Changes in rocky reef fish assemblages throughout an estuary with a restricted inlet.

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Abstract

Rocky reef habitat is common in many estuaries yet its role as a habitat for fishes is poorly known. There is also limited understanding of how access of coastal species into estuaries and habitat quality can affect the distribution of rocky reef fishes within estuaries. This study used baited remote underwater video stations (BRUVS) to determine spatial patterns in fish assemblages associated with rocky reef habitat throughout a barrier estuary with a permanently open but restricted inlet. Estuarine rocky reefs provided habitat for a diverse assemblage of fishes, many of which were large juveniles and subadults. In the absence of a pronounced salinity or temperature gradient a clear transition in fish assemblages occurred from coastal waters, through the inlet channel, to the central estuary, and into the inner estuary. The inlet channel, notably its narrowness and length, limit tidal input into this estuary which acts as a significant impediment to the dispersal of many coastal fishes and insufficient habitat excludes many coastal rocky reef species from the inner estuary. This study highlights the need to recognise estuarine rocky reefs as providing habitat for diverse fish assemblages and the role inlets play in restricting access of coastal species.

Introduction

Estuaries are highly productive systems providing refugia, feeding areas, nursery grounds and spawning habitat for numerous fishes (Turner et al. 2004, Gillanders 2007, Hughes et al. 2009), many of which are important commercial species (Gray et al. 1996, Roy et al. 2001). Estuarine fish assemblages include species of marine origin that are estuary residents, are passing through estuaries as migrants, or are using estuaries for only a particular life history stage (Roy et al. 2001, Vorwerk et al. 2003, Kaiser et al. 2005). Many of the latter group are coastal species that use estuaries as juvenile nurseries (Hannan & Williams 1998, Jenkins & Wheatley 1998, Beck et al. 2001, Jelbart et al. 2007b) after being transported as larvae from coastal spawning sites (Forward et al. 1999, Trinski 2002, Suthers et al. 2009). The high biological productivity in estuaries provides these juveniles with food, and the relatively high structural complexity and turbidity within many estuarine habitats provides refuge from predators, especially those relying on vision (Little 2000, Laegdsgaard & Johnson 2001, Turner et al. 2004, Kimirei et al. 2011). Many of these juveniles are then thought to undertake migrations to adult habitat in coastal waters (Beck et al. 2001, Gillanders et al. 2003, Becker et al. 2010).

The importance of estuaries for juveniles of many recreational and commercial fish species has resulted in numerous studies describing fish assemblages associated with estuarine habitats, especially those in the shallow fringes which are most easily sampled. The most intensely studied habitats are seagrasses (e.g. Ferrell et al. 1993, Hannan & Williams 1998, Scott et al. 2000, Jones & West 2005, Hindell 2006, York et al. 2006), mangroves (e.g. Laegdsgaard & Johnson 2001, Nagelkerken & Faunce 2008), and saltmarshes (e.g. Connolly et al. 1997, Paterson & Whitfield 2000, Mazumder 2004, Connolly 2009). Many studies have

also compared fish assemblages among these habitats (e.g. Dorenbosch et al. 2007, Jelbart et al. 2007a, Kimirei et al. 2011) or with unvegetated habitats such as bare sand and mud (e.g. Ferrell & Bell 1991, Connolly 1994, Edgar & Shaw 1995, Gray et al. 1996, Bloomfield & Gillanders 2005, Lugendo et al. 2007, França et al. 2012, Gladstone et al. 2012). These studies have found higher densities of juvenile fishes in vegetated habitats suggesting the structural complexity of seagrass, mangrove and saltmarsh plants provides an important habitat in the early life stages of many fishes (Beck et al. 2001, Edgar 2001, Turner et al. 2004, Gillanders 2007, Hogarth 2007).

Another habitat, often neglected but frequently found in estuaries, are rocky reefs (Little 2000, Turner et al. 2004, Gillanders 2007). Rocky reefs represent over 20% of the foreshore areas of many estuaries (e.g. Magalhães et al. 2003) and, in some estuaries, over 70% (Creese et al. 2009). Rocky reefs provide refuge for mobile species and hard substrate for the secure attachment of sessile and sedentary biota including macroalgae and filter feeders in coastal (Underwood et al. 1991, Turner et al. 2004) and estuarine waters (Glasby 1999, Creese et al. 2009). In coastal waters, these species are in turn preyed upon by various benthic predators, including an assortment of fishes (Gladstone 2007, Malcolm et al. 2010, Morton & Gladstone 2011), which are dependent on rocky reef habitat for prey as well as shelter and nocturnal refuge (Morton 2007, Morton et al. 2008). In estuaries, the structural complexity provided by rocky substrate and the associated macroalgae is likely to be equally important to estuarine fishes (Clynick et al. 2008, Edgar & Barrett 2010), yet estuarine rocky shores are largely unstudied (Magalhães et al. 2003, Creese et al. 2009). This is surprising given that artificial reefs have been successfully used as a fishery enhancement initiative in estuaries (Lowry et al. 2012) and that high densities of fishes occur on rocky reefs even where other habitats such as seagrasses and mangroves occur (Jenkins & Wheatley 1998, Guidetti 2000, Huijbers et al. 2008).

Where extensive within-estuary surveys have been conducted, fish assemblages are found to differ in response to salinity and temperature gradients, turbidity, oxygen levels, and distance from the estuary mouth (Loneragan et al. 1986, Marshall & Elliott 1998, Martino & Able 2003, Barletta et al. 2005, Jelbart et al. 2007b, Selleslagh & Amara 2008). These studies have, however, sampled habitats other than rocky reefs and occurred in tide-dominated estuaries, such as drowned river valleys, with a pronounced salinity gradient from the estuary mouth to the upper reaches and characteristically large entrances allowing significant tidal exchange with truly marine waters and easy passage for coastal fishes (Roy et al. 2001, Short & Woodroofe 2009). For estuaries with a restricted entrance, the inlet plays a significant role in the passage of fishes (Potter et al. 1990; Potter & Hyndes 1994; Strydom et al. 2003, Vorwerk et al. 2003). Estuary inlets can provide significant temporal barriers to fish passage, as in the case of intermittently closed/open estuaries (Bell et al. 2001, Lill et al. 2013), or permanent restricted passage as is the case for wave-dominated barrier estuaries (Edgar et al. 1999, Roy et al. 2001, Gillanders et al. 2011). Wave-dominated estuaries have an extensive

sand barrier separating the central basin of the estuary from the sea and a restricted inlet dominated by strong tidal velocities that transport marine sand into the estuary forming extensive flood tide deltas and that reduce tidal ranges to ~5-10% that in the ocean (Roy et al. 2001, Turner et al. 2004, Short & Woodroffe 2009).

Despite the likely significance for fishes and indirect benefits these fishes provide to humans, fish assemblages associated with estuarine rocky reefs are currently poorly studied despite many studies highlighting the need to more fully understand fish-habitat associations in estuaries (e.g. Ferrell & Bell 1991, Gray et al. 1996, Guidetti 2000, Kimirei et al. 2011). Therefore, the current understanding of estuarine fish assemblages, including the value of rocky reef as another potential estuarine nursery area, is incomplete. Conservation planning aimed at countering threatening processes to fishes is likely to be more effective with a better understanding of fish-habitat associations and the constraints estuary inlets have on fish passage (Rowley 1994, West & King 1996, Beck et al. 2001, Malcolm et al. 2010). The present study aimed to describe spatial patterns in the fish assemblages associated with rocky reef habitat throughout an estuary with a restricted inlet using the large, wave-dominated barrier estuary of Lake Macquarie as a case study. It was hypothesised that the inlet would limit the dispersal of coastal fishes into the estuary resulting in a change in fish assemblages from coastal waters to the inner estuary. This study also aimed to determine whether the described spatial patterns were temporally consistent by conducting the fish surveys on two occasions separated by 6 mo.

