

# Fish Movement Through an Estuary Mouth Is Related to Tidal Flow

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**Abstract** Many species of fish move between ocean and estuarine habitats; however, there is little evidence of the magnitude of fish undertaking these movements particularly over short time scales. Such information is critical in understanding the connectivity between these major habitats. We used an acoustic camera to observe the entire entrance of a small estuary over a 4-month period during 3 h of ebb and flood tides and during day and night, which allowed us to count all fish passing through the entrance and observe their schooling behaviour. Nearly 30,000 fish transited in 60 h of observation over the study period, with a mean of 1396 ( $\pm 240$  S.E.) fish per 3 h deployment and a maximum of 4636 fish per 3 h. Of these, 20,170 entered the estuary while 7751 exited. Movements of fish were closely related to tidal flow when fish movement peaked during the middle of the tide. While the majority of fish swam with the tide, approximately 32 % swam against the tidal current. The schooling behaviour of transiting fish varied between fish entering and exiting the estuary, with incoming fish far more likely to school than those exiting. This may be an antipredator behaviour but also related to group navigation. This study has provided insights into the tight coupling of estuaries and ocean, and the tidal influence on the mass movements of fish.

**Keywords** Connectivity · Tidal flow · Diel · Estuary · Ocean · Fish behaviour · Acoustic camera

## Introduction

Many marine fish species move between ocean habitats and sheltered estuarine systems at various stages of their lives (Berkstrom et al. 2012; Sheaves, Baker, Nagelkerken, & Connolly 2015). Estuarine ecosystems often contain critical habitats not found on open coastlines, such as mangroves, marshes, or shallow seagrass beds, which are used as nursery areas and foraging grounds (Beck et al. 2001). The timing and ontogenetic patterns of fish movements between estuaries and open coasts can be elucidated by chemical analysis of otoliths and other hard body structures (Gillanders 2005; Elsdon et al. 2008). A recent proliferation of acoustic telemetry studies has also highlighted how open coasts and estuaries are linked by the movements of fish between these two distinct ecosystems. While otolith microchemistry and acoustic telemetry have provided general insight into connectivity of estuaries and the ocean, and even species-specific information in this environment, they have not shed any light on the magnitude of fish that regularly move between estuaries and the ocean. We therefore have little knowledge of the timing, direction, and magnitude of fish movements through estuary mouths during a single day/night or tidal cycle. Quantifying these fine-scale movements would provide valuable insights into the ecology and function of marine ecosystems, fisheries, bioenergetics; the structure; and even the social behaviour. This type of information is valuable for initiatives such as marine conservation planning or the development of fisheries management plans.

Collective motion, such as flocking, herding, or schooling, is a common social behaviour of animals undertaking large-

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scale movements (Herbert-Read et al. 2011; Cavagna, Queiros, Giardina, Stefanini, & Viale 2013). Forming groups may help reduce predation (Lee, Pak, & Chon 2006; Cavagna et al. 2010) and aid decision-making regarding navigation (Grunbaum 1998; Codling, Pitchford, & Simpson 2007). Making behavioural observations of wild aquatic animals has proved difficult, particularly in turbid ecosystems such as estuaries. Existing otolith microchemistry and telemetry tools are not suitable for determining behaviours such as collective movements. Thus, it is unknown whether schooling is essential for fish passing between estuaries and the ocean. Furthermore, whether fish are entering or leaving an estuary and time of day (i.e., daylight or night) may influence whether individuals form schools (Rieucou, Boswell, Kimball, Diaz, & Allen 2015). Observations of wild fish may further our understanding of predator avoidance and decision-making by animals undertaking movements among coastal landscapes.

The lack of fine-scale information on fish movements through estuary mouths is largely due to the difficulty in surveying these areas with traditional sampling gear like nets. Over the past decade, aquatic ecologists have used high-resolution sonar (Dual-frequency Identification SONar—DIDSON) to make underwater observations in dark or turbid conditions, addressing a range of ecological questions which would be impossible using other techniques (Becker, Cowley, Whitfield, Järnegren, & Næsje 2011; Able, Grothues, & Kemp 2013; Becker & Suthers 2014). Also known as “acoustic cameras,” they emit very high frequency sound waves providing near-video quality footage, regardless of light levels, to a range of 20 m (Moursund, Carlson, & Peters 2003; Becker, Whitfield, Cowley, Järnegren, & Næsje 2013). The DIDSON allows, for the first time, an opportunity to estimate the abundance of fish moving between estuaries and the ocean, and to make behavioural observations of these fish.

