Predator driven diel variation in abundance and behaviour of fish in deep and shallow habitats of an estuary

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ABSTRACT

Our traditional understanding of the behaviour of large predatory fish and their smaller prey in estuarine ecosystems is often restricted by different gear types and visibility. In this study we determined the diel distribution and inferred movements of fish in an estuary in shallow and deep habitats ($<$1 m and 4 m deep respectively), using an unbaited acoustic camera (DIDSON). Baitfish ($<$100 mm TL) formed small and large shoals during the day in both shallow and deep habitats, compared to loose aggregations during the night or when they were inactive and not observed. Three larger size classes of fish (small, 100−300 mm Total Length (TL); medium, 301−500 mm TL and large $>$500 mm TL) were also more abundant during the day, likely due to general higher activity. This coincided with predatory activity with attacks by larger fish (301−500 mm and $>$500 mm) witnessed during the day but not at night. This heightened activity is the likely cause for changes in the schooling behaviour of the baitfish. The proportion of medium and large fish in the shallow habitat at night increased by over 50% as they moved from deeper areas of the estuary, showing the abundance of large predators in shallow water can be related to diel period. This highlights the pervasive top down influence even small numbers of predators can exert on the behaviour and distribution of estuarine fish assemblages.

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1. Introduction

The interaction between predators and prey is a key ecological process influencing the distribution and behaviour of fish (Rose and Leggett, 1990; Hixon and Beets, 1993). Prey species can moderate their mortality rates by changing their behaviour, such as forming schools (Magurran and Pitcher, 1987; Rangeley and Kramer, 1998) or alter their distribution and seek areas where mortality is reduced in structurally complex habitats (Sogard and Olla, 1993). Interactions between predator and prey fish may also be mediated by a range of factors such as stressful abiotic conditions (Suthers and Gee, 1986; Menge and Sutherland, 1987; Greig et al., 2013) or changing light and turbidity of the water column (Reid et al., 1999; Wegner et al., 2013).

Many piscivorous fish use sight and visibility to locate and capture their prey and altered visibility can change the distribution and behaviour of estuarine predators and prey (Becker et al., 2013).

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Diel periods can result in changes in the composition of fish communities within certain estuarine habitats (Rountree and Able, 1993; Hagan and Able, 2008; Becker et al., 2011a). This has implications for the way in which we recognise both the value of particular habitats for fish and the functional role they play. Shallow littoral regions of estuaries may be important to small prey species and juveniles as larger predators are thought to be depth limited (Ruiz et al., 1993; Paterson and Whitfield, 2000). There is increasing evidence however, that predators do enter these habitats for significant portions of time (Baker and Sheaves, 2006; Becker et al., 2011a). The value of shallow areas as refuge for prey species or foraging grounds for predators may depend on light levels. Prey may be constrained to shallow waters during the day by visual predators but not at night (Clark et al., 2003), since predatory fish may enter shallow waters (Baker and Sheaves, 2006). Antipredator behaviour such as schooling may also have less importance at night if predators are less active (Ryer and Olla, 1998). Therefore the distribution and behaviour of fish within estuaries in relation to risk and diel cycles in light is poorly understood. The way we perceive habitat use and behaviour of fish, particularly predator−prey interactions, may be a function of our bias towards day time observations and shallow water sampling.

Intermittently closed and open lakes and lagoons (ICOLLs) are common in temperate regions with high energy coastlines, low tidal ranges and intermittent rainfall (Roy et al., 2001). In particular, they are located in southern Australia, South Africa and parts of the north east Atlantic, such as Portugal (Allanson and Baird, 1999; Roy et al., 2001). Typically, the geomorphology of ICOLLs includes a deeper central basin and shallow fringing littoral habitats (Roy et al., 2001). Therefore ICOLLs are an ideal location for observations of how fish distribute themselves among shallow and deep habitats, between day and night.

Recent advances in acoustic technology, including the high resolution sonar (DIDSON) now allow scientists to observe the abundance and size distribution of fish in a range of freshwater and marine habitats (Boswell et al., 2008; Becker et al., 2011b). The ability to create up to 21 frames sec^{-1} means free flowing videos can be created and the behaviour of fish observed (Handegard et al., 2012; Becker et al., 2013). Since the DIDSON operates independent of light and bait plumes, it is a powerful tool for studying the behaviour and distribution of actively moving fish in turbid environments and at night. It is also able to collect comparable data on small and large fish, overcoming bias problems in using a traditional single gear type, or comparison difficulties when multiple gears are deployed. The species composition however, can only be inferred by video, complementary netting data (Becker et al., 2011a,b), or associated literature — as in this study.