Materials and methods

Study location

Lake Macquarie (33°05′S 151°35′E), with an estuary area of ~110 m^2 and a foreshore length of over 170 km, is the largest coastal lake in eastern Australia (Morton et al. 1996, Lowry et al. 2012). Its maximum length from north to south is ~24 km, and the maximum width from west to east is ~13.5 km (Figure 1). Its waters, which average only 7 m depth (max. 11 m), contain the third largest area of seagrass beds in New South Wales (Howe 2008). Lake Macquarie is permanently connected to the ocean at Swansea Channel. This 5.5 km long, 100-400 m wide and generally 2-5 m deep channel experiences strong tidal currents of up to 2 m.s^{-1} and restricts tidal fluctuations of ~2 m in coastal waters to <0.1 m within the Lake Macquarie basin (Spencer 1959, AWACS 1995, Manly Hydraulics Laboratory 1996). This results in only 1% of the volume of the basin exchanging with coastal waters in an average tidal cycle (Spencer 1959), and is likely to restrict the passage of marine fishes into Lake Macquarie (Hannan & Williams 1998, Roy et al. 2001). Having freshwater inflow estimated to be only 4% of its volume (Baas Becking et al. 1959) and salinity levels close to those in marine waters (Spencer 1959, Hannan & Williams 1998), Lake Macquarie is classified as a marine-dominated estuary that has high sediment trapping efficiency and naturally low turbidity (Gillanders 2007).

Sampling design and data collection

Preliminary investigations revealed that subtidal rocky reef habitat fringes ~40 km (25%) of the Lake Macquarie shoreline, and was also found in the inlet channel and coastal waters outside the inlet. Twenty sites with characteristics as similar as possible were chosen from major rocky reef areas suitable for sampling: one in coastal waters, two in the inlet channel and 17 in the central basin of Lake Macquarie (Figure 1). Each site was allocated to one of four zones: coastal, inlet channel, central estuary, and inner estuary. Within each site, four baited remote underwater video stations (BRUVS) were deployed from a motorised boat onto, or adjacent to, rocky reef in waters 1.5 to 6 m depth with replicate BRUVS separated by ~150 m. Depths of <2 m were sampled only at sites where rocky reef terminated in shallow water. BRUVS were the chosen method of sampling as the substratum complexity and depth associated with rocky reefs in this study complicated the use of traditional sampling methods used in estuaries such as trawls, seines and fyke nets (Rozas & Minello 1997, Franco et al. 2012). BRUVS are easily deployed for repeated surveys and, as they use bait to attract fishes to a feeding station, they are useful in mitigating the constraints of conducting surveys of fish assemblages in waters with reduced visibility (Gladstone et al. 2012).

The rocky reefs sampled generally consisted of mixed algal assemblages (particularly turfing and foliose brown alga) and, where sediment had accumulated near rocks, patches of the seagrass Zostera and associated epiphytic algae (AWACS 1995, Creese et al. 2009). Most sites were natural rocky reefs but artificial reefs occurred within the inlet channel and within the central basin of Lake Macquarie at site 9. Rocky reef in the inlet channel consisted of training walls composed of various sized boulders aggregated at a steep gradient to sandy sediment at a depth of ~6 m (AWACS 1995). The artificial reef at site 9 consisted of 180 reef modules (Mini-Bay Reef Balls®) arranged on a 5 m depth contour in six clusters, each located approximately 180 m apart (Lowry et al. 2010).

The BRUVS recording system consisted of a standard-definition digital Sony handycam fitted with a wide-angle lens converter that recorded video footage onto mini-DV tapes. Crushed pilchards, *Sardinops neopilchardus*, were placed within plastic mesh and set on bait poles ~60 cm in front of the camera's viewing port. BRUVS were deployed for 40 min to allow sufficient time for fish to become accustomed to the system and to be attracted to the bait. At each site, data collection occurred on two sampling occasions, hereafter termed 'sampling times'. The first occurred from October to December 2008, approximately 2-3 months prior to warmest temperatures in Lake Macquarie (Spencer 1959, Hannan & Williams 1998), and the second occurred in April and May 2009 soon after warmest temperatures are experienced. In total, 160 surveys were conducted (i.e. twenty sites, each with four BRUVS, conducted over two sampling times).

Each 40 min segment of continuous video footage was saved onto a computer for storage and reviewing. Video footage was reviewed to identify fish species and the relative abundance (MaxN) of each species. MaxN was defined as the maximum number of individuals of each species in the field of view at any one time during the 40 minutes of recorded footage (Malcolm et al. 2007, McKinley et al. 2011, Lowry et al. 2012), and total MaxN was the sum of MaxN for each species (Gladstone et al. 2012). Fish species were identified using Kuiter (1993, 1996) and Hutchins & Swainston (1996). All data collected from the video footage was verified by a second observer.

Data analyses

The null hypotheses that total MaxN and species richness of fishes did not differ among zones, sites (within zones) and between sampling times were each tested with a three-factor permutational multivariate analysis of variance (PERMANOVA) using PERMANOVA+ for PRIMER (Anderson et al. 2008) in PRIMERv6 (Clarke & Gorley 2006). Zone with four levels and sampling time with two levels were both considered fixed factors, whilst site (nested in zone) was considered a random factor. Assumptions of homogeneity of variance were tested using Cochran's C test and, when necessary, data were transformed to eliminate heterogeneity (Underwood 1981) before three-factor PERMANOVA tests based on Euclidean distances were conducted (Anderson 2001). When heterogeneity could not be eliminated a more conservative P-value of <0.01 was used to establish significance (Underwood 1981). Significant main effects and interactions were examined using *post-hoc* Student-Newman-Keuls (SNK) multiple comparisons of means tests (Underwood 1981). Monte Carlo P-values were used when there were not enough possible permutations to get a reasonable test (Anderson et al. 2008).

The null hypothesis that fish assemblages did not differ among zones, sites (within zones) and between sampling times was tested by PERMANOVA with the same design as the univariate tests but instead based on a Bray-Curtis similarity matrix and $\ln(x+1)$ transformed data to reduce the influence of numerically abundant species and increase the importance of rare species. Differences among assemblages at each site in both sampling times were visualised using non-metric multidimensional scaling (nMDS) ordination plots in PRIMERv6 and the similarity percentages (SIMPER) routine was used to determine the species that typified the fish assemblages of each zone and those used to distinguish between zones (Clarke & Gorley 2006). The correlation between the multivariate patterns in fish assemblages and the environmental variables of distance from coastal waters were determined using the BIO-ENV procedure in PRIMERv6 (Clarke & Gorley 2006).

Results

Species richness and abundances

In total, 14,492 individuals representing 80 species and 43 families were sampled (Table 1). A total of 30 species were found in coastal waters, 50 species in the inlet channel, 44 species in the central estuary, and 22 species in the inner estuary. The number of species sampled exclusively in coastal waters, the inlet channel, central estuary and inner estuary was 6, 14, 11 and 5, respectively. Six species could not be accurately identified to determine the family to which they belonged. The most species-rich families were Labridae (8 species), Carangidae (5 species), Mullidae and Monocanthidae (4 species each), and Muraenidae, Sparidae and Blennidae (3 species each). The most abundant species were *Ambassis jacksoniensis* (42.2% of all individuals), *Pelates sexlineatus* (19.6%), *Acanthopagrus australis* (9.3%), *Rhabdosargus sarba* (9.0%), *Atypichthys strigatus* (4.6%) and *Scorpis lineolata* (3.2%).

