Relationships between faunal assemblages and habitat types in Broke Inlet, Western Australia

Submitted by

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Declaration

I declare that the information contained in this thesis is the result of my own research unless otherwise cited, and has as its main content work which has not previously been submitted for a degree at any university.

James Richard Tweedley

Shifting Sands: The sand bar at the mouth of Broke Inlet in (top) summer and (bottom) winter 2008. Bottom photo by Bryn Farmer.

Abstract

The work for this thesis was undertaken in Broke Inlet, a seasonally-open estuary on the south coast of Western Australia and the only estuary in that region which is regarded as "near-pristine" (Commonwealth of Australia, 2002). The only previous seasonal studies of the environmental and biotic characteristics of this estuary involved broad-based descriptions of the trends in salinity, temperature and ichthyofaunal characteristics at a limited number of sites. Furthermore, no attempt has been made to identify statistically the range of habitats present in the nearshore and offshore waters of this system, and the extents to which the characteristics of the fish and benthic invertebrate faunas are related to habitat type. These types of data provide not only reliable inventories of the habitat and faunal characteristics of Broke Inlet, but also a potential basis for predicting the likely impact of anthropogenic and climatic changes in Broke Inlet in the future.

The main aims of this thesis were as follows. (1) To use the method of Valesini *et al.* (2010), which employs enduring environmental characteristics, to identify quantitatively the range of habitats present throughout the nearshore and offshore waters of Broke Inlet. The enduring environmental characteristics represent three broad categories, *i.e.* the location of any site in terms of its proximity to marine and freshwater sources, the degree of exposure to wave activity and the type of substrate and/or submerged vegetation. (2) To test the hypothesis that the species richness, density, diversity and species compositions of the fish and benthic macroinvertebrate faunas differ among habitat types, seasons and, in the case of the fish fauna, also years. (3) To test the hypothesis that the pattern of relative differences among habitat types, as exhibited by their faunal compositions, is correlated with that defined by their (i) enduring environmental characteristics and (ii) non-enduring environmental characteristics (water physico-chemical variables and sediment characteristics).

A high resolution satellite image and a digital elevation model of Broke Inlet were used to measure the enduring environmental characteristics at 104 and 36 widely-distributed sites in nearshore and offshore waters, respectively. These data were used to construct separate Manhattan distance matrices for nearshore and offshore waters, which were then subjected to the CLUSTER and SIMPROF routines in PRIMER v6 to identify the various groups of sites that did not differ significantly in their environmental characteristics and which were thus considered to represent habitat types.

Twelve and four distinct habitat types were identified in nearshore and offshore waters, respectively.

The ichthyofaunas at sites representing 11 nearshore (A-K) and three offshore (A-C) habitat types were sampled seasonally for two consecutive years using seine and gill nets, respectively. A total of 83,047 fish was collected from nearshore waters, representing 27 species from 19 families, with 99.6% of those fish belonging to six species which represent the Atherinidae (*Atherinosoma elongata, Leptatherina wallacei* and *Leptatherina presbyteroides*) or Gobiidae (*Afurcagobius suppositus, Pseudogobius olorum* and *Favonigobius lateralis*) and complete their life cycles within the estuary. Each of these species were found at each nearshore habitat type, except for *P. olorum,* which was not caught at habitat A.

The species richness, density and diversity of the nearshore fish fauna differed significantly among habitats, seasons and years, with habitat being the most influential factor. Generally, mean species richness and density were greatest at habitat types located in the entrance channel (B, G and H) and/or on the southern shore of the basin (C and G), while the fish assemblages were most depauperate at habitats near freshwater sources (A and J).

The nearshore ichthyofaunal composition of Broke Inlet differed significantly among habitats, seasons and years, with the first again being the most influential. However, the extents of the overall differences in composition during each sampling occasion were moderate. The lack of very pronounced ichthyofaunal differences among the various habitat types reflects the widespread distributions and high abundances of the above atherinid and gobiid species, and particularly of *A. elongata* and *L. wallacei,* which typified the fish fauna of each habitat type on almost all sampling occasions. The most distinctive of the faunas were those at habitat types in the entrance channel, where *L. presbyteroides* and *F. lateralis,* which are typically found in higher salinities, were in their greatest densities, and where several marine straggler species, such as the labrids *Notolabrus parilus* and *Achoerodus gouldii,* were occasionally caught. Seasonal and inter-annual changes in ichthyofaunal composition were small and often not consistent across habitats.

The pattern of relative differences among nearshore habitats in terms of their ichthyofaunal composition was correlated at a moderate level with that defined by their enduring environmental characteristics in all but one of the eight seasons. Such findings

indicate that the ichthyofaunal composition likely to be found at any site in the nearshore waters of Broke Inlet at any time of year can be predicted, simply by assigning that site to its most appropriate habitat type on the basis of its enduring environmental characteristics. Differences in ichthyofaunal composition among habitat types were also correlated, but to a slightly greater extent, with those among the suite of non-enduring water physico-chemical variables, with salinity and the biomass of macrophytes being particularly relevant.

Gill netting in the three offshore habitats yielded 1,050 fish representing 31 species. Species richness, catch rates and diversity all varied significantly among habitats, with the values for each of these biotic characteristics always being greatest at habitat A in the entrance channel and lowest at habitat B near the Shannon River mouth. These biotic variables did not always vary, however, among seasons and/or years. In contrast to the situation in nearshore waters, the offshore ichthyofauna comprised mainly marine estuarine-opportunists and marine stragglers, which contributed 84% to the number of species and 80% to the total number of fishes. The contribution of individuals belonging to the marine straggler guild was only 5% and no estuarine resident species were caught.

Ichthyofaunal composition in offshore waters differed significantly among habitats, seasons and years, with habitat being the most influential factor. Faunal composition only differed among habitats in spring and autumn, and even then the extent of those differences was low. During those seasons, habitat B contained the most distinct and depauperate fauna, which was typified mainly by *Mugil cephalus* and *Aldrichetta forsteri*. In contrast, the fish assemblages at habitats A and C were also typified by *Arripis georgianus, Arripis truttaceus, Rhabdosargus sarba, Pagrus auratus, Pseudocaranx dentex* and *Engraulis australis.*

The pattern of relative differences among offshore sites in terms of their ichthyofaunal composition was significantly correlated with that defined by their enduring environmental characteristics only in autumn, but was moderately correlated with that exhibited by the suite of non-enduring water physico-chemical variables in each season except summer.

Seasonal sampling of benthic macroinvertebrates at six of the nearshore habitat types (A, C, D, F, H and K) for a year yielded 7,485 individuals representing 28 species and seven phyla and, at the three offshore habitat types (A-C), 2,459 individuals

representing 26 species and eight phyla. Polychaetes (64 and 57%) and crustaceans (24 and 34%) were the most abundant taxa in nearshore and offshore waters, respectively. The mean density of invertebrates in the nearshore waters did not differ significantly among habitats, but did vary significantly among seasons, and was greatest in summer. The mean densities of invertebrates in offshore waters did not differ significantly, however, among habitats or seasons.

The compositions of nearshore benthic macroinvertebrate assemblages differed significantly among habitats and, less conspicuously, seasons. Comparisons between the faunal compositions in each pair of habitats in spring and summer were almost invariably significantly different and to a moderate extent. However, such pairwise comparisons were rarely significant in autumn and winter. Habitats A and K contained the most distinct and depauperate invertebrate fauna, comprising mainly the polychaete *Capitella capitata* and amphipod *Corophium minor*, whereas the other habitats also contained large numbers of the polychaete *Ceratonereis aequisetis*. In offshore waters, the composition of the benthic macroinvertebrate assemblages differed to a low to moderate degree among habitats, with habitat B containing the most distinct fauna due to large densities of *C. minor*. The extent of seasonal differences in these faunal compositions was small.

The pattern of relative differences among nearshore habitats in terms of their benthic macroinvertebrate composition was highly correlated with that defined by both their (i) enduring environmental characteristics and (ii) non-enduring water physico-chemical and sediment characteristics in spring and/or summer. Although the faunal and enduring environmental data were not correlated at offshore sites, the fauna and non-enduring environmental variables at those sites were correlated to a moderate extent.

In summary, the composition of the nearshore fish fauna at any site in Broke Inlet at any time of year can now be predicted by allocating that site to a particular habitat type on the basis of its enduring environmental characteristics. The less consistent spatial correlations between the compositions of the offshore fish fauna and benthic macroinvertebrate faunas and the enduring environmental variables largely reflected the ubiquitous nature of the majority of the abundant species representing those faunas, *i.e.* they are typically at least moderately abundant in all habitats and thus have no strong preferences for a particular habitat type.

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Chapter 1
General introduction

1.1: What is an estuary?

The paradigm states that an estuary is where the river meets the sea (Lyell, 1833; Ketchum, 1951), however, the scientific definition of an estuary has attracted much debate (see Day, 1980; Perillo, 1995; Elliott & McLusky, 2002; Potter *et al.*, 2010). Despite all definitions sharing a number of common attributes, *i.e.* (i) the dilution of seawater by water derived from land drainage, (ii) the presence of tides for some or all of the year, and (iii) the degree of enclosure (Tagliapietra *et al.*, 2009), there was little agreement on a suitable scientific definition until the 1964 Estuaries symposium (Lauff, 1967) when support was given for the following; "*an estuary is a semi-enclosed body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage*" (Pritchard, 1967). This definition, however, focused on salinity whereas the word "estuary" was derived from *aestus* meaning "of tide". Therefore, numerous authors have denounced a semantic misuse of the term estuary when describing non-tidal environments (Perillo, 1995; Elliott & McLusky, 2002). In response, a new definition with greater emphasis on tidal influences gained acceptance; "*an inlet of the sea reaching into a river valley as far as the upper limit of tidal rise, usually being divisible into three sections; a) a marine or lower estuary, in free connection with the open sea; b) a middle estuary, subject to strong salt and freshwater mixing; and c) an upper or fluvial estuary, characterised by fresh water but subject to daily tidal action*" (Dionne, 1963).

Both these definitions reflect the historical development of the term by researchers working on estuaries along temperate North Atlantic coasts where these systems are typically macrotidal with a free connection to the ocean, as opposed to many of those in southern Australia (*e.g.* Pollard, 1994b; Hodgkin & Hesp, 1998; Roy *et al.*, 2001), South Africa, (*e.g.* Reddering & Rust, 1990; Whitfield, 1992; 1998), New Zealand (*e.g.* Hume *et al.*, 2007) and also some systems in North America (*e.g.* Webb *et al.*, 1991; FitzGerald *et al.*, 2002; Kraus *et al.*, 2008). In these regions, estuaries become isolated from the marine environment through the formation of a sand bar across their mouth. Thus, Day (1980) modified Pritchard's original definition to include these estuaries with a periodic open connection to the sea by substituting "*free connection with the open sea*" with "*either permanently or periodically open to the sea"*. Although the definition by Day (1980) was developed primarily to incorporate South African estuaries, this modification was also particularly poignant for some estuaries in south-western Australia which vary both in their morphology and degree of isolation from the sea (Hodgkin & Hesp, 1998; Brearley, 2005). Furthermore, estuaries in this latter region are found along microtidal coasts which restrict the amount of water exchange with the ocean through their narrow mouths and have wide, shallow basins that facilitate high evaporation and thus can become hypersaline. With this in mind, an amendment to the Day (1980) definition was proposed by Potter *et al.* (2010), *i.e.* that an estuary is, "*a partially enclosed coastal body of water that is either permanently or periodically open to the sea and which receives at least periodic discharge from a river(s), and thus, while its salinity is typically less than that of natural sea water and varies temporally and along its length, it can become hypersaline in regions when evaporative water loss is high and freshwater and tidal inputs are negligible*". It is also noteworthy that these workers excluded intermittently closed and open lakes and lagoons from their definition as these systems lack fluvial input (Potter *et al.*, 2010).

1.2: Characteristics of south-western Australian estuaries

The morphology of many estuaries in temperate Australia differ markedly from those in the temperate northern hemisphere, which generally maintain a free connection with the ocean and are strongly influenced by the tide, *e.g.* Severn Estuary (Bassindale, 1943). Such estuaries in southern Australia can be classified into four geomorphic types, (i) riverine estuaries, which comprise narrow riverine channels throughout their length, *e.g.* Moore River Estuary, (ii) inter-barrier estuaries, *i.e.* elongate lagoons parallel to the coast situated behind barrier dunes or on-shore reefs, *e.g.* Leschenault Estuary, (iii) valley estuaries, *i.e.* drowned river valleys *e.g.*the Swan-Canning Estuary and, (iv) basin estuaries, which are flooded depressions in the coastal plain, *e.g.* Broke

Inlet (Hodgkin & Hesp, 1998; Potter & Hyndes, 1999). Non-riverine systems, *i.e.* inter-barrier, valley and basin estuaries, all exhibit a similar morphology generally comprising three main regions; (i) the upper estuary which includes the lower reaches of the tributary river(s), whose lower reaches are saline and undergo pronounced seasonal changes in hydrology (Hodgkin & Hesp, 1998; Chuwen *et al.*, 2009a), (ii) the middle estuary containing a large shallow basin(s), and (iii) the lower region which consists of an entrance channel which is usually short and narrow having marine-like characteristics. The microtidal oceanic tides of southern Australia, which are typically < 1 m, in combination with the narrow estuary mouths that attenuate 90% of the tide, result in limited tidal water movement within these estuaries (Hodgkin & Di Lollo, 1958; Hodgkin & Hesp, 1998).

When first flooded by the Holocene marine transgression *ca* 7,000 years ago estuaries in south-western Australia had a permanent connection with the ocean which they maintained until *ca* 3,500 years ago. In more recent times, however, littoral drift and tidal action accumulate sand at the mouths of these estuaries, which, when sufficient, result in the isolation of the estuary from the ocean. Some estuaries in south-western Australia have maintained, either naturally or artificially, a permanent connection to the ocean since the Holocene marine transgression and are termed "permanently-open" (Lenanton & Hodgkin, 1985; Hodgkin & Hesp, 1998). Conversely, in "seasonally-open" systems, sand accumulates at the estuary mouths during the very dry summer and early autumn period which isolate the estuary from the ocean. This sand bar is breached (either naturally or artificially) when the volume of water behind the bar increases markedly as a result of heavy winter rainfall (Hodgkin & Hesp, 1998; Chuwen *et al.*, 2009a). The bar at the mouth of some systems may remain either closed for years at a time and only breach following exceptional rainfall and are thus termed "normally-closed" or alternatively may never break, in which case these estuaries become salt lakes with no replenishment from the ocean and classified as "permanently-closed" (Lenanton & Hodgkin, 1985; Hodgkin & Hesp, 1998).

Approximately fifty estuaries occur along the 2,400 km coastline of south-western Australia, from the Murchison River at the northern extent of this region on the west coast through to Poison Creek at the eastern extent of the south coast of Western Australia (Potter & Hyndes, 1999; Brearley, 2005). The majority of estuaries along the lower west coast are either permanently-open (*e.g.* Swan-Canning and Peel-Harvey estuaries) or seasonally-open (*e.g.* Margaret River). Extending east from Cape Leeuwin *ca* 400 km to Albany the majority of estuaries are seasonally-open (*e.g.* Broke, Irwin and Wilson inlets) with several permanently-open estuaries, *i.e.* Blackwood River and Walpole-Nornalup estuaries and Oyster Harbour. East of Albany rainfall decreases markedly and as a result almost all estuaries are either normally-closed (*e.g.* Wellstead Estuary and Hamersley Inlet) or permanently-closed (*e.g.* Culham Inlet) (Potter & Hyndes, 1999; Brearley, 2005).

1.3: Estuarine fish assemblages and their use of estuaries

Numerous studies have highlighted the importance of estuaries for many fish species as they provide nursery and feeding areas (Beck *et al.*, 2001; McLusky & Elliott, 2004), areas of refuge (Elliott *et al.*, 1990) and migration routes (Able, 2005; Bottom *et al.*, 2005; Guelinckx *et al.*, 2006), and thus support large and productive fish communities (Schelske & Odum, 1961; Haedrich, 1983). Due to the environmental and economic importance of these systems, the compositions of estuarine fish assemblages have been well studied throughout the world (see Potter *et al.*, 1990; Pihl *et al.*, 2002; Nordlie, 2003 for reviews). These studies on the ichthyofauna of estuaries in western Europe, eastern North America, south-western Australia and South Africa highlight the diversity of both fish species (225, 237, 194 and 147, respectively) and families (79, 80, 90 and 62, respectively) present within these systems. Commonalities in taxonomic composition among these regions are low with only nine families and two species represented in all four regions (Nordlie, 2003). Although it should be noted that commonalities between south-western Australia and South Africa are slightly greater with these regions sharing 45 of 112 families and 15 of 326 species (Potter *et al.*, 1990).

Further to taxonomic descriptions of estuarine fish faunas, some studies have also included details based on functional analysis of community structure, where each species is assigned to a guild based on its use of an estuary (see Elliott *et al.*, 2007 for a review). The ichthyofaunal species in south-western Australian estuaries can be assigned into one of seven life cycle guilds. (i) Marine stragglers, *i.e.* species that spawn at sea and enter estuaries in low numbers, *e.g.* Brownspotted Wrasse (*Notolabrus parilus*). (ii) Marine estuarine-opportunists, *i.e.* marine species that regularly enter estuaries particularly as juveniles but may also use nearshore marine waters, *e.g.* Yelloweye Mullet (*Aldrichetta forsteri*). (iii) Estuarine residents, *i.e.* species that complete their entire life cycle within estuaries, *e.g.* Wallace's Hardyhead (*Leptatherina wallacei*). (iv) Estuarine and marine species, *i.e.* species which are represented by estuarine and marine populations *e.g.* Southern Longfin Goby (*Favonigobius lateralis*). (v) Freshwater stragglers, *i.e.* species found in low numbers in estuaries and whose distribution is usually limited to the low salinity, upper reaches of estuaries, *e.g.* Western Pygmy Perch (*Edelia vittata*). (vi) Anadromous species, *i.e.* species that undergo their greatest growth at sea and which, prior to the attainment of maturity, migrate into rivers where spawning subsequently occurs, *e.g.* Pouched Lamprey (*Geotria australis*), and (vii) semi anadromous species, *i.e.* species whose spawning run from the sea extends only as far as the upper estuary, *e.g.* Western Australian Gizzard Shad (*Nematalosa vlaminghi*) (Potter & Hyndes, 1999).

The various contributions of the different life cycle guilds to the overall species richness and abundance reflect the different ways fish use estuaries around the world. For example, the contribution of marine straggler taxa to the species richness of south-western Australian and South African estuarine ichthyofaunas was *ca* 70% in both regions but only 5% in western Europe. Conversely, marine estuarine-opportunists comprised 45% of the taxa in the last region but only 12-13% in estuaries in south-western Australia and South Africa (Potter *et al.*, 1990; Elliott & Dewailly, 1995). In holarctic estuaries, such as the Severn Estuary, the contribution of marine estuarine-opportunists to the species richness is also mirrored in their abundance with representatives of this guild contributing 92% of the individuals, while estuarine resident species contributed < 1% (Potter & Hyndes, 1999). In contrast, the nearshore waters of estuaries in south-western Australia contain a fauna numerically dominated by individuals of estuarine resident species. For example, a recent study of five estuaries along the south coast of Western Australia, which differ in their extent of connectivity to the ocean, found that the nearshore fish fauna of each estuary was numerically dominated by estuarine residents and estuarine and marine species which represented between 93.3 and 99.9% of the fish caught, while those of marine estuarine-opportunists represented only 0.1 to 3.8% of the ichthyofauna (Hoeksema *et al.*, 2009). The offshore waters of these same south-western Australian estuaries was found to be dominated by marine estuarine-opportunists which represented between 57.3 and 86.1% of the individuals, with the relative abundance of estuarine residents varying considerably among estuaries ranging between 0.4 and 25.4% (Chuwen *et al.*, 2009b).

1.4: Estuarine benthic macroinvertebrate assemblages

Benthic macroinvertebrates, *i.e.* those invertebrates > 500 μm in size, are a vital component of estuarine ecosystems and perform a number of crucial ecosystem functions. For instance, their bioturbation activities, such as feeding, tube-building, burrowing, irrigation of burrows, excretion and locomotion substantially influence the exchange of materials between the sediment and the overlying water column (Rhoads, 1974; Aller & Aller, 1986; Hansen & Kristensen, 1997). Thus, tube-building and burrowing enhance nutrient cycling by increasing the area of the oxic-anoxic interface and the transport of ions through the sediment (Kristensen *et al.*, 1991; Pennifold & Davis, 2001; De Roach *et al.*, 2002). Furthermore, turbidity levels are reduced through filter feeding and biodeposition and quantities of detrital matter are substantially reduced by grazing deposit feeders (Nielson *et al.*, 1996). These faunas also represent a major component of food webs within estuarine ecosystems, not only because they consume detrital material and primary food sources (Riisgård, 1991), but they also provide a major food source to both fish (*e.g.* Humphries & Potter, 1993; Sá *et al.*, 2006; Chuwen *et al.*, 2007) and avian predators (*e.g.* Moreira, 1997; Lourenço *et al.*, 2008).

The distribution of particular benthic macroinvertebrate species and/or faunal compositions have been linked to abiotic changes in the environment, including sediment grain size and organic matter content, salinity, dissolved oxygen concentrations, the presence of a bar at the mouth of the estuary, aquatic macrophytes, nutrient loadings, light penetration, freshwater flushing and a range of anthropogenic effects (*e.g.* Warwick, 1986; Edgar, 1991; Edgar & Cresswell, 1991; Ysebaert *et al.*, 1993; Snelgrove & Butman, 1994; Diaz & Rosenberg, 1995; Heck *et al.*, 1995; McLachlan, 1996; Edgar *et al.*, 1999; Edgar & Barrett, 2002; Hirst, 2004; Hastie & Smith, 2006). Furthermore, the strong associations between particular benthic species and an abiotic variable or suite of variables, has enabled the prediction of the distribution of many of those species (*e.g.* Ysebaert *et al.*, 2002; Ellis *et al.*, 2006).

Within permanently-open holarctic estuaries, benthic macroinvertebrate species richness and diversity is generally greatest in the lower saline reaches and declines progressively in an upstream direction with decreasing salinity (McLusky, 1987; Ysebaert *et al.*, 1993). The same trend occurs in some permanently-open estuaries in the southern hemisphere (*e.g.* Jones *et al.*, 1986; Edgar *et al.*, 1999), however, within seasonally-open estuaries, differences in salinity appear to have less of a structuring effect (*e.g.* Teske & Wooldridge, 2003; Dye & Barros, 2005b).

Many authors have recorded greater benthic invertebrate densities in macrophyte beds as opposed to nearby unvegetated areas (*e.g.* Edgar *et al.*, 1994; Heck *et al.*, 1995; Connolly, 1997; Mattila *et al.*, 1999). Such trends have generally been related to the increased structural complexity of the habitat which provides protection from predators (Heck & Thoman, 1981; Orth *et al.*, 1984; Warfe & Barmuta, 2004) and increased food availability either from the macrophytes themselves in the form of detritus (Rossi & Underwood, 2002; Smit *et al.*, 2006), epiphytic algal growth (Kitting *et al.*, 1984; Orth & Van Montfrans, 1984) or by trapping allochthonous food sources (Hori, 2006).

Sediment characteristics, such as grain size and organic matter content, can also influence the distribution and abundance of benthic macroinvertebrate species within estuaries. For example, suspension feeders, such as bivalves, are typically more abundant on the coarse, well oxygenated substrate of sand flats where high water velocities prevent detritus and fine sediments from settling and thus provide an adequate supply of suspended particulate food (Sanders, 1958; Wood, 1987). Conversely, areas with weaker currents allow fine sediments and organic matter to settle out of the water column often resulting in deoxygenation of the sediment and the raising of the depth of the transition zone closer to the surface (Jørgensen, 1980; Barnes & Hughes, 1999). In these situations, the benthic fauna is typically dominated by opportunistic deposit feeders, such as capitellid and spionid polychaetes (Pearson & Rosenberg, 1978; Wilson *et al.*, 1998). Few suspension feeders colonise these areas as fine sediment particles clog their filtering structures and the deposition of sediment can bury settling larvae (Rhoads & Young, 1970).

Temporal changes have also been detected in benthic macroinvertebrate composition. For example, seasonal changes in faunal composition have been related to the timing of reproduction and/or recruitment of certain species and species tolerances to seasonal changes in water physico-chemistry (*e.g.* Rainer, 1981; Kalejta & Hockey, 1991; Sardá *et al.*, 1995; Platell & Potter, 1996; Kanandjembo *et al.*, 2001). Long-term changes in the composition of benthic communities in estuaries and marine embayments have also been detected following attempts to remediate these environments from anthropogenic effects (*e.g.* Wilson *et al.*, 1998; Wildsmith *et al.*, 2009). Nevertheless, in seasonally-open estuaries the extents of spatial differences in benthic faunal composition have been generally shown to be more influential than temporal differences (*e.g.* Teske & Wooldridge, 2001; Edgar & Barrett, 2002; Gladstone *et al.*, 2006).

1.5: The conservation and management of aquatic environments

Conservation efforts have traditionally been centred around a single or “focal species” and its associated habitat (Zacharias & Roff, 2001). This single species is perceived to be of value to a particular natural environment and thus attracts management and conservation attention. Such species can be categorised as either, (i) an indicator species, whose presence denotes the composition or condition of a habitat, (ii) a keystone species, whose impacts on the habitat are disproportionally large relative to its abundance, (iii) an umbrella species, whose presence will conserve other species or (iv) a flagship species, whose presence will enlist public support (Power *et al.*, 1996; Simberloff, 1998; Zacharias & Roff, 2001). These concepts were popular in the 1980s as they provided a shortcut to maintaining and protecting a habitat through the management and monitoring of a single species. However, despite some authors suggesting these single species concepts are still of relevance in the management of aquatic environments today (Wilson, 1994; Kearney *et al.*, 1996; Piraino *et al.*, 2002; Christianou & Ebenman, 2005) a number of criticisms exist. Such criticisms focus on, (i) a lack of a firm definition for each category of focal species and criteria for selecting representative species (Simberloff, 1998; Zacharias & Roff, 2001) and (ii) the effectiveness of using a single species as a surrogate for a habitat/ecosystem (Simberloff, 1998).

Although these single species concepts still have some ecological relevance, in the last twenty years emphasis has shifted to conversing spaces, *i.e.* an “ecosystem approach” (Pearce, 1991; Crowder & Norse, 2008). This is based on the paradigm that if the ecosystem is protected then so will the biota which inhabit it (Edgar *et al.*, 1999; Pauly *et al.*, 2002; Lubchenco *et al.*, 2003) and the implementation of this approach has led to an increase in the number of marine protected areas (Pérez-Ruzafa *et al.*, 2008). However, the location of a marine protected area was often chosen either in a haphazard or *ad hoc* manner (McNeill, 1994; Pressey, 1994; Williams & Bax, 2001) or based on the aforementioned single species management concept (Roff & Evans, 2002), rather than to allow effective management of the resources within the park (Aguilar-Perera *et al.*, 2006; Stamieszkin *et al.*, 2009), or the need to protect local characteristics (Gubbay, 1988). More recently, there has been an impetus to develop scientifically credible methods of reserve selection (Stevens, 2002), which may be based on a suite of factors, such as high species richness, taxonomic diversity, presence of locally endemic or rare species, high productivity or the importance to particular species as spawning grounds, nursery areas, migratory pathways and/or feeding grounds (Fairweather & McNeill, 1993; Norse, 1993). These schemes which use habitats as surrogates for biodiversity (*e.g.* Vanderklift *et al.*, 1998; Ward *et al.*, 1999) require characterisation and classification of the marine environment at an appropriate scale which allows planners to design marine protected areas such that they incorporate representatives of every habitat type within a candidate area (Stevens & Connolly, 2005).

1.5.1: Approaches to classifying aquatic environments

Habitats are defined as ‘‘*a particular environment which can be distinguished by its abiotic characteristics and associated biological assemblage, operating at particular, but dynamic spatial and temporal scales in a recognisable geographic area*” (ICES, 2006). In order to classify areas of the aquatic environment a range of approaches have been developed which generally fall into two categories, *i.e.* habitat classification schemes and habitat mapping. Benthic habitat maps are defined in terms of seabed characteristics (topography, sediment texture, benthic cover) that can be readily detected and mapped (Diaz *et al.*, 2004). This approach to geoscientific seabed characterisation is primarily concerned with the identification, spatial extent, and geometrical relationship of geological units (*e.g.* Todd *et al.*, 1999; Kostylev *et al.*, 2001; Urbanski & Szymelfenig, 2003). However, these conventions may not be biologically meaningful as they often employ lithostratigraphic or chronostratigraphic criteria that may not be closely related to grain size and/or benthos (Orpin & Kostylev, 2006). Furthermore, many studies do not include direct biological sampling to verify the extent of concordance between substrate characteristics and the biotic distribution (Diaz *et al.*, 2004). Given the topographic emphasis of the benthic mapping concept, its application to the water column is not valid, as topographic distinctions cannot be applied to the water column (Connor *et al.*, 2006), whereas the pelagic environment can be classified using hydrographic characteristics (*e.g.* temperature, salinity and light) in a way which is ecologically relevant (Roff & Taylor, 2000). Furthermore, although habitat maps (*e.g.* UK sea map; Connor *et al.*, 2006) provide an important component of coastal marine habitat classification (*e.g.* Connor *et al.*, 2004; EUNIS, 2010) they do not provide a framework, hierarchical or otherwise, to allow the delineation or prediction of habitat types that are of direct interest to environmental managers.

Habitat classification schemes, however, comprise a set of decision rules for identifying and characterising the habitats of a given type of fauna within an area of interest (Robinson & Levings, 1995). These schemes have been used widely as a tool to aid the management and conservation of aquatic habitats and have the potential to provide information on (i) the environmental characteristics of the habitats classified,

(ii) quantitative data on the faunal assemblages present with the habitats, (iii) an ability to predict the faunal assemblage at a new site of interest and (iv) the likely consequences of any anthropogenic or environmental changes (Valesini *et al.*, 2003; Stevens & Connolly, 2004; Fujii, 2007).

1.5.2: Existing habitat classification schemes

A multitude of habitat classification schemes for marine and estuarine waters have been developed in recent years (*e.g.* Roff & Taylor, 2000; Valesini *et al.*, 2003; Connor *et al.*, 2004; Madden *et al.*, 2005; Hume *et al.*, 2007; Snelder *et al.*, 2007). While there are numerous ways of distinguishing among such schemes, one major difference depends on whether they have been based on (i) biotic characteristics, *i.e.* the distribution of a particular species (*e.g.* Paine, 1966; Estes & Palmisano, 1974) or faunal assemblage (*e.g.* Monaco *et al.*, 1992; Araújo & Costa de Azevedo, 2001; Ellis *et al.*, 2006), (ii) abiotic characteristics (*e.g.* Dethier, 1992; Digby *et al.*, 1998; Zacharias *et al.*, 1998; Roff & Taylor, 2000; Valesini *et al.*, 2003; Engle *et al.*, 2007; Gregr & Bodtker, 2007) or (iii) a combination of both (*e.g.* Mumby & Harborne, 1999; Zacharias *et al.*, 1999; Allee *et al.*, 2000; Connor *et al.*, 2004).

Classification schemes based on the single species approach have been criticised as only a small proportion of marine habitats are dominated by a single species (*e.g.* kelp forests, bivalve beds and maerl beds), while even these habitats have been shown to support diverse faunas (Grall *et al.*, 2006; Norderhaug *et al.*, 2007; Çinar *et al.*, 2008; Commito *et al.*, 2008). Thus, there has been an increase in the use of ecosystem-based approaches to management (Crowder & Norse, 2008). It is important to note that, as the distribution of all species exhibits spatio-temporal variability, the use of even a large suite of taxa offers a less robust mechanism for structuring a classification than the physical habitat in which they occur (Connor *et al.*, 2004). Moreover, the cost of adequately sampling biotic assemblages for this purpose is typically prohibitive and once completed the scheme is applicable only to the particular biotic group on which it was based and the geographical area for which it was devised.

Conversely, a variety of abiotic criteria have been used as variables in classification schemes to differentiate between habitats. These criteria generally fall into two categories, (i) enduring or (ii) non-enduring environmental criteria, *i.e.* variables that remain unchanged or which vary temporally, respectively. Numerous classification schemes have been developed which rely solely on the use of non-enduring environmental criteria and which employ variables that undergo pronounced temporal changes, such as salinity and water temperature (*e.g.* Schoch & Dethier, 1996; Brogueira & Cabeçadas, 2006). However, as with those schemes which rely on fauna, the measurement of non-enduring criteria over suitable spatial and temporal scales requires extensive *in situ* sampling and subsequent laboratory analysis, particularly in dynamic ecosystems such as estuaries, which typically undergo pronounced seasonal and inter-annual changes in environmental variables (*e.g.* Chuwen *et al.*, 2009a).

In contrast, schemes based on enduring environmental criteria are generally more cost-effective as the data required to generate the criteria tend to be readily available from mapped and/or digital sources, such as bathymetry, or generated through the use of Geographical Information Systems (GIS), *e.g.* estimating catchment size or fetch distances. As such, the use of enduring environmental criteria has been advocated in a number of classification schemes (*e.g.* Roff & Taylor, 2000; Banks & Skilleter, 2002; Roff *et al.*, 2003; Valesini *et al.*, 2003; Hume *et al.*, 2007; Snelder *et al.*, 2007). These criteria are beneficial for use in habitat classification schemes as they can act as surrogates for a suite of non-enduring criteria that may be costly to measure *in situ*. These characteristics are able to be calculated and mapped from digital sources, *e.g.* aerial photography, satellite imagery or multibeam bathymetrical data using GIS and, unlike non-enduring characteristics which vary temporally once classified these habitat types will remain distinct irrespective of time.

Habitat classification schemes also differ in their structural design. Thus, many comprise a hierarchical (nested) framework based on a set of decision rules (*e.g.* Interim Marine and Coastal Regionalisation for Australia Technical Group, 1998; Roff & Taylor, 2000; Connor *et al.*, 2004; Madden *et al.*, 2005), which can be devised using either a top down or bottom up approach. The former initially incorporates the environment of interest as a whole, which is subsequently divided up into sequentially smaller categories based on an interconnected set of decision rules, while the latter starts at the finest level of the classification and sequentially groups units into successively broader categories (Connor *et al.*, 2004). Whilst the majority of classification schemes are hierarchical, a number have been developed that typically operate at a single spatial scale and employ the use of multivariate statistical techniques, such as principle component analysis (PCA) or cluster analysis to group sites into habitat types based on a selected suite of variables (*e.g.* Zacharias *et al.*, 1998; Edgar *et al.*, 2000; Araújo & Costa de Azevedo, 2001; Valesini *et al.*, 2003; 2010).

The spatial scale encompassed by a habitat classification scheme varies greatly, with some schemes covering entire continents or countries (*e.g.* Zacharias *et al.*, 1998; Roff & Taylor, 2000; Hume *et al.*, 2007; Snelder *et al.*, 2007), while others are devised for use at regional (*i.e.* 100-1,000 km^2) (*e.g.* Edgar *et al.*, 2000; Banks & Skilleter, 2002; Valesini *et al.*, 2003) or local scales (*i.e.* 1-100 km^2) and have been developed to operate within specific systems *e.g.* an estuary (*e.g.* Brogueira & Cabeçadas, 2006; Valesini *et al.*, 2010). Several hierarchical schemes encompass all of these scales with the broadest level of classification incorporating all marine and estuarine waters within a country, while the finest level represents “biotopes” at the scale of metres (*e.g.* Allee *et al.*, 2000; Connor *et al.*, 2004; Madden *et al.*, 2005).

Finally, classification schemes differ in the extent to which they employ quantitative criteria. Many schemes, which employ qualitative or at best, semi-quantitative criteria (*e.g.* Zacharias *et al.*, 1998; Roff & Taylor, 2000; Connor *et al.*, 2004) are able to identify and use known habitat parameters to assess where biological communities may occur (Connor *et al.*, 1997). However, these classification schemes are unable to statistically test, using sound quantitative data, the relationship between habitat types and their associated fauna and predict biotic communities based on habitat characteristics. This predictive ability is of great interest to environmental managers as the model of community composition can be reliably applied to any unsampled area within the geographical area of the scheme (Zacharias *et al.*, 1999; Valesini *et al.*, 2009). In contrast, qualitative schemes are limited to describing only those areas sampled during the classification.

1.6: Rationale and overall aims

The ecological, commercial and recreational values of estuaries are well documented (*e.g.* Costanza *et al.*, 1997; Potter & Hyndes, 1999; Commonwealth of Australia, 2002), as are the range of anthropogenic and climate change related pressures that threaten their "health" and ecological functioning (*e.g.* Dyer, 1995; Kennish, 2002; McLusky & Elliott, 2004; Thompson *et al.*, 2007; Defeo *et al.*, 2009). Furthermore, whilst there has been a tendency to apply knowledge of estuarine processes and ecology, derived from northern hemisphere systems, into management strategies (Saunders & Taffs, 2009), it is important to recognise that the structure, function and ecology of estuaries in southern Australia differ markedly from those in the well studied holarctic estuaries (Potter & Hyndes, 1999; Roy *et al.*, 2001; Scanes *et al.*, 2007). Consequently, there is a real need to understand estuarine ecosystem processes in Australian estuaries, and thus develop realistic and appropriate management strategies for these systems (Saunders & Taffs, 2009). Critical to this, is a rigorous quantitative classification of estuarine habitats and an assessment of the extent to which the distribution of key faunal assemblages are related to those habitats, and the ability to successfully predict the habitat type to which any new site of interest belongs to and the suite of fauna likely to be present at that location. The current study was thus aimed at:

(1) Using the method of Valesini *et al.* (2010), which employs enduring environmental characteristics, to identify quantitatively the range of habitats present in the nearshore and offshore waters of Broke Inlet.

(2) To test the hypothesis that the species richness, density, diversity and species compositions of the fish and benthic macroinvertebrate faunas differ among habitat types, seasons and, in the case of the fish fauna, also years.

(3) To test the hypothesis that the pattern of relative differences among habitat types, as exhibited by their faunal compositions, is correlated with that defined by their (i) enduring environmental characteristics and (ii) non-enduring environmental characteristics (water physico-chemical variables and sediment characteristics).

Chapter 2

Quantitative classification and prediction of habitat types in Broke Inlet

2.1: Introduction

The ecosystem health of estuaries in south-western Australia, like that of many others throughout the world, is under increasing pressure from the detrimental influences of anthropogenic activities in these systems and their catchments (Kennish, 1992, 2002) and the influence of climate change (Dyer, 1995; Scavia *et al.*, 2002). The former include eutrophication (Cross, 1974; Lukatelich *et al.*, 1987; McComb & Lukatelich, 1995; McComb *et al.*, 1998; Robson *et al.*, 2008), anoxia and algal blooms (Robson & Hamilton, 2003; Swan River Trust, 2005), heavy metal contamination (Gerritse *et al.*, 1998; Rate *et al.*, 2000), sedimentation (Viney & Sivapalan, 2001), acid-sulphate leachate (Appleyard *et al.*, 2004) and habitat fragmentation (Hillman *et al.*, 1995). As a result, estuaries, and particularly those in temperate regions, are considered among the most degraded of all marine ecosystems (Jackson *et al.*, 2001). Furthermore, reductions in rainfall associated with climate change have resulted in decreasing stream flow and groundwater supply (Rogers & Ruprecht, 1999; Berti *et al.*, 2004), and the predicted intensification of the hydrological cycle (Easterling *et al.*, 2000; Huntington, 2006) may lead to a further reduction in rainfall (Sheffield & Wood, 2008). For example, average rainfall in the catchment of the Broke Inlet has decreased from 1,465 mm in 1956-1965 to 1,046 mm in 2006-2009 (Hodgkin & Clark, 1989a; Bureau of Meteorology, 2010). The above types of environmental changes have been shown by many workers throughout the world to have adverse impacts on estuarine fauna (see Attrill *et al.*, 1996; Hoeksema *et al.*, 2006; Martinho *et al.*, 2007; Dolbeth *et al.*, 2008; Pillay & Perissinotto, 2008, 2009), as well as for estuarine fisheries production (Gillson *et al.*, 2009), and water quality (Attrill & Power, 2000).

Despite the range of deleterious environmental influences affecting many estuaries throughout the world, there is insufficient understanding of such impacts on these ecosystems (Scavia *et al.*, 2002; Roessig *et al.*, 2004; Graham & Harrod, 2009).

Moreover, as estuaries typically (i) contain a diverse range of habitats, each with a unique set of environmental characteristics and inhabited by distinct biotic assemblages and (ii) experience considerable abiotic and biotic changes over various temporal scales (França *et al.*, 2009a; Valesini *et al.*, 2009), the influence of the above environmental impacts are likely to vary considerably over both space and time. Thus, in order to successfully manage resources and to better understand ecosystem function in estuarine environments, managers and ecologists initially require a sound understanding of the various habitats present within those systems over appropriate spatio-temporal scales. This is best achieved by firstly categorising those habitats on the basis of their collective environmental differences. This classification framework then provides a reliable foundation upon which to investigate the biota that occupy those habitats at various times (*e.g.* Stevens & Connolly, 2004; França *et al.*, 2009a; Valesini *et al.*, 2009).

As outlined in Chapter 1, a large number of habitat classification schemes, covering a wide variety of approaches, have been produced for coastal and estuarine waters throughout the world. However, the most useful schemes are typically those that (i) are based on a fully quantitative set of decision rules, (ii) employ temporally-enduring environmental criteria that are relevant to the distribution of biota and that can be accurately measured from readily-available mapped data, (iii) are developed at scales that are of most use to the majority of estuarine managers and ecologists, *i.e.* local to regional scales, (iv) are flexible in their ability to allow new data to be added and to be applied to other areas, (v) are easy to use, (vi) produce habitat types that can be demonstrated statistically to differ significantly in their environmental characteristics, and (vii) enable prediction of the habitat type to which any new site belongs (see Valesini *et al.*, 2010).

The importance of such schemes is demonstrated by their development at national levels to assist legislation aimed at improving the condition of estuarine and coastal waters (*e.g.* Vincent *et al.*, 2002; Connor *et al.*, 2004; Madden *et al.*, 2005). This is particularly relevant to Australia, where 30% of estuaries and their catchments were recently identified in a national audit as being either modified or extensively modified

(Commonwealth of Australia, 2002). Moreover, in south-western Australia, only one estuary, Broke Inlet, was considered by that audit to be in a “near-pristine” state.

The main aim of this component of the study is to apply the habitat classification scheme that has been recently developed by Valesini *et al.* (2010) for south-western Australian estuaries to the nearshore and offshore waters of Broke Inlet. Unlike many other habitat classification schemes for estuarine and/or coastal waters that are available in the scientific or grey literature, this scheme meets all of the criteria outlined above. The resulting categorisation of habitats in Broke Inlet will then provide the foundation for investigating the extent to which particular faunal assemblages differ among habitat types, and how the relationships between fauna and their habitats changes over time, *i.e.* seasonally and/or inter-annually (see Chapters 3, 4 and 5).

2.2: Materials and methods

2.2.1: Study area

2.2.1.1: Climate

The climate in south-western Australia is of a Mediterranean type (Gentilli, 1971), characterised by hot, dry summers (average maximum temperature in Perth 30°C) and cool, wet winters (average maximum 19°C; Bureau of Meteorology, 2010). The prevailing weather conditions are largely determined by seasonal movements of a belt of high pressure (anticyclonic) systems between 35°S and 45°S in summer and 26°S and 34°S in winter. Rain in the latter season is brought by cold fronts between high pressure systems in their west to east passage (Hodgkin & Hesp, 1998; Brearley, 2005). Mean annual rainfall in the region is greatest in the extreme south-west, *i.e.* around Broke Inlet, where it reaches *ca* 1,300 mm (Hodgkin & Hesp, 1998). Precipitation is highly seasonal, with 60-70% occurring between May and September, but deteriorating cyclonic storms may produce unseasonal downpours in summer (Hodgkin, 1998; Hodgkin & Hesp, 1998). Pan evaporation levels are around that of annual rainfall (1,362 mm), although surface evaporation may only be 85% of pan evaporation (Black & Rosher, 1980; Hodgkin, 1998; Hodgkin & Hesp, 1998).

The prevailing winds along the south coast in summer are south-westerly to south-easterly, with wind speeds exceeding 30 km h^{-1} for approximately 30% of the summer days, while southerlies prevail in winter (Sanderson *et al.*, 2000). Offshore marine waters are dominated by a persistent swell wave regime, which approaches the coast from a south to south-westerly direction and has a wave height of between 2-3 m with a period of 10-14 seconds (Lemm *et al.*, 1999). Unlike the lower west coast, which is protected by limestone reefs, there are few offshore islands or submerged features along the south coast to attenuate swell wave energy (Sanderson *et al.*, 2000). Furthermore, as the continental shelf is only *ca* 25-30 km wide along the south coast of Western Australia this coast is exposed to the most extreme wave energy of the entire Australian coastline (Harris *et al.*, 1991; Hemer, 2006).

Ocean currents in the region are dominated by the Leeuwin current system, consisting of the Leeuwin current, Leeuwin undercurrent and Capes current (Woo & Pattiaratchi, 2008). The Leeuwin current is a narrow (*ca* 50 km) eastern boundary current that transports warm, low salinity tropical water southwards along the continental shelf of Western Australia to Cape Leeuwin then eastward towards the Great Australian Bight (Cresswell, 1991; Smith *et al.*, 1991). The current is weakest during summer and strongest in winter when the opposing southerly winds are weaker. The Leeuwin undercurrent transports oxygen rich, nutrient depleted, high salinity water northward (Thompson, 1984), and the Capes current which also flows northward is strongest in summer (Pearce & Pattiaratchi, 1999). These currents strongly influence the marine environment of Western Australia and are responsible for the presence of some tropical marine organisms along the south-western coast of the continent (Maxwell & Cresswell, 1981; Pearce & Walker, 1991; Hutchins & Pearce, 1994; Pearce & Hutchins, 2009; Lenanton *et al*., 2009).

2.2.1.2: Geomorphology

Broke Inlet is situated on the south coast of Western Australia (34.5°S, 116.3°E) within the Ravensthorpe Ramp, which forms part of the Albany-Frazer geological province, basement Precambrian igneous and metamorphic rocks slope down from the

Yilgarn block (300 m above sea level) to the Southern Ocean, where they outcrop as headlands and islands (Hodgkin & Hesp, 1998). The coastline around the estuary is comprised of calcareous and siliceous sands and aeolian dunes, some of which were formed in the Pleistocene and have lithified to form limestone cliffs up to 150 m high in places. The inland margin of these dunes drops sharply into extensive, seasonally-inundated swampy plains, created by coastal dunes blocking surface water flow (CALM, 2005).

The estuary itself is a seasonally-open basin system which is 15 km long, up to 4 km wide and has a surface area of 48 km^2, making it one of the largest estuaries in south-western Australia (Hodgkin & Clark, 1989a). The large basin of the estuary, which is fed by the Shannon, Forth and Inlet rivers, comprises three subregions namely the Shannon, Middle and Clarke basins, which have an average and maximum depth of 1.5 and 4.5 m below mean sea level, respectively (Fig. 2.1). These subregions are often separated by shallow and dynamic sand bars (*ca* 0.5 m deep). Connection to the sea is via a 3.5 km long and 250 m wide entrance channel with an average and maximum depth of 3 and 7 m below mean sea level, respectively. The northern shore of the entrance channel is characterised by steep cliffs comprised of Pleistocene dune rock, whereas the southern shore is wide and sandy and is bordered by vegetated dunes.

Tidal exchange with the Southern Ocean is seasonal due to the formation of a large sand bar at the estuary mouth, typically between summer and early winter, as a result of the alongshore and onshore transport of marine sediments by ocean swell and local seas (Ranasinghe & Pattiaratchi, 1999b). This bar, which can be up to 500 m wide and 1.8 m high (Hodgkin & Clark, 1989a), is closed for the first half of the year and is breached either naturally or artificially in the winter or early spring, as a result of the marked increases in the volume of water in the estuary from seasonal rainfall (Chuwen *et al.*, 2009a). The bar has opened every year between 1964 and 1989 with the exception of 1969 and 1986 during which there was reduced rainfall. The opening and duration of time the bar stays open for depends mainly on the timing and volume of river flow and thus it closes again between mid spring and mid summer, never remaining open for more than six months (Hodgkin & Clark, 1989a).

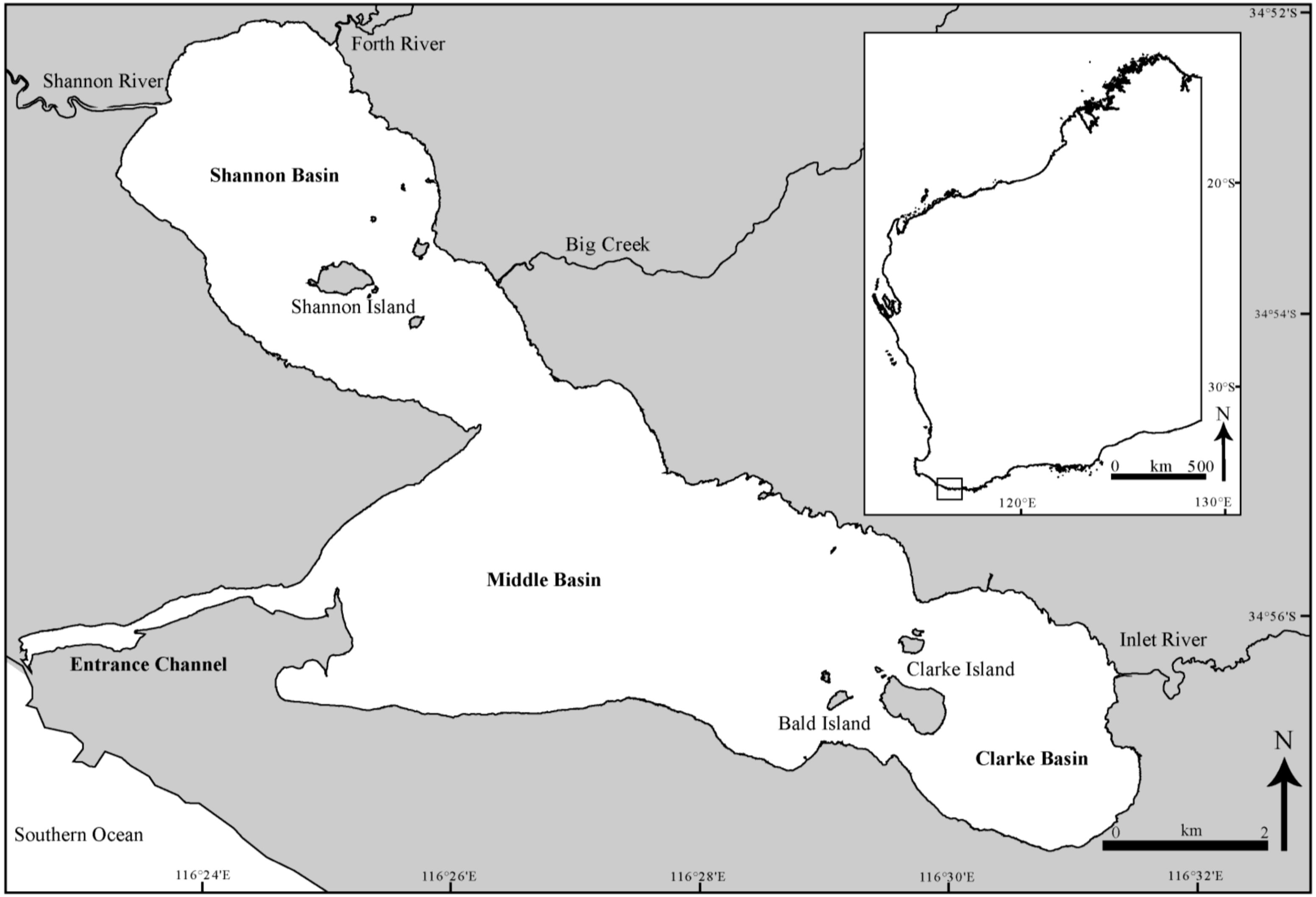


Fig. 2.1: Location of Broke Inlet within Western Australia and the main regions of the estuary basin, tributaries and islands within the estuary.

2.2.1.3: Hydrology

The catchment of Broke Inlet has three distinct drainage patterns, namely (i) a coastal belt, (ii) the dissected laterite plateau and (iii) a marine and alluvial swampy belt (CALM, 2005). The coastal belt is situated south-west of the estuary, where the soil is free draining. The dissected laterite plateau extends north-west of the estuary through dense Karri forest and reaches a height of 200 m above mean sea level where the Shannon River emanates from broad swampy head waters. The catchment of this river lies almost entirely within the Shannon National Park and comprises the majority (610 km^2) of the 928 km^2 catchment of Broke Inlet (Hodgkin & Clark, 1989a; Pen, 1999). The Shannon River, which is 47 km long, provides an estimated 141,000 ML or 86% of the mean annual flow into the estuary (Pen, 1999). Flow is highly seasonal, with 80% occurring between June and October (Hodgkin & Clark, 1989a). The marine and alluvial swampy belt, which surrounds the estuary, consists of seasonally-inundated flats where surface drainage forms a network of highly seasonal creeks (*e.g.* Big Creek) and the Forth (10 km long) and Inlet rivers (14 km long). These two rivers, which drain into the Shannon and Clarke basins, respectively (Fig. 2.1), have a mean annual flow of 6,900 and 15,700 ML, respectively (Pen, 1999). When the mouth of the estuary is open, the estuarine portion of the Shannon, Inlet and Forth rivers may extend 3 km, 2 km and 200 m from their mouths, respectively (Hodgkin & Clark, 1989a).

The salinity of the estuary exhibits pronounced intra and inter-annual variability, ranging from near fresh (< 5) to *ca* full-strength seawater (35-40) depending on the volume and timing of river flow and the time and duration of bar opening (Chuwen *et al.*, 2009a). Mixing is rapid in the basin due to its large size and shallow depth and thus salinity is generally uniform throughout the water column, except during times of high riverine flow.

Tides in south-western Australia are predominantly diurnal with a mean range of 0.6 m (Department of Defence, 2003). When the mouth of Broke Inlet is open, tidal heights within the estuary are dampened to *ca* 10% of the oceanic tide (Hodgkin & Clark, 1989a). These microtidal conditions may be overridden by changes in water level caused by atmospheric pressure, gravitational circulations and alongshore wind stress (*e.g.* Hamilton *et al.*, 2001; O'Callaghan *et al.*, 2007), which may increase water level changes by almost another metre (Hodgkin & Di Lollo, 1958).

Wave conditions within the estuary vary markedly due mainly to (i) large spatial differences in fetch and the orientation of the shoreline and (ii) pronounced temporal differences in wind speed, frequency and direction. Thus, wave heights in the narrow entrance channel and tidal portions of the rivers are typically very small, while those in the wide basin can reach 1.5 m.

2.2.1.4: Substrate and submerged aquatic vegetation

Sand banks and marginal shoals, comprised of medium to coarse siliceous sands, represent *ca* 56% of the substrate within Broke Inlet (Commonwealth of Australia, 2002). These extensive sand banks have formed from shoreline erosion, aeolian sand and the redistribution of river sediments. The substrate in the deeper areas of the estuary, however, consist of fine sand, mud and fine black gelatinous sediment (Hodgkin & Clark, 1989a).

Submerged aquatic vegetation is generally sparse throughout the basin of the estuary, particularly in Clarke Basin and the eastern shore of Shannon Basin (Tweedley, unpublished data). Most submerged aquatic vegetation occurs within the entrance channel and on the marginal shoals along the south coast of the basin, typically comprising the seagrass *Ruppia megacarpa* and to a lesser extent, the stonewort *Lamprothamnium papulosum*, the rhodophyte *Polysiphonia* and the chlorophyte *Cladophora* (Hodgkin & Clark, 1989a). Drift marine algae and seagrasses also often wash into the estuary during periods when the bar is open, and provide an ephemeral habitat and source of nutrients (Brearley, 2005).

2.2.1.5: Catchment and estuary use

Whilst substantial areas of native vegetation have been cleared for agricultural purposes from the catchments of the majority of estuaries in south-western Australia, the catchment of Broke Inlet has retained almost all of its natural vegetation and is thus in “near-pristine” condition (Commonwealth of Australia, 2002). The catchment and surrounding area have been gazetted as a component of the D’entrecasteaux and Shannon National Parks (CALM, 1987), however, the estuary itself is not protected under the current management plan (CALM, 2005). Present uses of the catchment and estuary focus largely on recreation, (*e.g.* fishing, bushwalking, horse riding, off-road-vehicle use and camping) but, a small number of commercial fishers (< 5) operate between May and October in Broke Inlet, with the majority of the catch comprising Yelloweye Mullet (*Aldrichetta forsteri;* 59%), Australian Salmon (*Arripis truttaceus*; 16%), King George Whiting (*Sillaginodes punctatus*; 12%) and Sea Mullet (*Mugil cephalus*; 5%) (Lenanton, 1984). However, total commercial catch rates which average 9,000 kg per annum have been declining since the late 1990's (Smith & Brown, 2008).

2.2.2: Measurement of enduring environmental variables

The waters of Broke Inlet were first classified as either nearshore or offshore, *i.e.* those with a depth below mean sea level of ≤ 1 or > 1 m, respectively. Numerous sites were then selected throughout both of these water depths, which were considered likely to reflect the full extent of environmental diversity throughout the system (*i.e.* 104 and 36 sites in the nearshore and offshore waters, respectively) (Fig. 2.2). No sites were selected in the tidal portions of the rivers due to the steep banks and numerous snags. Nearshore sites were defined by a point on the shoreline and all waters within a 100 m radius of that point, while offshore sites were defined as a point in the estuary and all waters within a 200 m radius of that point.

A suite of 14 enduring environmental variables, each of which represented one of three broad environmental categories, were chosen to characterise each site (Table 2.1). The first group reflected the location of each site within the estuary and was intended as a surrogate for a broad suite of water physico-chemical parameters, such as salinity, water temperature, tidal/riverine flow, and nutrient content that typically vary spatially within estuaries relative to their distance from marine and freshwater sources (see subsections 3.3.1.1 and 3.3.2.1). The second group of variables reflected the degree of exposure to wave activity generated by local winds and the impact of local bathymetry on waves as they approach the shoreline, which influence, for example, physical force generated by waves, sediment composition and turbidity. The third group comprised the contributions of the various substrate and submerged vegetation types present within the estuary.

Table 2.1: The suite of enduring environmental criteria employed in the nearshore and offshore habitat classification schemes, including their code (in brackets), the broad category to which they were assigned, their unit of measurement and the data transformation and weighting applied to each prior to analysis. MEF = Modified Effective Fetch. WSM = Wave Shoaling Margin. SAV = Submerged Aquatic Vegetation.

Enduring environmental variable	**Nearshore waters**			**Offshore waters**		
	Units	**Transformation**	**Weight**	**Units**	**Transformation**	**Weight**
Location						
Longitude (X)	Metres	None	50.00	Metres	None	50.00
Latitude (Y)	Metres	None	50.00	Metres	None	50.00
Exposure						
Northerly MEF (N)	Metres	Forth root	14.28	Metres	Forth root	11.11
Southerly MEF (S)	Metres	Forth root	14.28	Metres	Forth root	11.11
Easterly MEF (E)	Metres	Forth root	14.28	Metres	Forth root	11.11
Westerly MEF (W)	Metres	Forth root	14.28	Metres	Forth root	11.11
Northerly MEF to the WSM (NW)	Metres	-	-	Metres	Forth root	11.11
Southerly MEF to the WSM (SW)	Metres	-	-	Metres	Forth root	11.11
Easterly MEF to the WSM (EW)	Metres	-	-	Metres	Forth root	11.11
Westerly MEF to the WSM (WW)	Metres	-	-	Metres	Forth root	11.11
Direct MEF (D)	Metres	Forth root	14.28	Metres	-	-
Direct MEF to the WSM (DW)	Metres	Forth root	14.28	Metres	-	-
Average slope of the substrate (Sl)	Degrees	Square root	14.28	Degrees	Forth root	11.11
Substrate/ SAV						
% SAV (V)	Percentage	Forth root	100.00	Percentage	Forth root	100.00

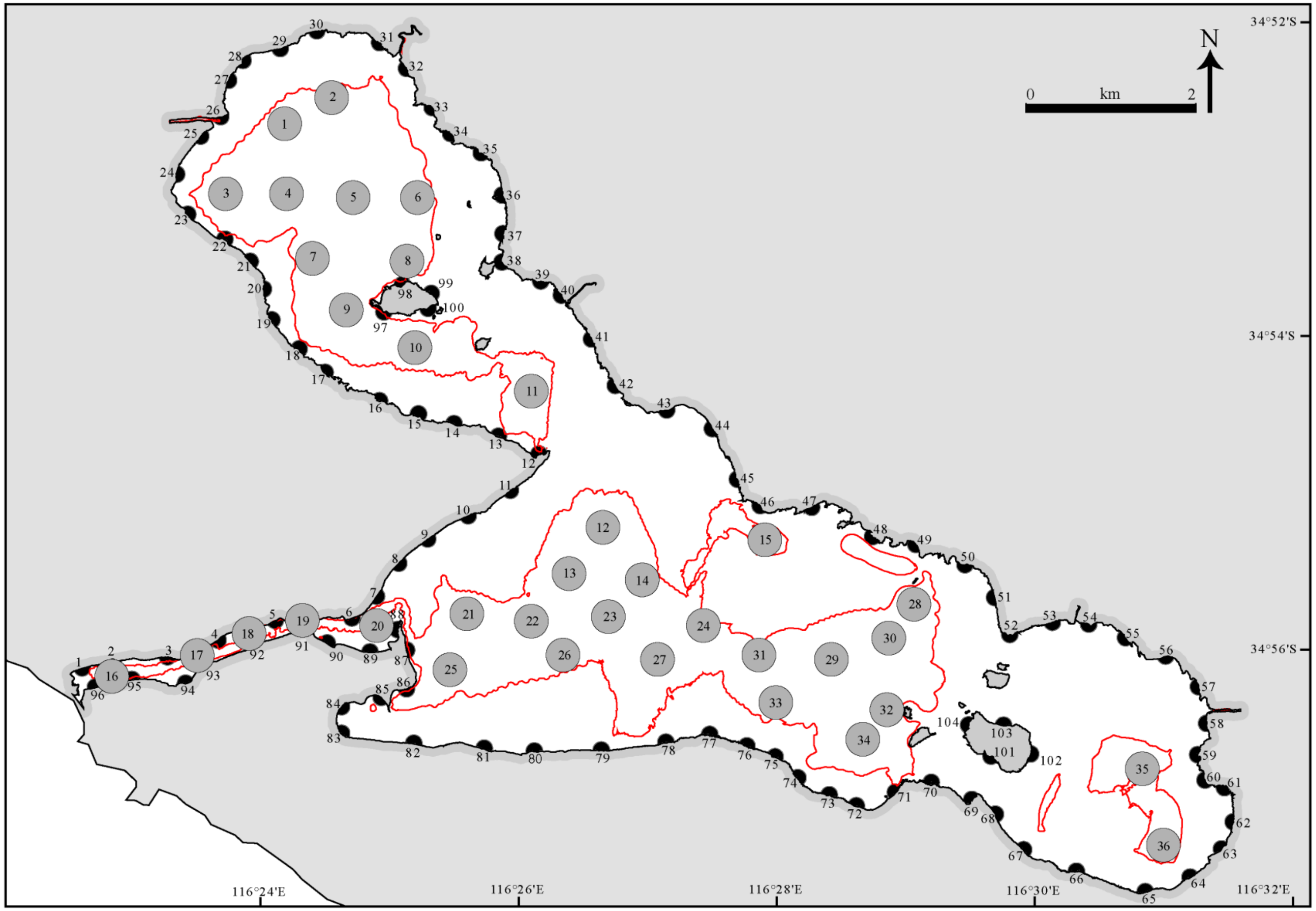


Fig. 2.2: Map of Broke Inlet showing the location of the 104 nearshore and 36 offshore sites selected for habitat classification. The red line represents the 1m depth contour and thus the boundary between nearshore and offshore waters.

2.2.2.1: Data sources and pre-processing

All enduring environmental variables were measured at each site from either a digitally georeferenced high resolution Quickbird satellite image of Broke Inlet (Dynamic Range Adjusted captured by Digital Globe in February 2007 under cloud free conditions) or from a Digital Elevation Model (DEM) of the system. ArcGIS 9.2 (ESRI, California, USA), together with the extension X Tools Pro 5 (Data East, Novosibirsk, Russia), was employed to measure the vector-based enduring environmental variables, while IDRISI v15.0 Andes (Clarke Labs, Massachusetts, USA) was used to measure the raster-based variables and Surfer 8 (Golden Software, Colorado, USA) was used to produce the DEMs. To ensure consistency among files, all were either created in or reprojected into the Universal Transverse Mercator Zone 50 South (UTM 50S) projection using the Geodetic Datum of Australia 1994 (GDA94).

Satellite image pre-processing

The satellite image of Broke Inlet, which was comprised of three separate images representing either the red, green or blue band of the colour spectrum, was initially subjected to pan sharpening (Zhang & Hong, 2005) to achieve a pixel resolution of 0.6 m. A 3x3 median filter was then applied to the image to reduce the influence of any “noisy pixels” (Eastman, 2006).

Masking out unwanted areas

The outline of the estuary, including that of any islands within the system, was firstly digitised and reclassed so that all pixels in land and aquatic areas were allocated the value 0 and 1, respectively. This reclassed image was then subjected to the OVERLAY module in combination with the satellite image, to produce a Boolean image of the estuary in which all terrestrial areas were masked out. This image was then overlaid with the DEM containing the 1 m depth contour to produce two new images of the nearshore (≤ 1 m) and offshore (> 1 m) waters, respectively.

Noise removal and water column correction

In order to remove any spectral “noise” that may have resulted from the misreading of light characteristics on the day the satellite image was taken, and thus improve the accuracy of the substrate classification, each of the three image bands were separately subjected to an unstandardised Principal Component Analysis (PCA). The principal component (PC) that accounted for the least variation was considered to represent mainly noise and was thus excluded, while the eigenvector values from the remaining PCs were subjected to reverse transformation using the IMAGE CALCULATOR module to produce three new “noiseless” bands. Water column correction techniques were then applied to the data for each noiseless band (Lyzenga, 1978, 1981), to account for the differences in the attenuation of light with water depth and clarity (Green *et al.*, 2002).

2.2.2.2: Collection of bathymetric data and construction of digital elevation model

Bathymetric data, (*i.e.* depth, latitude and longitude) and the Estimated Positional Error (EPE) were collected at a large number of sounding points throughout Broke Inlet during May and June 2007. All measurements were taken using a Garmin GPSMAP 185 Sounder with a Differential Global Positioning System (GA 29 GPS Antenna, Garmin, Kansas, USA) and recorded electronically on a laptop using Windmill Logger 4.07 (Windmill Software Ltd, Manchester, UK). The boat travelled at a speed of 6 km h^{-1} and depth soundings were recorded every 10 m in the basin and every 2 m in the entrance channel along numerous transects. Any soundings recorded where the depth was too shallow to give accurate data (*i.e.* < 40 cm) were removed from subsequent analysis, as were those with an EPE > 5 m. All depth data were corrected to the Australian Height Datum.

Interpolation was employed to estimate the depth of areas where no depth soundings were recorded (*i.e.* areas between transects). In order to choose the most appropriate interpolation methodology, nine techniques were trialled and the results subjected to the cross validation procedure in Surfer 8. The accuracy of the various techniques was tested using a series of descriptive and accuracy assessment statistics to compare the actual depth to the interpolated depth (see Desmet, 1997; Guan *et al.*, 1999) (Table 2.2). These statistics demonstrated that Triangular Irregular Networks (TIN) interpolated data was the most accurate (Table 2.2), and thus this interpolation method was subsequently used to produce a 3D DEM of the system (Fig. 2.3).

Table 2.2: Results and ranking of the descriptive and accuracy statistics used to assess the accuracy of each of the interpolation techniques trialled for producing a DEM of Broke Inlet. Max = maximum value. Min = minimum value. StDev = the standard deviation of the difference between actual and interpolated depth. ME = mean error. RSME = root mean square error. MAD = mean absolute difference. StDev MAD = standard deviation of the MAD. R^2 = coefficient of determination.

	Descriptive statistics				**Accuracy assessment statistics**						
	Max	**Min**	**Mean**	**StDev**	**ME**	**RSME**	**MAD**	**StDev MAD**	**R^2**	**Total**	**Ranking**
Actual depth	$0.00^{\cdot}$	$-6.70^{\cdot}$	$-0.80^{\cdot}$	$1.00^{\cdot}$							
Block Kriging	0.54^{6}	-7.00^{3}	-0.80^{1}	0.98^{3}	0.00^{1}	0.15^{2}	0.00^{1}	0.15^{1}	97.70^{2}	20	4
Inverse Distance to a Power	0.00^{1}	-5.93^{6}	-0.80^{1}	0.93^{6}	0.01^{7}	1.24^{7}	0.01^{7}	0.23^{4}	94.60^{6}	45	6
Local Polynomial	0.35^{5}	-4.39^{7}	-0.80^{1}	0.85^{7}	0.01^{7}	1.24^{7}	0.00^{1}	0.39^{7}	85.00^{7}	49	7
Moving Average	-0.78^{8}	-0.93^{8}	-0.85^{9}	0.04^{9}	-0.05^{9}	8.72^{9}	-0.05^{9}	1.00^{9}	00.20^{9}	79	9
Natural Neighbour	0.00^{1}	-6.50^{1}	-0.80^{1}	0.99^{1}	0.00^{1}	0.46^{5}	0.00^{1}	0.23^{4}	94.90^{4}	19	2
Near Neighbour	0.00^{1}	-6.50^{1}	-0.80^{1}	0.99^{1}	0.00^{1}	0.46^{5}	0.00^{1}	0.23^{4}	94.90^{4}	19	2
Point Kriging	0.54^{6}	-7.00^{3}	-0.80^{1}	0.98^{3}	0.00^{1}	0.15^{2}	0.00^{1}	0.15^{1}	97.70^{2}	20	4
Radial Basis Functions	30.00^{9}	-38.78^{9}	-0.80^{1}	1.22^{8}	0.00^{1}	0.13^{1}	-0.04^{8}	0.63^{8}	66.30^{8}	53	8
Triangular Irregular Network	0.00^{1}	-6.39^{5}	-0.80^{1}	0.98^{3}	0.00^{1}	0.45^{4}	0.00^{1}	0.15^{1}	97.90^{1}	18	1

Fig. 2.3: The digital elevation model of Broke Inlet produced from triangular irregular network interpolation. Depth shown in metres below mean sea level.

2.2.2.3: Calculation of enduring environmental variables

Location variables

The longitude (X) and latitude (Y) co-ordinates of each site were calculated using the ADD X, Y and Z CO-ORDINATES module in X Tools Pro.

Exposure variables

Modified Effective Fetch (MEF) along northerly, southerly, easterly, and westerly bearings (Fig. 2.4a) and, in the case of nearshore sites, also that along a bearing perpendicular to shore, *i.e.* direct fetch (Fig. 2.4b) were calculated for each site throughout the estuary using the following formula:

$$\text{MEF} = \sum(X_i * \text{Cos}\gamma_i) / \sum \text{Cos}\gamma$$

where X_i is the length of fetch $_i$ and γ_i is the angle of deviation from that fetch (Coastal Engineering Research Centre, 1977).

This method employs multiple fetch measurements that deviate, within a given arc, from either side of the bearing of interest. It provides a more robust reflection of wave exposure than fetch measured along a single bearing, as it reduces the influence

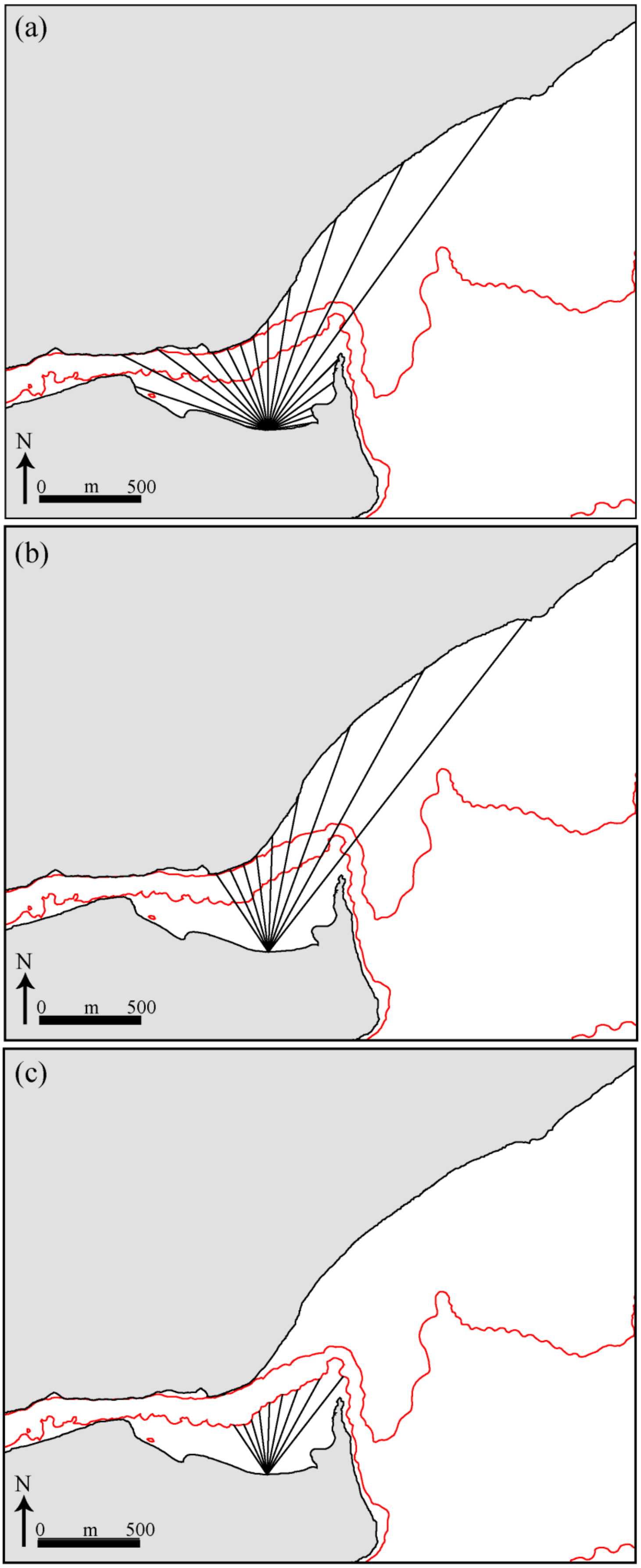


Fig. 2.4: Examples of the modified effective fetch bearings used to calculate (a) the fetch in all cardinal directions [note that all fetch lines overlying land have been removed] (b) direct fetch and (c) direct fetch to the wave shoaling margin at site 89. The red line indicates the position of the wave shoaling margin.

that any fine scale coastal indentation or emergent feature, *e.g.* a rocky outcrop, may have on the latter method. For each of the above bearings, four fetch lines oriented at successive 9° increments on both sides of the true bearing were used to calculate MEF, with any lines that lay entirely over land recorded as zero.

The distance of each nearshore site from the wave shoaling margin, which was considered to be adequately reflected by the 1 m depth contour, was determined by trimming the MEF lines for direct fetch at the point at which they intersected that depth contour (Fig. 2.4c). In those cases in which a fetch line did not extend over waters greater than 1 m in depth, it was terminated at the opposite shoreline. For offshore sites, this variable was replaced with a series of modified effective cardinal fetches that extend from each site to the 1 m depth contour, which collectively reflected the extent of the water depth surrounding each site (Table 2.1). The average slope of the substrate at each nearshore and offshore site was calculated by subjecting the DEM of the estuary to the SLOPE module in IDRISI.

Substrate classification and quantification of substrate/SAV type

Preliminary visual analysis of the pretreated satellite image, in conjunction with several extensive reconnaissance trips in the field identified two main substrate types, namely bare unconsolidated substrate and submerged aquatic vegetation. The latter group represented both seagrass and macroalgae, as they could not be reliably discriminated from each other on the image, due either to the fact that they often grew in mixed stands and/or their spectral signatures were not sufficiently distinct. Minimum-distance-to-means classification (MINDIST; Eastman, 2006), a supervised classification methodology, was employed to classify the nearshore areas of the estuary into two benthic classes (Fig. 2.5). The accuracy of the resultant benthic classification was determined by nominating a subplot of 5 m radius around a pixel in each class at all sites on the classified map, visiting each of those subplots in the field, then calculating the number of times the benthic class derived from the classified map matched that observed in the field. The overall accuracy of the benthic map was 94%. The area (m^2)

occupied by each benthic class at each site was then calculated and converted to a percentage using the EXTRACT module.

The offshore areas of the entrance channel, which contained clear marine waters at the time the satellite image was captured, facilitated classification and ground-truthing of the benthos in this region using the methods described above (accuracy 85%). However, the benthos at the offshore sites throughout the basin could not be classified in this way as their overlying waters were too tannin stained. Thus, 200 subplots across all offshore sites in the basin were surveyed in the field using a drop camera (Canon Power Shot 540, Canon, Tokyo, Japan), which revealed that the only substrate type present was bare unconsolidated sand/mud.

Fig. 2.5: Classification of the benthos in the nearshore waters of the entrance channel and Middle Basin of Broke Inlet produced using MINDIST classification. Yellow and red areas represent vegetated and unvegetated areas, respectively.

2.2.3: Classification and prediction of habitat types

The following suite of statistical procedures were carried out to assign each of the nearshore and offshore sites in Broke Inlet to their appropriate habitat type on the basis of the measurements for their enduring environmental characteristics. All analyses were carried out using the PRIMER v6 multivariate statistics package (Clarke & Gorley, 2006). The procedures employed in this methodology are based on those developed by Valesini *et al*. (2010) for the nearshore waters of estuaries in south-western Australia, and have been redescribed here to highlight the components that are unique to Broke Inlet.

2.2.3.1: Data pretreatment

The values for each of the enduring environmental variables recorded at the various nearshore and offshore sites were initially examined using pairwise Draftsman plots to (i) visually assess the extent to which the distribution of values for each variable were skewed and thus the type of transformation required to ameliorate any such effect and (ii) determine whether any pair of variables were highly correlated. The transformations carried out on each variable are listed in Table 2.1. Furthermore, as the percentage contributions of bare unconsolidated substrate and submerged aquatic vegetation were found to be highly correlated for both the nearshore and offshore sites, the former variable was removed from subsequent analyses.

As data for several of the enduring environmental variables were not directly comparable due to their different units of measurement, the data for each was normalised to place all variables on a common scale (Clarke & Gorley, 2006). Furthermore, in order to ensure that each of the three broad categories of enduring environmental variables contributed equally to the habitat classifications for both the nearshore and offshore waters, a weighting procedure was carried out in which each category was given an arbitrary weight of 100, which was then divided equally amongst its component variables. For example, both variables in the location category were assigned an equal weighting of 50. The weights assigned to each variable are provided for the nearshore and offshore waters in Table 2.1. The pretreated enduring environmental data for each site in the nearshore and offshore waters were then used to construct separate Manhattan distance matrices. Manhattan rather than Euclidean distance was employed as the distance coefficient as it operates with absolute and not squared differences and thus is less prone to distortion by outliers (Clarke *et al.*, 2006).

