	104	40	93	9	3	74
<i>Lutjanus malabaricus</i> (Schneider, 1801) ‡	T,1	104	32		7	6		28
<i>Lutjanus quinquelineatus</i> (Bloch, 1790)	T,1	54				2		29
<i>Lutjanus rivulatus</i> (Cuvier, 1828)	T,2	2			1		1	
<i>Lutjanus russelli</i> (Bleeker, 1849) ‡	T,1	245	1	1		23	25	120
<i>Lutjanus sebae</i> (Cuvier, 1828) ‡	T,1	267	2		34	87	21	105
<i>Lutjanus vitta</i> (Quoy & Gaimard, 1824)	T,15	65				18	6	14
<i>Syphorus nematophorus</i> (Bleeker, 1860) ‡	T,5	25			4		16	3
Family CAESONIDAE (Fusiliers)								
<i>Caesio cuning</i> (Bloch, 1791)	T,4	17	2	7	2			5
Family HAEMULIDAE (Grunts, Sweetlips, Javelinfishes)								
<i>Diagramma labiosum</i> Macleay, 1883 ‡	T,5	334	29	73	53	46	101	27
<i>Plectrohinchus gibbosus</i> Lacepède, 1802	T,4	9	2	2	3		2	
<i>Plectrohinchus multivittatus</i> (Macleay, 1878)	T,A	17		1	4	9	3	
<i>Plectrohinchus polytaenia</i> (Bleeker, 1852)	T,4	33			28	3	2	
<i>Plectrohinchus vittatus</i> (Linnaeus, 1758)	T,2	1					1	
<i>Pomadasys kaakan</i> (Cuvier, 1830)	T,4	33	33					
Family SPARIDAE (Breams, Snappers, Porgies)								
<i>Chrysophrys auratus</i> (Bloch & Schneider, 1801)	Te,13	1						1
Family LETHRINIDAE (Emperors, Emperor breams)								
<i>Lethrinus atkinsoni</i> Seale, 1910	T,9	278					74	204
<i>Lethrinus genivittatus</i> Valenciennes, 1830 ‡	T,4	359				9	46	155
<i>Lethrinus laticaudis</i> Alleyne & Macleay, 1877 ‡	T,13	2875	365	556	1103	275	174	229
<i>Lethrinus lentjan</i> (Lacepède, 1802)	T,2	180	15	25	23	6		101
<i>Lethrinus miniatus</i> (Bloch & Schneider, 1801)	T,5	10				2		8
<i>Lethrinus nebulosus</i> (Forsskål, 1775) ‡	T,1	322			20	2		94
<i>Lethrinus olivaceus</i> Valenciennes, 1830	T,2	18			7		1	206
<i>Lethrinus punctulatus</i> (Macleay, 1878)	T,A	9353	14	68	1672	3582	1210	1627
<i>Lethrinus ravus</i> Carpenter & Randall, 2003	T,5	2						1180
Family NEMIPTERIDAE (Threadfin breams)								
<i>Nemipterus furcosus</i> (Valenciennes, 1830)	T,4	22			1	7		14
<i>Nemipterus hexodon</i> (Quoy & Gaimard, 1824)	T,4	2	2					
<i>Pentapodus emeryii</i> (Richardson, 1843)	T,5	371			106	130	38	30
<i>Pentapodus porosus</i> (Valenciennes, 1830)	T,3	54	1	2		14	7	3
<i>Scolopsis monogramma</i> (Kuhl & van Hasselt, 1830)	T,4	74	3	2	15	32	8	4

Appendix 2 continued.