Differences occurred in the mean number of species among zones and between sampling times (Table 2), with higher species richness in coastal waters and the inlet channel than the central estuary and inner estuary, and an increase in species richness from October-December 2008 to April-May 2009 (all $P<0.05$, Figure 2). A significant Si(Zo)xTi interaction also occurred with *post hoc* analyses revealing differences often occurred in the number of species found in sites within the central estuary and also in the inner estuary in both sampling times, but not in the inlet channel.

The mean total MaxN in each zone ranged from 45 to 138 individuals with the highest abundances occurring in the inner estuary due to the occurrence of large schools of juvenile *Ambassis jacksoniensis* that often numbered >500 individuals (Figure 3). This species represented nearly half of the total abundance of all fishes which masked other trends in total MaxN. Excluding this species, no significant differences occurred in the MaxN among zones or between sampling times (both $P>0.01$, Table 2). Differences did occur among some sites within the central estuary and also in the inner estuary, but not in the inlet channel.

Species assemblages

The nMDS ordination for both sampling times showed points representing coastal waters and those in the inlet channel on the left of the plot separated from the points representing sites in the central and inner estuary on the right side of the plot (Figure 4). In both sampling times, the points on the plot progressed from left to right with increasing distance from coastal waters (Figure 5), with BIO-ENV analyses indicating a strong correlation between fish assemblages and distance in both October-December 2008 ($\rho=0.68$) and April-May 2009 ($\rho=0.72$).

PERMANOVA found significant ZoxTi and Si(Zo)xTi interactions in the analysis of species assemblages (Table 2). *Post hoc* analysis revealed differences occurred in the assemblages among all zones in both sampling times (all *P<0.01*), except coastal waters and the inlet channel. Sites within a zone were also found to often differ from one another in both sampling times (*P<0.05*). *Post hoc* analysis also revealed that assemblages within the inlet channel and central estuary differed between sampling times but the nMDS plot revealed that sites within each of these zones typically remained within the same cluster in both sampling times (Figure 4).

Contributing to differences between zones was the presence of species in coastal waters and in the inlet channel that were not found in the central and inner estuary (e.g. *Brachaelurus waddi*, *Parma microlepis*, *Chironemus marmoratus*, *Crinodus lophodon*, *Cheilodactylus fuscus* and several labrids) and the absence of several species in coastal waters and the inlet channel (e.g. *Ambassis jacksoniensis*, *Pomatomus saltatrix* and *Mugil cephalus*) (Table 1). Species found to have a particularly high MaxN at the coastal waters site compared to elsewhere included *Brachaelurus waddi*, *Gymnothorax prasinus*, *Dinolestes lewini*, *Pempheris compressa*, *Schuettea scalaripinnis*, *Atypichthys strigatus*, *Notolabrus gymnogenis* and *Opthalmolepis lineolatus* (Table 1 & 3). Species found to have a particularly high MaxN in the inlet channel compared to elsewhere include *Scorpis lineolata*, *Girella tricuspidata*, *Pseudolabrus guentheri*, *Acanthurus dussumieri*, mullids, cheilodactylids and tetraodontids (Table 1 & 3).

Contributing to overall differences between the central and inner estuary clusters was a relatively higher MaxN in the central estuary of *Pelates sexlineatus, Acanthopagrus australis*, *Chrysophrys auratus, Girella tricuspidata* and *Mugil cephalus*, and higher MaxN in the inner estuary of *Ambassis jacksoniensis, Rhabdosargus sarba* and *Monocanthus chinensis* (Table 1 & 3). In the inner estuary there was also an absence of twenty-five species which were present in the central estuary, including *Apogon limenus*, *Pseudocaranx dentex*, *Parupeneus signatus*, *Scorpis lineolata*, *Atypichthys strigatus* and *Pseudolabrus guentheri* (Table 1).

Discussion

Rocky reef as a habitat for estuarine fish assemblages

Use of BRUVS was found to be a very effective method for surveying rocky reef fish assemblages in this study with many of these fishes, including species within the families Muraenidae, Apogonidae, Mullidae, Chaetodontidae, Pomacentridae, Cheilodactylidae and Labridae, having not previously been reported in studies of fish fauna in other habitats in Lake Macquarie (Thomson 1959a & b, Hannan & Williams 1998, Steffe et al. 2005). The

overall success of BRUVS was due to the relatively good water clarity in coastal waters, the inlet channel and at the majority of sites within the estuary basin. Similarly, the success of BRUVS for monitoring fish assemblages in coastal waters (Willis & Babcock 2000, Malcolm et al. 2007, Stobart et al. 2007), entrances to drowned river valley estuaries (McKinley et al. 2011) and temporarily open/closed coastal lagoons (Becker et al. 2010) is dependent on the relatively low turbidity experienced in these environments. However, the use of BRUVS in estuaries experiencing high turbidity is likely to be limited. Even in the present study, all sampling occurred when surface winds were light as, being a shallow water body, the sediments of Lake Macquarie quickly mobilise with wind-generated surface waves and currents (Roy et al. 2001, Short & Woodroffe 2009), increasing turbidity and rendering the use of BRUVS impractical.

Seagrass, saltmarsh and mangrove habitats are recognised worldwide as important estuarine habitats for various taxa including fishes (Beck et al. 2001). However, the present study has revealed that estuarine rocky reef habitat also supports diverse fish assemblages which are unlike those associated with other estuarine habitats. For example, Hannan & Williams (1998) found fish assemblages associated with seagrass habitat in Lake Macquarie consisted of high abundances of clupeids, engraulidids, hemiramphids, atherinids, and the apogonid *Siphamia cephalotes*, which were not represented on rocky reefs in the present study, and sillaginids, blennids, gobiids, monocanthids and tetraodontids, which were represented in the present study but only by few individuals. Differences in the methods used in these studies do, however, make assemblage comparisons between these two habitats difficult. In other locations, studies have compared rocky reef with other nearby habitats (e.g. seagrass beds, bare sands) using a common sampling method and found these habitats to contain distinct fish assemblages (Garcis-Rubies & Macpherson 1995, Jenkins & Wheatley 1998, Guidetti 2000). Future studies are needed to test whether estuarine rocky reef habitat supports fish assemblages different to those in other estuarine habitats, and the use of BRUVS as a standard method for making such comparisons is recommended to counter logistical constraints associated with fish surveys in diverse habitats (Cappo et al. 2007, Murphy & Jenkins 2010).

It was evident in the present study that rocky reef fish assemblages consisted of predominantly post-settlement juveniles and subadults, supporting the conclusion of other studies that estuarine habitats are particularly important for juvenile fishes (Beck et al. 2001). Hannan & Williams (1998) noted the absence of larger juvenile fishes from seagrass habitat in Lake Macquarie and suggested a possible ontogenetic movement of individuals to other habitats, including rocky reefs. Although fish lengths were not measured in the present study, it was evident that the majority of individuals of the most abundant species, for example, *Pelates sexlineatus*, *Acanthopagrus australis*, and *Rhabdosargus sarba*, were large juveniles. The presence of these predominantly large juveniles and subadults suggests that many fishes may use estuarine rocky reefs as a transitional habitat between nursery grounds in seagrass

habitat and adult habitat in coastal waters or estuarine soft bottoms. To test this, studies incorporating the length measurements of individuals in each habitat are needed using, for example, stereo BRUVS (Cappo et al. 2007, Langlois et al. 2010, Watson et al. 2010).