2.2.3.2: Classification of habitat types

To identify those groups of sites that did not differ significantly in their suite of enduring environmental characteristics and thus represented distinct habitat types, each Manhattan distance matrix was subjected to hierarchical agglomerative clustering with group-average linking (CLUSTER) and an associated Similarity Profiles (SIMPROF) test (Clarke *et al.*, 2008). A SIMPROF test was performed at each node of the dendrogram to ascertain whether the particular group of samples being subdivided contains significant internal structure. This routine thus provides a sound basis for ascertaining the points in the clustering procedure at which further subdivision of the samples (sites) is unwarranted. The null hypothesis that there were no significant environmental differences among sites was rejected if the significance level (p) associated with the test statistic (π) was < 0.01. Habitat types represented by only one site were considered to be outliers and were thus removed from subsequent analyses.

2.2.3.3: Prediction of habitat types

Any new nearshore or offshore site in Broke Inlet (*i.e.* one not used in the habitat classification procedure) was able to be quantitatively assigned to its most appropriate habitat type on the basis of measurements for its enduring environmental variables, by employing a novel application of the Linkage Tree (LINKTREE) and SIMPROF routines (Clarke *et al.*, 2008). This approach was used to produce a binary decision tree whose terminal nodes represented each of the habitat types identified by the classification procedure and at each branch of the tree identified the quantitative thresholds of the enduring environmental variables that best separated sites into their most appropriate habitat types.

To produce linkage trees for the nearshore and offshore waters of Broke Inlet, a fixed “model” resemblance matrix was constructed by (i) averaging the pretreated data for each enduring environmental variable across the various sites representing any given habitat type, (ii) replicating those average values for each site representing that habitat type and (iii) employing these data to construct a Manhattan distance matrix. This distance matrix thus reflected the pattern of environmental differences among habitats identified by the classification procedure, but without any heterogeneity among sites from the same habitat type, *i.e.* pairs of sites belonging to the same habitat type had a distance of zero, while those belonging to different habitats had a distance that reflected their average dissimilarity. The complementary data matrix employed in the routine was that containing the untreated “true” measurements for the suite of enduring environmental variables recorded at each site. A SIMPROF test was also used in conjunction with LINKTREE to terminate construction of the tree at those nodes at which there was no significant structure among the remaining samples. The null hypothesis criteria for rejecting it were the same as those described in subsection 2.2.3.2. The use of the LINKTREE and SIMPROF routines in this manner resulted in separate linkage trees for the nearshore and offshore waters that provided a set of binary divisions of habitat types, each with the quantitative thresholds for the variable(s) which best explain those divisions.

In order to assign any of the “new” nearshore or offshore sites in Broke Inlet to their appropriate habitat type, each of the enduring environmental variables were firstly measured at that site using the methods given in subsection 2.2.2.3. The resultant site measurements were then compared with the thresholds for the environmental variable(s) specified at each successive branching node of the linkage tree, and the directed path followed until a terminal node, *i.e.* habitat type, was reached.

2.3: Results

2.3.1: Nearshore waters

2.3.1.1: Habitat classification

The CLUSTER and SIMPROF routines performed on the data for the suite of enduring environmental variables recorded at each of the 104 nearshore sites identified 12 significantly different habitat types (Fig. 2.6). This classification also contained two other habitats represented by a single site (*i.e.* sites 8 and 31), which were considered to be outliers and were thus removed from further analyses. The resultant habitat types were labelled according to the dissimilarity level at which they separated from the other habitat types, with habitat A being the most environmentally-distinct. The location of the sites assigned to each of the 12 habitat types are provided in Fig. 2.7 and representative site photos are shown in Fig. 2.8.

The nearshore habitat types split into two broad groups at a relatively high dissimilarity level, the first group of which was characterised by habitats containing either very small amounts of submerged vegetation or a bare/unconsolidated substrate (*i.e.* A, B, E, I, J, K and L), while the second group contained those habitats with moderate amounts of submerged aquatic vegetation (*i.e.* C, D, F, G and H) (Fig. 2.9).

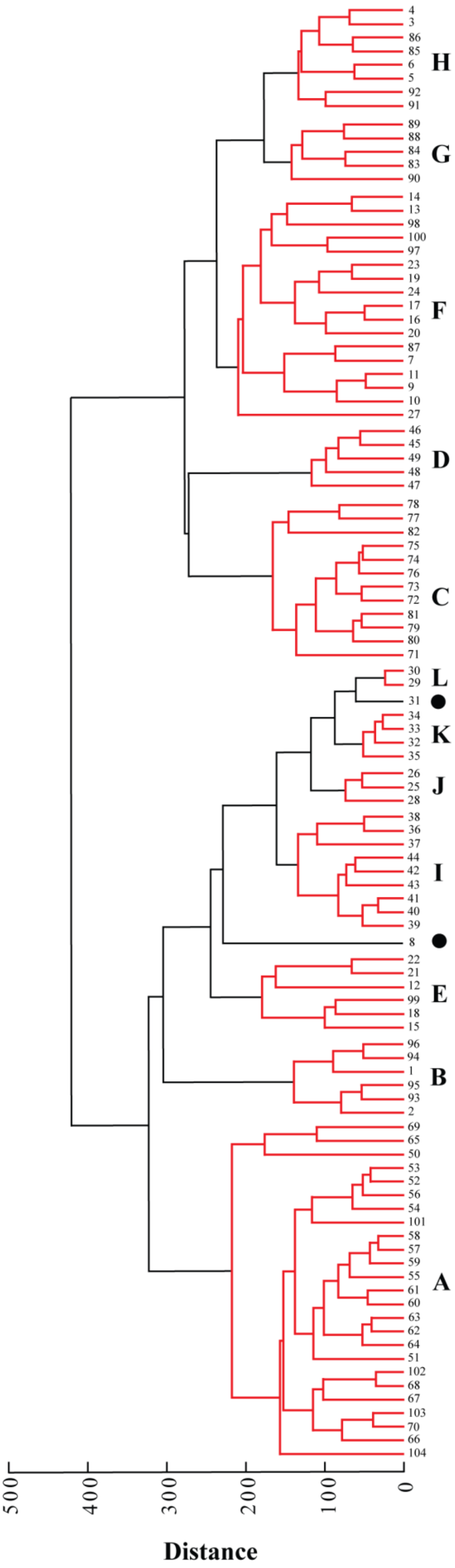


Fig. 2.6: Dendrogram derived from subjecting the enduring environmental data from each nearshore site in Broke Inlet to CLUSTER and SIMPROF. Groups of sites marked by red lines do not contain significant environmental differences and thus represent habitat types. ● denotes single sites considered to be outliers.

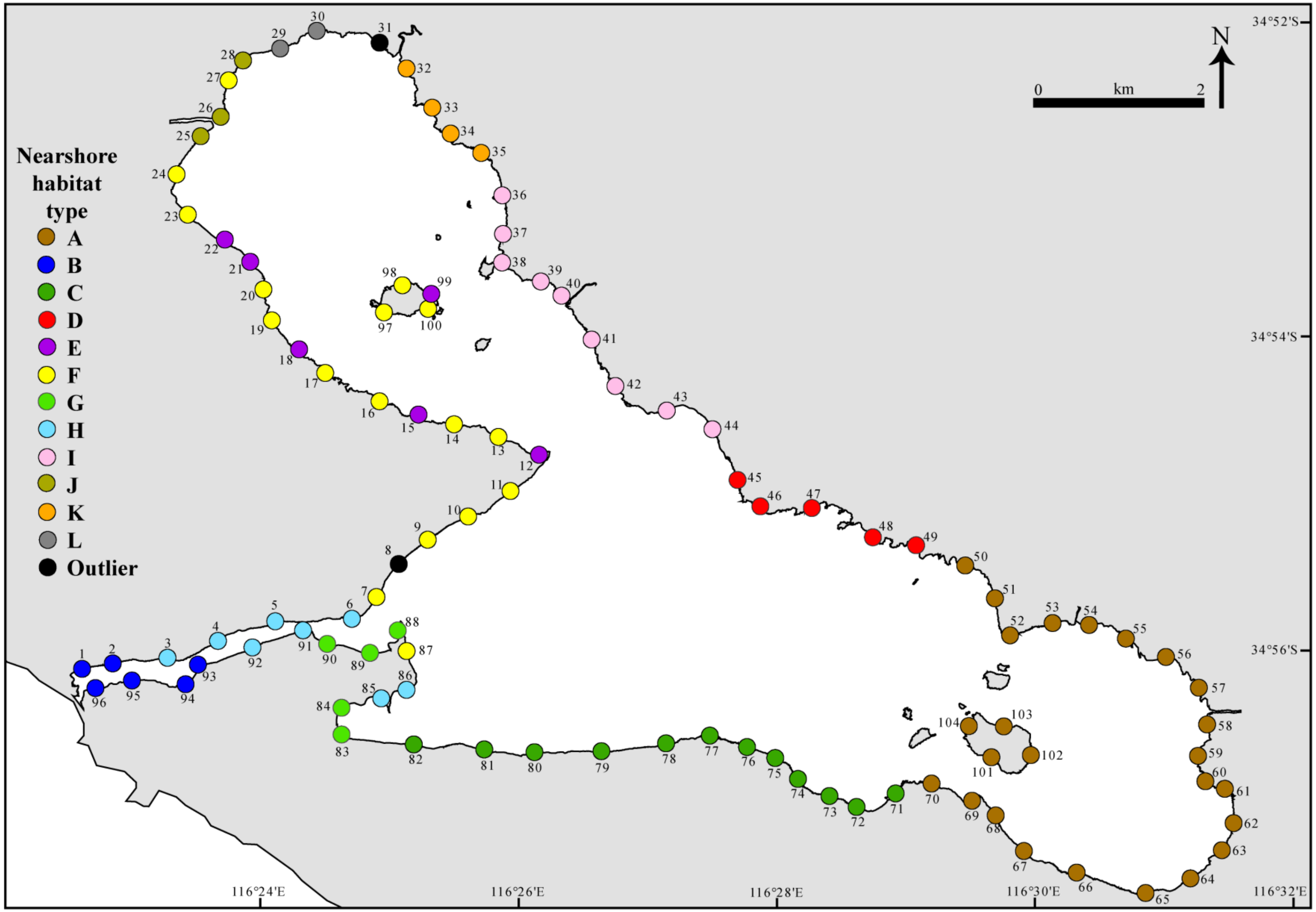


Fig. 2.7: Sites representing the 12 nearshore habitat types in Broke Inlet identified by the CLUSTER and SIMPROF procedures.

(a) Habitat type A; site 57

(b) Habitat type B; site 94

(c) Habitat type C; site 76

(d) Habitat type D; site 46

(e) Habitat type E; site 18

(f) Habitat type F; site 20

(g) Habitat type G; site 90

(h) Habitat type H; site 5

Fig. 2.8: Photographs of characteristic sites representing each nearshore habitat type in Broke Inlet.

(i) Habitat type I; site 39

(j) Habitat type J; site 26

(k) Habitat type K; site 32

(l) Habitat type L; site 30

Fig. 2.8 Continued: Photographs of characteristic sites representing each nearshore habitat type in Broke Inlet.

The most distinct habitat in the first group, A, was the largest and encompassed all 25 sites in Clarke Basin. This habitat was characterised by moderate to large direct and westerly fetches but was relatively sheltered from other prevailing winds. It also contained the largest wave shoaling margin of any habitat in the estuary. Habitat B was situated closest to the estuary mouth and was well distinguished from all other habitats in this group in the fact that it had the smallest fetches overall and the most steeply sloping substrate. The remaining habitat types in the first broad group were all located within Shannon Basin (Fig. 2.7). The most distinctive of these, E, comprised sites situated along the south-western shore and thus exhibited moderate northerly and easterly fetches and negligible to non-existent southerly and westerly fetches and a relatively narrow wave shoaling margin (Fig. 2.8). Conversely, habitats I and K, located on the opposite shore, were mainly exposed to winds from the south or west and particularly in the case of the former habitat, had a far wider wave shoaling margin than E. The remaining habitats in this group, J and L, were located around the mouth of

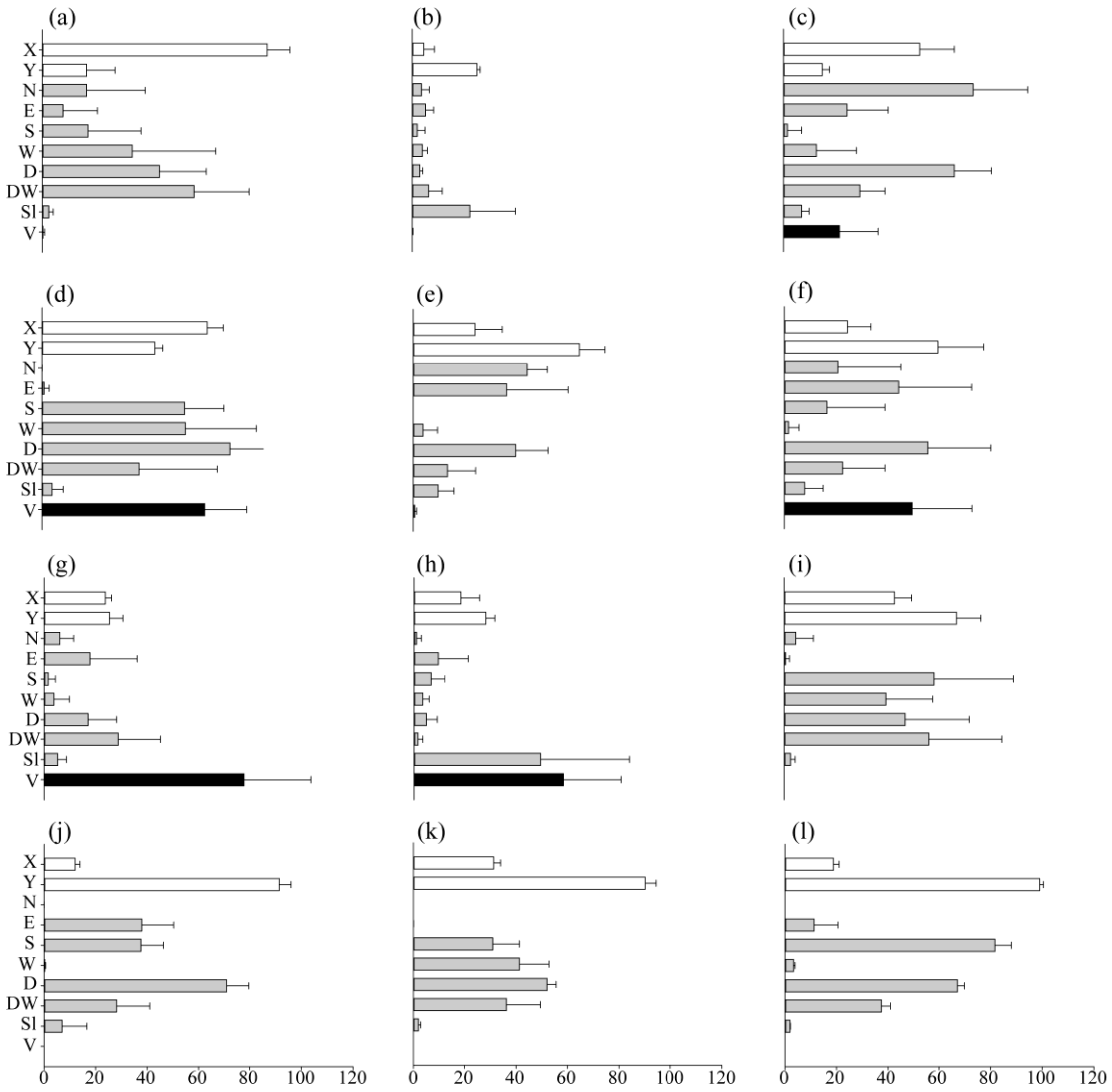


Fig. 2.9: Means and standard deviations of each nearshore enduring environmental variable at each nearshore habitat type (a-l), expressed as a percentage of the maximum value recorded at any site throughout the estuary. Note in the cases of the longitude (X) and latitude (Y) variables, prior to being expressed as a percentage the minimum values have been subtracted. Full variable names are given in Table 2.1.

the Shannon River and were distinguished mainly by their exposure to winds from various directions.

The most distinct habitat type in the second broad group, C, was represented by 12 sites located on the southern shore of Middle Basin, and was easily distinguished from the remaining habitat types in this group by the fact that it had by far the largest northerly fetch and least benthic vegetation within the group. In contrast, habitat D, situated on the north-eastern shore, was entirely fetch limited in a northerly direction, and was also nearly completely sheltered from easterly winds. However, the opposite was true for winds from all remaining directions, with habitat D having the greatest direct, westerly and southerly fetches of any habitats in this group. Sites within this habitat had the widest wave shoaling margin compared to those at other habitats in this group. The next most distinctive habitat, F, located on the south-western shore of the Shannon and Middle basins, was best distinguished by its level of exposure to various winds, while the remaining habitats in this group, G and H, were distinctive not only because of their location in the middle to upper reaches of the entrance channel, but also because of the high degree of shelter from wind activity and, in the case of H, a very steeply sloping substrate.

2.3.1.2: Habitat prediction

The linkage tree representing the separation of the nearshore sites into the habitat types identified by the above CLUSTER and SIMPROF procedures, and the quantitative thresholds of the enduring environmental variable(s) that best reflect the division at each branching node of the tree, is provided in Fig. 2.10. This tree thus provides a set of quantitative decision rules that enable the habitat type of any “new” nearshore site (*i.e.* one not used in the habitat classification procedure) to be identified. These decision rules also provide an indication of which particular enduring environmental variables from the full suite are the most important in differentiating between the various habitat types. While each of the suite of ten environmental variables were selected at some point in the linkage tree, five were the only ones to be selected at particular branching nodes, *i.e.* latitude, longitude, submerged aquatic vegetation and northerly and direct fetch (Fig. 2.10).

To test the ability of the linkage tree to reliably predict the habitat type to which a “new” site belongs, 20 additional nearshore sites were randomly nominated throughout Broke Inlet (see Fig. 2.11) and their suite of enduring environmental variables measured using the methodology given in subsection 2.2.2.3 (Table 2.3). The measurements for each of the sites were then compared to the threshold values given at each branching node of the linkage tree until a terminal node (habitat type) was reached. Comparison of the habitat type derived for each of the new sites with that of the closest existing (*i.e.* classified) site demonstrated that, in all cases, the habitat prediction was appropriate (Fig. 2.11).

Table 2.3: Measurements for the suite of enduring environmental variables recorded at each of the 20 additional nearshore sites throughout Broke Inlet that were used to trial the habitat prediction tool. Full variable names and their units of measurement are given in Table 2.1.

Site	X	Y	N	S	E	W	D	DW	Sl	V
i	6,130,000	444,000	0	113	252	333	280	77	1.94	29.54
ii	6,140,000	446,000	0	4,020	446	0	1,518	33	2.49	77.78
iii	6,140,000	448,000	0	3,971	2,597	0	1,937	35	4.12	80.09
iv	6,140,000	448,000	2,035	574	0	292	5,176	860	0.60	2.18
v	6,140,000	446,000	2,940	561	0	25	2,331	651	0.36	0.00
vi	6,140,000	445,000	1,838	3,740	0	91	2,949	162	0.65	14.04
vii	6,140,000	445,000	84	2,698	721	0	2,788	115	0.76	0.00
viii	6,140,000	446,000	0	144	3,952	435	2,468	1,110	0.04	0.07
ix	6,140,000	448,000	508	0	268	3,221	3,800	787	0.24	0.00
x	6,140,000	449,000	0	4	2,535	2,073	2,322	906	0.33	0.00
xi	6,140,000	450,000	0	2	3,596	1,405	2,375	1,025	0.16	0.00
xii	6,140,000	453,000	0	256	2,518	0	4,481	1,907	0.10	76.00
xiii	6,130,000	456,000	0	264	2,342	1,855	2,436	321	0.59	0.00
xiv	6,130,000	455,000	2,657	643	0	0	2,521	1,296	0.21	0.00
xv	6,130,000	453,000	2,310	1,388	0	1	2,698	1,094	0.56	0.00
xvi	6,130,000	451,000	2,247	1,974	38	0	1,228	900	0.25	34.57
xvii	6,130,000	448,000	3,655	2,145	0	1,067	3,074	389	0.61	64.00
xviii	6,130,000	446,000	60	2,458	7	0	4,031	945	0.73	89.02
xix	6,130,000	445,000	265	77	0	429	2,120	1,033	0.44	0.00
xx	6,130,000	444,000	312	270	0	54	272	255	0.76	0.00

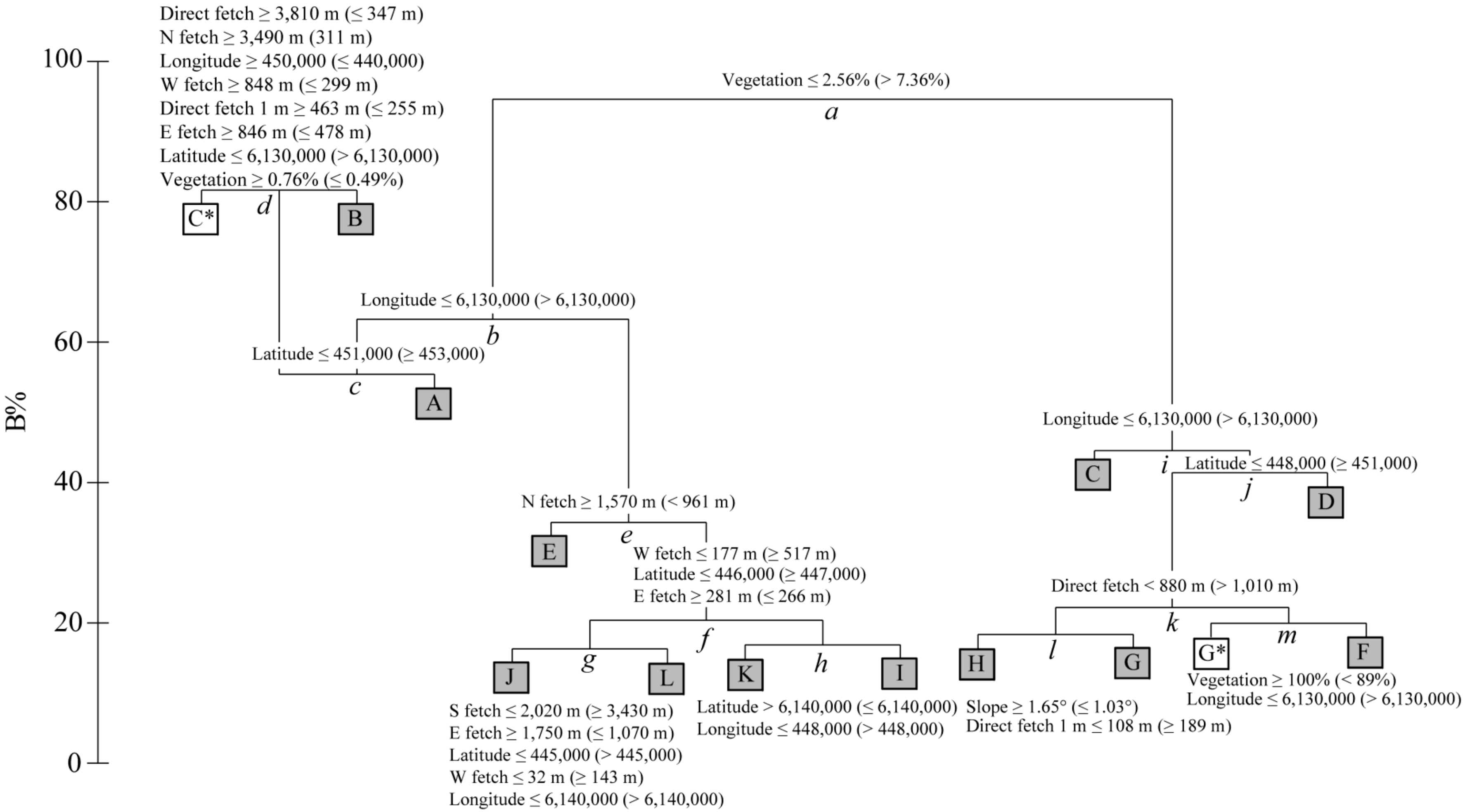


Fig. 2.10: Linkage tree and associated enduring environmental variable thresholds for assigning new nearshore sites to their appropriate habitat type. Unbracketed and bracketed thresholds given at each branching node indicate that a left or right path should be followed, respectively. Note that all threshold values have not been subjected to any form of data pretreatment. The terminal node represented by the white box with a habitat type marked by an asterisk denotes an alternative path for assigning to that habitat (n=1). B% reflects the extent of inter-habitat differences as a proportion of that between the most dissimilar habitat types.

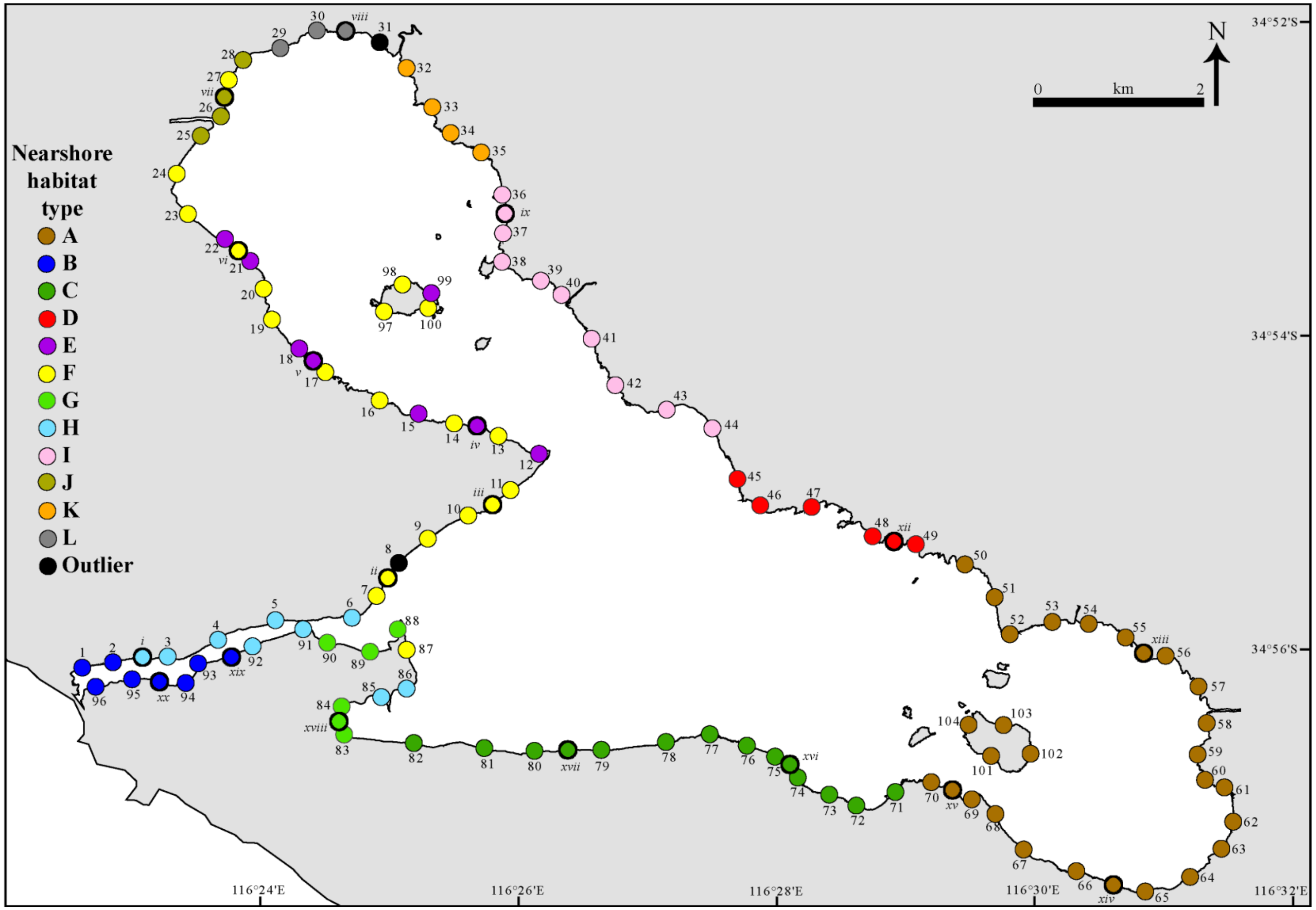


Fig. 2.11: Habitat classification of the nearshore sites (1-104) produced using the CLUSTER and SIMPROF procedures with the additional 20 nearshore sites (*i*-*xx*) classified using the LINKTREE procedure. The circles demark the existing sites and their respective habitat type, while the circles with a black edge and roman numerals identify the number and representative habitat type of the new sites.

2.3.2: Offshore waters

2.3.2.1: Habitat classification

The CLUSTER and SIMPROF routines performed on the data for the full suite of enduring environmental variables measured at each of the 36 offshore sites produced four significantly different habitat types (Figs 2.12, 2.13). As for the nearshore waters, each of the four offshore habitat types were coded according to the position along the distance axis at which they separated from the other habitat types, with the most environmentally-distinct habitat type labelled as A.

Habitat A was represented by five sites located within the entrance channel and was best differentiated from the remaining habitat types by small fetches and narrow areas of deeper water in all cardinal directions, by far the largest areas of submerged aquatic vegetation and the most relatively steeply sloping substrate (Fig. 2.14). In contrast, the next most distinctive habitat, B, which comprised sites located within Shannon Basin, was characterised by moderate to large fetches and areas of deeper waters in all cardinal directions and an unvegetated and gently sloping substrate (Fig. 2.14). The remaining habitats, C and D, which represented sites in the Middle and Clarke basins, respectively, both had unvegetated substrates but were distinguished by their locations within the estuary and the fact that C typically had larger fetch distances to surrounding areas of deeper waters (Fig. 2.14).

2.3.2.2: Habitat prediction

The linkage tree containing the separation of the offshore sites into their respective habitat types identified by the CLUSTER and SIMPROF procedures, along with the quantitative thresholds for the enduring environmental variables that reflected the division at each branching node is shown in Fig. 2.15. As for the nearshore waters the predictive capacity of this linkage tree was tested by nominating ten new sites throughout previously unclassified areas of the offshore waters (Table 2.4; Fig. 2.16), measuring their enduring environmental characteristics using the methodology given in subsection 2.2.2.3, then comparing the resultant data to the thresholds at each successive split of the tree until a habitat type was reached. The linkage tree successfully allocated each of the ten new sites to one of the four existing habitat types, and comparison of those habitat predictions with the habitat type of nearby classified sites demonstrated that, in each case, these predictions were appropriate (Fig. 2.16).

Table 2.4: Measurements for the suite of enduring environmental variables recorded at each of the 10 additional offshore sites throughout Broke Inlet that were used to trial the habitat prediction tool. Full variable names and their units of measurement are given in Table 2.1.

Site	X	Y	N	E	S	W	NW	EW	SW	WW	Sl	V
i	6,140,261	446,599	1,232	1,073	3,033	2,084	654	454	1,895	1,657	0.10	0
ii	6,139,034	446,530	2,228	3,139	1,048	1,851	1,781	743	933	1,335	0.00	0
iii	6,137,919	446,459	2,413	2,644	733	1,103	1,826	1,002	338	709	0.12	0
iv	6,137,747	447,584	1,767	2,136	961	1,805	491	536	431	1,165	0.53	0
v	6,134,052	444,083	118	523	209	488	55	209	87	245	1.99	47
vi	6,134,237	448,074	2,186	4,427	1,261	1,385	911	1,691	438	1,058	0.19	0
vii	6,133,683	449,680	3,706	3,634	625	2,529	1,866	580	437	326	0.08	0
viii	6,133,598	452,065	3,177	1,656	1,129	3,663	1,217	1,033	794	1,593	0.16	0
ix	6,132,820	455,201	1,722	1,387	1,375	1,285	327	510	256	194	0.08	0
x	6,132,365	455,873	2,158	779	941	2,169	314	193	533	199	0.04	0

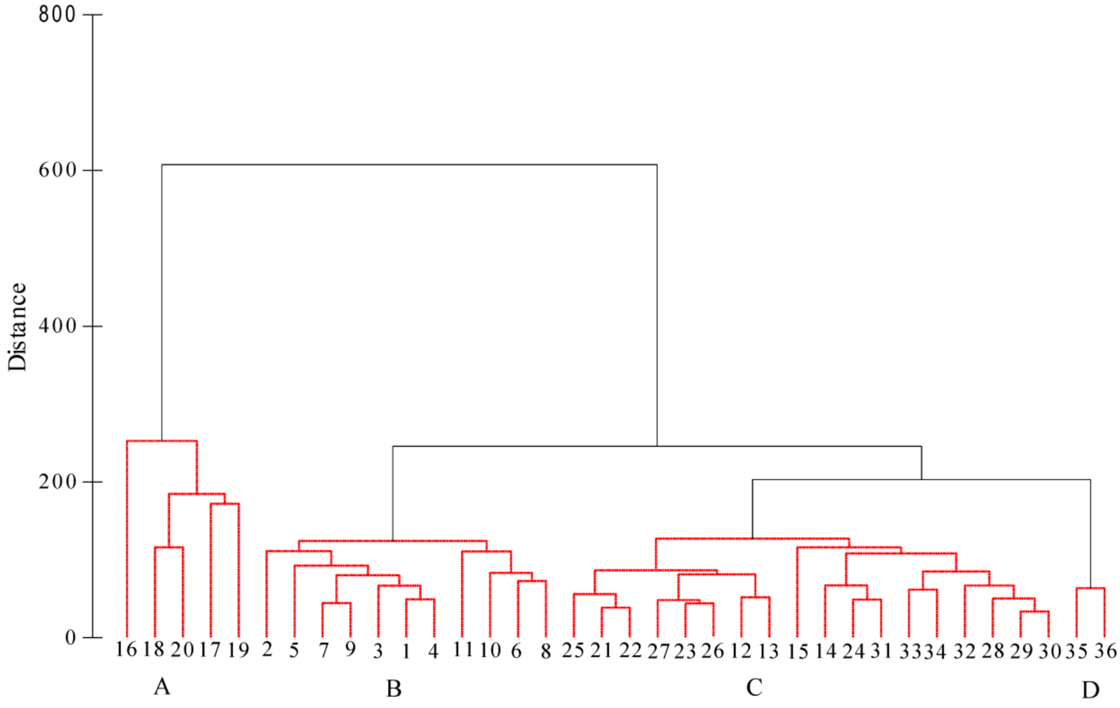


Fig. 2.12: Dendrogram derived from subjecting the enduring environmental data from each offshore site in Broke Inlet to CLUSTER and SIMPROF. Groups of sites marked by red lines do not contain significant environmental differences and thus represent habitat types.

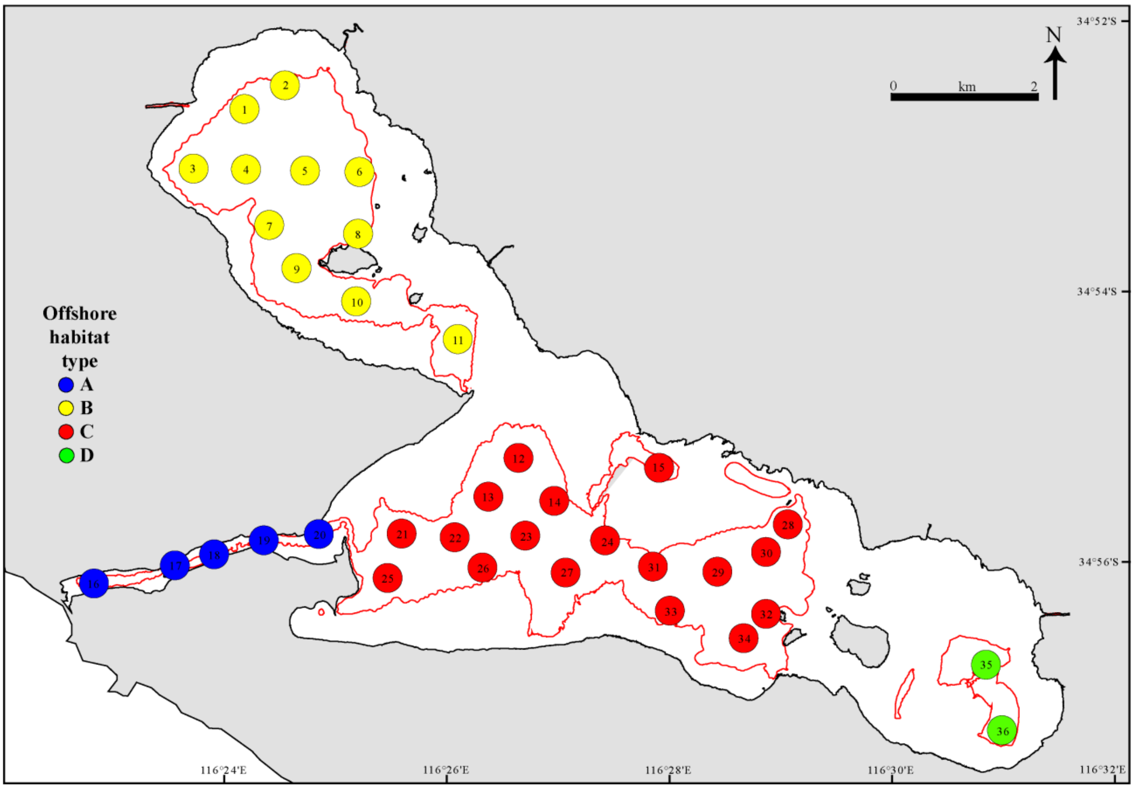


Fig. 2.13: Sites representing the four offshore habitat types in Broke Inlet identified by the CLUSTER and SIMPROF procedures.

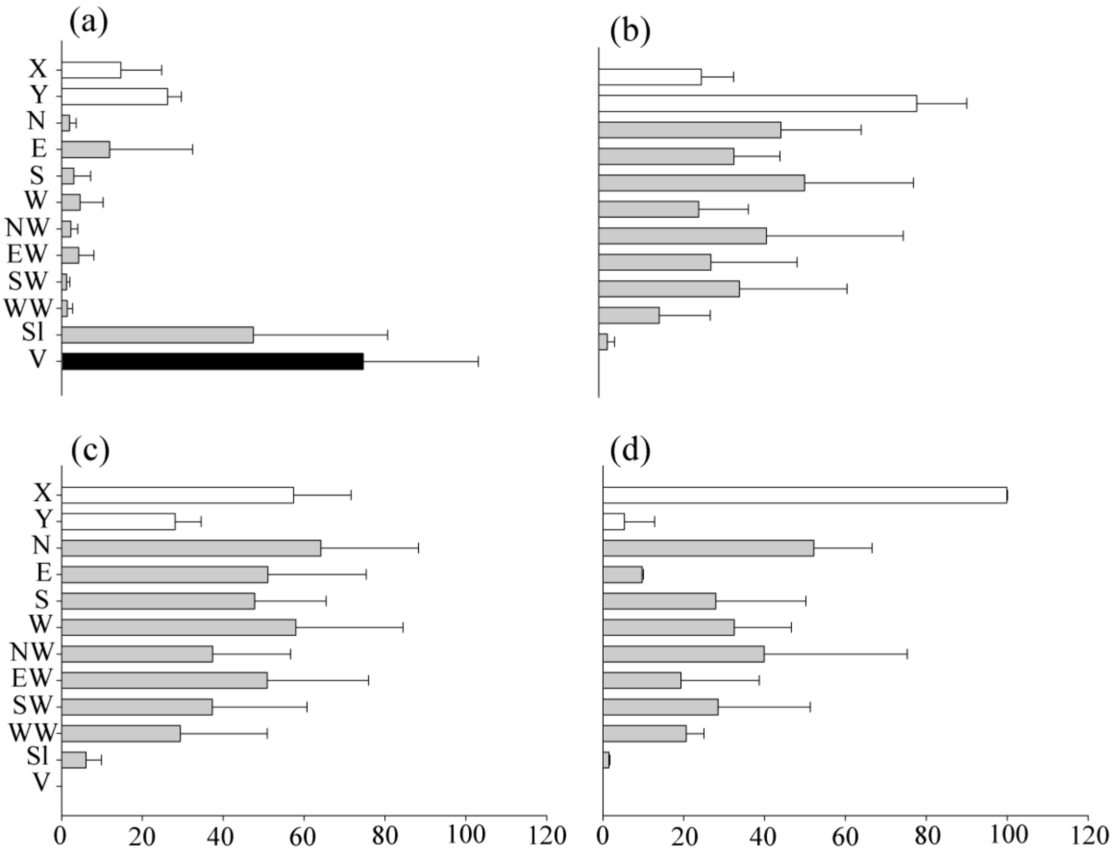


Fig. 2.14: Means and standard deviations of each offshore enduring environmental variable at each offshore habitat type (a-d), expressed as a percentage of the maximum value recorded at any site throughout the estuary. Note in the cases of the longitude (X) and latitude (Y) variables, prior to being expressed as a percentage the minimum values have been subtracted. Full variable names are given in Table 2.1.

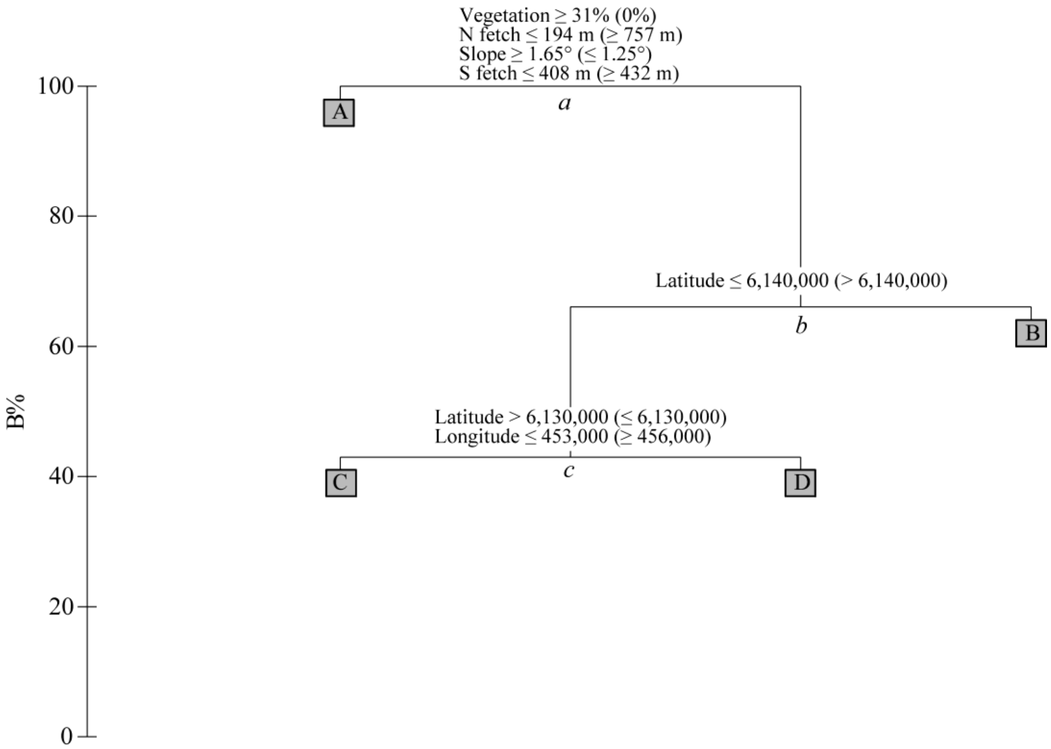


Fig. 2.15: Linkage tree and associated enduring environmental variable thresholds for assigning new offshore sites to their appropriate habitat type. Unbracketed and bracketed thresholds given at each branching node indicate that a left or right path should be followed, respectively. Note that all threshold values have not been subjected to any form of data pretreatment. B% reflects the extent of inter-habitat differences as a proportion of that between the most dissimilar habitat types.

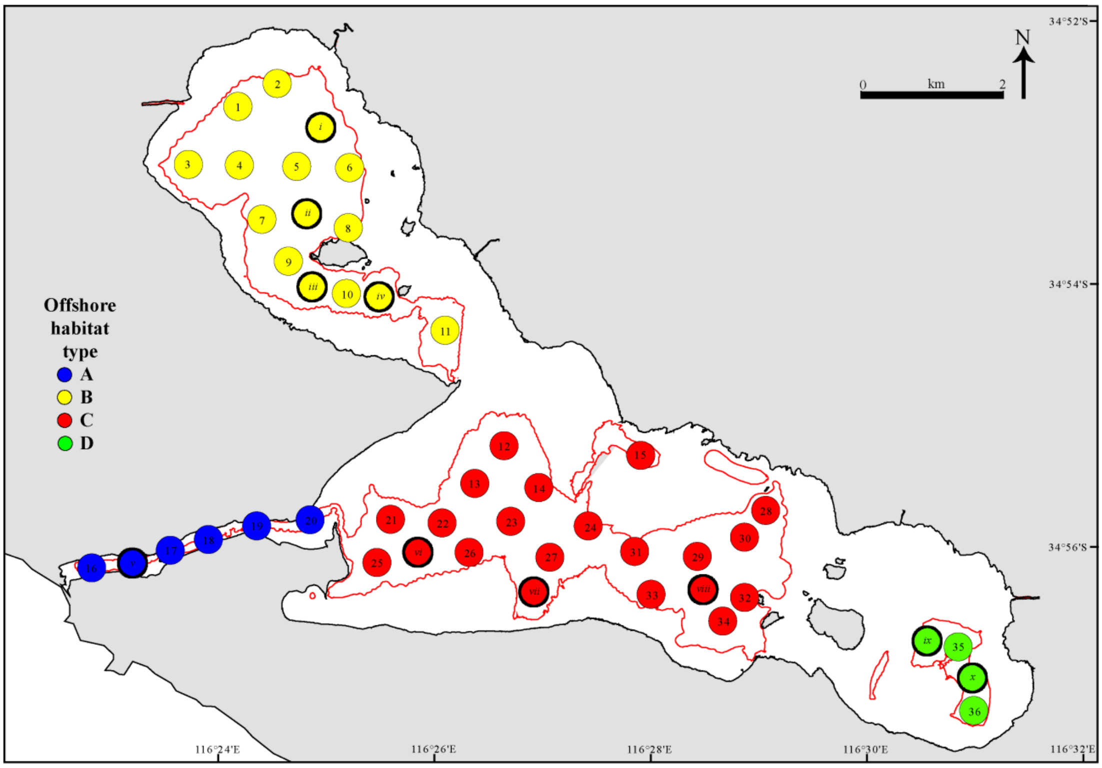


Fig. 2.16: Habitat classification of the offshore sites (1-36) produced using the CLUSTER and SIMPROF procedures with the additional 10 offshore sites (*i*-*x*) classified using the LINKTREE procedure. The circles demark the existing sites and their respective habitat type, while the circles with a black edge and roman numerals identify the number and representative habitat type of the new sites. The red line identifies the offshore areas.

2.4: Discussion

2.4.1: Critical appraisal of the Valesini et al. (2010) Habitat Classification Scheme (VHCS)

A critical appraisal of each "step" of the VHCS and its application to Broke Inlet is provided below.

2.4.1.1: Capturing spatial and temporal variability

Estuaries are among the most difficult aquatic environments to classify with respect to the habitats they contain, due to the large spatial and temporal variability in environmental conditions that typically occur within these systems over a variety of scales. Therefore, any successful scheme for classifying the various habitat types within estuaries must encompass a significant proportion of their environmental variability. Adequately capturing spatial variation may be complex in hierarchical schemes with nested spatial scales (*e.g.* Madden *et al.*, 2005) as the scales used in the classification are dependent on the aims of that particular study (see Keefer *et al.*, 2008) and thus two studies could theoretically classify the same sites within an estuary into different habitat types. However, such confusion is avoided in the VHCS as all waters from the mouth of the estuary to the estuarine extent of the rivers are classified. Thus, this scheme has been used as the basis for surveying a range of fauna, the distribution of which change at different spatial levels, *i.e.* meiofauna, hyperbenthic fauna, benthic macroinvertebrate fauna and ichthyofauna (Valesini *et al.*, 2009; Chapters 3, 4 and 5).

Capturing temporal variability in estuarine environmental conditions is more challenging, as a restricted or "snapshot" approach to data collection will usually not be adequate to characterise these dynamic systems (Keefer *et al.*, 2008). In order to overcome the influence of temporal variability in environmental characteristics, the VHCS employs a suite of temporally-enduring abiotic variables which were selected as the criteria for classifying the various habitat types within estuaries, rather than non-enduring environmental variables such as salinity and water temperature. The use of such criteria has several advantages, namely that they (i) are applicable at any temporal scale, (ii) can be measured from remotely sensed imagery in GIS, (iii) are time and cost-effective, relative to the resources required to obtain quantitative non-enduring environmental data at suitable spatio-temporal scales with appropriate levels of replication, (iv) often act as good surrogates for complex suites of non-enduring environmental characteristics (Roff & Taylor, 2000; Zacharias & Roff, 2000; Roff *et al.*, 2003) and (v) can be employed in systems, such as Broke Inlet, were comprehensive long term water quality data are not available.

2.4.1.2: Selection of sites

The selection of sites for classification into habitat types is of fundamental importance, as any bias or misrepresentation of the environmental diversity in an area of interest will be incorporated into the resultant classification scheme. One advantage of the VHCS is that the initial step involves the selection of as many sites throughout the estuary as are required to encompass as much of the environmental diversity as possible using, primarily, the digital image as a reference and, secondly, experience gained from field reconnaissance. However, it is difficult in heavily tannin-stained systems like Broke Inlet to ensure that the large majority of benthic diversity in deeper waters is captured by the suite of sites selected using only the above two methods. This can only be ensured through the extensive ground-truthing that was required to validate the benthic classification map of the estuary (Kenny *et al.*, 2003).

2.4.1.3: Selection of the enduring environmental characteristics

The environmental characteristics employed to delineate habitat types in the VHCS were required to be (i) fully quantitative, (ii) temporally-enduring, (iii) able to be calculated from mapped sources and (iv) biologically relevant to fish and benthic macroinvertebrates. The merits of using such environmental characteristics as habitat classification criteria have previously been described in Chapter 1 and addressed by other authors (*e.g.* Banks & Skilleter, 2002; Snelder *et al.*, 2005; Hume *et al.*, 2007; Snelder *et al.*, 2007). Those variables employed in the VHCS (see Table 1) were considered to fall into three categories, namely site location with respect to marine and freshwater sources, exposure to wave activity and substrate/submerged aquatic vegetation composition, each of which was selected on the basis that they were considered to influence the distribution of estuarine fish and benthic macroinvertebrate faunas (*e.g.* Ysebaert *et al.*, 1993; Bell *et al.*, 1997; Clark, 1997; Mattila *et al.*, 1999; Beyst *et al.*, 2001; Akin *et al.*, 2003; Brogueira & Cabeçadas, 2006).

Despite the sound logic and reasoning behind the three categories of environmental characteristics employed in the VHCS, some of the variables selected to represent each of the categories were not optimal. These included the use of the latitude and longitude variables in the location category as surrogates for a wide range of water physico-chemical variables. Whilst these provide a good depiction of the spatial differences among sites, they do not entirely capture the location of a site relative to marine and freshwater sources, as was their aim. In contrast, when the VHCS was recently applied to the Swan-Canning Estuary, a permanently-open, elongate drowned river valley system on the lower west coast of Australia, a "midline" drawn down the longitudinal axis of the estuary was used to measure the distance of the site from the ocean (Valesini *et al.*, 2010). This technique provides a more accurate representation of the vicinity of each site to marine and freshwater sources than that employed in Broke Inlet, and also several other "non-linear" estuarine systems in south-western Australia by Valesini *et al.* (2009), *i.e.* Wilson Inlet and the Peel-Harvey Estuary. The reasoning provided by these workers for this difference in methodology among estuaries with essentially "linear" *vs* "non-linear" morphologies was the difficulty in objectively identifying a middle longitudinal axis in the latter type of system. However, it is proposed that for Broke Inlet, and other basin estuaries, a line could be constructed from the site to the nearest river and connection to the ocean, either in the form of a straight line, *i.e.* as the crow flies or a along the waterline, *i.e.* as the fish swims. Such a measurement would accurately measure the distance to marine/freshwater sources and overcome the problem of multiple water sources. For example, if the distance from a site to each marine/freshwater source was calculated, theoretically two sites on opposite shores of the estuary, each of which is situated near the mouth of a river, would be distinguished during the classification procedure.

With regard to the percentage cover of submerged aquatic vegetation variable, some workers may not consider this to be an enduring environmental characteristic, as some species undergo an annual period of senescence (*e.g.* Critchley *et al.*, 1990) and, in some seasonally-open estuaries, dramatic changes in water level may result in macrophyte desiccation (*e.g.* Riddin & Adams, 2008). During the present study, however, the distribution of submerged aquatic vegetation was relatively consistent throughout the year, despite seasonal changes in biomass of *Ruppia megacarpa* (see Chapter 3). Similar trends in the distribution and biomass of this macrophyte have also been observed in the nearby and seasonally-open Wilson Inlet (Carruthers *et al.*, 1999).

Although the use of variables to account for wave exposure are common place in large-scale habitat classification schemes (*e.g.* Roff & Taylor, 2000; Zacharias & Roff, 2000; Connor *et al.*, 2004), they are typically less prominent amongst schemes developed for estuaries (*e.g.* Stevens & Connolly, 2004). Nevertheless, exposure to wave activity has been shown to influence faunal composition (*e.g.* Bell *et al.*, 1997; Clark, 1997; Hewitt *et al.*, 2003; Félix *et al.*, 2007). It is thus suggested that the lack of incorporation of wave exposure variables into estuarine classification schemes is reflective of the degree of difficulty in accurately measuring this variable. However, the fetch calculations employed in the VHCS were simple to undertake in GIS (see Ekebom *et al.*, 2003) and similar fetch calculations have been employed in other studies (*e.g.* Tolvanen & Suominen, 2005; Boström *et al.*, 2006; Harborne *et al.*, 2006; Allen *et al.*, 2007).

Another feature of the VHCS with respect to the variables it employs is the plasticity of the approach. Thus, the classification procedure allows any enduring environmental variable that is able to be accurately measured from mapped sources to be employed, therefore allowing the approach to be successfully applied to any estuary (see Valesini *et al.*, 2009). Although the choice of categories and/or representative variables is somewhat subjective, this is typical of many classification schemes and is also required to facilitate wide application of the approach.

2.4.1.4: Measurement of the enduring environmental characteristics

The initial stage in the measurement of the environmental characteristics employed in the VHCS is the acquisition of a high resolution remotely-sensed image and a digital elevation model or depth soundings of the estuary of interest. For estuaries situated around population centres, this information is commonly available through local government agencies, thus negating the potentially high costs of acquiring it independently. These requirements, however, are substantially less than those for several other classification schemes that are applicable to estuaries, such as Madden *et al.* (2005), which requires a large suite of non-enduring variables (*i.e.* modifiers or classifiers, which are a set of attribute-based descriptors that may be physico-chemical, physical, geomorphologic, or biological in nature, such as salinity, water velocity, substrate relief and sediment grain-size data) to be measured using expensive and complex equipment (*e.g.* acoustic Doppler current profilers and sidescan sonar) over various spatial and temporal scales before classification can proceed (Keefer *et al.*, 2008).

Preparation of the satellite image for use in the VHCS (see 2.2.2.1) is both relatively time consuming and computationally intense, moreover, *in situ* ground-truthing was required to validate the accuracy of the benthic classes identified from the image. However, such image preparation and/or ground-truthing requirements are standard for most types of work involving measurements from remotely-sensed imagery. Furthermore, the extent of the image pretreatment stage and, to a lesser extent, the variable measurement stages are not influenced by the number of sites chosen throughout the system, unlike in schemes requiring non-enduring or biotic criteria (*e.g.* Connor *et al.*, 2004; Madden *et al.*, 2005; Mount *et al.*, 2007).

2.4.1.5: Classification procedure

The fundamental aim of a habitat classification scheme is to group sites into a series of distinct habitat types based on their collective abiotic and/or biotic differences. However, very few schemes actually demonstrate that the characteristics of the resultant habitat types are significantly different, but instead simply assume this to be the case.

This is especially true for large hierarchical schemes which operate over a range of spatial and/or temporal scales (*e.g.* Roff & Taylor, 2000; Madden *et al.*, 2005; Mount *et al.*, 2007). In contrast, hierarchical agglomerative cluster analysis in combination with the SIMPROF test (Clarke *et al.*, 2008) is employed in the VHCS to (i) identify groups of sites which do not differ significantly in their environmental characteristics and thus represent distinct habitats and (ii) ensure that any such group does not contain more than one habitat type. Similar hierarchical clustering approaches have been used previously in other habitat classification schemes, however, those approaches have typically assigned an arbitrary resemblance level as the “cut-off” point, at which those groups of sites identified during the clustering process are presumed to represent different habitat types each with homogenous characteristics (*e.g.* Edgar *et al.*, 2000; Snelder *et al.*, 2007). Various non-hierarchical clustering techniques, such as K-means clustering, have also been widely used to classify habitat types (*e.g.* Zharikov *et al.*, 2005; Orpin & Kostylev, 2006). However, these techniques require an arbitrary pre-selection of the number of classes (*i.e.* habitat types) to which the data can be assigned, and the number of “true” classes remains unknown (*e.g.* Jordan & Vaas, 2000; Gregr & Bodtker, 2007). While some others have employed a range of statistical techniques to identify the optimal number of classes including cubic clustering criterion (*e.g.* Engle *et al.*, 2007), Calinski-Harabasz criterion (*e.g.* Legendre *et al.*, 2002; Orpin & Kostylev, 2006; Verfaillie *et al.*, 2009), and classification and regression tree algorithms (*e.g.* Zharikov *et al.*, 2005), these approaches still lack a statistical demonstration that the resultant classes are significantly distinct.

Another feature of the classification approach employed in the VHCS is that it is completely objective and repeatable among users. This is a major advantage over several large hierarchical schemes (*e.g.* Connor *et al.*, 2004; Madden *et al.*, 2005), in which the numerous modifiers or classifiers available, may be applied to any level of these schemes, meaning that the resultant classification of an area of interest can potentially vary considerably depending on the particular choices a user may make. Such problems have been highlighted by workers such Keefer *et al.* (2008).

2.4.1.6: Habitat prediction

The ability to predict the habitat type to which a new estuarine site belongs is widely advocated as a management tool (Zacharias *et al.*, 1999; De'ath, 2002) but has rarely been developed. The habitat prediction tool in the VHCS offers a number of advantages over existing methods. For example, having reached the terminal node of the linkage tree in the VHCS, there is no ambiguity over the identification of the habitat type. In the scheme developed by Zacharias *et al*. (1999), however, there were at least two habitat types presented as potential options at each terminal node of the predictive tree. Critically, at the fourth tier of the decision tree, which identified six of the seven habitat types, a particular habitat type was found to occur on both sides of the binary split, thus suggesting that the decision rule and associated threshold value for that split was the not the most appropriate, or potentially that the habitat types separated by that split were not statistically different. Furthermore, the linkage tree produced by the prediction tool in the VHCS clearly identifies which environmental criteria and its quantitative thresholds are most responsible for the divisions among habitats as opposed to the PCA approach adopted by Valesini *et al*. (2003).

The VHCS habitat predication method, although ultimately successful, has a number of issues. Firstly, the initial habitat classification employed a hierarchical agglomerative (“bottom-up”) approach, whereas the prediction technique employed a divisive (“top-down”) approach. This systematic difference in the methodology of these approaches may result in the subdivision of a habitat type across multiple nodes, this occurred in the predictive linkage tree produced for the nearshore waters of Broke Inlet. However, despite this minor inconsistency the classification rules for assigning sites to those habitats proved to be appropriate when the scheme was tested using “new” or “dummy” sites. Furthermore, there were some instances in that latter testing procedure in which a site met one/or more of the requirements for both habitats on either side of a terminal node. However, this generally only occurred for habitat types that lay adjacent to each other, and were thus typically similar.

2.4.2: Future developments

Valesini *et al.* (2010) envisaged the VHCS as a component of the lower levels of a hierarchical habitat classification scheme developed at a national scale (*e.g.* Mount *et al.*, 2007). If this scheme were to be widely employed, there are a number of ways of optimising the classification methodology to save time and resources. For example, in estuaries where bathymetric data is not available, as was the case with Broke Inlet, this information can be measured remotely using laser altimetry, such as LIDAR, rather than extensive "*in situ"* surveying using SONAR (Yang, 2005; Chust *et al.*, 2010). It is also possible to automat processes in GIS using routines, such as the macro-modeler in IDRISI, which could "automatically" perform the image pre-processing. Furthermore, the Wave Exposure Model (WEMo) developed by NOAA could be employed in conjunction with ArcGIS to calculate the exposure variables automatically at each nearshore and offshore site. The use of such processes to automate the image pre-processing and calculation of some of the enduring environmental variables would save considerable time and allow the production of a spatially continuous classification, whereby the entire margin of an estuary could be classified, thus alleviating the need for a predictive tool.

In order to fully validate the results of the VHCS for Broke Inlet, quantitative sampling of the fish and benthic macroinvertebrate faunas have been undertaken and the level of "agreement" between differences in the characteristics of those assemblages and those of the various habitat types have been statistically tested (see Chapters 3, 4 and 5). A good match between the habitat types and faunas will allow the habitat prediction tool to reliably predict the abundant fish or benthic macroinvertebrate species most likely to occur at any new site of interest.

Chapter 3

Ichthyofaunal composition among habitat types in Broke Inlet

3.1: Introduction

Estuaries comprise a complex mix of inter-connected habitat types due to the strong physico-chemical gradients and the diversity of benthic environments that are often present within these systems (Pihl *et al.*, 2002). Habitat structure and their spatial arrangement are thus typically important predictors of the composition of estuarine faunal assemblages, and sometimes also of species richness, diversity and abundance (Thrush *et al.*, 2005; França *et al.*, 2009a; Hourston *et al.*, 2009). While biotic interactions such as predation and competition also play a role in structuring faunal composition in estuaries, many of the spatial differences in these assemblages can consistently be related to those in a suite of physico-chemical characteristics (including those within the water column and those related to hydrological processes), the substrate and structural heterogeneity (*e.g.* Marshall & Elliott, 1998; Mattila *et al.*, 1999).

The majority of studies on spatial differences in faunal assemblages within estuaries have focused on their relationships with either extremes of habitat, *e.g.* riverine *vs* basin regions (*e.g.* Potter & Hyndes, 1994; Chuwen *et al.*, 2009b), vegetated *vs* unvegetated substrata (*e.g.* Sogard & Able, 1991; Humphries *et al.*, 1992; Rozas & Minello, 1998; Castellanos & Rozas, 2001) or gradational patterns along the length of the estuary (*e.g.* Loneragan & Potter, 1990; Ysebaert *et al.*, 1993; Hourston *et al.*, 2009). However, relatively few studies have attempted to determine the relationships between the spatial distribution of estuarine fauna and larger suites of environmental criteria that more adequately characterise differences among habitat types within those systems. Moreover, even fewer studies have focused on establishing quantitative, rather than qualitative, links between spatial differences in faunal composition and those of comprehensively-defined habitats, particularly at scales that are most useful for estuarine management, *i.e.* local to regional scales. Ascertaining solid relationships between faunal composition and habitat types within estuaries provides the foundation for predicting a range of faunal characteristics on the basis of the environmental criteria that collectively define habitats, which has an extensive range of applications for estuarine management and research.

To date, the only published studies of spatial differences in the fish assemblages of Broke Inlet have been undertaken at relatively broad scales, focusing primarily on their differences among subjectively-defined regions and their relationships with a limited suite of water physico-chemical parameters, *i.e.* salinity, water temperature and dissolved oxygen concentration. This is also the case for a range of other estuaries on the south coast of Western Australia, including those for Wilson Inlet, for which only differences in the fish fauna among broad regions and vegetated *vs* unvegetated habitats have been examined (Humphries *et al.*, 1992; Potter *et al.*, 1993), and the Walpole-Nornalup Estuary, Irwin Inlet, Oyster Harbour and Wellstead Estuary, where again ichthyofaunal differences were investigated among broad regions (Potter & Hyndes, 1994; Chuwen *et al.*, 2009b; Hoeksema *et al.*, 2009) and in the case of the latter estuary along the length of the estuary (Young & Potter, 2002).

In order to better characterise the spatial differences in the fish fauna of Broke Inlet, and to understand the extent of their relationships with those in a comprehensive suite of environmental characteristics, the fish assemblage was sampled seasonally for two years at 11 of the nearshore and three of the offshore habitat types that were identified quantitatively in Chapter 2. These data were used to address the following aims.

(1) To test whether the species richness, density/catch rate, diversity and composition of the fish fauna differed significantly among habitat types in both the nearshore and offshore waters.

(2) To test whether the classification of the nearshore and offshore habitat types provided a sound basis for predicting spatial differences in the nearshore and offshore fish faunas, respectively, by determining if the pattern of relative differences among habitat types, as defined by their enduring environmental criteria, was significantly correlated with that defined by the composition of their fish assemblages.

3.2: Materials and methods

3.2.1: Sampling regime

The fish fauna of Broke Inlet was sampled during the last month of each season between spring 2007 and winter 2009 at each of the habitat types identified in the nearshore and offshore waters of Broke Inlet (see Chapter 2). The only exceptions were habitats L in the nearshore waters and D in the offshore waters, which were not sampled as these habitats comprised only two sites. For convenience, spring 2007 to winter 2008 and spring 2008 to winter 2009 are subsequently referred to as the years 2007/2008 and 2008/2009, respectively. During each of the above sampling occasions, samples of the fish fauna were collected during the day at four sites representing each of the nearshore habitat types, with the exception of habitat J, for which there were only three representative sites and at night from three sites representing each offshore habitat type (Fig. 3.1). Moreover, two replicate samples were collected at each nearshore site and, within each season, samples from any given nearshore habitat type were collected on two separate days to reduce the likelihood of the resultant data being influenced by an atypical catch. Due to extremely low water levels, fish could not be collected from nearshore habitat A during the summer and autumn of both years. The number of sites sampled per habitat type and the number of replicates sampled per site were considered great enough to be representative of the nearshore and offshore waters of Broke Inlet.

Samples of the fish fauna at nearshore habitat types were collected using a seine net that was 21.5 m long and consisted of two 10 m long wings (6 m of 9 mm mesh and 4 m of 3 mm mesh) and a 1.5 m long bunt made of 3 mm mesh. The net, which was laid parallel to the shore and then hauled onto the beach, fished to a depth of 1.5 m and swept an area of 116 m^2. Fishes in the offshore waters were collected using sunken composite multifilament gill nets comprising seven 20 m long panels, each with a height of 2 m, but containing a different stretched mesh size, *i.e.* either 35, 51, 63, 76, 89 102 or 127 mm. Gill nets were set at dusk and retrieved at dawn (10-13 hours later).

Upon capture, all fish were immediately euthanised in an ice slurry (Murdoch University Animal Ethics Permit # R2086/07). The total number of individuals of each fish species in each sample was then recorded and the total length of each individual measured to the nearest 1 mm, except when a large number of any one species was caught, in which case the lengths of a random subsample of 100 fish were measured.

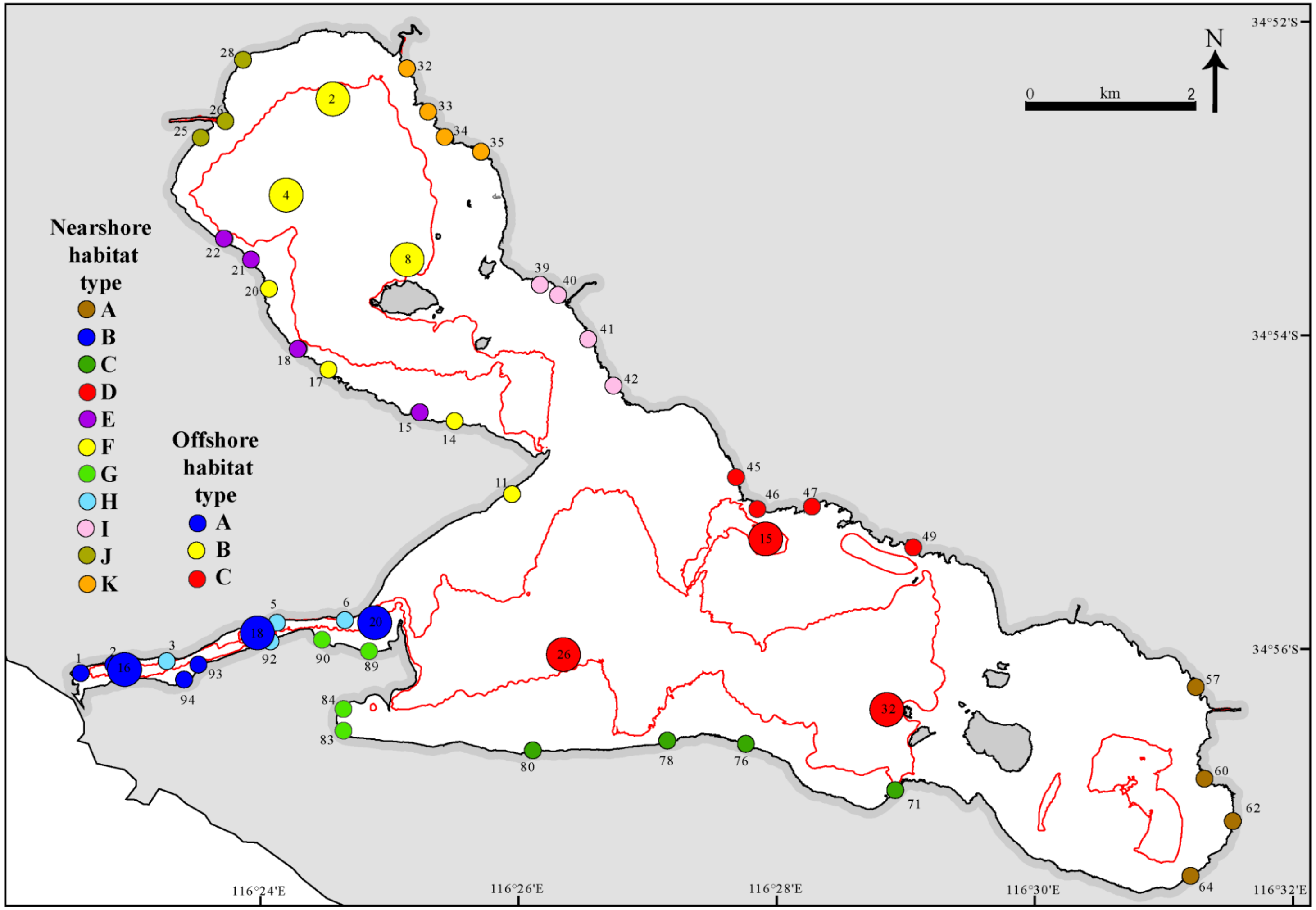


Fig. 3.1: Map showing location of the sampling sites in each nearshore and offshore habitat type in Broke Inlet at which the fish fauna was sampled seasonally between spring 2007 and winter 2009. Circles represent the actual size of the site and the red line (1 m depth contour) indicates the demarcation between the nearshore and offshore waters.

A range of non-enduring environmental variables were measured at each site at the same time at which fish were collected. These included water physico-chemical parameters, namely salinity, water temperature, dissolved oxygen concentration and pH and, in the nearshore waters, any submerged aquatic vegetation retained in the seine net during fish collection. Each of the water physico-chemical variables were measured using a YSI 556 Handheld Multiparameter Instrument (Yellow Spring International, Ohio, USA), with two replicate measurements of each variable being recorded in the middle of the water column at each nearshore site and at the surface and bottom of the water column at each offshore site. All samples of submerged vegetation were dried for 24 hours at 60°C, subsequent drying for three hours and weighing was then employed to ensure each sample was completely dry (Short & Coles, 2001).

3.2.2: Statistical analyses

Each of the following statistical analyses were performed using the PRIMER v6 multivariate software package (Clarke & Gorley, 2006) with the PERMANOVA+ add-on module (Anderson *et al.*, 2008). Although habitat was the main factor of interest, differences among seasons and years were accounted for so that their confounding influence could be quantified and "removed" if necessary.

3.2.2.1: Univariate analyses

Differences in non-enduring environmental variables among habitat types, seasons, and/or water depth

Prior to undertaking PERMANOVA, data for each of the dependent variables (*i.e.* salinity, water temperature, dissolved oxygen concentration, pH and dry weight of detached macrophytes), was examined to ascertain the type of transformation required, if any, to meet the test assumptions of homogenous dispersions among groups (Anderson, 2001). This was achieved by determining the extent of the linear relationship between the $\log_e$ (mean) and the $\log_e$ (standard deviation) of all groups of replicate samples, and then using the slope criteria provided by Clarke & Warwick (2001) to select an appropriate transformation. This methodology showed that, for the nearshore waters, salinity, water temperature, dissolved oxygen concentration and pH required a square root transformation and the dry weight of detached macrophytes a $\log_e(X+1)$ transformation. None of the non-enduring environmental variables in the offshore waters required transformation. Note that here, as in all other cases where trends in univariate data were employed, PERMANOVA rather than ANOVA was employed as the former test does not make assumptions about the distribution of the data (Anderson, 2001; McArdle & Anderson, 2001).

Euclidean distance matrices containing all pairs of replicate samples were then constructed separately for each non-enduring environmental variable in both the nearshore and offshore waters. These matrices constructed from the nearshore data were then subjected to a four-way PERMANOVA to test whether each dependent variable differed significantly among habitats, sites (nested within habitats), seasons and years. All factors except the nested term were considered fixed. If this analysis did not detect significant site differences then the replicate data recorded at each site was pooled to represent habitat, and these data were subjected to habitat x season x year PERMANOVA, with all factors considered fixed. If significant site differences were detected, the replicate data at each site on each sampling occasion was averaged and subjected to the above three-way PERMANOVA. The data for each non-enduring environmental variable in the offshore waters was subjected to a four-way crossed habitat x season x year x depth PERMANOVA with all factors being considered fixed. In all PERMANOVA tests, the null hypothesis of no significant differences among groups was rejected if the significance level (p) was < 0.05, and the relative influence of each term in the model was quantified using the components of variation. The main source of significant differences detected by PERMANOVA were identified by examining plots of the marginal means of the dependent variable, back transformed where necessary, with associated 95% confidence intervals.

Differences in species richness, density and diversity among habitat types, seasons and years

Species richness and Shannon-Wiener diversity were initially calculated for each replicate fish sample using the DIVERSE routine in PRIMER v6 (Clarke & Gorley, 2006). The density of fish in each nearshore sample (number of fish 100 m^{-2}) and the catch rate of fish in each offshore sample (number of fish h^{-1}) were also calculated. Each of these dependent variables in the nearshore and offshore waters were then individually examined using the method devised by Clarke and Warwick (2001) to ascertain the type of transformation required, if any, to satisfy the assumption of homogenous group dispersions for PERMANOVA (see above). These analyses indicated that, in the nearshore waters, species richness and Shannon-Wiener diversity required a square-root transformation and density a $\log_e(X+1)$, while in the offshore waters, species richness and catch rates required a square-root transformation and Shannon-Wiener diversity a fourth-root transformation. Separate Euclidean distance matrices containing all pairs of samples were then constructed for each of the above variables in the nearshore and offshore waters, which were then each subjected to the same PERMANOVA tests described above for non-enduring water physico-chemical variables. The only exception was the removal of the depth term for the tests for the offshore data. The method of interpretation for each of these PERMANOVA analyses was the same as that described earlier.

3.2.2.2: Multivariate analyses

Differences in fish faunal composition among habitat types

The replicate fish species abundance data recorded at each nearshore site in each season and year was initially subjected to dispersion weighting to down-weight the contributions of those species that exhibited erratic differences in abundance between replicate samples (Clarke *et al.*, 2006b). The resultant data was then subjected to a square-root transformation to balance the contributions of highly abundant species with those that were less abundant. This pretreated data was then used to construct a Bray-Curtis similarity matrix, which was subjected to the same PERMANOVA analyses as described above.

As the above PERMANOVA tests detected significant interactions between habitat and season and/or year (see subsections 3.3.1.4 and 3.3.2.4) the Bray-Curtis matrix was separated for each level of the relevant temporal factor(s) in order to remove their confounding influence, and the various sub-matrices were then each subjected to one-way Analysis of Similarities (ANOSIM) tests (Clarke & Green, 1988) to elucidate, in more detail, the extent to which ichthyofaunal composition differed among habitats. In this and all subsequent ANOSIM tests, the null hypothesis that there were no significant differences in ichthyofaunal composition among habitats was rejected if the significance level (p) was < 0.05. The extent of any significant differences were determined by the magnitude of the test statistic (R), which typically ranges between 0 (*i.e.* no group differences) to 1 (*i.e.* the similarities between samples from different groups are all less than those between samples belonging to the same group). The same Bray-Curtis submatrices were also subjected to non-metric Multidimensional Scaling (nMDS) ordination in order to display visually the differences in the fish faunal composition among habitats.

When ANOSIM detected a significant difference among habitats and the associated R-statistic was ≥ 0.2, Similarity Percentages (SIMPER; Clarke, 1993) was then used to elucidate which species typified the assemblages at each habitat and those which contributed most to differences between each pair of habitats. Focus was placed on those typifying and distinguishing species that had the highest similarity/standard deviation ratio and dissimilarity/standard deviation ratio, respectively, and those that were the most abundant.

The offshore fish faunal composition data in each replicate sample was initially subjected to an overall square-root transformation, *i.e.* the same approach as was considered appropriate for overall catch-rate (see subsection 3.2.2.1). Note that dispersion weighting could not be applied to the offshore species composition data as, unlike that for the nearshore waters, it comprised catch-rates and not species counts (Clarke *et al.*, 2006b). The transformed data was then used to construct a Bray-Curtis similarity matrix, which was in turn subjected to the same three-way PERMANOVA as described in subsection 3.2.2.1 for the other biotic variables in the offshore waters.

The extent and nature of significant habitat differences in offshore fish faunal compositions detected by PERMANOVA were further explored using one-way ANOSIM tests, nMDS ordinations and one-way SIMPER analyses, carried out separately for each season and/or year where necessary. The methods of interpretation of those analyses were the same as for those described above for the nearshore waters.

Relationships between the fish community and environmental characteristics of habitat types

The RELATE routine was used to test, for each season and/or year, the extent to which the relative differences among habitat types, as defined by their fish faunal composition, were significantly correlated with those defined by their suite of (i) enduring environmental characteristics and (ii) non-enduring environmental characteristics, *i.e.* water physico-chemisty and, in the case of the nearshore waters, the dry weight of detached macrophytes. This routine was thus used to determine how similar the pattern of the rank orders of resemblance were between the Bray-Curtis similarity matrix constructed from the pretreated fish assemblage data at each habitat type and the complementary Manhattan distance matrices constructed, respectively, from the transformed and normalised (i) enduring environmental data (see subsection 2.2.2) and (ii) non-enduring environmental data (see subsection 3.2.1). Note that, for the nearshore waters, the complementary fish assemblage and environmental matrices were constructed from data which had been averaged for each habitat type, while in the offshore waters, where there were three habitat types, these matrices were constructed from the data recorded at each site. The latter was required to increase the number of samples in the matrices, and thus power in the RELATE tests. The null hypothesis that there was no relationship in the pattern of rank order similarities between the complementary matrices was rejected if the significance level (p) was < 0.05. The test statistic, rho (ρ), was used to gauge the extent of any significant differences, with values close to 0 reflecting little correlation in rank order agreement and close to 1 reflecting a near perfect match. nMDS ordinations of the ichthyofaunal and environmental data for each habitat type or site in each season and/or year were also constructed to provide a visual indication of any matching between the complementary data sets.