Using the DIDSON acoustic camera, our aim was to observe the distribution of fish within unvegetated shallow littoral (>1 m) and deeper offshore (3–4 m) habitats of an ICOLL during the day and night. We expect more observations of larger fish at deep sites, especially during the day when their activity levels are higher due to a reliance on light to capture prey.

Our second aim was to observe the distribution and behaviour of prey fish in relation to depth and diel period. We expect that the abundance of small shoaling baitfish (<100 mm) will be significantly higher in shallow waters due to the protection from predation this area affords, especially during the day.

2. Methods

2.1. Study location

Smiths Lake is a large ($\approx$10 km^2) ICOLL, located on the warm temperate, mid north coast of New South Wales, Australia (152°28′51″ E, 32°23′26″S). The lake consists of a deep central basin ($\approx$3–4 m) with fringing shallow littoral habitats (<1 m) consisting of bare sand and seagrass beds composed of a combination of *Zostera capricorni* and *Ruppia* sp, along most of its length (Fig. 1). The mouth region contains large shallow sand flats with a few braided channels which lead to a shifting intermittently open entrance channel. Due to surrounding topography, the catchment of the estuary is small, with the main lake being fed by a number of small creeks. The mouth of Smiths Lake opened several weeks prior to deployments in 2012 and 2013 and remained open for the duration of the fieldwork.

2.2. Field deployments

Fieldwork was conducted during April 2012 and 2013. Deployments of the DIDSON were made at four sites within Smiths Lake (Fig. 1), two of these sites were located within the deep central basin (4 m deep), and two sites located within shallow littoral areas ($\approx$1 m deep). Because no structure is present within the deep central basin, we chose unvegetated littoral habitat sites so that depth was not confounded with any form of habitat structure. During 2012, two replicate deployments were made at the four sites during the day (09:00 h–16:00 h), and again during the night (20:00 h–01:00 h). Deployments among sites was randomized and no site was sampled twice in a single day or night. In 2013 an identical sampling regime was employed, however three replicate deployments were conducted. Each deployment consisted of positioning the DIDSON and ensuring that a clear image, free of visual obstructions was captured. The DIDSON itself was attached to a small frame with the sonar orientated so it was pointed slightly
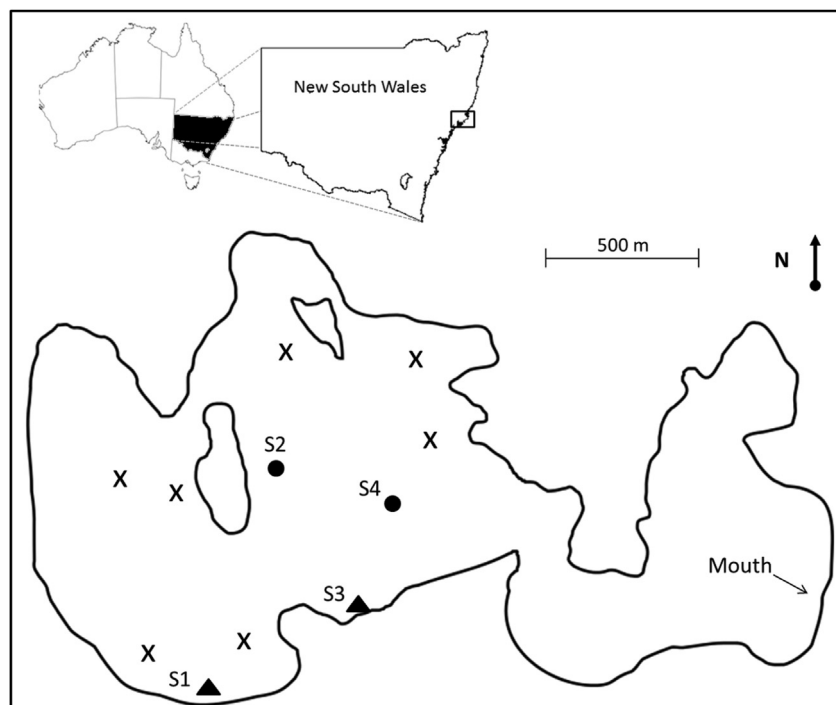