Spatial variation in fish assemblages

The present study identified four major 'zones' – coastal waters, inlet channel, central estuary, and the inner estuary – that represented a transition in fish assemblages with increasing distance from coastal waters. Although only 30 species were represented in the coastal waters zone compared with 50 in the inlet channel, 44 in the central estuary and 22 in the inner estuary, the different sampling intensity used in this study (i.e. one coastal waters site compared with two in the inlet channel, ten in the central estuary and seven in the inner estuary) would suggest that an overall higher species density occurs on rocky reefs in coastal waters and the inlet channel compared with those within the central and inner estuary (hereafter collectively termed the central basin). Whilst a more extensive survey in coastal waters would give a better representation of fish assemblages on coastal rocky reefs in the region there were significant constraints on available sites. The nearest rocky reefs to the north of the inlet channel are located in excess of 9.5 km away. As the greatest variation in assemblages of fishes on coastal rocky reefs occurs at scales of kilometres (Curley et al. 2002), it is likely that these assemblages would differ from those nearby the inlet channel. Nearby rocky reefs were located to the south but, unlike the coastal site selected in this study which is protected by an outer island and reef, these southern reefs have high wave exposure and are likely to be represented by distinct fish assemblages (Bellwood et al. 2002, Fulton and Bellwood 2004). Past studies that have been conducted on coastal reefs in the region (e.g. Curley et al. 2002, Gladstone 2007, Malcolm et al. 2007, Morton & Gladstone 2011) revealed fish assemblages were represented by many of the species found at the coastal site in this study and that these assemblages were similarly distinct from those found in the inlet channel and the central basin of Lake Macquarie.

The inlet channel provided a transition zone between assemblages found in coastal waters and those within the central basin. In total, 23 of the 30 species (i.e. 77% of species) found at the coastal site and 26 of the 50 species (52%) found in the central basin were represented in the inlet channel. In contrast, only 14 of 50 species (28%) in the central basin were found in coastal waters. Overall, the assemblages within the inlet channel resembled those at the coastal site more than they resembled those in the central basin, however, transitions occurred within the inlet channel along its length. For example, of the 30 species recorded in coastal waters, 22 were sampled within the inlet channel at its coastal inlet but only 14 near the entrance to the central basin. This suggests the restricted entrance as well as the 5.5 km length of the inlet channel provides a significant impediment to the dispersal of many coastal species into the central basin of wave-dominated, barrier estuaries.

Whether physical or chemical barriers, or a combination of both, limit dispersal along the length of the inlet channel is not yet known so studies focusing on this question are needed. Of importance is also the determination of whether the transition in fish assemblages within the inlet channel reflects limitations to larval supply or impediments to the settlement of fishes. For example, coastal-spawned larvae are known to be entrained into the inlet channel of Lake Macquarie (Trnski 2001), yet they may not meet features in the environment that are suitable for successful settlement (Carr 1994, Tupper & Boutilier 1997). As salinity levels within the inlet channel of this study are similar to those of the coast (Hannan & Williams 1998), it is probable that physical barriers, such as fast tidal currents and the abrasive action of sand transported by the tides (AWACS 1995), or lack of suitable natural rocky habitat, provide a significant impediment to the settlement of many coastal rocky reef species into the inlet channel of wave dominated, barrier estuaries.

Fish assemblages associated with rocky reefs in the central basin were distinct from those in the inlet channel and coastal waters. The dispersal of many fishes to rocky reef habitat in the central basin is likely to be restricted by reef isolation and low habitat connectivity (Ault & Johnson 1998, McClanahan & Mangi 2000, Fernández et al. 2008) as distances between rocky reef habitat in the inlet channel and the nearest reefs in the central basin are in excess of 3 km. Tidal flushing of the central basin is limited to 1% of its volume (Spencer 1959) so coastal larval entrained in the inlet channel must rely on wind-driven surface currents for dispersal to favourable habitat within the central basin or actively swim to favourable settlement sites (Montgomery et al. 2001, Trnski 2002). The entrance to the central basin at the western end of the inlet channel also consists of an extensive area of sand shoals (Witt et al. 1996), with these 'sandy back barriers' being a common feature of barrier estuaries (Short & Woodroffe 2009). Whilst post-settlement juveniles, subadults and adults of many species are capable of crossing bare sand (Ambrose & Anderson 1990, Langlois et al. 2005), many species are reluctant to do so (Coll et al. 1998, Chapman & Kramer 2000, Fernández et al. 2008). For the latter species, sandy shoals associated with the inlet of wave-dominated barrier estuaries are likely to be a significant barrier to prevent many coastal rocky reef species from entering the central basin.

Despite attempts to conduct surveys at times with likely low turbidity, visibility estimates from recorded footage were higher in coastal waters and the inlet channel compared with sites in the central basin. This reduced visibility did not result in a reduction in the abundances in the central basin compared with zones with higher visibility as mean total MaxN was similar among zones and, when *Ambassis jacksoniensis* was included, highest MaxN occurred at sites in the inner estuary where estimated visibility was lowest. It is possible that some of the many species present in high abundances in coastal waters and the inlet channel were observed infrequently or absent in the central basin due to reduced visibility which could lead to apparent differences in assemblages. These species, including *Gymnothorax prasinus*, *Atypichthys strigatus*, several labrids and *Scorpis lineolata*, were

typically attracted to the bait and, if present, would easily have been observed in the visibility experienced in the central and inner estuary. Many of these species were notably absent from the central basin despite a comprehensive sampling effort involving seventeen sites, each with four BRUVS replicates, sampled on two occasions. Also, emphasising the differences in fish assemblages was the low abundances or absence of many species in coastal waters and the inlet channel, including *Pelates sexlineatus*, *Ambassis jacksoniensis* and *Mugil cephalus*, that were abundant in the central basin. These species were highly likely to be observed in coastal waters and the inlet channel, which experience high visibility, if they were in similarly high abundances to those in the central basin.

Within the central basin there was a distinction between fish assemblages in the central estuary and those in the inner estuary. Assemblages in the central estuary consisted of species with abundances typically in transition between zones and defined the maximum extent of the distribution of many coastal species into the central basin. In many estuaries, salinity is the most important environmental variable in structuring fish assemblages (Martino & Able 2003, Selleslagh & Amara 2008, Selleslagh et al. 2009, de Moura et al. 2012). For example, Barletta et al. (2005) recognised distinct fish assemblages in the upper, middle and lower sections of a tropical estuary in Brazil, and Jaureguizar et al. (2003) identified three fish assemblages associated with the inner, central and external areas of a Uruguayan estuary. In the present study, it is unlikely changes in salinity restrict coastal species from the inner estuary as the two main freshwater inputs into Lake Macquarie contribute less than 4% to its volume (Baas Becking et al. 1959), making salinities within the central basin, which are typically uniform and range between 32 and 36 g/L (Morton et al. 1996; Hannan & Williams 1998), similar to the 35 g/L found in adjacent coastal waters (Kaiser et al. 2005). The boundary between the central estuary and the inner estuary in the present study instead reflects the furthest extent of extensive rocky reef habitat adjacent to relatively deep water (i.e. >5 m depth). In the inner estuary the reef typically fringes the shore and ends abruptly at depths of often less that 1.5 m. Many of the species in the central estuary may therefore be excluded from the inner estuary due to insufficient areas of appropriate rocky reef habitat. The central basin of barrier estuaries are constantly infilling with fine sediment delivered from incoming streams (Turner et al. 2004, Short & Woodroffe 2009) and in the present study much of this was found to overlay rocky reefs in the inner estuary reducing habitat complexity and the likely availability of refuge, nocturnal retreats and prey resources.