The Biota and Environment matching routine (BIOENV; Clarke & Ainsworth, 1993) was then employed to ascertain whether a greater correlation between the complementary faunal and non-enduring environmental matrices could be obtained using only a particular subset of the non-enduring variables, rather than the full suite as employed in RELATE. The matrices used in this procedure were identical to those employed in the RELATE routine described above. The null hypothesis, and test statistic for these BIOENV tests were the same as those for the above RELATE tests. Comparisons of the relative differences among habitat types in the fish composition *vs* the non-enduring environmental variables selected by BIOENV were displayed visually by subjecting the above Bray-Curtis similarity matrices to nMDS ordination and then overlaying circles (“bubbles”) of proportionate sizes that represented the magnitude at each habitat/site of the selected environmental variable.

3.3: Results

3.3.1: Nearshore waters

3.3.1.1: Differences in non-enduring environmental variables among nearshore habitat types, seasons and years

A three-way crossed PERMANOVA of the nearshore salinity data in each habitat, season and year detected significant differences among each of these main effects and all possible interactions between main effects were also significant (*p*=0.001-0.011; Table 3.1a). As indicated by the associated components of variation, differences between years exerted by far the greatest influence on salinity, followed by those among seasons and, to a notably lesser extent, among habitats. With the exception of the season x habitat interaction, whose relative importance was similar to that of habitat, the influence of the remaining interaction terms were far lower than that for any of the main effects (Table 3.1a).

Salinities were generally higher in 2007/2008 than 2008/2009, except during winter when a similar range of values were recorded in both years among the various habitats (Fig. 3.2a). Salinities were consistently the highest during summer and autumn at all habitats (*i.e.* 27-33 in 2007/2008 and 15-22 in 2008/2009). During winter, however, salinity exhibited marked differences among habitats. Thus, whereas salinities remained similar or exhibited relatively small declines from summer and autumn to winter and spring in the channel habitats (B, G and H), they were markedly higher than those at habitats within Middle Basin (C and D), and particularly those located near the vicinity of Inlet River and within Shannon Basin (A, E, F, J, K and I) during those latter

Table 3.1: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (*p*) from PERMANOVA tests on the data for mean (a) salinity, (b) water temperature, (c) dissolved oxygen concentration, (d) pH and (e) macrophyte dry weight recorded at the 11 nearshore habitat types in Broke Inlet sampled in each season between spring 2007/2008 and winter 2008/2009. df = degrees of freedom. Significant results are highlighted in bold.

		(a) Salinity				**(b) Water temperature**				**(c) Dissolved oxygen concentration**			
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***	**MS**	**Pseudo-F**	**COV**	***p***	**MS**	**Pseudo-F**	**COV**	***p***
Year	1	**9493.500**	**1175.900**	**60.933**	**0.001**	2.096	0.400	-0.020	0.591	**0.244**	**16.531**	**0.001**	**0.001**
Season	3	**2986.600**	**369.930**	**37.193**	**0.001**	**26.475**	**5.049**	**0.265**	**0.001**	**4.557**	**308.910**	**0.057**	**0.001**
Habitat	10	**387.380**	**47.982**	**12.789**	**0.001**	5.050	0.963	-0.007	0.609	**0.288**	**19.511**	**0.009**	**0.001**
Interactions													
Year x Season	3	**260.170**	**32.225**	**6.296**	**0.001**	9.021	1.720	0.094	0.104	**10.901**	**738.970**	**0.272**	**0.001**
Year x Habitat	10	**19.287**	**2.389**	**0.756**	**0.011**	5.284	1.008	0.003	0.469	**0.075**	**5.061**	**0.004**	**0.001**
Season x Habitat	28	**95.920**	**11.881**	**11.260**	**0.001**	4.930	0.940	-0.040	0.669	**0.089**	**6.049**	**0.010**	**0.001**
Year x Season x Habitat	28	**17.452**	**2.162**	**2.404**	**0.002**	5.734	1.094	0.126	0.249	**0.061**	**4.139**	**0.012**	**0.001**
Residual	244	8.074		8.074		5.244		5.244		0.015		0.015	

		(d) pH				**(e) Macrophyte dry weight**			
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***	**MS**	**Pseudo-F**	**COV**	***p***
Year	1	**0.005**	**5.487**	**0.0001**	**0.006**	**16.664**	**15.178**	**0.100**	**0.001**
Season	3	0.316	9.631	0.0043	0.094	**66.161**	**60.263**	**0.812**	**0.001**
Habitat	10	**0.011**	**3.401**	**0.0004**	**0.001**	**53.553**	**48.780**	**1.769**	**0.001**
Interactions									
Year x Season	3	**0.032**	**37.364**	**0.0008**	**0.001**	**7.254**	**6.608**	**0.154**	**0.002**
Year x Habitat	10	**0.004**	**4.542**	**0.0004**	**0.001**	1.904	1.734	0.054	0.067
Season x Habitat	28	**0.008**	**2.639**	**0.0008**	**0.016**	**3.574**	**3.255**	**0.317**	**0.001**
Year x Season x Habitat	28	**0.003**	**3.628**	**0.0006**	**0.001**	**2.970**	**2.705**	**0.480**	**0.001**
Residual	244	0.001		0.0009		1.098		1.098	

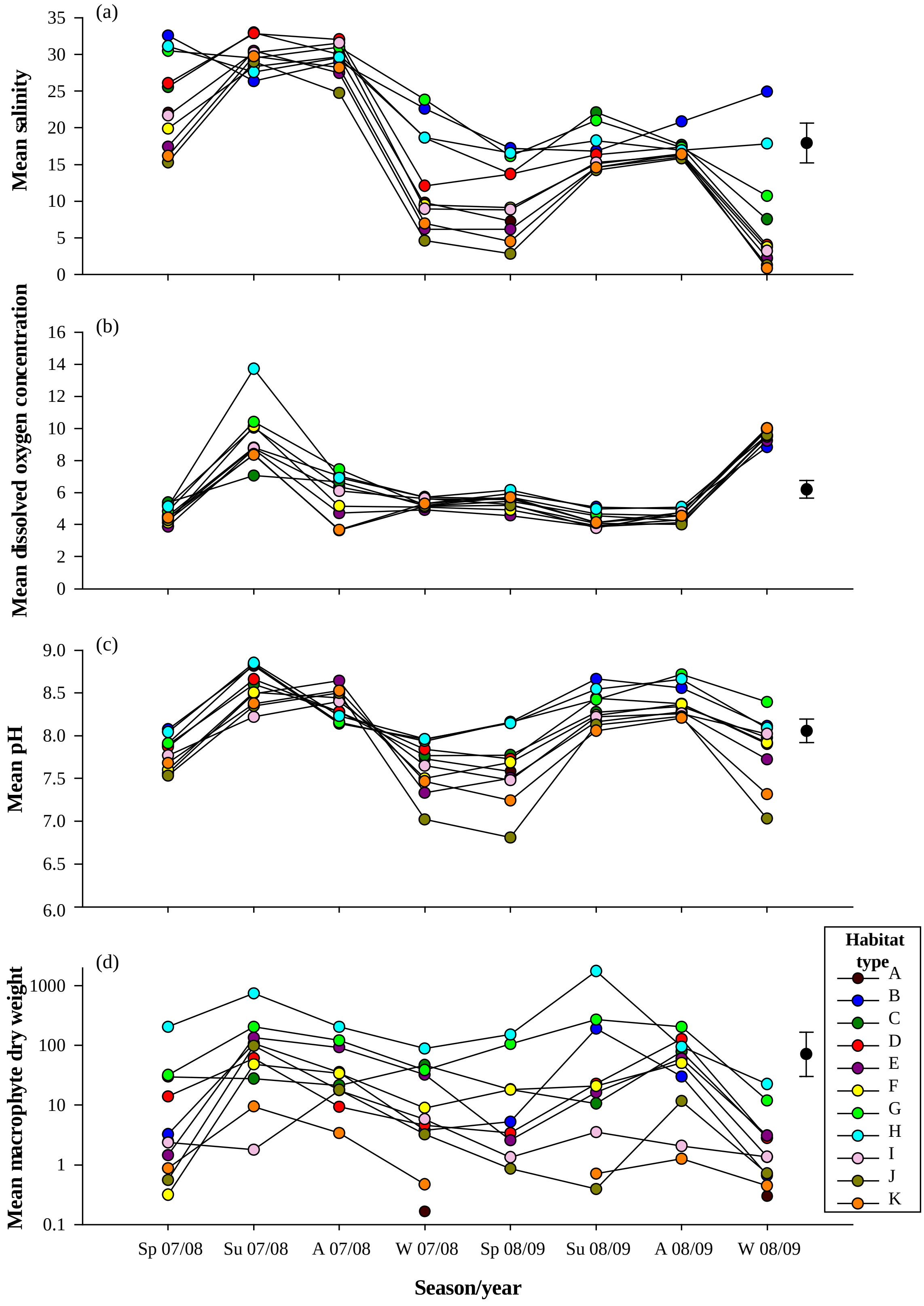


Fig. 3.2: Mean (a) salinity, (b) dissolved oxygen concentration (mg L^{-1}), (c) pH and (d) dry weight of detached macrophytes (g) at each the 11 nearshore habitat types in Broke Inlet sampled in each season between spring 2007/2008 and winter 2008/2009. For the sake of clarity, the average ± 95% confidence intervals have been presented for each of these plots.

two seasons. Thus, during winter 2008/2009 and at some habitats in spring of the same year, salinities < 5 were recorded and, in some cases, 1 (Fig. 3.2a).

Water temperature exhibited significant differences only among seasons (p=0.001, Table 3.1b). Temperatures were highest during spring and summer (22 and 20°C, respectively) and decreased substantially during autumn and winter (*ca* 15°C; figure not shown). Dissolved oxygen concentration differed significantly among habitats, seasons and years and all interaction terms between these main effects (all p=0.001; Table 3.1c). By far the greatest proportion of the variance was explained by the year x season interaction, which was due mainly to the markedly greater values recorded in winter 2008/2009 than in winter 2007/2008 (*ca* 9 and 5 mg L^{-1}, respectively) and the much greater range of values recorded during summer 2007/2008 (*i.e.* 7-14 mg L^{-1}) than in summer 2008/2009 (*i.e.* 5-6 mg L^{-1}). Dissolved oxygen concentrations were often greatest at channel habitat H and among the lowest at habitats E and K located within Shannon Basin (Fig. 3.2b).

Mean pH differed significantly between habitats and years and among all interactions (p=0.001-0.016; Table 3.1d). The year x season and season x habitat interactions explained the largest proportion of the variance, followed by the three-way interaction. The first of these interactions was caused mainly by differences between the two years in the range of values recorded during spring (*i.e.* 7.5 and 8 among all habitats in 2007/2008 compared to 6.8 and 8.2 in 2008/2009) and winter (*i.e.* 7 and 8 in 2007/2008 and 7 and 8.4 in 2008/2009). The second and, to some extent, the last of these interactions was due to the variability among sampling occasions in the pattern of pH differences between habitats. For example, whereas values at habitat J were either the lowest or among the lowest on most sampling occasions, they were among the highest in autumn 2007/2008. The opposite was true for the channel habitats B, G and H (Fig. 3.2c).

The dry weight of macrophytes also differed significantly among all main effects and interactions (p=0.001-0.002), with the exception of the year x habitat interaction term (Table 3.1e). The majority of the variance in this dependent variable was explained by differences in habitat and to a lesser extent, season. Macrophyte biomass was greatest at habitat H, followed by G, on almost all sampling occasions, and was commonly among the lowest at habitats A, I, J and K (Fig. 3.2d). The greatest quantities of detached macrophytes were recorded in summer and/or autumn, while the least was often recorded in winter (Fig. 3.2d). The significant interactions detected for this dependent variable were attributable to the notable differences among sampling occasions in the pattern and extent of macrophyte biomass among habitats (Fig. 3.2d).

3.3.1.2: Fish species mean density and life cycle contribution at each nearshore habitat type

A total of 71,593 fish were caught (*i.e.* after the number of fish in each sample was adjusted to that in 100 m^{-2} and summed) in the nearshore waters throughout Broke Inlet between spring 2007/2008 and winter 2008/2009. These fish comprised 27 species which represented 19 families. The Atherinidae and Gobiidae were the most speciose, each represented by three species, and together accounted for 99.6% of all fish caught (Table 3.2).

Of the 11 nearshore habitat types sampled throughout the estuary, habitat H located in the vegetated areas of the entrance channel was the most speciose (18), followed closely by habitat B at the mouth of the entrance channel (17) and C on the southern shore of Middle Basin (15) (Table 3.2). Conversely, habitat A situated on the eastern shore near the mouth of Inlet River was the most depauperate and harboured only five species. However, it should be noted that, due to the extensive shallow sandbanks which surround this habitat, sampling could only be carried out during winter and spring of both years. The remaining habitats (D, E, F, G, I, J and K), which were all located within either the Shannon or Middle basins, each contained between seven to ten species in total. The overall mean density of fish was also highest at habitat H (342 fish 100 m^{-2}), followed by that at habitats B and G (232 and 124 fish 100 m^{-2}, respectively). The lowest mean densities of fish were recorded at habitat A (30 fish 100 m^{-2}), while those at the remaining habitats (*i.e.* C, D, E, F, I, J and K) ranged between 47 and 105 fish 100 m^{-2} (Table 3.2).

The most speciose life cycle guild of fish throughout the nearshore waters of Broke Inlet was the marine stragglers, represented by eight species, followed by the

Table 3.2: Mean density (fish 100 m^{-2}; M), standard error (^{SE}), percentage contribution to the overall catch (%), rank by density (R), mean biomass (g; B), mean total length (mm; L) and length range (r) of each fish species recorded at each of the 11 nearshore habitat types in Broke Inlet in each season between spring 2007/2008 and winter 2008/2009. Abundant species at each habitat type (*i.e.* those that contribute ≥ 5% to the catch) are highlighted in grey. The life cycle category (LC) of each species is also provided (E = estuarine resident, EM = estuarine and marine, MEO = marine estuarine-opportunist, MS = marine straggler and FS = freshwater straggler). The species richness, mean overall density, number of samples and adjusted number of individuals (*i.e.* after the number of individuals in each sample had been adjusted to that in 100 m^{-2}) are given for each habitat type. Species are ranked by total abundance.

		A					**B**					**C**					**D**				
Species	**LC**	M^{SE}	%	R	B^{SE}	L^{r}	M^{SE}	%	R	B^{SE}	L^{r}	M^{SE}	%	R	B^{SE}	L^{r}	M^{SE}	%	R	B^{SE}	L^{r}
Atherinosoma elongata	E	$14.74^{2.56}$	49.15	1	$11.59^{5.84}$	$38^{(17-87)}$	$91.31^{12.12}$	39.42	2	$63.91^{8.32}$	$46^{(12-90)}$	$52.67^{12.80}$	49.97	1	$41.71^{10.45}$	$45^{(16-95)}$	$26.68^{4.69}$	53.56	1	$25.43^{7.92}$	$47^{(16-110)}$
Leptatherina wallacei	E	$14.68^{4.79}$	48.97	2	$4.22^{1.34}$	$34^{(18-73)}$	$44.63^{7.09}$	16.61	3	$13.68^{2.40}$	$38^{(11-67)}$	$27.17^{4.79}$	25.78	2	$13.39^{2.41}$	$39^{(20-83)}$	$12.94^{2.24}$	25.98	2	$6.10^{1.14}$	$40^{(21-71)}$
Leptatherina presbyteroides	EM	$0.27^{0.20}$	0.90	3	$0.16^{0.63}$	$40^{(31-60)}$	$108.31^{27.99}$	40.31	1	$41.00^{18.16}$	$37^{(10-78)}$	$17.34^{19.30}$	16.45	3	$9.18^{5.17}$	$43^{(21-69)}$	$3.60^{1.21}$	7.22	4	$0.91^{0.30}$	$39^{(19-63)}$
Afurcagobius suppositus	E	$0.19^{0.06}$	0.63	4	$0.81^{0.32}$	$36^{(30-49)}$	$2.48^{0.67}$	1.07	5	$3.52^{1.61}$	$36^{(30-49)}$	$5.38^{0.74}$	5.10	4	$6.53^{1.30}$	$45^{(19-93)}$	$5.47^{1.04}$	10.98	3	$2.41^{0.41}$	$35^{(19-73)}$
Pseudogobius olorum	E						$1.09^{0.67}$	0.47	6	$0.72^{0.40}$	$35^{(21-52)}$	$0.97^{0.31}$	0.92	6	$0.36^{0.11}$	$32^{(20-53)}$	$0.30^{0.13}$	0.59	6	$0.24^{0.12}$	$37^{(26-52)}$
Favonigobius lateralis	EM	$0.11^{0.05}$	0.36	5	$0.80^{0.40}$	$42^{(35-45)}$	$3.62^{0.74}$	1.56	4	$3.69^{0.60}$	$41^{(16-77)}$	$1.14^{0.26}$	1.09	5	$1.16^{0.25}$	$44^{(17-64)}$	$0.62^{0.17}$	1.24	5	$0.89^{0.25}$	$50^{(28-72)}$
Notolabrus parilus	MS						$0.35^{0.27}$	0.15		$0.55^{0.39}$	$36^{(22-105)}$	$0.01^{0.01}$	0.01	10	$0.09^{0.09}$	$74^{(74)}$					
Hyporhamphus melanochir	EM											$0.59^{0.33}$	0.56	7	$6.73^{3.11}$	$138^{(59-268)}$	$0.01^{0.01}$	0.03	8	$0.03^{0.03}$	$97^{(97)}$
Achoerodus gouldii	MS						$0.16^{0.11}$	0.07	9	$0.14^{0.09}$	$37^{(20-52)}$										
Engraulis australis	EM						$0.11^{0.10}$	0.05	11	$0.27^{0.25}$	$73^{(59-86)}$										
Aldrichetta forsteri	MEO						$0.12^{0.10}$	0.05	11	$1.90^{1.56}$	$94^{(55-159)}$	$0.03^{0.03}$	0.03	8	$0.06^{0.06}$	$44^{(43-45)}$	$0.20^{0.19}$	0.41	7	$11.00^{10.23}$	$191^{(154-483)}$
Ammotretis rostratus	MEO						$0.32^{0.08}$	0.14	8	$1.05^{0.35}$	$56^{(24-88)}$	$0.01^{0.01}$	0.01	10	$0.01^{0.01}$	$41^{(41)}$					
Neoodax balteatus	MS						$0.03^{0.02}$	0.01	13	$0.20^{0.15}$	$100^{(87-112)}$	$0.01^{0.01}$	0.01	10	$0.15^{0.15}$	$109^{(109)}$					
Ammotretis elongatus	EM						$0.13^{0.10}$	0.06	10	0.44-0.31	$36^{(36)}$										
Enoplosus armatus	MS											$0.03^{0.02}$	0.03	8	$0.02^{0.01}$	$30^{(26-33)}$					
Edelia vittata	FS																				
Mugil cephalus	MEO						$0.03^{0.02}$	0.01	13	$0.01^{0.01}$	$26^{(26)}$										
Platycephalus speculator	EM						$0.03^{0.03}$	0.01	13	$0.49^{0.49}$	$140^{(133-146)}$										
Girella zebra	MS																				
Haletta semifasciata	MS																				
Galaxias occidentalis	FS											$0.01^{0.01}$	0.01	10	$0.05^{0.05}$	$86^{(86)}$					
Lepidogalaxias salamandroides	FS																				
Urocampus carinirostris	EM											$0.01^{0.01}$	0.01	10	$0.01^{0.01}$	$52^{(52)}$					
Pseudocaranx dentex	MS											$0.01^{0.01}$	0.01	10	$0.02^{0.02}$	$44^{(44)}$					
Rhabdosargus sarba	MEO																				
Pseudorhombus jenynsii	MEO						$0.01^{0.01}$	0.01	13	$1.40^{1.40}$	$195^{(195)}$										
Cynoglossus broadhursti	MS						$0.01^{0.01}$	0.01	13	$0.24^{0.24}$	$135^{(135)}$										
Species richness		**5**					**17**					**15**					**8**				
Mean overall density		**30**					**232**					**105**					**50**				
Number of samples		**32**					**64**					**64**					**64**				
Adjusted number of individuals		**960**					**14,848**					**6,720**					**3,200**				
Actual number of individuals		**1,113**					**17,198**					**7,824**					**3,699**				

Table 3.2 Continued:

		E					F					G					H				
Species	**LC**	M^{SE}	%	R	B^{SE}	L^{r}	M-SE	%	R	B-SE	L-r	M-SE	%	R	B-SE	L-r	M-SE	%	R	B-SE	L-r
Atherinosoma elongata	E	$30.15^{5.18}$	52.38	1	$24.29^{4.24}$	$44^{(16-110)}$	$28.62^{5.39}$	58.75	1	$26.88^{0.18}$	$47^{(17-97)}$	$77.22^{11.88}$	62.49	1	$66.34^{8.08}$	$48^{(15-108)}$	$131.74^{18.98}$	38.55	1	$114.17^{14.27}$	$48^{(6-124)}$
Leptatherina wallacei	E	$20.03^{3.42}$	34.80	2	$10.45^{2.20}$	$41^{(16-88)}$	$15.38^{3.02}$	31.57	2	$8.15^{0.65}$	$41^{(21-79)}$	$25.48^{6.15}$	20.62	2	$11.4^{2.34}$	$40^{(19-78)}$	$94.36^{17.97}$	27.61	3	$36.88^{7.16}$	$40^{(17-85)}$
Leptatherina presbyteroides	EM	$2.18^{0.93}$	3.79	4	$0.69^{0.31}$	$42^{(26-68)}$	$1.01^{0.32}$	2.07	4	$0.49^{0.11}$	$42^{(26-68)}$	$9.81^{1.74}$	7.93	3	$3.46^{0.64}$	$38^{(16-62)}$	$94.37^{35..49}$	27.62	2	$33.77^{15.05}$	$38^{(16-76)}$
Afurcagobius suppositus	E	$4.54^{0.73}$	7.89	3	$3.57^{0.56}$	$39^{(19-82)}$	$2.79^{0.42}$	5.72	3	$3.00^{0.11}$	$43^{(21-94)}$	$6.91^{1.19}$	5.59	4	$6.66^{1.08}$	$41^{(15-93)}$	$9.42^{1.55}$	2.76	4	$15.50^{3.88}$	$48^{(15-96)}$
Pseudogobius olorum	E	$0.38^{0.13}$	0.66	5	$0.24^{0.10}$	$36^{(20-64)}$	$0.61^{0.28}$	1.24	5	$0.27^{0.10}$	$34^{(23-47)}$	$3.57^{0.85}$	2.89	5	$1.66^{0.42}$	$33^{(16-59)}$	$4.54^{1.13}$	1.33	5	$2.29^{0.46}$	$36^{(19-78)}$
Favonigobius lateralis	EM	$0.18^{0.07}$	0.30	6	$0.23^{0.13}$	$47^{(36-61)}$	$0.26^{0.12}$	0.53	6	$0.24^{0.65}$	$42^{(26-57)}$	$0.39^{0.12}$	0.32	6	$0.49^{0.17}$	$47^{(31-65)}$	$3.51^{1.40}$	1.02	6	$2.80^{0.52}$	$53^{(25-84)}$
Notolabrus parilus	MS											$0.11^{0.06}$	0.09	7	$0.39^{0.25}$	$57^{(31-93)}$	$1.26^{0.37}$	0.37	7	$4.08^{1.28}$	$46^{(19-134)}$
Hyporhamphus melanochir	EM	$0.01^{0.01}$	0.02	8	$0.03^{0.03}$	$104^{(104)}$	$0.04^{0.01}$	0.08	7	$0.95^{0.00}$	$187^{(124-233)}$						$0.38^{0.18}$	0.11	10	$12.37^{6.59}$	$187^{(60-413)}$
Achoerodus gouldii	MS											$0.05^{0.04}$	0.04	8	$0.03^{0.02}$	$34^{(32-36)}$	$0.73^{0.23}$	0.21	8	$6.87^{3.19}$	$68^{(26-102)}$
Engraulis australis	EM																$0.73^{0.49}$	0.21	8	$2.38^{1.59}$	$77^{(61-92)}$
Aldrichetta forsteri	MEO																$0.36^{0.27}$	0.10	11	$3.18^{3.06}$	$93^{(32-126)}$
Ammotretis rostratus	MEO	$0.01^{0.01}$	0.02	8	$0.14^{0.14}$	$87^{(87)}$											$0.05^{0.02}$	0.01	15	$2.98^{2.29}$	$132^{(28-207)}$
Neoodax balteatus	MS											$0.01^{0.01}$	0.01	10	$0.20^{0.20}$	$119^{(119)}$	$0.17^{0.10}$	0.05	12	$1.41^{1.20}$	$93^{(31-134)}$
Ammotretis elongatus	EM																				
Enoplosus armatus	MS						$0.01^{0.01}$	0.03	8	$0.01^{0.00}$	$24^{(24)}$	$0.03^{0.02}$	0.02	9	$0.10^{0.10}$	$52^{(27-76)}$	$0.06^{0.04}$	0.02	13	$0.27^{0.27}$	$71^{(68-74)}$
Edelia vittata	FS	$0.07^{0.06}$	0.12	7	$0.02^{0.02}$	$21^{(17-27)}$															
Mugil cephalus	MEO																$0.05^{0.02}$	0.01	14	$0.79^{0.79}$	$74^{(24-168)}$
Platycephalus speculator	EM																				
Girella zebra	MS																$0.03^{0.03}$	0.01	15	$0.34^{0.34}$	$116^{(116)}$
Haletta semifasciata	MS																$0.03^{0.03}$	0.01	15	$0.5^{0.5}$	$95^{(95)}$
Galaxias occidentalis	FS																				
Lepidogalaxias salamandroides	FS	$0.01^{0.01}$	0.02	8	$0.06^{0.06}$	$26^{(26)}$															
Urocampus carinirostris	EM																				
Pseudocaranx dentex	MS																				
Rhabdosargus sarba	MEO																$0.01^{0.01}$	0.00	18	$0.06^{0.06}$	$23^{(23)}$
Pseudorhombus jenynsii	MEO																				
Cynoglossus broadhursti	MS																				
Species richness		**10**					**8**					**10**					**18**				
Mean overall density		**58**					**49**					**124**					**342**				
Number of samples		**64**					**64**					**64**					**64**				
Adjusted number of individuals		**3,712**					**3,136**					**7,936**					**21,888**				
Actual number of fish individuals		**4,273**					**3,617**					**9,175**					**25,369**				

Table 3.2 Continued:

		I					**J**					**K**				
Species	**LC**	M^{SE}	%	R	B^{SE}	L^{r}	M^{SE}	%	R	B^{SE}	L-r	M^{SE}	%	R	B^{SE}	L-r
Atherinosoma elongata	E	$42.89^{7.39}$	69.53	1	$26.46^{4.83}$	$42^{(14-89)}$	$25.92^{4.29}$	52.80	1	$17.34^{5.97}$	$39^{(15-108)}$	$22.91^{5.58}$	49.06	3	$11.22^{3.20}$	$39^{(6-119)}$
Leptatherina wallacei	E	$14.66^{2.86}$	23.76	2	$5.99^{1.11}$	$37^{(6-82)}$	$15.86^{2.91}$	32.31	2	$6.24^{1.63}$	$37^{(15-95)}$	$12.47^{2.38}$	26.71	1	$3.82^{0.76}$	$34^{(17-68)}$
Leptatherina presbyteroides	EM	$2.01^{0.65}$	3.25	3	$0.69^{0.21}$	$38^{(16-57)}$	$1.58^{1.25}$	3.22	4	$0.46^{0.41}$	$37^{(22-63)}$	$10.56^{9.62}$	22.61	2	$5.54^{5.21}$	$40^{(20-67)}$
Afurcagobius suppositus	E	$0.96^{0.20}$	1.55	5	$0.54^{0.13}$	$35^{(21-64)}$	$5.24^{1.46}$	10.68	3	$1.87^{0.45}$	$31^{(18-54)}$	$0.58^{0.17}$	1.24	4	$0.40^{0.12}$	$37^{(20-72)}$
Pseudogobius olorum	E	$0.11^{0.06}$	0.17	6	$0.04^{0.02}$	$29^{(22-43)}$	$0.23^{0.10}$	0.48	5	$0.08^{0.04}$	$30^{(18-50)}$	$0.04^{0.02}$	0.09	6	$0.02^{0.01}$	$30^{(16-40)}$
Favonigobius lateralis	EM	$1.02^{0.23}$	1.66	4	$0.87^{0.23}$	$41^{(23-63)}$	$0.23^{0.12}$	0.48	5	$0.22^{0.11}$	$43^{(26-63)}$	$0.09^{0.05}$	0.20	5	$0.10^{0.05}$	$41^{(28-57)}$
Notolabrus parilus	MS															
Hyporhamphus melanochir	EM											$0.03^{0.03}$	0.06	7	$0.20^{0.20}$	$147^{(141-152)}$
Achoerodus gouldii	MS															
Engraulis australis	EM											$0.01^{0.01}$	0.03	8	$0.02^{0.02}$	$57^{(57)}$
Aldrichetta forsteri	MEO															
Ammotretis rostratus	MEO	$0.04^{0.02}$	0.07	7	$0.70^{0.42}$	$106^{(95-114)}$										
Neoodax balteatus	MS															
Ammotretis elongatus	EM															
Enoplosus armatus	MS															
Edelia vittata	FS						$0.02^{0.02}$	0.04	7	$0.03^{0.03}$	$49^{(49)}$					
Mugil cephalus	MEO															
Platycephalus speculator	EM															
Girella zebra	MS															
Haletta semifasciata	MS															
Galaxias occidentalis	FS															
Lepidogalaxias salamandroides	FS															
Urocampus carinirostris	EM															
Pseudocaranx dentex	MS															
Rhabdosargus sarba	MEO															
Pseudorhombus jenynsii	MEO															
Cynoglossus broadhursti	MS															
Species richness		**7**					**7**					**8**				
Mean overall density		**62**					**49**					**47**				
Number of samples		**64**					**48**					**64**				
Adjusted number of individuals		**3,968**					**2,352**					**3,008**				
Actual number of fish individuals		**4,579**					**2,733**					**3,467**				

estuarine and marine (seven species), marine estuarine-opportunist (five species) estuarine residents (four species) and freshwater (three species) guilds. The atherinids *Atherinosoma elongata* and *Leptatherina wallacei*, both of which are estuarine residents, ranked within the top three most abundant species at all habitats and together represented between 56 and 98% of the total fish caught in each habitat type. Conversely, the other atherinid species captured, *Leptatherina presbyteroides*, an estuarine and marine species, contributed ≥ 5% of the catch at only six of the 11 habitats (*i.e.* B, C, D, G, H and K) despite representing over 21% of the total fish caught. Three goby species, *Afurcagobius suppositus*, *Pseudogobius olorum* and *Favonigobius lateralis*, were captured at all habitats with the exception of *P. olorum* at habitat A. *Afurcagobius suppositus* was the most abundant of the three gobies, representing > 5% of the catch at habitats C, E, F, G and J. While *F. lateralis* and *P. olorum* were never particularly abundant, their densities were highest at habitats B and H, and H and G, respectively, all of which are located within the entrance channel.

Estuarine and marine and marine straggler species exhibited a restricted spatial distribution and were recorded mainly in those habitats located within or close to the entrance channel, *i.e.* B, C, G and H (Table 3.2). Some of the more numerous marine stragglers, *i.e. Notolabrus parilus* and *Achoerodus gouldii*, were only caught in habitats situated in the entrance channel. Three freshwater stragglers were caught, *i.e. Edelia vittata*, *Galaxias occidentalis* and *Lepidogalaxias salamandroides*, of which the most numerous, *E. vittata*, was caught at habitats located at the mouth of the Shannon River (J) or in the vicinity (E). The other two freshwater species were caught only in habitats C and E, respectively.

3.3.1.3: Differences in species richness, density and diversity among nearshore habitat types, season and years

Mean species richness differed significantly among nearshore habitats, seasons and years and all interaction terms among those main effects (*p*=0.001; Table 3.3a). As indicated by the associated components of variation, differences among habitats explained the large majority of the variance in this dependent variable. The influences

Table 3.3: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (*p*) from PERMANOVA tests on the data for mean fish (a) species richness, (b) density and (c) Shannon-Wiener diversity at the 11 nearshore habitat types in Broke Inlet sampled in each season between spring 2007/2008 and winter 2008/2009. df = degrees of freedom. Significant results are highlighted in bold.

	(a) Species richness				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Year	1	**1.489**	**26.602**	**0.009**	**0.001**
Season	3	**1.381**	**24.677**	**0.017**	**0.001**
Habitat	10	**1.939**	**34.640**	**0.063**	**0.001**
Interactions					
Year x Season	3	**0.432**	**7.721**	**0.009**	**0.001**
Year x Habitat	10	**0.213**	**3.802**	**0.011**	**0.001**
Season x Habitat	28	**0.138**	**2.460**	**0.010**	**0.001**
Year x Season x Habitat	28	**0.139**	**2.476**	**0.021**	**0.001**
Residual	244	0.056		0.056	

	(b) Density				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Year	1	**22.446**	**31.664**	**0.140**	**0.001**
Season	3	**13.806**	**19.476**	**0.164**	**0.001**
Habitat	10	**14.592**	**20.585**	**0.468**	**0.001**
Interactions					
Year x Season	3	**12.235**	**17.260**	**0.288**	**0.001**
Year x Habitat	10	**1.311**	**1.849**	**0.041**	**0.047**
Season x Habitat	28	**1.390**	**1.960**	**0.087**	**0.006**
Year x Season x Habitat	28	0.974	1.374	0.068	0.123
Residual	244	0.709		0.709	

	(c) Shannon-Wiener diversity				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Year	1	0.206	3.497	0.001	0.071
Season	3	**1.149**	**19.534**	**0.014**	**0.001**
Habitat	10	**0.701**	**11.916**	**0.022**	**0.001**
Interactions					
Year x Season	3	**0.608**	**10.341**	**0.014**	**0.001**
Year x Habitat	10	**0.290**	**4.935**	**0.016**	**0.001**
Season x Habitat	28	**0.087**	**1.487**	**0.004**	**0.045**
Year x Season x Habitat	28	**0.117**	**1.993**	**0.015**	**0.001**
Residual	244	0.059		0.059	

of the three-way interaction and the season main effect were the next most important (Table 3.3a). In all seasons and years, habitat H contained the greatest mean number of species, ranging from 3.2 in winter 2008/2009 to 8.1 in spring 2008/2009 (Fig. 3.3a). Habitats B, C, and G also contained relatively high mean numbers of species during most sampling occasions, *i.e.* between 4 and 5.5, while the least were generally recorded at those habitats located near freshwater sources, *i.e.* A, J and K, at which a mean of 1 to 4 species were recorded (Fig. 3.3a). Despite differences in the rank orders and range among habitats during the various sampling occasions with respect to their mean species richness, which accounted for the significant interactions between all combinations of the main effects, the highest number of species were generally recorded

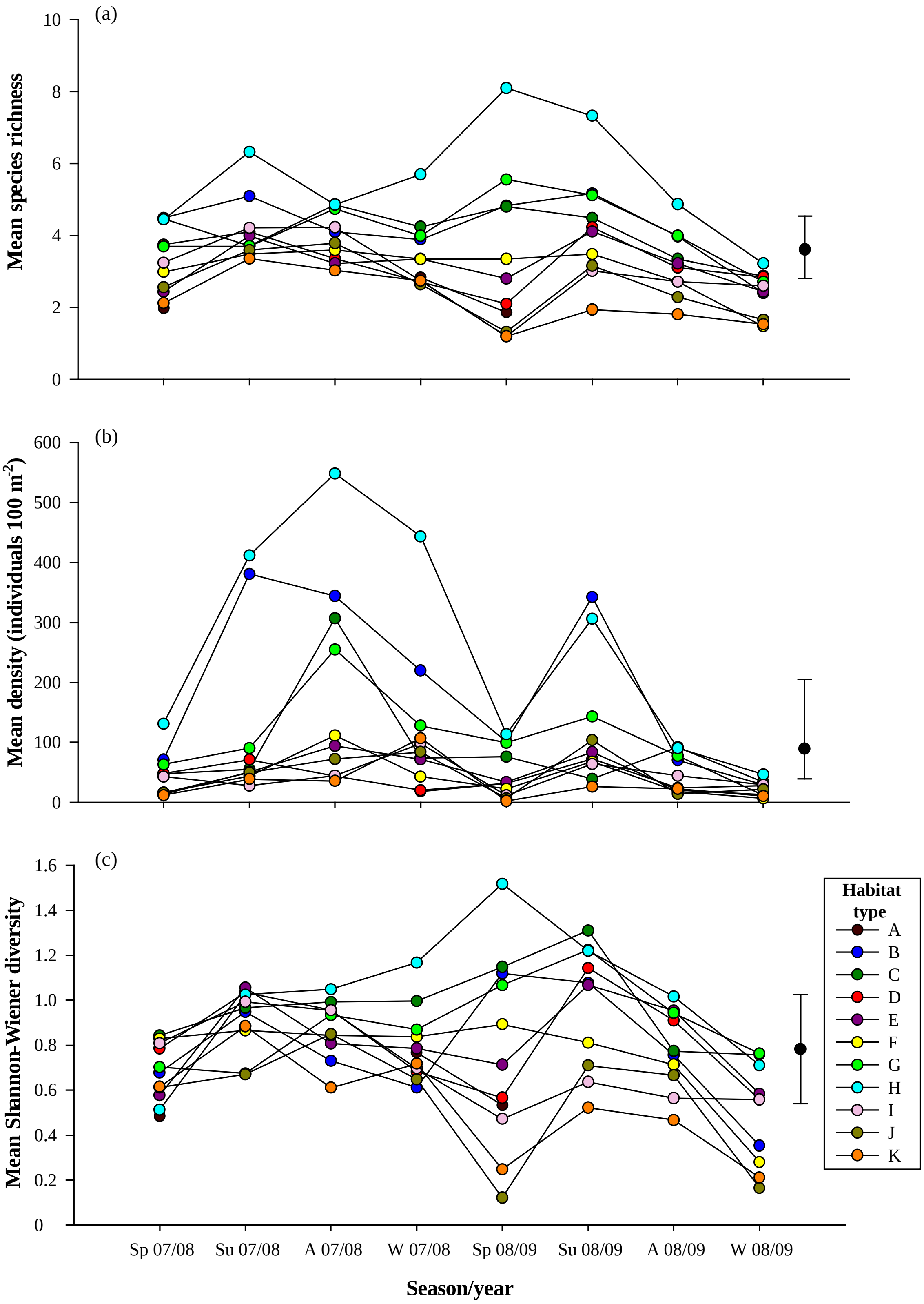


Fig. 3.3: Mean (a) species richness, (b) density (individuals 100 m^{-2}) and (c) Shannon-Wiener diversity of the nearshore fish fauna at each of the 11 nearshore habitat types in Broke Inlet sampled in each season between spring 2007/2008 and winter 2008/2009. For the sake of clarity, the average ± 95% confidence intervals have been presented for each of these plots.

in summer 2007/2008 and/or 2008/2009 and the lowest in winter 2008/2009. During spring 2008/2009, in which the greatest range of mean species richness was recorded, *i.e.* 1.2 to 8.1, habitats such as G and H reached their maximums, while those such as J and K fell to their minimum (Fig. 3.3a).

Mean density also differed among all main effects and interactions, except for the habitat x season x year interaction (*p*=0.001-0.047; Table 3.3b). Differences among habitats had by far the greatest influence on this dependent variable, followed by those attributable to the year x season interaction, while the influences of the remaining significant terms were far lower (Table 3.3b). Habitat H contained the highest mean density of fish in almost all seasons and years, with values of up to 550 fish m^{-2} in autumn 2007/2008. The other channel habitats B and, to a lesser extent, G, also contained relatively high mean fish densities during most sampling occasions (*i.e.* 63-381 fish 100 m^{-2}). Habitats located near freshwater sources (*i.e.* A, I, J and K) often had among the lowest mean fish densities (≤ 50 fish 100 m^{-2}), while the remaining habitats generally contained mean densities of around 50-100 fish 100 m^{-2} (Fig. 3.3b). The relatively important interaction between season and years was due mainly to the large differences in the range of fish densities recorded in autumn and winter across years, with those in 2007/2008 being markedly larger. During each year, fish densities at most habitats reached their maximum during summer or autumn.

PERMANOVA detected significant differences in Shannon-Wiener diversity among habitats and seasons and all interaction terms (*p*=0.001-0.045; Table 3.3c). Like both the mean number of species and density of fish, Shannon-Wiener diversity varied to the greatest extent among habitats. The remaining significant terms made relatively moderate contributions, with the exception of the season x habitat interaction, which was far less important (Table 3.3c). Also like the above two dependent variables, habitats H, C and/or G often contained the highest species diversity, whilst the least diverse assemblages were typically recorded at habitats J and K (Fig. 3.3c). The least diverse assemblages were typically recorded during winter at most habitats, but there was considerable variability in the order and range among habitats during the remaining sampling occasions, thus explaining the relative importance of the various interaction terms. Most noticeably, the range in diversity during spring and, to a lesser extent, summer 2008/2009 (0.12-1.52 and 0.52-1.31, respectively) was far greater than those for the same seasons in 2007/2008 and indeed, for any other sampling occasion. These trends paralleled those exhibited by the mean number of species (*cf.* Figs 3.3c, a).

3.3.1.4: Differences in fish assemblage composition among nearshore habitat types

Three-way crossed PERMANOVA identified significant differences in the species composition of the nearshore fish communities among habitats, seasons and years and all of their interaction terms (all *p*=0.001; Table 3.4). The components of variation for habitat was over twice that of the next most influential term, *i.e.* the year x season x habitat interaction, closely followed by the year x season interaction. On the basis of these results, subsequent analyses were then employed to more thoroughly investigate the differences among habitats in the nearshore fish community composition. Note that, these analyses were carried out separately for each season in each year in order to remove the confounding influence of these temporal factors.

One-way ANOSIM tests identified significant differences among habitats in each season and year combination (all *p*=0.001; Table 3.5). However, the overall extent of those differences were low to moderate (Global *R*=0.237-0.485), with the greatest being detected in spring 2007/2008, followed closely by summer and spring 2008/2009, and the least in winter 2008/2009 (Table 3.5).

Table 3.4: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (*p*) from a three-way PERMANOVA of the nearshore ichthyofaunal composition recorded at the 11 nearshore habitat types throughout Broke Inlet in each season between spring 2007/2008 and winter 2008/2009. df = degrees of freedom. Significant results are highlighted in bold.

	Nearshore fish assemblage composition				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Year	1	**13935.000**	**16.097**	**83.958**	**0.001**
Season	3	**8664.300**	**10.008**	**97.380**	**0.001**
Habitat	10	**11539.000**	**13.329**	**359.870**	**0.001**
Interactions					
Year x Season	3	**6711.100**	**7.752**	**145.980**	**0.001**
Year x Habitat	10	**1827.300**	**2.111**	**64.841**	**0.001**
Season x Habitat	28	**1804.000**	**2.084**	**120.270**	**0.001**
Year x Season x Habitat	28	**1470.900**	**1.699**	**155.140**	**0.001**
Residual	244	865.730		865.730	

Table 3.5: *R*-statistic and/or significance level (*p*) values derived from one-way ANOSIM tests of the nearshore fish faunal composition among the 11 nearshore habitat types during each season sampled between spring 2007/2008 and winter 2008/2009. Insignificant pairwise comparisons are highlighted in grey.

(a) Spring 2007/2008; *p*=0.001, Global *R*=0.485

	A	B	C	D	E	F	G	H	I	J
B	0.885									
C	0.969	0.302								
D	0.948	0.635	-0.042							
E	0.344	0.813	0.646	0.490						
F	0.167	0.740	0.240	0.198	-0.083					
G	1.000	0.719	0.010	0.031	0.771	0.313				
H	0.979	0.594	0.115	0.083	0.823	0.406	0.052			
I	0.708	0.385	0.521	0.365	0.844	0.573	0.958	0.823		
J	0.815	0.796	0.481	0.315	0.093	0.037	0.407	0.630	0.981	
K	0.167	0.708	0.677	0.365	-0.167	-0.229	0.833	0.865	0.552	0.278

(b) Summer 2007/2008; *p*=0.001, Global *R*=0.379

	B	C	D	E	F	G	H	I	J
C	0.958								
D	0.990	-0.042							
E	1.000	-0.083	0.073						
F	0.990	-0.073	0.094	0.010					
G	0.844	-0.177	0.083	0.073	-0.021				
H	0.594	0.521	0.604	0.594	0.750	0.469			
I	0.969	0.375	0.604	0.302	0.135	0.219	0.844		
J	0.963	-0.093	0.148	0.000	-0.130	-0.222	0.556	-0.074	
K	1.000	0.146	0.156	0.229	0.135	0.000	0.896	-0.052	-0.056

(c) Autumn 2007/2008; *p*=0.001, Global *R*=0.322

	B	C	D	E	F	G	H	I	J
C	-0.156								
D	0.542	0.552							
E	0.375	0.510	-0.031						
F	0.333	0.375	0.385	-0.125					
G	0.198	0.167	0.708	0.385	0.292				
H	0.094	0.031	0.958	0.875	0.813	0.229			
I	0.302	0.333	0.208	0.427	0.219	0.635	0.854		
J	0.352	0.481	0.056	-0.148	-0.148	0.500	0.833	0.315	
K	0.167	0.271	0.406	0.250	0.156	0.375	0.479	0.156	-0.093

(d) Winter 2007/2008; *p*=0.001, Global *R*=0.346

	A	B	C	D	E	F	G	H	I	J
B	0.615									
C	0.854	0.271								
D	0.292	0.458	0.677							
E	0.198	0.385	0.260	0.396						
F	0.083	0.250	0.250	0.073	-0.021					
G	0.719	-0.042	0.167	0.729	0.292	0.125				
H	1.000	-0.146	0.490	0.938	0.781	0.729	0.219			
I	0.417	0.479	0.667	0.510	-0.146	0.167	0.531	0.969		
J	0.296	0.130	0.222	0.444	-0.259	-0.019	0.352	0.778	-0.148	
K	0.427	0.458	0.583	0.615	-0.260	0.135	0.354	0.927	-0.219	-0.352

Table 3.5 Continued:

(e) Spring 2008/2009; *p*=0.001, Global *R*=0.467

	A	B	C	D	E	F	G	H	I	J
B	0.781									
C	0.771	0.219								
D	-0.188	0.813	0.646							
E	-0.115	0.427	0.302	-0.094						
F	0.448	0.573	0.219	0.354	-0.021					
G	0.927	0.198	0.063	0.896	0.479	0.563				
H	0.979	0.542	0.615	1.000	0.719	0.885	0.698			
I	-0.094	0.313	0.229	-0.146	-0.135	0.135	0.500	0.563		
J	0.296	0.963	0.907	0.389	0.111	0.426	0.981	1.000	0.046	
K	0.448	1.000	1.000	0.677	0.448	0.875	1.000	1.000	0.344	0.296

(f) Summer 2008/2009; *p*=0.001, Global *R*=0.483

	B	C	D	E	F	G	H	I	J
C	0.969								
D	0.760	0.292							
E	0.833	0.292	0.302						
F	0.875	0.333	0.688	-0.042					
G	0.323	0.563	0.427	0.125	0.385				
H	0.365	0.854	0.729	0.708	0.781	0.094			
I	0.427	0.302	0.313	0.208	0.010	0.344	0.573		
J	0.815	0.926	0.722	0.093	-0.315	0.315	0.741	0.148	
K	0.990	0.865	0.958	0.875	0.396	0.917	0.990	0.198	0.500

(g) Autumn 2008/2009; *p*=0.001, Global *R*=0.344

	B	C	D	E	F	G	H	I	J
C	0.094								
D	0.469	0.208							
E	0.677	0.469	0.135						
F	0.667	0.552	0.073	-0.073					
G	0.313	0.167	0.604	0.563	0.385				
H	-0.021	-0.167	0.427	0.552	0.646	-0.063			
I	0.125	0.073	0.021	0.083	0.073	0.323	0.323		
J	0.667	0.630	0.056	0.241	-0.074	0.907	0.963	0.056	
K	0.719	0.729	0.448	0.740	0.354	0.844	0.927	0.250	0.056

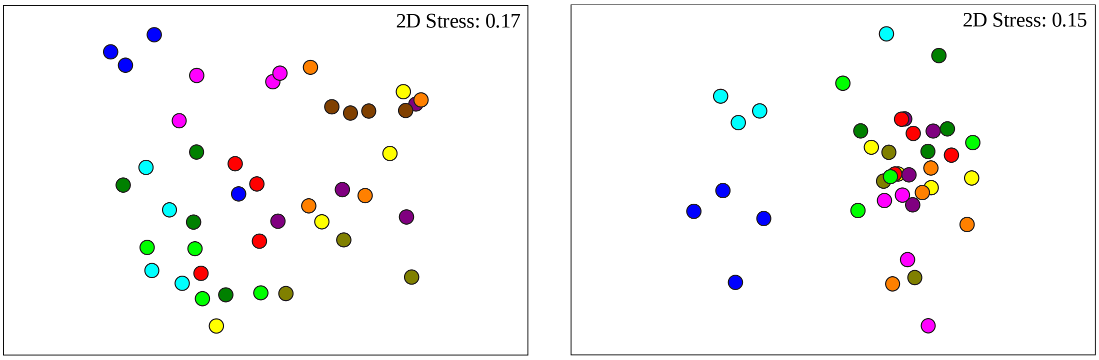
(h) Winter 2008/2009; *p*=0.001, Global *R*=0.237

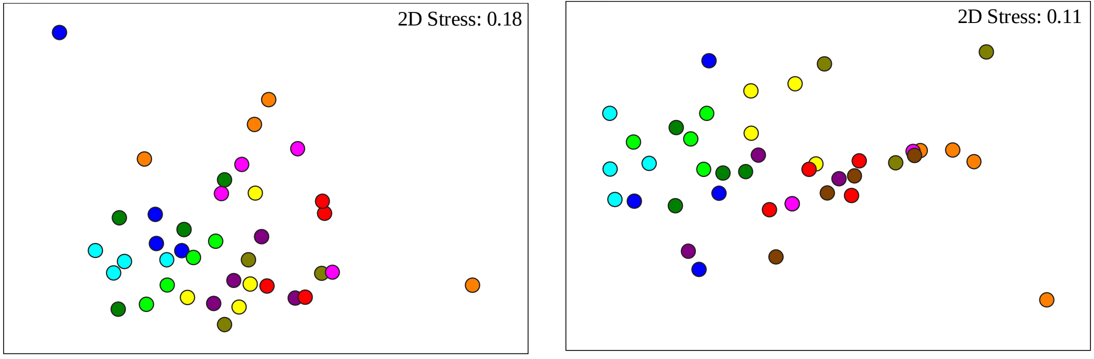
	A	B	C	D	E	F	G	H	I	J
B	0.063									
C	0.260	0.490								
D	0.135	0.281	-0.042							
E	0.427	0.771	0.177	0.073						
F	0.271	0.698	0.427	0.260	0.083					
G	0.417	0.563	0.073	0.042	-0.042	0.271				
H	0.094	0.115	-0.042	-0.115	0.000	0.323	-0.073			
I	0.115	0.333	0.094	-0.042	0.063	0.177	0.156	-0.125		
J	0.306	0.444	0.315	0.093	0.296	0.139	0.370	0.315	0.222	
K	0.542	0.875	0.583	0.448	0.208	0.104	0.563	0.417	0.323	0.148

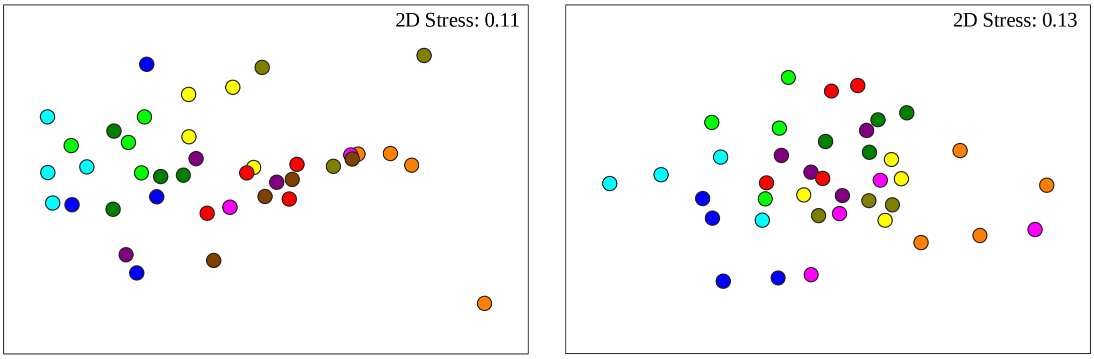
During spring 2007/2008 and spring and summer 2008/2009 the pairwise differences involving habitats A, B, H and K were typically large (*i.e.* *R* > 0.800), thereby reflecting the relatively distinct fish faunal compositions, with samples representing those habitats, in particular B and H forming discrete groups on the nMDS ordinations (Figs 3.4a, e, f). In the case of habitats A and K, the estuarine atherinids *A. elongata* and *L. wallacei* typified the fish fauna in these seasons, however, as these species distinguished the ichthyofaunas of almost all habitats in all seasons of both years, the distinctness of these habitats was more attributable to the low densities of these species and the depauperate nature of the ichthyofauna (Appendix 3.1a, e, f). Conversely, the channel habitats B and H were, in addition to the above species, also characterised by several other species including the estuarine and marine *F. lateralis* and *L. presbyteroides* and in the case of H, the gobiids *P. olorum* and *A. suppositus*. Species such as *Hyporhamphus melanochir, A. gouldii* and *N. parilus* also distinguished this latter habitat from the others in spring and summer 2008/2009 (Appendix 3.1e, f).

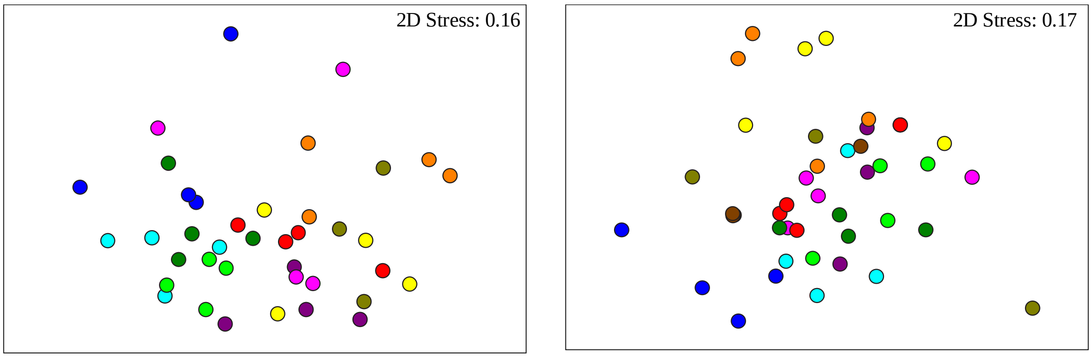
The next largest differences in fish faunal composition among habitats were detected in summer 2007/2008 (Global *R*=0.379), but only 20 of the 45 pairwise comparisons were significant, which almost invariably involved the channel habitats B and H (Table 3.5b). As reflected by the associated nMDS ordination (Fig. 3.4b), these habitats harboured a distinct fauna (pairwise *R* generally > 0.750) during this sampling season, paralleling the findings above for spring 2007/2008 and spring and summer 2008/2009. Aside from *A. elongata* and *L. wallacei*, which once again characterised the fauna at almost all habitats during this sampling occasion, the flounder *Ammotretis rostratus* and *L. presbyteroides* also distinguished habitat B from the remainder, while the notably greater abundances of *A. elongata, L. wallacei, A. suppositus* and *N. parilus* best distinguished H from other habitats (Appendix 3.1b).

The extent of the overall ichthyofaunal differences among habitats were similar and relatively low in autumn and winter 2007/2008 and autumn 2008/2009 (Global *R*=0.322-0.346), with habitats G and H being the most faunally distinct thus, samples from these seasons formed relatively discrete groups on the nMDS ordinations (Figs 3.4c, d, g). Once again *A. elongata* and *L. wallacei* typified the fauna at all habitats, however, the distinctness of the fish at habitats G and H was due mainly to the high abundances of *A. elongata, L. wallacei* and *A. suppositus*, while the opposite was true for habitat K during autumn 2008/2009. The fish faunas of habitats G and H were distinguished by a prevalence of *A. suppositus* in autumn and winter 2007/2008 and


(a) Spring 2007/2008 (b) Summer 2007/2008


(c) Autumn 2007/2008 (d) Winter 2007/2008


(e) Spring 2008/2009 (f) Summer 2008/2009


(g) Autumn 2008/2009 (h) Winter 2008/2009

Habitat type ● A ● B ● C ● D ● E ● F ● G ● H ● I ● J ● K

Fig. 3.4: nMDS ordination plots of the fish faunal composition at each of the 11 nearshore habitat types sampled in Broke Inlet in each season between spring 2007/2008 and winter 2008/2009.

autumn 2008/2009, *L. presbyteroides* during the former two seasons and *P. olorum* in habitat G in both winter 2007/2008 and autumn 2008/2009.

Ichthyofaunal differences among habitats were lowest in winter 2008/2009 (Global R=0.237), with many pairwise comparisons being insignificant. However, most comparisons involving habitat B and, to a lesser extent, K were significantly different and had notably high R-statistics (*i.e.* > 0.500) in several cases. The distinctness of habitat B was due mainly to higher catches of *F. lateralis* and *A. elongata*, while that of K was largely attributable to the relatively greater abundance of *L. wallacei* and lower abundances of *A. suppositus*. The fish faunas of all other habitats were characterised by similar abundances of *A. elongata* and *L. wallacei* (Appendix 3.1h).

3.3.1.5: Relationships between the fish community and environmental characteristics of nearshore habitat types

RELATE demonstrated that, with the exception of winter 2008/2009, the pattern of relative differences among habitats as defined by their suite of enduring environmental characteristics was significantly correlated with that defined by their average fish faunal composition in each season and year (p=0.001-0.044; Table 3.6a). However, the extents of the significant correlations between those complementary environmental and ichthyofaunal resemblance matrices were moderate (*i.e.* ρ=0.305-0.475), with the greatest matches being detected in spring 2008/2009, followed by winter 2007/2008, *i.e. cf.* the spatial arrangement of habitats in the nMDS ordination plots shown in Fig. 3.5a with those in Figs 3.5e and f, respectively.

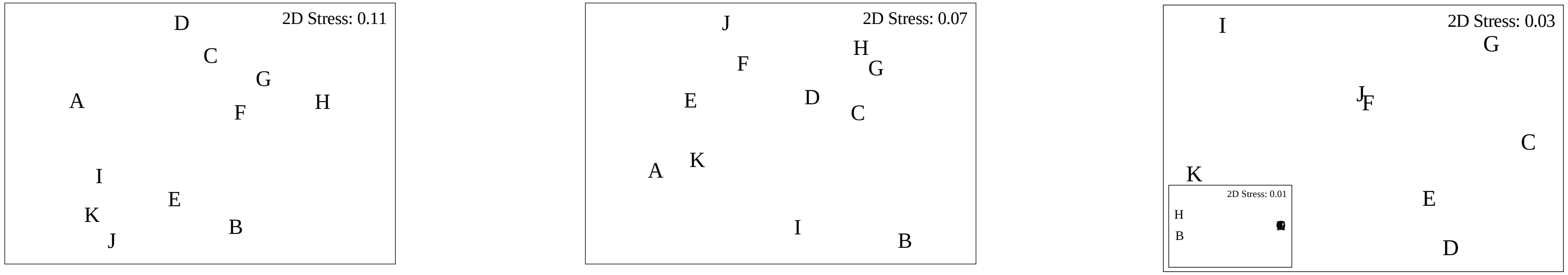
RELATE was then used to determine the extent to which the pattern of the relative differences among nearshore habitats, as defined by their suite of non-enduring environmental characteristics (*i.e.* water physico-chemistry and biomass of detached macrophytes) provided a good surrogate for that exhibited by their fish fauna in each season and year. Significant correlations between those complementary matrices were detected again on all occasions except winter 2008/2009. However, the extent of those significant correlations were often substantially greater than the corresponding values obtained when the enduring environmental data was employed (Table 3.6b).

Table 3.6: Significance level (*p*) and rho statistic (ρ) values for the correlation between a resemblance matrix constructed from the average fish fauna data at each nearshore habitat and complementary matrices constructed from (a) enduring environmental variables (EEVs), (b) the full suite of non-enduring environmental variables (NEVs) and (c) the subset of the non-enduring environmental variables (NEV subset) selected by the BIOENV routine. Analyses were repeated for each season between spring 2007/2008 and winter 2008/2009. Significant correlations are highlighted in bold. Temp = water temperature, Sal = salinity, DO = dissolved oxygen concentration, DMB = detached macrophyte biomass.

	(a) EEVs		**(b) NEVS**		**(c) NEV subset**		
Season/Year	***p***	**ρ**	***p***	**ρ**	***p***	**ρ**	**Variables selected**
Spring 2007/2008	**0.020**	**0.305**	**0.001**	**0.527**	**0.003**	**0.613**	**pH**
Summer 2007/2008	**0.007**	**0.308**	**0.035**	**0.438**	0.073	0.558	
Autumn 2007/2008	**0.022**	**0.338**	**0.043**	**0.318**	**0.009**	**0.586**	**Temp**
Winter 2007/2008	**0.003**	**0.381**	**0.041**	**0.315**	**0.023**	**0.464**	**Sal, DO, DMB**
Spring 2008/2009	**0.001**	**0.475**	**0.001**	**0.786**	**0.001**	**0.819**	**Temp, pH, DMB**
Summer 2008/2009	**0.009**	**0.363**	**0.003**	**0.648**	**0.006**	**0.700**	**DO, pH, DMB**
Autumn 2008/2009	**0.044**	**0.311**	**0.021**	**0.398**	**0.023**	**0.537**	**Temp, Sal, DO, pH**
Winter 2008/2009	0.395	0.032	0.053	0.315	0.244	0.386	

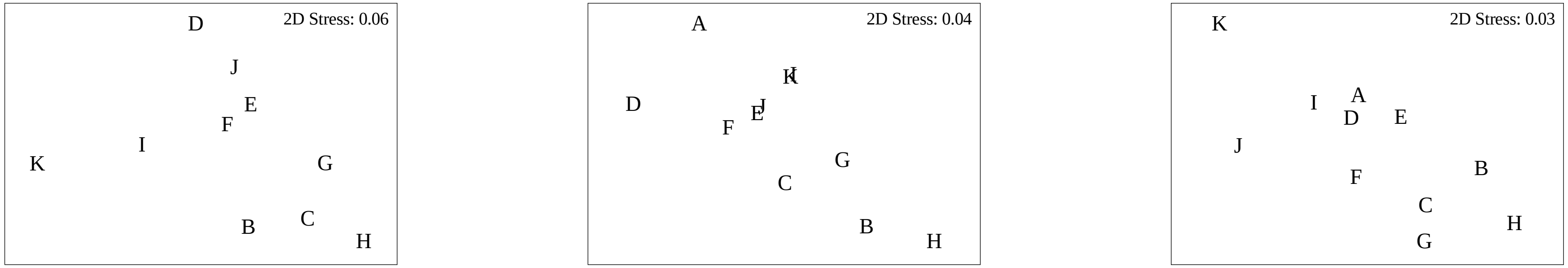
BIOENV was then employed to determine whether a greater correlation could be achieved between the non-enduring environmental and fish faunal matrices by only using a subset of those environmental variables, rather than the full suites as employed in RELATE. The extent of the relationship between these complementary matrices was considerably improved during almost all sampling occasions, and the subsets of NEVs that were responsible in each case are given in Table 3.6c.

The relationships between the patterns among habitats exhibited by the nearshore fish faunas and the magnitude of the NEVs selected by BIOENV in each season and year are illustrated by the nMDS and associated bubble plots shown in Fig. 3.6. The channel habitats B, G and H exhibited slightly elevated levels of pH and water temperature during spring 2007/2008 and autumn 2007/2008 respectively, compared to C and D, which in turn were higher than those values recorded in habitats A, J and K (Figs 3.6a, b). The presence of increasing amounts of macrophyte biomass was accompanied by an increase in salinity diagonally from top left to bottom right in the associated nMDS plots in both winter 2007/2008 and spring 2008/2009, a trend also mirrored in pH and water temperature values in the latter season (Figs 3.6c, e, f, g, h). In both summer and autumn 2008/2009, channel habitats, B, G and H formed a cluster on the right of the associated nMDS plot. This shift in the fish faunal composition was mirrored in the non-enduring environmental variables by an increase in pH and dissolved oxygen concentration in both seasons and macrophyte biomass in


(a) Enduring environmental data

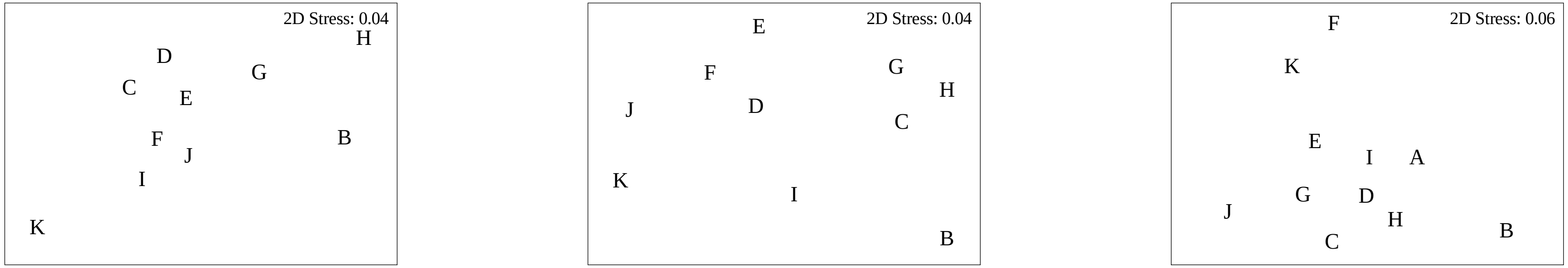
(b) Spring 2007/2008; p=0.020, ρ=0.305

(c) Summer 2007/2008; p=0.007, ρ=0.308


(d) Autumn 2007/2008; p=0.022, ρ=0.338

(e) Winter 2007/2008; p=0.003, ρ=0.381

(f) Spring 2008/2009; p=0.001, ρ=0.475

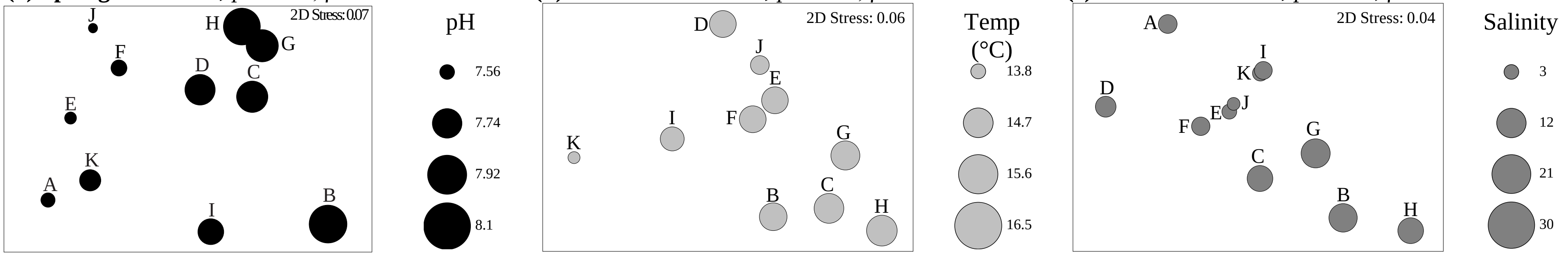

(g) Summer 2008/2009; p=0.009, ρ=0.363

(h) Autumn 2008/2009; p=0.044, ρ=0.311

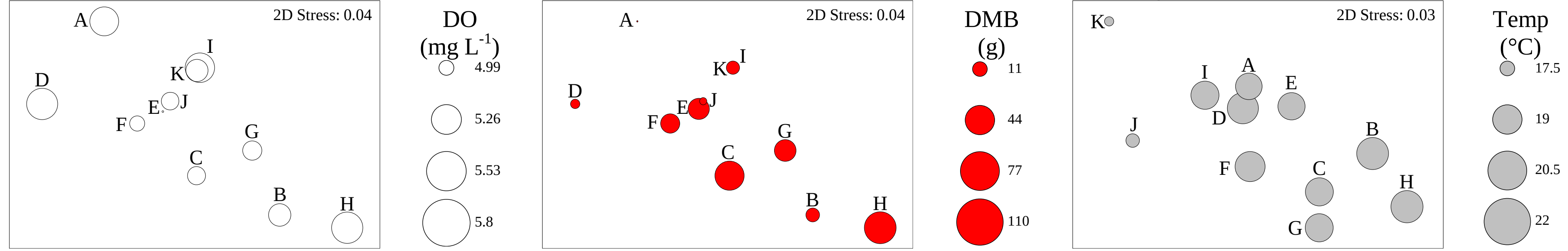
(i) Winter 2008/2009; p=0.390, ρ=0.032

Fig. 3.5: nMDS ordination plots constructed from the averages of the (a) enduring environmental variables and (b-i) the fish faunal composition in each season from spring 2007/2008 to winter 2008/2009 at each nearshore habitat type. The significance levels (p) and rho values (ρ) obtained from RELATE tests are also provided.

(a) Spring 2007/2008; *p*=0.003, ρ=0.613 **(b) Autumn 2007/2008;** *p*=0.009, ρ=0.586 **(c) Winter 2007/2008;** *p*=0.049, ρ=0.464



(d) Winter 2007/2008; *p*=0.049, ρ=0.464 **(e) Winter 2007/2008;** *p*=0.049, ρ=0.464 **(f) Spring 2008/2009;** *p*=0.001, ρ=0.819



(g) Spring 2008/2009; *p*=0.001, ρ=0.819 **(h) Spring 2008/2009;** *p*=0.001, ρ=0.819 **(i) Summer 2008/2009;** *p*=0.005, ρ=0.700

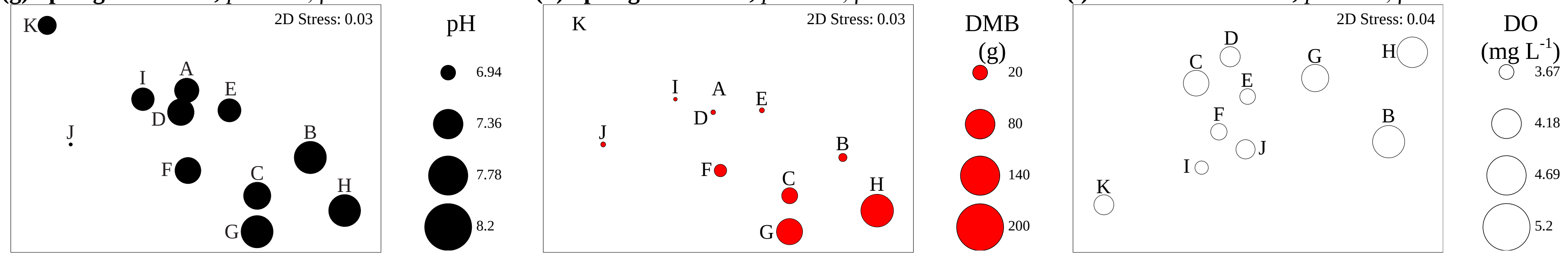
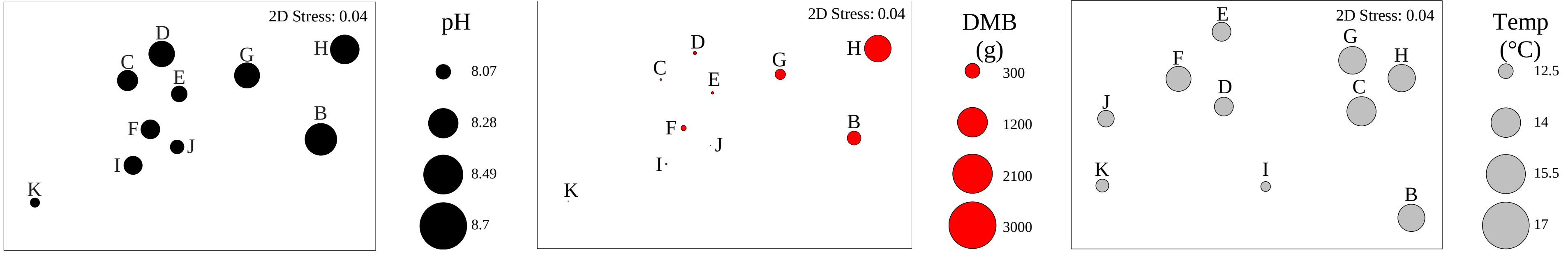
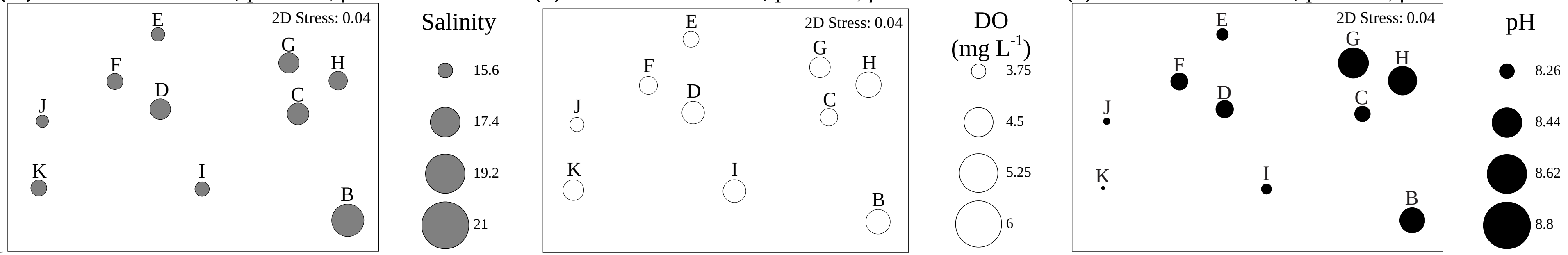


Fig. 3.6: nMDS ordination plots of the average fish faunal composition recorded at each nearshore habitat type in a particular sampling season. The magnitude of the non-enduring environmental variable(s) selected by the BIOENV routine that best match the spatial pattern displayed by the fish faunal composition are displayed for each habitat as circles of proportionate sizes. The significance levels (*p*) and rho values (ρ) obtained from the above BIOENV tests are also provided. Temp = water temperature, DMB = detached macrophyte biomass, DO = dissolved oxygen concentration.


(j) Summer 2008/2009; *p*=0.005, ρ=0.700

(k) Summer 2008/2009; *p*=0.005, ρ=0.700

(l) Autumn 2008/2009; *p*=0.035, ρ=0.537


(m) Autumn 2008/2009; *p*=0.035, ρ=0.537

(n) Autumn 2008/2009; *p*=0.035, ρ=0.537

(o) Autumn 2008/2009; *p*=0.035, ρ=0.537

Fig. 3.6 Continued: nMDS ordination plots of the average fish faunal composition recorded at each nearshore habitat type in a particular sampling season. The magnitude of the non-enduring environmental variable(s) selected by the BIOENV routine that best match the spatial pattern displayed by the fish faunal composition are displayed for each habitat as circles of proportionate sizes. The significance levels (*p*) and rho values (ρ) obtained from the above BIOENV tests are also provided. Temp = water temperature, DMB = detached macrophyte biomass, DO = dissolved oxygen concentration.

the former season and water temperature and salinity in the latter season (Figs 3.6j, k, m, o). Of the remaining habitats moderate pH values were recorded among C, D and F in both seasons whilst habitats I, J and K were distinguished by subtle differences in dissolved oxygen concentrations during both seasons and also water temperature in autumn 2008/2009 (Figs 3.6i, l, n).

3.3.2: Offshore waters

3.3.2.1: Differences in non-enduring environmental variables among offshore habitat types, seasons and years

Four-way PERMANOVA detected significant differences in salinity among habitats, seasons, years and depths and numerous two and three-way interactions between these main effects (p=0.001-0.039). By far the greatest proportion of the variance in this dependent variable was explained by differences between years, followed by those in the year x season interaction (Table 3.7a). In contrast, the depth main effect, and several interactions involving this factor, accounted for by far the least variation in salinity. Mean salinities were generally greater during 2007/2008 than 2008/2009, especially in summer and autumn (Fig. 3.7a). Thus, values during these seasons in 2007/2008 ranged between 29 and 41, whilst those in 2008/2009 ranged only between 14 and 23. Marked differences among habitats were observed during winter and spring of both years, with values of around 15-33 and mainly 16-26 at habitats A and C, respectively, as opposed to 2-12 at B (Fig. 3.7a). However, differences among habitats were not as marked in the remaining seasons, partly accounting for the habitat x season interaction. Variability in the seasonal trends among habitats also contributed to this latter interaction. Thus during 2007/2008 for example, values at habitat A mostly remained between 29 and 33 throughout the year, while those at C and B rose to their maximum of 40 and 41, respectively, in summer and fell to their minima of 16 and 6, respectively, in winter (Fig. 3.7a). Bottom and surface salinities were similar except at habitats A and C in winter 2007/2008 and/or spring 2008/2009, when bottom salinities were considerably greater (Fig. 3.7a).

Table 3.7: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (*p*) from four-way PERMANOVA tests on the data for mean (a) salinity, (b) water temperature and (c) dissolved oxygen concentration and a three-way PERMANOVA on the data for (d) pH recorded at the three offshore habitat types in Broke Inlet sampled in each season between spring 2007/2008 and winter 2008/2009. df = degrees of freedom. Significant results are highlighted in bold.