Even with the DIDSON, observing fish movements in estuaries with wide mouths is impractical, as it is difficult to survey the entire mouth at once. However, in temperate regions of the southern hemisphere, such as eastern and southern coasts of Australia and the coast of South Africa, coastal processes result in many estuaries having shallow and/or narrow mouths that are only temporarily open to the ocean (Roy et al. 2001). Similar systems are also found in parts of the northern hemisphere such as Portugal, Spain, and California (Tagliapietra & Ghirardini 2006; Collins & Melack 2014). Often known as intermittently closed/open lake or lagoon (hereafter referred to as ICOLLs), these estuaries often have openings that are shallow (<2 m) and narrow (<20 m), although the actual size of the ICOLL can vary considerably (Whitfield 1998; Roy et al. 2001). The small mouth width of many ICOLLs means the DIDSON's 20 m long field of view can observe a full cross section of the mouth. This allows for a near-total census of all passing fish between the estuary and

ocean. Basic behaviour of fish can also be easily interpreted due to the high frame rate of DIDSON videos, making it simple to identify whether or not fish are schooling (Handegard, Boswell, Ioannou, Leblanc, & Tjostheim 2012) and their direction of travel.

In this study, the abundance, movement direction, and schooling behaviour of fish moving through an estuary mouth was determined by deploying a DIDSON acoustic camera across the mouth of an ICOLL. The influence of tide and diel period on fish movement was examined by deploying the DIDSON during the day and night, and on ebb and flood tides. Specifically, we expected fish would predominantly travel in the same direction as the tide, with a peak in abundance coinciding with greatest tidal flow due to reduced energetic costs at these times. Secondly, we expected the social behaviour of fish to differ between diel periods, with schooling to occur more readily during the day than at night due to the increased threat of visual predators.