Limited dispersal of larvae into the central basin is also likely to be a major contributor to differences in fish assemblages between the central and inner estuary as ocean-spawned larvae in surface waters are largely confined to what has been identified as the central Lake Macquarie zone in the present study (Miskiewicz 1987). Due to the lack of salinity, temperature or turbidity gradients in Lake Macquarie, which are known to influence fish distributions in other locations (Cyprus & Blaber 1992, Marshall & Elliott 1998, Akin et al. 2005, Barletta et al. 2005), Hannan & Williams (1998) concluded that distance from the

ocean coupled with weak internal water circulation limits the dispersal of ocean-spawned larvae and recruitment of juveniles into seagrass habitat away from the central regions of Lake Macquarie where ocean-spawned larvae are largely confined. Similarly, in the Pittwater estuary located approximately 60 km south of Lake Macquarie, Jelbart et al. (2007b) concluded that changes in fish assemblages with increasing distance from the ocean were in response to impediments to the transport of ocean-spawned larvae as this estuary similarly does not experience a strong salinity gradient.

Temporal differences in fish assemblages

Although the present study was conducted over two sampling times (October-December 08 and April-May 09), and some sites showed large changes in their overall assemblages, overall zones were distinct and in most instances each site remained similar to others within the same zone for both sampling times. Superficially, results suggest that the boundary between the central and inner estuary is fixed, but these sampling events occurred over a period of only ~6 months. Within this time, no high rainfall events occurred to significantly alter the salinity of Lake Macquarie which could cause changes in the transition of fish assemblages similar to those that occur in estuaries with pronounced salinity gradients (West & King 1996, Martino & Able 2003, Jelbart et al. 2007a). Sampling also occurred outside the coolest and warmest water temperatures which are experienced in June-August and January-March, respectively (Spencer 1959, Hannan & Williams 1998). It could be suggested that a temperature gradient may exist in these months which restricts the distribution of species and alters the location of zones proposed in this study (Kaiser et al. 2005). However, despite the annual temperature in Lake Macquarie ranging from ~13-29°C, the temperature throughout Lake Macquarie is generally uniform at any point in time (Spencer 1959, Hannan & Williams 1998) and so temperature differences are unlikely to be a determinant in structuring fish assemblages in Lake Macquarie.

Conclusion

This study aimed to describe spatial patterns in the fish assemblages associated with rocky reef habitat throughout an estuary with a restricted inlet. Whilst estuarine rocky reef habitat has been largely neglected in past studies, this study highlights the need to recognise the importance of this habitat for estuarine fishes and the need for future studies to determine their potential as a transitional habitat for juvenile and subadult fishes. This study predicted that the inlet configuration would restrict the dispersal of coastal fishes into the estuary resulting in a change in fish assemblages from coastal waters to the inner estuary. This was indeed the case with four major zones representing relatively distinct rocky reef fish assemblages – coastal waters, inlet channel, central estuary, and inner estuary. These zones exist in the absence of a salinity or temperature gradient therefore suggesting that physical barriers to larval supply and insufficient areas of quality habitat have limited the dispersal and settlement of coastal fishes in this study. Future studies incorporating detailed site metrics

and larval distribution maps are recommended to explore their potential importance in driving changes in rocky reef fish assemblages within wave-dominated, barrier estuaries. The spatial patterns in the fish assemblages were found to be temporally consistent on two sampling times separated by 6 months, which was investigated as the second aim of this study. This study highlights a) the need for recognising estuarine rocky reef as a habitat for diverse fish assemblages, b) that characteristics of the estuary inlet of wave-dominated barrier estuaries is restrictive to the dispersal of many coastal fishes, c) the effectiveness of BRUVS for sampling fish assemblages in estuaries with relatively low turbidity, and d) there is a need to recognise zones of distinct estuarine fish assemblages to ensure each is represented in conservation planning.

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Table 1: Fish species showing the mean number of individuals recorded at each site in coastal waters (1 site), inlet channel (2 sites), central estuary (10 sites), and the inner estuary (7 sites). Total counts for each species is shown on the right and mean numbers of greater than one have been rounded to whole numbers. Distances from coastal waters are shown in brackets.

Family	Species	Site 1 (0 km) Coastal waters	Sites 2,3 (1-4 km) Inlet channel	Sites 4-13 (7-12 km) Central estuary	Sites 14-20 (13-18 km) Inner estuary	Total fish
HETERODONTIDAE	*Heterodontus galeatus*	1				**1**
BRACHAELURIDAE	*Brachaelurus waddi*	6	<1			**7**
UROLOPHIDAE	*Trygonoptera* sp.			<0.5	<0.5	**4**
DASYATIDIDAE	*Dasyatis* sp.			<0.5	<1	**6**
MYLIOBATIDIDAE	*Myliobatis australis*		2			**3**
ANGUILLIDAE	*Anguilla reinhardtii*				<0.5	**1**
MURAENIDAE	*Gymnothorax prasinus*	25	12	1	<0.5	**63**
	Gymnothorax cribroris		<1	<0.5		**2**
	Enchelycore ramosa		<1			**1**
MORIDAE	*Lotella rhacina*	2				**2**
BELONIDAE	*Tylosurus gavialoides*			<0.5	<0.5	**4**
PLATYCEPHALIDAE	*Platycephalus fuscus*		<1			**1**
SCORPAENIDAE	*Centropogon australis*		1	<0.5		**3**
SERRANIDAE	*Acanthistius ocellatus*	6				**6**
TERAPONTIDAE	*Pelates sexlineatus*		1	216	96	**2839**
CHANDIDAE	*Ambassis jacksoniensis*			59	791	**6122**
APOGONIDAE	*Apogon fasciatus*			<1		**9**
	Apogon limenus				<0.5	**2**
DINOLESTIDAE	*Dinolestes lewini*	12	<1	<0.5		**14**
SILLAGINIDAE	*Sillaginodes/Sillago* sp.				<0.5	**3**
POMATOMIDAE	*Pomatomus saltatrix*			3	4	**56**
CARANGIDAE	*Seriola dumerili*			<0.5		**1**
	Seriola rivoliana			<0.5		**3**
	Seriola lalandi	3		<0.5		**5**
	Pseudocaranx dentex	6	3	2		**30**
	Trachurus novaezelandiae			<1		**6**
SPARIDAE	*Acanthopagrus australis*	15	22	96	47	**1347**
	Rhabdosargus sarba	2	30	63	88	**1307**
	Chrysophrys auratus		6	3	<0.5	**48**
GERREIDAE	*Gerres subfasciatus*		3	11	9	**179**
LETHRINIDAE	*Lethrinus nebulosus*		1			**2**
MULLIDAE	*Parupeneus signatus*	5	39	1		**95**
	Parupeneus barberinoides		1			**2**
	Upeneichthys vlamingii		2			**3**
	Upeneus tragula			<0.5		**1**
PEMPHERIDIDAE	*Pempheris compressa*	40				**40**
MONODACTYLIDAE	*Schuettea scalaripinnis*	40				**40**
	Monodactylus argenteus			1	1	**22**
SCORPIDIDAE	*Scorpis lineolata*	72	171	5		**465**
GIRELLIDAE	*Girella tricuspidata*	17	89	6	<1	**254**
MICROCANTHIDAE	*Atypichthys strigatus*	356	155	<1		**673**
	Microcanthus strigatus	2	56	6	4	**201**