		(a) Salinity				**(b) Water temperature**				**(c) Dissolved oxygen concentration**			
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***	**MS**	**Pseudo-F**	**COV**	***p***	**MS**	**Pseudo-F**	**COV**	***p***
Year	1	**3755.500**	**232.190**	**90.887**	**0.001**	**50.098**	**30.942**	**1.178**	**0.001**	**188.390**	**380.640**	**4.567**	**0.001**
Season	5	**908.640**	**56.178**	**36.010**	**0.001**	**279.230**	**172.460**	**11.201**	**0.001**	**110.710**	**223.680**	**4.447**	**0.001**
Habitat	2	**1056.000**	**65.289**	**21.455**	**0.001**	**13.560**	**8.375**	**0.246**	**0.001**	0.170	0.343	-0.007	0.684
Depth	1	**325.440**	**20.121**	**4.256**	**0.001**	0.160	0.099	-0.020	0.773	**14.595**	**29.488**	**0.194**	**0.001**
Interactions													
Year x Season	1	**1068.500**	**66.062**	**51.155**	**0.001**	**54.889**	**33.901**	**2.590**	**0.001**	**48.578**	**98.152**	**2.337**	**0.001**
Year x Habitat	2	43.363	2.681	1.983	0.084	**30.809**	**19.029**	**2.128**	**0.001**	**3.042**	**6.147**	**0.186**	**0.005**
Year x Depth	1	26.945	1.666	0.524	0.174	0.045	0.028	-0.077	0.860	0.046	0.093	-0.022	0.774
Season x Habitat	10	**249.300**	**15.413**	**28.204**	**0.001**	**4.092**	**2.527**	**0.299**	**0.013**	**1.989**	**4.019**	**0.181**	**0.001**
Season x Depth	5	**47.563**	**2.941**	**2.533**	**0.013**	1.456	0.899	-0.013	0.481	0.811	1.638	0.025	0.163
Habitat x Depth	2	41.044	2.538	1.026	0.068	3.076	1.900	0.060	0.151	0.394	0.797	-0.004	0.427
Year x Season x Habitat	2	**62.646**	**3.873**	**6.777**	**0.027**	**17.288**	**10.678**	**2.285**	**0.002**	1.077	2.177	0.085	0.115
Year x Season x Depth	1	**69.193**	**4.278**	**5.155**	**0.037**	4.197	2.592	0.251	0.109	0.179	0.361	-0.031	0.564
Year x Habitat x Depth	2	**65.019**	**4.020**	**7.123**	**0.019**	2.958	1.827	0.195	0.159	0.949	1.918	0.066	0.143
Season x Habitat x Depth	10	**31.891**	**1.972**	**3.803**	**0.039**	2.368	1.462	0.181	0.144	0.376	0.759	-0.029	0.689
Year x Season x Habitat x Depth	2	12.728	0.787	-1.005	0.443	0.317	0.196	-0.380	0.807	0.453	0.916	-0.012	0.391
Residual	119	16.174		16.174		1.619		1.619		0.495		0.495	

		(d) pH			
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Year	1	0.058	2.009	0.001	0.171
Season	3	**1.885**	**65.534**	**0.103**	**0.001**
Habitat	2	**0.668**	**23.202**	**0.027**	**0.001**
Interactions					
Year x Season	3	**0.217**	**7.550**	**0.021**	**0.001**
Year x Habitat	2	0.076	2.632	0.004	0.077
Season x Habitat	6	**0.170**	**5.919**	**0.024**	**0.001**
Year x Season x Habitat	6	**0.094**	**3.281**	**0.022**	**0.006**
Residual	48	0.029		0.029	

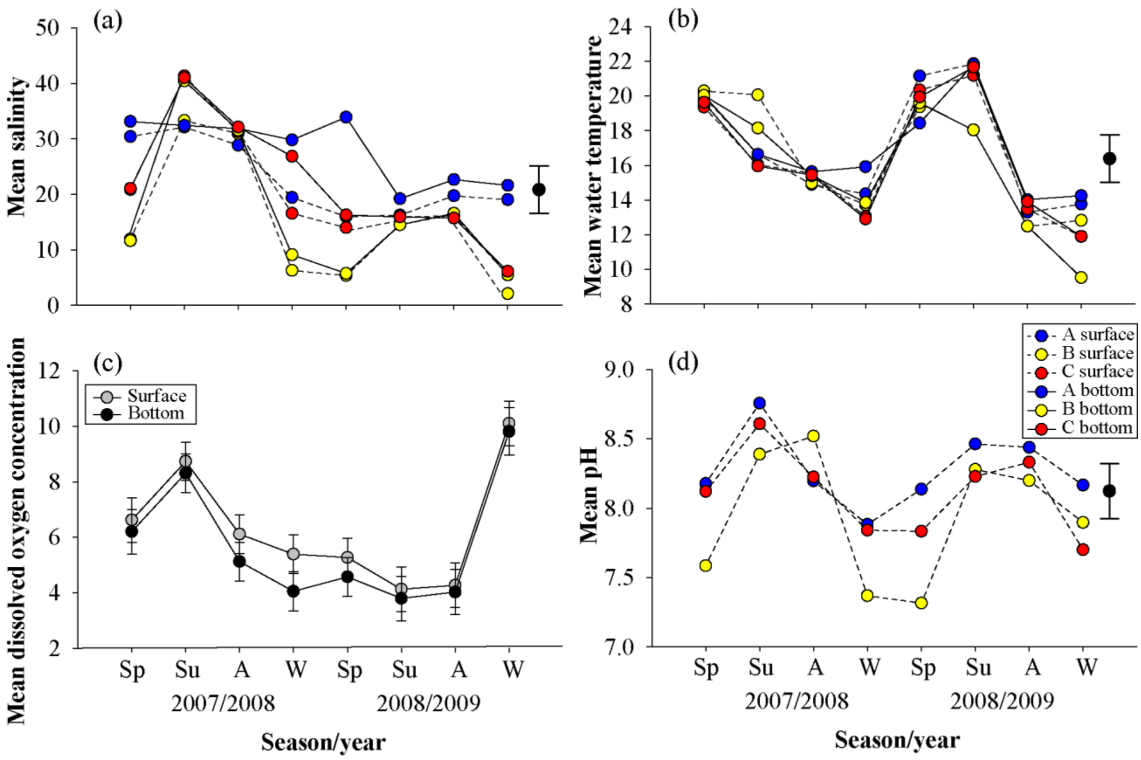


Fig. 3.7: Mean surface and bottom (a) salinity, (b) water temperature (°C), (c) dissolved oxygen concentration (mg L^{-1}) and (d) surface pH at each offshore habitat type in Broke Inlet during each season between spring 2007/2008 and winter 2008/2009 For the sake of clarity, the average ± 95% confidence intervals have been presented for plots a, b and d, and are given on all points on plot c.

Water temperature differed significantly among habitats seasons, years and all interactions involving two or all three of these main effects (p=0.001-0.013; Table 3.7b). Differences among seasons explained the majority of the variance in water temperature, and was more than four times greater than the next most influential term. In contrast, differences among habitats were the least important of the significant terms. Temperatures reached their maximum in spring and/or summer (*ca* 16-22°C) and fell to their minima in autumn and/or winter (*ca* 11-15°C). The significant interaction between habitats, seasons and years reflected differences in the order and range of water temperatures among habitats during the various sampling occasions. For example, water temperature was greatest at habitat B during summer 2007/2008 but the reverse was true in the corresponding season in 2008/2009 (Fig. 3.7b).

Significant differences in dissolved oxygen concentration were detected among years, seasons and depth, with the first two main effects also interacting significantly with both habitat and each other (p=0.001-0.005; Table 3.7c). However, differences between years and seasons, followed by their interaction term, exerted a considerably greater influence on this dependent variable than any other term. Seasonal trends in dissolved oxygen concentration differed considerably between 2007/2008 and 2008/2009, thus explaining the significant season x year interaction. Whereas values reached their maxima in summer and declined to their minima in winter during 2007/2008 (8.7 and 5.4, respectively), they remained relatively constant between spring and autumn (*i.e.* 4.5) then underwent a pronounced increase in winter (10.1) in the second year (Fig. 3.7c). Dissolved oxygen concentrations were always lower in the bottom than surface waters (Fig. 3.7c).

Mean pH in the surface waters differed significantly among both seasons and habitats and all interactions except that between year and habitat (*p*=0.001-0.006; Table 3.7d). The relative importance of seasonal differences was four times that of any other significant main effect or interaction term. The greatest mean pH values at each habitat were recorded during summer or autumn, while the lowest were recorded during spring or winter. Moreover, pH was often the greatest at habitat A and least at habitat B, sometimes markedly so. Inter-annually, higher mean values at each habitat were recorded in 2007/2008 than 2008/2009 during spring and summer, but this was often not the case for autumn and winter. Such findings explain, at least in part, the significant year x season x habitat interaction term for this variable.

3.3.2.2: Fish species mean density and life cycle contribution at each offshore habitat type

Sampling of the three offshore habitat types in Broke Inlet in each season between spring 2007/2008 and winter 2008/2009 yielded 1,050 fish. These fish comprised 31 species and represented 23 families, of which the Kyphosidae, Sillaginidae, Mugilidae, Arripidae, Labridae and Sparidae were represented by multiple species, *i.e.* two or three (Table 3.8). Unlike the fish fauna in the nearshore waters, that of the offshore waters was dominated by marine species, *i.e.* marine estuarine-opportunists and marine stragglers, which represented 84% of the species and 80% of the individuals caught. Habitat A, located in the entrance channel, contained all 31 species recorded in the offshore waters and was by far the most speciose, particularly

Table 3.8: Catch rate (fish 10 h^{-1}; C), standard error (^{SE}), percentage contribution to the overall catch (%), rank by catch rate (R), biomass (g; B), mean length (mm; L) and length range (^{r}) of each fish species recorded at each of the three offshore habitat types in Broke Inlet sampled in each season between spring 2007/2008 and winter 2008/2009. Abundant species at each habitat type (*i.e.* those that contribute ≥ 5% to the catch) are highlighted in grey. The life cycle category (LC) of each species is also provided (EM = estuarine and marine, MEO = marine estuarine-opportunists and MS = marine straggler). The species richness, mean total catch rates and adjusted number of individuals (*i.e.* after the number of individuals in each sample had been adjusted to caught in ten hours) are given for each habitat type. Species ranked according to their total catch rate.

		A					**B**					**C**				
Species	**LC**	C^{SE}	%	R	B^{SE}	L^{r}	C^{SE}	%	R	B^{SE}	L^{r}	C^{SE}	%	R	B^{SE}	L^{r}
Arripis georgianus	MEO	$3.98^{2.00}$	19.93	1	$1120.47^{623.82}$	$255^{(194-312)}$	$0.73^{0.54}$	10.61	3	$241.16^{196.15}$	$267^{(216-310)}$	$3.37^{0.91}$	29.01	1	$774.82^{247.63}$	$251^{(207-295)}$
Mugil cephalus	MEO	$2.75^{0.92}$	13.35	2	$1072.41^{342.18}$	$310^{(157-459)}$	$2.74^{0.87}$	41.34	1	$1322.65^{379.65}$	$299^{(118-459)}$	$1.06^{0.30}$	8.95	3	$457.17^{180.03}$	$309^{(158-432)}$
Engraulis australis	EM	$1.50^{0.97}$	6.95	4	$24.97^{18.27}$	$123^{(94-152)}$	$0.66^{0.42}$	10.06	4	$5.81^{4.85}$	$111^{(82-130)}$	$1.87^{0.68}$	15.43	2	$31.94^{13.60}$	$119^{(75-176)}$
Aldrichetta forsteri	MEO	$1.32^{0.36}$	6.76	7	$540.5^{156.74}$	$270^{(140-452)}$	$1.31^{0.56}$	19.55	2	$467.96^{206.31}$	$315^{(238-403)}$	$1.04^{0.34}$	8.64	4	$292.52^{85.04}$	$221^{(172-364)}$
Rhabdosargus sarba	MEO	$1.42^{0.51}$	6.95	4	$747.48^{332.53}$	$271^{(82-321)}$	$0.12^{0.09}$	1.68	7	$82.26^{67.45}$	$333^{(261-387)}$	$0.94^{0.40}$	7.41	6	$574.01^{212.43}$	$296^{(207-415)}$
Ammotretis rostratus	EM	$0.91^{0.41}$	4.57	9	$167.35^{93.95}$	$250^{(86-501)}$	$0.50^{0.21}$	7.82	5	$85.59^{35.76}$	$206^{(145-266)}$	$0.91^{0.19}$	7.72	5	$164.82^{46.70}$	$194^{(74-273)}$
Pseudocaranx dentex	MEO	$1.44^{0.76}$	6.95	4	$389.37^{227.38}$	$256^{(185-363)}$						$0.54^{0.28}$	4.32	8	$205.91^{98.21}$	$267^{(162-383)}$
Pagrus auratus	MEO	$1.59^{0.57}$	8.04	3	$665.88^{325.41}$	$283^{(152-410)}$						$0.15^{0.09}$	1.23	13	$58.12^{41.90}$	$269^{(230-343)}$
Arripis truttaceus	MEO	$1.06^{0.48}$	4.94	8	$765.75^{393.47}$	$375^{(304-430)}$	$0.08^{0.08}$	1.12	8	$98.52^{98.52}$	$450^{(442-457)}$	$0.34^{0.30}$	3.09	9	$12.58^{12.58}$	$283^{(283-283)}$
Sillaginodes punctatus	MEO	$0.47^{0.20}$	2.38	12	$102.44^{64.57}$	$325^{(244-383)}$	$0.04^{0.04}$	0.56	9	$13.97^{13.97}$	$376^{(376-376)}$	$0.80^{0.55}$	6.17	7	$236.22^{133.85}$	$321^{(240-410)}$
Gonorynchus greyi	MEO	$0.82^{0.40}$	4.20	10	$66.39^{39.75}$	$244^{(143-293)}$						$0.18^{0.09}$	1.54	11	$4.82^{4.46}$	$220^{(112-259)}$
Hyporhamphus melanochir	EM	$0.14^{0.11}$	0.73	21	$4.97^{4.97}$	$345^{(345-345)}$	$0.43^{0.43}$	7.26	6	$52.64^{38..12}$	$328^{(297-371)}$	$0.17^{0.07}$	1.54	11	$25.83^{19.12}$	$350^{(326-396)}$
Enoplosus armatus	MS	$0.63^{0.34}$	3.29	11	$39.39^{19.84}$	$139^{(85-204)}$										
Pomatomus saltatrix	MEO	$0.19^{0.13}$	0.91	18	$120.02^{97.91}$	$357^{(264-420)}$						$0.38^{0.27}$	3.09	9	$371.34^{263.56}$	$407^{(257-680)}$
Sillago bassensis	MS	$0.35^{0.27}$	1.65	13	$26.28^{19.93}$	$195^{(179-219)}$										
Cnidoglanis macrocephalus	EM	$0.24^{0.11}$	1.10	15	$220.56^{122.47}$	$516^{(335-635)}$						$0.04^{0.04}$	0.31	16	$16.23^{16.23}$	$431^{(431)}$
Platycephalus speculator	EM	$0.26^{0.12}$	1.28	14	$64.65^{33.58}$	$302^{(202-425)}$										
Pseudorhombus jenynsii	MEO	$0.23^{0.14}$	1.10	15	$100.72^{59.68}$	$314^{(283-349)}$						$0.04^{0.04}$	0.31	16	$12.29^{12.92}$	$321^{(321)}$
Achoerodus gouldii	MS	$0.22^{0.11}$	1.10	15	$49.94^{24.72}$	$192^{(120-240)}$										
Sillago schomburgkii	MEO	$0.19^{0.10}$	0.91	18	$17.38^{11.87}$	$226^{(206-244)}$										
Girella zebra	MS	$0.19^{0.11}$	0.91	18	$115.39^{72.01}$	$267^{(253-277)}$										
Mustelus antarcticus	MS	$0.04^{0.04}$	0.18	23	$556.82^{556.82}$	$1410^{1410-1410)}$						$0.12^{0.09}$	0.93	14	$1560.22^{1148.16}$	$1343^{(1190-1480)}$
Chelidonichthys kumu	MS	$0.04^{0.04}$	0.18	23	$6.54^{06..54}$	$362^{(362)}$										
Schuettea woodwardi	MS	$0.05^{0.05}$	0.18	23	$5.40^{5.40}$	$196^{(196-196)}$										
Scorpis georgiana	MS	$0.08^{0.06}$	0.37	22	$23.74^{16.45}$	$243^{(237-249)}$										
Notolabrus parilus	MS	$0.04^{0.04}$	0.18	23	$2.10^{2.10}$	$143^{(143)}$						$0.05^{0.05}$	0.31	16	$1.61^{1.61}$	$132^{(132)}$
Myliobatis australis	MS	$0.05^{0.05}$	0.18	23	$181.82^{181.82}$	$800^{(800)}$										
Lotella rhacina	MS	$0.04^{0.04}$	0.18	23	$5.87^{5.817}$	$307^{(307-307)}$										
Tilodon sexfasciatum	MS	$0.04^{0.04}$	0.18	23	$7.84^{7.84}$	$194^{(194-194)}$										
Cynoglossus broadhursti	MS	$0.07^{0.05}$	0.18	23	$0.68^{0.68}$	$136^{(136)}$										
Eubalichthys bucephalus	MS	$0.07^{0.05}$	0.18	23	$17.30^{17.30}$	$297^{(297)}$										
Total number of species		**31**					**9**					**17**				
Mean catch rate 10 h^{-1}		**20**					**7**					**12**				
Number of samples		**24**					**24**					**24**				
Adjusted number of individuals		**480**					**168**					**288**				
Actual number of individuals		**547**					**179**					**324**				

compared to habitat B in Shannon Basin, at which only nine species were recorded. The same trend was also observed for overall fish abundance, with *ca* 1.5 and 2.5 times as many fish caught at habitat A than C and B, respectively. Most of the catch at habitat A comprised the marine estuarine-opportunists Australian Herring *Arripis georgianus* (20%), the mugilids *Mugil cephalus* and *Aldrichetta forsteri* (13 and 7%, respectively) and, to a lesser extent, the sparids *Rhabdosargus sarba* and *Pagrus auratus*, (7 and 8%, respectively), and the Silver Trevally *Pseudocaranx dentex* (7%). The only relatively abundant species representing a different life cycle guild at this habitat were the Australian Anchovy *Engraulis australis* (7%) and the Longsnout Flounder *Ammotretis rostratus* (5%), both of which are estuarine and marine species (Table 3.8). Although 14 marine straggler species were caught at habitat A, they collectively comprised only *ca* 5% of the catch.

Four of the most abundant species at offshore habitats B and C were also abundant at A, although their rank orders differed in each case. These included the marine estuarine-opportunists, *A. georgianus*, *M. cephalus* and *A. forsteri*, and the estuarine and marine species, *E. australis*, each of which represented *ca* 10-41% and 9-29% of the individuals caught at habitats B and C, respectively. *Ammotretis rostratus* was also relatively abundant at habitats B and C, as were *H. melanochir* and *Sillaginodes punctatus*. However, habitat C harboured a far more diverse and abundant fauna compared to B, which was only represented by nine species (Table 3.8).

3.3.2.3: Differences in species richness, catch rates and diversity among offshore habitat types, seasons and years

Three-way crossed PERMANOVA identified significant differences in the mean number of species among both habitats and seasons (*p*=0.001-0.007), with the former of these main effects having a substantially greater influence on this dependent variable (Table 3.9a). Mean species richness was highest at habitat A (6) and lowest at habitat B (1.5; Fig. 3.8a), and while values were similar during spring, summer and autumn (*ca* 4.5), they were markedly lower during winter (3; Fig. 3.8b).

Table 3.9: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (*p*) from PERMANOVA tests on the data on the mean (a) species richness, (b) catch rate and (c) Shannon-Wiener diversity recorded at the three offshore habitat types in Broke Inlet sampled in each season between spring 2007/2008 and winter 2008/2009. df = degrees of freedom. Significant results are highlighted in bold.

	(a) Species richness				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Year	1	0.000	0.001	-0.002	0.977
Season	3	**0.386**	**5.172**	**0.019**	**0.007**
Habitat	2	**1.370**	**18.351**	**0.061**	**0.001**
Interactions					
Year x Season	3	0.182	2.433	0.013	0.059
Year x Habitat	2	0.085	1.144	0.001	0.343
Season x Habitat	6	0.136	1.815	0.011	0.110
Year x Season x Habitat	5	0.085	1.134	0.003	0.366
Residual	49	0.075		0.075	

	(b) Catch rate				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Year	1	**0.979**	**4.990**	**0.024**	**0.024**
Season	3	**0.667**	**3.401**	**0.029**	**0.021**
Habitat	2	**1.757**	**8.961**	**0.073**	**0.001**
Interactions					
Year x Season	3	0.313	1.596	0.014	0.192
Year x Habitat	2	0.021	0.108	-0.016	0.902
Season x Habitat	6	0.436	2.222	0.043	0.059
Year x Season x Habitat	5	0.410	2.093	0.070	0.073
Residual	49	0.196		0.196	

	(c) Shannon-Wiener diversity				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Year	1	0.152	1.242	0.001	0.311
Season	3	0.327	2.679	0.012	0.052
Habitat	2	**1.970**	**16.145**	**0.086**	**0.001**
Interactions					
Year x Season	3	**0.486**	**3.987**	**0.044**	**0.020**
Year x Habitat	2	0.245	2.011	0.012	0.144
Season x Habitat	6	0.137	1.125	0.003	0.342
Year x Season x Habitat	5	0.223	1.828	0.033	0.124
Residual	49	0.122		0.122	

Catch rates differed significantly among habitats, seasons and years (*p*=0.001-0.024), with the former main effect again being the most influential (Table 3.9b). Mean catch rates among habitats followed a similar trend to mean species richness, with the highest values occurring at habitat A (1.7 fish 1h^{-1}) and lowest at B (0.5 fish 1h^{-1}; Fig. 3.8c). Catch rates during 2007/2008 were greatest in spring and summer (1.5 fish 1h^{-1}) and least in autumn and winter (1.0 fish 1h^{-1}), while in 2008/2009 catch rates increased between spring (1.7 fish 1h^{-1}) and autumn (3 fish 1h^{-1}), and fell sharply in winter (0.5 fish 1h^{-1}; Fig. 3.8c). Greater values were detected during 2007/2008 than 2008/2009 (0.8 *vs* 1.5 fish 1h^{-1}).

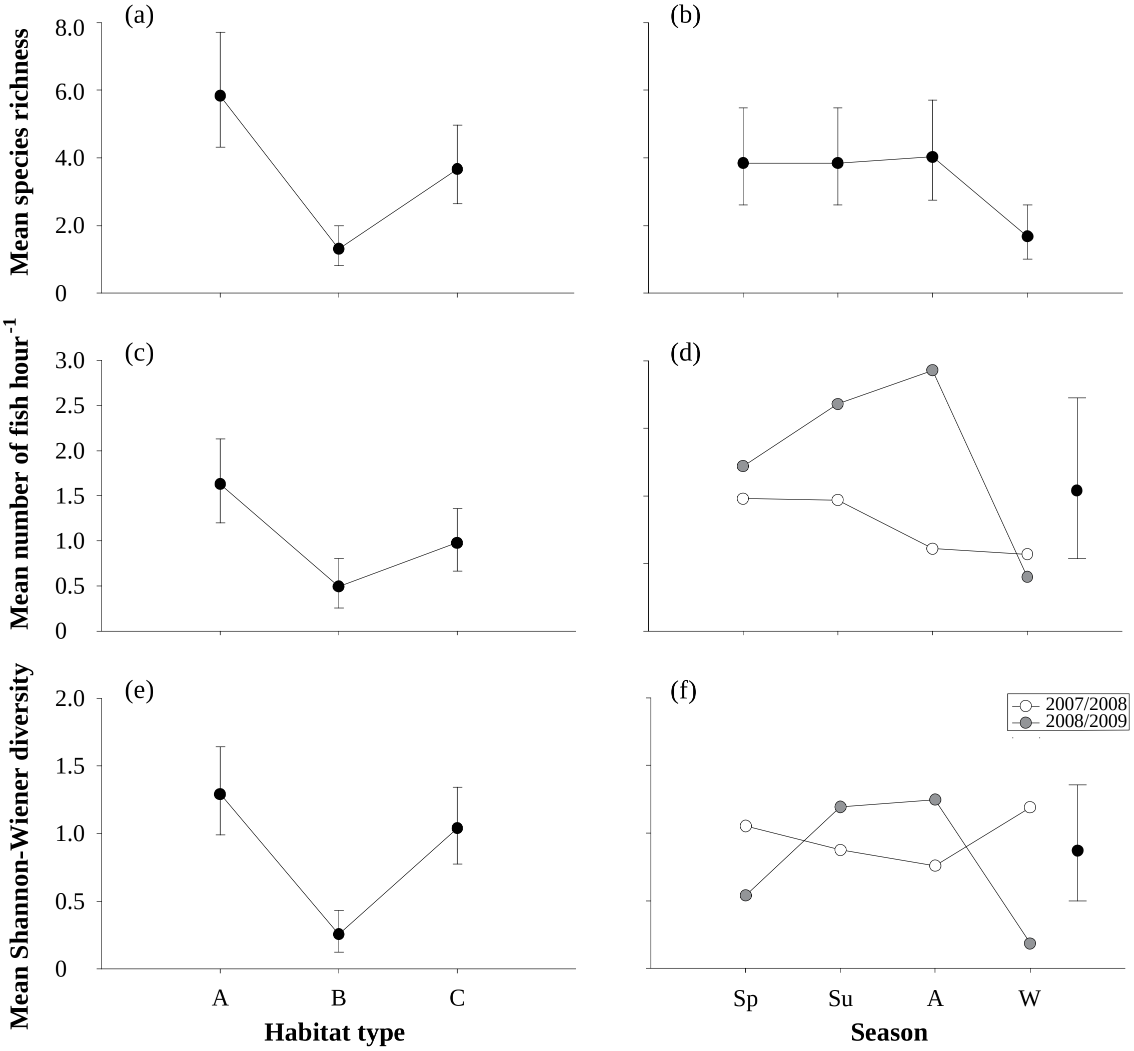


Fig. 3.8: Mean (a, b) species richness, (c, d) catch rates (fish per h^{-1}) and (e, f) Shannon-Wiener diversity of the offshore fish fauna among habitats, seasons and/or years. Error bars represent the ± 95% confidence intervals, which have been averaged on plots d and f for clarity.

Shannon-Wiener diversity differed significantly among habitats and the year x season interaction (p=0.001-0.020), with the former term being the greatest (Table 3.9c). Diversity was again highest at habitat A (1.3) and lowest at B (0.2; Fig. 2.8e). The significant interaction was due largely to the opposing seasonal trends exhibited by diversity in each of the two years. Thus, whereas it was highest in spring and winter 2007/2008 and lowest in summer and autumn, the reverse was true in 2008/2009 (Fig. 2.8f).

3.3.2.4: Differences in fish assemblage composition among offshore habitat types

The species composition of the fish assemblages in the offshore waters of Broke Inlet were shown by PERMANOVA to differ significantly among habitats, seasons and years, as well as with the year x season and season x habitat interactions (*p*=0.001-0.007; Table 3.10). Differences among habitats accounted for the majority of

Table 3.10: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (*p*) from a three-way PERMANOVA of the offshore ichthyofaunal composition recorded at the three offshore habitat types in Broke Inlet sampled in each season between spring 2007 and winter 2009. df = degrees of freedom. Significant results are highlighted in bold.

	Offshore fish assemblage composition				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Year	1	**7620.900**	**3.126**	**143.980**	**0.001**
Season	3	**6619.500**	**2.716**	**232.320**	**0.001**
Habitat	2	**9523.500**	**3.907**	**295.250**	**0.001**
Interactions					
Year x Season	3	**4645.200**	**1.906**	**245.280**	**0.007**
Year x Habitat	2	3363.100	1.380	77.120	0.135
Season x Habitat	6	**3901.200**	**1.600**	**243.930**	**0.006**
Year x Season x Habitat	6	3292.300	1.351	284.870	0.064
Residual	48	2437.700		2437.700	

the variation in ichthyofaunal composition, while those between years were the least influential of the significant effects. Given that habitat and season were by far the most influential main effects and the significant habitat x season interaction, the following analyses to further investigate habitat differences in offshore fish faunal composition were carried out separately for each season, with the data pooled over both years.

One-way ANOSIM tests detected significant differences in ichthyofaunal composition among offshore habitats only during spring and autumn (*p*=0.004 and 0.005, respectively), and the overall extent of those differences was relatively low (Global *R*=0.231-0.313; Table 3.11). The greatest differences were detected between habitats A and B in both of the above seasons (pairwise *R*=0.426 and 0.563, respectively). During spring, the composition of the fish fauna at habitat A, which was characterised by the arripids *A. georgianus* and *A. truttaceus* (Appendix 3.2a), was relatively consistent among replicate samples, as reflected by the tight group formed by these samples on the nMDS plot (Fig. 3.9a). However, the composition of the fish fauna at habitat B, which was characterised by the mugilids *A. forsteri* and *M. cephalus* (Appendix 3.2a), was far more variable, as reflected by the highly dispersed nature of the replicate samples on the nMDS plot (Fig. 3.9a). In autumn, samples from habitats A and B were similarly dispersed but tended to occupy opposite sides of the nMDS plot (Fig. 3.9c). The differences between these two habitats were caused by greater abundances of *A. georgianus, P. auratus* and *P. dentex* in A and greater abundances of *M. cephalus* in B (Appendix 3.2b).

Table 3.11: Global *R*-statistic and/or significance level (*p*) values derived from one-way ANOSIM tests of offshore fish faunal composition among the three habitat types, carried out separately for each season. Insignificant pairwise comparisons are highlighted in grey.

(a) Spring; *p*=0.004, Global *R*=0.231

	A	B
B	0.426	
C	0.154	0.113

(b) Summer; *p*=0.168, Global *R*=0.070

	A	B
B	0.164	
C	0.004	0.061

(c) Autumn; *p*=0.005, Global *R*=0.313

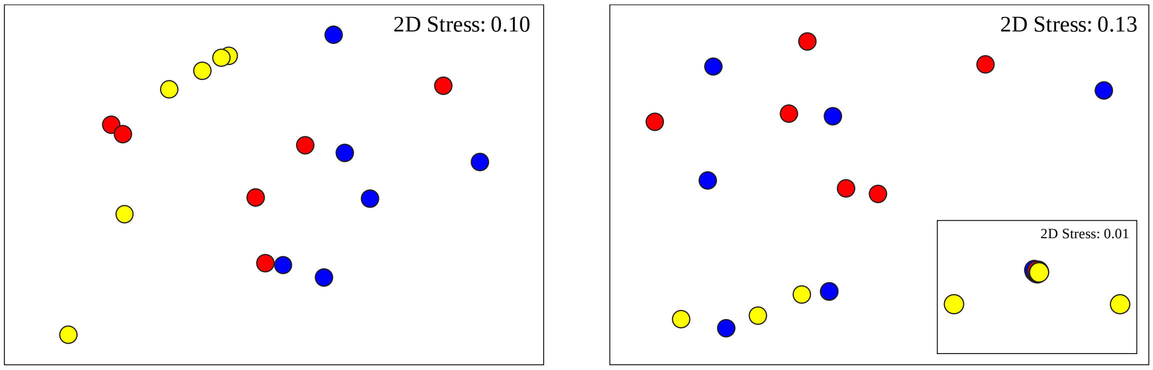
	A	B
B	0.563	
C	0.085	0.250

(d) Winter; *p*=0.104, Global *R*=0.104

	A	B
B	0.028	
C	-0.037	0.286

(a) Spring **(b) Summer**

(c) Autumn **(d) Winter**



Habitat type ● A ● B ● C

Fig. 3.9: nMDS ordination plots of the fish faunal composition at each of the three offshore habitat types in each season.

3.3.2.5: Relationships between the fish community and environmental characteristics of offshore habitat types

The RELATE procedure was employed to test the extent to which the pattern of relative differences among offshore sites, as defined by their suite of enduring environmental characteristics, was correlated with that defined by their offshore fish faunal composition in each season. Note that, as there were only three offshore habitats, these tests were carried out using the averages recorded at each site rather than habitat in order to improve statistical power. A significant correlation between these complementary matrices was detected only during autumn, and the extent of that correlation was moderate (ρ=0.416; Table 3.12a; Fig. 3.10).

Table 3.12: Significance level (*p*) and rho statistic (ρ) values for the correlation between a resemblance matrix constructed from the average fish fauna data at each offshore site and complementary matrices constructed from (a) enduring environmental variables (EEVs), (b) the full suite of non-enduring environmental variables (NEVs) and (c) the subset of the non-enduring environmental variables (NEV subset) selected by the BIOENV routine. Analyses were repeated for each calendar season. Significant correlations are highlighted in bold. DO = dissolved oxygen concentration.

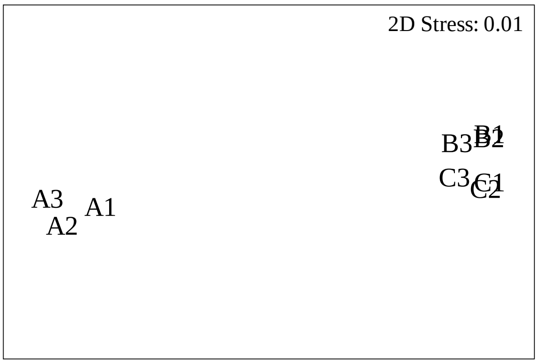
	(a) EEVs		**(b) NEVs**		**(c) NEV subset**		
Season	***p***	**ρ**	***p***	**P**	***p***	**ρ**	**Variables selected**
Spring	0.214	0.126	**0.024**	**0.389**	**0.011**	**0.534**	**Surface salinity**
Summer	0.332	0.066	0.516	-0.020	0.870	0.175	
Autumn	**0.016**	**0.416**	**0.022**	**0.362**	**0.049**	**0.465**	**Surface DO**
Winter	0.367	0.047	**0.046**	**0.337**	**0.004**	**0.530**	**pH**

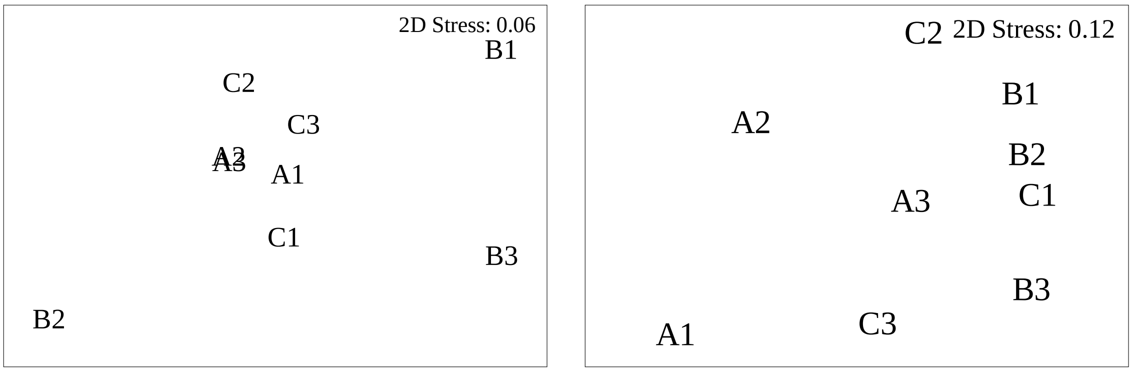
RELATE was then used to correlate the spatial patterns in the complementary fish faunal and non-enduring environmental, *i.e.* water physico-chemical, matrices constructed from the average data recorded at the various offshore sites in each season. These tests detected significant matches in all seasons except summer, with the extent of those matches being moderate (Table 3.12b). BIOENV was used to test whether a greater correlation could be obtained between complementary matrices by only employing particular subsets of the water physico-chemical variables, a significant match and greater correlation was obtained during spring, autumn and winter (Table 3.12).

The relationships between the pattern of differences among habitat as exhibited by the offshore fish faunas and the magnitude of the NEVs selected by BIOENV in each season are illustrated by nMDS ordinations and associated bubble plots (Fig. 3.11). On the ordination plot for spring sites representing habitat B exhibited markedly lower surface salinities compared to those representing habitats A and C (Fig. 3.11a). Surface dissolved oxygen and pH levels during autumn and winter, respectively, were highest in sites representing habitat A and lowest at those representing habitat B (Figs 3.11b, c).

However, the overall ranges of these last two variables among habitats were low, for example, pH only ranged from 7.5-8.2 (Fig. 3.11c).

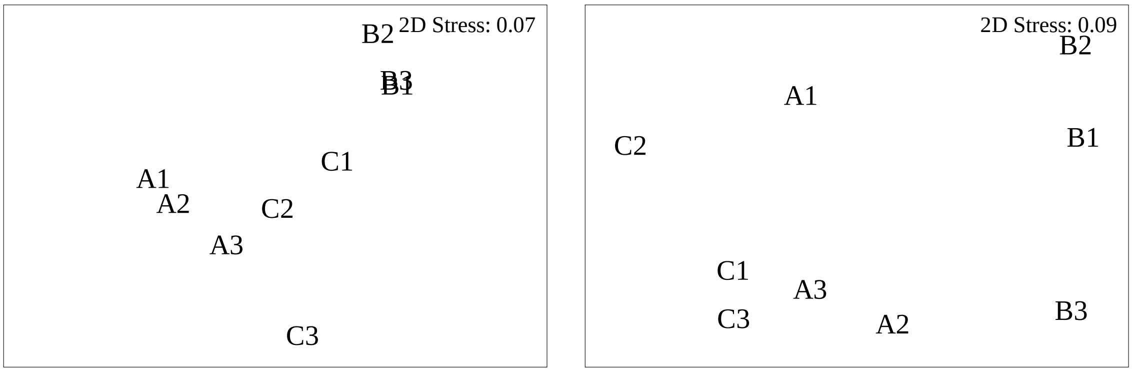
(a) Enduring environmental data





(b) Spring; *p*=0.214, ρ=0.126

(c) Summer; *p*=0.332, ρ=0.066

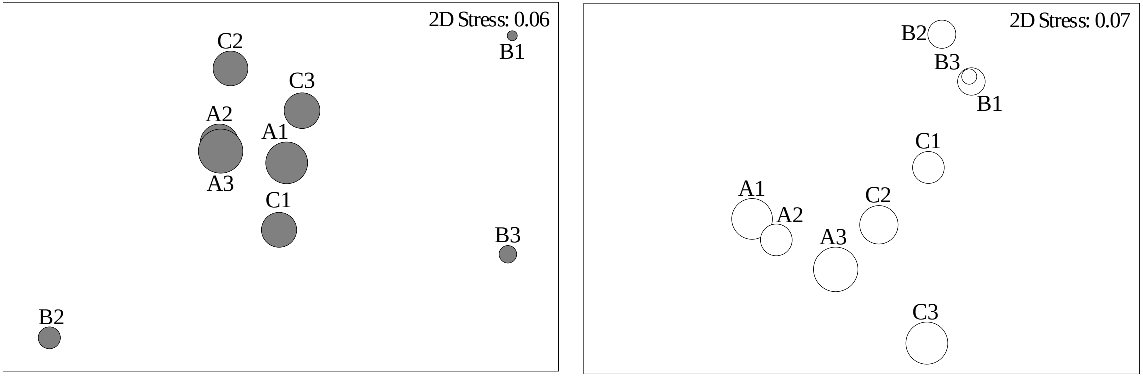


(d) Autumn; *p*=0.016, ρ=0.416

(e) Winter; *p*=0.367, ρ=0.047

Fig. 3.10: nMDS ordination plots constructed from the averages of the (a) enduring environmental variables and (b-e) the fish faunal composition in each season at each offshore site. The significance levels (*p*) and rho values (ρ) obtained from RELATE tests are also provided.

(a) Spring; *p*=0.011, ρ=0.534 **(b) Autumn;** *p*=0.049, ρ=0.465



(c) Winter; *p*=0.004, ρ=0.530

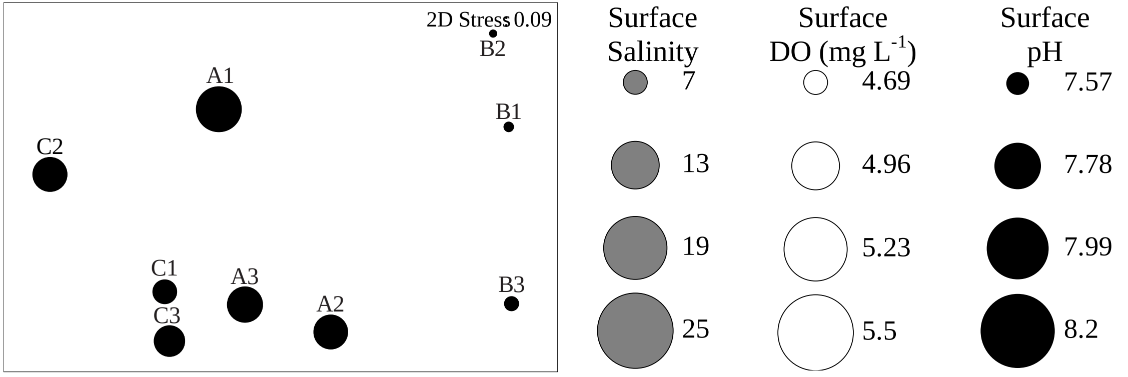


Fig. 3.11: nMDS ordination plots of the average fish faunal composition recorded at each offshore site in a particular season. The magnitude of the non-enduring environmental variable(s) selected by the BIOENV routine are displayed for each site as circles of proportionate sizes. The significance levels (*p*) and rho values (ρ) obtained from the above BIOENV tests are also provided. DO = dissolved oxygen concentration.

3.4: Discussion

3.4.1: Nearshore fish community

3.4.1.1: Nearshore fish assemblage characteristics

Analysis of the nearshore fish community sampled seasonally at 11 habitat types throughout Broke Inlet for two consecutive years demonstrated that these fauna were heavily dominated by a suite of six species, namely the atherinids *Atherinosoma elongata, Leptatherina wallacei* and *Leptatherina presbyteroides* and the gobiids *Afurcagobius suppositus*, *Pseudogobius olorum* and *Favonigobius lateralis*. These species collectively represented between 99 and 100% of the total catch at each habitat. Such findings parallel those in a recent study by Hoeksema *et al.* (2009) in the nearshore waters of Broke Inlet, where these species represented 99.7% of all fish caught. Moreover, the above species are also typically abundant in other estuaries along the south coast of Western Australia, irrespective of their degree of connectivity to the ocean (Potter *et al.*, 1993; Potter & Hyndes, 1994; Hoeksema *et al.*, 2009).

Each of the above atherinid and gobiid species are able to complete their life cycle within the estuary (Prince & Potter, 1983; Gill *et al.*, 1996). It is theorised that such a life history strategy could have developed as a response to estuaries in southern Australia being cut off at intervals from the ocean by the formation of sand bars, thus temporarily landlocking marine species and selecting those best able to adapt to estuarine conditions (Potter *et al.*, 1986b; Beheregaray *et al.*, 2000). Atherinids, for example, show a high degree of intra-specific morphological variability that is thought to be caused by the highly variable physico-chemical conditions of the estuarine environment, which has selected for generalist genotypes that are able to adjust their morphology, physiology and behaviour depending on environmental conditions (Bamber & Henderson, 1988; Beheregaray *et al.*, 2002). This plasticity has enabled *A. elongata,* the most numerous fish species in Broke Inlet, to become highly euryhaline and able to tolerate salinities from < 5-135 (Prince *et al.*, 1982a; Hoeksema *et al.*, 2006), and thus successfully colonise estuaries which undergo pronounced changes in salinity (Hoeksema *et al.*, 2006; Chuwen *et al.*, 2009a).

Atherinid and gobiid species in south-western Australian estuaries have also developed a number of methods to maximise reproductive success in these environments. These include a protracted spawning period during times of relative environmental stability (Prince & Potter, 1983; 1992b; Neira & Potter, 1994; Gill *et al.*, 1996), demersal and adhesive eggs (Prince & Potter, 1983; White *et al.*, 1984; Potter & Hyndes, 1994) and, in the case of atherinids, well developed larvae upon hatching (Watts, 1991). These characteristics presumably developed as a result of selection pressures favouring those species which are able to complete their life cycle in these estuaries (Potter *et al.*, 1986b). However, such characteristics are not unique to Australian estuarine species, as the reproductive biology of the Brazilian atherinid *Odontesthes argentinensis* differs between populations inhabiting the Patos Lagoon and nearshore marine waters in terms of their spawning period, site selection and egg morphology (Bemvenuti, 1987; Phonlor & Vinagre, 1989; Phonlor & Cousin, 1997).

In order for the aforementioned atherinid and gobiid species to collectively dominate the ichthyofaunas of many south-western Australian estuaries, they have also evolved to partition resources within these environments. Thus, for example, *L. presbyteroides* and *F. lateralis* are typically most abundant in areas of bare sand and salinities of around 35, *L. wallacei* and *A. suppositus* have a tendency to occur in areas with dense seagrass beds and reduced salinities (sometimes < 5), *A. elongata,* usually prefer seagrass beds with intermediate salinities and *P. olorum* patchy seagrass areas with a silty substrate (Prince *et al.*, 1982a; Gill & Potter, 1993; Humphries & Potter, 1993; Gill & Humphries, 1995). In addition to differences in “preferred” habitat, these atherinid and gobiid species each possess different jaw morphology (Prince *et al.*, 1982b; Gill & Miller, 1990; Gill, 1993), thus enabling them to specialise in the types of prey they consume (Humphries, 1993). Differences in the diets of these species within south-western Australian estuaries have been shown to support such morphological differences (Gaughan, 1992; Gill & Potter, 1993; Humphries & Potter, 1993).

The relative contribution of marine species to the nearshore ichthyofauna of Broke Inlet was minimal, *i.e.* < 1% of the total catch. Such findings are obviously closely related to the seasonally-open nature of Broke Inlet, thereby reducing the opportunity for marine species to potentially migrate into the estuary. In contrast, the nearshore fish fauna of Oyster Harbour, a permanently-open estuary located *ca* 150 km east of Broke Inlet, has a far larger proportion of marine species (Hoeksema *et al.*, 2009). Secondly, the spawning time of many of the marine estuarine-opportunist species that occur along the south coast of Western Australia is at a time of year when the bar at the mouth of Broke Inlet it typically closed (Malcolm, 1960; Chubb *et al.*, 1981; Hyndes *et al.*, 1998; Fairclough *et al.*, 2000a, b). However, even in permanently-open estuaries in the region, such as the Swan-Canning and Walpole-Nornalup estuaries, the recruitment of larvae from marine species into these estuaries is low, contributing only *ca* 1% to the total ichthyoplankton in those systems (Gaughan *et al.*, 1990; Neira & Potter, 1994). Similar trends have also been reported in seasonally-open estuaries such as the nearby Wilson Inlet and the Hopkins River Estuary in Victoria (Neira & Potter, 1992a; Newton, 1996). Nevertheless, the recruitment of marine species must occur at some stage of their life cycle, as marine species dominate the offshore waters of these systems, including Broke Inlet (see subsection 3.4.2.1). It has therefore been suggested that the majority of the individuals are of a substantial size (*i.e.* > 100 mm) upon entering estuaries on the south coast of Western Australia and thus do not utilise the nearshore waters of these systems as a nursery area to the same extent as in other regions (Chuwen *et al.*, 2009b; Hoeksema *et al.*, 2009).

3.4.1.2: Differences in fish assemblages among nearshore habitat types

Significant differences in ichthyofaunal composition were detected among the various nearshore habitats within Broke Inlet during each of the eight sampling seasons between spring 2007/2008 and winter 2008/2009. However, the extent of those spatial differences were low to moderate. Such findings reflect the fact that, as described in subsection 3.4.1.1, the nearshore ichthyofauna of this system is dominated by a suite of six estuarine species that, despite exhibiting preferences for particular environmental conditions, are able to tolerate a wide range of those conditions.

During all sampling occasions, the most distinct ichthyofaunal assemblages were recorded at one or more of the habitats located in the entrance channel, *i.e.* B, G and/or H. These habitats also had highly distinct enduring environmental characteristics from many of those located in the estuary basin, such as small fetches, narrow wave shoaling margins, steeply sloping substrates and, in the case of habitats H and G, dense and extensive *Ruppia megacarpa* beds. The distinctiveness of the fish assemblages at these channel habitats was due firstly to the far higher abundances of atherinids and gobiids compared to basin habitats, and secondly to the presence of a relatively large suite of marine species which were largely or entirely unique to these habitats, *e.g. Notolabrus parilus*, *Hyporhamphus melanochir* and *Achoerodus gouldii*.

The persistently higher fish densities recorded at the above channel habitats is possibly related to the greater level of shelter and food they provide and the physico-chemical characteristics of the water column. Thus, Humphries *et al*. (1992) demonstrated that the densities of *A. elongata, L. wallacei*, *A. suppositus* and *P. olorum* in the nearby and seasonally-open Wilson Inlet were greatest in areas of patchy or dense *R. megacarpa*. Furthermore, the latter two species have been shown in other south-western Australian estuaries to occur predominantly in highly sheltered areas (Gill & Potter, 1993). In addition, *Pseudogobius olorum* feeds mainly on algae, detritus and bacterial mats, all of which are associated with seagrass habitats (Gill & Potter, 1993), and *A. elongata, A. suppositus* and *L. wallacei* all feed on nereidid polychaetes and/or the shrimp *Palaemonetes australis*, which are also typically associated with *R. megacarpa* beds (Humphries & Potter, 1993; Platell & Potter, 1996). Lastly, although the highly abundant and ubiquitous *A. elongata* is extremely euryhaline, it has been shown to have a preference for salinities between 20 and 36 in other south-western Australian estuaries (Prince *et al.*, 1982a). These findings parallel those of the current study, in which the densities of this species were far greater at the channel habitats where salinities ranged between 17 and 33, and were least in the basin habitats in which salinities during six of the eight sampling occasions were *ca* 15 and fell to < 5 on some occasions.

Further distinction of the fish assemblages among the channel habitats was also apparent. Thus, the estuarine and marine species *L. presbyteroides* and *F. lateralis* were more prevalent at habitat B than G and/or H during the majority of sampling occasions, reflecting the unvegetated and coarse sandy substrates present at this habitat, which these species are known to prefer (Prince *et al.*, 1982a; Gill & Potter, 1993; Humphries & Potter, 1993). Despite large areas of unvegetated sediment being present in many of the basin habitats, the notably lower abundances of the above two species, both of which have marine affinities (Prince *et al.*, 1982a; Gill & Potter, 1993), is presumably related to the lower salinities in those areas. The presence of marine species only or mainly at habitat B in certain seasons also helped distinguish the ichthyofauna at this habitat from those at the other entrance channel habitats. These included *Ammotretis rostratus*, *Ammotretis elongatus*, *Platycephalus speculator*, *Pseudorhombus jenynsii* and *Cynoglossus broadhursti*, all of which are well camouflaged against the sandy substrate at habitat B. Likewise, several weed-associated marine species, namely *N. parilus*, *A. gouldii*, *H. melanochir*, *Neoodax balteatus*, *Enoplosus armatus* and *Girella zebra*, also helped to distinguish the fish fauna at the vegetated habitat H in certain seasons.

Several marine species, such as *E. armatus*, *G. zebra* and *H. melanochir*, were also recorded at habitat G, at the uppermost end of the channel, and further into the estuary at habitat C, located on the southern shore of Middle basin. This probably reflects the fact that both these habitats were relatively sheltered from wave action, contained *R. megacarpa* beds and maintained relatively high salinities throughout the year. Moreover, the moderately large densities of *A. elongata* and *L. wallacei* recorded at habitats G and C also helped distinguish their fish faunas from those of most other basin habitats.

Habitat A, situated at the mouth of Inlet River and surrounded by extensive, shallow and unvegetated shoals, was among the most distinct of the basin habitats with regard to its fish fauna, most notably due to its depauperate composition. Thus, this very shallow habitat could only be sampled during winter and spring of both study years and, in those seasons, fish densities were always low.

It is interesting to note that freshwater species were seldom caught during this study, even though habitats A, J and K, which were situated at the mouths of the Inlet, Shannon and Forth rivers, respectively, experienced salinities of < 5 during three of the eight sampling occasions. Such findings may reflect the limited abundance of fish in these rivers, which are oligotrophic and harbour a sparse and depauperate fish fauna (Bunn & Davies, 1990; Morgan *et al.*, 1998) or a tendency for these freshwater species not to stray from the rivers and into the basin. Furthermore, the mean densities of fish at these three habitats were typically among the lowest, despite the fact that *L. wallacei* and *P. olorum* are known to exhibit a preference for reduced salinities in other south-western Australian estuaries (Prince *et al.*, 1982a; Gill & Potter, 1993).

The extent of the ichthyofaunal differences among the remaining basin habitats (D, E, F, and I) were typically low and, during several sampling occasions, were not significantly different. Any significant differences were usually due to varying densities of one or more of the six common estuarine species. Such findings reflect both the limited number of species found to inhabit the basin regions, and the apparent wide environmental tolerances of those species (see subsection 3.4.1.1).

3.4.1.3: Relationships between the fish community and environmental characteristics of nearshore habitat types

The pattern of relative differences among nearshore habitats in terms of their enduring environmental characteristics was significantly correlated with that exhibited by the fish fauna in all but one of the eight sampling seasons, with the extent of those correlations being moderate. This reflects the fact that, the two main channel habitats (B and H) both had distinctive enduring environmental and ichthyofaunal characteristics, this trend was often not mirrored at many of the basin habitats. Thus, whereas the enduring environmental characteristics of basin habitats C, D and F were distinct from those of A, E, I, J and K, due mainly to presence of submerged aquatic macrophytes at the former habitats, their fish faunas were each largely dominated by the same suite of six common atherinid and goby species, which, only sometimes differed considerably in their relative densities with reduced abundances in typically recorded in habitat A and, to a lesser extent, J and K. However, the significant correlation with the enduring environmental variables and limited suite of species that occur in Broke Inlet make it possible to predict the species likely to typify any new site of interest within the estuary.

The relative differences among habitats, as defined by the suite of non-enduring water physico-chemical variables were significantly matched with those of the ichthyofauna on all but one sampling occasion. Furthermore, the extents of those significant matches were often slightly greater than those for the enduring environmental data. This was particularly so for those seasons in which the mouth of the estuary had been open for a relatively prolonged period or recently closed, *i.e.* spring or summer. During those seasons, pronounced spatial differences in non-enduring environmental variables, such as salinity, pH and macrophyte biomass, were present due to current or recent freshwater input into Shannon and Clarke basins and saltwater intrusion from the ocean and the annual growth cycle of *R. megacarpa*. Such environmental heterogeneity was coupled with greater differences in ichthyofauna among habitats. However, the extent of the matches between both the enduring and non-enduring environmental and fish faunal data in Broke Inlet were often considerably lower than those recorded in the permanently-open Swan-Canning Estuary which reflects the greater diversity of habitats and environmental conditions present within this system (Valesini *et al.*, 2009).

3.4.2: Offshore fish community

3.4.2.1: Offshore fish assemblage characteristics

In contrast to the nearshore waters, which were overwhelmingly dominated by estuarine species (*i.e.* estuarine residents and estuarine and marine species), only 5 of the 31 species and 20% of the individuals caught in the offshore waters, belonged to the estuarine and marine guild, while no estuarine residents were caught. Instead, marine estuarine-opportunists were the most numerous, constituting *ca* 75% of the individuals caught in each habitat. While marine stragglers were the most speciose guild, they contributed the least to the overall abundance of fishes (5%). The contribution of this latter guild is strongly influenced by the length of time Broke Inlet is open to the ocean (Chuwen *et al.*, 2009b) and, as in many other estuaries in south-western Australia, the distance upstream from the estuary mouth (Loneragan *et al.*, 1989; Potter *et al.*, 1993; Potter & Hyndes, 1994; Chuwen *et al.*, 2009b). Thus, during this study, marine stragglers were only recorded at offshore habitat A, which was located in the entrance channel. However, regardless of the degree of connectivity to the ocean, marine estuarine-opportunists have been shown to numerically dominate the ichthyofauna of the deeper, offshore waters of estuaries along the southern coast of Western Australia (Potter *et al.*, 1993; Potter & Hyndes, 1994; Chuwen *et al.*, 2009b). The abundance of these species is primarily due to the immigration of individuals > 100 mm in length entering these systems from nearshore marine environments at times when the mouths of these estuaries are open. These productive and sheltered environments act as important areas for these species (Potter *et al.*, 1997; Potter & Hyndes, 1999; Potter *et al.*, in prep), compared to the exposed nearshore marine waters, which are situated only 30 km from the continental shelf and are subject to large swells, as this coast is not protected by a chain of offshore reefs like those present on the lower west coast of Australia (Sanderson *et al.*, 2000).

It is also noteworthy that, unlike the nearshore waters, no estuarine resident species were caught in the offshore waters of Broke Inlet during this study. This is due to the paucity of the sparid *Acanthopagrus butcheri*, which is the only estuarine resident in the offshore waters of estuaries in south-western Australia. Although this species is abundant in other estuaries in this region, the fact that this species was not caught in this study parallels that by Chuwen *et al.* (2009b), where no individuals were captured in the basin of Broke Inlet during two years of seasonal sampling, which may reflect the low salinities present in the estuary and riverine reaches during winter and spring when this species spawns (Willams *et al.*, 2009). Furthermore, the abundances of the estuarine spawning *Cnidoglanis macrocephalus* were lower than those recorded in other nearby seasonally-open estuaries (Chuwen *et al.,* 2009b). As this species utilises detached macrophytes as a nursery area (Lenanton & Caputi, 1989; Crawley *et al.,* 2006) the reduced catches recorded in Broke Inlet may be related to the paucity of macrophytes in this system. It is also important to note that the absence of small estuarine species, such as atherinids and gobiids, is likely to be related to these fishes not being susceptible to capture by gillnets rather than them not being present in the offshore waters.

3.4.2.2: Differences in fish assemblages among offshore habitat types

Significant differences in fish assemblage composition among the offshore habitats were only detected during spring and autumn and, during these seasons, the overall extent of those spatial differences was low. The most distinct differences occurred between habitat A in the entrance channel and B in Shannon Basin, the latter of which receives the greatest freshwater input. These differences were mainly due to higher abundances of *Arripis truttaceus, Pagrus auratus, Pseudocaranx dentex* and *Arripis georgianus* at habitat A than B, while the opposite was true for *Mugil cephalus* and *Aldrichetta forsteri*. These two mugilids are known to exhibit an apparent preference for upper estuarine/lower riverine reaches with reduced salinities (Chubb *et al.*, 1981; Chuwen *et al.*, 2009b). As only five of the 31 species recorded during this study belong to the estuarine and marine guild it is reasonable to assume the paucity of these species in habitat B may be related to the lower salinities present within that habitat and the relative distance from the ocean. A similar trend was detected in the offshore waters of the Swan-Canning Estuary where the contribution of marine estuarine-opportunists declined from 39 and 32% in the lower and middle estuary to only 5% in the upper estuary (Loneragan *et al.*, 1989).

Conversely, the greater abundances of the marine species *A. georgianus* and *A. truttaceus* in habitat A during spring may be related to the higher salinities present in this habitat and the fact that at this time of year they make a westward migration from South Australia to spawn (Fairclough *et al.*, 2000a, b). Furthermore, these species, along with *P. auratus* and *P. dentex*, are known to feed on fish and crustaceans, particularly *Palaemonetes australis* (Edgar & Shaw, 1995; Hindell *et al.*, 2000; Platell *et al.*, 2006), which are most abundant in the entrance channel and related to the presence of *Ruppia megacarpa* (Tweedley & Valesini, 2008; Chapter 5).

The lack of a significant difference in ichthyofaunal composition among offshore habitats in winter may be due to the paucity of fish caught during this season, which was one third of that in other seasons. Such a trend was probably related to the very low salinities present throughout the estuary at this time and the recent breaching of the bar at the mouth of the estuary, thus providing an emigratory route to the ocean.

3.4.2.3: Relationships between the fish community and environmental characteristics of offshore habitat types

The pattern of relative differences among offshore sites in terms of their enduring environmental characteristics were significantly correlated with those exhibited by their fish fauna only during autumn. Such findings are a consequence of the rank order of similarities among habitats, thus, whereas the enduring environmental characteristics of the channel habitat A were the most distinct, habitat B contained by far the most distinctive ichthyofaunal assemblage and non-enduring water physico-chemical variables. Although the pattern of spatial differences in ichthyofaunal composition was significantly correlated with that exhibited by the non-enduring environmental characteristics in all seasons except summer, only in the case of spring was the result “reliable”. In the case of the other significant correlations, *i.e.* those recorded in autumn and winter, BIOENV selected a single variable which exhibited little spatial variation. For example, pH was *ca* 7.5 at sites representing habitat B and *ca* 7.8 at the remaining sites (habitats A and C). Such subtle variations in pH or dissolved oxygen concentrations, which ranged from 4.7-5 mg L^{-1} in autumn, are unlikely to affect the offshore fish faunal composition and thus these variables in these seasons are not considered to provide a reliable “explanation”.

3.5: Appendices

Appendix 3.1: Species that consistently typified (provided along the diagonal) and distinguished (provided in the sub-diagonal) the fish assemblages at each nearshore habitat between spring 07/08 and winter 08/09 as detected by one-way SIMPER. The habitat type in which each species was most abundant is given in superscript for each pairwise comparison. Insignificant pairwise comparisons are highlighted in grey. Asterisks denote the relative consistency of each species in either typifying or distinguishing the faunal composition of habitat types, as measured by the similarity to standard deviation ratio and dissimilarity to standard deviation ratio, respectively; > 1.5-3*, > 3-5**, > 5***.

(a) Spring 2007/2008

	A	B	C	D	E	F	G	H	I	J	K
A	*L. wallacei**** *A. elongata****										
B	*F. lateralis*^{B**} *A. elongata*^{B*} *L. presbyteroides*^{B*}	*F. lateralis*** *A. elongata** *L. presbyteroides**									
C	*A. suppositus*^{C*} *A. elongata*^{C*} *P. olorum*^{C*}	▨	*L. wallacei*** *A. elongata***								
D	*A. suppositus*^{D***} *P. olorum*^{D*} *L. wallacei*^{D*}	*A. suppositus*^{D*} *F. lateralis*^{B*} *P. olorum*^{D*} *L. presbyteroides*^{B*}	▨	*A. suppositus**** *A. elongata** *L. wallacei**							
E	*A. suppositus*^{E*}	*F. lateralis*^{B**} *A. elongata*^{B*}	*P. olorum*^{C*} *A. elongata*^{C*}	*A. elongata*^{D*} *P. olorum*^{D*}	*A. elongata*** *L. wallacei**						
F	▨	*F. lateralis*^{B*} *A. elongata*^{B*}	▨	▨	▨	*A. elongata** *L. wallacei**					
G	*A. suppositus*^{G***} *P. olorum*^{G*} *F. lateralis*^{G*}	*A. suppositus*^{G**} *P. olorum*^{G*} *L. presbyteroides*^{B*}	▨	▨	*P. olorum*^{G*} *A. suppositus*^{G*} *F. lateralis*^{G*}	*P. olorum*^{G} *A. suppositus*^{G} *A. elongata*^{G}	*A. suppositus**** *P. olorum** *A. elongata**				
H	*P. olorum*^{H*} *A. elongata*^{H*}	*A. suppositus*^{H***} *F. lateralis*^{B*} *A. elongata*^{H} *A. rostratus* ^{B} *P. olorum*^{H*}	▨	▨	*P. olorum*^{H*} *A. elongata*^{H*}	▨	▨	*P. olorum*** *L. wallacei*** *A. elongata***			
I	*F. lateralis*^{I**} *A. elongata*^{I*}	▨	*A. suppositus*^{C*} *A. elongata*^{C*} *P. olorum*^{C*}	*A. suppositus*^{D}** *P. olorum*^{D*}	*F. lateralis*^{I*} *A. elongata*^{I*} *A. suppositus*^{E*}	*F. lateralis*^{I*} *A. elongata*^{I*}	*A. suppositus*^{G**} *P. olorum*^{G*}	*P. olorum*^{H*} *F. lateralis*^{I*}	*L. wallacei**** *A. elongata*** *F. lateralis**		
J	*A. suppositus*^{J**}	*F. lateralis*^{B*} *P. olorum*^{J*} *A. rostratus* ^{B}	*A. suppositus*^{J*} *F. lateralis*^{C} *A. elongata*^{C*}	▨	▨	▨	▨	*A. elongata*^{H*} *A. suppositus*^{H*}	*F. lateralis*^{I*} *A. suppositus*^{J*}	*A. suppositus*** *A. elongata**	
K	▨	*F. lateralis*^{B*} *A. elongata*^{B*}	*A. elongata*^{C*} *A. suppositus*^{C*} *P. olorum*^{C*}	▨	▨	▨	*A. suppositus*^{G*} *P. olorum*^{G*}	*A. elongata*^{H*} *P. olorum*^{H*}	*F. lateralis*^{I*} *A. elongata*^{I*}	▨	*A. elongata**** *L. wallacei***

(b) Summer 2007/2008

	B	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**
B	*A. rostratus**** *L. presbyteroides**** *L. wallacei*** *A. elongata***									
C	*A. rostratus*^{B***} *L. presbyteroides*^{B**} *L. wallacei*^{B**} *A. elongata*^{B*}	*A. suppositus**** *A. elongata**								
D	*A. rostratus*^{B***} *L. presbyteroides*^{B**} *A. elongata*^{B*} *L. wallacei*^{B*}		*A. suppositus**** *A. elongata*** *L. wallacei**							
E	*A. rostratus*^{B***} *L. presbyteroides*^{B**} *L. wallacei*^{B*} *F. lateralis*^{B*}			*A. elongata*** *A. suppositus*** *L. wallacei**						
F	*A. rostratus*^{B***} *L. presbyteroides*^{B**} *L. wallacei*^{B*} *F. lateralis*^{B*}				*A. suppositus**** *A. elongata**** *L. wallacei***					
G	*A. rostratus*^{B**} *L. presbyteroides*^{B**} *L. wallacei*^{B*} *F. lateralis*^{B*}					*A. elongata*** *A. suppositus**				
H	*A. rostratus*^{B**} *A. suppositus*^{H*} *L. wallacei*^{H*} *N. parilus*^{H*}	*A. elongata*^{H*} *L. wallacei*^{H*} *A. suppositus*^{H*} *F. lateralis*^{H}	*A. elongata*^{H*} *A. suppositus*^{H*} *L. wallacei*^{H*} *N. parilus*^{H*}	*A. elongata*^{H*} *A. suppositus*^{H*} *N. parilus*^{H*} *L. wallacei*^{H*}	*A. elongata*^{H*} *A. suppositus*^{H*} *N. parilus*^{H*} *L. wallacei*^{H*}	*L. wallacei*^{H*} *A. elongata*^{H*} *A. suppositus*^{H*} *L. presbyteroides*^{H}	*A. suppositus**** *A. elongata*** *L. presbyteroides** *L. wallacei**			
I	*A. rostratus*^{B**} *L. presbyteroides*^{B**} *F. lateralis*^{B*} *L. wallacei*^{B*}	*F. lateralis*^{I*} *A. suppositus*^{C*} *L. wallacei*^{I*}	*L. presbyteroides*^{D*} *F. lateralis*^{I*} *A. suppositus*^{D*} *A. elongata*^{D*}			*A. elongata*^{G*}	*A. suppositus*^{H*} *A. elongata*^{H*} *N. parilus*^{H*} *L. wallacei*^{H*}	*A. elongata**** *L. wallacei**** *F. lateralis***		
J	*A. rostratus*^{B***} *L. presbyteroides*^{B**} *F. lateralis*^{B*} *L. wallacei*^{B*}						*A. elongata*^{H*} *A. suppositus*^{H*} *N. parilus*^{H*} *L. wallacei*^{H*}		*A. elongata**** *F. lateralis**** *A. suppositus** *L. wallacei**	
K	*A. rostratus*^{B***} *L. presbyteroides*^{B**} *L. wallacei*^{B*} *A. elongata*^{B*}						*A. suppositus*^{H*} *A. elongata*^{H*} *N. parilus*^{H*} *L. wallacei*^{H*}			*L. wallacei**** *A. elongata*** *L. presbyteroides**

(c) Autumn 2007/2008

	B	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**
B	*F. lateralis**** *L. presbyteroides**									
C		*A. elongata*** *A. suppositus** *L. presbyteroides** *L. wallacei**								
D	*L. wallacei*^{B*} *A. elongata*^{B*} *F. lateralis*^{B*}	*L. presbyteroides*^{C*} *L. wallacei*^{C*} *A. elongata*^{C*}	*A. suppositus**** *A. elongata**** *L. wallacei**							
E	*F. lateralis*^{B*} *A. elongata*^{B*} *L. presbyteroides*^{B*}	*L. wallacei*^{C*} *L. presbyteroides*^{C*}		*L. wallacei*** *A. suppositus** *A. elongata**						
F	*L. wallacei*^{B*} *A. elongata*^{B*} *L. presbyteroides*^{B*}				*A. elongata**** *A. suppositus*** *L. wallacei**					
G			*L. presbyteroides*^{G***} *L. wallacei*^{G*} *A. elongata*^{G*} *F. lateralis*^{D*}	*L. wallacei*^{G} *A. elongata*^{G} *P. olorum*^{G*} *L. presbyteroides*^{G*}		*A. elongata**** *A. suppositus**** *L. wallacei*** *L. presbyteroides**				
H			*L. wallacei*^{H**} *L. presbyteroides*^{H*} *A. elongata*^{H*}	*L. presbyteroides*^{H*} *L. wallacei*^{H*} *A. elongata*^{H*}	*L. presbyteroides*^{H*} *L. wallacei*^{H*} *A. elongata*^{H*}		*A. suppositus**** *A. elongata**** *F. lateralis*** *L. wallacei***			
I	*L. wallacei*^{B**} *A. elongata*^{B*} *A. suppositus*^{B*}					*L. wallacei*^{G*} *A. elongata*^{G} *P. olorum*^{G*} *A. suppositus*^{G*}	*L. wallacei*^{H***} *A. suppositus*^{H*} *A. elongata*^{H*} *L. presbyteroides*^{H*}	*L. presbyteroides*** *A. suppositus*** *L. wallacei*** *A. elongata**		
J						*L. wallacei*^{G} *A. elongata*^{G} *P. olorum*^{G*} *A. suppositus*^{G}	*A. elongata*^{H*} *L. wallacei*^{H*} *A. suppositus*^{H*} *L. presbyteroides*^{H*}		*A. elongata*** *A. suppositus*** *L. wallacei**	
K			*A. suppositus*^{D*} *F. lateralis*^{D} *L. presbyteroides*^{K}	*A. suppositus*^{E*} *A. elongata*^{E} *L. wallacei*^{E} *L. presbyteroides*^{K}		*A. suppositus*^{G*} *A. elongata*^{G*} *L. wallacei*^{G*} *P. olorum*^{G*}	*A. suppositus*^{H*} *L. wallacei*^{H*} *A. elongata*^{H*} *L. presbyteroides*^{H*}			*A. elongata**

(d) Winter 2007/2008

	A	B	C	D	E	F	G	H	I	J	K
A	*A. elongata**** *L. wallacei***										
B	*L. presbyteroides*^{B*} *A. suppositus*^{B*} *A. elongata*^{B*}	*A. elongata*** *L. presbyteroides*** *L. wallacei**									
C	*P. olorum*^{C***} *A. suppositus*^{C**} *L. wallacei*^{C*} *A. elongata*^{C*}	*L. presbyteroides*^{B*} *P. olorum*^{B} *A. elongata*^{B} *F. lateralis*^{B}	*P. olorum**** *A. suppositus**** *L. wallacei*** *A. elongata**								
D		*L. presbyteroides*^{B*} *A. suppositus*^{B*} *L. wallacei*^{B} *P. olorum*^{B}	*P. olorum*^{C***} *A. suppositus*^{C*} *L. wallacei*^{C*} *F. lateralis*^{C}	*A. elongata***							
E		*L. presbyteroides*^{B*} *A. suppositus*^{B*} *L. wallacei*^{E}			*L. wallacei**** *A. suppositus*** *A. elongata***						
F						*L. wallacei*** *A. elongata*** *A. suppositus**					
G	*P. olorum*^{G***} *A. elongata*^{G*} *L. wallacei*^{G}			*P. olorum*^{G***} *A. elongata*^{G*} *L. wallacei*^{G*}			*P. olorum**** *A. elongata** *A. suppositus**				
H	*A. suppositus*^{H*} *L. presbyteroides*^{H*} *A. elongata*^{H*} *P. olorum*^{H}		*L. presbyteroides*^{H*}	*A. suppositus*^{H*} *L. presbyteroides*^{H*} *L. wallacei*^{H*}	*A. suppositus*^{H*} *L. presbyteroides*^{H*}	*A. suppositus*^{H*} *L. presbyteroides*^{H*}		*A. suppositus*** *A. elongata*** *L. wallacei**			
I	*A. elongata*^{I*} *L. wallacei*^{I*}	*L. presbyteroides*^{B*} *A. suppositus*^{B*}	*P. olorum*^{C***} *A. suppositus*^{C**} *A. elongata*^{I*}	*L. wallacei*^{I*} *A. elongata*^{I*} *A. suppositus*^{D}			*P. olorum*^{G**} *A. elongata*^{G*}	*A. suppositus*^{H*} *L. presbyteroides*^{H*}	*L. wallacei**** *A. elongata***		
J								*L. presbyteroides*^{H*} *A. suppositus*^{H*}		*L. wallacei**** *A. elongata***	
K	*A. elongata*^{K*} *L. wallacei*^{K*}	*A. suppositus*^{B*} *L. presbyteroides*^{B*}	*A. suppositus*^{C**} *P. olorum*^{C*} *A. elongata*^{K*}	*L. wallacei*^{K**} *A. elongata*^{K*} *A. suppositus*^{D*}				*A. suppositus*^{H*} *L. presbyteroides*^{H*}			*L. wallacei**** *A. elongata****

(e) Spring 2008/2009

	A	B	C	D	E	F	G	H	I	J	K
A	*L. wallacei*** *A. elongata**										
B	*F. lateralis*^{B*} *L. presbyteroides*^{B*} *L. wallacei*^{B*} *A. suppositus*^{B}	*A. elongata*** *F. lateralis*** *L. presbyteroides** *L. wallacei*									
C	*L. presbyteroides* ^{C**} *A. suppositus*^{C**} *L. wallacei*^{C*} *P. olorum*^{C}		*A. suppositus**** *A. elongata*** *L. presbyteroides*** *L. wallacei***								
D		*L. presbyteroides*^{B*} *L. wallacei*^{B*} *A. elongata*^{B*} *A. suppositus*^{B*}	*L. presbyteroide* ^{C**} *A. suppositus*^{C**} *L. wallacei*^{C} *A. elongata*^{C}	*L. wallacei*** *A. elongata***							
E		*L. wallacei*^{B*} *L. presbyteroides*^{B} *F. lateralis*^{B*}	*F. lateralis*^{C} *P. olorum*^{C} *A. elongata*^{C}		*L. wallacei** *A. elongata**						
F		*L. presbyteroides*^{B*} *L. wallacei*^{B*} *A. elongata*^{B*} *F. lateralis*^{B*}				*A. elongata**** *L. wallacei***					
G	*A. suppositus*^{G***} *P. olorum*^{G*} *L. presbyteroides*^{G*} *F. lateralis*^{G*}			*A. suppositus*^{G***} *L. presbyteroides*^{G*} *P. olorum*^{G*} *A. elongata*^{G*}	*P. olorum*^{G*} *A. suppositus*^{G} *F. lateralis*^{G} *L. presbyteroides*^{G}	*A. elongata*^{G*} *L. presbyteroides*^{G*} *P. olorum*^{G} *A. suppositus*^{G}	*A. suppositus**** *A. elongata**** *P. olorum**** *L. presbyteroides**				
H	*A. suppositus*^{H**} *F. lateralis*^{H**} *P. olorum*^{H**} *L. presbyteroides*^{H*}	*P. olorum*^{H*} *N. parilus*^{H} *A. suppositus*^{H*} *A. gouldii*^{H}	*N. parilus*^{H*} *L. presbyteroides*^{H*} *L. wallacei*^{H*} *A. gouldii*^{H*}	*A. suppositus*^{H***} *L. presbyteroides*^{H*} *P. olorum*^{H*} *N. parilus*^{H*}	*F. lateralis*^{H**} *P. olorum*^{H*} *N. parilus*^{H*} *L. wallacei*^{H*}	*P. olorum*^{H*} *L. presbyteroides*^{H*} *N. parilus*^{H*} *L. wallacei*^{H*}	*P. olorum*^{H*} *A. suppositus*^{H*} *L. wallacei*^{H*} *H. melanochir*^{H*}	*A. suppositus**** *F. lateralis**** *A. elongata*** *P. olorum***			
I		*F. lateralis*^{B*} *L. presbyteroides*^{B*} *A. suppositus*^{B} *A. elongata*^{B}					*A. elongata*^{G*} *P. olorum*^{G*} *A. suppositus*^{G**} *L. presbyteroides*^{G*}	*A. suppositus*^{H***} *F. lateralis*^{H**} *P. olorum*^{H**} *L. presbyteroides*^{H*}	*A. elongata**		
J		*A. elongata*^{B**} *F. lateralis*^{B*} *L. presbyteroides*^{B*} *L. wallacei*^{B*}	*L. presbyteroides*^{C**} *A. elongata*^{C**} *A. suppositus*^{C*} *L. wallacei*^{C*}	*A. elongata*^{D*} *L. wallacei*^{D}			*A. elongata*^{G*} *P. olorum*^{G*} *L. presbyteroides*^{G*} *A. suppositus*^{G*}	*F. lateralis*^{H**} *P. olorum*^{H**} *A. elongata*^{H**} *A. suppositus*^{H*}		*L. wallacei***	
K	*L. wallacei*^{A*} *A. elongata*^{A*}	*A. elongata*^{B**} *F. lateralis*^{B*} *L. presbyteroides*^{B*} *L. wallacei*^{B*}	*A. suppositus*^{C**} *L. presbyteroides*^{C**} *A. elongata*^{C**} *L. wallacei*^{C}	*L. wallacei*^{D*} *A. elongata*^{D*}	*L. wallacei*^{E*} *A. elongata*^{E*}	*A. elongata*^{F**} *L. wallacei*^{F*} *A. suppositus*^{F}	*A. suppositus*^{G***} *P. olorum*^{G**} *A. elongata*^{G*} *L. presbyteroides*^{G*}	*A. suppositus*^{H***} *F. lateralis*^{H**} *P. olorum*^{H**} *A. elongata*^{H*}	*L. wallacei*^{I*} *A. elongata*^{I}		*A. elongata****

(f) Summer 2008/2009

	B	C	D	E	F	G	H	I	J	K
B	*L. wallacei**** *A. elongata**** *F. lateralis**** *L. presbyteroides**									
C	*A. elongata*^{B***} *L. wallacei*^{B**} *A. suppositus*^{C} *L. presbyteroides*^{B}	*A. elongata**** *L. wallacei**** *L. presbyteroides**** *A. suppositus****								
D	*L. wallacei*^{B*} *A. elongata*^{B*} *A. suppositus*^{D} *L. presbyteroides*^{B}	*A. suppositus*^{D} *L. wallacei*^{D**} *A. elongata*^{D} *F. lateralis*^{D}	*F. lateralis*** *L. presbyteroides*** *A. suppositus*** *A. elongata**							
E	*L. wallacei*^{B*} *A. elongata*^{B*} *F. lateralis*^{B*} *L. presbyteroides*^{B}		*A. suppositus*^{D*} *L. wallacei*^{D} *F. lateralis*^{D*} *L. presbyteroides*^{D*}	*L. wallacei**** *A. suppositus*** *A. elongata*** *L. presbyteroides**						
F	*A. elongata*^{B}** *L. wallacei*^{B*} *A. suppositus*^{B*} *F. lateralis*^{B*}		*L. presbyteroides*^{D*} *F. lateralis*^{D*} *A. suppositus*^{D*} *L. wallacei*^{F}		*L. wallacei**** *A. elongata**** *A. suppositus***					
G		*A. elongata*^{G*} *L. presbyteroides*^{G*} *P. olorum*^{G*} *A. suppositus*^{G}	*F. lateralis*^{D*} *P. olorum*^{G} *L. wallacei*^{G*} *A. suppositus*^{D*}							
H		*P. olorum*^{H***} *L. presbyteroides*^{H*} *A. elongata*^{H*} *A. gouldii*^{H*}	*P. olorum*^{H**} *L. presbyteroides*^{H*} *N. parilus*^{H} *A. gouldii*^{H}	*P. olorum*^{H*} *L. presbyteroides*^{H*} *N. parilus*^{H*} *A. gouldii*^{H*}	*L. presbyteroides*^{H*} *P. olorum*^{H*} *A. suppositus*^{H*} *A. gouldii*^{H*}		*F. lateralis**** *P. olorum*** *L. presbyteroides*** *A. suppositus***			
I	*L. wallacei*^{B*} *L. presbyteroides*^{B} *A. suppositus*^{B} *A. elongata*^{B}	*A. suppositus*^{C*} *A. elongata*^{I*} *L. wallacei*^{I*} *F. lateralis*^{I}	*A. suppositus*^{D*} *A. elongata*^{I} *L. presbyteroides*^{D} *L. wallacei*^{I}			*P. olorum*^{G*} *A. elongata*^{G} *A. suppositus*^{G} *L. wallacei*^{G}	*P. olorum*^{H**} *L. presbyteroides*^{H*} *A. suppositus*^{H*} *A.s gouldii*^{H*}	*A. elongata*** *L. wallacei***		
J	*A. elongata*^{B}** *F. lateralis*^{B*} *L. wallacei*^{B*} *A. suppositus*^{B*}	*L. presbyteroides*^{C**} *A. elongata*$^{J **}$ *A. suppositus*^{C} *L. wallacei*^{J}	*F. lateralis*^{D***} *L. presbyteroides*^{D*} *A. suppositus*^{D*} *L. wallacei*^{J}				*L. wallacei*^{H} *F. lateralis*^{H} *P. olorum*^{H**} *L. presbyteroides*^{H*}		*L. wallacei**** *A. suppositus**** *A. elongata****	
K	*L. wallacei*^{B***} *A. elongata*^{B*} *F. lateralis*^{B*} *L. presbyteroides*^{B*}	*L. presbyteroides*^{C**} *A. suppositus*^{C*} *A. elongata*^{K*}	*F. lateralis*^{D***} *L. presbyteroides*^{D**} *A. suppositus*^{D*} *L. wallacei*^{D*}	*A. suppositus*^{E**} *L. presbyteroides*^{E*} *L. wallacei*^{E*} *A. elongata*^{E}	*A. suppositus*^{F*} *A. elongata*^{F} *L. presbyteroides*^{F} *L. wallacei*^{F}	*L. presbyteroides*^{G*} *A. suppositus*^{G*} *P. olorum*^{G*} *A. elongata*^{G*}	*P. olorum*^{H**} *L. presbyteroides*^{H**} *A. suppositus*^{H*} *L. wallacei*^{H*}			*L. wallacei**** *A. elongata**

(g) Autumn 2008/2009

	B	C	D	E	F	G	H	I	J	K
B	*A. elongata**** *A. suppositus**** *L. wallacei**									
C		*A. elongata**** *A. suppositus*** *L. wallacei**								
D	*A. elongata*^{B*} *F. lateralis*^{B} *A. suppositus*^{D} *L. wallacei*^{B}		*L. wallacei**** *A. suppositus**** *A. elongata**							
E	*A. elongata*^{B*} *A. suppositus*^{E*} *F. lateralis*^{B} *L. wallacei*^{B}	*L. wallacei*^{C} *L. presbyteroides*^{C} *A. elongata*^{C}		*L. wallacei**** *A. suppositus*** *A. elongata***						
F	*A. elongata*^{B*} *F. lateralis*^{B*} *L. wallacei*^{B}	*A. suppositus*^{C*} *L. wallacei*^{C} *A. elongata*^{C} *L. presbyteroides*^{C}			*A. elongata**** *L. wallacei*** *A. suppositus***					
G	*P. olorum*^{G*} *A. elongata*^{B*} *F. lateralis*^{B*} *L. wallacei*^{G}		*P. olorum*^{G***} *L. wallacei*^{G*} *A. elongata*^{G*} *A. suppositus*^{G}	*P. olorum*^{G*} *A. elongata*^{G*} *L. wallacei*^{G*} *A. suppositus*^{G}	*A. elongata*^{G*} *A. suppositus*^{G} *L. wallacei*^{G}	*P. olorum**** *A. suppositus*** *A. elongata*** *L. wallacei**				
H			*L. presbyteroides*^{H*} *L. wallacei*^{H*} *A. elongata*^{H} *F. lateralis*^{H}	*L. presbyteroides*^{H*} *L. wallacei*^{H*} *A. elongata*^{H*} *A. suppositus*^{H}	*L. presbyteroides*^{H*} *A. suppositus*^{H*} *A. elongata*^{H*} *L. wallacei*^{H*}		*A. suppositus**** *A. elongata**** *L. wallacei****			
I						*A. suppositus*^{G} *L. wallacei*^{G} *P. olorum*^{G***}	*F. lateralis*^{H*} *A. elongata*^{H*} *L. wallacei*^{H}	*A. elongata*** *L. wallacei**		
J	*A. elongata*^{B**} *F. lateralis*^{B*} *L. wallacei*^{B} *L. presbyteroides*^{B}	*A. suppositus*^{C} *A. elongata*^{C} *L. wallacei*^{C} *L. presbyteroides*^{C}				*P. olorum*^{G***} *A. elongata*^{G**} *L. wallacei*^{G*} *A. suppositus*^{G}	*L. presbyteroides*^{H***} *L. wallacei*^{H*} *A. elongata*^{H*} *A. suppositus*^{H*}		*L. wallacei*** *A. elongata**	
K	*A. elongata*^{B**} *F. lateralis*^{B*} *A. suppositus*^{B*} *L. wallacei*^{B}	*A. suppositus*^{C} *L. wallacei*^{C} *L. presbyteroides*^{C} *A. elongata*^{C}	*A. suppositus*^{D*} *L. wallacei*^{D*}	*A. suppositus*^{E*} *L. wallacei*^{K} *A. elongata*^{K}	*A. suppositus*^{F*} *P. olorum*^{F} *A. elongata*^{K}	*P. olorum*^{G***} *A. suppositus*^{G*} *A. elongata*^{G*} *L. wallacei*^{G}	*A. suppositus*^{H**} *L. presbyteroides*^{H**} *L. wallacei*^{H*} *A. elongata*^{H*}			*A. elongata**** *L. wallacei***

(h) Winter 2008/2009

	A	B	C	D	E	F	G	H	I	J	K
A	*A. elongata**** *L. wallacei***										
B		*F. lateralis** *A. elongata**									
C		*F. lateralis*^{B*} *A. elongata*^{B*} *A. suppositus*^{C*} *L. wallacei*^{C}	*A. elongata*** *L. wallacei** *A. suppositus**								
D		*A. elongata*^{B*} *A. suppositus*^{D} *L. wallacei*^{D} *F. lateralis*^{B}		*A. suppositus*** *A. elongata** *L. wallacei**							
E	*A. suppositus*^{E*} *A. elongata*^{A*} *F. lateralis*^{A*}	*F. lateralis*^{B*} *A. elongata*^{B*} *A. suppositus*^{E} *L. wallacei*^{E}			*A. elongata** *A. suppositus** *L. wallacei**						
F		*F. lateralis*^{B**} *A. elongata*^{B*}				*L. wallacei***					
G		*A. suppositus*^{G*} *A. elongata*^{B*} *F. lateralis*^{B} *L. wallacei*^{G}					*L. wallacei*** *A. suppositus** *A. elongata**				
H								*A. suppositus**** *L. wallacei** *A. elongata**			
I		*F. lateralis*^{B*} *A. elongata*^{B} *A. suppositus*^{I}							*A. suppositus**** *L. wallacei**		
J	*A. suppositus*^{J} *A. elongata*^{A*} *F. lateralis*^{A}	*A. elongata*^{B*} *A. suppositus*^{J} *L. wallacei*^{B}			*A. suppositus*^{J} *L. wallacei*^{E*} *A. elongata*^{E*}					None	
K	*A. elongata*^{A*} *F. lateralis*^{A*}	*F. lateralis*^{B*} *A. elongata*^{B*} *L. wallacei*^{K}	*A. elongata*^{C*} *A. suppositus*^{C*} *L. wallacei*^{C}	*L. wallacei*^{D*} *A. elongata*^{D*} *A. suppositus*^{D}			*L. wallacei*^{K*} *A. elongata*^{K*} *A. suppositus*^{G*}	*A. elongata*^{H*} *A. suppositus*^{H} *F. lateralis*^{H}			*L. wallacei**

Appendix 3.2: Species that consistently typified (provided along the diagonal) and distinguished (provided in the sub-diagonal) the fish assemblages at each offshore habitat in (a) spring, (b) summer, (c) autumn and (d) winter as detected by one-way SIMPER. The habitat type in which each species was most abundant is given in superscript for each pairwise comparison. Insignificant pairwise comparisons are highlighted in grey. Asterisks denote the relative consistency of each species in either typifying or distinguishing the faunal composition of habitat types, as measured by the similarity to standard deviation ratio and dissimilarity to standard deviation ratio, respectively; > 1-3*, > 3-5**, > 5***.