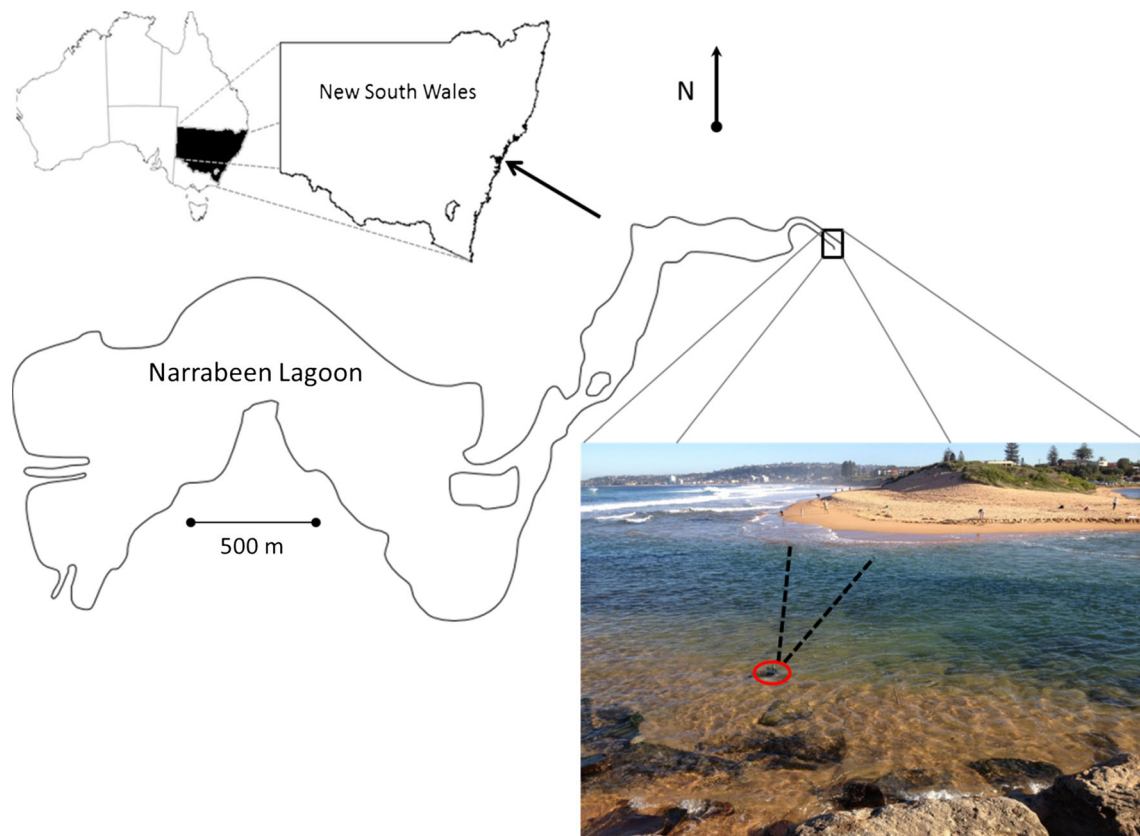
## Materials

### Study Location

Fieldwork was conducted at Narrabeen Lagoon, a medium-sized ICOLL on the warm temperate east coast of Australia (33° 43' S; 151° 18' E). The lagoon covers an area approximately 2 km<sup>2</sup> with a catchment size of 55 km<sup>2</sup> (Fig. 1) which is typical of the many smaller estuaries in south-eastern Australia. The southern shoreline and much of the area near the mouth are urbanised; however, the northern shore and catchment is located within remnant patches of dry heath and woodland forest. The lagoon contains extensive beds of seagrass including *Zostera capricorni*, *Halophila* sp., and smaller patches of *Ruppia spiralis*. The intertidal zone consists of small patches of saltmarsh (*Sarcocornia quinqueflora* and *Samolus repens*) and mangroves. During periods when the mouth is open, the lagoon discharges into the Tasman Sea through a relatively narrow channel that is normally less than 20 m wide and 200 m long. Closed mouth phases are short in duration, as the entrance is usually mechanically opened due to flood mitigation issues in the surrounding urban catchment. The mouth of Narrabeen had opened several months prior to the commencement of fieldwork and remained open for the duration of the project. There was no major change in the morphology of the mouth throughout the course of the fieldwork. The coastline at Narrabeen Lagoon experiences semi-diurnal tides with a maximum spring tide amplitude of 1.8 m.

### Field Deployments

Fieldwork was conducted between July and October 2013. Fish movements through the entrance channel of Narrabeen



**Fig. 1** Location of Narrabeen Lagoon on the Pacific coast of New South Wales. The *black rectangle* on the map of Narrabeen Lagoon shows the location of the sampling site, positioned at the mouth of the system. The photo shows the setup of the field equipment; the DIDSON is highlighted

by the *red circle*, and its field of view covering the mouth channel is shown by the *black dashed lines*. The DIDSON was positioned on the northern bank; therefore, the photograph is taken facing south with the Tasman Sea to the *left*

Lagoon were recorded with a DIDSON acoustic camera (Soundmetrics, Bellevue, WA, USA). The DIDSON was attached to a weighted stainless steel frame and deployed at the boundary of the surf-zone and estuary mouth, and directed so its field of view covered a full cross section of the entrance channel (Fig. 1.). The beam pattern of the DIDSON results in a narrower field of view, both horizontally and vertically, closer to the sonar, leading to the potential of fish swimming above the beams at short distances from the unit. Because of this, we positioned the sonar on the northern side of the channel which had a shallow sloping substrate and tilted the DIDSON so it was pointing slightly below horizontal. The combination of tilt angle and shallower water closer to the DIDSON resulted in the full water column being visible even at close ranges. The DIDSON was operated in a low-frequency mode (1.1 MHz) enabling a window length (field of view) of 20 m, allowing the full cross section of the entrance channel to be viewed. The window length limited the frame rate to 7 frames/s, though this is still sufficient for the creation of free-flowing videos (Becker et al. 2013). It is difficult to identify species in DIDSON footage, but the associated software does permit measurement of total length (TL). At window lengths used in this study, we could clearly

identify and count all fish greater than 80 mm TL. While at times we did measure fish below this length, these individuals were not included in the dataset as we were not confident the DIDSON settings would allow all fish of these sizes to be observed. Because the entrance channel of Narrabeen Lagoon is short (50 m), we could be confident fish observed passing through the field of view were transiting between the estuary and ocean.