Family	Species					
CHAETODONTIDAE	*Chaetodon auriga*		2	<0.5		**5**
	Chelmonops truncatus			<0.5		**1**
POMACENTRIDAE	*Parma microlepis*	8	<1			**9**
	Abudefduf vaigiensis			<0.5		**4**
CHIRONEMIDAE	*Chironemus marmoratus*	9	<1			**10**
APLODACTYLIDAE	*Crinodus lophodon*	1	<1			**2**
CHEILODACTYLIDAE	*Cheilodactylus vestitus*		3	<0.5		**7**
	Cheilodactylus fuscus	3	4			**11**
MUGILIDAE	*Mugil cephalus*			17	10	**241**
SPHYRAENIDAE	*Sphyraena obtusata*		<1	<0.5		**5**
LABRIDAE	*Pseudolabrus guentheri*	4	14	1		**44**
	Notolabrus gymnogenis	17	3			**22**
	Eupetrichthys angustipes	3	1			**5**
	Coris picta		4			**7**
	Achoerodus viridis	2	<1			**3**
	Pictilabrus laticlavius	9	4			**16**
	Opthalmolepis lineolatus	29	2			**32**
	Thalassoma lunare		1	<0.5		**3**
ODACIDAE	*Odax cyanomelas*	4				**4**
	Odax acroptilus		<1			**1**
BLENNIIDAE	*Plagiotremus tapeinosoma*		1			**2**
	Unidentified sp.			<0.5		**1**
	Unidentified sp.				<0.5	**1**
GOBIIDAE	Unidentified sp.		<1		<0.5	**2**
ACANTHURIDAE	*Acanthurus dussumieri*	1	6	<1		**17**
MONOCANTHIDAE	*Meuschenia freycineti*		<1			**1**
	Monocanthus chinensis		<1	<1	2	**24**
	Meuschenia trachylepis	4	8	<1		**27**
	Brachaluteres jacksonianus		2			**3**
TETRAODONTIDAE	*Torquigener pleurogramma*		20	<0.5		**41**
	Torquigener squamicauda		<1			**1**
DIODONTIDAE	*Dicotylichthys punctulatus*		4	<0.5		**8**
Unidentified taxa	Unidentified 1				<0.5	**1**
	Unidentified 2			<0.5		**4**
	Unidentified 3		22.5			**45**
	Unidentified 4			<0.5		**1**
	Unidentified 5		<1			**1**
	Unidentified 6			<0.5		**1**
	Total species	**30**	**50**	**44**	**22**	**80**

Table 2: Summary of PERMANOVA results for mean species richness, mean total MaxN (excluding *Ambassis jacksoniensis*) and species assemblages. [a]data is square-root transformed, [b]data is ln(x+1) transformed. Significant *P*-values are in bold.

Source of variation	df	Species richness[a] (Cochran's C = 0.0972, $P>0.05$)			Total MaxN[b] (Cochran's C = 0.1338, $P<0.05$)			Species assemblage[b]		
		MS	Pseudo-F	P	MS	Pseudo-F	P	MS	Pseudo-F	P
Zone	3	13.11	75.78	**0.001**	10.30	3.50	0.046	38627.0	8.53	**0.001**
Site (Zo)	16	0.68	3.94	**0.001**	2.95	6.94	**0.001**	4530.6	3.90	**0.012**
Time	1	1.49	8.63	**0.047**	4.74	5.69	0.021	6699.1	3.40	**0.001**
ZoxTi	3	0.60	3.44	0.189	0.47	0.56	0.655	4219.4	2.14	**0.030**
Si(Zo)xTi	16	0.35	2.03	**0.011**	0.83	1.96	0.024	1971.5	1.70	**0.001**
Res.	120	0.17			0.42			1162.8		
Total	159									

Table 3: Species contributing over 10% to typifying (shaded) and over 6% to distinguishing (non-shaded) between the fish assemblages of each zone as identified using SIMPER. Asterisks denote a higher abundance in the zone at the top of the column. Species are listed in descending order of contribution.