(a) Spring

	A	B	C
A	*Arripis georgianus**** *Arripis truttaceus**		
B	*Arripis georgianus*^{A*} *Arripis truttaceus*^{A*} *Engraulis australis*^{A} *Aldrichetta forsteri*^{B*}	*Aldrichetta forsteri* *Mugil cephalus*	
C			*Arripis georgianus** *Aldrichetta forsteri*

(b) Autumn

	A	B	C
A	*Arripis georgianus* *Gonorynchus greyi* *Pagrus auratus*		
B	*Arripis georgianus*^{A*} *Mugil cephalus*^{B*} *Pagrus auratus*^{A*} *Pseudocaranx dentex*^{A*}	*Ammotretis rostratus*$*$ *Aldrichetta forsteri* *Engraulis australis*	
C		*Mugil cephalus*^{B*}	*Ammotretis rostratus*$*$ *Arripis georgianus*

Chapter 4

Temporal differences in ichthyofaunal composition among habitat types in Broke Inlet

4.1: Introduction

Estuaries are dynamic ecosystems which undergo considerable changes in physico-chemical conditions across a range of temporal scales, such as diel/tidal (*e.g.* Hoguane *et al.*, 1999), seasonal (*e.g.* Uncles *et al.*, 2000), inter-annual (*e.g.* Chuwen *et al.*, 2009a) and/or longer time scales driven by large climatic events, for instance the El Niño Southern Oscillation (*e.g.* Tolan, 2007) or climate change (*e.g.* Najjar *et al.*, 2010). While faunal species that spend considerable portions of their life cycle within estuaries have typically developed a suite of adaptations for coping with variability in water and/or sediment conditions (*e.g.* Kinne, 1964, 1966; Lockwood, 1976), their distributions often reflect their "preference" for a particular range of these conditions. As a result, temporal changes in the ichthyofaunal composition of estuaries have frequently been related to concurrent changes in a range of environmental parameters (Marshall & Elliott, 1998; Jaureguizar *et al.*, 2003; Selleslagh & Amara, 2008), and in particular salinity (Barletta *et al.*, 2005; Hoeksema *et al.*, 2006), due to its effect on fish growth, survival and reproductive success (Gilchrist, 1995; Boeuf & Payan, 2001).

Temporal changes in estuarine fish assemblages are also driven by the manner in which particular species use estuaries throughout their life cycle, *i.e.* estuarine-use guilds (see subsection 1.2; Elliott *et al.*, 2007). The consistent and pronounced seasonal changes in fish faunal composition, in many holarctic systems, including the Severn, Thames, Elbe and Scheldt estuaries, have been attributed to the sequential immigration and emigration of marine estuarine-opportunist species in downstream regions, the migrations of diadromous species and the influx of freshwater species into upstream regions (Potter *et al.*, 1986a; Potter *et al.*, 1997; Araújo *et al.*, 1998, 1999; Thiel & Potter, 2001; Maes *et al.*, 2005). Despite marked differences in the relative abundances of species representing the various estuarine-use guilds between estuaries in holarctic regions and those in south-western Australia (*cf.* Potter & Hyndes, 1999; Nordlie, 2003), monthly or seasonal changes in fish faunal composition have also been demonstrated in some permanently-open systems in the latter region, such as the Peel-Harvey and Swan-Canning estuaries (Young & Potter, 2003; Hoeksema & Potter, 2006). In the former system, these changes were generally attributable to differences in the relative abundances of marine species, augmented by estuarine resident species (Young & Potter, 2003). In the upper Swan-Canning Estuary, however, monthly changes in ichthyofaunal composition were due primarily to the time-staggered differences in peak abundances of several estuarine resident species, reflecting differences in their recruitment patterns and, to a lesser extent, the migration of marine species into those upper reaches (Hoeksema & Potter, 2006).

Temporal changes in fish fauna have also been detected in estuaries with an ephemeral connection to the ocean (*e.g.* Pollard, 1994a; Chuwen *et al.*, 2009b). The pattern of these changes are governed by the timing and duration over which the sand bar at the mouths of these systems are breached (Bennett, 1989; Whitfield & Kok, 1992; Young *et al.*, 1997) and thus estuary type, *e.g.* permanently-open *vs* seasonally-open (Kok & Whitfield, 1986; Potter & Hyndes, 1994; Whitfield, 1999). For example, prolonged phases of estuary closure to the ocean not only prevent the recruitment and subsequent emigration of marine estuarine-opportunist species, but may also cause dramatic increases in estuarine salinity, and thus the mortality of less tolerant species (Young & Potter, 2002; Hoeksema *et al.*, 2006).

Given the wide range of habitats that typically occur in estuaries, and thus their different fish faunas, the types of temporal changes that are observed in ichthyofaunal composition are also likely to differ spatially throughout a given system. In the Peel-Harvey Estuary for instance, the nature and extent of seasonal changes in the fish fauna varied among regions (Young & Potter, 2003). Moreover, given the differences in environmental change that are likely to be experienced by different habitats in Broke Inlet throughout the year (*e.g.* those closest to the mouth of the tributaries will undergo a considerably greater decline in salinity than those near the entrance channel; see Fig. 3.2), it is expected that temporal differences in ichthyofaunal composition will also vary spatially throughout this estuary.

The nearshore fish fauna of Broke Inlet is heavily dominated by a suite of estuarine species (Hoeksema *et al.*, 2009; Chapter 3), many of which have a one year life cycle (Prince & Potter, 1983; Gill *et al.*, 1996) and have been shown to undergo monthly changes in their abundance in other estuaries in south-western Australia (Hoeksema & Potter, 2006). In contrast, the offshore ichthyofauna is dominated by marine species which immigrate and emigrate from the estuary following the breaching of the bar at the mouth of the estuary (Chuwen *et al.*, 2009b; Chapter 3). With this in mind, temporal variation in the characteristics of the fish fauna at the various nearshore and offshore habitats within Broke Inlet were investigated to address the following aims.

(1) Determine the extent of any seasonal and inter-annual changes in species richness, density/catch rate and composition of the fish fauna in each nearshore and offshore habitat.

(2) Identify whether any seasonal changes occur in a cyclical pattern.

(3) Determine whether temporal changes in the characteristics of the ichthyofauna in each habitat are influenced by non-enduring environmental variables (*e.g.* salinity, water temperature, dissolved oxygen concentration).

(4) Investigate whether the pattern of relative differences in ichthyofaunal composition among seasons and years varies among nearshore habitats.

4.2: Materials and methods

4.2.1: Sampling regime

Details on the methodology for site selection, collection of fish samples and the measurement of fish lengths and weights are described in subsection 3.2.1 along with the measurement of non-enduring environmental variables

4.2.2: Statistical analyses

All statistical analyses were performed using the PRIMER v6 multivariate software package (Clarke & Gorley, 2006) and the PERMANOVA+ add-on (Anderson *et al.*, 2008). Seasonal and inter-annual changes in the non-enduring water physico-chemical variables, *i.e.* salinity, water temperature, dissolved oxygen content, pH and macrophyte biomass, and fish species richness, density/catch rate and diversity in both the nearshore and offshore waters were investigated in conjunction with their spatial differences. The methodology for which is described in section 3.2.2.1.

4.2.2.1: Temporal differences in ichthyofaunal composition

The statistical methodology employed to investigate the overall extent of spatio-temporal differences in the composition of the nearshore and offshore ichthyofauna, which incorporated analyses of their differences among seasons and years, are described in subsection 3.2.2.2.

Where PERMANOVA detected significant interactions between habitat type and season and/or year, temporal differences in the ichthyofaunal composition of both the nearshore and offshore waters were investigated for each habitat separately in order to remove the confounding influence of that factor (see Table 3.4, 3.10). Thus, appropriate Bray-Curtis sub-matrices containing samples from the various seasons and/or years in any one habitat were constructed and each subjected to two-way Analysis of Similarities (ANOSIM) tests (Clarke & Green, 1988) to determine whether the ichthyofaunal composition was significantly influenced by season and/or year. The null hypothesis and test statistic are the same as that used in subsection 3.2.2.2. Non-metric Multidimensional Scaling (nMDS) was then employed to display visually any differences detected in the fish faunal composition among seasons and/or years in each habitat.

When ANOSIM detected a significant difference among any temporal factor and the associated *R*-statistic was ≥ 0.2, Similarity Percentages (SIMPER) was then used to elucidate which species typified the assemblages in that season and/or year and those which contributed most to differences between each pair of the above two factors (Clarke, 1993). Focus was placed on those species that had the highest similarity (or dissimilarity)/standard deviation ratio, and those that were the most abundant.

Temporal cyclicity in fish composition, whereby consecutive units (*e.g.* seasons) form a circular pattern in which the first unit is situated near the last, was investigated for each nearshore and offshore habitat type using the RELATE routine. The pretreated, replicate fish assemblage data recorded within each habitat type was averaged for each season and year combination (*e.g.* spring 2007/2008), and the resultant data used to construct a Bray-Curtis similarity matrix. Each of the matrices from each habitat was then subjected to nMDS ordination, to allow trends among the samples from different seasons and years to be displayed. To test for cyclicity, a Euclidean distance model matrix was constructed from the inter-point distances of two sets of four points, each of which represented a season in a particular year, *e.g.* spring 2007/2008 and spring 2008/2009. Within each year, the seasonal points were "positioned" at 90° increments from each other, such that summer *vs* winter and autumn *vs* spring were the most dissimilar (180°), but consecutive seasons, such as summer *vs* autumn, were the most similar (90°). The two "circles" representing each year were slightly offset to account for any inter-annual differences. The RELATE routine was then employed to determine, for each nearshore and offshore habitat type separately, how similar the patterns of the rank orders of resemblance were between the model matrix and the matrix constructed from the fish faunal data. The null hypothesis that there was no relation in the pattern of rank order similarities between the two matrices was rejected if the significance level (p) was < 0.05. For significant results, the magnitude of the test statistic, rho (ρ) was used to determine the extent of the correlation, with values close to 0 reflecting no correlation and those close to 1 representing a perfect match.

4.2.2.2: Matching temporal patterns between the fish community and non-enduring environmental characteristics at each habitat type

The Biota and Environment matching routine (BIOENV; Clarke & Ainsworth, 1993) was employed to elucidate which subset of the non-enduring environmental variables recorded concurrently with the collection of all fish samples provided the best correlation with the temporal patterns displayed by the fish assemblage data in each habitat averaged for each season and year combination. The non-enduring environmental variables employed in these analyses, including their collection methods and subsequent data pre-treatment, are described in subsections 3.2.1 and 3.2.2.1, respectively. However, one extra variable was added here which was not used in those previous analyses, namely bar state, with positive values reflecting the number of days that the bar had been open to the ocean and negative values those since the bar had closed. The use of Draftsman plots (see subsection 2.2.3.1) between this variable and the other non-enduring environmental variables indicated that it did not require any transformation prior to analysis. The resultant transformed non-enduring environmental variable matrix was then normalised to place all variables on a common scale. The reference resemblance matrix employed in the BIOENV analysis was a Bray-Curtis matrix constructed from the pretreated fish assemblage data averaged for each season and year, while the secondary matrix was the complementary pretreated (*i.e.* transformed and normalised) non-enduring environmental data. Manhattan distance was used to construct resemblance matrices from this data during the matching procedure. For each of the above BIOENV tests the null hypothesis, criteria for rejecting it and the interpretation of significant results were the same as those described for the RELATE test above.

Comparisons between the temporal patterns exhibited by (i) the ichthyofaunal composition data and (ii) the non-enduring environmental variables selected by the BIOENV routine were illustrated by subjecting the relevant Bray-Curtis similarity matrix constructed from the former data to nMDS ordination, then overlaying circles ("bubbles") of proportionate sizes that represented the magnitude of the selected environmental variables in each corresponding sample.

4.2.2.3: Matching temporal patterns in fish faunal composition among habitat types

To investigate whether the temporal pattern of ichthyofaunal composition differed among nearshore habitats, the Bray-Curtis similarity matrices described in subsection 4.2.2.2, *i.e.* those constructed from the pretreated fish assemblage data, averaged for each season and year combination, in each individual habitat, were subjected to RELATE to test the null hypothesis of no correlation in the pattern of their rank order similarities, *i.e.* that the temporal pattern of ichthyofaunal composition in one habitat was unrelated to that in another. The resultant pairwise ρ values were then used to produce a second-stage resemblance matrix, which was then subjected to nMDS ordination. The distribution of the points on the resultant plot, each of which represented a particular habitat, enabled detection of whether the pattern of ichthyofaunal differences among sampling occasions differed among habitats. Note that, each of the matrices employed in this routine are required to contain complementary samples, therefore, habitat A, which was only able to be sampled during spring and winter of both years, was excluded from this analysis.

4.3: Results

4.3.1: Nearshore waters

4.3.1.1: Nearshore fish species mean density and life cycle contribution in each season

In both 2007/2008 and 2008/2009, the highest number of species were recorded during spring and summer (14-16) and lowest in autumn and winter (9-11). The mean density of fish averaged among habitats varied from *ca* 51 to 222 fish 100 m^{-2} in the first year to *ca* 37 to 141 fish 100 m^{-2} in the second. Moreover, the seasonal trends in mean density also differed among years. Thus, whereas by far the lowest mean density in the first year was recorded in spring, similarly low mean densities were recorded in all seasons of the second year except summer (Table 4.1).

The atherinid *Atherinosoma elongata* was the most abundant species in all but one season contributing between 36 and 76% to the total catch. *Leptatherina wallacei* and *Leptatherina presbyteroides* were also highly abundant, typically ranking either second or third in each season (Table 4.1). In spring 2008/2009 however, *L. wallacei* was the most abundant species throughout the nearshore waters of the estuary, while the winter of that year was the only season in which densities of *L. presbyteroides* were relatively low. The gobiids *Afurcagobius suppositus, Pseudogobius olorum* and *Favonigobius lateralis* frequently also ranked amongst the top five most abundant species. Each of these six atherinid and gobiid species is able to complete their entire

Table 4.1: Mean density (fish 100 m^{-2}; M), standard error (^{SE}), percentage contribution to the overall catch (%), rank by density (R), mean biomass (g; B), mean total length (mm; L) and length range (r) of each fish species recorded at the 11 nearshore habitat types in Broke Inlet in each season between spring 2007/2008 and winter 2008/2009. Abundant species in each season (*i.e.* those that contribute ≥ 5% to the overall mean density) are highlighted in grey. The life cycle category (LC) of each species is also provided (E = estuarine residents, EM = estuarine and marine, MEO = marine estuarine-opportunist, MS = marine straggler and FS = freshwater straggler). The species richness, mean overall density, number of samples and adjusted number of individuals (*i.e.* after the number of individuals in each sample had been adjusted to that in 100 m^{-2}) are given for each season sampled. Species are ranked by total abundance.

		Spring 2007/2008					**Summer 2007/2008**					**Autumn 2007/2008**					**Winter 2007/2008**				
Species	**LC**	M^{SE}	%	R	B^{SE}	L^{r}	M^{SE}	%	R	B^{SE}	L^{r}	M^{SE}	%	R	B^{SE}	L^{r}	M^{SE}	%	R	B^{SE}	L^{r}
Atherinosoma elongata	E	38.40$^{5.58}$	75.74	1	49.67$^{8.59}$	52$^{(17-108)}$	73.86$^{11.956}$	52.94	1	45.83$^{6.38}$	43$^{(14-119)}$	103.87$^{14.75}$	46.78	1	63.82$^{11.1}$	39$^{(15-89)}$	74.40$^{13.40}$	40.79	1	48.90$^{8.86}$	42$^{(16-97)}$
Leptatherina wallacei	E	5.20$^{1.35}$	10.26	2	2.94$^{0.58}$	43$^{(27-79)}$	23.33$^{5.28}$	16.72	3	10.46$^{2.06}$	42$^{(19-95)}$	58.11$^{11.38}$	26.17	2	20.13$^{3.43}$	38$^{(15-85)}$	33.40$^{7.64}$	18.31	3	15.44$^{4.45}$	37$^{(15-82)}$
Leptatherina presbyteroides	EM	1.99$^{0.72}$	3.93	4	1.37$^{0.45}$	46$^{(16-67)}$	27.85$^{8.41}$	19.96	2	5.59$^{1.71}$	34$^{(17-63)}$	49.81$^{15.36}$	22.43	3	20.58$^{7.68}$	38$^{(20-76)}$	67.25$^{31..63}$	36.87	2	33.72$^{16.92}$	41$^{(16-63)}$
Afurcagobius suppositus	E	2.37$^{0.59}$	4.67	3	5.14$^{2.11}$	55$^{(20-90)}$	8.62$^{1.37}$	6.18	4	4.54$^{0.94}$	34$^{(15-79)}$	7.57$^{0.95}$	3.41	4	4.9$^{0.51}$	37$^{(19-93)}$	4.61$^{0.74}$	2.53	4	10.50$^{2.52}$	53$^{(17-96)}$
Pseudogobius olorum	E	1.62$^{0.50}$	3.20	5	1.00$^{0.31}$	38$^{(25-52)}$	1.89$^{0.77}$	1.35	6	0.49$^{0.19}$	26$^{(16-62)}$	0.49$^{0.18}$	0.22	6	0.13$^{0.06}$	30$^{(18-44)}$	1.94$^{0.76}$	1.07	5	0.61$^{0.25}$	30$^{(17-64)}$
Favonigobius lateralis	EM	0.88$^{0.25}$	1.74	6	0.97$^{0.35}$	43$^{(17-72)}$	2.60$^{0.86}$	1.86	5	1.30$^{0.30}$	35$^{(16-67)}$	1.70$^{0.35}$	0.77	5	2.02$^{0.35}$	48$^{(22-77)}$	0.58$^{0.14}$	0.32	6	1.01$^{0.29}$	51$^{(21-84)}$
Notolabrus parilus	MS	0.03$^{0.02}$	0.06	9	0.37$^{0.21}$	90$^{(86-94)}$	0.14$^{0.08}$	0.10	10	0.58$^{0.44}$	61$^{(41-80)}$	0.01$^{0.01}$	0.00	9	0.4$^{0.24}$	92$^{(85-100)}$					
Hyporhamphus melanochir	EM	0.03$^{0.02}$	0.06	9	0.38$^{0.34}$	162$^{(124-184)}$	0.23$^{0.13}$	0.17	8	3.05$^{2.22}$	151$^{(60-214)}$	0.39$^{0.27}$	0.17	7	4.23$^{3.53}$	128$^{(59-257)}$					
Achoerodus gouldii	MS						0.18$^{0.11}$	0.13	9	2.53$^{1.57}$	83$^{(51-101)}$										
Engraulis australis	EM						0.69$^{0.41}$	0.49	7	2.17$^{1.32}$	77$^{(59-92)}$	0.01$^{0.01}$	0.00	9	0.02$^{0.02}$	57$^{(57)}$					
Aldrichetta forsteri	MEO	0.01$^{0.01}$	0.02	11	0.01$^{0.01}$	46$^{(46)}$											0.15$^{0.14}$	0.08	7	8.18$^{7.62}$	191$^{(154-483)}$
Ammotretis rostratus	MEO	0.09$^{0.04}$	0.18	7	0.06$^{0.03}$	33$^{(24-45)}$	0.07$^{0.03}$	0.05	11	0.34$^{0.19}$	72$^{(55-88)}$	0.08$^{.04}$	0.03	8	1.17$^{0.73}$	90$^{(62-160)}$	0.01$^{0.01}$	0.01	8	1.60$^{1.60}$	207$^{(207)}$
Neoodax balteatus	MS											0.01$^{0.01}$	0.00	9	0.12$^{0.12}$	109$^{(109)}$					
Ammotretis elongatus	EM	0.01$^{0.01}$	0.02	11	0.01$^{0.01}$	36$^{(36)}$															
Enoplosus armatus	MS	0.04$^{0.02}$	0.08	8	0.02$^{0.02}$	28$^{(24-33)}$															
Edelia vittata	FS																				
Mugil cephalus	MEO																0.02$^{0.01}$	0.01	8	0.01$^{0.01}$	27$^{(24-29)}$
Platycephalus speculator	EM						0.02$^{0.02}$	0.02	12	0.41$^{0.41}$	140$^{(133-146)}$										
Girella zebra	MS						0.02$^{0.02}$	0.02	12	0.27$^{0.28}$	116$^{(116)}$										
Haletta semifasciata	MS						0.02$^{0.02}$	0.02	12	0.42$^{0.42}$	95$^{(95)}$										
Galaxias occidentalis	FS																				
Lepidogalaxias salamandroides	FS																				
Urocampus carinirostris	EM																0.01$^{0.01}$	0.01	8	0.01$^{0.01}$	52$^{(52)}$
Pseudocaranx dentex	MS	0.01$^{0.01}$	0.02	11	0.01$^{0.01}$	44$^{(44)}$															
Rhabdosargus sarba	MEO																				
Pseudorhombus jenynsii	MEO	0.01$^{0.01}$	0.02	11	1.04$^{1.04}$	195$^{(195)}$															
Cynoglossus broadhursti	MS																				
Species richness		**14**					**14**					**11**					**10**				
Mean overall density		**51**					**140**					**222**					**182**				
Number of samples		**86**					**78**					**78**					**86**				
Adjusted number of individuals		**4,386**					**10,920**					**17,316**					**15,652**				
Actual number of individuals		**5,058**					**12,624**					**20,091**					**18,194**				

Table 4.1 Continued:

		Spring 2008/2009					**Summer 2008/2009**					**Autumn 2008/2009**					**Winter 2008/2009**				
Species	**LC**	M^{SE}	%	R	B^{SE}	L^{r}	M^{SE}	%	R	B^{SE}	L^{r}	M^{SE}	%	R	B^{SE}	L^{r}	M^{SE}	%	R	B^{SE}	L^{r}
Atherinosoma elongata	E	$21.15^{2.53}$	35.77	2	$25.57^{3.56}$	$52^{(20-124)}$	$56.44^{.45}$	40.08	1	$46.93^{5.68}$	$48^{(12-97)}$	$30.69^{4.45}$	58.51	1	$27.50^{5.11}$	$45^{(16-60)}$	$20.98^{4.47}$	56.67	1	$23.61^{7.61}$	$47^{(19-96)}$
Leptatherina wallacei	E	$24.82^{3.65}$	41.97	1	$12.04^{1.69}$	$41^{(20-84)}$	$47.13^{9.80}$	33.46	2	$19.10^{3.32}$	$42^{(11-88)}$	$16.61^{2.38}$	31.67	2	$7.03^{1.27}$	$45^{(16-87)}$	$13.42^{2.29}$	36.26	2	$5.25^{0.96}$	$35^{(17-67)}$
Leptatherina presbyteroides	EM	$9.08^{2.14}$	15.36	3	$3.62^{0.79}$	$40^{(23-67)}$	$27.48^{6.34}$	19.51	3	$9.34^{2.34}$	$38^{(10-78)}$	$1.77^{0.60}$	3.37	4	$0.69^{0.37}$	$34^{(16-60)}$	$0.01^{0.01}$	0.03	7	$0.01^{0.01}$	$46^{(46)}$
Afurcagobius suppositus	E	$1.08^{0.21}$	1.83	5	$2.64^{0.63}$	$59^{(25-93)}$	$5.68^{1.02}$	4.03	4	$2.97^{0.69}$	$34^{(19-93)}$	$2.11^{0.28}$	4.02	3	$1.73^{0.32}$	$39^{(19-96)}$	$1.84^{0.46}$	4.98	3	$1.33^{0.40}$	$36^{(15-90)}$
Pseudogobius olorum	E	$1.38^{0.38}$	2.34	4	$0.76^{0.20}$	$37^{(24-57)}$	$1.40^{0.38}$	1.00	6	$1.36^{0.37}$	$44^{(21-78)}$	$0.33^{0.14}$	0.63	6	$0.21^{0.09}$	$37^{(21-54)}$	$0.08^{0.04}$	0.22	5	$0.03^{0.02}$	$26^{(16-41)}$
Favonigobius lateralis	EM	$0.23^{0.05}$	0.39	7	$0.71^{0.17}$	$63^{(38-84)}$	$1.46^{0.93}$	1.04	5	$0.84^{0.26}$	$48^{(20-72)}$	$0.75^{0.29}$	1.43	5	$0.77^{0.28}$	$45^{(26-77)}$	$0.63^{0.18}$	1.71	4	$0.79^{0.22}$	$47^{(26-76)}$
Notolabrus parilus	MS	$0.69^{0.31}$	1.17	6	$0.49^{0.29}$	$31^{(19-105)}$	$0.42^{0.17}$	0.30	7	$2.03^{0.88}$	$59^{(22-134)}$	$0.06^{0.03}$	0.11	8	$0.24^{0.18}$	$57^{(41-93)}$					
Hyporhamphus melanochir	EM	$0.18^{0.09}$	0.31	8	$7.17^{3.94}$	$197^{(69-413)}$	$0.02^{0.02}$	0.02	12	$1.05^{0.75}$	$236^{(204-268)}$										
Achoerodus gouldii	MS	$0.30^{0.11}$	0.51	9	$0.22^{0.09}$	$36^{(20-52)}$	$0.27^{0.15}$	0.19	9	$3.00^{1.96}$	$80^{(56-102)}$										
Engraulis australis	EM																				
Aldrichetta forsteri	MEO	$0.10^{0.07}$	0.17	10	$1.25^{0.32}$	$68^{(32-159)}$	$0.29^{0.22}$	0.20	8	$2.82^{2.29}$	$101^{(55-126)}$										
Ammotretis rostratus	MEO	$0.01^{0.01}$	0.02	13	$0.01^{0.01}$	$28^{(28)}$	$0.04^{0.03}$	0.03	11	$0.19^{0.12}$	$62^{(53-87)}$	$0.04^{0.03}$	0.08	9	$0.48^{0.30}$	$86^{(63-114)}$					
Neoodax balteatus	MS	$0.03^{0.02}$	0.05	12	$0.01^{0.01}$	$36^{(31-41)}$	$0.13^{0.08}$	0.09	10	$1.47^{0.91}$	$110^{(87-134)}$										
Ammotretis elongatus	EM						$0.01^{0.01}$	0.01	13	$0.03^{0.03}$	$63^{(63)}$	$0.09^{0.08}$	0.17	7	$0.33^{0.26}$	$66^{(54-93)}$					
Enoplosus armatus	MS	$0.01^{0.01}$	0.02	13	$1.25^{1.14}$	$27^{(27)}$	$0.04^{0.03}$	0.03	11	$0.29^{0.21}$	$72^{(68-76)}$										
Edelia vittata	FS	$0.05^{0.04}$	0.08	11	$0.02^{0.02}$	$21^{(17-27)}$											$0.01^{0.01}$	0.03	7	$0.02^{0.02}$	$49^{(49)}$
Mugil cephalus	MEO																$0.03^{0.02}$	0.08	6	$0.59^{0.32}$	$73^{(26-168)}$
Platycephalus speculator	EM																				
Girella zebra	MS																				
Haletta semifasciata	MS																				
Galaxias occidentalis	FS																$0.01^{0.01}$	0.03	7	$0.04^{0.04}$	$86^{(86)}$
Lepidogalaxias salamandroides	FS						$0.01^{0.01}$	0.01	13	$0.01^{0.01}$	$46^{(46)}$										
Urocampus carinirostris	EM																				
Pseudocaranx dentex	MS																				
Rhabdosargus sarba	MEO	$0.01^{0.01}$	0.02	13	$0.01^{0.01}$	$23^{(23)}$															
Pseudorhombus jenynsii	MEO																				
Cynoglossus broadhursti	MS						$0.01^{0.01}$	0.01	13	$0.19^{0.19}$	$135^{(135)}$										
Species richness		**15**					**16**					**9**					**9**				
Mean overall density		**59**					**141**					**52**					**37**				
Number of samples		**86**					**78**					**78**					**86**				
Adjusted number of individuals		**5,074**					**10,998**					**4,056**					**3,182**				
Actual number of individuals		**5,899**					**12,743**					**4,746**					**3,693**				

life cycle in the estuary. The number of marine estuarine-opportunists and marine straggler species was greatest during spring and summer of both years, although their mean densities were always relatively low. Juveniles of the labrid species *Notolabrus parilus* and *Achoerodus gouldii* (*i.e.* individuals < 100 mm total length), both of which are marine stragglers, were relatively prevalent, *i.e.* totalling 199 individuals. The former labrid species was caught in all seasons except winter and the latter species in three of the eight sampling occasions. Other marine species that were recorded in two or more seasons included juveniles of the marine estuarine-opportunists *Aldrichetta forsteri* and *Ammotretis rostratus.*

4.3.1.2: Differences in nearshore fish assemblage composition among seasons and years

Three-way PERMANOVA of the spatio-temporal trends in the composition of the nearshore fish community of Broke Inlet detected significant differences among all main effects, *i.e.* habitats, seasons and years and also for the three-way interaction term (p=0.001; see subsection 3.3.1.4, Table 3.3). Thus, in order to investigate temporal differences in the nearshore ichthyofauna without the confounding influence of habitat, the following analyses were carried out separately for each habitat.

Two-way crossed season x year ANOSIM tests detected significant ichthyofaunal differences between years and seasons in all habitats, with the exception of year in habitat A (p=0.287; Table 4.2). The overall extent of those significant inter-annual differences ranged from low to moderate (Global R=0.141-0.569), with the most pronounced differences detected in habitats G, H and J, while the lowest were recorded in habitats C, E and I. These findings were reflected on the nMDS plots constructed for each habitat, whereby samples collected in 2007/2008 were typically situated on the opposite side of the plot from those collected in 2008/2009 at habitat J, whereas they were more intermingled in the other habitats in particular C and E (Fig. 4.1). Two-way crossed SIMPER demonstrated that the significant inter-annual differences detected at all habitats except A were caused, in part, by greater densities of the atherinids *A. elongata* and *L. presbyteroides* and the gobiids *F. lateralis* and *A. suppositus* in

Table 4.2: *R*-statistic and/or significance level (*p*) values derived from two-way crossed year x season ANOSIM tests on the nearshore fish faunal composition data recorded at habitat types A-K (a-k). Insignificant pairwise comparisons are highlighted in grey.

(a) Habitat A

Year: *p*=0.287, Global *R*=0.042
Season: *p*=0.027, Global *R*=0.286

(b) Habitat B

Year: *p*=0.001, Global *R*=0.326
Season: *p*=0.001, Global *R*=0.284

	Spring	Summer	Autumn
Summer	0.349		
Autumn	0.172	0.359	
Winter	0.328	0.500	0.047

(c) Habitat C

Year: *p*=0.001, Global *R*=0.263
Season: *p*=0.001, Global *R*=0.269

	Spring	Summer	Autumn
Summer	0.206		
Autumn	0.318	0.401	
Winter	0.333	0.281	0.260

(d) Habitat D

Year: *p*=0.001, Global *R*=0.365
Season: *p*=0.001, Global *R*=0.457

	Spring	Summer	Autumn
Summer	0.729		
Autumn	0.609	0.479	
Winter	0.292	0.531	0.234

(e) Habitat E

Year: *p*=0.020, Global *R*=0.258
Season: *p*=0.001, Global *R*=0.330

	Spring	Summer	Autumn
Summer	0.448		
Autumn	0.453	0.370	
Winter	0.271	0.370	0.073

(f) Habitat F

Year: *p*=0.007, Global *R*=0.315
Season: *p*=0.008, Global *R*=0.205

	Spring	Summer	Autumn
Summer	0.182		
Autumn	0.208	0.260	
Winter	0.141	0.286	0.042

(g) Habitat G

Year: *p*=0.001, Global *R*=0.477
Season: *p*=0.003, Global *R*=0.294

	Spring	Summer	Autumn
Summer	0.031		
Autumn	0.443	0.255	
Winter	0.441	0.380	0.313

(h) Habitat H

Year: *p*=0.001, Global *R*=0.568
Season: *p*=0.001, Global *R*=0.377

	Spring	Summer	Autumn
Summer	0.349		
Autumn	0.823	0.391	
Winter	0.766	0.344	0.010

(i) Habitat I

Year: *p*=0.050, Global *R*=0.141
Season: *p*=0.013, Global *R*=0.177

	Spring	Summer	Autumn
Summer	0.016		
Autumn	0.214	0.031	
Winter	0.245	0.297	0.255

(j) Habitat J

Year: *p*=0.001, Global *R*=0.569
Season: *p*=0.010, Global *R*=0.237

	Spring	Summer	Autumn
Summer	0.519		
Autumn	0.136	0.259	
Winter	0.352	0.204	0.065

(k) Habitat K

Year: *p*=0.001, Global *R*=0.378
Season: *p*=0.001, Global *R*=0.331

	Spring	Summer	Autumn
Summer	0.422		
Autumn	0.339	-0.047	
Winter	0.609	0.349	0.333

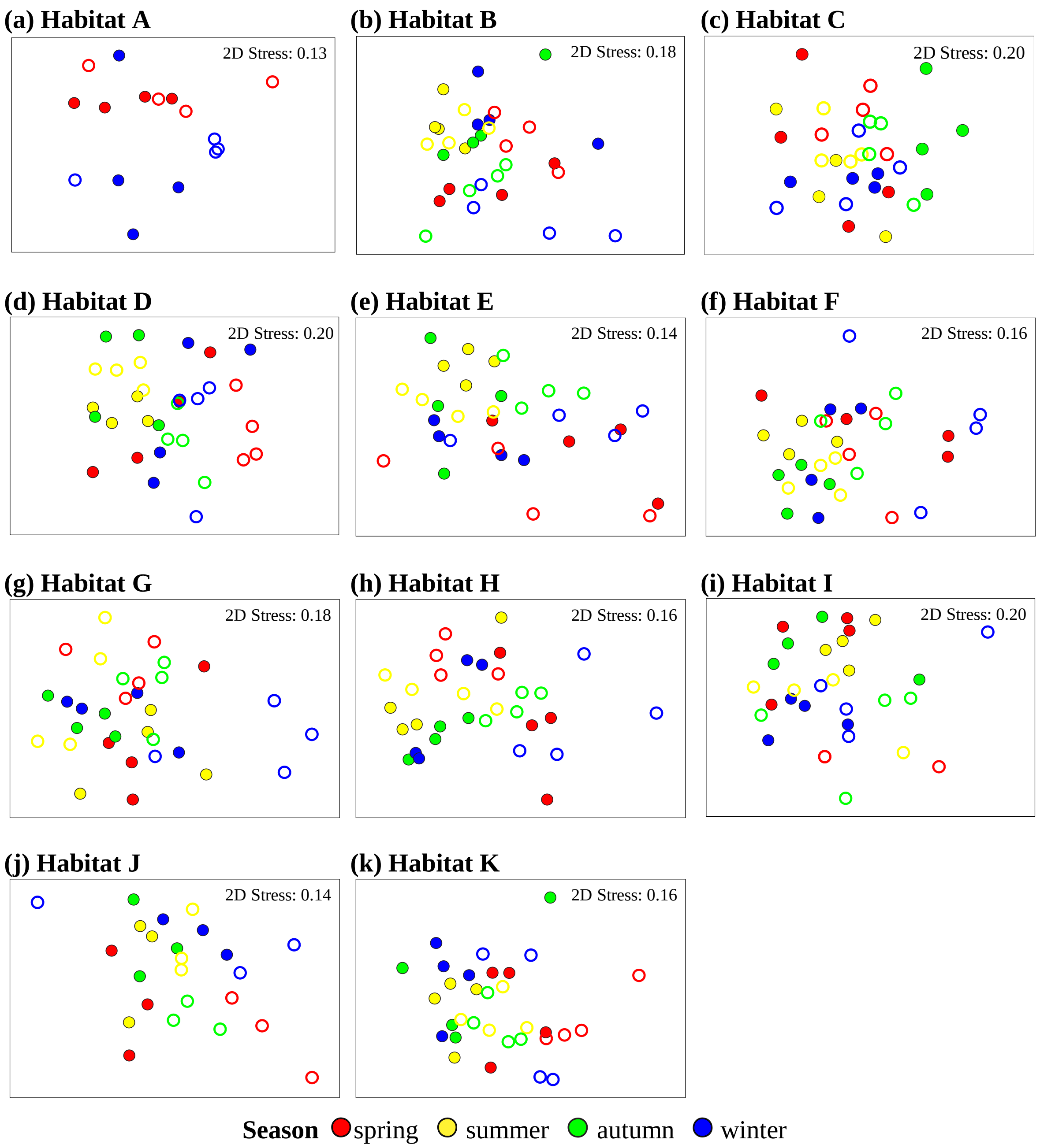


Fig. 4.1: nMDS ordination plots of the fish faunal composition at each nearshore site in each season and year at habitat types A–K (a-k). Closed circles represent samples from 2007/2008, while open circles 2008/2009. Note that habitat A was only able to be sampled in spring and winter in both years.

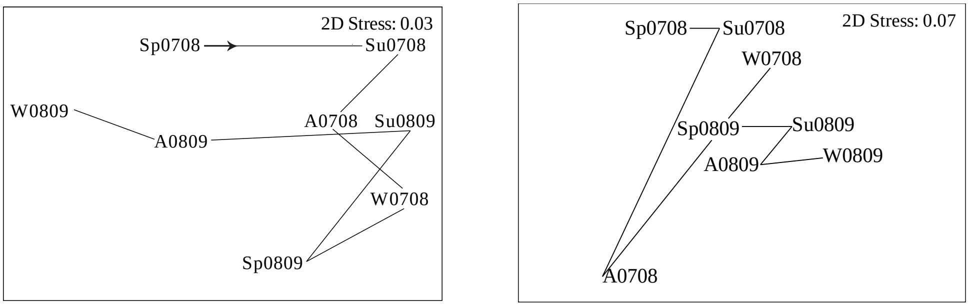
2007/2008 than 2008/2009 (Appendix 4.1b-k). In contrast, the densities of *L. wallacei* did not exhibit consistent inter-annual trends in each of the various habitats, with greater densities being recorded in 2007/2008 in habitats located in Shannon and Clarke basins (E, F, J and K) and habitat H in the entrance channel while the reverse was true for habitats located in the Middle basin (C, D, G, and I) and habitat B in the entrance channel.

The overall extent of seasonal differences in ichthyofaunal composition in each habitat was generally less than that of year, *i.e.* Global *R*=0.177-0.457, with the greatest differences occurring at habitats D and H and the least at habitats F and I (Table 4.2). At least one pair of seasons did not differ significantly in every habitat. At habitat D, moderately large to large differences were detected for spring *vs* summer and autumn, and moderate differences were also recorded for summer *vs* autumn and winter. These findings were clearly illustrated on the associated nMDS ordination plots in which samples from summer formed a cluster on the middle left of the plot (Fig. 4.1d). SIMPER showed that these differences were due to the highest densities of the three atherinid species in summer, followed by spring, which in turn were greater than those in either autumn or winter, while densities of the gobiid species *F. lateralis* and *A. suppositus* were lowest in spring (Appendix 4.1d). At habitat H however, by far the most pronounced differences were detected for spring *vs* autumn and winter (pairwise *R*=0.766-0.823). Samples from the former season were relatively distinct from those in the latter two seasons (Fig. 4.1h), which were caused, in some part, by the lower densities of *L. wallacei* and *L. presbyteroides* and higher densities of *P. olorum* present during spring (Appendix 4.1h). In most of the remaining habitats, namely, E, K and J, the greatest differences were recorded between spring and one or more of the other seasons which generally contained lower densities of atherinid species with the exception of winter in habitat J when these species were more abundant (Appendix 4.1e, k and j).

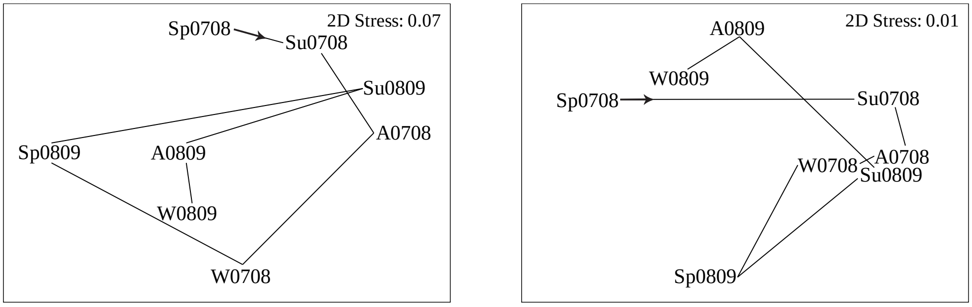
4.3.1.3: Cyclical temporal changes in nearshore ichthyofaunal composition

No significant cyclical changes in the composition of the nearshore fish fauna were detected among the various seasons in each year in any habitat except C. However, the extent of the correlation between the temporal patterns recorded in that latter habitat and the cyclical model matrix was low (p=0.020; ρ=0.250). The lack of temporal cyclicity was clearly demonstrated, for each habitat, by the nMDS plots of the average fish faunal composition in each season and year (Fig. 4.2). Note that habitat A was not included in this analysis as insufficient data was recorded at this habitat.

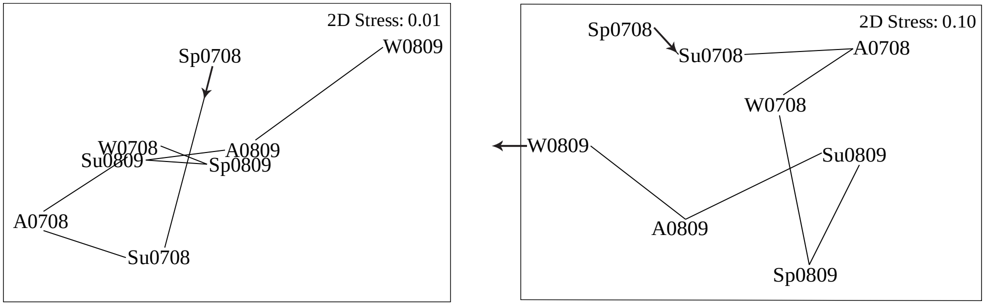
(a) Habitat B; *p*=0.555, ρ=-0.037 **(b) Habitat C; *p*=0.020, ρ=0.250**



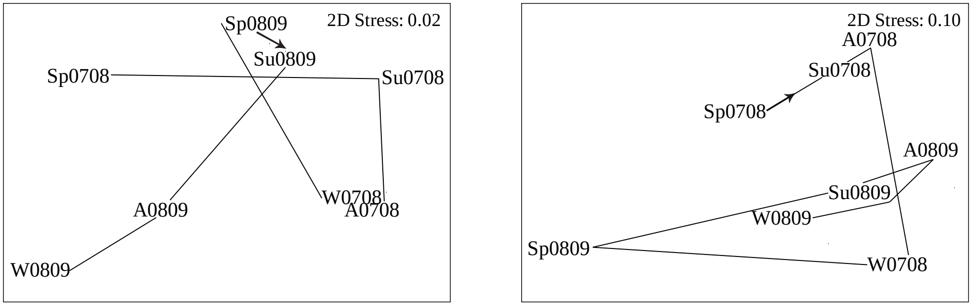
(c) Habitat D; *p*=0.068, ρ=0.263 **(d) Habitat E**; *p*=0.449, ρ=0.02



(e) Habitat F; *p*=0.798, ρ=-0.095 **(f) Habitat G**; *p*=0.461, ρ=0.018



(g) Habitat H; *p*=0.330, ρ=0.111 **(h) Habitat I**; *p*=0.258, ρ=0.101



(i) Habitat J; *p*=0.699, ρ=-0.105 **(j) Habitat K**; *p*=0.121, ρ=0.122

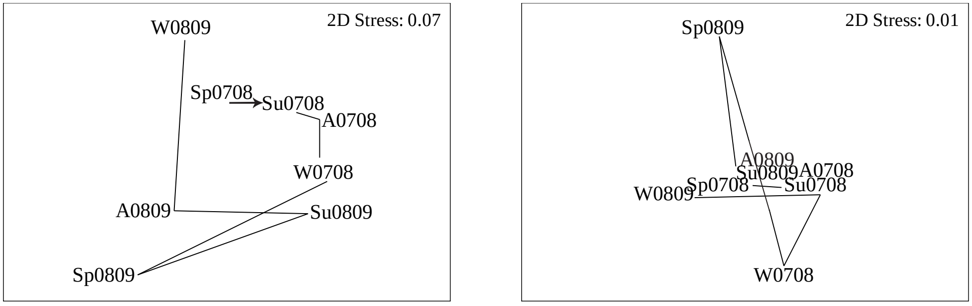


Fig. 4.2: nMDS ordination plots of the average fish faunal composition recorded in each season and year for habitats B-K (a-j). The lines join consecutive seasons from spring 2007/2008 to winter 2008/2009. The significance levels (*p*) and rho values (ρ) obtained from RELATE tests between the matrices used to construct each nMDS plot and cyclical model matrix are also provided.

4.3.1.4: Matching temporal patterns between the fish community and non-enduring environmental characteristics at each nearshore habitat type

The RELATE procedure was employed to determine the extent to which the pattern of relative differences in the fish faunal composition in each season and year matched that displayed by the complementary suite of non-enduring environmental variables. These analyses, which were carried out separately for each habitat, did not detect a significant correlation in any case (Table 4.3). Moreover, when BIOENV was employed to determine whether a better correlation with the fish faunal data could be achieved by only employing a particular subset of those non-enduring environmental variables, no significant matches were detected, with the exception of habitat G, located at the basin end of the entrance channel, at which salinity alone provided a moderately good correlation (p=0.042, ρ=0.619).

4.3.1.5: Matching temporal patterns in nearshore fish faunal composition among habitat types

Temporal patterns in fish faunal compositions were compared among each of the 11 nearshore habitats, with the exception of A, at which sampling was only able to be conducted during spring and winter of both years. This analysis, which was conducted using the RELATE routine, detected a significant match in 19 of the 45 pairwise comparisons among habitats, with the greatest correlations in temporal patterns typically being detected between pairs of habitats that were located in close proximity to each other, *e.g.* B *vs* H, F *vs* H and K *vs* I (Table 4.4). Such findings were summarised by the second-stage ordination of the correlation values shown in Table 4.4 (Fig. 4.3). On this plot, adjacent habitats tended to be closely grouped, *e.g.* I, J and K, reflecting the similarity in their underlying temporal patterns of fish faunal composition, whereas habitat C, whose temporal patterns was not significantly correlated with those of any other habitat, was distantly separate from the remaining habitats (Table 4.4; Fig. 4.3).

Table 4.3: Significance levels (*p*) and rho statistic (ρ) values for the correlation between a resemblance matrix constructed from the average fish faunal data in each season and year and complementary matrices constructed from (a) the full suite of non-enduring environmental variables (NEVs), and (b) the subset of the non-enduring environmental variables (NEV subset) selected by the BIOENV routine. Analyses were repeated for each nearshore habitat type (with the exception of A, at which insufficient data was collected). Significant correlations are highlighted in bold.

	(a) NEVs		**(b) NEV subset**		
Habitat	***p***	**ρ**	***p***	**ρ**	**Variables selected**
B	0.809	-0.166	0.965	0.038	
C	0.469	0.002	0.821	0.201	
D	0.814	-0.168	0.384	0.331	
E	0.115	0.242	0.255	0.405	
F	0.053	0.294	0.071	0.589	
G	0.577	-0.086	**0.042**	**0.619**	**Salinity**
H	0.602	-0.057	0.714	0.212	
I	0.432	0.257	0.185	0.459	
J	0.577	-0.046	0.766	0.105	
K	0.130	0.292	0.197	0.499	

Table 4.4: Rho statistic (ρ) and significance level (*p*) derived from the RELATE routines in which complementary matrices constructed from the average fish faunal data recorded in each season and year were correlated for all pairs of nearshore habitat types (except A at which insufficient data was recorded). Insignificant pairwise comparisons are highlighted in grey.

	B	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**
C	-0.215								
D	0.057	-0.061							
E	0.551	-0.025	0.327						
F	0.495	0.386	-0.209	0.337					
G	0.501	0.227	0.001	0.595	0.568				
H	0.807	0.184	-0.057	0.584	0.669	0.445			
I	0.048	-0.229	0.401	0.224	-0.271	0.117	-0.127		
J	0.498	-0.283	0.304	0.375	0.241	0.539	0.310	0.383	
K	0.349	-0.144	0.403	0.333	-0.022	-0.023	0.209	0.517	0.447

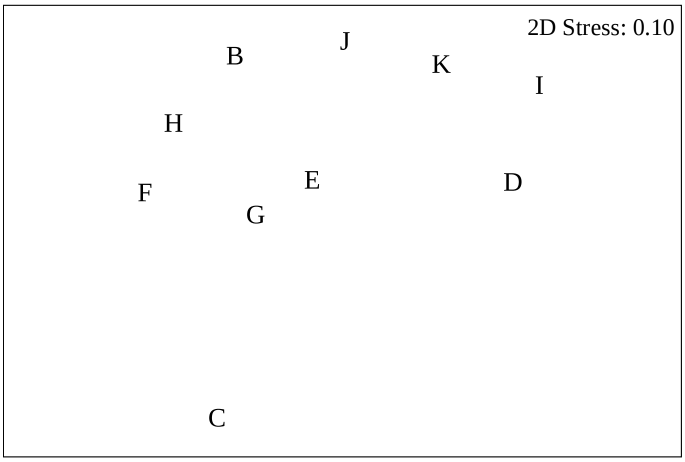


Fig. 4.3: nMDS ordination of the second-stage matrix shown in Table 4.4.

4.3.2: Offshore waters

4.3.2.1: Offshore fish species mean density and life cycle contribution in each season

The number of species caught in the offshore waters in spring and summer in both 2007/2008 and 2008/2009 was relatively consistent, ranging between 16 and 18 species. While similar numbers of species were also caught in autumn and winter of the first year, 21 and 6 species, respectively, were caught in those seasons in the second year (Table 4.5). The total number of fish caught in spring and summer of both years was similar *i.e.* 122-188 fish. However, while notably lower total catches were recorded in autumn 2007/2008 (92 fish), they were far higher in autumn 2008/2009 than any other occasion (258 fish). Total catches in the winters of both years were similar (59-65 fish), and were by far the lowest recorded in any season (Table 4.5).

Australian Herring (*Arripis georgianus*), a marine estuarine-opportunist, was ranked between first and third in terms of their catch rate in all seasons except winter 2008/2009. *Mugil cephalus*, *Engraulis australis* and, to a lesser extent, *Aldrichetta foresteri*, were also frequently ranked in the top four species. However, the remaining abundant species, *i.e.* those that contributed > 5% to the total catch, varied considerably among seasons and years. Despite this, marine estuarine-opportunists numerically dominated the offshore fish fauna on all sampling occasions, representing between 59 and 86% of the fish collected. This guild was also the most speciose comprising between eight and 11 representatives in all seasons and years except winter 2008/2009, during which only four species were caught. The number of estuarine and marine species caught also remained largely consistent among sampling occasions (3-4), with the exception of winter 2008/2009 (2 species). Marine stragglers, in contrast, exhibited pronounced temporal changes, both in the number of species caught (0-7) and their contributions to the total catch (0-13%). This variability is reflected in the fact that, of the 14 marine straggler species caught throughout the duration of this study, only four, *Enoplosus armatus*, *Sillago bassensis*, *Achoerodus gouldii* and *Girella zebra* were caught on more than two occasions (Table 4.5).

Table 4.5: Catch rate (fish 10 h^{-1}; C), standard error (^{SE}), percentage contribution to the overall catch (%), rank by catch rate (R), biomass (g; B), mean length (mm; L) and length range (^{r}) of each fish species recorded at the three offshore habitat types in Broke Inlet in each season sampled between spring 2007/2008 and winter 2008/2009. Abundant species in each season (*i.e.* those that contribute > 5% to the catch) are highlighted in grey. The life cycle category (LC) of each species is also provided (EM = estuarine and marine, MEO = marine estuarine-opportunist, MS = marine straggler). The species richness, mean total catch rates and adjusted number of individuals (*i.e.* after the number of individuals in each sample have been adjusted to caught in ten hours and summed) are given for each season sampled. Species ranked according to their total catch rate.

Species	LC	**Spring 2007/2008**					**Summer 2007/2008**					**Autumn 2007/2008**					**Winter 2007/2008**				
		C^{SE}	%	R	B^{SE}	L^{r}	C^{SE}	%	R	B^{SE}	L^{r}	C^{SE}	%	R	B^{SE}	L^{r}	C^{SE}	%	R	B^{SE}	L^{r}
Arripis georgianus	MEO	$3.34^{1.60}$	23.26	1	$517.09^{261.39}$	$236^{(202-2880)}$	$1.44^{0.38}$	10.66	3	$320.32^{82.75}$	$237^{(194-282)}$	$4.33^{2.63}$	42.39	1	$910.69^{553.63}$	$249^{(212-290)}$	$1.11^{0.35}$	15.38	3	$315.46^{133.35}$	$236^{(200-257)}$
Mugil cephalus	MEO	$1.45^{0.84}$	10.08	3	$567.28^{299.57}$	$326^{(213-407)}$	$1.33^{0.94}$	9.84	4	$694.42^{494.09}$	$352^{(299-396)}$	$0.11^{0.11}$	1.09	12	$56.75^{56.75}$	$352^{(352)}$	$1.22^{0.22}$	16.92	2	$937.19^{214.33}$	$316^{(214-411)}$
Engraulis australis	EM	$1.34^{0.65}$	9.30	4	$13.50^{7.32}$	$114^{(84-128)}$	$0.67^{0.29}$	4.92	7	$4.57^{2.03}$	$102^{(84-119)}$	$0.44^{0.24}$	4.35	6	$6.66^{3.53}$	$91^{(76-110)}$	$1.33^{0.62}$	18.46	1	$31.22^{17.29}$	$121^{(98-141)}$
Aldrichetta forsteri	MEO	$1.12^{0.43}$	7.75	7	$317.03^{111.37}$	$317^{(247-414)}$	$2.44^{0.82}$	18.03	2	$839.04^{323.07}$	$313^{(168-383)}$	$0.67^{0.55}$	6.52	5	$207.6^{180.11}$	$315^{(291-340)}$	$1.00^{0.41}$	13.85	4	$529.22^{222.84}$	$207^{(140-452)}$
Rhabdosargus sarba	MEO	$0.45^{0.25}$	3.10	9	$179.68^{111.67}$	$279^{(225-397)}$	$0.56^{0.29}$	4.10	8	$258.69^{163.17}$	$278^{(82-387)}$	$0.11^{0.11}$	1.09	12	$102.46^{102.46}$	$283^{(382)}$	$0.22^{0.22}$	3.08	7	$17.27^{17.27}$	$173^{(171-174)}$
Ammotretis rostratus	EM	$0.78^{0.58}$	5.43	8	$154.40^{123.78}$	$305^{(188-501)}$	$0.22^{0.15}$	1.64	12	$61.47^{41.09}$	$277^{(263-291)}$	$0.89^{0.26}$	8.70	3	$49.19^{18.61}$	$139^{(74-212)}$	$0.89^{0.42}$	12.31	5	$156.23^{72.9}$	$208^{(127-251)}$
Pseudocaranx dentex	MEO	$0.12^{0.12}$	0.78	13	$27.37^{27.37}$	$269^{(269)}$	$2.78^{1.98}$	20.49	1	$777.39^{546.77}$	$274^{(250-290)}$	$0.22^{0.22}$	2.17	10	$28.85^{28.85}$	$212^{(208-215)}$					
Pagrus auratus	MEO	$1.34^{0.90}$	9.30	4	$151.67^{98.52}$	$191^{(174-210)}$	$1.33^{0.67}$	9.84	4	$315.8^{171.01}$	$241^{(82-387)}$	$0.33^{0.33}$	3.26	0	99^{99}	$257^{(245-266)}$	$0.11^{0.11}$	1.54	10	$43.47^{43.47}$	$290^{(290)}$
Arripis truttaceus	MEO	$1.34^{0.99}$	9.30	4	$740.44^{528.29}$	$361^{(339-380)}$															
Sillaginodes punctatus	MEO	$0.23^{0.15}$	1.55	11	$65.86^{43.60}$	$373^{(370-376)}$						$0.44^{0.44}$	4.35	6	$87.43^{19.12}$	$285^{(244-304)}$	$0.33^{0.17}$	4.62	6	$73.12^{44.68}$	$325^{(307-362)}$
Gonorynchus greyi	MEO	$0.23^{0.15}$	1.55	11	$17.09^{11.37}$	$241^{0230-251)}$	$0.33^{0.24}$	2.46	11	$23.26^{18.12}$	$233^{(210-246)}$	$1.00^{0.53}$	9.78	2	$323.12^{69.61}$	$263^{(238-293)}$	$0.11^{0.11}$	1.54	10	$10.86^{10.86}$	$246^{(246)}$
Hyporhamphus melanochir	EM	$1.89^{1.43}$	13.18	2	$129.03^{154.56}$	$339^{(297-386)}$	$0.11^{0.11}$	0.82	14	$12.14^{12.14}$	$345^{(345)}$	$0.22^{0.15}$	2.17	9	$126.64^{3.03}$	$343^{(343-340)}$	$0.11^{0.11}$	1.54	10	$41.34^{41.34}$	$341^{(326-364)}$
Enoplosus armatus	MS						$0.11^{0.11}$	0.82	14	$4.71^{4.71}$	$150^{(150)}$	$0.78^{0.78}$	7.61	4	$29.15^{29.15}$	$121^{(85-131)}$	$0.11^{0.11}$	1.54	10	$3.17^{3.17}$	$131^{(131)}$
Pomatomus saltatrix	MEO						$0.89^{0.61}$	6.56	6	$570.66^{383.85}$	$388^{(351-420)}$										
Sillago bassensis	MS																				
Cnidoglanis macrocephalus	EM						$0.11^{0.11}$	0.82	14	$19.87^{19.87}$	$335^{(335)}$						$0.11^{0.11}$	1.54	10	$37.87^{37.87}$	$431^{(431)}$
Platycephalus speculator	EM	$0.12^{0.12}$	0.78	13	$30.99^{30.99}$	$355^{(355)}$	$0.22^{0.22}$	1.64	12	$13.77^{13.77}$	$224^{(222-226)}$	$0.11^{0.11}$	1.09	12	48^{48}	$202^{(202)}$					
Pseudorhombus jenynsii	MEO	$0.12^{0.12}$	0.78	13	$13.12^{13.12}$	$225^{(225)}$	$0.56^{0.38}$	4.10	8	$185.21^{132.22}$	$307^{(283-336)}$										
Achoerodus gouldii	MS											$0.33^{0.33}$	3.26	8	$36.82^{36.82}$	$167^{(120-195)}$					
Sillago schomburgkii	MEO	$0.12^{0.12}$	0.78	13	$30.14^{30.14}$	$320^{(320)}$											$0.22^{0.15}$	3.08	7	$14.58^{9.67}$	$209^{(206-212)}$
Girella zebra	MS																$0.22^{0.22}$	3.08	7	$157.07^{157.07}$	$268^{(253-277)}$
Mustelus antarcticus	MS						$0.44^{0.24}$	3.28	10	$5001.62^{2712.38}$	$1357^{(1190-1480)}$										
Chelidonichthys kumu	MS	$0.34^{0.17}$	2.33	10	$90.70^{45.51}$	$290^{(275-304)}$											$0.11^{0.11}$	1.54	10	$59.83^{59.83}$	$362^{(362)}$
Schuettea woodwardi	MS	$0.12^{0.12}$	0.78	13	$6.36^{6.36}$	$166^{(166)}$															
Scorpis georgiana	MS																				
Notolabrus parilus	MS																				
Myliobatis australis	MS																				
Lotella rhacina	MS											$0.11^{0.11}$	1.09	12	$34.16^{34.16}$	$362^{(362)}$					
Tilodon sexfasciatum	MS																				
Cynoglossus broadhursti	MS																				
Eubalichthys bucephalus	MS											$0.11^{0.11}$	1.09	12	$42.29^{42.29}$	$297^{(297)}$					
Species richness		17					16					16					15				
Mean total catch rate		14					14					10					7				
Number of samples		9					9					9					9				
Adjusted number of individuals		126					126					90					63				
Actual number of individuals		129					122					92					65				

Table 4.5 Continued:

Species	LC	Spring 2008/2009					Summer 2008/2009					Autumn 2008/2009					Winter 2008/2009				
		C^{SE}	%	R	B^{SE}	L^{r}	C^{SE}	%	R	B^{SE}	L^{r}	C^{SE}	%	R	B^{SE}	L^{r}	C^{SE}	%	R	B^{SE}	L^{r}
Arripis georgianus	MEO	$4.12^{1.23}$	26.06	2	$808.62^{273.39}$	$256^{(242-264)}$	$3.33^{1.48}$	15.96	2	$903.59^{456.38}$	$268^{(225-310)}$	$7.00^{.5.89}$	24.42	1	$1814.12^{1528.17}$	$267^{(232-312)}$					
Mugil cephalus	MEO	$0.23^{0.15}$	1.41	9	$90.75^{60.31}$	$332^{(327-336)}$	$6.44^{2.10}$	30.85	1	$2729.99^{638.89}$	$351^{(118-459)}$	$5.33^{1.50}$	18.60	2	$1771.4^{661.85}$	$274^{(148-420)}$	$3.44^{1.75}$	52.54	1	$640.79^{349.66}$	$243^{(156-396)}$
Engraulis australis	EM	$4.67^{2.83}$	29.58	1	$78.24^{48.82}$	$125^{(93-176)}$	$2.00^{1.18}$	9.57	4	$19.39^{11.44}$	$117^{(107-136)}$	$0.56^{0.56}$	1.94	11	$8.33^{5.75}$	$120^{(109-131)}$	$0.78^{0.78}$	11.86	3	$8.04^{8.04}$	$111^{(75-132)}$
Aldrichetta forsteri	MEO	$0.34^{0.17}$	2.11	7	$120.39^{73.51}$	$307^{(203-365)}$	$2.67^{1.27}$	12.77	3	$815.89^{356.25}$	$305^{(238-403)}$	$1.56^{0.85}$	5.43	7	$482.46^{281.67}$	$315^{(247-364)}$	$1.33^{0.94}$	20.34	2	$153.06^{102.45}$	$216^{(172-268)}$
Rhabdosargus sarba	MEO	$1.12^{0.88}$	7.04	5	$321.22^{204.30}$	$239^{(207-374)}$	$1.67^{0.78}$	7.98	5	$1002.14^{561.30}$	$290^{(234-387)}$	$2.67^{1.32}$	9.30	3	$1344.29^{684.76}$	$296^{(258-354)}$	$0.44^{0.18}$	6.78	4	$321.55^{144.04}$	$344^{(280-415)}$
Ammotretis rostratus	EM	$0.67^{0.29}$	4.23	6	$103.74^{50.49}$	$217^{(180-252)}$	$0.78^{0.36}$	3.72	7	$156.26^{83.01}$	$246^{(208-270)}$	$2.44^{1.07}$	8.53	4	$365.61^{225.03}$	$213^{(85-292)}$	$0.44^{0.24}$	6.78	4	$79.79^{45.50}$	$210^{(136-273)}$
Pseudocaranx dentex	MEO	$0.34^{0.34}$	2.11	7	$72.98^{72.98}$	$256^{(242-264)}$	$0.22^{0.22}$	1.06	11	$92.23^{92.23}$	$273^{(162-383)}$	$2.11^{1.12}$	7.36	5	$460.77^{170.76}$	$243^{(185-363)}$					
Pagrus auratus	MEO						$0.32^{0.24}$	1.60	10	$192.03^{162.01}$	$326^{(254-410)}$	$1.89^{1.21}$	6.59	6	$1067.3^{771.83}$	$322^{(152-392)}$					
Arripis truttaceus	MEO	$1.34^{0.67}$	8.45	4	$796.26^{398.16}$	$361^{(334-384)}$	$1.22^{1.22}$	5.85	6	$903.20^{903.20}$	$386^{(304-409)}$	$0.33^{0.24}$	1.16	13	$339.27^{248.51}$	$443^{(430-457)}$	$0.11^{0.11}$	1.69	6	$29.34^{29.34}$	$283^{(283)}$
Sillaginodes punctatus	MEO	$1.67^{1.43}$	10.56	3	$344.97^{297.56}$	$310^{(291-331)}$	$0.67^{0.47}$	3.19	8	$196.89^{154.74}$	$335^{(240-383)}$	$0.44^{0.24}$	1.55	12	$186.6^{107.32}$	$388^{(372-410)}$					
Gonorynchus greyi	MEO						$0.11^{0.11}$	0.53	13	$13.58^{13.58}$	$272^{(272)}$	$1.44^{1.08}$	5.04	8	$125.83^{94.29}$	$224^{(112-264)}$					
Hyporhamphus melanochir	EM						$0.11^{0.11}$	0.53	13	$18.94^{18.94}$	$396^{(396)}$										
Enoplosus armatus	MS											$1.00^{0.78}$	3.49	9	$59.27^{39.61}$	$152^{(121-204)}$					
Pomatomus saltatrix	MEO						$0.67^{0.55}$	3.19	8	$556.67^{532.32}$	$407^{(257-680)}$	$0.11^{0.11}$	0.39	15	$32.49^{32.49}$	$312^{(312)}$					
Sillago bassensis	MS	$0.12^{0.12}$	0.70	13	$7.92^{7.92}$	$194^{(194)}$	$0.11^{0.11}$	0.53	13	$8.12^{8.12}$	$204^{(204)}$	$0.78^{0.78}$	2.71	10	$48.20^{48.20}$	$194^{(179-219)}$					
Cnidoglanis macrocephalus	EM	$0.23^{0.15}$	1.41	9	$108.47^{72.84}$	$441^{(406-475)}$						$0.33^{0.24}$	1.16	13	$410.82^{287.73}$	$627^{(615-635)}$					
Platycephalus speculator	EM						$0.22^{0.22}$	1.06	11	$57.45^{57.45}$	$343^{(320-365)}$	$0.11^{0.11}$	0.39	15	$55.81^{55.81}$	$425^{(425)}$					
Pseudorhombus jenynsii	MEO											$0.11^{0.11}$	0.39	15	$61.00^{61.00}$	$349^{(349)}$					
Achoerodus gouldii	MS	$0.12^{0.12}$	0.70	13	$23.66^{23.66}$	$210^{(210)}$	$0.11^{0.11}$	0.53	13	$44.04^{44.04}$	$240^{(240)}$	$0.11^{0.11}$	0.39	15	$17.56^{17.56}$	$199^{(199)}$					
Sillago schomburgkii	MEO	$0.23^{0.23}$	1.41	9	$27.91^{27.91}$	$243^{(242-244)}$															
Girella zebra	MS	$0.23^{0.23}$	1.41	9	$81.31^{81.31}$	$262^{(253-271)}$	$0.11^{0.11}$	0.53	13	$43.68^{43.68}$	$273^{(273)}$										
Mustelus antarcticus	MS																				
Chelidonichthys kumu	MS																				
Schuettea woodwardi	MS	$0.12^{0.12}$	0.70	13	$13.19^{13.19}$	$239^{(207-374)}$															
Scorpis georgiana	MS	$0.12^{0.12}$	0.70	13	$31.62^{31.62}$	$249^{(249)}$						$0.11^{0.11}$	0.39	15	$26.39^{26.39}$	$237^{(237)}$					
Notolabrus parilus	MS	$0.12^{0.12}$	0.70	13	$3.75^{3.75}$	$132^{(132)}$						$0.11^{0.11}$	0.39	15	$5.14^{5.14}$	$143^{(143)}$					
Myliobatis australis	MS	$0.12^{0.12}$	0.70	13	$444.45^{444.45}$	$800^{(800)}$															
Lotella rhacina	MS																				
Tilodon sexfasciatum	MS						$0.11^{0.11}$	0.53	13	$19.16^{19.16}$	$194^{(194)}$										
Cynoglossus broadhursti	MS											$0.11^{0.11}$	0.39	15	$1.65^{1.65}$	$136^{(136)}$					
Eubalichthys bucephalus	MS																				
Species richness		18					18					21					6				
Mean total catch rate		16					21					29					7				
Number of samples		9					9					9					9				
Adjusted number of individuals		144					189					261					63				
Actual number of individuals		142					188					258					59				

4.3.2.2: Differences in offshore fish composition among seasons and years

Initial investigation of the spatial and temporal differences in the composition of the offshore ichthyofaunal community, employing PERMANOVA, detected significant differences among all main effects, *i.e.* habitat, season and year, and also the two-way interactions between year and season, and season and habitat (*p*=0.001-0.007; see subsection 3.3.2.4; Table 3.10). Thus, in order to more fully investigate temporal differences in the offshore ichthyofauna without the confounding influence of habitat, the subsequent analyses were conducted for each habitat separately.

Two-way crossed ANOSIM tests detected significant differences in ichthyofaunal compositions among both seasons and years in each of the three offshore habitats (*p*=0.005-0.039). The overall extent of those differences, however, were low (Global *R*=0.173-0.316) with slightly larger *R* values detected for season than year in habitats A and B, while the reverse was true for habitat C (Table 4.6). Within habitat A, the greatest seasonal differences were recorded between spring and each of the other seasons (pairwise *R*=0.370-0.481), which was also reflected by the fact that the samples from this season formed the most discrete group on the ordination plot (Fig. 4.4a). Two-way crossed SIMPER showed that while *A. georgianus* typified the fauna in all seasons at habitat A, it was particularly prevalent in spring. Moreover, greater catch rates of another arripid, *Arripis truttaceus*, also distinguished the fish fauna recorded in spring from that in other seasons (Appendix 4.2a). Significant differences were also detected between autumn and winter at habitat A, which was mainly due to greater catches of several marine estuarine-opportunist species in the former season, namely *A. georgianus*, *Pagrus auratus*, *Gonorynchus greyi* and *Pseudocaranx dentex*.

Mugilids dominated the offshore fish fauna of habitat B, with *M. cephalus* typifying the catch throughout most of the year and *A. forsteri* characterising that during spring and summer (Appendix 4.2b). The greatest seasonal differences at this habitat were between summer and winter and also between summer and autumn. The relative distinctness of the fish fauna in the first of these seasons was illustrated on the ordination, in which samples collected in summer were situated in a broad cluster below those from autumn and winter (Fig. 4.4b). SIPMER demonstrated that the ichthyofaunal

Table 4.6: *R*-statistic and/or significance level (*p*) values derived from two-way crossed year x season ANOSIM tests on the offshore fish faunal composition data recorded at habitat types A-C (a-c). Insignificant pairwise comparisons are highlighted in grey.