Deployments were conducted on both flood and ebb tides during the day and at night. Five replicate deployments were made for each combination of tidal direction (ebb or flood) and diel period (day or night), resulting in a total of 20 deployments. For practical reasons, deployments lasted 3 h, but the start time of deployments were staggered throughout the tidal cycle to generate a dataset which covered the full tidal cycle. Most deployments were conducted during a neap tidal cycle; however, it was impossible for all deployments to be made on identical tidal amplitudes. Differences between mean tidal amplitudes for treatments were small (day flood tides =  $1.04 \text{ m} \pm 0.08 \text{ S.E.}$ , day ebb tides =  $0.97 \text{ m} \pm 0.09 \text{ S.E.}$ , night flood tides =  $0.84 \text{ m} \pm 0.05 \text{ S.E.}$ , night ebb tides =  $1.12 \text{ m} \pm 0.04 \text{ S.E.}$ ).

Water quality was measured at the beginning and end of each deployment using a YSI 556. Salinity ranged between

34.3 and 36.8, turbidity fluctuated between 0.6 and 6.7 NTU, and pH between 8.02 and 8.32. Temperature showed the greatest variation (15.3–21.8 °C), with warmer waters recorded towards the end of the field program. However, as we randomized the dates, we sampled each tide/diel combination; ANOVA revealed no significant differences in temperatures between tidal direction (ebb and flood;  $P = 0.48$ ), diel period (day and night;  $P = 0.058$ ), or an interaction between these factors ( $P = 0.778$ ).

### DIDSON Footage Processing

Footage was processed manually using the Soundmetrics DIDSON software V5.25.48. The full 3 h of each deployment was analysed from start to finish in “Background Subtraction” mode, which eliminates static objects such as the substrate. This makes moving objects, like fish, easier to identify and measure. Every fish passing through the DIDSON field of view was counted, measured (total length) using the software measurement tool (Burwen, Fleischman, & Miller 2010; Becker & Suthers 2014), and its swimming direction recorded (into the estuary, “incoming,” or leaving the estuary, “outgoing”). Most fish passed from one side of the field of view to the other, in an obvious and deliberate swimming direction within a matter of seconds. An individual was not counted if it swam into the field of view but then returned back in the direction from which it came. Some fish were observed to be foraging in the mouth itself and did not appear to be passing between the estuary and ocean. Therefore, if an individual spent more than 3 min within the field of view, its swimming direction became ambiguous and it was also not counted. By counting all fish, there is a chance we may have counted the same individual as it swam past in one direction and then returned from the other. Some individuals may have been counted more than once if they repeatedly passed through the mouth over the 3-h deployment. Fish occasionally formed large dense schools, making it impossible to get an accurate length measurement of all individuals. In these cases, a minimum of 10 fish were measured and their mean length interpreted as the length of all fish in the school. The schooling behaviour of fish was also recorded. Each fish was noted as either belonging to a school or moving as an individual. Definitions of a “school” vary widely in the literature (Shaw 1970; Pitcher & Parrish 1993), but we define a school as three or more fish in close proximity, which was defined as approximately 2 body lengths and travelling in the same direction.

### Statistical Analysis

A generalized additive mixed model (GAMM) was used to test whether the number of fish moving in or out of the estuary varied throughout the tidal cycle and whether this was dependent on tidal direction. A separate analysis was done for

incoming and outgoing fish. “Tidal direction” (ebb or flood) was included as a factor, “hours since tide turn” (from 0 to 6 h) was included as a smoother (with an interaction with tidal direction), and “day” (from 1 to 10) was included as a random factor. A smoother was used for hours since tide turn based on the clear non-linearity between this covariate and the response variable. Smoothers were penalized thin plate regression splines. Hours since tide turned was used to put the tide cycle on a ~6-h scale to discern any trends in movement between tidal highs and lows. The complete tidal cycle was tested by stratifying this variable across tidal direction (ebb and flood), and stratifying this variable improved the model based on Akaike information criterion (AIC). Diel period was also evaluated in both models but was not significant and did not improve the final model based on AIC. A negative binomial family (NB2 model; (Hilbe 2011)) was used to account for considerable overdispersion. Thus, the selected model used for both incoming and outgoing fish was