Zone	Coastal waters	Inlet channel	Central estuary	Inner estuary
Coastal waters	*Atypichthys strigatus* *Gymnothorax prasinus* *Opthalmolepis lineolatus* *Notolabrus gymnogenis* (Av. similarity = 48.12)			
Inlet channel	*Atypichthys strigatus** *Scorpis lineolata* *Girella tricuspidata* (Av. dissimilarity = 71.80)	*Scorpis lineolata* *Girella tricuspidata* *Pseudolabrus guentheri* (Av. similarity = 36.63)		
Central estuary	*Atypichthys strigatus** *Pelates sexlineatus* *Acanthopagrus australis* *Rhabdosargus sarba* (Av. dissimilarity = 91.94)	*Pelates sexlineatus* *Scorpis lineolata** *Atypichthys strigatus** *Acanthopagrus australis* *Girella tricuspidata** *Rhabdosargus sarba* (Av. dissimilarity = 83.53)	*Acanthopagrus australis* *Pelates sexlineatus* *Rhabdosargus sarba* (Av. similarity = 47.75)	
Inner estuary	*Atypichthys strigatus** *Ambassis jacksoniensis* *Rhabdosargus sarba* *Pelates sexlineatus* (Av. dissimilarity = 95.86)	*Ambassis jacksoniensis* *Scorpis lineolata** *Atypichthys strigatus** *Rhabdosargus sarba* *Girella tricuspidata** *Pelates sexlineatus* (Av. dissimilarity = 89.64)	*Ambassis jacksoniensis* *Pelates sexlineatus** *Acanthopagrus australis** *Rhabdosargus sarba* (Av. dissimilarity = 60.60)	*Rhabdosargus sarba* *Ambassis jacksoniensis* *Acanthopagrus australis* *Pelates sexlineatus* (Av. similarity = 43.22)
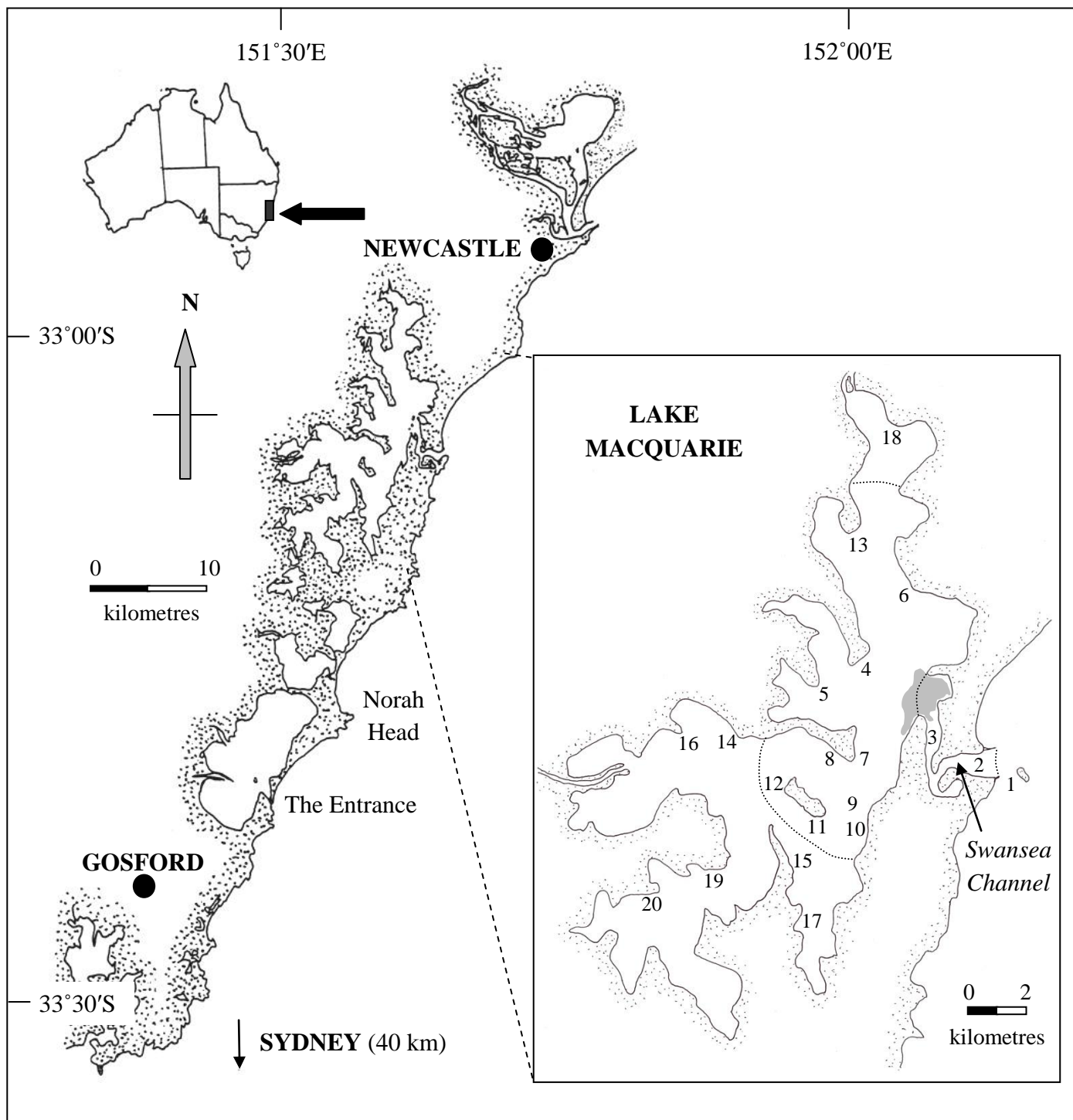
Fig. 1 The twenty sites used for sampling rocky reef fish assemblages in the Lake Macquarie estuary with site number increasing with greater distance from coastal waters. Dotted lines separate the four zones identified in this study (coastal waters = site 1, inlet channel = sites 2-3, central estuary = sites 4-13, inner estuary = sites 14-20). Light grey shading represents an area with extensive sand shoaling.
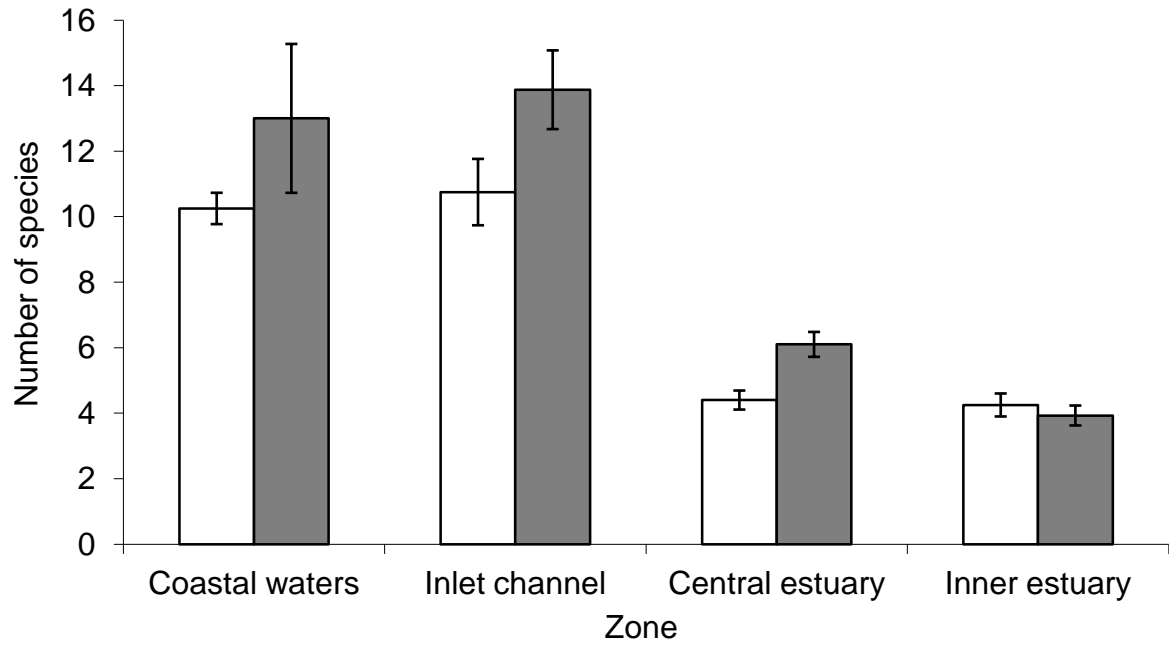
Fig. 2 Mean number of species in each zone during October-December 2008 (unshaded) and April-May 2009 (shaded). Standard error bars are shown where *n* is the number of sites within the zone multiplied by the four BRUVS deployments per site.