(a) Habitat A

Year: *p*=0.039, Global *R*=0.278
Season: *p*=0.005, Global *R*=0.316

	Spring	Summer	Autumn
Summer	0.370		
Autumn	0.444	0.000	
Winter	0.481	0.204	0.204

(b) Habitat B

Year: *p*=0.031, Global *R*=0.242
Season: *p*=0.006, Global *R*=0.299

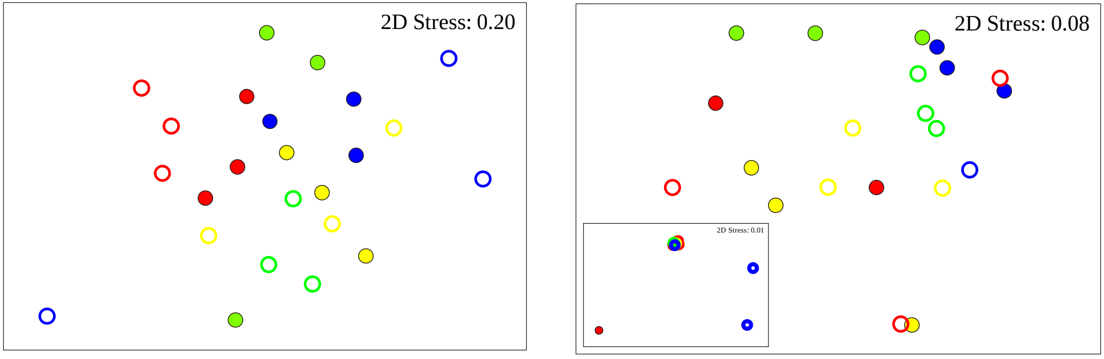
	Spring	Summer	Autumn
Summer	0.046		
Autumn	0.259	0.407	
Winter	0.167	0.539	0.333

(c) Habitat C

Year: *p*=0.027, Global *R*=0.227
Season: *p*=0.038, Global *R*=0.173

	Spring	Summer	Autumn
Summer	-0.176		
Autumn	0.306	-0.056	
Winter	0.343	0.241	0.333

(a) Habitat A: **(b) Habitat B:**



(c) Habitat C:

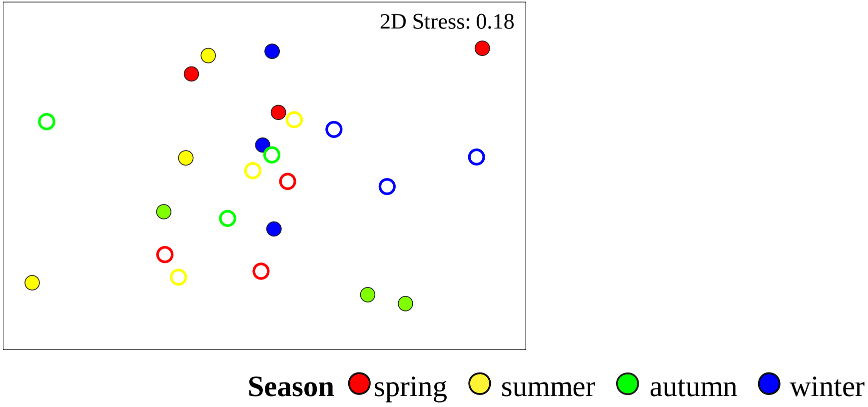


Fig. 4.4: nMDS ordination plots constructed from the offshore fish assemblage data recorded at each site in each sampling season at habitat A (a), B (b) and C (c). Closed circles represent samples from 2007/2008, while open circles 2008/2009.

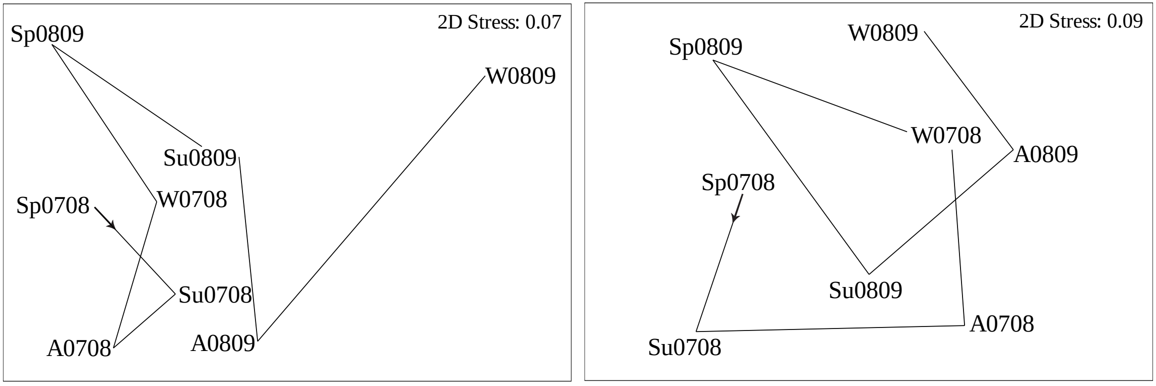
differences among these seasons were mainly due to higher catch rates during summer of the estuarine and marine species, *E. australis,* and the marine estuarine-opportunists *A. georgianus* and *A. forsteri*. The next greatest difference detected was between autumn and winter and was due mainly to greater catches of *M. cephalus* and *A. rostratus* (Appendix 4.2b).

The extent of the pairwise seasonal differences at habitat C were low to moderate, half of which were not significant (Table 4.6c). The greatest differences in fish composition were recorded for winter *vs* spring and autumn. SIMPER showed that while the ichthyofauna of this habitat was characterised by *A. georgianus* in all seasons and *A. forsteri* in most, the former species was more abundant during spring and summer, while *M. cephalus, A. forsteri* and *E. australis* were more abundant during winter. Autumn and winter were distinguished by higher abundances of *A. georgianus* and *A. rostratus* during the former season and *E. australis* and *M. cephalus* in winter (Appendix 4.2c).

The significant but small inter-annual differences (p=0.027-0.039; Global R=0.227-0.278) detected at each offshore habitat were generally attributable to greater catches of *A. forsteri* during 2007/2008 than 2008/2009, while the opposite was true for *M. cephalus.* Furthermore, greater catches of *Rhabdosargus sarba* were recorded in 2008/2009 at habitats A and C, while *P. auratus* was more prevalent in 2007/2008 at the first of these habitats (Appendix 4.3).

4.3.2.3: Cyclical temporal changes in offshore ichthyofaunal composition

RELATE identified that the temporal changes in ichthyofaunal composition matched that in the model cyclical matrix only at habitat B, with the extent of the cyclical relationship being moderate (ρ=0.432). Thus, seasonal samples from the first year form a cyclical pattern that was slightly offset from that in the second year (Fig. 4.5b). Although the seasonal fish composition in the first year at habitats A and C exhibited a small tendency to form a cyclical temporal pattern this was not the case in the second year. In particular, the fish fauna in winter 2008/2009 was markedly different from that recorded in all other sampling occasions (Figs 4.5a, c).



(a) Habitat A; p=0.062, ρ=0.170

(b) Habitat B; p=0.014, ρ=0.432

(c) Habitat C; p=0.603, ρ=-0.020

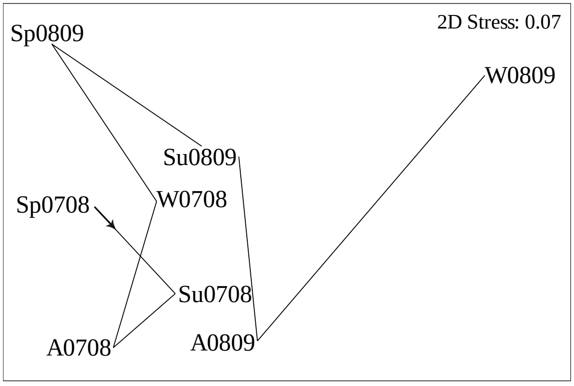


Fig. 4.5: nMDS ordination plots of the average fish faunal composition recorded in each season and year for habitats A-C (a-c). The lines join consecutive seasons from spring 2007/2008. The significance levels (p) and rho values (ρ) obtained from RELATE tests between the matrices used to construct each nMDS plot and cyclical model matrix are also provided.

4.3.2.4: Matching temporal patterns between the fish community and non-enduring environmental characteristics at each offshore habitat type

RELATE was employed to determine, separately for each offshore habitat, the extent to which the relative differences in fish faunal composition among the various sampling occasions matched that defined by the suite of complementary non-enduring environmental variables recorded during fish sampling. A significant and moderately high correlation between those complementary matrices was detected only at habitat B (p=0.002; ρ=0.595).

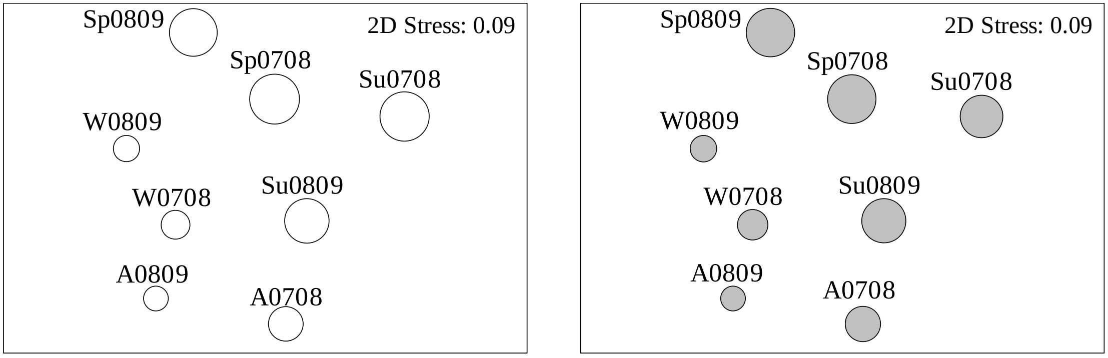
BIOENV was then employed to test whether a better match between each pair of complementary matrices could be detected if a subset of the non-enduring environmental variables were employed, rather than the full suite. Considerable improvements were detected for habitats B and C by using only surface and bottom water temperature, bottom salinity and bar state at the former habitat and surface salinity at the latter.

Relationships between the temporal patterns exhibited by the fish fauna and the magnitude of those non-enduring environmental variables selected by the BIOENV routine are illustrated, for habitats B and C by the nMDS and associated bubble plots shown in Fig. 4.6. In the first of these habitats, the notable shift in fish composition between samples collected in winter and autumn to those in summer and spring was well mirrored by the notably greater surface and bottom water temperatures during the latter two seasons (Figs 4.6a, b). Moreover, the relative distinctness of samples collected in autumn and summer at this habitat, particularly in 2007/2008, was well reflected by considerably higher bottom salinities and prolonged bar closure, *i.e. ca* 30 and 120 days in summer and autumn, respectively (Figs 4.6c, d). At habitat C, the differences in the fish composition among several sampling occasions was reasonably well reflected by differences in surface salinity. Thus, samples collected in summer and autumn 2007/2008 and winter 2008/2009, which contained notably distinct fish fauna, had the highest and lowest surface salinities, respectively (Fig. 4.6e).

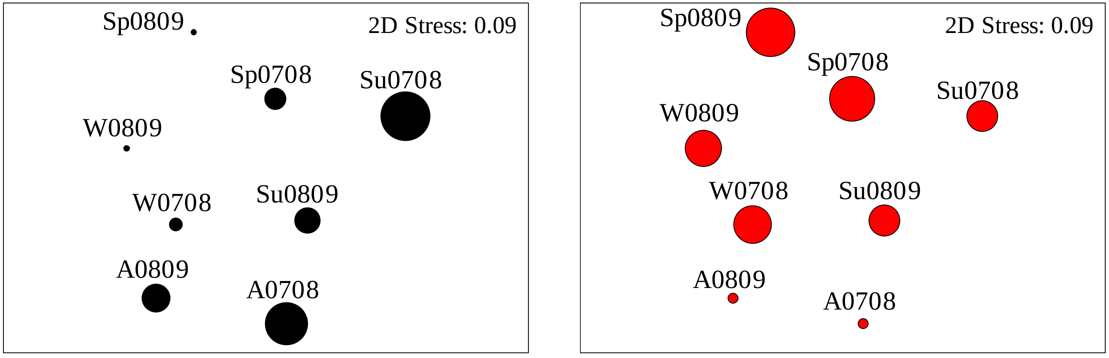
4.3.2.5: Matching temporal patterns in offshore fish faunal composition among habitat types

The pattern of temporal differences in offshore fish faunal composition in each season and year combination was found to be moderately similar between habitats A and C (p=0.05 ρ=0.454). However, the cyclical pattern in the extent of seasonal differences exhibited in habitats B was found to be unrelated to that in either habitat A or C (p=0.364 and 0.095, respectively).

(a) Habitat B; *p*=0.001, ρ=0.740 **(b) Habitat B;** *p*=0.001, ρ=0.740



(c) Habitat B; *p*=0.001, ρ=0.740 **(d) Habitat B;** *p*=0.001, ρ=0.740



(e) Habitat C; *p*=0.034, ρ=0.608

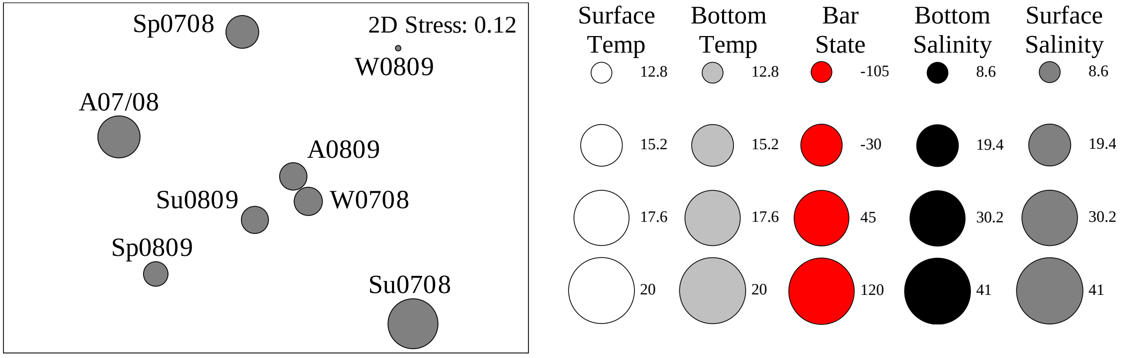


Fig. 4.6: nMDS ordination plots of the average fish faunal composition recorded in each season and year in offshore habitats B (a-d) and C (e). The magnitude of the non-enduring environmental variables selected by the BIOENV routine that best matched the temporal pattern displayed by the fish faunal composition are displayed for season and year as circles of proportionate sizes. The significance levels (*p*) and rho values (ρ) obtained from the above BIOENV tests are also provided.

4.4: Discussion

4.4.1: Nearshore fish community

4.4.1.1: Temporal changes in nearshore ichthyofaunal composition

The nearshore fish faunal composition of Broke Inlet exhibited both seasonal and inter-annual differences, however, the extent of those differences were low to moderate, with seasonal changes generally being slightly less than those of inter-annual changes. Inter-annual trends in the abundances of species were generally consistent among habitats, with greater densities of *Atherinosoma elongata*, *Afurcagobius suppositus, Leptatherina presbyteroides* and *Favonigobius lateralis* observed during 2007/2008 than 2008/2009. The latter two species, which are also represented by nearshore marine populations (Potter & Hyndes, 1999; Valesini *et al.*, 2004), are typically most abundant in areas of the estuary where salinities are closest to that of the marine environment (Prince *et al.*, 1982a; Gill & Potter, 1993; Humphries & Potter, 1993). Thus, the reduced abundance of these species during 2008/2009 is consistent with the marked reductions in salinity recorded during that year across all habitats. Furthermore, despite *A. elongata* being able to osmoregulate over a wide range of salinities, peak abundances of this species tend to be associated with salinities of between 20-36 (Prince *et al.*, 1982a) and thus, the reduced abundance of this species in 2008/2009 may be a consequence of the lower salinities recorded throughout that year. Conversely, densities of *L. wallacei*, an estuarine resident species that often exhibits an apparent preference for reduced salinities (Prince *et al.*, 1982a), increased in a number of habitats during 2008/2009 and particularly those that exhibited the highest salinities in the preceding year.

Despite significant seasonal changes being detected in the nearshore fish faunal composition of Broke Inlet, the extent of those differences were moderate at best, which mirrors research in other seasonally-open Australian estuaries (*e.g.* Griffiths, 2001; Hoeksema *et al.*, 2009). This reflects not only the adaptability of the suite of small and short-lived estuarine species that dominate the nearshore fish fauna of Broke Inlet to variable water physico-chemical conditions, but also the seasonally-open nature of the estuary. Seasonal changes in the ichthyofauna of such estuaries have been related to the timing and duration of bar opening events (*e.g.* Bennett, 1989). For example, periods of bar closure prevent the migration of marine species into and out of estuaries (Chuwen *et al.*, 2009a). Thus it is relevant that the seasonal changes recorded in Broke Inlet and other nearby seasonally-open estuaries on the south coast of Western Australia were considerably less pronounced than those exhibited by the nearshore fish faunas of permanently-open estuaries on the lower west coast (*e.g.* Young & Potter, 2003;

Hoeksema & Potter, 2006). The increased temporal differences in ichthyofaunal composition of these systems can be related to their permanent and free connection to the ocean, particularly those estuaries that have a linear morphology. For example the Swan-Canning Estuary exhibits a pronounced longitudinal water physico-chemical gradient from mouth to source within which species tended to distribute themselves according to their environmental tolerances (*e.g.* Prince *et al.*, 1982a; Gill & Potter, 1993). These distributions subsequently change with the seasonal movements of the salt wedge and river plume that result from changes in the relative contributions of tidal *vs* riverine water movements (Stephens & Imberger, 1996; Hamilton *et al.*, 2001). Moreover, seasonal changes in the ichthyofauna of these estuaries are also enhanced by marine species whose often highly seasonal migrations between these systems and the marine environment are facilitated by their permanent connection with the sea (Maes *et al.*, 2005; Hoeksema & Potter, 2006).

Significant cyclical changes in ichthyofaunal composition were not detected at any of the nearshore habitats of Broke Inlet except C, where a low degree of cyclicity was recorded. These results parallel the findings of a recent study in five estuaries along the south coast of Western Australia, in which any seasonal changes in nearshore fish faunal composition were not associated with a clearly definable cyclical progression (Hoeksema *et al.*, 2009). Such results may be attributed to the limited contributions of the juveniles of marine species whose passage into these systems is determined by the state of the bar and the timing of duration over which they have a free connection with the ocean and a lack of a distinct breeding season among estuarine species, as found in the upper reaches of the Swan-Canning Estuary (Prince & Potter, 1983; Gill *et al.*, 1996).

In the nearshore waters of the Swan-Canning Estuary, which are also dominated by estuarine species, significant and cyclical changes were detected in ichthyofaunal composition, particularly in those years and regions of the estuary that exhibited marked and consistent seasonal variations in environmental variables, due to the differential recruitment of juveniles of different species and thus time-staggered differences in their peak abundances (Hoeksema & Potter, 2006). However, despite the fact that several of the species that were most responsible for the cyclical changes observed in the upper Swan-Canning Estuary are among the most numerous fish species in Broke Inlet, *i.e. L. wallacei, P. olorum* and *A. suppositus*, similar cyclical changes were not observed in the latter system. Moreover, whereas *A. elongata* and *L. presbyteroides*, which were also highly abundant in Broke Inlet, have been shown to have distinct spawning periods in the Swan-Canning Estuary, this was not the case in the current study. Thus, comparisons of the length class compositions of *A. elongata* among seasons and years in each habitat demonstrated that juveniles of this species, *i.e.* individuals ≤ 20 mm, were present in each season (data not presented), therefore strongly suggesting that the spawning period of this species in Broke Inlet is far more protracted than in the Swan-Canning Estuary.

The ability of atherinids to complete their life cycle in estuaries has been attributed to selection pressures associated with the landlocking of these species in systems which were closed to the sea (Potter *et al.*, 1986b). Although these atherinids in the Swan-Canning Estuary exhibit a preferred spawning period in which environmental conditions are optimal for juvenile survival and recruitment, seasonally-open estuaries do not always undergo the same consistent seasonal and inter-annual changes in water physico-chemistry. For example, in spring, when *A. elongata* spawns in the Swan-Canning Estuary, salinities in Broke Inlet ranged from 12-35 in 2007/2008 and 1-18 in 2008/2009 and thus did not undergo the progressive increase in salinity during that season that is typically observed in the Swan-Canning Estuary. Therefore in response to the lack of consistent seasonal changes in water physico-chemistry that act to stimulate the onset of spawning (Prince & Potter, 1983), it is suggested that this species does not have a clearly defined spawning period in Broke Inlet and may spawn on multiple occasions over a given year, as is the case with some other atherinid species (*e.g.* Bayliff, 1950; Hubbs, 1976; Conand, 1993). It is therefore noteworthy that the spawning period in several atherinid species has been shown to vary with latitude (*e.g.* Henderson & Bamber, 1987; Conand, 1993) and that the latitudes of Broke Inlet and the Swan-Canning Estuary differ substantially, *i.e.* by 3°. Furthermore, another estuarine species present in Broke Inlet, the gobiid *P. olorum*, has been shown to spawn in both spring and autumn, with the lack of summer spawning attributed to water temperatures exceeding 25°C (Gill *et al.*, 1996). It is therefore relevant that, the water temperature in Broke Inlet rarely exceeded this upper thermal limit for reproductive success (Chuwen *et al.*, 2009a; Chapter 3) and thus this species may be able to spawn throughout spring, summer and autumn.

4.4.1.2: Matching temporal patterns between the fish community and non-enduring environmental characteristics at each nearshore habitat type

The pattern of temporal differences in the composition of the nearshore fish fauna were not significantly correlated with that exhibited by the non-enduring environmental variables. Furthermore, when BIOENV was employed to identify the particular subset of those environmental variables that was best correlated with the temporal trends in ichthyofaunal composition, a significant correlation was still only detected in a single habitat. Such findings indicate that temporal changes in the suite of non-enduring environmental variables have little influence on the composition of the nearshore fish faunas of Broke Inlet. The fact that a similar suite of estuarine species dominates the ichthyofauna in all seasons at all habitats regardless of the environmental conditions is likely to account for such findings. The extensive adaptation of these species to the variable environmental conditions in south-western Australian estuaries is exemplified by the fact that the most abundant species, *A. elongata,* can survive in salinities ranging from < 5-136 (Prince *et al.*, 1982a; Hoeksema *et al.*, 2006). Indeed, this atherinid was the sole surviving species in Culham Inlet, a normally-closed estuary on the south coast of Western Australia when salinities exceeded 80. Furthermore, another estuarine species, the gobiid *P. olorum* which generally occurs in the upper reaches of estuaries, was recorded in Culham Inlet in salinities of up to 76 (Hoeksema *et al.*, 2006). It has been hypothesised that the large variations in water physico-chemistry experienced by estuarine fish species has led to the selection for generalist genotypes that enable morphological, physiological and behavioural characteristics to be expressed that suit a wide range of environmental conditions (Bamber & Henderson, 1988). Thus, despite displaying “preferences” for particular environmental conditions and exhibiting predictable distributions in those systems that have clearly defined progressions in water physico-chemistry, such as the Swan-Canning Estuary (*e.g.* Prince *et al.*, 1982a; Gill & Potter, 1993), the generalist nature of those species enables them to maintain ubiquitous distributions throughout estuaries along the south coast of Western Australia irrespective of the environmental conditions present within those systems (Hoeksema *et al.*, 2009).

4.4.1.3: Matching temporal patterns in nearshore fish faunal composition among habitat types

The patterns of temporal changes in ichthyofaunal composition were found to be similar in numerous combinations of habitats, particularly those situated in close proximity. Such findings demonstrate that temporal similarity was influenced more by the spatial location of the habitat within the estuary rather than the suite of enduring environmental variables used to distinguish those habitats. Thus, for example, habitat B, the second most distinct habitat with respect to its enduring environmental characteristics, was correlated with the highest number of other habitats on the basis of its fish fauna. This suggests that neither the individual enduring environmental characteristics of a habitat nor its level of dissimilarity to nearby habitats in terms of those environmental characteristics that determine the extent of the temporal changes exhibited by that habitat and that it is the spatial location of the habitat within the estuary which governs its temporal similarity to other habitats. The environmental forces influencing the temporal changes in ichthyofauna therefore, act at a “regional” scale within the estuary, which may be augmented by subtle differences on a habitat basis, *i.e.* depending on the characteristic of individual habitats.

4.4.2: Offshore fish community

4.4.2.1: Temporal changes in offshore ichthyofaunal composition

Significant seasonal and inter-annual differences in ichthyofaunal composition were detected in each offshore habitat, with the extent of those differences being slightly greater for season than years in habitats A and B. While the overall extent of these seasonal differences was low, moderate differences were detected between particular pairs of seasons. In the channel habitat A, in which the greatest overall seasonal differences were recorded, for example, the most distinct differences were recorded between spring and each of the other three seasons. This was due mainly to the greater prevalence of adult *Arripis georgianus* and *Arripis truttaceus* in this habitat the former of which undertake a westward migration from waters in South Australia to their spawning grounds on the lower west and south coasts of Western Australia around that time of year (Fairclough *et al.*, 2000a). It has been suggested that the adults of these marine estuarine-opportunists enter these estuaries during their migration to their spawning grounds, when these systems are freely connected with the ocean, as they typically provide increased shelter from the highly exposed marine waters of the south coast and an abundant source of food (Haedrich, 1983; Beck *et al.*, 2001).

The ichthyofaunal differences between spring and summer at habitat A were also due to the fact that various other marine estuarine-opportunists characterised this habitat in summer, namely the mugilids *Aldrichetta forsteri* and *Mugil cephalus* and the sparid *Pagrus auratus.* Although the bar at the mouth of the estuary closed during the summer of both years, preventing the movement of the above species from the estuary, it typically reopens in late winter, allowing species with marine affinities the chance to emigrate from the estuary to the nearshore marine environment.

The significant seasonal changes in the composition of the offshore fish fauna at habitat B, in Shannon Basin, were found to exhibit strong temporal cyclicity, which was due largely to the sequential immigration and subsequent emigration from that habitat of the various marine fish species. Thus, during spring the ichthyofauna was typified by *A. forsteri* which subsequently moved into the lower estuary during autumn, a trend also recorded in the Swan-Canning Estuary (Chubb *et al.*, 1981). During summer, this habitat was also characterised by *A. georgianus* and *Engraulis australis,* with the spawning in *E. australis* occurring during this season in the nearby Walpole-Nornalup Estuary and Wilson Inlet (Neira & Potter, 1992a; Neira & Potter, 1994). Furthermore, individuals of this species are known to immigrate into the estuaries in southern Australia at this time to spawn (Blackburn, 1950). The abundances of these two species decreased in autumn while those of the estuarine and marine species *Ammotretis rostratus* increased, and characterised the offshore fish fauna at this habitat until spring. This period coincides with the spawning time of this species, which extends from May to November (Crawford, 1984; Jenkins, 1986). Adult *M. cephalus* also typified the fish assemblages at habitat B in autumn and also winter, which may reflect their movement out of the rivers and into the upper reaches of the estuary which they are known to undertake at this time of year on route to the marine environment to spawn (Thomson, 1955; Chubb *et al.*, 1981; Chuwen *et al.*, 2009b). It is also thus relevant that by far the lowest numbers of this species in all habitat were caught during spring.

The offshore ichthyofauna of habitat C also differed seasonally, although to a lesser extent than the other habitats. In the first year the fish fauna followed a seasonal cyclical pattern with greater abundances of arripids during spring, an influx of marine estuarine-opportunists that had recently entered the system when it was freely connected with the sea, such as *P. auratus, Rhabdosargus sarba, Gonorynchus greyi* and *Pseudocaranx dentex,* during summer and autumn as salinities increased. These species emigrated from this habitat in winter when fluvial discharge increases markedly, reducing salinity and re-establishing the connection with the ocean. This cycling in the fish fauna is likely to be driven by the seasonal changes in salinity which underwent a “typical” and pronounced seasonal pattern during the first year of sampling, but did not follow the same pattern in the second year in which salinities were consistent, *i.e. ca* 15 until winter. This pattern of temporal differences in surface salinity at this habitat was found to be strongly correlated with those exhibited by fish faunal composition (Fig. 4.6). Furthermore, the lack of a cyclical trend in the second year conforms with other research on seasonally-open estuaries in southern Australia in which seasonal changes in ichthyofauna are typically small (*e.g.* Pollard, 1994a; Griffiths, 2001). On the south coast of Western Australia the estuaries which underwent the greatest seasonal changes in ichthyofauna were also found to experience the most pronounced changes in salinity (Chuwen *et al.*, 2009b). It is therefore hypothesised that the small seasonal changes observed during the second year of sampling at habitat C may reflect the relatively small seasonal fluctuations in salinity at that habitat during spring, summer and autumn 2008/2009.The small inter-annual differences in the composition of the offshore ichthyofauna detected at each habitat was due to marine species, such as *A. forsteri* and *P. auratus*, being more abundant during 2007/2008 than 2008/2009. Such findings may reflect the fact that salinities in Broke Inlet during this year were higher than in 2008/2009. Furthermore, this reduction in salinity between the two sampling years may have contributed to the increase in *M. cephalus* during 2008/2009, as this species is capable of occupying regions of reduced salinities in estuaries and, as such, was found to be more abundant in the saline reaches of rivers than in the basins of five estuaries on the south coast of Western Australia (Chuwen *et al.*, 2009b).

4.4.2.2: Matching temporal patterns between the fish community and non-enduring environmental characteristics at each offshore habitat type

The pattern of temporal differences in non-enduring environmental characteristics, *i.e.* those reflecting water physico-chemistry was significantly correlated with that exhibited by the offshore fish fauna in habitats B and C, with the extent of those correlations ranging from moderately high to high. Unlike some of the variables selected by the BIOENV procedure in subsection 3.3.2.5, which were identified as being correlated with spatial differences in fish faunal composition in a particular season, the BIOENV procedure in these analyses selected variables with a large range of values which was well distributed among the samples (*e.g.* surface salinity at habitat B ranged from *ca* 8-41). These selected non-enduring environmental variables were thus considered to provide a more reliable “explanation” of differences in fish faunal composition than some of those referred to above.

Temporal changes in the ichthyofauna of habitat B were strongly correlated those exhibited by surface and bottom water temperature, bar state and bottom salinity, while those at habitat C were correlated only with changes in surface salinity. Salinities at both of those habitats underwent pronounced temporal changes ranging between *ca* 3 in winter 2008/2009 to 40 in summer 2007/2008. Salinity has been shown to influence the distribution of fish species, and particularly marine species, in numerous other south-western Australian estuaries (*e.g.* Loneragan *et al.*, 1987; Loneragan & Potter, 1990; Hoeksema & Potter, 2006). At habitat A however, salinities ranged only between 20 and 35 and were generally always highest at this habitat. It is therefore proposed that this habitat provides a refuge for species with marine affinities when the bar is closed and salinities in other habitats have declined markedly.

Significant correlations between the temporal patterns of differences in offshore ichthyofaunal composition were detected between habitats A and C, however, neither of these patterns were correlated with those recorded in habitat B. This reflects the fact that habitat B was the only habitat in which temporal changes in offshore fish composition exhibited a significant cyclical pattern due to the immigration and emigration of various marine species. It is also noteworthy that, while the offshore water at habitats A and C are directly linked, this is not the case with habitat B. As such, the movement of fish from this habitat, which harboured the most distinct and depauperate ichthyofaunal assemblage, and other habitats is restricted by a *ca* 1.5 km stretch of very shallow water, *i.e.* < 50 cm over an extensive sand bar (Fig. 2.3), greatly influencing temporal patterns of fish movement between habitats and distinguishing it from the rest of the estuary.

4.5: Appendices

Appendix 4.1: Species that consistently typified (provided along the diagonal) and distinguished (provided in the sub-diagonal) the nearshore fish assemblages at each habitat in each season and/or year between spring 2007 and winter 2009 as detected by two-way crossed SIMPER. The season or year in which each species was most abundant is given in superscript for each pairwise comparison. Insignificant pairwise comparisons are highlighted in grey. Asterisks denote the relative consistency of each species in either typifying or distinguishing the faunal composition in that season or year, as measured by the similarity to standard deviation ratio and dissimilarity to standard deviation ratio, respectively; > 1.5-3*, > 3-5**, > 5***.

(a) Habitat A:

	Spring	**Winter**
Spring	*L. wallacei**** *A. elongata**	
Winter	*L. wallacei*^{Sp} *A. elongata*^{Sp} *F. lateralis*^{W} *A. suppositus*^{W}	*L. wallacei*** *A. elongata**

(b) Habitat B:

	2007/2008	**2008/2009**
2007/2008	*A. elongata** *L. presbyteroides** *F. lateralis* *L. wallacei*	
2008/2009	*L. presbyteroides*$^{07/08}$ *A. elongata*$^{07/08}$ *L. wallacei*$^{08/09}$ *F. lateralis*$^{07/08}$	*A. elongata** *F. lateralis* *L. wallacei** *L. presbyteroides*

	Spring	**Summer**	**Autumn**	**Winter**
Spring	*L. presbyteroides* *A. elongata* *L. wallacei* *F. lateralis*			
Summer	*L. wallacei*^{Su*} *L. presbyteroides*^{Su*} *A. elongata*^{Su*} *F. lateralis*^{Su}	*A. elongata** *F. lateralis*** *L. presbyteroides** *L. wallacei*		
Autumn	*L. presbyteroides*^{A} *L. wallacei*^{A*} *A. elongata*^{A} *F. lateralis*^{Sp}	*L. presbyteroides*^{Su*} *L. wallacei*^{Su*} *A. elongata*^{Su} *F. lateralis*^{Su*}	*A. elongata** *L. wallacei* *F. lateralis* *A. suppositus*	
Winter	*L. presbyteroides*^{W*} *L. wallacei*^{Sp} *A. elongata*^{W} *A. suppositus*^{W}	*L. wallacei*^{Su*} *L. presbyteroides*^{Su*} *A. elongata*^{Su} *F. lateralis*^{Su}		*A. elongata** *F. lateralis* *L. presbyteroides* *L. wallacei*

(c) Habitat C:

	2007/2008	2008/2009
2007/2008	*A. suppositus** *A. elongata*** *L. wallacei**	
2008/2009	*A. suppositus*$^{07/08}$ *L. wallacei*$^{08/09*}$ *A. elongata*$^{07/08}$ *F. lateralis*$^{07/08}$	*L. wallacei** *A. suppositus** *A. elongata***

	Spring	Summer	Autumn	Winter
Spring	*A. elongata*** *L. wallacei** *A. suppositus* *P. olorum*			
Summer		*A. suppositus**** *A. elongata** *L. wallacei*		
Autumn	*L. wallacei*^{A*} *F. lateralis*^{A} *P. olorum*^{Sp} *L. presbyteroides*^{A}	*L. wallacei*^{A*} *A. elongata*^{A} *F. lateralis*^{A} *L. presbyteroides*^{A}	*A. elongata*** *L. wallacei** *A. suppositus**	
Winter	*A. suppositus*^{W} *L. wallacei*^{W*} *P. olorum*^{Sp} *A. elongata*^{Sp*}	*L. wallacei*^{W*} *F. lateralis*^{W} *A. elongata*^{W*} *L. presbyteroides*^{Su}	*L. wallacei*^{A*} *A. elongata*^{A} *F. lateralis*^{A} *L. presbyteroides*^{A}	*A. suppositus*** *L. wallacei** *A. elongata**

(d) Habitat D:

	2007/2008	2008/2009
2007/2008	*A. suppositus** *A. elongata** *L. wallacei**	
2008/2009	*A. suppositus*$^{07/08*}$ *L. wallacei*$^{08/09}$ *F. lateralis*$^{07/08}$ *A. elongata*$^{07/08}$	*L. wallacei** *A. suppositus** *A. elongata**

	Spring	Summer	Autumn	Winter
Spring	*L. wallacei** *A. elongata** *A. suppositus*			
Summer	*A. suppositus*^{Su*} *L. presbyteroides*^{Su*} *A. elongata*^{Su*} *L. wallacei*^{Su}	*A. suppositus**** *A. elongata** *L. wallacei** *L. presbyteroides*		
Autumn	*A. suppositus*^{A*} *A. elongata*^{Sp} *F. lateralis*^{A*} *P. olorum*^{Sp}	*A. suppositus*^{Su} *F. lateralis*^{A} *A. elongata*^{Su*} *L. presbyteroides*^{Su*}	*A. suppositus**** *L. wallacei** *A. elongata**	
Winter	*L. wallacei*^{Sp} *A. suppositus*^{W} *A. elongata*^{Sp} *F. lateralis*^{W}	*A. suppositus*^{Su*} *L. wallacei*^{Su} *L. presbyteroides*^{Su*} *A. elongata*^{Su*}		*A. elongata** *A. suppositus* *L. wallacei* *F. lateralis*

(e) Habitat E:

	2007/2008	2008/2009
2007/2008	*A. suppositus** *L. wallacei** *A. elongata***	
2008/2009	*L. wallacei*$^{07/08}$ *A. elongata*$^{07/08}$ *A. suppositus*$^{07/08}$ *P. olorum*$^{08/09}$	*A. suppositus** *L. wallacei** *A. elongata**

	Spring	Summer	Autumn	Winter
Spring	*L. wallacei** *A. elongata** *A. suppositus*			
Summer	*A. suppositus*^{Su*} *A. elongata*^{Su} *L. wallacei*^{Su*}	*A. suppositus*** *A. elongata*** *L. wallacei***		
Autumn	*A. suppositus*^{A} *L. wallacei*^{Sp*} *A. elongata*^{A}	*A. elongata*^{Su*} *A. suppositus*^{Su*} *L. wallacei*^{Su*} *P. olorum*^{Su}	*A. suppositus*** *A. elongata** *L. wallacei***	
Winter		*A. suppositus*^{Su*} *L. wallacei*^{W*} *A. elongata*^{Su*} *L. presbyteroides*^{Su}		*A. suppositus** *L. wallacei** *A. elongata**

(f) Habitat F:

	2007/2008	2008/2009
2007/2008	*A. suppositus** *A. elongata*** *L. wallacei**	
2008/2009	*A. suppositus*$^{07/08}$ *A. elongata*$^{07/08}$ *L. wallacei*$^{07/08}$ *P. olorum*$^{07/08}$	*L. wallacei*** *A. elongata** *A. suppositus*

	Spring	Summer	Autumn	Winter
Spring	*L. wallacei** *A. elongata*** *A. suppositus*			
Summer		*A. suppositus** *A. elongata*** *L. wallacei***		
Autumn		*L. wallacei*^{A*} *A. elongata*^{A*} *A. suppositus*^{Su} *F. lateralis*^{Su}	*A. elongata**** *A. suppositus*** *L. wallacei**	
Winter		*A. elongata*^{Su*} *A. suppositus*^{Su*} *L. wallacei*^{Su} *F. lateralis*^{Su}		*L. wallacei** *A. elongata* *A. suppositus*

(g) Habitat G:

	2007/2008	**2008/2009**
2007/2008	*A. elongata*** *A. suppositus** *P. olorum* *L. wallacei*	
2008/2009	*A. elongata*$^{07/08}$ *P. olorum*$^{07/08*}$ *L. wallacei*$^{08/09*}$ *A. suppositus*$^{07/08}$	*A. suppositus** *A. elongata** *L. wallacei** *P. olorum*

	Spring	**Summer**	**Autumn**	**Winter**
Spring	*A. elongata*** *A. suppositus** *P. olorum**			
Summer	▨	*A. elongata** *A. suppositus** *L. wallacei*		
Autumn	*L. wallacei*^{A} *A. elongata*^{A} *P. olorum*^{Sp} *L. presbyteroides*^{A*}	*L. wallacei*^{A} *P. olorum*^{Su*} *A. suppositus*^{Su} *A. elongata*^{A}	*A. elongata**** *L. wallacei*** *A. suppositus**** *P. olorum**	
Winter	*A. elongata*^{Sp*} *P. olorum*^{Sp*} *L. presbyteroides*^{Sp*} *L. wallacei*^{W*}	*P. olorum*^{Su*} *A. elongata*^{Su*} *A. suppositus*^{Su} *L. wallacei*^{Su*}	*L. wallacei*^{A*} *A. elongata*^{A} *P. olorum*^{A*} *A. suppositus*^{A}	*A. suppositus** *A. elongata** *L. wallacei*

(h) Habitat H:

	2007/2008	**2008/2009**
2007/2008	*A. elongata** *A. suppositus** *L. wallacei**	
2008/2009	*L. wallacei*$^{07/08}$ *L. presbyteroides*$^{07/08}$ *A. elongata*$^{07/08*}$ *A. suppositus*$^{07/08*}$	*L. wallacei** *A. suppositus*** *A. elongata**

	Spring	**Summer**	**Autumn**	**Winter**
Spring	*A. elongata* *P. olorum*** *L. wallacei** *A. suppositus**			
Summer	*L. wallacei*^{Su} *A. suppositus*^{Su} *L. presbyteroides*^{Su} *H. melanochir*^{Su}	*A. elongata** *A. suppositus** *L. wallacei** *L. presbyteroides**		
Autumn	*L. wallacei*^{A} *L. presbyteroides*^{A} *P. olorum*^{Sp} *N. parilus*^{Sp}	*L. wallacei*^{A} *F. lateralis*^{Su} *L. presbyteroides*^{Su*} *A. suppositus*^{Su*}	*L. wallacei*** *A. elongata**** *A. suppositus**** *L. presbyteroides**	
Winter	*L. presbyteroides*^{W} *L. wallacei*^{W} *P. olorum*^{Sp*} *A. elongata*^{W*}	*L. wallacei*^{Su} *L. presbyteroides*^{W*} *P. olorum*^{Su*} *F. lateralis*^{Su}	▨	*A. suppositus**** *A. elongata** *L. wallacei** *L. presbyteroides*

(i) Habitat I:

	2007/2008	**2008/2009**
2007/2008	*A. elongata** *L. wallacei** *F. lateralis* *A. suppositus*	
2008/2009	*F. lateralis*$^{07/08}$ *A. elongata*$^{07/08}$ *L. wallacei*$^{08/09}$ *A. suppositus*$^{07/08}$	*A. elongata* *L. wallacei* *A. suppositus*

	Spring	**Summer**	**Autumn**	**Winter**
Spring	*A. elongata* *L. wallacei* *F. lateralis*			
Summer		*A. elongata*** *F. lateralis* *L. wallacei***		
Autumn	*A. suppositus*^{A} *A. elongata*^{A} *L. wallacei*^{Sp} *A. rostratus*^{A}		*A. elongata** *A. suppositus* *L. wallacei**	
Winter	*A. elongata*^{W} *L. wallacei*^{W} *A. suppositus*^{W} *F. lateralis*^{Sp}	*A. elongata*^{Su} *L. wallacei*^{W*} *F. lateralis*^{Su} *A. suppositus*^{W}	*A. elongata*^{W*} *L. wallacei*^{W*} *A. suppositus*^{A} *F. lateralis*^{A}	*L. wallacei** *A. elongata** *A. suppositus*

(j) Habitat J:

	2007/2008	**2008/2009**
2007/2008	*A. elongata*** *A. suppositus** *L. wallacei*	
2008/2009	*A. suppositus*$^{07/08}$ *A. elongata*$^{07/08}$ *L. wallacei*$^{07/08}$	*L. wallacei** *A. elongata* *A. suppositus*

	Spring	**Summer**	**Autumn**	**Winter**
Spring	*L. wallacei* *A. suppositus* *A. elongata*			
Summer	*A. elongata*^{Su} *A. suppositus*^{Su} *L. wallacei*^{Su} *F. lateralis*^{Su}	*A. elongata** *A. suppositus*** *L. wallacei** *F. lateralis*		
Autumn			*A. elongata** *L. wallacei** *A. suppositus*	
Winter	*A. suppositus*^{Sp} *L. wallacei*^{Sp*} *A. elongata*^{Sp} *F. lateralis*^{Sp}			*L. wallacei* *A. elongata* *A. suppositus*

(k) Habitat K:

	2007/2008	2008/2009
2007/2008	*A. elongata** *L. wallacei** *A. suppositus*	
2008/2009	*A. elongata*$^{07/08}$ *L. wallacei*$^{07/08}$ *A. suppositus*$^{07/08}$ *L. presbyteroides*$^{07/08}$	*L. wallacei** *A. elongata*

	Spring	Summer	Autumn	Winter
Spring	*A. elongata*** *L. wallacei*			
Summer	*A. elongata*^{Su} *L. wallacei*^{Su} *A. suppositus*^{Su}	*L. wallacei** *A. elongata** *A. suppositus*		
Autumn	*A. elongata*^{A*} *L. wallacei*^{A} *A. suppositus*^{A} *L. presbyteroides*^{A}	▨	*A. elongata** *L. wallacei*	
Winter	*L. wallacei*^{W} *A. elongata*^{W*} *A. suppositus*^{W}	*A. elongata*^{W} *L. wallacei*^{W*} *A. suppositus*^{Su}	*A. elongata*^{W} *L. wallacei*^{W*} *A. suppositus*^{W}	*L. wallacei** *A. elongata*

Appendix 4.2: Species that consistently typified (provided along the diagonal) and distinguished (provided in the sub-diagonal) the offshore fish assemblages at each habitat in each season and year between spring 2007 and winter 2009 as detected by two-way crossed SIMPER. The season or year in which each species was most abundant is given in superscript for each pairwise comparison. Insignificant pairwise comparisons are highlighted in grey. Asterisks denote the relative consistency of each species in either typifying or distinguishing the faunal composition in that season or year, as measured by the similarity to standard deviation ratio and dissimilarity to standard deviation ratio, respectively; > 1.5-3*, > 3-5**, > 5***.

(a) Habitat A:

	2007/2008	2008/2009
2007/2008	*A. georgianus** *A. forsteri* *P. auratus* *M. cephalus*	
2008/2009	*M. cephalus*$^{08/09}$ *A. forsteri*$^{07/08}$ *R. sarba*$^{08/09}$ *P. auratus*$^{07/08}$	*M. cephalus* *A. georgianus* *A. truttaceus* *R. sarba*

	Spring	Summer	Autumn	Winter
Spring	*A. georgianus**** *A. truttaceus*			
Summer	*M. cephalus*^{Su} *A. truttaceus*^{Sp} *A. forsteri*^{Su*} *A. georgianus*^{Sp}	*M. cephalus* *A. forsteri* *P. auratus* *A. georgianus*		
Autumn	*P. auratus*^{A} *R. sarba*^{A*} *A. georgianus*^{A} *A. truttaceus*^{Sp}	▨	*A. georgianus* *M. cephalus* *R. sarba* *G. greyi*	
Winter	*A. truttaceus*^{Sp*} *A. georgianus*^{Sp} *M. cephalus*^{W*} *A. rostratus*^{Sp}	▨	*A. georgianus*^{A} *P. auratus*^{A} *G. greyi*^{A} *P. dentex*^{A}	*M. cephalus* *A. forsteri* *A. georgianus*

(b) Habitat B:

	2007/2008	**2008/2009**
2007/2008	*M. cephalus* *A. rostratus* *E. australis* *A. forsteri*	
2008/2009	*M. cephalus*$^{08/09}$ *A. rostratus*$^{08/09}$	*M. cephalus* *A. rostratus* *A. forsteri*

	Spring	**Summer**	**Autumn**	**Winter**
Spring	*A. forsteri*			
Summer		*M. cephalus* *A. forsteri* *A. georgianus* *E. australis*		
Autumn	*M. cephalus*^{A} *A. rostratus*^{A} *A. forsteri*^{Sp}	*A. forsteri*^{Su} *A. georgianus*^{Su} *A. rostratus*^{A} *E. australis*^{Su}	*M. cephalus* *A. rostratus* *E. australis*	
Winter	*M. cephalus*^{W} *A. forsteri*^{Sp}	*A. forsteri*^{Su} *A. georgianus*^{Su} *E. australis*^{Su}	*M. cephalus*^{A} *A. rostratus*^{A}	*M. cephalus* *A. rostratus*

(c) Habitat C:

	2007/2008	**2008/2009**
2007/2008	*A. georgianus* *A. rostratus* *E. australis* *A. forsteri*	
2008/2009	*A. georgianus*$^{08/09}$ *E. australis*$^{08/09}$ *M. cephalus*$^{08/09}$ *R. sarba*$^{08/09}$	*A. georgianus* *A. rostratus* *R. sarba* *A. forsteri*

	Spring	**Summer**	**Autumn**	**Winter**
Spring	*A. georgianus* *A. rostratus* *A. forsteri*			
Summer		*A. georgianus* *A. forsteri*		
Autumn	*A. georgianus*^{Sp} *A. rostratus*^{A} *M. cephalus*^{Sp} *A. forsteri*^{Sp}		*A. rostratus* *A. georgianus* *H. melanochir* *P. dentex*	
Winter	*A. georgianus*^{Sp} *M. cephalus*^{W} *A. forsteri*^{W} *A. rostratus*^{W}		*A. georgianus*^{A*} *E. australis*^{W} *M. cephalus*^{W} *A. rostratus*^{A}	*E. australis* *R. sarba* *A. forsteri* *A. georgianus* *M. cephalus*

Chapter 5

Benthic macroinvertebrate composition among habitat types and seasons in Broke Inlet

5.1: Introduction

Benthic macroinvertebrate communities, which comprise mainly polychaetes, molluscs and crustaceans, are a vital component of estuarine environments. These small benthic fauna perform a range of crucial functions, such as aiding the decomposition of organic matter, recycling nutrients and translocating materials (Riisgård, 1991; Wallace & Webster, 1996; Constable, 1999; Pennifold & Davis, 2001; De Roach *et al.*, 2002). They also provide an important food source for many fish and avian species (Kalejta & Hockey, 1991; Humphries & Potter, 1993; Platell *et al.*, 2006).

The species richness, density and composition of the benthic macroinvertebrate faunas of estuaries have been shown by many workers throughout the world to vary spatially and temporally (*e.g.* Edgar & Barrett, 2002; Giberto *et al.*, 2004; França *et al.*, 2009b; Wildsmith *et al.*, 2009). Thus, numerous studies have demonstrated that the spatial distributions of the various benthic macroinvertebrate species within estuaries are strongly related to spatial differences in certain environmental variables and in particular salinity (*e.g.* Ysebaert *et al.*, 2002; Ellis *et al.*, 2006), the grain size and organic content of the sediment (*e.g.* Gray, 1974; Teske & Wooldridge, 2003), benthic structural heterogeneity (*e.g.* Gilinsky, 1984; Attrill *et al.*, 2000; Basset *et al.*, 2007) and water flow/wave exposure (*e.g.* Warwick *et al.*, 1991; Mettam, 1994). The strong links between benthic macroinvertebrate composition and environmental variables are reflected in the demonstration that the pattern of relative differences in the compositions of these faunas among habitat types in the Swan-Canning Estuary are strongly correlated with the suite of enduring environmental characteristics that were used to identify those habitat types (Valesini *et al.*, 2009). This presumably reflects differences in the tolerances to and/or preferences of the various species for particular enduring environmental conditions (Valesini *et al.*, 2009).

Temporal changes in the characteristics of benthic macroinvertebrate assemblages within estuaries have been related to differences in the timing of the recruitment of certain species and in the extent of their mortality at different times of the year, both of which typically reflect the marked seasonal changes that often occur in estuarine hydrology, and especially salinity, water temperature and river flow (*e.g.* Rainer, 1981; Kalejta & Hockey, 1991; Sardá *et al.*, 1995; Platell & Potter, 1996; Kanandjembo *et al.*, 2001).

Most studies of the spatial and/or temporal differences in benthic macroinvertebrate composition in estuaries in Western Australia have been undertaken in the large permanently-open systems of the lower west coast (*e.g.* Semeniuk & Wurm, 2000; Kanandjembo *et al.*, 2001; Wildsmith, 2007; Valesini *et al.*, 2009; Wildsmith *et al.*, 2009). However, studies of the benthic macroinvertebrate faunas in estuaries on the south coast of Western Australia are largely restricted to limited qualitative surveys of those assemblages in a number of these systems (*e.g.* Hodgkin & Clark, 1987-1990) and to molluscs in Oyster Harbour (*e.g.* Wells & Roberts, 1980; Wells & Threlfall, 1980). The only detailed study of the benthic macroinvertebrate fauna in estuaries on this coast is that undertaken by Platell & Potter (1996) in Wilson Inlet, which is located approximately 100 km to the east of Broke Inlet and is likewise seasonally-open (Brearley, 2005).

Environmental conditions in the Broke and Wilson inlets differ markedly, with the former being essentially oligotrophic and containing only small areas of macrophytes, whereas the latter is eutrophic and contains large and dense stands of the aquatic macrophyte *Ruppia megacarpa* (Lukatelich *et al.*, 1987; Carruthers *et al.*, 1999; Brearley, 2005). The study of Wilson Inlet by Platell and Potter (1996) yielded 41 benthic macroinvertebrate species, which were numerically dominated by capitellid and spionid polychaetes and the gastropod *Hydrococcus brazieri*. The densities of benthic macroinvertebrates at sites in the shallows varied markedly throughout the estuary, ranging from about 300 to 3,000 individuals 0.1m^{-2}, with a mean overall density of approximately 1,000 0.1m^{-2}. This mean density is similar to those recorded in the permanently-open Peel-Harvey and Swan-Canning estuaries on the lower west coast of

Australia (Valesini *et al.*, 2009; Wildsmith *et al.*, 2009) and comparable with that in the Gippsland Lakes in south-eastern Australia (Poore, 1982). The presence of fewer species of benthic macroinvertebrates in Wilson Inlet (41) than in the Peel-Harvey (63) and Swan-Canning (69) estuaries parallels the findings in both South African and eastern Australian estuaries that are seasonally-open to the ocean *vs* those that are permanently-open (*e.g.* Teske & Wooldridge, 2001; Dye & Barros, 2005a, b).

The study of the benthic macroinvertebrate fauna of Wilson Inlet was undertaken at relatively broad scales and focused primarily on an area in each of the upper and lower regions and water depths and their relationships with a limited suite of water physico-chemical parameters (*i.e.* salinity, water temperature) and the presence of *R. megacarpa* and shell debris (Platell & Potter, 1996). During the present study in four consecutive seasons the benthic macroinvertebrate assemblages in Broke Inlet were sampled quantitatively at six of the nearshore habitat types and at each of the three offshore habitats identified in Chapter 2 to test the following hypotheses.

(1) The species richness, density, diversity and the composition of the benthic macroinvertebrate fauna differ significantly among the various habitat types sampled in both the nearshore and offshore waters.

(2) The pattern of relative differences among habitat types exhibited by the compositions of the benthic macroinvertebrate faunas is significantly correlated with that defined by the suite of enduring environmental variables used to identify those habitats in both the nearshore and offshore waters.

(3) The species richness, density, diversity and species composition of benthic macroinvertebrates in both the nearshore and offshore waters differ significantly among the four seasons.

5.2: Materials and methods

5.2.1: Sampling regime

Benthic macroinvertebrates were sampled at four sites at each of six of the 11 nearshore and at all three of the offshore habitats that were identified in Broke Inlet during the current study (Chapter 2; Fig. 5.1). Three randomly-located cores of sediment (that contained invertebrates) were collected subtidally at each site in the nearshore and offshore waters, using a pole-mounted cylindrical corer, which was 11 cm in diameter, had a surface area of 96 cm^2 and sampled to a depth of 15 cm. Sampling was undertaken seasonally between spring 2007 and winter 2008 at nearshore sites and between summer and spring 2008 at offshore sites. The sediment samples were preserved in 5% formalin buffered in estuarine water and then wet-sieved through a 500 μm mesh. The invertebrates were removed from any sediment retained on the mesh, identified to the lowest possible taxonomic level and counted. The number of individuals of each macroinvertebrate taxon in each replicate sample was converted to a density, *i.e.* number of individuals 0.1 m^{-2}.

Various non-enduring environmental water physico-chemical variables were recorded at the time at which the benthic macroinvertebrate fauna was sampled, *i.e.* salinity, water temperature, dissolved oxygen concentration, pH and macrophyte biomass, the methods for which are described in subsection 3.2.1. A range of other non-enduring environmental variables that were related directly to the sediment, *i.e.* percentage contributions of various sediment grain size fractions and particulate organic matter (%POM) and the depth of the transitional zone were also measured at the time of faunal collection. The methods for these latter parameters are given below.

Two further sediment cores were collected seasonally at each site in each nearshore and offshore habitat type using a cylindrical corer that was 3.57 cm in diameter (10 cm^2 in area) and sampled to a depth of 10 cm. The depth in each of these cores of the transitional zone, where the colour of the sediment changes from light to dark and demarks the region of biologically available oxygen (Hourston *et al.*, 2009), was recorded to the nearest 0.5 cm. The cores were dried for 24 h at 80°C, weighed to the nearest 1 mg and then ashed for 2 h at 550°C and re-weighed (Heiri *et al.*, 2001).

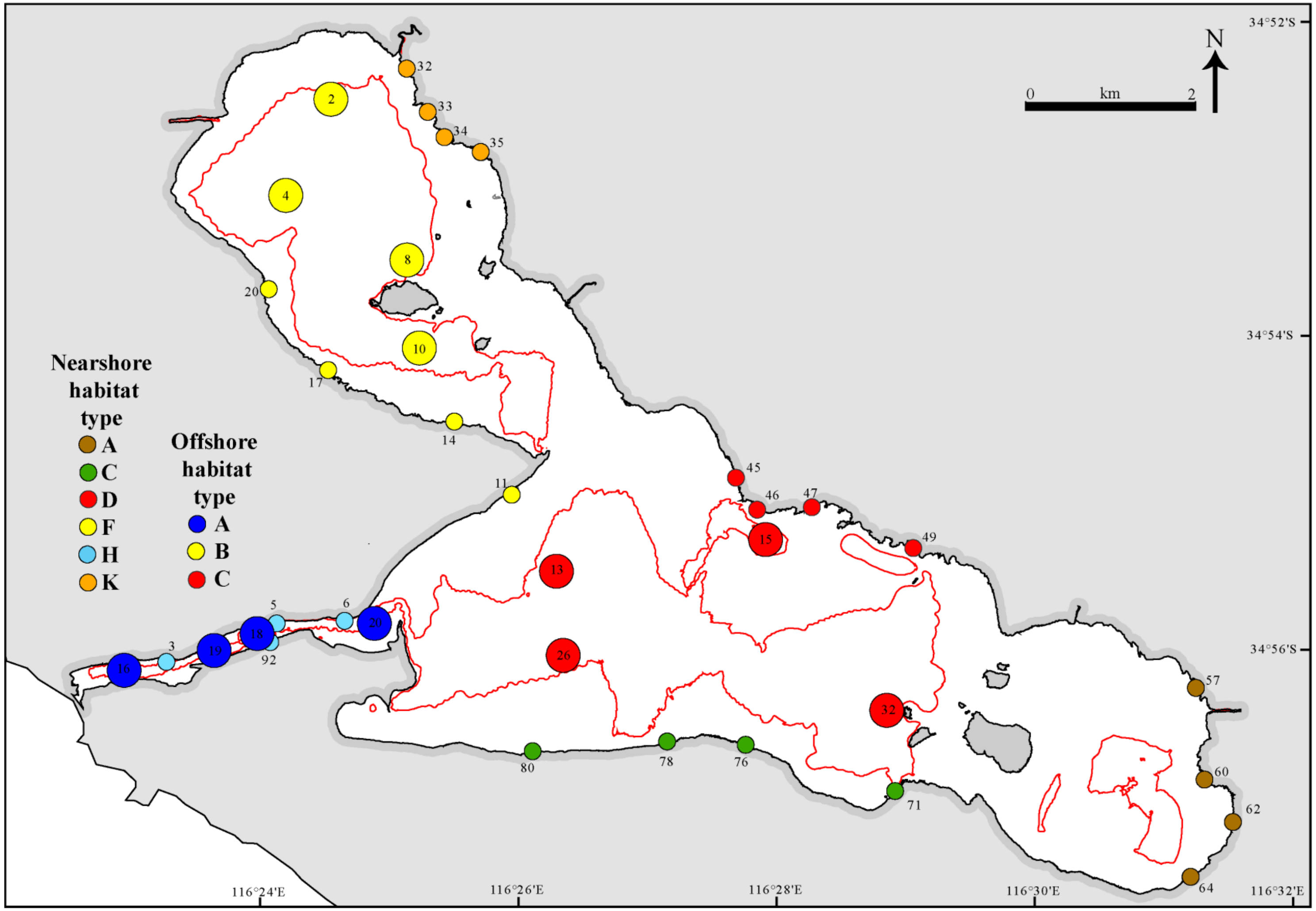


Fig. 5.1: Map showing location of the sampling sites in each nearshore and offshore habitat type in Broke Inlet at which the benthic macroinvertebrate fauna was sampled. Circles represent the area of the site and the red line (1 m depth contour) demarcates the nearshore and offshore waters.

The difference between the dry and ashed weight enabled the percentage contribution of POM in each sample to be calculated.

Each ashed sample was wet-sieved through a 63 µm sieve to remove the fine sediment particles, dried and re-weighed. The remaining material was wet-sieved through a stack of sieves with mesh sizes corresponding to the Wentworth Scale for grain size, *i.e.* 2,000, 1,000, 500, 250, 125 and 63 µm (Wentworth, 1922). After separation, the samples for each grain size were dried for 24 h and weighed to the nearest mg, enabling their percentage contributions by weight to be calculated.

5.2.2: Statistical analyses

All statistical analyses were performed using the PRIMER v6 multivariate software package (Clarke & Gorley, 2006) with the PERMANOVA+ add-on (Anderson *et al.*, 2008).

5.2.2.1: Univariate analyses

Differences in the non-enduring environmental variables among habitat types and seasons

Permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001; Anderson *et al.*, 2008) was employed to determine the extent to which each of the non-enduring environmental variables were related to habitat type and season. The statistical methodology for each of the water physico-chemical parameters, *i.e.* salinity, water temperature, dissolved oxygen concentration, pH and the dry weight of any detached macrophytes, are given in subsection 3.2.2.1.

With respect to the sediment characteristics, the percentage contribution of each of the seven sediment grain sizes in both the nearshore and offshore waters were subjected to a square-root transformation. In the case of both %POM and the depth of the transition zone in the nearshore and offshore waters, the relationship between the $\log_e$ (mean) and $\log_e$ (standard deviation) of each group of replicate samples was examined to ascertain which type of transformation was required, if any, to meet the test assumption of homogenous sample dispersions among groups (Clarke & Warwick, 2001). This procedure showed that %POM in both the nearshore and offshore waters required a $\log_e(X+0.1)$ transformation, while the depth of the transition zone required a fourth root transformation in nearshore waters and no transformation in offshore waters.

Following the approach adopted in Chapters 3 (see subsection 3.2.2.1), preliminary PERMANOVA tests were performed on Euclidean distance matrices constructed from replicate data for each sediment characteristic at each site in both the nearshore and offshore waters, *i.e.* employing habitat, season and site (nested within habitat) as main effects, to determine if there were any significant differences among sites, and thus which level of replication was most appropriate for examining differences among habitat types. Habitat and season were considered fixed, while site was treated as a random factor. As a significant site and/or site x season interaction effect was detected in all cases, the replicate data recorded at each nearshore and offshore site on each sampling occasion was averaged. These data were then used to construct three separate Euclidean distance matrices for the sediment characteristics, *i.e.* the collective multivariate suite of sediment grain size contributions, %POM and depth of the transition zone. Each resemblance matrix was then subjected to PERMANOVA to test whether the above three non-enduring environmental variables differed among habitats and seasons, both of which were considered fixed factors. In all PERMANOVA tests, the null hypothesis that there were no significant differences among *a priori* groups was rejected if the significance level (p) was < 0.05. The relative influence of each of the terms in the model was quantified using their components of variation. The main causes of any significant differences in each dependent variable were identified from plots of their estimated marginal means and associated 95% confidence levels, which were back transformed when appropriate. Note that 95% confidence levels were not calculated for the sediment grain size contributions as these were multivariate analyses.

Differences in species richness, density and diversity among habitat types and seasons

The number of individuals of each benthic macroinvertebrate species in each replicate sample at each nearshore and offshore site in each season was used to calculate the species richness, density (individuals 0.1m^{-2}), Shannon-Weiner diversity and average quantitative taxonomic distinctness for each sample using the DIVERSE routine. The latter variable is a measure of species diversity that accounts for the extent to which individuals from different species are related based on their taxonomic separation through the hierarchical levels of the Linnaean tree (Warwick & Clarke, 1995). The extent of the slope of the $\log_e$ (mean) and the $\log_e$ (standard deviation) of the various groups of replicates for each of the above variables indicated that species richness and density in both the nearshore and offshore waters required a square-root and log(X+1) transformation, respectively, to approximate the assumptions of PERMANOVA. In contrast, Shannon-Weiner diversity and average quantitative taxonomic distinctness did not require transformation. Euclidean distance matrices, constructed separately for each variable in the nearshore and offshore waters, were subjected to the same PERMANOVA tests as described above for the non-enduring sediment characteristics. The methods for interpreting these tests were the same as those described above.

5.2.2.2: Multivariate analyses

Differences in benthic macroinvertebrate composition among habitat types and seasons

The abundances of the various benthic macroinvertebrate species in replicate samples collected from each nearshore and offshore site in each season were initially subjected to dispersion weighting in order to down-weight the contributions of those species that exhibited erratic differences in abundance between replicate samples (Clarke *et al.*, 2006b). These data were subjected to a square root transformation to reduce the influence of any very abundant and consistently occurring species and then used to construct separate Bray-Curtis similarity matrices for both the nearshore and offshore waters. These matrices were then each subjected to the same PERMANOVA tests as described above.

Any significant habitat and/or seasonal differences detected by PERMANOVA were investigated in more detail by subjecting the above matrices to one-way Analysis of Similarities (ANOSIM) tests (Clarke & Green, 1988). In those cases in which PERMANOVA detected a significant habitat x season interaction, the ANOSIM tests for the first of these factors were carried out for each level of the second factor (and *vice versa*) to remove any confounding influences. In these and all subsequent ANOSIM tests, the null hypothesis that there were no significant differences in benthic macroinvertebrate composition among *a priori* groups was rejected if the significance level (p) was < 0.05. The extent of any such significant differences was determined by the magnitude of the test statistic (R), which typically ranges between 0, *i.e.* no group differences, to 1, *i.e.* the similarities between samples from different groups are always less than those between samples belonging to the same group. Non-metric Multidimensional Scaling (nMDS) ordination was then employed to display visually the ways in which the samples from each *a priori* group are distributed in low dimensional space (2D or 3D) according to their faunal compositions.

When ANOSIM detected a significant difference in the compositions of benthic macroinvertebrates among habitats and/or seasons and the associated R-statistic was ≥ 0.2, one-way Similarity Percentages (SIMPER; Clarke, 1993) was used to elucidate which species typified the assemblages at each habitat and/or in each season and which species contributed most to differences between each pair of those combinations. Focus was placed on those species that had the highest similarity/dissimilarity to standard deviation ratio and were most abundant.

Relationships between the benthic macroinvertebrate community and environmental characteristics of habitat types

The RELATE routine was used to test whether the relative pattern of differences among habitats in benthic macroinvertebrate composition were significantly correlated with those defined by their (i) enduring environmental characteristics and (ii) non-enduring characteristics, *i.e.* water physico-chemical variables and sediment characteristics. This routine was thus used to determine the extent to which the pattern of the rank orders of resemblance in the Bray-Curtis similarity matrix constructed from the nearshore or offshore faunal assemblage data averaged for every habitat type or site, respectively, matched the complementary Manhattan distance matrices constructed from the pretreated (i) enduring environmental data (see Chapter 2) and (ii) non-enduring environmental data (see subsections 3.2.2.1; 5.2.1). Note that the matrices employed for the offshore analyses were constructed from the averages recorded at each site rather than habitat type in order to increase the number of samples in the reference (faunal) matrices and thus minimize the likelihood of RELATE finding a significant match between the complementary matrices by chance. Note also that the RELATE analyses for the nearshore waters were carried out separately for each season as significant interactions between habitats and seasons were detected for the faunal and/or non-enduring environmental data (see subsections 5.3.1.4 and 3.3.1.1). However, this was not the case for the offshore waters (see subsections 5.3.2.4 and 5.3.2.1) and thus those analyses were carried out using data averaged over all seasons. The null hypothesis that there is no relationship in the pattern of the rank orders of resemblance between the two matrices was rejected if the significance level (p) was < 0.05. The test statistic, rho (ρ), was used to determine the relative extent of any significant differences, with a value of 0 reflecting no correlation in rank order pattern and a value of 1 indicating a perfect match. nMDS ordinations were also constructed from the aforementioned matrices to provide a visual indication of any matching in the spatial arrangement of habitat types as defined by their faunal *vs* environmental characteristics.

The Biota and Environment matching routine (BIOENV; Clarke & Ainsworth, 1993) was then employed to ascertain whether a better correlation between complementary faunal and non-enduring environmental matrices could be achieved by using only a particular subset of the non-enduring variables, rather than the full suite. The faunal (reference) resemblance matrices used in this procedure were identical to those employed in the RELATE routine described above, while the non-enduring (secondary) matrices employed were the same as those used to produce the non-enduring resemblance matrices used in the above RELATE tests. Manhattan distance was considered an appropriate resemblance coefficient for these latter data for the BIOENV procedure, as this distance measure was employed for these variables in the classification procedure. The null hypothesis and test statistic for these were the same as those described above for RELATE. Comparisons of the spatial patterns among the different habitat types exhibited by (i) the average benthic macroinvertebrate faunal composition *vs* (ii) the averages of the complementary non-enduring environmental variables selected by BIOENV, were displayed visually by subjecting the Bray-Curtis similarity matrices constructed from the faunal data to nMDS ordination, then overlaying circles ("bubbles") of proportionate sizes that represented the magnitude of the selected non-enduring environmental variables at each habitat/site.

5.3: Results

5.3.1: Nearshore waters

5.3.1.1: Differences in the non-enduring environmental variables among nearshore habitat types and seasons

The ways in which the range of non-enduring water physico-chemical variables (*i.e.* salinity, water temperature, dissolved oxygen concentration and pH) and detached macrophyte biomass varied among habitats and seasons have been described in subsections 3.3.1.1 and 3.3.2.1, respectively, for all nearshore and offshore habitats at which benthic macroinvertebrates were sampled.

Two-way PERMANOVA showed that sediment grain size composition differed significantly among habitats and seasons and that there was no interaction between these two main effects (*p*=0.001-0.016; Table 5.1a). On the basis of the values for the components of variation, habitat made by far the greatest contribution to the variance in this dependent variable. However, these spatial differences were not extreme. Thus, the sediment at all habitats was dominated by medium sands with grain sizes of 250-499 μm. The differences in grain size composition among habitats were greatest between A and K, which contained the greatest amount of sediment in the 250-499 μm fraction (68%), and F and H, which had the least amount of this fraction (50-55%; Fig. 5.2a). The last of these habitats and C contained the least amount of the 125-249 μm fraction, *i.e.* 7-11% *vs* 15-19%, while D contained the greatest proportion of sediment in the < 2000, 1000-1999, 63-124 and > 63 μm size fractions (Fig. 5.2a). Differences among seasons were not pronounced, with the largest differences being that between winter and spring. The 250-499 μm size fraction again dominated in samples for each season, but the percentage contribution of the 500-999 μm fraction was greater in winter (30%)

Table 5.1: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (*p*) from PERMANOVA tests on the data for mean (a) sediment grain size composition, (b) percentage organic matter content and (c) transition zone depth at the six nearshore habitat types in Broke Inlet sampled in each season between spring 2007 and winter 2008. df = degrees of freedom. Significant results are highlighted in bold.

	(a) Sediment grain size composition				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Season	3	**14.348**	**2.422**	**0.395**	**0.016**
Habitat	5	**38.115**	**6.434**	**2.236**	**0.001**
Interactions					
Season x Habitat	13	4.328	0.731	-0.389	0.877
Residual	66	5.927		5.924	

	(b) Particulate organic matter				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Season	3	0.505	2.688	0.0148	0.062
Habitat	5	**1.192**	**6.343**	**0.0697**	**0.001**
Interactions					
Season x Habitat	13	0.218	1.159	0.007	0.327
Residual	66	0.188		0.188	

	(c) Transition zone depth				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Season	3	0.010	1.722	0.019	0.168
Habitat	5	**0.016**	**2.663**	**0.068**	**0.030**
Interactions					
Season x Habitat	13	0.010	1.705	0.010	0.073
Residual	72	0.006		0.062	

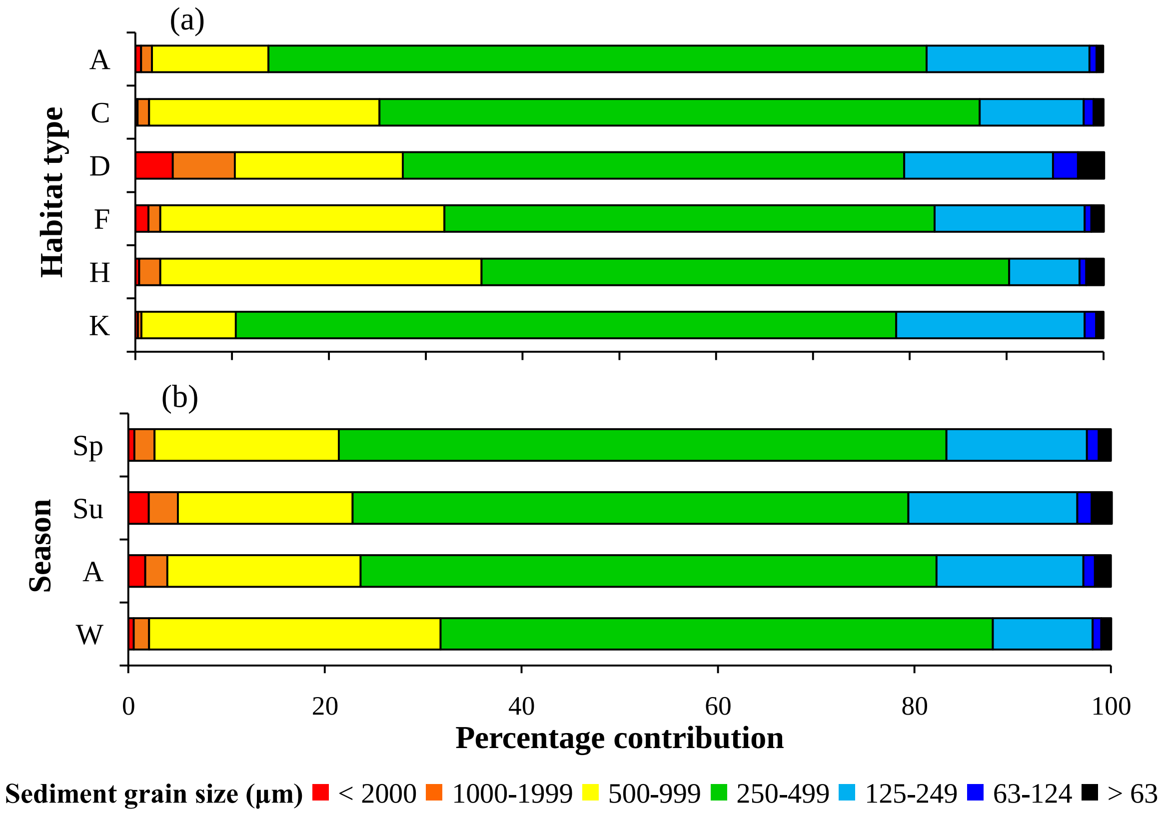


Fig. 5.2: Mean percentage sediment grain size contributions recorded at each of the six nearshore habitat types in Broke Inlet among (a) habitat types and (b) seasons sampled between spring 2007 and winter 2008.

than spring (18%), and the contribution of the 125-249 μm fraction was least during winter (10%; Fig. 5.2b).

The percentage contribution of POM and the depth of the transition zone both differed significantly only among habitats (p=0.001 and 0.030, respectively; Table 5.1). Mean values for the former variable were greatest at habitats D and H, *i.e.* 2 and 1.6%, respectively, and lowest at C and K, *i.e.* 0.5% (Fig. 5.3a). The mean depth of the transition zone exceeded the length of the core (*i.e.* 10 cm) at habitats A, H and K but was shallowest at D (*ca* 8 cm; Fig. 5.3b).

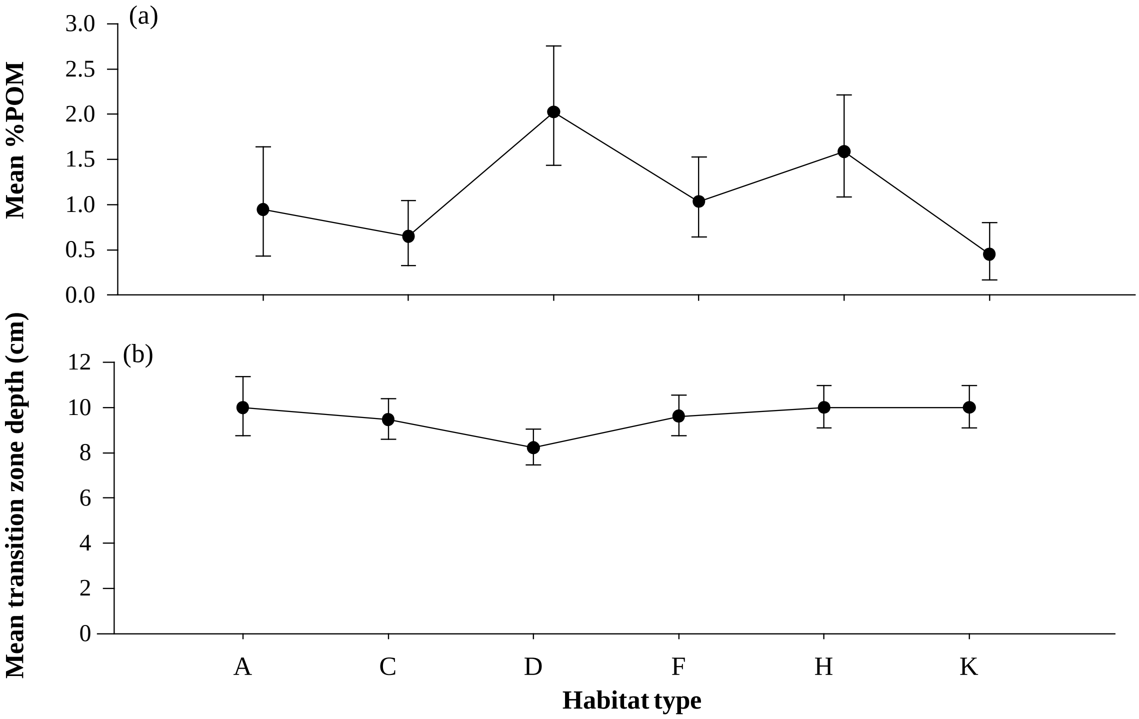


Fig. 5.3: Mean (a) percentage particulate organic matter content (%POM) and (b) depth of the transition zone at each of the six nearshore habitat types in Broke Inlet sampled in each season between spring 2007 and winter 2008.

5.3.1.2: Densities of benthic macroinvertebrate phyla, species and feeding guilds among nearshore habitat types

A total of 7,162 benthic macroinvertebrates were collected from sites throughout the nearshore waters of Broke Inlet between spring 2007 and winter 2008. These fauna comprised 28 species belonging to seven phyla (Table 5.2). The Annelida, represented by nine polychaete species from seven families, accounted for 64% of the individuals collected. The Arthropoda was the next most speciose and abundant phyla, comprising two species of both amphipod and isopod and a single decapod and mysid species, and

Table 5.2: Mean density (number of individuals 0.1m^{-2}; M), standard error (^{SE}), percentage contribution to the overall mean density (%) and the rank by density (R) of the benthic macroinvertebrate taxa recorded at the six nearshore habitat types sampled in Broke Inlet in each season between spring 2007 and winter 2008. Abundant taxa at each habitat type (*i.e.* those that contribute ≥ 5% to the mean overall density) are highlighted in grey. Each taxon has been assigned to its respective phyla and class (P/C; *i.e.* A = Annelida, Ar = Arthropoda, C = Cnidaria, H = Hemichordata, M = Mollusca, N = Nemertea, Pl = Platyhelminthes, S = Sipuncula and B = Bivalvia, I = Insecta, Ma = Malacostraca, P = Polychaeta, Sc = Scyphozoa, T = Thaliacea) and predominant feeding mode (F; *i.e.* Dp = deposit feeder, Dt = detritus feeder, S = suspension feeder, P = predator, U = Unknown). The total number of species, overall mean density and adjusted number of individuals sampled (*i.e.* after the number of individuals in each sample had been adjusted to that in 0.1 m^{-2} and summed) are also provided for each habitat type. Species ranked by total abundance.