Fig. 1. Smiths Lake showing the Shallow sampling sites S1 and S3 (black triangles) and Deep sampling sites S2 and S4 (black circles). Water quality readings were taken at the seven locations marked with an X. The black box shows the location of Smiths Lake on the New South Wales coastline.

below horizontal. Following a 5 min acclimation period, recording commenced for a 30 min deployment. The DIDSON was operated in high frequency mode (1.8 Mhz) with a window length (range) set to 10 m and a starting point 2 m in front of the sonar. Water quality parameters including salinity (PSU), dissolved oxygen (mg.L^{-1}), turbidity (NTU) and temperature (°C) were measured at seven locations across the lake (Fig. 1) using a YSI 6920 probe. Measurements were made at least 3 times at each location during 2013.

Water quality had little variation among the seven locations. Salinity (PSU) reflected the open state of the mouth with levels within the central basin relatively high for intermittently open systems (mean = 26.59; ±0.11 s.e.). Dissolved oxygen (mg.L^{-1}) levels were consistently high across the lake (mean = 6.37; ±0.47 s.e.) although levels below 3 mg.L^{-1} were recorded on two occasions in the early morning. Turbidity (NTU) was low across the lake (mean = 2.78; ±0.13 s.e.), again reflecting the open mouth state and marine influence of the system at the time of sampling. Temperature (°C) was typical for Smiths Lake during the mid-Austral autumn (mean = 21.39; ±0.1 s.e.) (Robinson et al. 1982). Patterns observed in our fish dataset are therefore not likely to be influenced by any significant changes in this suite of physico–chemical parameters among sites within the estuary.

2.3. Footage processing

Footage was processed manually using the Soundmetrics DIDSON software V5.25.24. It is usually not possible to assign fish in DIDSON footage to specific taxonomic groups. However, the software does allow for accurate length measurements, meaning individual fish can be placed into size classes which can act as proxies for broad functional ecological categories (Becker et al., 2011a, 2011b, 2013). Fish were therefore placed into four size categories. The smallest consisted of baitfish <100 mm total length (TL), while the remaining three (100–300 mm; 301–500 mm and >500 mm TL) represent medium and large bodied fish.

No robust data on the abundance and diversity of medium and large bodied fish in Smiths Lake has been collected to allow us to relate size classes with likely species. We therefore collated data on the size range of common east Australian estuarine fish from published studies conducted in New South Wales estuaries (Supplementary Table 1). This provided a comprehensive dataset on the size range of many larger fish collected within estuarine systems of this region. Species for which length data existed in three or more independent studies, the average median length over those studies could be plotted (Fig. 2). This shows that fish within the 100–300 mm size class are likely to be benthic carnivores such as *Acanthopagrus australis* and *Sillago ciliata* or herbivores such as *Girella tricuspidata*. Fish within the 301–500 mm class probably consist of a combination of mugilids including *Mugil cephalus*, as well as piscivores such as *Pomatomus saltatrix* (Fig. 2). The largest size class (>500 mm) is probably dominated by piscivores including *Platycephalus fuscus* (Fig. 2), *Argyrosomus japonicas*, *Tylosurus gavialoides* (Supplementary Table 1), and *Dasyatis fluviorum* (personal observation).

The relative abundance for the three larger size classes (100–300 mm, 301–500 mm, >500 mm) was calculated using MaxN, the maximum number of fish observed during the 30 min deployment (Cappo et al., 2007). This common method does not attempt to accurately count the number of fish at a site, but produces a relative abundance estimate, while also eliminating the chance of multiple counts of the same individuals. Over a half hour period, a single MaxN estimation may not provide a representative estimation of the average abundance of fish during that time, particularly when bait is not used to attract fish within the field of view. This is due to the schooling behaviour of many estuarine species and may create a situation where a half hour deployment is totally void of fish for all
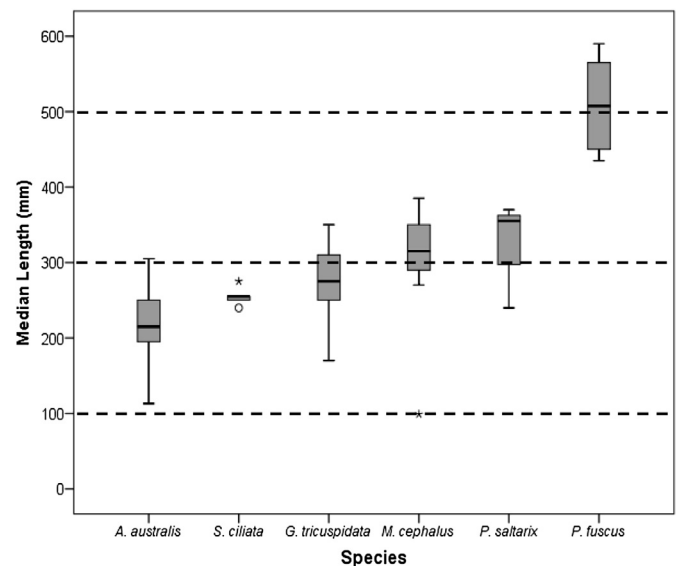