Ambassis jacksoniensis included

Ambassis jacksoniensis excluded
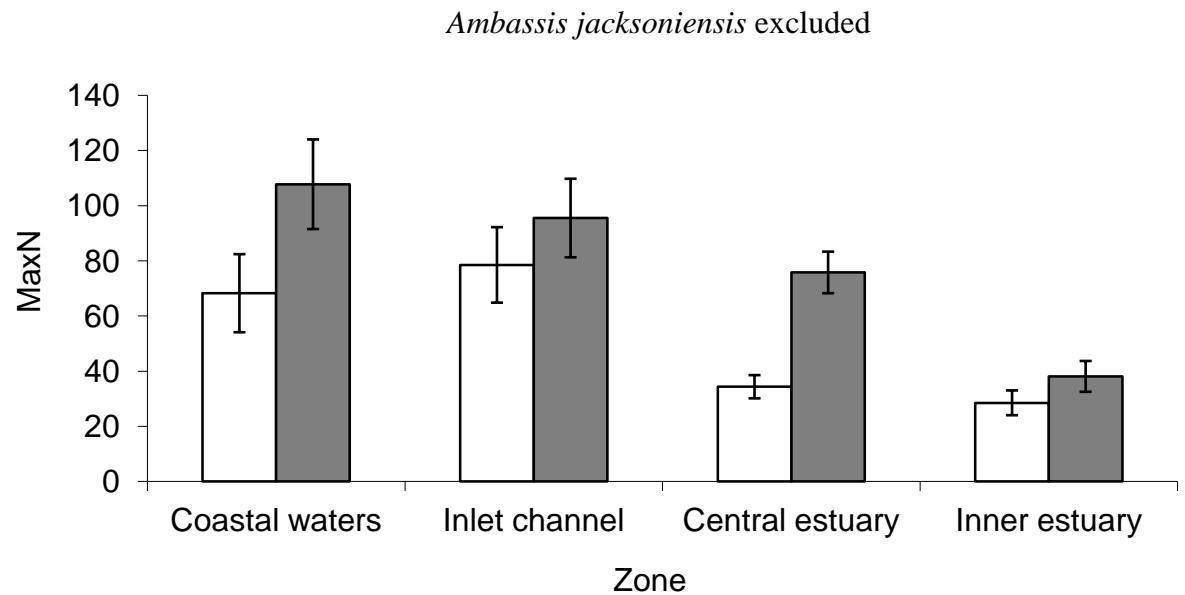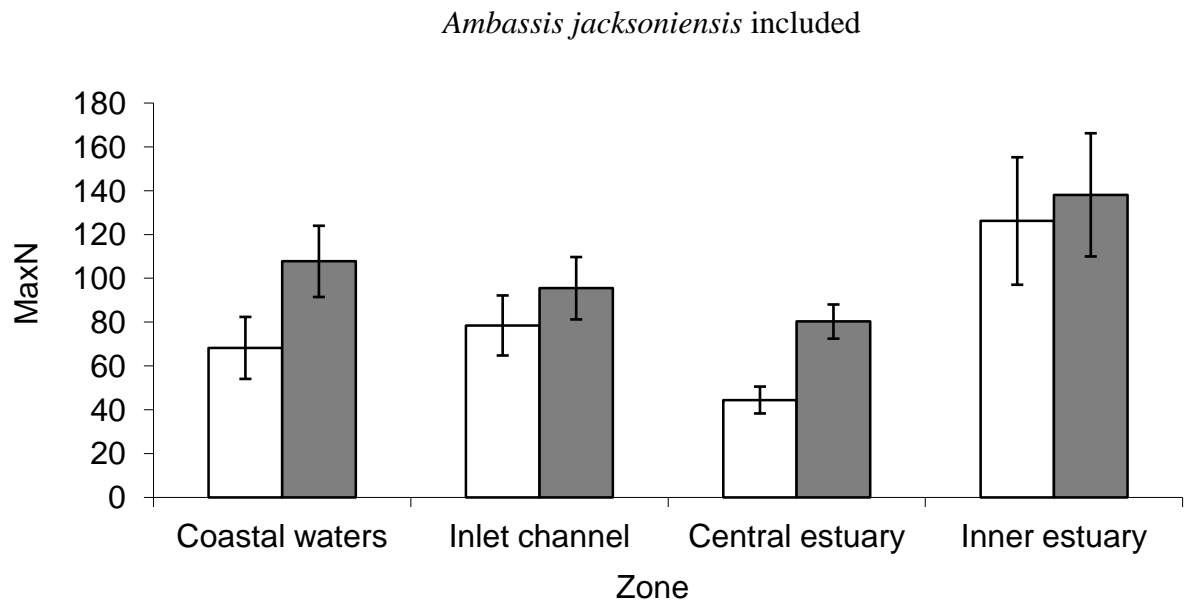
Fig. 3 Mean total MaxN in each zone during October-December 2008 (unshaded) and April-May 2009 (shaded). Standard error bars are shown where *n* is the number of sites within the zone multiplied by the four BRUVS deployments per site.
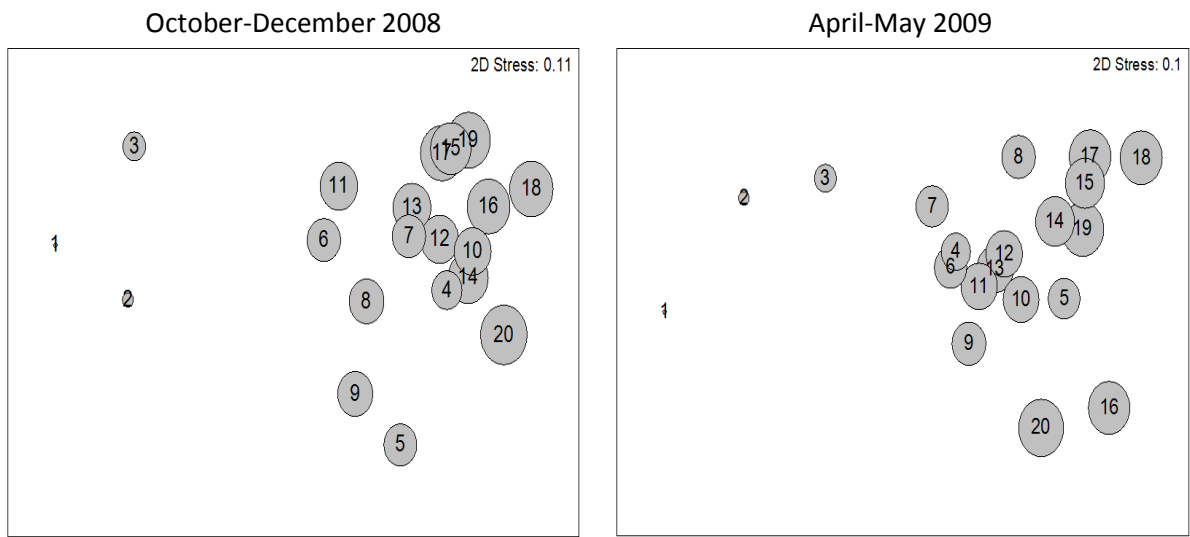
Fig. 4
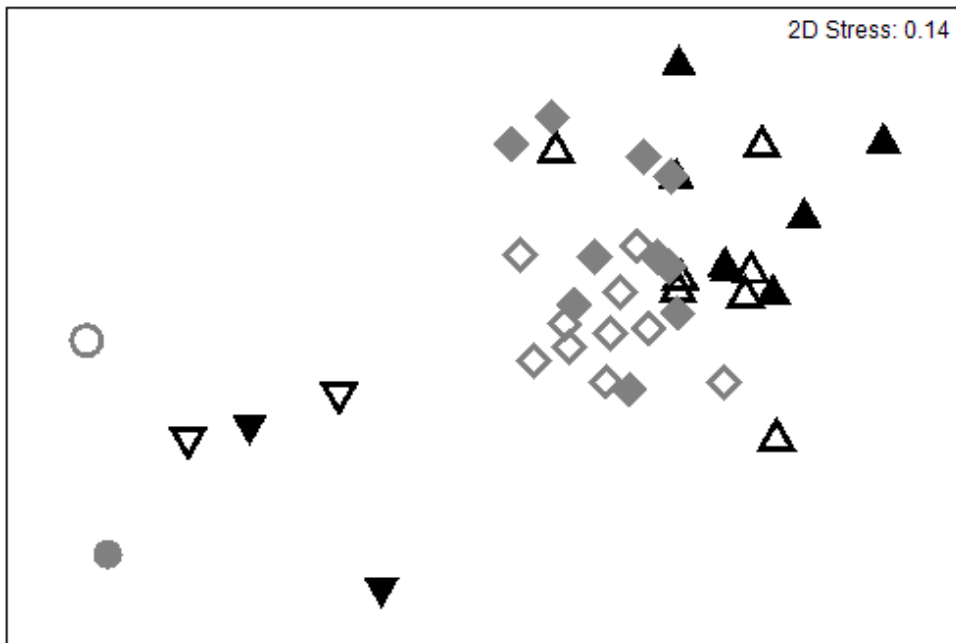
Fig. 4 nMDS ordination comparing fish assemblages within coastal waters (circles), the inlet channel (downward triangles), central estuary (diamonds) and inner estuary (upward triangle) for the October-December 2008 (unshaded) and April-May 2009 (shaded) sampling times. Each point represents the average of four BRUVS replicates.

Fig. 5

Fig. 5 nMDS ordinations comparing fish assemblages and distance from coastal waters for the two sampling times. Site numbers are shown with each point representing the average of four BRUVS replicates. Bubble size represents relative distance from coastal waters ranging from 0 to 18 km.