			A			**C**			**D**			**F**			**H**			**K**		
Species	**P/C**	**F**	**M ^{SE}**	**%**	**R**	**M ^{SE}**	**%**	**R**	**M ^{SE}**	**%**	**R**	**M ^{SE}**	**%**	**R**	**M ^{SE}**	**%**	**R**	**M ^{SE}**	**%**	**R**
Capitella capitata	A/P	Dp	$73.3^{18.0}$	43.46	1	$31.1^{11.7}$	11.71	3	$16.5^{11.0}$	8.63	3	$140.4^{20.6}$	34.94	1	$167.9^{32.4}$	39.18	1	$63.4^{13.9}$	34.60	1
Ceratonereis aequisetis	A/P	Dp/Dt	$2.9^{1.3}$	1.73	8	$81.2^{14.5}$	30.55	1	$77.9^{10.7}$	40.64	1	$35.9^{7.9}$	8.94	3	$133.2^{24.6}$	31.10	2	$5.7^{1.7}$	3.09	6
Corophium minor	Ar/Ma	Dt/S	$29.6^{14.2}$	17.53	2	$18.1^{6.8}$	6.8	6	$0.7^{0.4}$	0.34	9	$99.9^{25.5}$	24.86	2	$12.8^{6.7}$	3.00	7	$51.4^{13.7}$	28.06	2
Cyathura hakea	Ar/Ma	P	$1.7^{1.4}$	0.99	9	$49.0^{9.1}$	18.43	2	$35.9^{6.1}$	18.73	2	$20.7^{5.5}$	5.15	4	$13.1^{3.7}$	3.05	6	$2.2^{0.7}$	1.19	10
Armandia intermedia	A/P	Dp				$30.7^{6.4}$	11.55	4	$15.7^{5.3}$	8.17	4	$19.2^{5.1}$	4.77	5	$4.4^{2.5}$	1.02	10	$27.0^{5.6}$	14.74	3
Pontomyia sp.	Ar/I	Dt	$25.0^{6.0}$	14.81	3	$27.4^{8.2}$	10.32	5	$13.7^{3.9}$	7.15	5	$12.6^{4.4}$	3.14	7	$6.3^{1.9}$	1.47	9	$4.8^{1.6}$	2.62	7
Fluviolanatus subtorta	M/B	S				$0.7^{0.5}$	0.25	13	$11.1^{4.4}$	5.79	7	$13.1^{4.0}$	3.25	6	$28.7^{7.6}$	6.71	3	$0.4^{0.3}$	0.24	14
Scoloplos normalis	A/P	Dp	$9.6^{2.9}$	5.68	5	$11.3^{2.1}$	4.26	7	$12.0^{2.2}$	6.24	6	$9.6^{1.4}$	2.38	10	$3.0^{1.0}$	0.71	12	$4.6^{1.0}$	2.50	8
Arthritica semen	M/B	Dp/S	$10.0^{4.1}$	5.93	4	$3.5^{1.0}$	1.31	9				$8.7^{2.6}$	2.17	11	$13.7^{4.9}$	3.20	5	$9.6^{2.9}$	5.23	4
Melita matilda	Ar/Ma	Dp	$6.7^{2.9}$	3.95	6	$6.1^{4.4}$	2.29	8	$6.7^{2.9}$	3.52	8	$12.0^{6.8}$	2.98	8	$2.4^{2.2}$	0.56	13	$5.9^{3.7}$	3.21	5
Prionospio cirrifera	A/P	Dp										$6.1^{4.1}$	1.52	12	$22.0^{11.3}$	5.13	4	$0.2^{0.2}$	0.12	17
Cirolanidae sp.	Ar/Ma	P	$5.0^{1.7}$	2.96	7	$1.3^{0.7}$	0.49	11				$9.8^{2.7}$	2.44	9	$0.2^{0.2}$	0.05	19	$2.0^{1.3}$	1.07	11
Pseudopolydora sp.	A/P	Dp/Dt				$0.9^{0.5}$	0.33	12				$3.9^{2.5}$	0.98	14	$10.5^{4.0}$	2.44	8			
Nemertea sp.	N	P										$4.8^{1.9}$	1.19	13	$2.4^{1.2}$	0.56	13	$2.4^{1.6}$	1.31	9
Capitellid sp.	A/P	Dp	$1.7^{0.8}$	0.99	9	$0.7^{0.5}$	0.25	13	$0.2^{0.2}$	0.11	11	$2.4^{1.5}$	0.60	15	$0.9^{0.4}$	0.20	16	$1.5^{1.3}$	0.83	12
Palaemonetes australis	Ar/Ma	S/Dp				$0.2^{0.2}$	0.08	18	$0.2^{0.2}$	0.11	11				$3.9^{1.3}$	0.91	11	$0.2^{0.2}$	0.12	17
Desdemona ornata	A/P	S				$0.2^{0.2}$	0.08	18	$0.2^{0.2}$	0.11	11	$2.0^{0.9}$	0.49	16	$0.4^{0.4}$	0.10	18	$0.9^{0.7}$	0.48	13
Ficopomatus enigmaticus	A/P	S				$0.4^{0.3}$	0.16	16	$0.4^{0.3}$	0.23	10				$1.7^{1.0}$	0.41	15			
Sanguinolaria biradiata	M/B	S	$1.3^{1.0}$	0.74	12	$0.7^{0.4}$	0.25	13	$0.2^{0.2}$	0.11	11				$0.7^{0.4}$	0.15	17	$0.2^{0.2}$	0.12	17
Chironomidae sp.	Ar/I	Dt				$1.7^{1.2}$	0.66	10												
Ceratopogonidae sp.	Ar/I	U	$1.7^{1.7}$	0.99	9													$0.4^{0.3}$	0.24	14
Gastrosaccus sorrentoensis	Ar/Ma	S	$0.4^{0.4}$	0.25	13							$0.2^{0.2}$	0.05	17				$0.4^{0.3}$	0.24	14
Bivalvia spp.	M/B	U				$0.4^{0.3}$	0.16	16	$0.2^{0.2}$	0.11	11									
Sipuncula sp.	S	Dp													$0.2^{0.2}$	0.05	19			
Diptera sp.	Ar/I	U										$0.2^{0.2}$	0.05	17						
Triplectides australis	Ar/I	Dt										$0.2^{0.2}$	0.05	17						
Rhizostomeae sp.	C/Sc	U										$0.2^{0.2}$	0.05	17						
Salpida sp.	H/T	S				$0.2^{0.2}$	0.08	18												
Species richness			**13**			**20**			**15**			**20**			**20**			**19**		
Overall mean density			**169**			**266**			**192**			**402**			**429**			**183**		
Number of samples			**24**			**48**			**48**			**48**			**48**			**48**		
Adjusted number of individuals			**4,056**			**12,768**			**9,216**			**19,296**			**20,592**			**8,784**		
Actual number of individuals			**405**			**1,221**			**881**			**1846**			**1968**			**841**		

which together contributed 24% to the total number of benthic macroinvertebrates. The Mollusca and Uniramia, represented by four bivalve and five insect species, accounted for 6 and 5%, respectively, of the invertebrates sampled (Table 5.2).

The faunas at habitats C, F and H were the most speciose (20), closely followed by K (19), while habitat A contained the least number of species (13; Table 5.2). It should be noted, however, that due to the extensive shallow sandbanks that surround the last habitat, sampling could be carried out only during spring and winter. Similarly, the mean densities of benthic macroinvertebrates were greatest at habitat H, which is located in the vegetated areas of the entrance channel, and at F on the south-western shore of Shannon Basin, *i.e.* 429 and 402 individuals 0.1 m^{-2}, respectively, while, as with species richness, the lowest mean densities were recorded at habitat A (169 individuals $0.1m^{-2}$). Relatively low densities were also recorded at habitats K and D at the mouth of the Forth River in Shannon Basin and in the northern shore of Middle Basin, respectively (*i.e.* 183 and 192 individuals $0.1m^{-2}$, respectively; Table 5.2).

Deposit feeders were the most numerous feeding guild at habitats A, F, K and H, representing between 47 and 56% of individuals, with detritus/suspension feeders making the next largest contribution at the first three habitats (18-28% of the individuals; Table 5.2). At habitats C and D, deposit/detritus feeders were most numerous, comprising between 31 and 41% of the total number of individuals, respectively, followed by deposit feeders (27-30%) and predators (19%). Conversely, suspension feeders contributed only 4 to 7% in habitats D, F and H and *ca* 1% in habitats A, C and K (Table 5.2).

The Polychaeta was the most abundant class, contributing to between 51 and 81% of the individuals collected from each habitat, with their mean density being greatest at habitats H and F. The dominance of polychaetes at habitat H was due to the presence of high densities of *Capitella capitata* and *Ceratonereis aequisetis,* with the former species ranking first or third in terms of abundance at each habitat (Table 5.2). At habitat F, *C. capitata* and the amphipod *Corophium minor* collectively represented 60% of the total number of individuals. These two species also ranked first and second, respectively, in terms of density and contributed a similarly high proportion of the invertebrate fauna sampled at habitats A and K. Other abundant species at A and K were the insect larvae of *Pontomyia* sp. and the opheliid polychaete *Armandia intermedia,* which represented 15% of the fauna sampled at these habitats, respectively. The most numerous species at habitat D were the nereidid polychaete *C. aequisetis* (40%) and the anthurid isopod *Cyanthura hakea* (19%), while *C. capitata* and *A. intermedia* (both 8%) were also relatively abundant. Molluscs were most abundant at habitat H and, to a lesser extent, at F, due mainly to relatively high densities of the bivalves *Fluviolanatus subtorta* (7 and 3%, respectively) and *Arthritica semen* (3 and 2%, respectively; Table 5.2).

5.3.1.3: Differences in species richness, density and diversity among nearshore habitat types and seasons

The species richness of the nearshore benthic macroinvertebrate fauna differed significantly among both habitats and seasons (*p*=0.03-0.034), with the components of variation for the latter variable being about twice that of the former (Table 5.3a). Mean species richness was greatest in summer (5.1) and spring (4.6) and least in autumn and winter (3.3) (Fig. 5.4a). The fauna was most speciose at habitat F (5.3) and least speciose at D and K, at which an average of *ca* 3.3 species were recorded in each sample (Fig. 5.4b).

PERMANOVA demonstrated that mean density differed significantly among seasons (*p*=0.044) but not habitats (Table 5.3b), with the densities being highest in summer (398 individuals 0.1m^{-2}) and lowest during autumn and winter (220 and 239 individuals 0.1m^{-2}, respectively; Fig. 5.4c).

Shannon-Wiener diversity was shown by PERMANOVA to differ among habitats and seasons, with an interaction being detected between these two main effects (*p*=0.001-0.012; Table 5.3c). Differences among seasons and the season x habitat interaction each explained approximately twice the variance in this dependent variable than did differences among habitats. Diversity in the majority of habitats was greatest in spring and/or summer, with the values in these seasons being highest at habitats C, F and H and lowest at K. The significant season x habitat interaction was attributable to differences in the rank order and extent of differences among habitats in the various

Table 5.3: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (*p*) from PERMANOVAs on the data for mean (a) species richness, (b) density, (c) Shannon-Weiner diversity and (d) average quantitative taxonomic distinctness of the benthic macroinvertebrate assemblages at the six nearshore habitat types in Broke Inlet sampled in each season between spring 2007 and winter 2008. df = degrees of freedom. Significant results are highlighted in bold.

	(a) Species richness				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Season	3	**1.063**	**6.405**	**0.040**	**0.003**
Habitat	5	**0.480**	**2.892**	**0.022**	**0.034**
Interactions					
Season x Habitat	13	0.281	1.692	0.287	0.100
Residual	66	0.166		0.166	

	(b) Density				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Season	3	**2.105**	**2.859**	**0.064**	**0.044**
Habitat	5	1.296	1.760	0.038	0.132
Interactions					
Season x Habitat	13	0.868	1.178	0.032	0.334
Residual	66			0.736	

	(c) Shannon-Weiner diversity				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Season	3	**0.993**	**11.781**	**0.039**	**0.001**
Habitat	5	**0.230**	**2.931**	**0.015**	**0.012**
Interactions					
Season x Habitat	13	**0.213**	**2.713**	**0.035**	**0.003**
Residual	66	0.078		0.783	

	(d) Average quantitative taxonomic distinctness				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***P***
Season	3	**1056.800**	**3.829**	**36.600**	**0.018**
Habitat	5	**910.710**	**3.300**	**44.079**	**0.011**
Interactions					
Season x Habitat	13	467.380	1.694	47.853	0.081
Residual	66	275.970		275.970	

seasons. For example, diversity at habitat H was the third highest in both spring and summer, but was the lowest during autumn and second lowest during winter.

Species diversity, as measured using average quantitative taxonomic distinctness, differed among both habitats and seasons (*p*=0.011-0.018), with the latter of these main effects explaining a greater proportion of the variance in this dependent variable (Table 5.3d). Values of this variable was greatest at habitat A (95), even though this habitat type could be sampled only during spring and winter, and was least at habitat H (69). The values for average quantitative taxonomic distinctness at the remaining habitats ranged between 84 and 87 (Fig. 5.4e). As with species richness and density, the values for average quantitative taxonomic distinctness were highest during spring and summer and lowest in autumn and winter (Fig. 5.4f).

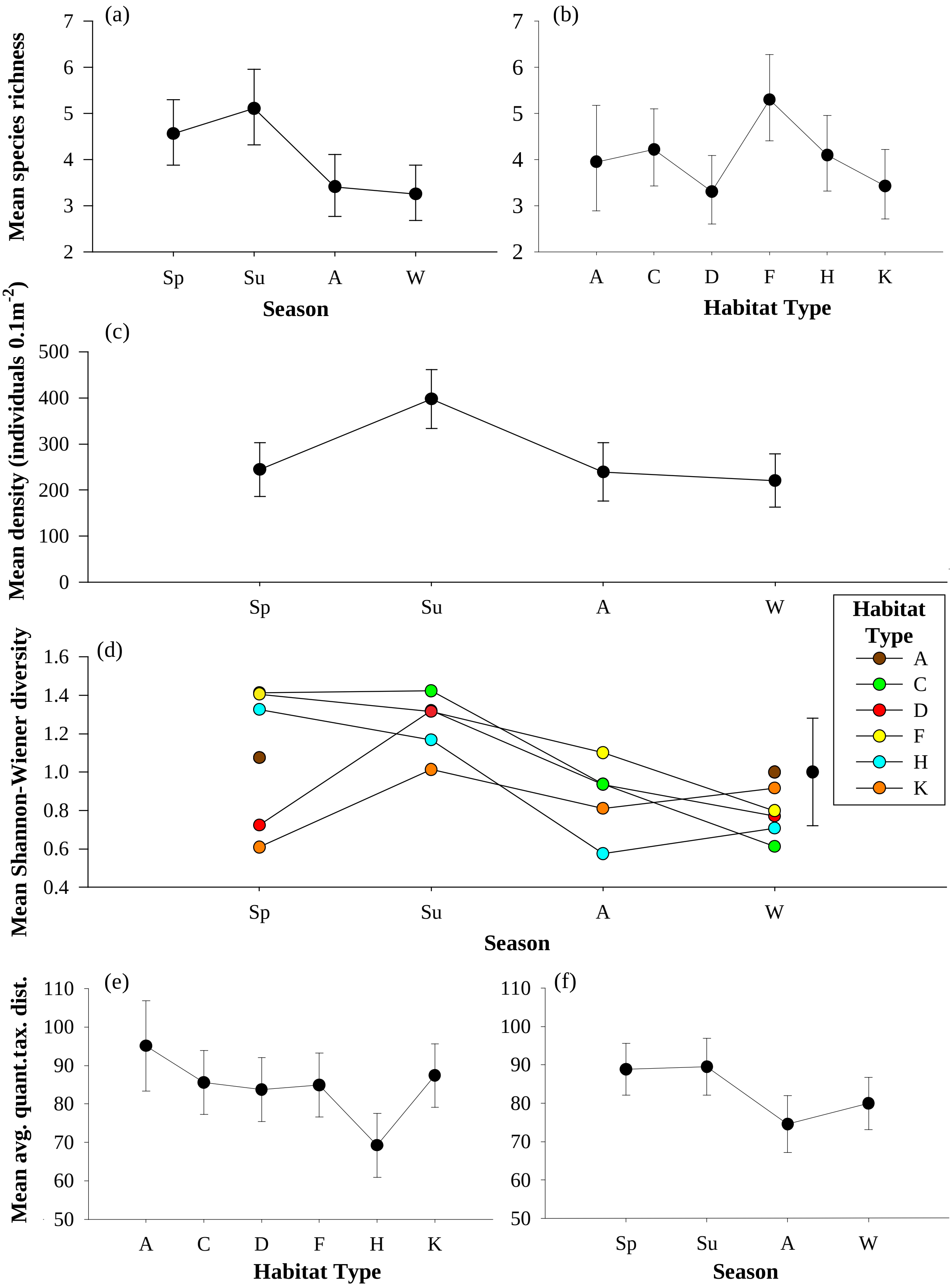


Fig. 5.4: Mean (a, b) species richness, (c) density (individuals 0.1 m^{-2}), (d) Shannon-Weiner diversity and (e, f) average quantitative taxonomic distinctness of the benthic macroinvertebrate assemblages at each of the six nearshore habitat types and/or seasons in Broke Inlet sampled between spring 2007 and winter 2008.

5.3.1.4: Differences in benthic macroinvertebrate assemblage composition among nearshore habitat types

Two-way crossed PERMANOVA demonstrated that the species composition of the nearshore benthic macroinvertebrate communities differed significantly among habitats and seasons and that there was an interaction between those main effects (*p*=0.001; Table 5.4). The components of variation were by far the highest for habitat and were least for the season x habitat interaction (Table 5.4). However, given the significance of this interaction term, subsequent analyses to more fully elucidate the nature and extent of habitat differences in the composition of the nearshore benthic macroinvertebrate assemblages were carried out separately for each season.

Table 5.4: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (*p*) from a two-way PERMANOVA of the benthic macroinvertebrate compositions at six of the nearshore habitat types in Broke Inlet sampled in each season between spring 2007 and winter 2008. df = degrees of freedom. Significant results are highlighted in bold.

	Nearshore benthic macroinvertebrate composition				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Season	3	**9656.100**	**6.108**	**378.530**	**0.001**
Habitat	5	**9125.800**	**5.773**	**523.950**	**0.001**
Interactions					
Season x Habitat	13	**2426.700**	**1.535**	**211.450**	**0.001**
Residual	66	1580.900		1580.900	

One-way ANOSIM tests demonstrated that the benthic macroinvertebrate composition differed significantly among habitats in each season (*p*=0.001-0.007), with the overall extent of those differences being low to moderate (Global *R*=0.277-0.591; Table 5.5). The differences among habitats were greatest in spring, with almost every pair of habitats differing significantly from each other. In this season, the faunal composition at habitat K was the most distinct, with all but one of the pairwise comparisons involving this habitat generating *R* values > 0.800 (Table 5.5a). These findings were reflected on the ordination plot derived from composition data for spring, with samples from habitat K forming a tight and discrete group to one side of the plot (Table 5.5a; Fig. 5.5a). The fauna at this habitat, which is located near the mouth of the Forth River (Fig. 5.1), was characterised by the presence of relatively high densities of the polychaete *C. capitata* and the bivalve *A. semen*, which were also mainly

Table 5.5: *R*-statistic and/or significance level (*p*) values derived from one-way ANOSIM tests of nearshore benthic macroinvertebrate composition among the six nearshore habitat types during each season sampled between spring 2007 and winter 2008. Insignificant pairwise comparisons are highlighted in grey. Note, habitat A was not sampled in either summer or autumn.

(a) Spring; *p*=0.001, Global *R*=0.591

	A	**C**	**D**	**F**	**H**
C	0.490				
D	0.396	0.167			
F	0.771	-0.063	0.396		
H	0.969	0.729	0.510	0.573	
K	0.688	0.896	0.813	0.896	0.896

(b) Summer; *p*=0.001, Global *R*=0.521

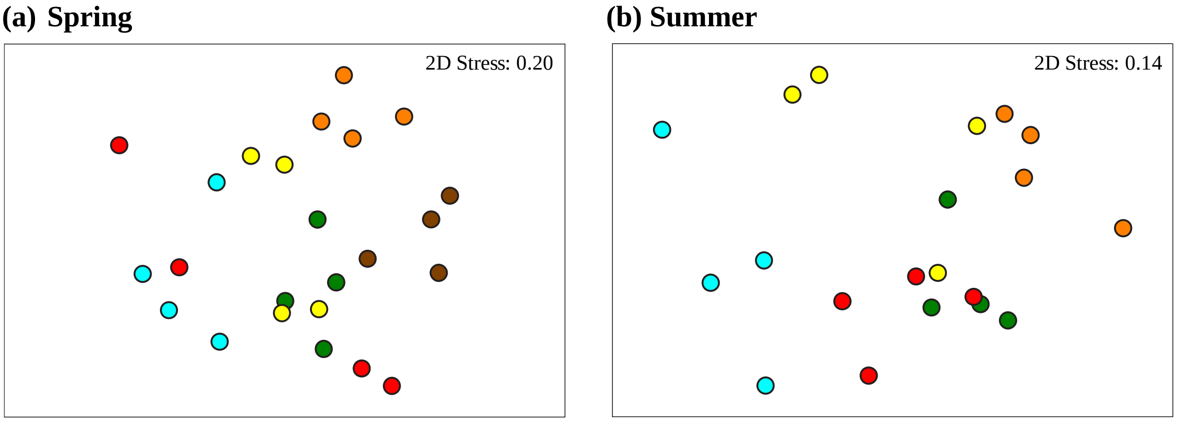
	C	**D**	**F**	**H**
D	0.063			
F	0.313	0.469		
H	0.823	0.396	0.396	
K	0.896	0.833	0.417	1.000

(c) Autumn; *p*=0.003, Global *R*=0.322

	C	**D**	**F**	**H**
D	0.063			
F	0.719	0.719		
H	0.063	0.208	0.146	
K	0.333	0.500	0.260	0.271

(d) Winter; *p*=0.007, Global *R*=0.277

	A	**C**	**D**	**F**	**H**
C	0.646				
D	0.958	-0.281			
F	0.219	0.135	0.229		
H	0.510	0.063	0.146	0.219	
K	0.021	0.375	0.615	0.010	0.427


(a) Spring **(b) Summer**

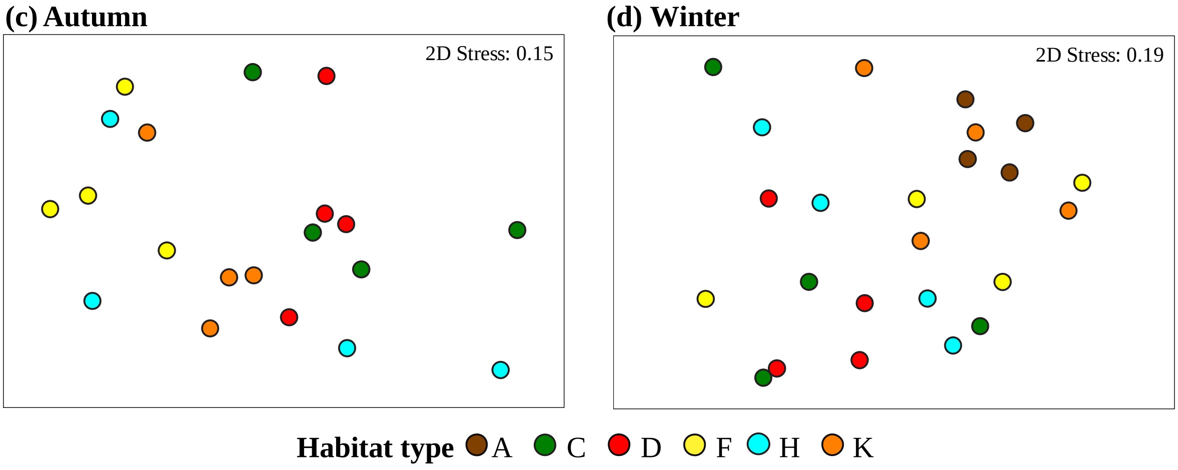

(c) Autumn **(d) Winter**

Fig. 5.5: nMDS ordination plots of the benthic macroinvertebrate composition at each of the six nearshore habitat types sampled in Broke Inlet in each season between spring 2007 and winter 2008. Plots derived from Bray-Curtis similarity matrices constructed from the average benthic macroinvertebrate assemblage data recorded at each site representing each habitat type.

responsible for distinguishing the fauna at K from those at A, D and H (Appendix 5.1a). The habitat with the next most distinct fauna during spring, *i.e.* A (Table 5.5a; Fig. 5.5a), was typified by the presence of appreciable numbers of *Pontomyia* sp. and *A. semen*, with greater numbers of the former species being important in distinguishing the fauna at this habitat from those at the others. *Ceratonereis aequisetis* typified the benthic macroinvertebrate assemblages at habitats C, F and H, with the fauna at the last of these habitats also being distinguished from those of others by greater densities of the bivalves *A. semen* and *F. subtorta* and the polychaete *C. aequisetis* (Appendix 5.1a).

The pattern of differences in the benthic macroinvertebrate faunas among the various habitats in spring remained the same during summer, with significant differences being recorded between each pair of habitats except for C *vs* D (Table 5.5b). Thus, the fauna at habitat K was again the most distinct (Table 5.5b; Fig. 5.5b), but, in this season, this was due to relatively high densities of the polychaete *A. intermedia* and low densities of species such as *C. aequisetis, C. hakea* and *F. subtorta* (Appendix 5.1b). The fauna at habitat H was distinguished from those at C and F by greater densities of *F. subtorta* and *C. aequisetis*, while those at habitats C and D contained greater densities of *C. hakea* than those at habitats F and K (Appendix 5.1b).

The differences in faunal composition among habitats were not as pronounced in autumn and particularly winter (Global *R*=0.322 and 0.277, respectively), with significant differences typically being found only between habitats near the mouths of rivers (A and K) and those elsewhere in the basin (C, D and F; Table 5.5c,d). This less marked seasonal distinction in faunal composition among most habitats is reflected by the fact that the samples for each of those habitats did not form discrete groups on the ordination plots constructed from the data recorded in these two seasons (Figs 5.5c, d). The fauna at habitats A and K in winter and K in autumn were characterised, in particular, by the consistent presence of appreciable densities of the polychaetes *S. normalis* and *C. capitata* and of the amphipod *C. minor*. These species were also mainly responsible for distinguishing the fauna at habitats A and K and from those at other habitats in winter (Appendix 5.1d).

5.3.1.5: Relationships between the benthic macroinvertebrate community and environmental characteristics of nearshore habitat types

RELATE demonstrated that the pattern of relative differences among habitats, as exhibited by their suite of enduring environmental variables, was significantly matched with that defined by the benthic macroinvertebrate composition only during spring (p=0.004), with the extent of that correlation being strong, *i.e.* ρ=0.764 (Table 5.6a). These findings were reflected in the similarity between the distributions of the pairs representing the various habitats on the associated nMDS plots (*cf.* Fig. 5.6a, b). In the plots constructed from the faunal composition data recorded in each of the other three seasons, however, the points for habitats C and D lay closer together than in that constructed from the enduring environmental data, whereas the reverse trend occurred with habitats F and H. Such findings explain, at least in part, the lack of a significant correlation between the faunal and enduring environmental data in these seasons (p=0.133-0.858).

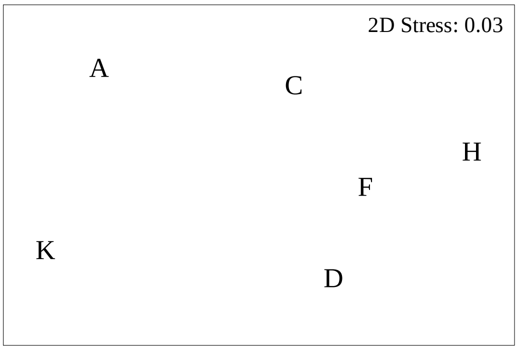
RELATE was then used to determine the extent to which the pattern of relative differences among habitats, as defined by their suite of non-enduring environmental variables (*i.e.* water physico-chemical variables and sediment characteristics), provided a good surrogate for those exhibited by the benthic macroinvertebrate fauna in each season. A significant correlation between the complementary faunal and water physico-chemical variables and amount of detached macrophytes matrices was detected in summer only (p=0.001) and the extent of that correlation was very high (ρ=0.891; Table 5.6b). When BIOENV was used to ascertain whether stronger correlations between the above matrices could be achieved by using only a particular subset of the water physico-chemical variables, a significant match was again obtained only during summer. This match employed, however, the same full set of variables as that used by RELATE and thus the extent of the correlation was the same (ρ=0.891; Table 5.6c).

RELATE detected a significant and moderately high correlation between the spatial patterns exhibited by the benthic macroinvertebrate fauna and the suite of sediment characteristics during spring (p=0.017; ρ=0.636), but not in the other seasons (Table 5.6d). Moreover, when BIOENV was used to correlate all possible

Table 5.6: Significance level (*p*) and rho statistic (ρ) values for the correlation between a resemblance matrix constructed from the average benthic macroinvertebrate fauna data at each offshore site in each season between spring 2007 and winter 2008 and complementary matrices constructed from (a) enduring environmental data (EEV), (b) water physico-chemical (W) and (d) sediment characteristic (S) data. The results of BIOENV tests between the above faunal data and the complimentary water /detached macrophytes physico-chemistry and sediment data are provided in (c) and (e) respectively. Significant correlations are highlighted in bold.

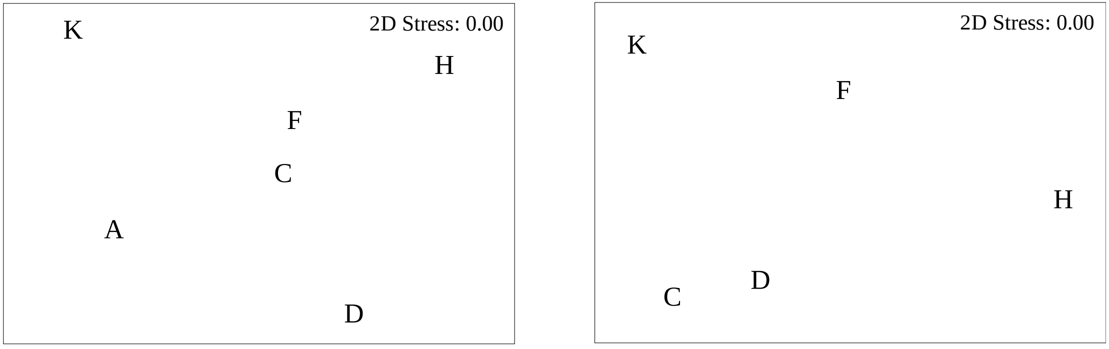
	(a) EEV		**(b) W**		**(c) W subset**		**(d) S**		**(e) S subset**	
	p	**ρ**	***p***	**ρ**	***p***	**ρ**	***p***	**ρ**	***p***	**ρ**
Spring	**0.004**	**0.764**	0.398	0.086	0.250	0.414	**0.017**	**0.636**	0.108	0.729
Summer	0.133	0.527	**0.011**	**0.891**	**0.009**	**0.891**	0.466	0.055	0.225	0.721
Autumn	0.858	-0.212	0.735	-0.212	0.862	0.127	0.887	-0.418	0.455	0.699
Winter	0.305	0.125	0.128	0.393	0.401	0.482	0.857	-0.254	0.919	0.096

(a) Enduring environmental variables



(b) Spring; *p*=0.004, ρ=0.764

(c) Summer; *p*=0.133, ρ=0.527



(d) Autumn; *p*=0.858, ρ=-0.212

(e) Winter; *p*=0.305, ρ=0.125

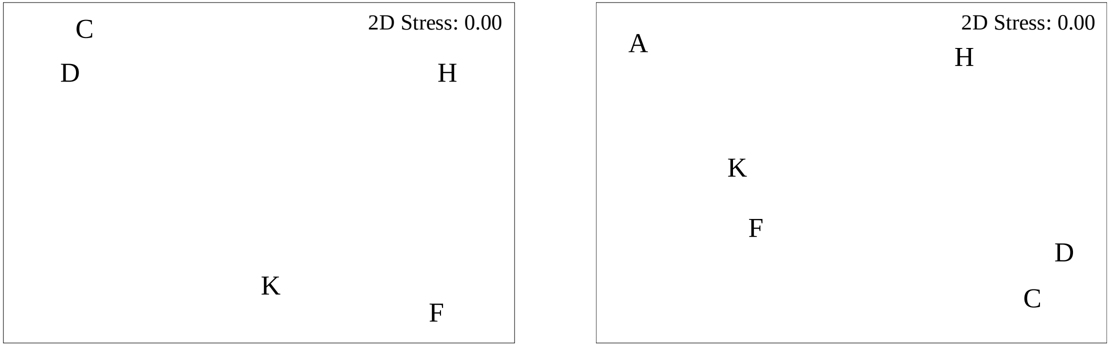


Fig. 5.6: nMDS ordination plots constructed from the averages of the (a) enduring environmental variables and (b-e) the benthic macroinvertebrate composition in each season from spring 2007 to winter 2008, at each of the six nearshore habitat types sampled. The significance levels (*p*) and rho values (ρ) obtained from the RELATE tests are also provided.

subsets of those sediment characteristics with the faunal data, a significant correlation was not detected in any season (Table 5.6e).

5.3.1.6: Differences in the mean density of the nearshore benthic macroinvertebrate species among seasons

The total number of benthic macroinvertebrate species recorded in the nearshore waters was similar in each season (21-22: Table 5.7), whereas the overall mean density was far higher in summer (415 individuals 0.1m^{-2}) than in the other three seasons (230-255 individuals 0.1m^{-2}).

Deposit feeding was the most prevalent feeding mode, comprising between 36 and 46% of all individuals in the various seasons. The contributions made by deposit/detritus feeders varied considerably among seasons, declining from 27% in spring and 34% in summer to 14-17% in autumn and winter (Table 5.7). Detritus/suspension feeders and predators each contributed between 6 and 17% to the number of individuals in each season, and suspension feeders contributed 6-9% in spring and summer and only 1% in autumn and winter (Table 5.7).

The polychaetes *C. capitata* and *C. aequisetis* and the amphipod *C. minor* were the three most abundant species in each season, and collectively comprised between 54 and 79% of the total number of individuals recorded. Other species, such as *C. hakea*, contributed more than 5% in each season and the same was true for *A. intermedia* in summer and autumn (Table 5.7).

5.3.1.7: Differences in nearshore benthic macroinvertebrate composition among seasons

Two-way PERMANOVA detected significant seasonal differences in benthic macroinvertebrate composition as well as a significant interaction between season and habitat (Table 5.4). Therefore, in order to further examine these seasonal trends without the confounding influence of habitat, one-way ANOSIM tests among seasons were carried out separately for each nearshore habitat type. These analyses identified significant seasonal differences in benthic macroinvertebrate composition in only three of the six habitats, namely C, H and K (p=0.001-0.033; Table 5.8).

Table 5.7: Mean density (number of individuals 0.1m^{-2}; M), standard error (^{SE}), percentage contribution to the overall mean density (%) and the rank by density (R) of the benthic macroinvertebrate taxa recorded in each season between spring 2007 and winter 2008 at the six nearshore habitat types sampled in Broke Inlet. Abundant taxa in each season (*i.e.* those that contribute ≥ 5% to the overall mean density) are highlighted in grey. Keys for phylum and class (P/C) and predominant feeding guild (F) of each taxon are provided in Table 5.2. The total number of species, overall mean density and adjusted number of individuals sampled (*i.e.* after the number of individuals in each sample had been adjusted to that in 0.1 m^{-2} and summed) are also provided for each season. Species ranked by total abundance.

			Spring			**Summer**			**Autumn**			**Winter**		
Species	**P/C**	**F**	**Mean** ^{SE}	**%**	**R**	**Mean** ^{SE}	**%**	**R**	**Mean** ^{SE}	**%**	**R**	**Mean** ^{SE}	**%**	**R**
Capitella capitata	A/P	Dp	$94.1^{12.0}$	36.94	1	$82.4^{19.7}$	19.83	2	$43.5^{14.6}$	17.41	2	$106.1^{21.5}$	46.06	1
Ceratonereis aequisetis	A/P	Dp/Dt	$60.1^{11.3}$	23.60	2	$103.3^{17.1}$	24.86	1	$42.8^{9.1}$	17.13	3	$41.8^{9.1}$	18.15	2
Corophium minor	Ar/M	Dt/S	$16.1^{4.0}$	6.33	3	$52.3^{17.4}$	12.58	3	$46.5^{15.3}$	18.59	1	$33.8^{9.7}$	14.68	3
Cyathura hakea	Ar/M	P	$14.8^{3.5}$	5.82	5	$28.2^{5.8}$	6.79	5	$30.5^{7.4}$	12.19	5	$17.4^{3.4}$	7.56	4
Armandia intermedia	A/P	Dp	$0.7^{0.5}$	0.29	15	$36.9^{5.8}$	8.89	4	$39.7^{5.6}$	15.88	4			
Pontomyia sp.	Ar/I	Dt	$14.9^{3.3}$	5.87	4	$28.2^{7.0}$	6.79	5	$6.4^{2.0}$	2.58	7	$8.1^{2.0}$	3.53	5
Fluviolanatus subtorta	M/B	S	$11.9^{3.6}$	4.68	6	$27.0^{6.3}$	6.50	7	$1.7^{1.0}$	0.70	12	$0.1^{0.1}$	0.06	17
Scoloplos normalis	A/P	Dp	$8.9^{1.8}$	3.48	8	$9.8^{1.4}$	2.35	9	$6.4^{1.3}$	2.58	7	$8.0^{1.3}$	3.47	6
Arthritica semen	M/B	Dp/S	$11.6^{2.0}$	4.56	7	$8.0^{3.2}$	1.93	10	$3.3^{2.8}$	1.32	9	$6.1^{1.9}$	2.65	7
Melita matilda	Ar/M	Dp	$2.9^{1.1}$	1.14	11	$5.6^{2.1}$	1.34	11	$18.5^{7.1}$	7.38	6	$1.5^{0.5}$	0.63	9
Prionospio cirrifera	A/P	Dp	$0.4^{0.2}$	0.17	17	$20.7^{9.5}$	4.99	8				$1.2^{1.0}$	0.50	10
Cirolanidae sp.	Ar/M	P	$3.8^{1.2}$	1.48	10	$5.2^{1.9}$	1.26	12	$1.7^{1.1}$	0.70	12	$1.0^{0.4}$	0.44	11
Pseudopolydora sp.	A/P	Dp/Dt	$8.4^{3.0}$	3.31	9	$0.7^{0.7}$	0.17	16	$1.0^{0.8}$	0.42	15	$0.3^{0.3}$	0.13	15
Nemertea sp.	N	P				$2.8^{1.3}$	0.67	13	$2.8^{1.2}$	1.11	10	$1.7^{1.1}$	0.76	8
Capitellid sp.	A/P	Dp	$2.5^{1.0}$	0.97	12	$0.2^{0.2}$	0.04	17	$2.1^{1.2}$	0.84	11			
Palaemonetes australis	Ar/M	S/Dp	$0.7^{0.4}$	0.29	15	$2.1^{1.0}$	0.50	14	$0.3^{0.2}$	0.14	16	$0.3^{0.2}$	0.13	15
Desdemona ornata	A/P	S	$0.9^{0.5}$	0.34	14	$1.4^{0.7}$	0.34	15	$0.3^{0.2}$	0.14	16	$0.1^{0.1}$	0.06	17
Ficopomatus enigmaticus	A/P	S	$1.0^{0.6}$	0.40	13	$0.2^{0.2}$	0.04	17	$0.2^{0.2}$	0.07	20	$0.4^{0.2}$	0.19	14
Sanguinolaria biradiata	M/B	S	$0.3^{0.3}$	0.11	18	$0.2^{0.2}$	0.04	17	$0.3^{0.2}$	0.14	16	$0.9^{0.3}$	0.38	12
Chironomidae sp.	Ar/I	Dt				$0.2^{0.2}$	0.04	17	$1.2^{0.9}$	0.49	14			
Ceratopogonidae sp.	Ar/I	U										$0.9^{0.6}$	0.38	12
Gastrosaccus sorrentoensis	Ar/M	S	$0.3^{0.2}$	0.11	18				$0.2^{0.2}$	0.07	20	$0.1^{0.1}$	0.06	17
Bivalvia spp.	M/B	U							$0.3^{0.2}$	0.14	16	$0.1^{0.1}$	0.06	17
Sipuncula sp.	S	Dp	$0.1^{0.1}$	0.06	20									
Diptera sp.	Ar/I	U										$0.1^{0.1}$	0.06	17
Triplectides australis	Ar/I	Dt	$0.1^{0.1}$	0.06	20									
Rhizostomeae sp.	Cn/S	U				$0.2^{0.2}$	0.04	17						
Salpida sp.	H/T	S										$0.1^{0.1}$	0.06	17
Species richness			**21**			**21**			**21**			**22**		
Overall mean density			**255**			**415**			**250**			**230**		
Number of samples			**72**			**60**			**60**			**72**		
Adjusted number of individuals			**18,329**			**24,923**			**15,006**			**16,584**		
Actual number of individuals			**1,754**			**2,385**			**1,436**			**1,587**		

Table 5.8: R-statistic and/or significance level (p) values derived from one-way ANOSIM tests among seasons carried out on the nearshore benthic macroinvertebrate composition data recorded in each habitat type seasonally between spring 2007 and winter 2008. Insignificant pairwise comparisons are highlighted in grey.

(a) Habitat A

Season: p=0.057, Global R=0.365

(b) Habitat C

Season: p=0.003, Global R=0.358

	Spring	Summer	Autumn
Summer	0.510		
Autumn	0.500	0.500	
Winter	0.292	0.417	0.021

(c) Habitat D

Season: p=0.109, Global R=0.135

	Spring	Summer	Autumn
Summer	0.125		
Autumn	0.125	0.083	
Winter	0.052	0.510	0.031

(d) Habitat F

Season: p=0.066, Global R=0.203

	Spring	Summer	Autumn
Summer	0.052		
Autumn	0.531	0.083	
Winter	0.031	0.229	0.344

(e) Habitat H

Season: p=0.033, Global R=0.234

	Spring	Summer	Autumn
Summer	0.021		
Autumn	0.469	0.302	
Winter	0.469	0.229	0.010

(f) Habitat K

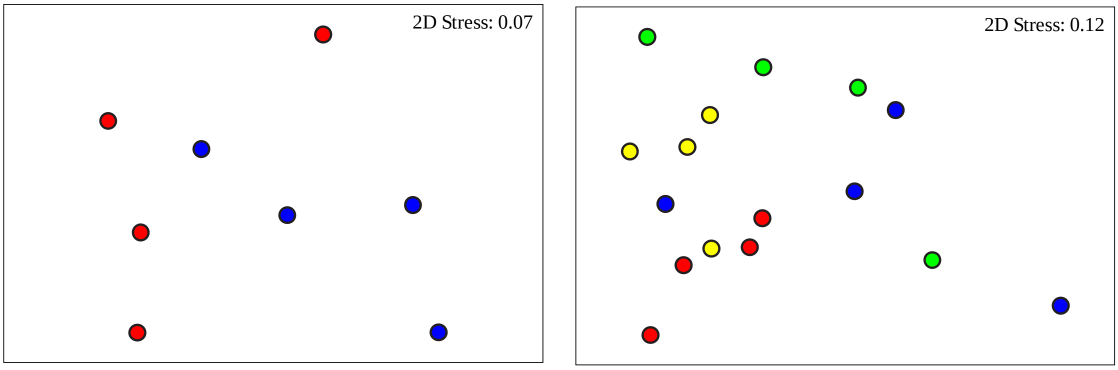
Season: p=0.001, Global R=0.688

	Spring	Summer	Autumn
Summer	1.000		
Autumn	1.000	0.115	
Winter	0.740	0.500	0.615

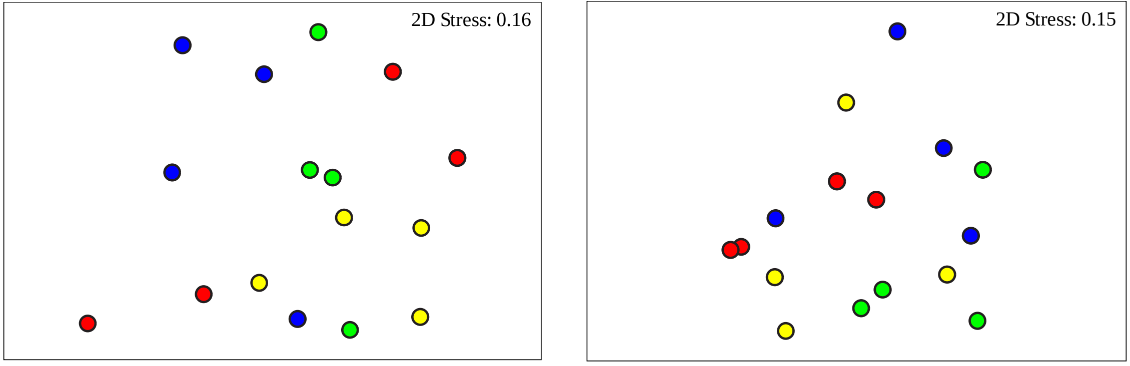
The most pronounced seasonal changes in faunal composition were those at habitat K, with the extent of those differences being large (Global R=0.688), and all but one of the pairwise comparisons being significant. The fauna in spring, which was characterised and distinguished by consistently high densities of the polychaete *C. capitata* and bivalve *A. semen*, was completely distinct from those in summer and autumn (pairwise R=1.000), with its representative samples forming a tight and distinct group to one side of the associated nMDS plot (Fig 5.7f). The fauna in spring was also distinguished from those in summer and autumn by lower densities of *A. intermedia*, and from those in winter by lower densities of *S. normalis* (Appendix 5.2c). Higher densities of the amphipod *C. minor* and lower densities of *A. intermedia* also distinguished the fauna in winter from those in the other seasons at habitat K.

The fauna at habitat C underwent moderate seasonal changes (Global R=0.358), with all pairwise comparisons involving either spring or summer being significant (Table 5.8b). The samples from these two seasons each formed relatively tight groups towards one side of the associated nMDS plot, while those representing autumn and winter were far more widely dispersed (Fig. 5.7b). The faunas in spring and summer at habitat C were characterised by and often distinguished by a relatively diverse assemblage, including *S. normalis*, *C. aequisetis*, *C. capitata*, *C. hakea* and *Pontomyia* sp. In contrast, those in autumn and winter were more depauperate and were typified mainly by only *C. haeka*. and *C. aequisetis* (Appendix 5.2a). The overall extent of the seasonal differences at habitat H was low (Global *R*=0.234) and, at a pairwise level, significant differences were only detected between spring and both autumn and winter (Table 5.8e). These differences were reflected in the greater prevalence of *F. subtorta* and *C. aequisetis* in spring than autumn and winter, and to the lower abundances of *C. capitata* in spring than in winter (Appendix 5.2b).

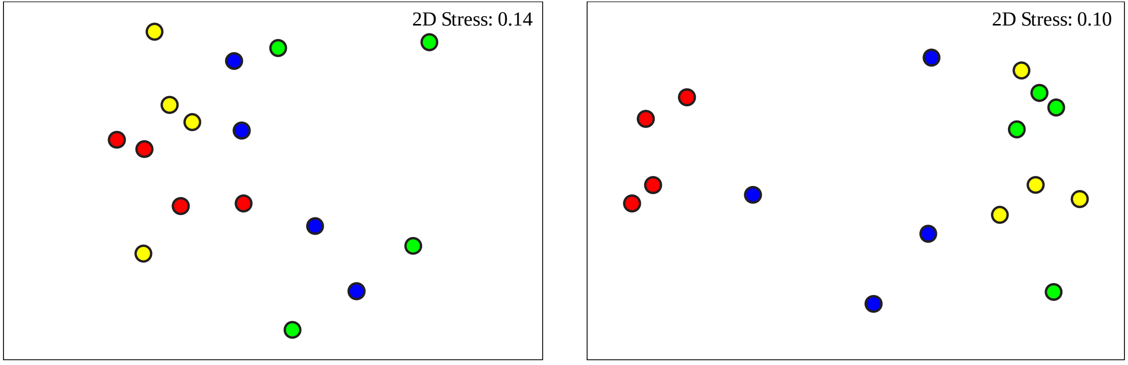
(a) Habitat A **(b) Habitat C**



(c) Habitat D **(d) Habitat F**



(e) Habitat H **(f) Habitat K**



Season 🔴spring 🟡 summer 🟢 autumn 🔵 winter

Fig. 5.7: nMDS ordination plots of the benthic macroinvertebrate composition at each nearshore site in each season between spring 2007 and winter 2008 at habitats (a) A, (b) C, (c) D, (d) F, (e) H and (f) K.

5.3.2: Offshore waters

5.3.2.1: Differences in the non-enduring environmental variables among offshore habitat types and seasons

Analysis of the spatio-temporal differences in each of a range of non-enduring water physico-chemical parameters, *i.e.* salinity, water temperature, dissolved oxygen concentration and pH, have previously been described for the full range of offshore habitats at which the benthic macroinvertebrate fauna was sampled (see subsection 3.3.2.1).

Sediment grain size composition was found by PERMANOVA to differ significantly among offshore habitats (*p*=0.001) but not seasons, and neither was there an interaction between these two main effects (Table 5.9a). The grain size composition of the substrate at habitat A, situated in the entrance channel, was the most distinct, containing by far the greatest proportion of sediment in the 500-999 µm fraction, *i.e.* 46%, compared to 10-16% at habitats B and C in the basin (Fig. 5.8). Conversely, the composition of sediment at habitats B and C, which were similar, contained higher proportions of the 125-249 µm, 63-124 µm and fine fractions and, to a lesser extent, also the 250-499 µm faction.

PERMANOVA also detected a significant difference among offshore habitats in %POM (*p*=0.043; Table 5.9b), with the sediments at habitats B and C containing over three times the %POM of habitat A (Fig. 5.9a). The depth of the transition zone was also found to differ among habitats (*p*=0.001; Table 5.9c), with the depth of this zone extending beyond the length of the core at habitat A, but being *ca* 2 and 0 cm below the sediment surface at habitats C and B, respectively (Fig. 5.9b).

5.3.2.2: Densities of benthic macroinvertebrate phyla, species and feeding guilds among offshore habitat types

A total of 2,459 benthic macroinvertebrates were collected from the substrate of the offshore waters in Broke Inlet between summer and spring 2008. These fauna comprised 26 species, which represented five phyla (Table 5.10). The Annelida, represented by nine polychaete species from seven families, accounted for 57% of the

Table 5.9: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (*p*) from PERMANOVA tests on the data on the mean (a) sediment grain size composition, (b) particulate organic matter content and (c) transition zone depth at the three offshore habitat types in Broke Inlet sampled in each season between summer and spring 2008. df = degrees of freedom. Significant results are highlighted in bold.

	(a) Sediment grain size composition				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Season	3	10.621	1.131	0.105	0.342
Habitat	2	**106.080**	**11.291**	**6.201**	**0.001**
Interactions					
Season x Habitat	6	2.933	0.312	-1.655	0.990
Residual	35	9.395		9.395	

	(b) Percentage organic matter				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Season	3	0.510	0.369	0.075	0.792
Habitat	2	**4.760**	**3.448**	**0.217**	**0.043**
Interactions					
Season x Habitat	6	0.334	0.242	-0.268	0.963
Residual	35	1.381		1.381	

	(c) Transition zone depth				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Season	3	2.250	0.258	-0.538	0.871
Habitat	2	**370.77**	**42.577**	**22.629**	**0.001**
Interactions					
Season x Habitat	6	1.689	0.193	-1.755	0.985
Residual	36	8.708		8.708	

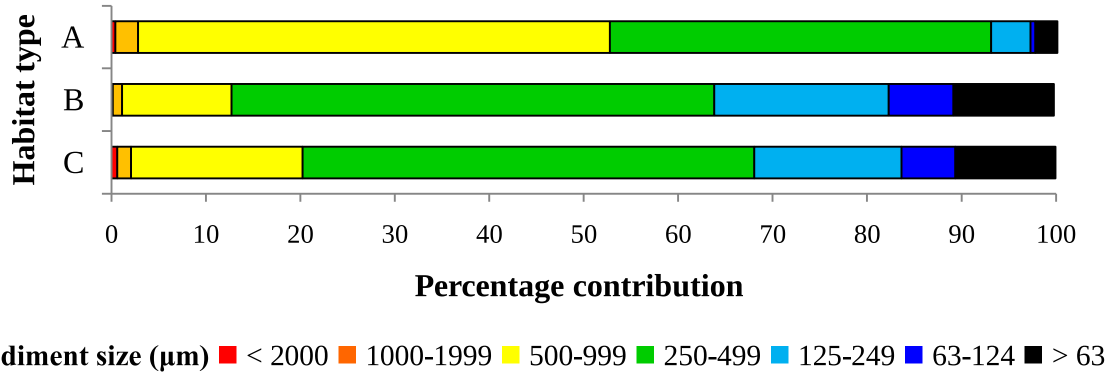


Fig. 5.8: Mean percentage sediment grain size contributions recorded at each of the three offshore habitat types in Broke Inlet sampled in each season between summer and spring 2008.

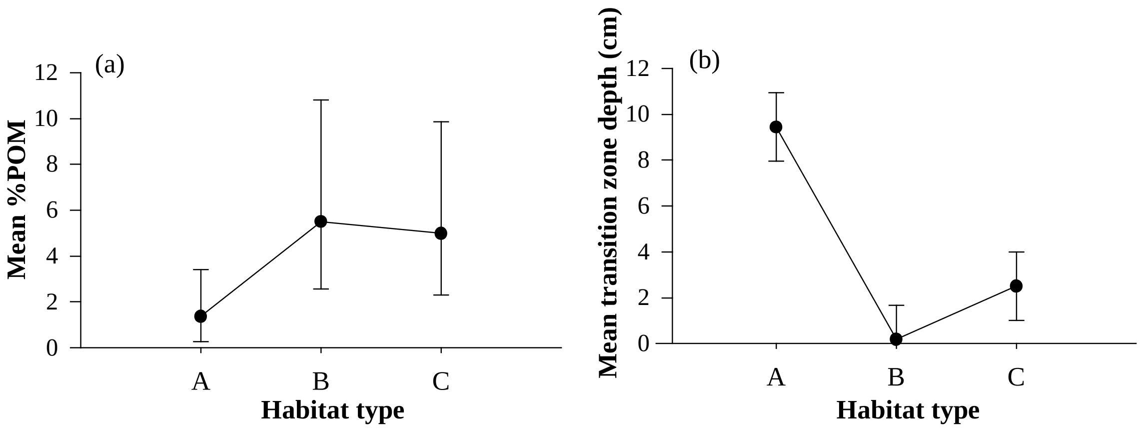


Fig. 5.9: Mean (a) particulate organic matter content (%POM) and (b) depth of the transition zone at each of the three offshore habitat types in Broke Inlet sampled in each season between summer and spring 2008.

Table 5.10: Mean density (individuals 0.1 m^{-2}; M), standard error (^{SE}), percentage contribution to the overall mean density (%) and the rank by density (R) of the benthic macroinvertebrate taxa recorded at the three offshore habitat types sampled in Broke Inlet in each season between summer and spring 2008. Abundant taxa at each habitat type (*i.e.* those that contribute > 5% to the overall mean density) are highlighted in grey. Keys for phylum and class and predominant feeding guild of each taxon are provided in Table 5.2. The total number of species, overall mean density and adjusted number of individuals sampled (*i.e.* after the number of individuals in each sample had been adjusted to that in 0.1 m^{-2} and summed) are also provided for each habitat type. Species ranked by total abundance.

			A			B			C		
Species	**P/C**	**F**	**M^{SE}**	**%**	**R**	**M^{SE}**	**%**	**R**	**M^{SE}**	**%**	**R**
Corophium minor	Ar/M	Dt/S	3.0$^{1.5}$	1.41	9	93.8$^{31.0}$	50.83	1	6.7$^{2.2}$	5.02	7
Capitella capitata	A/P	Dp	56.2$^{15.7}$	25.98	1	37.2$^{7.4}$	20.17	2	2.6$^{0.9}$	1.94	9
Ceratonereis aequisetis	A/P	Dp/Dt	41.6$^{8.9}$	19.23	2	1.3$^{0.6}$	0.71	9	37.2$^{6.5}$	27.67	1
Cyathura hakea	Ar/M	P	30.0$^{6.2}$	13.90	4	6.3$^{1.6}$	3.42	6	36.4$^{7.3}$	27.02	2
Armandia intermedia	A/P	Dp	35.1$^{10.4}$	16.21	3	19.8$^{4.8}$	10.73	3	12.4$^{3.7}$	9.22	3
Scoloplos normalis	A/P	Dp	8.5$^{2.9}$	3.93	7	8.7$^{2.2}$	4.72	5	10.7$^{2.8}$	7.93	5
Prionospio cirrifera	A/P	Dp	14.6$^{8.7}$	6.75	6	0.7$^{0.4}$	0.35	12	7.0$^{2.0}$	5.18	6
Pontomyia sp.	Ar/I	Dt	15.0$^{3.7}$	6.95	5	1.3$^{0.7}$	0.71	9	2.4$^{1.0}$	1.78	10
Desdemona ornata	A/P	S							12.0$^{5.2}$	8.90	4
Melita matilda	Ar/M	Dp	3.9$^{1.3}$	1.81	8	2.4$^{1.0}$	1.30	7	4.1$^{1.8}$	3.07	8
Nemertea sp.	N	P	0.4$^{0.3}$	0.20	15	8.9$^{2.3}$	4.83	4	0.4$^{0.4}$	0.32	13
Gastrosaccus sorrentoensis	Ar/M	S	1.5$^{0.6}$	0.70	11	0.2$^{0.2}$	0.12	13	0.4$^{0.3}$	0.32	13
Arthritica semen	M/B	Dp/S	0.9$^{0.6}$	0.40	13	1.3$^{0.6}$	0.71	9			
Sanguinolaria biradiata	M/B	S	2.2$^{1.2}$	1.01	10						
Cirolanidae sp.	Ar/M	P				2.0$^{0.9}$	1.06	8			
Tanaidacea sp.	Ar/M	Dt	1.1$^{0.6}$	0.50	12				0.7$^{0.5}$	0.49	11
Capitellid sp.	A/P	Dp	0.9$^{0.5}$	0.40	13				0.2$^{0.2}$	0.16	16
Ficopomatus enigmaticus	A/P	S							0.7$^{0.5}$	0.49	11
Fluviolanatus subtorta	M/B	S				0.2$^{0.2}$	0.12	13	0.4$^{0.3}$	0.32	13
Bivalvia sp.	M/B	U	0.4$^{0.4}$	0.20	15						
Ceratopogonidae sp.	Ar/I	U	0.4$^{0.3}$	0.20	15						
Prionospio sp. 2	A/P	Dp	0.2$^{0.2}$	0.10	18						
Turbellarian sp.	Pl/T	P							0.2$^{0.2}$	0.16	16
Palaemonetes australis	Ar/M	S/Dp	0.2$^{0.2}$	0.10	18						
Xenostrobus inconstans	M/B	S				0.2$^{0.2}$	0.12	13			
Triplectides australis	Ar/I	Dt				0.2$^{0.2}$	0.12	13			
Number of species			**19**			**16**			**17**		
Overall mean density			**216**			**185**			**135**		
Number of samples			**48**			**48**			**48**		
Adjusted number of individuals			**10,377**			**8,862**			**6,458**		
Actual number of individuals			**993**			**848**			**618**		

individuals sampled. The Arthropoda was the next most speciose and abundant phyla, comprising two species of amphipods, two of the isopods and one decapod, tanaid and mysid species, which together contributed 36% of the invertebrates collected. The Uniramia and Mollusca, represented by three insect and five bivalve species, accounted for 4 and 1% of the total number of invertebrates, respectively, while nemerteans contributed 2% (Table 5.10).

The benthic macroinvertebrate fauna at habitat A was the most speciose (19), followed by those at C (17) and B (16). The overall mean density of invertebrates was greatest at habitat A, and least at C (Table 5.10). Deposit feeding was the dominant feeding mode in habitat A (55% of the individuals) and was also well represented in habitats B and C (37 and 28%, respectively). In addition habitat B was dominated by detritus/suspension feeders (51%) and habitat C by equal abundances of deposit/detritus feeders and predators (28%; Table 5.10).

Polychaetes dominated the benthic macroinvertebrate faunas at habitats A and C, representing 73 and 61%, of the total number of individuals, respectively. *Capitella capitata*, *C. aequisetis* and *A. intermedia* were notably abundant and ranked first, second and third, respectively, at habitat A, with the latter two species also being abundant at habitat C ranking first and third, respectively (Table 5.10). Other abundant species at habitat C included the polychaetes *Desdemona ornata* and *S. normalis* which were most abundant at this habitat and the crustaceans *C. hakea* and *C. minor*. Crustaceans dominated the fauna at habitat B (56%), with the amphipod *C. minor* being particularly abundant, *i.e.* 94 individuals 0.1 m^{-2} (Table 5.10). Nemerteans were also markedly more abundant in habitat B, *i.e.* 8.9 individuals 0.1 m^{-2} in comparison to both habitats A and C, *i.e.* 0.4 individuals 0.1 m^{-2} (Table 5.10).

5.3.2.3: Differences in species richness, density and diversity among offshore habitat types and seasons

The mean species richness of the benthic macroinvertebrate fauna, in the sediments of the offshore waters differed significantly among seasons (*p*=0.049) but not habitats (Table 5.11a). The highest values were recorded in summer (4.5) and the lowest in winter (2.7), with intermediate values in spring (3.2) and autumn (3.8; data not shown). In contrast, the mean density, Shannon-Weiner and average quantitative taxonomic distinctness of benthic macroinvertebrates in the offshore waters did not differ significantly among habitats, seasons or the interaction between these main effects (*p*=0.07-0.701; Table 5.11b-d). Mean densities of invertebrates in each habitat in each season ranged from 120-200 individuals 0.1m^{-2}, and the values for Shannon-

Table 5.11: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (*p*) from PERMANOVA tests on the data for mean (a) species richness, (b) density, (c) Shannon-Weiner diversity and (d) average quantitative taxonomic distinctness of the benthic macroinvertebrate assemblages at the three offshore habitats in Broke Inlet sampled in each season between summer and spring 2008. df = degrees of freedom. Significant results are highlighted in bold.

	(a) Species richness				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Season	3	**0.533**	**2.970**	**0.0295**	**0.049**
Habitat	2	0.318	0.886	-0.001	0.441
Interactions					
Season x Habitat	6	0.581	0.540	-0.002	0.748
Residual	36	0.180		0.180	

	(b) Density				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Season	3	1.831	2.504	0.091	0.070
Habitat	2	1.057	1.446	0.020	0.254
Interactions					
Season x Habitat	6	0.515	0.704	-0.054	0.632
Residual	36			0.731	

	(c) Shannon-Weiner diversity				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Season	3	0.355	2.236	0.016	0.101
Habitat	2	0.059	0.376	-0.006	0.694
Interactions					
Season x Habitat	6	0.100	0.632	-0.014	0.701
Residual	36	0.159		0.159	

	(d) Average quantitative taxonomic distinctness				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Season	3	1230.400	2.154	54.923	0.105
Habitat	2	1288.900	2.256	44.845	0.127
Interactions					
Season x Habitat	6	569.430	0.997	-0.476	0.455
Residual	36	571.330		571.330	

Weiner diversity and average quantitative taxonomic distinctness between 0.5 and 1.1 and 54 and 91, respectively (data not shown).

5.3.2.4: Differences in benthic macroinvertebrate assemblage composition among offshore habitat types

The composition of benthic macroinvertebrate fauna in the offshore waters of Broke Inlet differed significantly among both habitats and seasons (*p*=0.001-0.007; Table 5.12). Differences among habitats explained a far greater proportion of the variability in faunal composition than those among seasons, the component of variation for the former factor being approximately four times that of the latter. As the interaction factor between these main effects was not significant, subsequent analyses to examine habitat differences in more detail were undertaken after pooling the data for all seasons.

Table 5.12: Mean squares (MS), pseudo F-ratios, components of variation (COV) and significance levels (*p*) from a two-way crossed PERMANOVA on the benthic macroinvertebrate composition at the three offshore habitats in Broke Inlet sampled in each season between summer and spring 2008. df = degrees of freedom. Significant results are highlighted in bold.

	Offshore benthic macroinvertebrate composition				
Main effects	**df**	**MS**	**Pseudo-F**	**COV**	***p***
Season	3	**4048.600**	**2.009**	**169.440**	**0.007**
Habitat	2	**13242.000**	**6.571**	**701.690**	**0.001**
Interactions					
Season x Habitat	6	2158.200	1.071	35.729	0.350
Residual	36	2015.300		2015.300	

One-way ANOSIM tests identified a significant difference in faunal composition among habitats overall (*p*=0.001) and between each pair of habitats (*p*=0.001). The extents of those differences, however, were low to moderate, being greatest between A and B (*R*=0.489), least between A and C (*R*=0.189) and intermediate between B and C (*R*=0.382).

The fauna at habitat B was the most distinct, as illustrated by the fact that the majority of samples representing that habitat formed a group on the top of the nMDS plot (Fig. 5.10). The fauna at this habitat was characterised by relatively high densities of *C. capitata, S. normalis, C. minor* and Nemertea sp. (Appendix 5.3), and the first two species were also important in distinguishing the fauna at this habitat from those at C and A, respectively. The small difference in faunal composition between habitats A and C is reflected in the considerable intermingling of the samples from these habitats on the nMDS plot (Fig. 5.10). These differences were partly caused by the greater densities of *Pontomyia* sp. and *C. aequisetis* at habitat A compared to C, while the opposite was true for *S. normalis* and the anthurid *C. hakea* (Appendix 5.3).

5.3.2.5: Relationships between the benthic macroinvertebrate community and environmental characteristics of offshore habitat types

RELATE demonstrated that the pattern of relative differences among offshore sites, in terms of their suite of average enduring environmental characteristics, was not significantly correlated with that derived from their average benthic macroinvertebrate composition (*p*=0.072, ρ=0.230). When the matrix constructed from the enduring

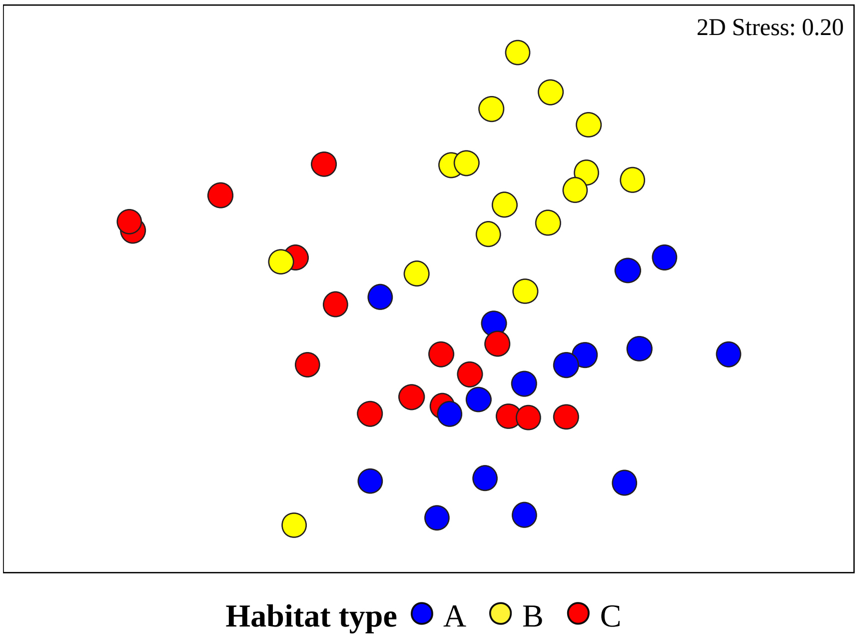
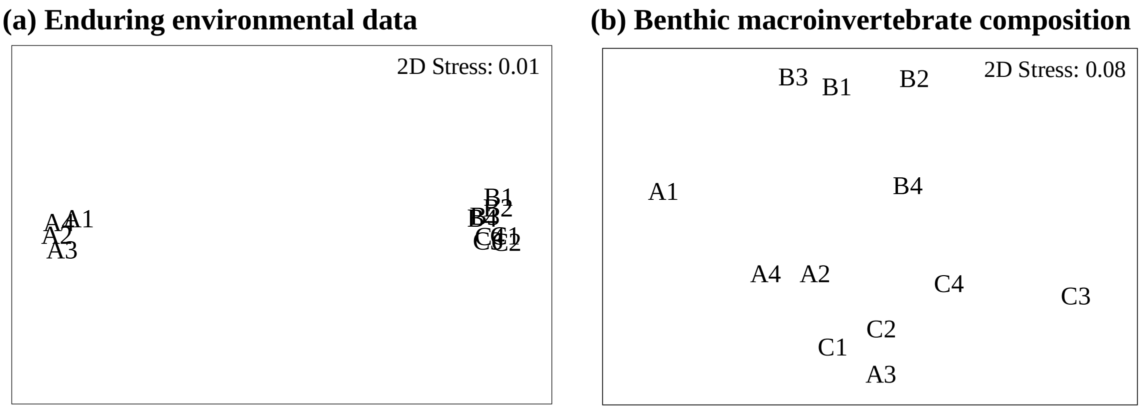


Fig. 5.10: nMDS ordination plot of the benthic macroinvertebrate composition at each of the sites representing three offshore habitat types in Broke Inlet sampled in each season between summer and spring 2008.

environmental data was subjected to nMDS ordination, the sites formed two distinct groups on the resultant plot, one containing those from habitat A and the other containing those from habitats B and C (Fig. 5.11a). However, when the mean data for the benthic macroinvertebrate composition across all seasons was subjected to ordination, the samples for habitat B were generally distinct, while particularly, samples from habitats A and C lay close to each other (Fig. 5.11b).

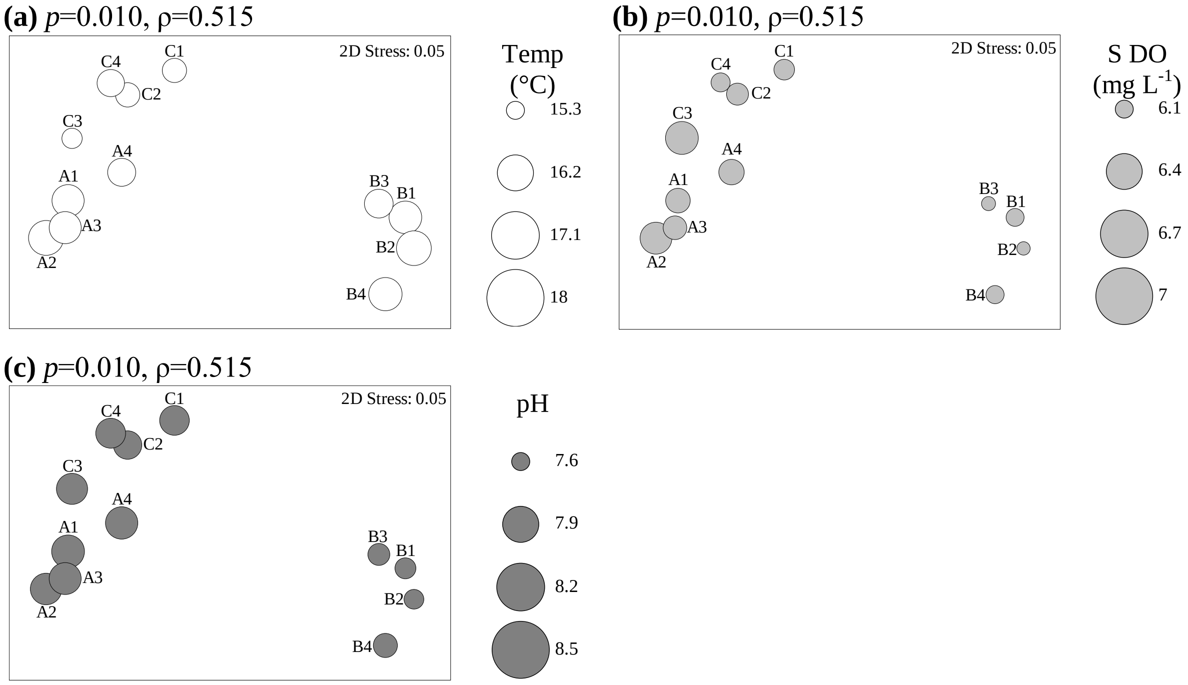
The RELATE procedure was then used to identify whether the pattern of differences among offshore sites in either the suite of non-enduring water physico-chemical variables or sediment characteristics were correlated with those exhibited by the invertebrate fauna. In both cases, a significant correlation was detected (p=0.008 and 0.016). Furthermore, the values for the correlations between both the water and sediment parameters and the faunal composition (ρ=0.388 and 0.287, respectively) were greater than was the case with the enduring environmental characteristics. BIOENV was then employed to ascertain whether the extent of these matches could be improved using a subset of both suites of variables. In the case of the water physico-chemical variables, BIOENV achieved a greater correlation (ρ=0.515) using three variables, *i.e.* surface water temperature, dissolved oxygen concentration and pH (Fig. 5.12).

However, in the case of all three water physico-chemical variables the ranges of those values were low, with pH for example, ranging between 7.6 and 8.5. Although the extent of the correlation with the sediment characteristics was improved slightly by using only percentage fines, organic material and the 500 and 63μm fractions (*R*=0.336), this correlation was not significant (*p*=0.123).



(a) Enduring environmental data **(b) Benthic macroinvertebrate composition**

Fig. 5.11: nMDS ordination plots constructed from the averages at each offshore site of the (a) enduring environmental variables and (b) benthic macroinvertebrate composition recorded between summer and spring 2008.



(a) *p*=0.010, ρ=0.515 **(b)** *p*=0.010, ρ=0.515 **(c)** *p*=0.010, ρ=0.515

Fig. 5.12: nMDS ordination plots of the average benthic macroinvertebrate composition recorded at each offshore site. The magnitude of the non-enduring environmental variable(s) selected by the BIOENV routine that best match the spatial pattern displayed by the benthic macroinvertebrate composition are displayed for each habitat as circles of proportionate sizes. The significance levels (*p*) and rho values (ρ) obtained from the above BIOENV tests are also provided. Temp = surface water temperature and DO = dissolved oxygen concentration.

5.3.2.6: Differences in the mean density of the offshore benthic macroinvertebrate species among seasons

A greater number of species was recorded during summer and autumn (18-19) than during winter and spring (14-16; Table 5.13). Similar trends were evident in the mean density of individuals, with 206-266 0.1m^{-2} invertebrates being recorded in the first two seasons and 115-127 0.1m^{-2} invertebrates in the latter two seasons.

Deposit feeders were the best represented of the feeding modes, with their numbers contributing between 43 and 56% to the total number of individuals during summer and autumn and between 21 and 35% in winter and spring. Other important feeding modes included deposit/detritus feeders and predators, which contributed more in winter and spring (21-26%) than in summer and autumn (10-12%). The detritus/suspension feeding *C. minor* contributed between 7 and 27%, with the highest values of 24-27% being recorded in autumn and winter.

The benthic macroinvertebrate fauna in each season was dominated by the crustaceans *C. minor* and *C. haeka* and the polychaetes *C. capitata* and *C. aequisetis*, which always ranked in the top five species and together contributed 53-82% to the total number of individuals collected (Table 5.13). However, *A. intermedia* contributed approximately 19% to the total number of individuals in both summer and autumn, but was not recorded during either winter or spring (Table 5.13). Several other species were also relatively abundant in one or two seasons, such as *S. normalis, Prionospio cirrifera* and *D. ornata*.

5.3.2.7: Differences in offshore benthic macroinvertebrate composition among seasons

PERMANOVA identified that the composition of the offshore benthic macroinvertebrate faunas differed significantly among seasons (*p*=0.007), but this main effect explained only a quarter of the variance as habitat and did not significantly interact with habitat (Table 5.12). One-way ANOSIM, which was then used to examine the nature and extent of these seasonal differences in more detail, demonstrated that only two of the six pairwise comparisons were identified as significant (*i.e.* spring *vs*

Table 5.13: Mean density (number of individuals 0.1m^{-2}; M), standard error (^{SE}), percentage contribution to the overall mean density (%) and the rank by density (R) of the benthic macroinvertebrate taxa recorded in each season between summer and spring 2008 at the three offshore habitat types sampled in Broke Inlet. Abundant taxa in each season (*i.e.* those that contribute ≥ 5% to the overall mean density) are highlighted in grey. Keys for phylum and class (P/C) and predominant feeding guild (F) of each taxon are provided in Table 5.2. The total number of species, overall mean density and adjusted number of individuals sampled (*i.e.* after the number of individuals in each sample had been adjusted to that in 0.1 m^{-2} and summed) are also provided for each season. Species ranked by total abundance.

			Summer			**Autumn**			**Winter**			**Spring**		
Species	**P/C**	**F**	**M^{SE}**	**%**	**R**	**M^{SE}**	**%**	**R**	**M^{SE}**	**%**	**R**	**M^{SE}**	**%**	**R**
Corophium minor	Ar/M	Dt/S	$29.3^{9.5}$	14.23	3	$71.4^{40.3}$	26.89	1	$27.6^{12.2}$	23.93	1	$9.9^{3.5}$	7.78	5
Capitella capitata	A/P	Dp	$40.1^{10.2}$	19.44	1	$52.8^{19.6}$	19.89	2	$14.8^{5.2}$	12.85	4	$20.3^{7.2}$	16.02	3
Ceratonereis aequisetis	A/P	Dp/Dt	$19.7^{6.1}$	9.58	4	$31.9^{9.4}$	12.02	4	$26.7^{8.1}$	23.17	2	$28.0^{7.8}$	22.43	1
Cyathura hakea	Ar/M	P	$19.7^{4.0}$	9.58	4	$26.1^{8.0}$	9.84	5	$25.3^{7.1}$	21.91	3	$25.8^{7.5}$	20.37	2
Armandia intermedia	A/P	Dp	$39.5^{10.3}$	19.15	2	$50.2^{10.2}$	18.91	3						
Scoloplos normalis	A/P	Dp	$13.1^{3.0}$	6.34	7	$2.9^{1.0}$	1.09	10	$2.0^{0.9}$	1.76	9	$19.2^{4.6}$	15.10	4
Prionospio cirrifera	A/P	Dp	$18.6^{11.6}$	9.01	6	$5.5^{2.5}$	2.08	7	$3.8^{1.1}$	3.27	5	$1.7^{0.7}$	1.37	10
Pontomyia sp.	Ar/I	Dt	$6.7^{3.3}$	3.24	8	$9.9^{3.6}$	3.72	6	$2.3^{1.3}$	2.02	8	$6.1^{2.4}$	4.81	7
Desdemona ornata	A/P	S	$6.1^{5.5}$	2.96	9	$1.5^{1.2}$	0.55	11				$8.4^{4.2}$	6.64	6
Melita matilda	Ar/M	Dp	$4.6^{2.3}$	2.25	10	$3.5^{1.4}$	1.31	9	$2.9^{1.2}$	2.52	6	$2.9^{1.4}$	2.29	8
Nemertea sp.	N	P	$4.4^{2.2}$	2.11	11	$5.5^{2.0}$	2.08	7	$2.6^{1.6}$	2.27	7	$0.6^{0.6}$	0.46	11
Gastrosaccus sorrentoensis	Ar/M	S	$1.2^{0.6}$	0.56	12	$1.5^{0.7}$	0.55	11	$0.3^{0.3}$	0.25	14			
Arthritica semen	M/B	Dp/S	$0.6^{0.6}$	0.28	13	$1.2^{0.8}$	0.44	13	$1.2^{0.6}$	1.01	11			
Sanguinolaria biradiata	M/B	S	$0.6^{0.6}$	0.28	13	$0.6^{0.4}$	0.22	14	$1.7^{1.5}$	1.51	10			
Cirolanidae sp.	Ar/M	P	$0.6^{0.4}$	0.28	13				$2.0^{1.2}$	1.76	9			
Tanaidacea sp.	Ar/M	Dt										$2.3^{1.0}$	1.83	9
Capitellid sp.	A/P	Dp	$0.3^{0.3}$	0.14	17	$0.3^{0.3}$	0.11	15	$0.9^{0.6}$	0.76	12			
Ficopomatus enigmatius	A/P	S				$0.3^{0.3}$	0.11	15	$0.6^{0.6}$	0.50	13			
Fluviolanatus subtorta	M/B	S	$0.6^{0.4}$	0.28	13							$0.3^{0.3}$	0.23	13
Bivalvia sp.	M/B	U							$0.6^{0.6}$	0.50	13			
Ceratopogonidae sp.	Ar/I	U										$0.6^{0.4}$	0.46	11
Prionospio sp. 2	A/P	Dp				$0.3^{0.3}$	0.11	15						
Turbellaria sp.	Pl/T	P	$0.3^{0.3}$	0.14	17									
Palaemonetes australis	Ar/M	S/Dp	$0.3^{0.3}$	0.14	17									
Xenostrobus inconstans	M/B	S										$0.3^{0.3}$	0.23	13
Triplectides australis	Ar/I	Dt				$0.3^{0.3}$	0.11	15						
Species richness			**19**			**18**			**16**			**14**		
Overall mean density			**206**			**266**			**115**			**127**		
Number of samples			**36**			**36**			**36**			**36**		
Adjusted number of individuals			**7,420**			**9,562**			**4,149**			**4,567**		
Actual number of individuals			**710**			**915**			**397**			**437**		

autumn and summer *vs* winter), with the extents of those differences being low (*R*=0.161 and 0.103, and *p*=0.013 and 0.031, respectively). The small influence of season is illustrated by the fact that none of the samples for any season formed discrete groups on the nMDS plot shown in Fig. 5.13. For this reason, SIMPER was not subsequently used to identify which species best typified and/or distinguished between those samples.