Fig. 2. Boxplot showing the median lengths of six medium and large bodied estuarine species recorded in multiple published studies conducted in New South Wales estuaries. Boxes represent 25th and 75th percentiles, the dotted lines highlight the three size classes (100–300 mm; 301–500 mm; >500 mm) used in this study.

but the few seconds when a large school passes the field of view. In this instance, a single MaxN value for the half hour deployment can provide misleading estimates of fish abundance for the majority of the filming period (Smith et al., 2011; Becker et al., 2013). The problem is overcome by selecting multiple shorter sections (subsamples) of footage and calculating a separate MaxN for each, then calculating their mean. We selected five random, 3 min subsamples from each deployment for which separate MaxN values were calculated. The mean of these five values represented our abundance estimates for each of the three size classes and is referred to as 'mean MaxN' or mMaxN (Becker et al., 2013).

Fish within the smallest 'baitfish' size class (<100 mm) could not be accurately individually counted. To make robust comparisons between our treatments, we placed the abundance of these baitfish into categories, which not only reflected the numbers of fish, but also their behaviour and whether they formed schools or were more widely dispersed. These categories included 'Large Shoal'; 'Small Shoal'; 'Loose Aggregation' and 'No Fish'.' In terms of abundance, 'Large Shoal' represented the highest levels of abundance and that fish were displaying schooling behaviour (many hundreds of fish). 'Small Shoal' represents a decrease in abundance while still displaying schooling behaviour (approximately 100 fish). 'Loose Aggregation' constitutes the same abundance as 'Small Shoal' but discerns that fish behaviour had changed and fish were not forming schools. 'No Fish' represents periods when no baitfish were present. Assignment to these categories was based on visual assessments of the footage by a single observer. A single category which reflected the abundance and behaviour of the small fish was selected for each 3 min sub-sample. If more than one abundance category was observed during the 3 min sub-sample, following the MaxN convention, the higher abundance category was selected. Fish behaviour during the 3 min sub-samples was always consistent, that is we never saw a shoal form or disperse during our observation periods. Therefore the behaviour categories represent the behaviour of fish throughout each sub-sample.

2.4. Statistical analysis

Comparisons of the relative abundance (mMaxN) for each of the size classes 100–300 mm; 301–500 mm; >500 mm was made

using ANOVA. Factors included in the analysis consisted of Year (two levels; '2012' and '2013'; fixed), Depth (two levels; 'deep' and 'shallow'; fixed), Diel Period (two levels; 'day' and 'night'; fixed) and Site (two levels nested in Depth; random). Homogeneity was assessed with residual plots and p plots observed to ensure normality of the dataset (Quinn and Keough, 2002), subsequently data for the >500 mm size class was square root transformed. When significant effects were detected Tukey's post hoc comparisons were conducted. All analysis was conducted with SPSS Inc.

To compare the frequency of observations for the four categories of small baitfish among Day vs. Night and Deep vs. Shallow, Chi-square tests of independence were employed separately for data collected during 2012 and 2013. An initial Chi-square test between years showed there was no significant difference in the tendency of fish to form schools between years ($\chi^2 = 6.15$, d.f. $= 3$, $p > 0.05$), therefore direct comparison of proportions between years is valid.

3. Results

There was a large range in size of fish observed, with the smallest length <100 mm while the largest recorded length was 850 mm. The taxa of most fish could not be identified, other than those with distinctive morphology such as sting rays (Dasyatidae) and eels (Anguillidae) which were each observed on two occasions. On four occasions distinct behaviour such as predatory attacks by fish sized 301–500 mm and >500 mm were witnessed on the shoaling baitfish (<100 mm).