	Category	Total	Kimberley		Canning			Pilbara	
			Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Keraudren	Cape Preston	Locker Point
Family SCIAENIDAE (Croakers)									
<i>Protonotaria diacanthus</i> (Lacepède, 1802)	T,1	5	3		2				
Family MULLIDAE (Goatfishes)									
<i>Parupeneus barberinus</i> (Lacepède, 1801)	T,2	3							3
<i>Parupeneus chrysopleuron</i> (Temminck & Schlegel, 1843)	T,4	1							1
<i>Parupeneus heptacanthus</i> (Lacepède, 1801)	T,2	2							2
<i>Parupeneus indicus</i> (Shaw, 1803)	T,2	51		2	36	5	1	3	4
<i>Parupeneus spilurus</i> (Bleeker, 1854)	T,5	9						2	7
Family GLAUCOSOMATIDAE (Pearl perches)									
<i>Glaucosoma magnificum</i> (Ogilby, 1915)	T,A	126		6	41	50	23		6
Family CHAETODONTIDAE (Butterflyfishes)									
<i>Chaetodon aureofasciatus</i> Macleay, 1878	T,3	5			1	2			2
<i>Chaetodon trifascialis</i> Quoy & Gaimard, 1824	T,2	2					2		
<i>Chelmon marginalis</i> Richardson, 1842	T,A	46	1	2	20	1	4	9	9
<i>Chelmon muelleri</i> (Klunzinger, 1880)	T,A	2	1	1					
<i>Coradion chrysozonus</i> (Cuvier, 1831)	T,4	19	1		5	12			1
<i>Heniochus acuminatus</i> (Linnaeus, 1758)	T,2	10		2	4			2	2
<i>Parachaetodon ocellatus</i> (Cuvier, 1831)	T,4	10		1		7		1	1
Family POMACANTHIDAE (Angelfishes)									
<i>Chaetodontoplus duboulayi</i> (Günther, 1867)	T,5	55	5	15	13	8	7	3	4
<i>Chaetodontoplus personifer</i> (McCulloch, 1914)	T,A	2				1			1
<i>Pomacanthus semicirculatus</i> (Cuvier, 1831)	T,2	1							1
Family POMACENTRIDAE (Damselfishes)									
<i>Abudefduf bengalensis</i> (Bloch, 1787)	T,4	42	1		13	5		9	14
<i>Abudefduf septemfasciatus</i> (Cuvier, 1830)	T,2	1							1
Family LABRIDAE (Wrasses)									
<i>Bodianus bilunulatus</i> (Lacepède, 1801)	T,2	5							5
<i>Bodianus solatus</i> Gomon, 2006	T,W	1							1
<i>Choerodon anchorago</i> (Bloch, 1791)	T,4	1							1
<i>Choerodon cauteroma</i> Gomon & Allen, 1987	T,A	109	1		6	21	40	31	10
<i>Choerodon cephalotes</i> (Castelnau, 1875)	T,5	1				1			
<i>Choerodon cyanodus</i> (Richardson, 1843)	T,A	283	12	30	145	52	1	28	15
Family SCARIDAE (Parrotfishes)									
<i>Scarus ghobban</i> Forsskål, 1775	T,12	9		3					6
Family EPHIPPIDAE (Batfishes, Spadefishes)									
<i>Platax batavianus</i> Cuvier, 1831	T,5	7			2	3	2		
<i>Platax teira</i> (Forsskål, 1775) ‡	T,1	6			1			1	4
<i>Zabidius novemaculeatus</i> (McCulloch, 1916)	T,3	3	1	1	1				
Family SIGANIDAE (Rabbitfishes)									
<i>Siganus argenteus</i> (Quoy & Gaimard, 1825)	T,2	1							1
<i>Siganus doliatus</i> Cuvier, 1830	T,9	5			3				2
<i>Siganus fuscescens</i> (Houttuyn, 1782)	T,4	424	14	3	84	209	42	44	28

Appendix 2 continued.

	Category	Total	Kimberley		Canning			Pilbara	
			Cape Voltaire	Hall Point	Emeriau Point	Cape Bossut	Cape Keraudren	Cape Preston	Locker Point
Family ACANTHURIDAE (Surgeonfishes)									
<i>Acanthurus grammoptilus</i> Richardson, 1843	T,5	4				4			
<i>Acanthurus xanthopterus</i> Valenciennes, 1835	T,12	4		1		3			
Family SPHYRAENIDAE (Barracudas)									
<i>Sphyraena jello</i> Cuvier, 1829	T,1	17	1	1	11	1			3
<i>Sphyraena putnamiae</i> Jordan & Seale, 1907	T,2	1		1					
Order TETRAODONTIFORMES									
Family BALISTIDAE (Triggerfishes)									
<i>Abalistes stellatus</i> (Anonymous, 1798)	T,1	539			42	220	74	182	21
<i>Sufflamen fraenatus</i> (Latrelle, 1804)	T,2	9							9
Family MONACANTHIDAE (Leatherjackets, Filefishes)									
<i>Chaetodermis penicilligera</i> (Cuvier, 1817)	T,5	4				3			1
<i>Monacanthus chinensis</i> (Osbeck, 1765)	T,5	77		8	9	36	4	12	8
<i>Pseudomonacanthus peroni</i> (Holland, 1854) ‡	T,3	10		1	8			1	
Family OSTRACIIDAE (Boxfishes, Cowfishes)									
<i>Rhynchostracion nasus</i> (Bloch, 1785)	T,4	1					1		
<i>Rhynchostracion rhinorhynchus</i> (Bleeker, 1852)	T,1	1				1			
Family TETRAODONTIDAE (Pufferfishes, Blowfishes)									
<i>Arothron hispidus</i> (Linnaeus, 1758)	T,2	1		1					
<i>Arothron stellatus</i> (Bloch & Schneider, 1801)	T,2	1				1			
<i>Feroxodon multistriatus</i> (Richardson, 1854)	T,A	12			1	9	1		1
Family DIODONTIDAE (Porcupinefishes)									
<i>Diodon holocanthus</i> Linnaeus, 1758	T,6	1			1				
<i>Tragulichthys jaculiferus</i> (Cuvier, 1818)	T,A	1				1			
Total number of individuals		25740	1874	2794	5865	6593	2327	3495	2792
Total number of species		132	47	51	62	60	49	56	71
Total number of Australian endemic species		16	6	8	8	11	9	5	10
Total number of Western Australian endemic species		3	2	1	2	2	3	2	3