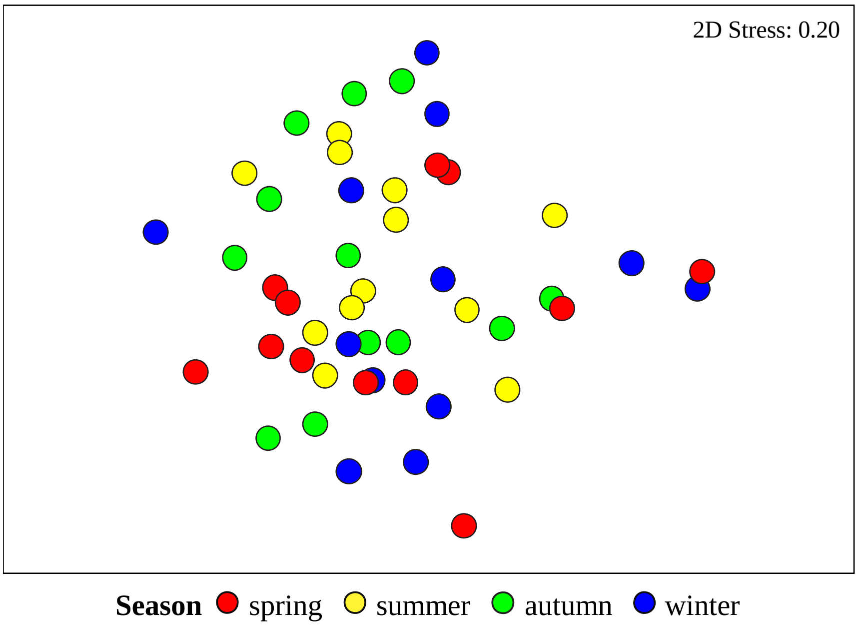


Fig. 5.13: nMDS ordination of the benthic macroinvertebrate composition at each offshore site in each season between summer and spring 2008.

5.4: Discussion

5.4.1: Benthic macroinvertebrate community

This study showed that the benthic macroinvertebrate faunas in both the nearshore and offshore waters of Broke Inlet were dominated by polychaetes (64 and 57% of the individuals collected, respectively) and crustaceans (24 and 36% of the individuals collected, respectively), as is typical for estuaries in both south-western Australia (*e.g.* Platell & Potter, 1996; Wildsmith *et al.*, 2009) and temperate regions of the northern and southern hemispheres (*e.g.* Jones *et al.*, 1986; Kalejta & Hockey, 1991; Ysebaert *et al.*, 1993). Furthermore, the majority of benthic macroinvertebrate species recorded during this study have been found in previous qualitative surveys of the fauna in Broke Inlet and/or quantitative studies of those in nearby seasonally-open estuaries (Hodgkin & Clark, 1987-1990; Forbes, 1994; Platell & Potter, 1996) and permanently-open estuaries on the lower west coast of Australia (Wildsmith, 2007; Valesini *et al.*, 2009; Wildsmith *et al.*, 2009). Sampling of the benthic macroinvertebrate fauna of 13 permanently and seasonally-open estuaries in South Africa likewise yielded similar suites of species in both estuary types (Teske & Wooldridge, 2001).

The number of benthic macroinvertebrate species recorded during extensive sampling of the nearshore and offshore waters of Broke Inlet, *i.e.* 28 and 26, respectively, is similar to the 40 and 33 species, respectively, recorded in the nearshore and offshore waters of the nearby and seasonally-open Wilson Inlet (Platell & Potter, 1996) and the 21-30 species recorded in seasonally-open South African estuaries (Teske & Wooldridge, 2001). However, species richness in the nearshore waters of Broke Inlet is considerably lower than the 69 and 63 species, recorded, respectively, during comparable sampling of the nearshore waters of the permanently-open Swan-Canning and Peel-Harvey estuaries (Valesini *et al.*, 2009; Wildsmith *et al.*, 2009).

The relatively small number of benthic macroinvertebrate species found in the seasonally-open estuaries of south-western Australia and South Africa presumably reflects, in part, the fact that the mouths of these systems are closed to the ocean for a period during the year when marine benthic macroinvertebrate species typically spawn (*i.e.* summer and autumn), thus preventing the recruitment of their larvae into these systems (Kalejta & Hockey, 1991; Wooldridge, 1999). Furthermore, the narrow entrance channel and microtidal environment of estuaries in these regions results in limited water exchange between the estuary and adjacent marine environment (Ranasinghe & Pattiaratchi, 1999a), and thus the absence of a mechanism for transporting larvae into these systems (*e.g.* Neira & Potter, 1992b; Wooldridge, 1999). In addition, for much of the year, the salinities of seasonally-open estuaries, such as the Broke and Wilson inlets, are less than that of full-strength seawater and often markedly so, which would preclude colonisation by stenohaline species. This accounts for the observation that reduced salinities are often accompanied by a relatively low number of benthic macroinvertebrate species (Ysebaert *et al.*, 1993).

Irrespective of whether an estuary is permanently or seasonally-open in south-western Australia, the species richness of their benthic macroinvertebrate faunas are much lower than those of nearby marine waters. For example, the greatest number of benthic macroinvertebrate species recorded in any estuary in this region, *i.e.* 69 in the nearshore waters of the Swan-Canning Estuary (Valesini *et al.*, 2009), is far less than the 121 species recorded in nearshore marine waters along the same south-western Australian coast (Wildsmith *et al.*, 2005). Furthermore, the same trend has been reported in south-eastern Australia with 90 species being recorded in the Gippsland Lakes compared with 803 in nearby shallow coastal waters (*cf.* Poore, 1982; Coleman *et al.*, 1997).

The mean seasonal densities of benthic macroinvertebrates in the nearshore and offshore waters of Broke Inlet, *i.e.* 230-415 and 115-266 individuals 0.1 m^{-2}, respectively, are substantially less than those recorded in the corresponding waters of the nearby Wilson Inlet, *i.e.* 554-1,160 and 578-948 individuals 0.1 m^{-2}, respectively, despite the latter study employing a mesh size of 1 mm as opposed to 0.5 mm in the current study which would presumably exclude smaller individuals (Platell & Potter, 1996). The overall mean densities of benthic macroinvertebrates were even greater in the nearshore waters of the permanently-open Swan-Canning and Peel-Harvey estuaries, *i.e.* 959 and 1,220 individuals 0.1 m^{-2}, respectively (Wildsmith, 2007; Wildsmith *et al.*, 2009). However, while the mean seasonal densities of these fauna in Broke Inlet are relatively low for a south-western Australian estuary, they are far greater than the overall mean densities recorded in the nearshore waters of the lower west and east coasts of Australia, *i.e.* 61 and 94 individuals 0.1 m^{-2}, respectively (Dexter, 1984; Wildsmith *et al.*, 2005).

As the Broke and Wilson inlets are both seasonally-open, of a similar size and shape and separated by a distance of only *ca* 100 km, the very large differences in the mean densities of benthic macroinvertebrates are presumably related, at least in part, to differences in the primary productivity of those two systems. It is thus relevant that Broke Inlet is unique among south-western Australian estuaries in being oligotrophic and containing only a few areas of macrophytes whereas Wilson Inlet is eutrophic and contains large areas of macrophytes, and particularly of *Ruppia megacarpa* (Lukatelich *et al.*, 1987; Hodgkin & Clark, 1989a; Department of Environment, 2003; Brearley, 2005). The paucity of macrophyte growth in Broke Inlet partly reflects the fact that the water entering this estuary flows through a fully-forested catchment and is thus, low in nutrients (Bunn & Davies, 1990) and heavily stained with tannin, which severely limits light penetration (Edgar & Cresswell, 1991). The very substantial areas of macrophytes in Wilson Inlet would provide shelter and, after decomposition, also food for benthic macroinvertebrates (Connolly *et al.*, 2005; Hyndes & Lavery, 2005). The value of these macrophytes is emphasised by the correlation between the density of some macroinvertebrate species, including *Ceratonereis aequisetis* and *Capitella capitata*, and the biomass of *R. megacarpa* in Wilson Inlet (Platell & Potter, 1996).

5.4.2: Benthic macroinvertebrate composition among nearshore habitat types and seasons

The benthic macroinvertebrate composition differed significantly among the various nearshore habitats in Broke Inlet in each season between spring 2007 and winter 2008. However, the extent of those differences varied, being greatest in spring and summer and least in autumn and winter.

The most distinct of the faunal compositions were those recorded at habitat A in the two seasons in which it could be sampled, *i.e.* spring and winter, and at K in all seasons except autumn. The faunas at both of these habitats, which were unvegetated and experienced the lowest salinities, were particularly depauperate, a trend that has been associated with similar habitats in other estuaries (*e.g.* Ysebaert *et al.*, 1993; Edgar *et al.*, 1994; Connolly, 1997). Throughout this study, the benthic macroinvertebrate faunas at these habitats were characterised by *C. capitata* and *Arthritica semen*, both of which can tolerate a wide range of salinities (Warren, 1977; Wells & Threlfall, 1982) and contribute substantially to the benthic macroinvertebrate fauna of the upper region of the Swan-Canning Estuary (Kanandjembo *et al.*, 2001; Valesini *et al.*, 2009). The densities of these species are also inversely correlated with salinity in the nearby Wilson Inlet and the extents of those correlations were among the greatest for any benthic macroinvertebrate species recorded in that estuary (Platell & Potter, 1996). Wolff (1973) suggested that reduced salinities provide *C. capitata* with a competitive refuge by excluding less euryhaline species.

The next most distinct benthic macroinvertebrate fauna was found at habitat H. This habitat, which was located in the entrance channel and contained patches of dense vegetation, had the greatest mean densities of the polychaetes *C. aequisetis, C. capitata* and *Prionospio cirrifera*. and the bivalves *Fluviolanatus subtorta* and *A. semen*. Densities of the former two polychaete species and the last bivalve species were shown to be positively correlated with the biomass of the seagrass *R. megacarpa* in Wilson Inlet (Platell & Potter, 1996). This macrophyte species provides a food source for *C. aequisetis* and, upon decomposition, for the deposit-feeding *C. capitata* and *P. cirrifera* (Fauchald & Jumars, 1979; Connolly *et al.*, 2005). It also provides protection for all of those polychaete species, which are preyed on by atherinids and gobies, the most abundant fish taxa in the nearshore waters of this estuary (Humphries & Potter, 1993; Chapter 3). The coarse marine-derived sediment present at habitat H has also been positively correlated with the occurrence of *F. subtorta* in other estuaries, while the location of this habitat in the entrance channel means that it does not undergo the same dramatic seasonal reductions in salinity that may occur in other parts of the estuary, and which have been shown to lead to the mortality of this species (Jones *et al.*, 1986; Jones, 1987).

The benthic macroinvertebrate fauna at habitats C, D and F did not differ significantly between a number of their pairwise comparisons and particularly during winter when no significant differences were detected between any combination of these habitats. The faunas at these habitats were characterised by *Scoloplos normalis*, *C. aequisetis, Cyanthura hakea* and *Armandia intermedia* during summer and autumn, all of which are known to be associated with *R. megacarpa*, which occurred in patches at each of these habitats. Thus, the anthurid *C. hakea*, which is an active predator, is well camouflaged against vegetation (Poore & Lew Ton, 1985) and the densities of the remaining polychaete species have been found by other workers to be related to the presence of macrophytes (Platell & Potter, 1996; Hutchings, 2000a). Moreover, although *A. intermedia* is a marine species (Joydas & Damodaran, 2009), it was only recorded in seasons when the salinity was ~30. This species prefers fine sediments which may explain why it was more abundant in the basin habitats as opposed to that in the entrance channel (Hutchings, 1984).

The extents of the seasonal changes in the nearshore benthic macroinvertebrate fauna of Broke Inlet, were typically less than those among habitats, a trend also recorded in Tasmanian estuaries (*e.g.* Edgar & Barrett, 2002). Indeed, seasonal changes were only observed at habitats C, H and K. Traditionally, such changes in benthic macroinvertebrate composition have been related to differences in the time of year when species spawn, recruit or undergo mortality (*e.g.* Rainer, 1982; Sardá *et al.*, 1999; Ducrotoy & Ibanez, 2002; Reiss & Kröncke, 2005). However, the densities of some of the most numerous benthic macroinvertebrate species in Broke Inlet did not exhibit conspicuous seasonal trends in abundance. It is thus relevant that *C. capitata* and *A. semen,* which ranked first and ninth in terms of total abundance, respectively, have been shown to breed continuously (Wells & Threlfall, 1982; Hutchings, 2000b).

The small but significant seasonal differences in benthic macroinvertebrate composition in certain habitats were due, however, to the densities of some species peaking at a particular time. For example, *C. aequisetis* in south-eastern Australian estuaries has a one year life cycle, with sexual maturity being obtained in late spring and spawning occurring in summer (Glasby, 1986). Furthermore, at habitats H and K in which the benthic macroinvertebrate composition underwent some seasonal changes, *A. intermedia* was present in relatively large numbers only during summer and autumn, reflecting the life history of this marine species, which spawns in marine waters with some larvae being recruited into estuaries during spring and summer. The absence of this species in winter may be due to a seaward migration of its adults in winter and/or mortality due to the low salinities in winter and spring (Tamaki, 1985).

5.4.3: Benthic macroinvertebrate composition among offshore habitat types and seasons

The composition of the benthic macroinvertebrate fauna at the three offshore habitats within Broke Inlet differed significantly, but the extents of those differences were low to moderate. The most distinct assemblages were recorded at habitat B in Shannon Basin, which contained the lowest species richness and was dominated by three species that together represented 80% of the individuals. Although the most abundant of these species, the amphipod *C. minor*, was collected at all habitats, it occurred in appreciable numbers only at habitat B. As this species feeds on detritus, such findings are presumably related to the relatively large amount of organic matter in the substrate of this habitat. This is probably a consequence of the fact that the Shannon and Forth Rivers, which provide 90% of water input to the estuary, discharge into this habitat after flowing through dense Karri, Jarrah and Marri forests, and thus make the largest contribution to the allochthonous material in the estuary. Other abundant species at habitat B, *i.e. C. capitata* and *A. intermedia*, are non-selective deposit feeders (Fauchald & Jumars, 1979), and would thus similarly be able to exploit the relatively large amount of sedimentary organic matter present at this habitat.

The benthic macroinvertebrate fauna at the channel habitat A, the only vegetated offshore habitat, was the next most distinct and comprised species that have been related to the presence of macrophytes, *e.g. C. capitata*, *C. aequisetis*, *C. hakea* and *A. intermedia* (Hutchings, 1984; Poore & Lew Ton, 1986; Platell & Potter, 1996). Furthermore, the relatively high densities of *Pontomyia* sp. presumably reflects the close proximity of this habitat to the terrestrial marshes inhabited by the adults of this species (Davis & Christidis, 1997).

The extents of the seasonal differences in the benthic macroinvertebrate composition of the offshore waters were negligible, and far less than those related to habitat. In fact, densities of only two of the 26 species collected from the offshore waters underwent notable seasonal changes, *i.e. A. intermedia* and *C. minor*, which paralleled those exhibited by these species in the nearshore waters. The overall lack of seasonal differences in benthic macroinvertebrate composition parallels that recorded in other studies in seasonally-open estuaries in Tasmania and South Africa where seasonal differences were low (*e.g.* Teske & Wooldridge, 2001, 2003; Edgar & Barrett, 2002).

5.4.3: Relationships between the benthic macroinvertebrate community and environmental characteristics of habitat types

The pattern of relative differences in benthic macroinvertebrate composition among nearshore habitats was significantly correlated with the enduring environmental characteristics used to classify those habitats only in spring, while no such correlation was observed in the offshore waters. This reflects the fact that differences in benthic macroinvertebrate composition among nearshore habitats were greatest during this season and declined markedly in autumn and winter. The lack of significant differences in faunal composition among many habitat types in these last two seasons thus precluded the effectiveness of any correlations to the enduring environmental variables. Several other workers have also been unsuccessful in their attempts to correlate benthic macroinvertebrate composition in Australian estuaries with enduring environmental characteristics (*e.g.* Hirst, 2004; Stevens & Connolly, 2004). In contrast, strong and significant correlations between enduring environmental variables and benthic macroinvertebrates assemblages were detected in the Swan-Canning Estuary (Wildsmith, 2007; Valesini *et al.*, 2009). However, this study was undertaken in a large permanently-open estuary with marked longitudinal differences in salinity and sediment composition (Valesini *et al.*, 2009). Unlike the latter estuary, Broke Inlet does not exhibit longitudinal gradients in environmental conditions and sampling of the upper estuary (which includes the lower reaches of the tributaries) in Broke Inlet was not able to be conducted. These factors are thus considered to have precluded the range of differences in habitat, non-enduring environmental conditions and faunal compositions.

Numerous studies have related the spatial distribution of benthic macroinvertebrates in the permanently-open macrotidal estuaries of the northern hemisphere to a range of environmental variables, such as salinity and sediment composition (*e.g.* Holland *et al.*, 1987; Ysebaert *et al.*, 1993; Snelgrove & Butman, 1994). However, within the seasonally/temporarily-open microtidal estuaries of southern Australia and Africa, these trends are less clear. For example, Teske & Wooldridge (2003) found that the influence of salinity on the benthic macroinvertebrate fauna of 13 permanently and temporarily-open estuaries in South Africa was minimal, and decreased with increasing distance from the estuary mouth. Although the salinity in Broke Inlet ranged from 6 in winter to 33 in summer, the 10 most abundant species, representing *ca* 95% of the total number of individuals in both the nearshore and offshore waters, contained only one and two species, respectively, that were not recorded in a season or were recorded at a very low density compared with other seasons. This suggests that the benthic macroinvertebrate species in Broke Inlet are euryhaline, as is the case with many fish species that inhabit this estuary (Chapter 3; Hoeksema *et al.*, 2009). Such a trait would be obligatory for these fauna, given the marked seasonal and inter-annual changes in salinity that can occur in seasonally-open systems such as Broke Inlet (Chapter 3; Hoeksema *et al.*, 2006; Chuwen *et al.*, 2009a). It is thus relevant that individuals of the polychaete genus *Ceratonereis*, which occurs in estuarine environments including Broke Inlet, brood although atypical of nereidids, brooding reduces the osmotic stress for their larvae (Hutchings, 1999). Teske & Wooldridge (2003) also found that the benthic macroinvertebrate species of South African estuaries could be allocated to one of four categories, *i.e.* marine fauna, oligohaline fauna and two groups of estuarine fauna, one of which occurred in sandy sediments and the other in muddy sediments. Only species belonging to the “estuarine fauna” were present in temporarily/seasonal-open estuaries.

In the present study, the relative differences among nearshore habitats in the composition of their benthic macroinvertebrate fauna were significantly correlated with those exhibited by suites of non-enduring water physico-chemical variables and sediment characteristics, during only summer and spring, respectively. This was also true for offshore sites. However, the extents of those significant correlations were, at best, only moderate. Such findings parallel those of a study in the nearby Wilson Inlet, in which, although the densities of the eight most abundant species were significantly correlated with salinity, water temperature, shell debris and the biomass of *R. megacarpa*, significant correlations were recorded in only half of the comparisons and the extent of those matches were moderate at best (Platell & Potter, 1996). The relatively modest correlations between spatial differences in the benthic macroinvertebrate fauna and those in the non-enduring environmental variables in Broke Inlet also reflect the fact that some environmental variables exhibit limited variation among habitats. For example, mean salinity ranged only from 28 to 33 among the various nearshore habitats in summer and autumn. This was also the case for several of the sediment characteristics in the nearshore waters which were similar.

5.5: Appendices

Appendix 5.1: Species that consistently typified (provided along the diagonal) and distinguished (provided in the sub-diagonal) the benthic macroinvertebrate assemblages at each nearshore habitat between spring 2007 and winter 2008 as detected by one-way SIMPER. The habitat type in which each species was most abundant is given in superscript for each pairwise comparison. Insignificant pairwise comparisons are highlighted in grey. Asterisks denote the relative consistency of each species in either typifying or distinguishing the faunal composition of habitat types, as measured by the similarity to standard deviation ratio and dissimilarity to standard deviation ratio, respectively; > 1.5-3*, > 3-5**, > 5-10***, > 10****.

(a) Spring

	A	**C**	**D**	**F**	**H**	**K**
A	*Pontomyia* sp.** *A. semen*** *C. capitata**					
C	*S. normalis*^{C} *C. hakea*^{C} *C. aequisetis*^{C*} *Pontomyia* sp.^{A}	*S. normalis*** *C. hakea* *Pontomyia* sp.** *C. aequisetis**** *C. capitata*** *A. semen****				
D	*Pontomyia* sp.^{A} *A. semen*^{A*} *S. normalis*^{D} *C. aequisetis*^{D}	▨	*C. aequisetis* *Pontomyia* sp. *C. hakea* *S. normalis*			
F	*Pontomyia* sp.^{A*} *S. normalis*^{F*} *C. aequisetis*^{F} *C. minor*^{F}*	▨	*C. capitata*^{F**} *S. normalis*^{F*} *Pontomyia* sp.^{D}	*C. capitata***** *S. normalis***** *C. aequisetis** *C. minor**		
H	*C. aequisetis*^{H**} *F. subtorta*^{H**} *Pontomyia* sp.^{A*}	*F. suborta*^{H*} *S. normalis*^{C*} *C. aequisetis*^{H*}	*C. aequisetis*^{H*} *F. subtorta*^{H*} *A. semen*^{H} *S. normalis*^{D} *Pseudopolydora* sp.^{H*}	*S. normalis*^{F***} *C. capitata*^{F*} *F. subtorta*^{H*} *C. aequisetis*^{H*}	*C. aequisetis**** *F. subtorta*** *A. semen** *Pontomyia* sp.** *Pseudopolydora* sp.***	
K	*Pontomyia* sp.^{A*} *C. capitata*^{K*} *M. matilida*^{A}	*S. normalis*^{C*} *C. hakea*^{C*} *Pontomyia* sp.^{C*}	*C. capitata*^{K*} *A. semen*^{K**} *Pontomyia* sp.^{D} *S. normalis*^{D}	*S. normalis*^{F**} Cirolanidae sp.^{F}	*F. subtorta*^{H**} *C. aequisetis*^{H*} *C. capitata*^{K}	*C. capitata**** *A. semen****

(b) Summer

	C	D	F	H	K
C	*A. intermedia**** *S. normalis**** *Pontomyia* sp.* *C. hakea*** *C. aequisetis**				
D		*C. aequisetis**** *C. hakea*** *Pontomyia* sp.** *A. intermedia* *F. subtorta* *S. normalis*			
F	*Pontomyia* sp.^{C} Cirolanidae sp.^{F} *C. minor*^{F} *C. hakea*^{C}	Cirolanidae sp.^{F*} *C. minor*^{F} *C. hakea*^{D*}	Cirolanidae sp.* *S. normalis*** *C. aequisetis* *C. minor** *F. subtorta**** *A. intermedia*		
H	*A. intermedia*^{C*} *Pontomyia* sp.^{C*} *F. subtorta*^{H*} *C. capitata*^{H*} *S. normalis*^{C*}	*C. capitata*^{H*} *A. intermedia*^{D} *C. aequisetis*^{H*} *F. subtorta*^{H*}	Cirolanidae sp.^{F*} *C. aequisetis*^{H*} *C. minor*^{F}	*F. subtorta** *C. aequisetis* *C. capitata* *C. hakea*	
K	*Pontomyia* sp.^{C} *C. hakea*^{C**} *C. aequisetis*^{C*}	*C. aequisetis*^{D**} *C. hakea*^{D**} *F. subtorta*^{D} *A. intermedia*^{K*}	Cirolanidae sp.^{F} *C. aequisetis*^{F} *C. minor*^{F}	*C. aequisetis*^{H*} *F. subtorta*^{H*} *A. intermedia*^{K*} *C. capitata*^{H*}	*A. intermedia** *S. normalis**** *C. minor****

(c) Autumn

	C	D	F	H	K
C	*C. hakea** *A. intermedia* *C. aequisetis**				
D		*C. hakea** *S. normalis* *C. aequisetis* *A. intermedia*			
F	*C. minor*^{F*} *C. hakea*^{C*} *M. matilida*^{F}	*C. minor*^{F*} *M. matilida*^{F} *C. aequisetis*^{D*}	*A. intermedia*** *C. minor*** *Pontomyia* sp.*		
H				*C. aequisetis* *A. intermedia* *C. capitata*	
K	*C. hakea*^{C*} *A. intermedia*^{K} *M. matilida*^{C} *C. minor*^{K}	*C. aequisetis*^{D*} *A. intermedia*^{K*} *S. normalis*^{D*} *C. hakea*^{D*} *C. minor*^{K*} *M. matilida*^{K}		*A. intermedia*^{K} *C. minor*^{K} *M. matilida*^{K} *S. normalis*^{K}	*A. intermedia*** *C. minor* *S. normalis*

(d) Winter

	A	**C**	**D**	**F**	**H**	**K**
A	*S. normalis** *Pontomyia* sp.*** *C. capitata** *A. semen*****					
C	*S. normalis*^{A*} *C. capitata*^{A} *Pontomyia* sp.^{A*} *C. aequisetis*^{C*} *C. minor*^{A}	*C. aequisetis* *C. hakea* *S. normalis*				
D	*C. hakea*^{D*} *C. capitata*^{A*} *Pontomyia* sp.^{A*} *C. minor*^{A}		*C. hakea*** *C. aequisetis** *S. normalis*			
F				*S. normalis* *C. minor** *Pontomyia* sp. *C. hakea*		
H	*S. normalis*^{A} *C. capitata*^{H*} *C. minor*^{A} *C. aequisetis*^{H*} Cirolanidae sp.^{A}				*C. capitata** *C. aequisetis** *A. semen* *Pontomyia* sp.	
K		*C. minor*^{K} *C. aequisetis*^{C} *C. hakea*^{C} *S. normalis*^{K}	*C. minor*^{K*} *C. aequisetis*^{D*} *C. hakea*^{D} *C. capitata*^{K}		*C. capitata*^{H*} *C. minor*^{K} *C. aequisetis*^{H*} *A. semen*^{K}	*S. normalis*** *C. minor** *C. capitata** *Pontomyia* sp.

Appendix 5.2: Species that consistently typified (provided along the diagonal) and distinguished (provided in the sub-diagonal) the benthic macroinvertebrate assemblages in each season between spring 2007 and winter 2008 at each of the nearshore habitats where significant differences were detected. Species detected by one-way SIMPER analysis. The season in which each species was most abundant is given in superscript for each pairwise comparison. Insignificant pairwise comparisons are highlighted in grey. Asterisks denote the relative consistency of each species in either typifying or distinguishing the faunal composition of seasons, as measured by the similarity to standard deviation ratio and dissimilarity to standard deviation ratio, respectively; > 1-3*, > 3-5**, 5-10***, > 10****.

(a) Habitat C

	Spring	**Summer**	**Autumn**	**Winter**
Spring	*S. normalis*** *C. hakea* *Pontomyia* sp.** *C. aequisetis**** *C. capitata*** *A. semen****			
Summer	*A. intermedia*$^{\text{Su*}}$ *Pontomyia* sp.$^{\text{Su}}$ *C. capitata*$^{\text{Sp*}}$	*A. intermedia**** *S. normalis**** *Pontomyia* sp.* *C. hakea*** *C. aequisetis***		
Autumn	*S. normalis*$^{\text{Sp*}}$ *A. intermedia*$^{\text{A}}$ *C. capitata*$^{\text{Sp*}}$	*Pontomyia* sp.$^{\text{Su*}}$ *S. normalis*$^{\text{Su*}}$ *A. intermedia*$^{\text{Su}}$	*C. hakea** *A. intermedia* *C. aequisetis**	
Winter	*S. normalis*$^{\text{Sp}}$ *C. capitata*$^{\text{Sp*}}$ *Pontomyia* sp.$^{\text{Sp*}}$ *C. aequisetis*$^{\text{W*}}$	*Pontomyia* sp.$^{\text{Su*}}$ *A. intermedia*$^{\text{Su*}}$ *S. normalis*$^{\text{Su*}}$ *C. aequisetis*$^{\text{Su*}}$	▨	*C. aequisetis* *C. hakea*

(b) Habitat H

	Spring	**Summer**	**Autumn**	**Winter**
Spring	*C. aequisetis**** *F. subtorta*** *A. semen** *Pontomyia* sp.**			
Summer	▨	*F. subtorta** *C. aequisetis* *C. capitata* *C. hakea*		
Autumn	*F. subtorta*$^{\text{Sp*}}$ *C. aequisetis*$^{\text{Sp*}}$	▨	*C. aequisetis* *A. intermedia* *C. capitata*	
Winter	*F. subtorta*$^{\text{Sp*}}$ *C. capitata*$^{\text{W*}}$ *C. aequisetis*$^{\text{Sp}}$	▨	▨	*C. capitata** *C. aequisetis** *A. semen* *Pontomyia* sp.

(c) Habitat K

	Spring	**Summer**	**Autumn**	**Winter**
Spring	*C. capitata**** *A. semen****			
Summer	*A. intermedia*$^{\text{Su}*}$ *C. capitata*$^{\text{Sp}*}$ *A. semen*$^{\text{Sp}**}$ *S. normalis*$^{\text{Su}***}$	*A. intermedia** *S. normalis**** *C. minor***		
Autumn	*A. intermedia*$^{\text{A}**}$ *C. capitata*$^{\text{Sp}**}$ *A. semen*$^{\text{Sp}***}$		*A. intermedia*** *C. minor* *S. normalis*	
Winter	*A. semen*$^{\text{Sp}*}$ *C. capitata*$^{\text{Sp}}$ *S. normalis*$^{\text{W}**}$ *C. minor*$^{\text{W}}$	*A. intermedia*$^{\text{Su}*}$ *C. minor*$^{\text{W}}$	*A. intermedia*$^{\text{A}*}$ *C. minor*$^{\text{W}}$ *C. capitata*$^{\text{W}}$	*S. normalis*** *C. minor** *C. capitata**

Appendix 5.3: Species that consistently typified (provided along the diagonal) and distinguished (provided in the sub-diagonal) the benthic macroinvertebrate assemblages at each offshore habitat between summer and spring 2008 as detected by one-way SIMPER. The habitat type in which each species was most abundant is given in superscript for each pairwise comparison. Insignificant pairwise comparisons are highlighted in grey. Asterisks denote the relative consistency of each species in either typifying or distinguishing the faunal composition of habitat types, as measured by the similarity to standard deviation ratio and dissimilarity to standard deviation ratio, respectively; > 1.5-3*, > 3-5**, > 5-10***, > 10****.

	A	**B**	**C**
A	*Pontomyia* sp. *C. aequisetis* *C. hakea* *C. capitata*		
B	*Pontomyia* sp.$^{\text{A}}$ *S. normalis*$^{\text{B}}$ *C. aequisetis*$^{\text{A}}$	*C. capitata* *C. minor* Nemertea sp. *S. normalis*	
C	*Pontomyia* sp.$^{\text{A}}$ *C. aequisetis*$^{\text{A}}$ *S. normalis*$^{\text{C}}$ *C. hakea*$^{\text{C}}$	Nemertea sp.$^{\text{B}}$ *C. hakea*$^{\text{C}}$ *C. minor*$^{\text{B}}$ *C. capitata*$^{\text{B}}$	*C. hakea* *P. cirrifera* *C. aequisetis* *S. normalis*

Chapter 6
General Discussion

6.1: Classification of habitat types in Broke Inlet

This study represents the first attempt to statistically identify the different habitat types in the shallow, nearshore as well as the deeper, offshore waters of a south-western Australian estuary using a suite of enduring environmental variables. This habitat classification for the seasonally-open Broke Inlet on the south coast of Western Australia was achieved using the methodology developed by Valesini *et al.* (2010) for shallow, nearshore estuarine waters. The development of a quantitative habitat classification scheme for Broke Inlet will enable scientists and environmental managers to predict the habitat type to which any site in this estuary belongs, simply by using measurements for a range of its enduring environmental characteristics. It also provides a quantitative framework for exploring the extent to which the compositions of the fish and benthic macroinvertebrate faunas within the estuary are related to habitat type.

6.2: Relationships between faunal compositions and habitat type

The classification of sites in the nearshore and offshore waters of Broke Inlet into 11 and three habitat types, respectively, was shown to be ecologically relevant, in that the compositions of the ichthyofaunas in the nearshore waters and those of the benthic macroinvertebrate faunas in the nearshore and offshore waters, were shown to differ significantly among habitat types in all seasons. Thus, in the nearshore waters, the fish and benthic macroinvertebrate faunas varied most markedly in the case of habitats containing substantial amounts of macrophytes *vs* those with bare substrate. Moreover, nearshore habitats located in the entrance channel also had relatively distinct fish faunas from those in the basin. The composition of the benthic macroinvertebrate fauna in the offshore waters, differed mainly between habitat A in the entrance channel and habitat B in Shannon Basin. These differences were shown to be correlated with the consistently lower dissolved oxygen concentrations, pH, salinities, smaller sediment grain size and greater sedimentary organic content at the latter habitat, which receives direct freshwater input from the Shannon River. In contrast to the above, the ichthyofauna in the offshore waters differed significantly among habitat types only in spring and autumn. Like those for the offshore benthic macroinvertebrates, these differences were greatest between habitats A and B.

In addition to the demonstrated differences in fish composition among nearshore habitat types, the pattern of relative differences among those habitats in terms of their fish fauna was significantly correlated with that defined by their enduring environmental characteristics in all but one of the eight sampling seasons. This matching demonstrates that reliable predictions of the approximate composition of the fish fauna at any nearshore site in Broke Inlet can be made at any time of year.

The pattern of relative differences among nearshore habitat types, as defined by their benthic macroinvertebrate faunas, was significantly matched with that exhibited by their enduring environmental characteristics only during spring, although a moderate but non-significant correlation was detected during summer. The non-significant matches in the remaining seasons were often related to the relatively small differences in faunal composition among habitats. Thus, while the benthic macroinvertebrate compositions differed between *ca* 90% of the pairwise habitat comparisons during both spring and summer, this was true in only 40-50% of these comparisons during winter and autumn. A similar trend was recorded for the offshore ichthyofauna, where a significant correlation was detected between the fish and enduring environmental data only in the season in which the faunal differences among habitats were greatest, *i.e.* autumn. The lack of a significant correlation in the other three seasons reflects the fact that (i) the fish fauna did not differ significantly among habitats in summer or winter and (ii) that there was a mismatch in the rank orders of resemblance between the faunal and enduring environmental matrices, with habitat B being the most faunally-distinct, while habitat A was the most environmentally-distinct. The latter was also the case with regard to the offshore benthic macroinvertebrate fauna.

The strength of the spatial correlations between the benthic macroinvertebrate and offshore fish faunas and the enduring environmental data largely do not support their use for predicting the species likely to typify the assemblage at any “new” site within Broke Inlet. However, it is important to note that differences in benthic macroinvertebrate composition among sites were greatly reduced in autumn and winter as was the composition of the offshore ichthyofauna in summer and winter and thus in these seasons, any “new” site would likely contain a similar fauna to any other site.

The data collected during this study represent the most comprehensive quantitative sampling of the ichthyofauna and the only quantitative sampling of the benthic macroinvertebrate fauna undertaken in this system. These data therefore enable comparisons to be made between the fish and/or benthic macroinvertebrate fauna in this uniquely “near-pristine” estuary and those of other estuaries throughout south-western Australia.

6.3: The faunas of Broke Inlet: comparisons with other south-western Australian estuaries

The estuaries of south-western Australia are diverse, differing in their morphological, physico-chemical and biotic characteristics. They also vary in the extent to which they have suffered from detrimental anthropogenic effects (Table 6.1a). As a consequence, environmental conditions in these estuaries differ markedly (*e.g.* Potter & Hyndes, 1999; Hoeksema *et al.*, 2006; Chuwen *et al.*, 2009b). Since the 1970s, the ichthyofaunas of 14 estuaries in south-western Australia have been studied in detail. These estuaries range from the intermittently-open Moore River Estuary, *ca* 80 km north of Perth, and the permanently-open estuaries on the lower west coast to the seasonally-open and normally-closed estuaries of the south coast of Western Australia (Table 6.1; Fig. 6.1). The following subsections focus on comparing the faunal data obtained for the seasonally-open Broke Inlet during the present study with those collected for other estuaries. Note that for each estuary only the most comprehensive study of the nearshore and offshore ichthyofaunas has been selected for inclusion in the comparison with Broke Inlet.

Table 6.1: (a) Physical characteristics of 14 south-western Australian estuaries, including latitude, longitude, basin size (km^2), estuary type (*i.e.* PO = permanently-open, IO = intermittently-open, SO = seasonally-open and NC = normally-closed), catchment size (km^2), percentage of the catchment cleared (%), median rainfall (mm), mean annual flow (GL) and level of anthropogenic modification (NP = near-pristine, LU = largely unmodified, M = modified and EM = extensively modified). Mean density (fish 100 m^{-2}) or mean catch rates (fish h^{-1}), number of species and families and the contribution of the different life cycle (LC) guilds to the (b) nearshore and (c) offshore ichthyofauna of each estuary. The most abundant guilds (*i.e.* those that contribute > 15% to the total catch) are highlighted in grey. Moore = Moore River Estuary, Swan = Swan-Canning Estuary, Peel = Peel-Harvey Estuary, Lesch = Leschenault Estuary, Black = Blackwood River Estuary, Wal/Nor = Walpole-Nornalup Estuary, Broke = Broke Inlet, Irwin = Irwin Inlet, Wilson = Wilson Inlet, Oys H = Oyster Harbour, Well = Wellstead Estuary, Ham = Hamersley Inlet, Culham = Culham Inlet and Stokes = Stokes Inlet.

	Moore[d]	**Swan**[e,f]	**Peel**[e,g]	**Lesch**[h]	**Black**[i, j]	**Wal/Nor**[k]	**Broke**	**Irwin**[l, m]	**Wilson**[e, m]	**Oys H**[l, m]	**Well**[e, m]	**Ham**[n]	**Culham**[n]	**Stokes**[n]
(a) Physical Characteristics														
Latitude	31.4 °S	32.1 °S	32.5 °S	33.3 °S	34.2 °S	35.0 °S	**34.9 °S**	35.0 °S	35.0 °S	35.0 °S	34.4 °S	33.9 °S	33.5 °S	33.9 °S
Longitude	115.5 °E	115.7 °E	115.7 °E	115.7 °E	115.1 °E	116.7 °E	**116.4 °E**	116.9 °E	117.3 °E	117.9 °E	119.4 °E	119.9 °E	120.0 °E	121.1 °E
Basin size[a]	1.5	50	131	27	9	13	**48**	10	48	15.6	2.5	2.3	11.3	14
Estuary type[a]	IO	PO	PO	PO	PO	PO	**SO**	SO	SO	PO	NC	NC	NC	NC
Catchment size[b]	14,400	121,000	10,050	4,600	22,070	5,725	**680**	2,290	2,180	2,966	720	840	2,300	4,410
Percentage clearing[b]	82	60	42	36	83	44	**95**	39	46	72	75	10	34	65
Median rainfall[b]	500	450	850	925	700	1,200	**1,400**	800	850	800	465	440	400	400
Annual flow[b]	98	600	810	570	860	363.2	**162**	164	161.4	504	14	1.2	3.4	19
Modification[c]	EM	EM	EM	EM		LU	**NP**	LU	M	EM	M	M	EM	M
(b) Nearshore ichthyofauna														
Mean density	366	184	363	169	359		**81**	345	334	206	1192	744	680	236
Number of species	27	60	71	42	42		**27**	20	23	33	18	6	6	5
Number of families	14	26	34	26	25		**19**	15	14	17	12	5	4	5
LC contribution														
Anadromous	0.01	0.26												
Freshwater straggler	0.03	0.37	0.03				**0.17**	0.10					0.33	0.02
Estuarine resident	92.70	30.26	43.02	14.90	39.36		**81.94**	82.36	95.99	49.60	98.91	99.98	97.58	99.93
Estuarine and marine	2.08	36.05	10.15	52.96	43.14		**16.80**	14.57	3.87	43.24	1.08	0.00	2.10	0.06
Mar. est.-opportunist	4.91	32.43	46.59	30.60	17.23		**0.42**	2.97	0.10	3.98	0.01	0.01		
Marine straggler	0.28	0.62	0.21	1.54	0.27		**0.67**		0.03	3.18				
(c) Offshore ichthyofauna														
Catch rate		26.02	70.55	10.05	1.72	5.55	**0.91**	6.43	4.08	4.08	87.18	11.81	2.3	23.16
Number of species		22	20	26	14	23	**31**	27	27	45	17	6	1	8
Number of families		17	15	20	10	18	**22**	21	21	29	13	4	1	6
LC contribution														
Anadromous		61.10	12.80	18.16										
Freshwater straggler														
Estuarine resident		4.00	3.30			15.30		0.40	3.40	7.10	25.40	83.80	100.00	96.25
Estuarine and marine		10.00	7.10	4.26	13.77	20.70	**19.64**	23.40	38.70	6.70	1.80			1.14
Mar. est.-opportunist		15.90	72.80	74.11	84.81	57.40	**77.45**	75.60	57.20	76.50	72.70	16.20		2.61
Marine straggler		9.00	4.00	3.47	1.42	6.60	**2.91**	0.60	0.70	9.70	0.10			

[a] Brearley (2005), [b] Pen (1999), [c] Commonwealth of Australia (2002), [d] Young *et al.* (1997), [e] Valesini *et al.* (2009), [f] Loneragan *et al.* (1989), [g] Loneragan *et al.* (1987), [h] Potter *et al.* (2000), [i] Valesini *et al.* (1997), [j] Valesini (1995), [k] Potter & Hyndes (1994), [l] Hoeksema *et al.* (2009), [m] Chuwen *et al.* (2009b), [n] Hoeksema *et al.* (2006).

Table 6.2: List of species, families and life cycle (LC) categories of fish recorded in the nearshore waters of Broke Inlet during the present study and their presence (*) or absence in studies of the nearshore ichthyofauna of other estuaries in south-western Australia. Full estuary names and life cycle categories are given in Table 6.1. Species ranked by their total abundance during the present study. Data collected from the sources in Table 6.1.

Species	Family	LC	Moore	Swan	Peel	Lesch	Black	Wal/Nor	Irwin	Wilson	Oys H	Well	Ham	Culham	Stokes
Atherinosoma elongata	Atherinidae	E		*	*	*	*	*	*	*	*	*	*	*	*
Leptatherina wallacei	Atherinidae	E	*	*	*	*	*	*	*	*	*	*	*	*	
Leptatherina presbyteroides	Atherinidae	EM	*	*	*	*	*	*	*	*	*	*			
Afurcagobius suppositus	Gobiidae	E	*	*	*	*	*		*	*	*	*			
Pseudogobius olorum	Gobiidae	E	*	*	*	*	*	*	*	*	*	*	*	*	*
Favonigobius lateralis	Gobiidae	EM	*	*	*	*	*	*	*	*	*	*		*	*
Notolabrus parilus	Labridae	MS				*	*			*					
Hyporhamphus melanochir	Hemiramphidae	EM				*	*		*	*					
Achoerodus gouldii	Labridae	MS													
Engraulis australis	Engraulidae	EM		*	*	*	*		*	*		*			*
Aldrichetta forsteri	Mugilidae	MEO	*	*	*	*	*	*	*	*	*	*	*		*
Ammotretis rostratus	Pleuronectidae	MEO						*	*	*	*	*			
Neoodax balteatus	Odacidae	MS		*							*				
Ammotretis elongatus	Pleuronectidae	EM		*	*	*	*				*				
Enoplosus armatus	Enoplosidae	MS		*	*	*	*				*				
Edelia vittata	Percichthyidae	FS													
Mugil cephalus	Mugilidae	MEO	*	*	*	*	*	*	*	*	*	*			
Platycephalus speculator	Platycephalidae	EM		*	*	*	*			*					
Girella zebra	Kyphosidae	MS													
Haletta semifasciata	Odacidae	MS		*	*	*	*				*	*			
Galaxias occidentalis	Galaxiidae	FS		*	*										
Lepidogalaxias salamandroides	Lepidogalaxiidae	FS													
Urocampus carinirostris	Syngnathidae	EM		*	*	*	*		*	*	*	*			
Pseudocaranx dentex	Carangidae	MS			*		*								
Rhabdosargus sarba	Sparidae	MEO	*	*	*	*	*	*		*		*			
Pseudorhombus jenynsii	Paralichthyidae	MEO	*	*	*	*	*	*		*	*				
Cynoglossus broadhursti	Cynoglossidae	MS													

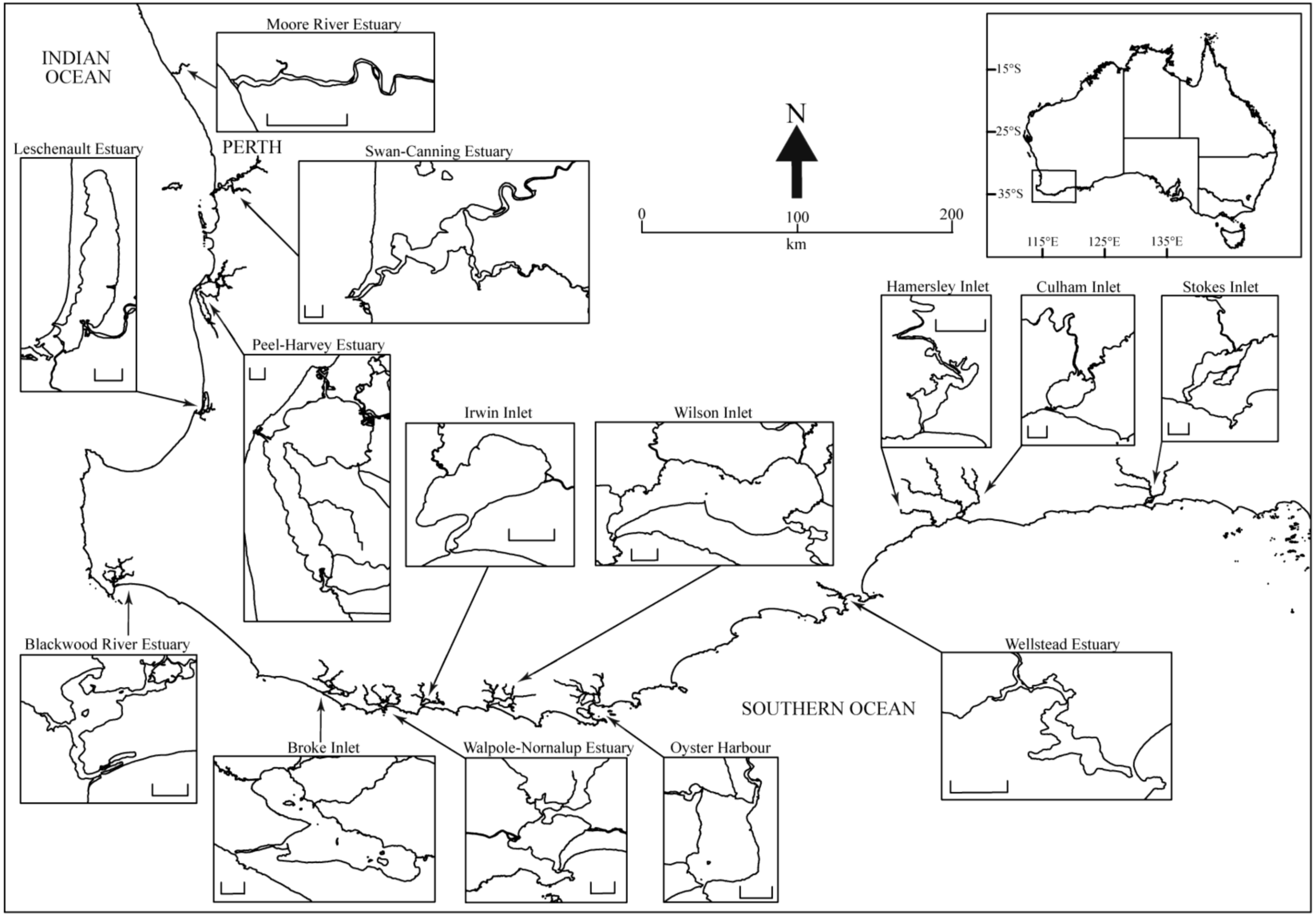


Fig. 6.1: Map of south-western Australia detailing 14 estuaries in which the ichthyofauna has been studied since the 1970s. The scale bar in the map of each estuary represents 2 km.

6.3.1: Ichthyofaunal community

6.3.1.1: Nearshore ichthyofauna

During the present study, 83,047 fish were caught from the nearshore waters of Broke Inlet over two consecutive years of seasonal sampling. These fish comprised 27 species, of which 22 had been recorded during recent studies of other south-western Australian estuaries (Table 6.2). The six most abundant species recorded in Broke Inlet, *i.e.* the atherinids *Atherinosoma elongata, Leptatherina wallacei* and *Leptatherina presbyteroides* and the gobiids *Afurcagobius suppositus, Pseudogobius olorum* and *Favonigobius lateralis*, are found in virtually all estuaries from the Moore River Estuary on the lower west coast to the Hamersley, Culham and Stokes inlets on the south coast of Western Australia (Table 6.2).

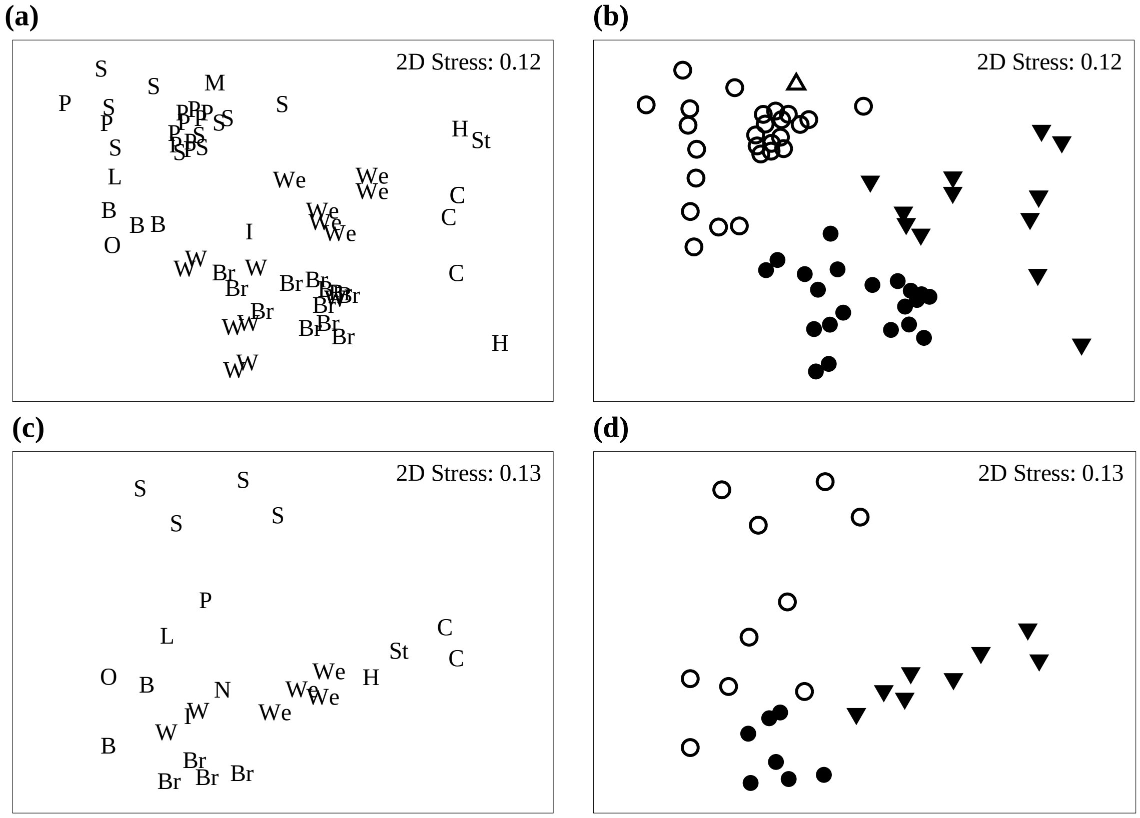
In contrast, five of the fish species collected from the nearshore waters of Broke Inlet, *i.e. Achoerodus gouldii, Cynoglossus broadhursti, Girella zebra*, *Edelia vittata* and *Lepidogalaxias salamandroides,* were not recorded during detailed studies of any other south-western Australian estuary. Although the first three of these species are typically characterised as marine stragglers and, in the case of the last two of those three, were represented by only one individual, *A. gouldii* was the ninth most abundant species in the nearshore waters of Broke Inlet. The small size of the individuals of *A. gouldii*, *i.e.* 26 to 105 mm total length, a labrid which grows to a large size, indicates that these fish had been transported inshore early in life into the vicinity of Broke Inlet and that currents then favoured their movement into that estuary at a time when its mouth was open. Another labrid, *Notolabrus parilus,* which is rarely found in south-western Australian estuaries and which was caught at similarly small sizes, ranked seventh in abundance in the nearshore waters of Broke Inlet. It must be recognized, however, that all 199 individuals of *A. gouldii* and *N. parilus* caught during this study were found in the entrance channel, and thus only used that restricted part of the estuary as a nursery area. Moreover, the juveniles of *N. parilus* and *Achoerodus viridis*, a similar species to *A. gouldii,* are known to occupy seagrass beds (Gillanders, 1997; Lek *et al.*, submitted), which were present in abundance at habitat H in the entrance channel.

Both of the other two species that were “unique” to the samples from Broke Inlet, *i.e. E. vittata* and *L. salamandroides*, are endemic freshwater species (Morgan *et al.*, 1998). The presence of these two species, and that of *Galaxias occidentalis*, in this estuary was thus presumably due to their having been flushed downstream in small numbers by heavy winter rains from their typical riverine habitats.

The number of species and families recorded in the nearshore waters of south-western Australian estuaries, are highest in the permanently-open systems of the lower west and south coasts and lowest in the normally-closed estuaries along the south coast (Table 6.1b), in which the opportunity for marine species to become recruited into these systems is limited. The number of fish taxa recorded in Broke Inlet during the present study is similar to that recorded in other seasonally-open estuaries in this region.

The mean density of fish in the nearshore waters of Broke Inlet, *i.e.* 81 fish 100 m^{-2}, is less than that recorded in any of the other 12 estuaries in south-western Australia which were sampled with the same type of seine net, *i.e.* a 21.5 m long net (Table 6.1b). This probably reflects the low productivity in Broke Inlet, which is most likely due to the low levels of nutrients (nitrogen and phosphorus) and consequently a paucity of aquatic macrophytes (Hodgkin & Clark, 1989a; Brearley, 2005). Substantial clearing of estuary catchments for urban development and/or agriculture (Pen, 1999) have resulted in a number of estuaries in south-western Australia becoming eutrophic (*e.g.* Lukatelich *et al.*, 1987; McComb & Lukatelich, 1995). For example, high levels of nutrient run-off into the nearby, similarly-sized and seasonally-open Wilson Inlet has led to the development of very extensive growths of the seagrass *Ruppia megacarpa* (Department of Environment, 2003). The fact that the overall fish density in the nearshore waters of that system was more than four times greater than that in the oligotrophic Broke Inlet (Table 6.1b) is consistent with the findings that the abundances of several of the dominant atherinid and gobiid species are positively correlated with the density of *R. megacarpa* (Humphries *et al.*, 1992).

The compositions of the fish faunas in the nearshore waters of Broke Inlet were compared to those of the 12 other estuaries in south-western Australia that had been sampled using a 21.5 m seine net (Figs 6.2a, b). These MDS ordination analyses used the mean density of each fish species in each habitat type in these systems in which the



○ Permanently-open ● Seasonally-open △ Intermittently-open ▼ Normally-closed
M=Moore, S=Swan-Canning, P=Peel-Harvey, L=Leschenault, B=Blackwood, Br=Broke, N=Walpole-Nornalup,
I=Irwin, W=Wilson, O=Oyster Harbour, We=Wellstead, H=Hamersley, C=Culham and St=Stokes

Fig. 6.2: nMDS plots constructed from the mean density data for each fish species caught in nearshore waters (a, b) and the mean percentage contribution of each fish species caught in offshore waters (c, d) of each of the estuaries detailed in Fig. 6.1. Each point represents either an estuary or habitat type/region of an estuary if that system was spatially subdivided during the original study. Points coded for estuary (a, c) and estuary type (b, d).

Valesini *et al.* (2010) classification scheme had been applied, *i.e.* Broke Inlet (current study) the Swan-Canning Estuary, Peel-Harvey Estuary, Wilson Inlet and Wellstead Estuary (Valesini *et al.*, 2009). Where such habitat-related data were not available for an estuary, the densities of each species in each well-defined region (*i.e.* channel, basin and/or upper estuary) were employed for the analyses, *i.e.* Blackwood River Estuary and Hamersley, Culham and Stokes inlets. When no habitat or regional data were available for an estuary, as with that of the Moore River Estuary, Leschenault Estuary, Irwin Inlet and Oyster Harbour, the mean density for each species throughout the whole estuary was used. The above density data were forth-root transformed and used to construct a Bray-Curtis similarity matrix, which was subjected to nMDS ordination. On the resultant plot, the samples from each estuary formed relatively discrete groups that progress in an anticlockwise direction from the most northern estuary on the west coast

(Moore River Estuary) and the nearby Swan-Canning and Peel-Harvey estuaries (top left hand corner of the plot), downwards to those from the Blackwood River Estuary on the south-western tip of Western Australia and then further around to those for the Wilson, Irwin and Broke inlets on the western part of the south coast (Fig 6.2a). The samples for the Hamersley, Culham and Stokes inlets, which are located the furthest east of all the estuaries studied along the south coast of Western Australia lay a notable distance to the right of those from Broke Inlet and also Wellstead Estuary, the latter of which formed a group close to the centre of the plot. The single sample for Oyster Harbour lay to the left of those for Wilson and Broke inlets, even though that estuary is located further to the east.

When the samples in Fig. 6.2a were coded for estuary type rather than estuary, they each formed discrete groups on the basis of that factor (Fig 6.2b). Thus, the samples from permanently and intermittently-open estuaries lay mostly on the opposite side of the plot from those for the normally-closed estuaries, while the samples from the seasonally-open estuaries occupied an intermediate position (Fig 6.2b).

In terms of abundance, the nearshore ichthyofauna of Broke Inlet is dominated (82%) by species which are restricted to estuaries, a situation which parallels that in the other nearby seasonally-open systems, *i.e.* Irwin (82%) and Wilson (96%) inlets (Table 6.1b). This life cycle guild made an even greater contribution (> 98%) to the nearshore fish faunas of the Wellstead Estuary and the Hamersley, Culham and Stokes inlets, which is hardly surprising given that these estuaries are not normally connected to the ocean. However, the contribution of this guild to the nearshore ichthyofaunas of the Swan-Canning, Peel-Harvey, Leschenault and Blackwood River estuaries and Oyster Harbour is far lower (15-50%), largely reflecting the ability of marine species to enter these permanently-open estuaries.

6.3.1.2: Offshore ichthyofauna

Sampling in the offshore waters of Broke Inlet yielded 1,050 fish, the five most abundant of which were *Arripis georgianus*, *Mugil cephalus*, *Engraulis australis*, *Aldrichetta forsteri* and *Rhabdosargus sarba.* All of these species with the exception of

A. georgianus in the Swan-Canning and Peel-Harvey estuaries and *R. sarba* in the Swan-Canning Estuary have been recorded in the offshore waters of all permanently and seasonally-open estuaries in south-western Australia and are likewise abundant in those systems (Table 6.3). However, some other species found in Broke Inlet, such as *Ammotretis rostratus, Pagrus auratus, Enoplosus armatus, Sillago bassensis, Achoerodus gouldii* and *Mustelus antarcticus* have been recorded only in estuaries on the south coast. Although seven species (*Girella zebra, Schuettea woodwardi, Scorpis georgiana, Lotella rhacina, Tilodon sexfasciatum, Cynoglossus broadhursti* and *Eubalichthys bucephalus*) found in Broke Inlet during the current study have not been recorded in any other south-western Australian estuary, it should be recognised that all of these species were rare and are classified as marine stragglers (Table 6.3).

There are two notable omissions from the list of fish species found in the offshore waters of Broke Inlet. The first of these species, the sparid *Acanthopagrus butcheri,* is abundant in the offshore waters of all other estuaries in south-western Australia and especially in those of normally-closed estuaries, in which it can represent up to 100% of the individuals (Hoeksema *et al.*, 2006; Chuwen *et al.*, 2009b). Furthermore, previous sampling at regular intervals of the offshore waters of the basin of Broke Inlet and those of its major tributary, the Shannon River, yielded only two individuals (Chuwen *et al.*, 2009b). These data clearly demonstrate that, unlike the situation in other south-western Australian estuaries and particularly in the saline reaches of their tributaries, *A. butcheri* is rare in Broke Inlet. It has been proposed that the paucity of this species in Broke Inlet is related to the very low salinities found during winter in the tributary rivers, which provide the “preferred” habitat of this species (Hodgkin & Clark, 1989a; Chuwen *et al.*, 2009b) and often also in spring when *A. butcheri* typically use this region of estuaries to spawn (Willams *et al.*, 2009).

The second species that was a notable omission from the samples from Broke Inlet was the Western Striped Grunter *Pelates octolineatus,* which is abundant in the offshore waters of other estuaries in this region, comprising, for example, 29% of the total catch obtained from Oyster Harbour (Chuwen *et al.*, 2009b). The absence of this species from Broke Inlet (previously referred to as *Pelates sexlineatus* in Western Australia) is probably related to the fact that seagrass constitutes its main habitat and

Table 6.3: List of species, families and life cycle (LC) categories of fish recorded in the offshore waters of Broke Inlet during the present study and their presence (*) or absence in studies of the offshore ichthyofauna of other estuaries in south-western Australia. Full estuary names and life cycle categories are given in Table 6.1. Species ranked by their total abundance during the present study. Data collected from the sources in Table 6.1.

Species	**Family**	**LC**	**Swan**	**Peel**	**Lesch**	**Black**	**Wal/Nor**	**Irwin**	**Wilson**	**Oys H**	**Well**	**Ham**	**Culham**	**Stokes**
Arripis georgianus	Arripidae	MEO			*	*	*	*	*	*	*	*		*
Mugil cephalus	Mugilidae	MEO	*	*	*	*	*	*	*	*	*	*		*
Engraulis australis	Engraulidae	EM	*	*	*	*	*	*	*	*	*			*
Aldrichetta forsteri	Mugilidae	MEO	*	*	*	*	*	*	*	*	*	*		*
Rhabdosargus sarba	Sparidae	MEO		*	*	*	*	*	*	*	*	*		
Ammotretis rostratus	Pleuronectidae	EM					*	*	*	*	*			
Pseudocaranx dentex	Carangidae	MEO			*	*	*	*	*	*	*	*		
Pagrus auratus	Sparidae	MEO				*	*	*	*	*	*			
Arripis truttaceus	Arripidae	MEO			*	*		*	*	*	*	*		
Sillaginodes punctata	Sillaginidae	MEO		*	*	*	*	*	*	*	*			
Gonorynchus greyi	Gonorynchidae	MEO					*	*	*	*				
Hyporhamphus melanochir	Hemiramphidae	EM		*	*			*	*	*	*			
Enoplosus armatus	Enoplosidae	MS				*		*	*	*				
Pomatomus saltatrix	Pomatomidae	MEO	*	*	*	*	*	*	*	*	*			
Sillago bassensis	Sillaginidae	MS					*							
Cnidoglanis macrocephalus	Plotosidae	EM	*	*	*	*	*	*	*	*	*			*
Platycephalus speculator	Platycephalidae	EM					*	*	*	*	*			
Pseudorhombus jenynsii	Paralichthyidae	MEO	*	*	*		*	*	*	*				
Achoerodus gouldii	Labridae	MS						*	*	*				
Sillago schomburgkii	Sillaginidae	MEO		*	*	*		*	*	*				
Girella zebra	Kyphosidae	MS												
Mustelus antarcticus	Triakidae	MS			*		*							
Chelidonichthys kumu	Triglidae	MS	*			*								
Schuettea woodwardi	Monodactylidae	MS												
Scorpis georgiana	Kyphosidae	MS												
Notolabrus parilus	Labridae	MS							*	*				
Myliobatis australis	Myliobatidae	MS			*		*							
Lotella rhacina	Moridae	MS												
Tilodon sexfasciatum	Kyphosidae	MS												
Cynoglossus broadhursti	Cynoglossidae	MS												
Eubalichthys bucephalus	Monacanthidae	MS												

macrophyte growths are not abundant in this system (Connolly, 1994; Sanchez-Jerez *et al.*, 2002).

The number of species and families recorded in Broke Inlet during the present study are similar to those recorded by Chuwen *et al.* (2009b) in the seasonally-open Irwin and Wilson inlets. The number of taxa recorded in Oyster Harbour by Chuwen *et al.* (2009b), however, was greater than in those three estuaries due to the presence of a greater number of marine species, which reflects the fact that this estuary is permanently-open and thus provides a continuous potential route for the entry of marine species. This type of difference parallels that recorded for seasonally and permanently-open estuaries in South Africa in which marine species likewise contribute greatly to the ichthyofaunas of those systems (*e.g.* Bennett, 1989; Harrison & Whitfield, 2006).

As with the mean densities of fishes in the nearshore waters, the mean catch rates of fishes in the offshore waters of Broke Inlet were the lowest of all estuaries in south-western Australia for which there are comprehensive and comparable data on gill net catches (Table 6.1c). Such findings also presumably reflect the oligotrophic nature of Broke Inlet and, in particular, the sparseness of its macrophyte growth (Brearley, 2005). This is reinforced by the fact that, the greatest mean catch rates in offshore waters were recorded in the normally-closed Wellstead Estuary, which contains extensive growths of *R. megacarpa* (Brearley, 2005; Chuwen *et al.*, 2009b).

The compositions of the offshore fish faunas in Broke Inlet were compared with those from the other 12 estuaries in south-western Australia that have also been sampled using composite gill nets (Figs 6.2c, d). In the case of Broke Inlet, this analysis used the percentage contribution of each fish species in each habitat type. Where such habitat-related data were not available for a system, the percentage contribution of each species in each well-defined region of the estuary were employed, *i.e.* Swan-Canning, Blackwood River and Wellstead estuaries and Stokes Inlet. Where no habitat or regional data were available for an estuary, as with the Peel-Harvey, Leschenault and Walpole-Nornalup estuaries, Oyster Harbour and the Wilson, Irwin, Hamersley and Culham inlets, the percentage contribution of each species throughout the whole estuary was used. Percentage contribution data was employed in this analysis as the gill nets used in the various studies differed slightly in their mesh sizes.

The above percentage contribution data were square-root transformed, used to construct a Bray-Curtis similarity matrix and subjected to nMDS ordination. On the resultant plot, the samples from the various estuaries followed the same anticlockwise progression according to location as was exhibited on the corresponding ordination plot for the nearshore fish faunas (*cf.* Fig. 6.2a, c). Thus, samples from the Swan-Canning Estuary lie in the top left-hand corner of the plot, above those, in sequence, for the Peel-Harvey, Leschenault and Blackwood River estuaries, while those for Broke Inlet, Wilson Inlet, Wellstead Estuary and the Hamersley, Stokes and Culham inlets form a progressive line to the right along the bottom of the plot (Fig. 6.2c).

When the offshore samples were coded for estuary type rather than estuary, they formed essentially discrete groups according to that factor (Fig. 6.2d). Thus, as with the samples from nearshore waters, most of those for permanently-open estuaries lie on the opposite side of the plot from those for normally-closed estuaries, with those for seasonally-open estuaries forming a tight group between them.

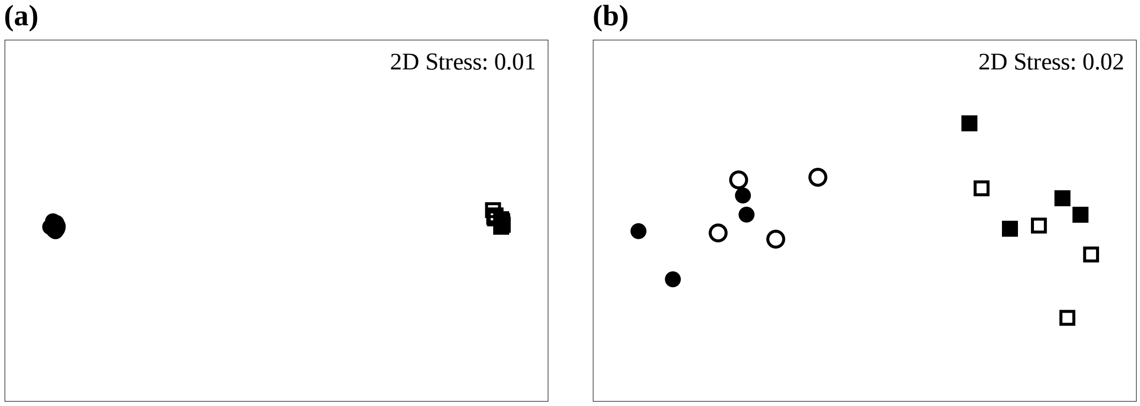
In terms of percentage composition, the offshore ichthyofauna of Broke Inlet is dominated by marine estuarine-opportunists (77%) and, to a lesser extent, estuarine and marine species (20%; Table 6.1c). Representatives of these life cycle guilds were also abundant in the other seasonally-open estuaries. In contrast, estuarine resident species were moderately to remarkably abundant in normally-closed estuaries (25-100%), while the permanently-open estuaries on the lower west coast were the only systems to contain anadromous species and thus help to account for the marked differences observed for the different estuary types (Table 6.1c).

6.3.2: Benthic macroinvertebrate community

The only extensive quantitative data on the composition of the benthic macroinvertebrate assemblages for any estuary on the south coast of Western Australia, excepting that collected during the current study, is that published by Platell and Potter (1996) for Wilson Inlet. It should be noted, however, that although these workers used a 1 mm mesh as opposed to the 0.5 mm mesh employed in the current study, a trial within that original study indicated that no additional species were recorded in samples employing a 0.5 mm mesh and that > 90% of the biomass was retained on the 1 mm sieve (Platell, 1990). The mean number of benthic macroinvertebrate species recorded seasonally in the nearshore and offshore waters of Broke Inlet, *i.e.* 21-22 and 14-19, respectively, were less than those recorded in the corresponding water depths in Wilson Inlet, *i.e.* 28-32 and 19-26, respectively. Furthermore, mean seasonal densities of benthic macroinvertebrates in the nearshore waters of Broke Inlet (230-415 individuals 0.1 m^{-2}) were far less than those recorded in Wilson Inlet (470-1,740 individuals 0.1 m^{2}), and the same was true for the offshore waters (115-266 *vs* 570-1,140 individuals 0.1 m^{-2}, respectively). The greater densities of benthic macroinvertebrates in Wilson than Broke Inlet reflect the fact that the former estuary is eutrophic while the latter is oligotrophic (Lukatelich *et al.*, 1987; Department of Environment, 2003; Brearley, 2005). High densities of benthic macroinvertebrates are typically an indication of eutrophication in other parts of the world (Gray *et al.*, 2002; Karlson *et al.*, 2002).

Following nMDS ordination of the mean square-root transformed densities of each benthic macroinvertebrate species in samples collected seasonally from the nearshore and offshore waters of Broke and Wilson inlets, the samples for the two estuaries formed very tight and widely separated groups on the resultant plot (Fig. 6.3a). This marked inter-estuarine difference in faunal composition at the species level was attributable, in particular, to the far greater densities of *Corophium minor*, *Mesanthura* sp. and *Armandia intermedia* in Broke Inlet and of *Heteromastus filiformis*, *Capitella capitata* and *Hydrococcus brazieri* in Wilson Inlet.

The groups of samples from the two estuaries remained discrete on the ordination plot even when the benthic macroinvertebrate data were analysed at the phylum rather than species level (*cf.* Fig. 6.3a, b). Such differences were due mainly to the greater contributions made by polychaetes to the nearshore and offshore faunas of Wilson Inlet (69 and 91%, respectively) than Broke Inlet (64 and 57%, respectively), and to the reverse situation for crustaceans, *i.e.* 1 and 0.3%, respectively, for Wilson Inlet *vs* 24 and 36%, respectively, for Broke Inlet. The pronounced trend for the densities of polychaetes to be greater in the eutrophic Wilson Inlet (particularly in the offshore waters) and for those of crustaceans to be greater in the oligotrophic Broke Inlet is consistent with the generalisation that polychaetes often thrive in eutrophic and disturbed environments and that crustaceans are particularly sensitive to such conditions (Reise, 1982; Warwick & Clarke, 1993; Wildsmith *et al.*, 2009).



Broke Inlet: ○ nearshore waters ● offshore waters
Wilson Inlet: ☐ nearshore waters ■ offshore waters

Fig. 6.3: nMDS ordination plots constructed from the mean density data for each benthic macroinvertebrate (a) species and (b) phylum caught seasonally in the nearshore and offshore waters of Broke and Wilson Inlets.

6.4: Future developments and management implications

This study has provided detailed, quantitative data on both the fish and benthic macroinvertebrate fauna present within Broke Inlet and their relationships with a range of environmental characteristics. Comparisons of the fauna in Broke Inlet to other estuaries in south-western Australia suggest that while this system harbours a similar ichthyofauna to other seasonally-open estuaries, such as the nearby Wilson Inlet, their invertebrate communities differ markedly. Since this study is only the second quantitative study on benthic macroinvertebrate community composition in seasonally-open estuaries on the south coast of Western Australia, these findings highlight the need for more detailed quantitative sampling of the benthic macroinvertebrate assemblages present in estuaries along this coast. The results of such a study would greatly enhance our knowledge on the faunal composition of these systems. Furthermore, as Broke Inlet has been suggested as a benchmark for detecting the affects of anthropogenic change given its “near-pristine” status (Commonwealth of Australia, 2002), the habitat classification framework and faunal data collected during this study provide a detailed and fully quantitative platform for gauging the extent of any future shifts in the abiotic and biotic characteristics of this estuary and for making comparisons with other more anthropogenically-degraded estuaries in south-western Australia.

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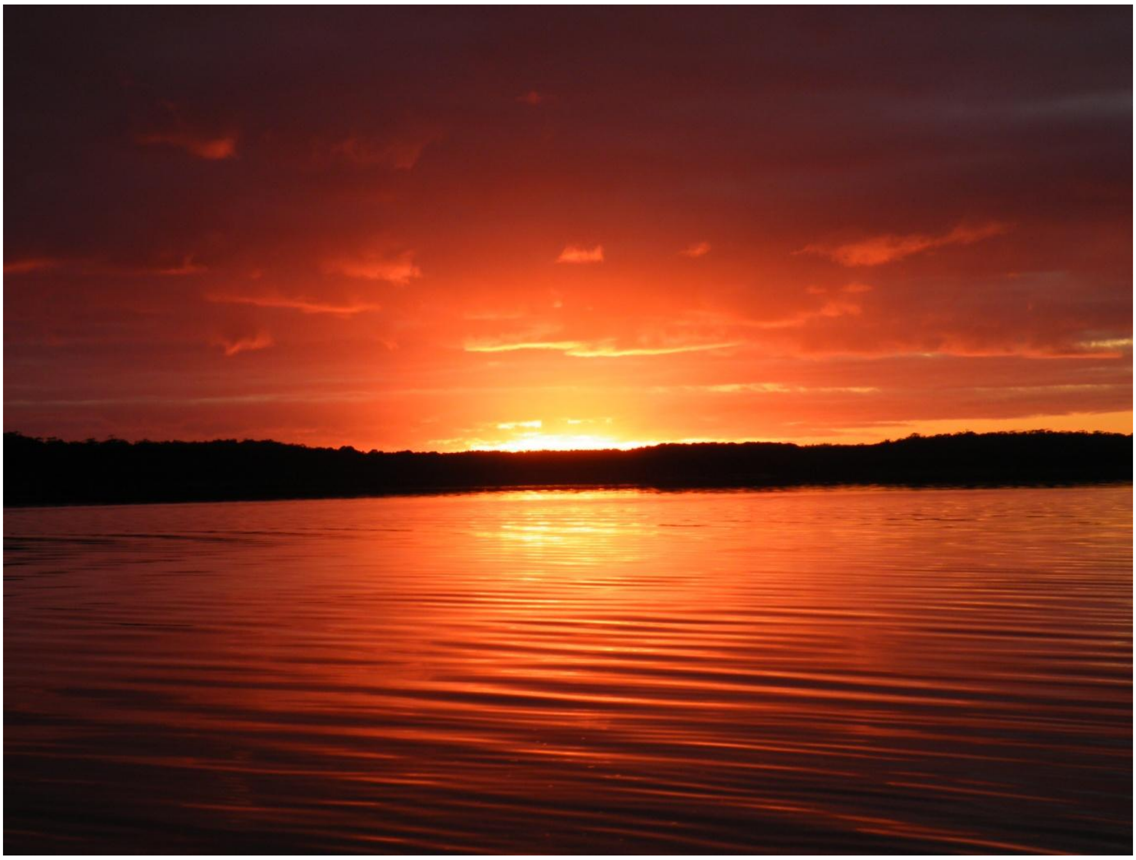

Home Time: Sunset over Broke Inlet after another hard day at the "office".