The relative abundance (mMaxN) of the 100–300 mm size class did not differ among any of the factors of interest (Table 1). An interaction between Diel and Depth was found for the 301–500 mm size class (Table 1). Post-hoc comparisons revealed this was caused by significant greater relative abundances (mMaxN) during the day in both deep and shallow sites (Fig. 3). The strength of this pattern was far greater at deep sites during both years, therefore driving the interaction. An interaction was also observed between Depth and Year. Post-hoc comparisons show this was due to a significantly increased relative abundance (mMaxN) at deep sites during 2013, but not within the shallows. For the >500 mm size class a main effect of diel period was observed (Table 1). Relative abundances of fish within this class were greater during the day during both years (Fig. 3).

Separating the mMaxN data into proportions of the total day and night abundance for deep and shallow habitats suggests many fish may be moving from deep areas during the day, into the shallows at night (Fig. 4). This pattern is clear for the 300–500 mm and >500 mm size classes where there is an equal proportional increase in abundance (mMaxN) at shallow sites at night, to the decrease observed at deep sites (Fig. 4).

Differences occurred in the frequency of observations regarding the descriptive categories for the small baitfish (<100 mm), with similar patterns occurring during 2012 and 2013 (Fig. 5). In 2012 significant differences were found in the proportions of observations for the categories between Deep and Shallow sites ($\chi^2 = 8.2$, d.f. $= 3$, $p < 0.05$), while a stronger pattern was observed between Day and Night samples ($\chi^2 = 34.3$, d.f. $= 3$, $p < 0.001$). The latter was largely driven by shoaling behaviour being observed exclusively during the day at both deep and shallow sites. A similar pattern occurred during 2013 with differences in the proportion of categories between Deep and Shallow ($\chi^2 = 19.9$, d.f. $= 3$, $p < 0.01$), but again a stronger effect occurring between Day and Night samples ($\chi^2 = 26.6$, d.f. $= 3$, $p < 0.01$). This was also due to fish in 2013, displaying shoaling behaviour predominantly during the day.

4. Discussion

4.1. Distribution and abundance of the three larger size classes in deep and shallow habitats

We have shown that the behaviour and distribution of fish undergo considerable changes between diel periods, but importantly these changes are not consistent across all size ranges. The shallow water nursery paradigm, in which predation on juvenile fish is believed to be reduced in shallow depths, is complex and may be dependent upon interconnected habitats which themselves can be greatly influenced by light levels (Nagelkerken et al., 2002; Baker and Sheaves, 2005; Becker et al., 2011a).

Significantly more fish of both the 301–500 mm and >500 mm size classes were observed during the day. Two explanations for this may be that fish are moving to a part of the estuary not sampled in this study at night, or that fish were more active during the day. Our sites spanned a large area in the main central section of the estuary making it unlikely we would not have detected active fish within this major portion of the system. Also, there are no previous studies which have demonstrated large scale night time longitudinal movements of fish within estuaries, making a mass migration of fish away from our sites towards the mouth region unlikely. Given the static nature of DIDSON deployments, this indicates these fish being more active during daylight hours and is consistent with previous studies which have examined activity levels of similar sized estuarine species (Payne et al., 2013). The metadata we collated indicates most fish within these size classes are probably piscivores, therefore elevated activity levels are expected during the day as most rely on sight to capture their prey (Benfield and Minello, 1996; Payne et al., 2013). This also complements telemetry studies which found piscivorous species such as *Pomatomus saltatrix* are more active during daylight hours (Hedger

Table 1
ANOVA output for each of the three larger fish size classes within Smiths Lake during April 2012 and 2013. Significant results are shown in bold.

| Source | df | 100–300 mm | | | 301 500 mm | | | >500 mm | | |
		MS	F	P	MS	F	P	MS	F	P
Year (Y)	1	16.96	2.63	0.246	5.22	78.91	**0.012**	0.54	9.10	0.095
Diel (Di)	1	32.71	15.09	0.06	59.00	154.93	**0.006**	3.47	20.91	**0.045**
Depth (De)	1	3.70	1.64	0.329	0.00	0.00	0.966	0.09	0.25	0.666
Site (Depth) Si (De)	2	2.25	3.93	0.979	1.84	9.28	0.482	0.36	174.44	0.999
Y × Di	1	1.77	0.22	0.685	0.84	3.38	0.208	0.01	0.03	0.875
Y × De	1	0.00	0.00	0.996	1.57	23.70	**0.04**	0.25	4.17	0.178
Y × Si (De)	2	6.45	0.80	0.555	0.07	0.27	0.79	0.06	0.27	0.789
Di × De	1	12.06	5.56	0.142	8.59	22.55	**0.042**	0.46	2.74	0.24
Di × Si (De)	2	2.17	0.27	0.788	0.38	1.53	0.395	0.17	0.74	0.574
Y × Di × De	1	2.44	0.30	0.637	3.13	12.57	0.071	0.07	0.33	0.626
Y × Di × Si (De)	2	8.05	1.87	0.176	0.25	0.22	0.801	0.22	1.55	0.232
Residual	24	4.31			1.11			0.14		
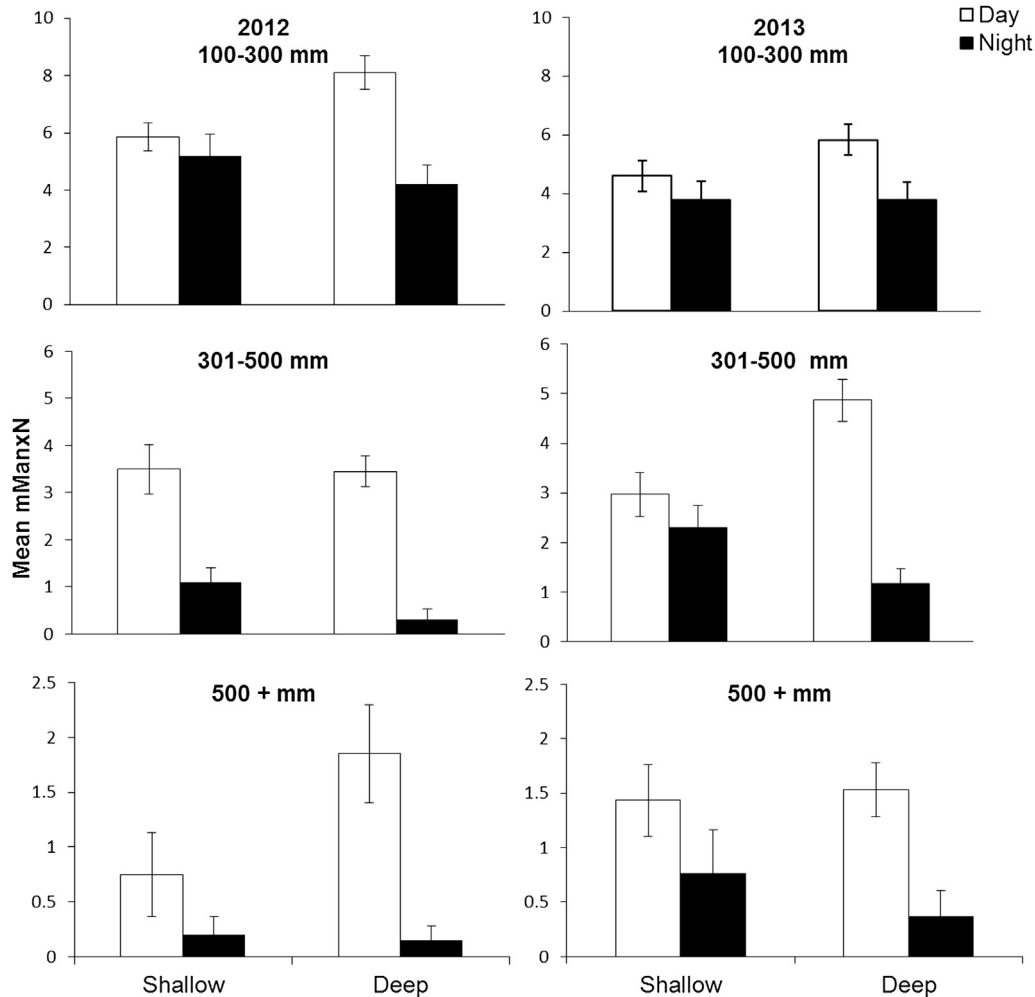
Fig. 3. Mean abundance (mMaxN) for the three larger fish size classes at shallow and deep sites from deployments made during the day and at night during April 2012 (left column) and 2013 (right column) ± S.E.

et al., 2010). For the 301–500 mm sized fish, this pattern was stronger in deeper water during both years. When our abundance data is viewed proportionally it appears this interaction is driven by many of the fish which were active at deeper sites during the day, moving to shallower regions at night. Such migrations by estuarine fish have been highlighted in the past, where fish make decisions based upon factors such as food availability, predation risk and environmental conditions, and as these alter between diel periods and depth, fish adjust their distribution accordingly (Rountree and Able, 2007). Moon phases during both years consisted of a waning gibbous, which may have provided sufficient light for some fish activity at shallow sites at night. Some fish may also move at night into the upper water column within offshore pelagic regions of the estuary (Fig. 4). This area was not sampled during this study and mid-water deployments of the DIDSON are needed.

4.2. Abundance, behaviour and distribution of shoaling baitfish

Shoaling baitfish were found to form schools far more often during the day than at night. Similar findings reveal prey fish are less likely to form schools during periods of low light (Major, 1977; Ryer and Olla, 1998), due to anti-predator behaviour (Pitcher and Parrish, 1993). Seine netting data from Smiths Lake suggests these fish are probably atherinids and ambassids (personal observations) and likely represent an important prey for known

piscivores within Smiths Lake, such as *Platycephalus fuscus* and *Pomatomus saltatrix* (Robinson et al., 1982). Both these predatory species rely on visual cues, feeding predominantly during the day (Buckel and Conover, 1997; Baker and Sheaves, 2005). Larger fish (301–500 and >500 mm) which may also consist of piscivorous species, were significantly more active during the day and on four occasions, attacks by fish in both size classes were witnessed in the DIDSON footage on shoals of the baitfish during daytime deployments. Although the numbers of fish in the >500 mm size class were comparatively low, in deep waters they were observed more than three times as often on average during the day. The shoaling response by the baitfish appears to indicate that these low numbers are still of ecological relevance and provide some insight into the effect even low numbers of predators may have on prey species.

It is of note that the abundance of small shoaling fish was greater in deeper waters during the day than at shallow sites and a greater overall abundance during the day was found in both depths. This contrasts with work conducted in South Africa, which found higher abundances of similar shoaling species (Atherinidae) within bare shallow littoral habitats during the day than at night (Becker et al., 2011a). That study, however, was restricted to sampling only shallow habitats, with no sampling conducted at deeper sites. An explanation for the low abundance of small shoaling species in the shallows during the day could be due to potential or perceived predation from avian predators. Birds are top order predators in
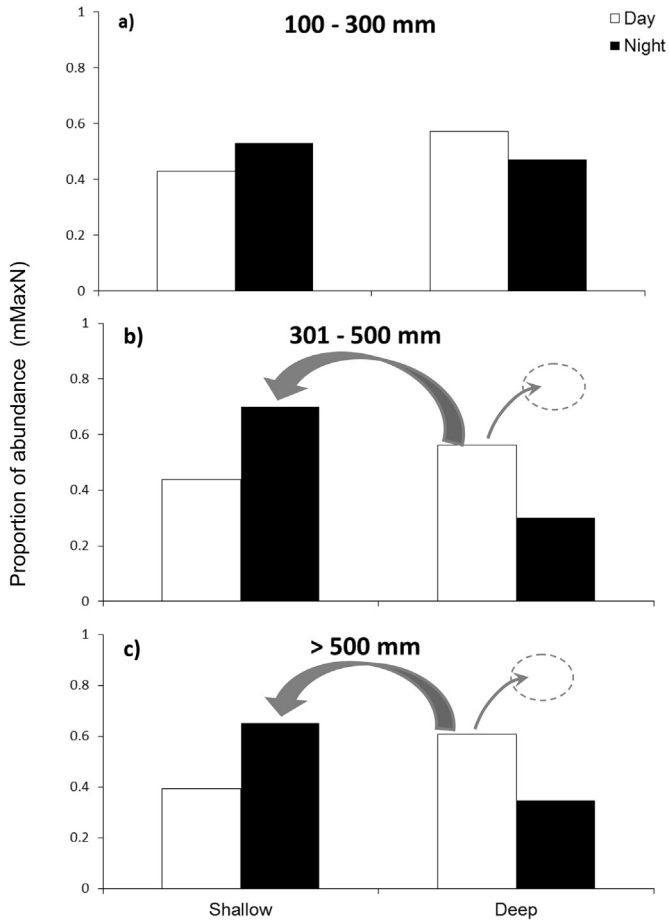
Fig. 4. Proportion of abundance (mMaxN) for the three larger fish size classes (a) 100–300 mm, (b) 301–500 mm, (c) > 500 mm, at shallow and deep sites from deployments made during the day and at night for data pooled across both years. Arrows indicate inferred movements and their magnitude. The dashed circle indicates fish potentially moving into the upper water column at night to forage.

These fish enter very shallow water to ambush prey including fish, particularly during the day (Baker and Sheaves, 2006). Whether small baitfish are capable of perceiving a potential threat from ambush predators such as *P. fuscus*, and therefore altering their distribution is difficult to ascertain. Although observations of baitfish at night were lower overall, they were particularly low in the shallow habitats. The proportional increase in predatory sized fish observed in these habitats at night may partly explain this pattern. It is important that our results provide additional evidence that the distribution and behaviour of small prey fish is greatly influenced by diel light levels and predator activity, and that shallow waters *per se* do not necessarily represent important refuges for small fish. The unique ability of the DIDSON to simultaneously collect information on abundance and behaviour, has revealed more baitfish will adopt shoaling behaviour while occupying deeper habitats than those which seek shallow regions. This challenges our traditional concept that shallow habitat is vital for small fish survival.

We did not sample during crepuscular periods, when shoaling baitfish also need some light for their own foraging. Our results may have also differed had we sampled in structured habitat within the littoral zone. We deliberately selected bare sandy areas for our shallow sites so that we could make direct comparisons with deeper areas of the lake which mostly do not contain any form of structure. Including an extra level in our design to include shallow structured habitat would make for useful comparisons with bare shallow and deep sites. The DIDSON itself may have attracted fish to the structure, however most fish seen in the footage were at least 5 m from the DIDSON and they were only loosely associated with the equipment. This study also demonstrates the capability of the DIDSON in collecting ecological data. The ability of the sonar to simultaneously collect abundance, length and behavioural data is a powerful tool for researchers interested in the interactions among fish and how environmental variables may influence any observed patterns.

In conclusion, we have shown that both the distribution and behaviour of predator and prey fish within a typical intermittently closed/open estuarine ecosystem undergo spatial and behavioural changes in relation to diel cycles of light. Behavioural and spatial responses of small baitfish, in conjunction with activity levels of larger predatory fish appear to point to predator—prey interactions driving most of our observations during both day and night. This highlights the influence top down effects has on the distribution of smaller fish within estuaries.
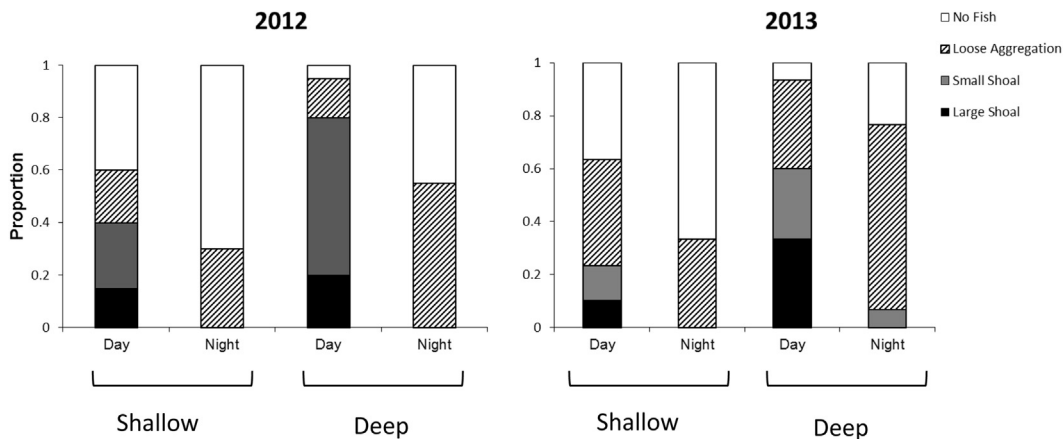
estuarine food webs and can exert significant top down pressure on fish assemblages (Steinmetz et al., 2003; Zydelis and Kontautas, 2008). Another potential reason may be that *Platycephalus fuscus* is one of the major piscivorous predators found in the estuary.

Fig. 5. Proportion of observations for each of the four categories of small shoaling fish during the day and at night in 2012 and 2013 in deep and shallow habitats. Each column during 2013 is based upon 30 observations; data during 2012 is based upon 20 observations.

Acknowledgements

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2014.04.012.

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