$$Fish_{ij} \sim NB(\mu_{ij}, k) \quad \log(\mu_{ij}) = \beta_1 + \beta_2 \times TideD_{ij} + s_{jd}(TideT_{ij}) + a_j + \varepsilon_{ij} \quad a_j \sim N(0, \sigma_{Day}^2) \quad \varepsilon_{ij} \sim N(0, \sigma^2)$$

where *Fish* is the number of fish moving in or out of the estuary, for sample *i*, on day *j*, and for tidal direction *d*, *TideD* is the direction of the tide, *TideT* is the hours since tide turned, *s* is a smoothing function, *a* is the *Day* random effect,  $\beta$  are constants, and  $\varepsilon$  is residual error; both *a* and  $\varepsilon$  are normally distributed. Models were evaluated by examining Pearson residuals against included and excluded covariates and against fitted values (Zuur, Ieno, Walker, Saveliev, & Smith 2009). Goodness-of-fit was estimated using percent deviance explained calculated by excluding the random effect. GAMMs were done using the *gamm* function in the “mgcv” package (Wood 2006; Wood 2011) in R (R Core Team 2014).

To compare the frequency of observations of fish schooling or swimming as individuals between incoming and outgoing fish, chi-square tests of independence were employed. Fish were separated into two size classes which have proved appropriate in previous estuarine studies using DIDSON (Becker et al. 2011; Becker & Suthers 2014) which included 100–300 mm and 301+ mm. A separate test was conducted for each combination of tidal direction and diel period resulting in four tests for each size class.

### Results

A total of 27,921 fish were observed to transit the mouth of Narrabeen Lagoon during the 20 deployments. Of these, 20,170 were observed swimming into the estuary, while 7751 were swimming out. We observed a mean of 1396 ( $\pm 240$  S.E.) fish per the 3-h deployment. Numbers of fish passing through the mouth among deployments was variable,

with the most observed for a single deployment totalling 4636 individuals and the least totalling 372.

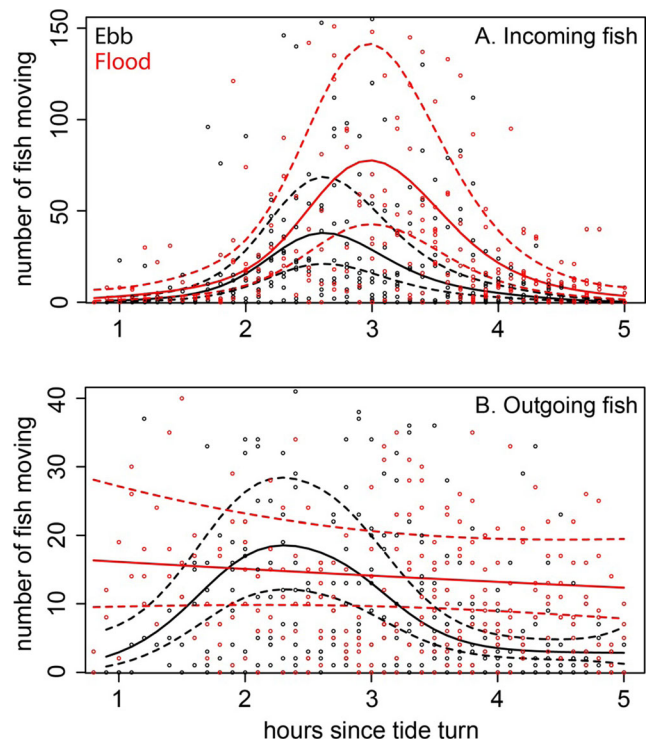
There was little difference in the size of fish in regard to the direction of travel. The overall mean length of fish was 257 mm ± 42 S.D., while the mean of incoming fish was 266 mm (±45 S.D.) and outgoing fish averaged 251 mm (±46 S.D.). The size of moving fish was also similar between the diel period, with fish observed during the day an average of 247 mm (±43 S.D.) and fish at night an average of 267 mm (±41 S.D.).

The GAMMs revealed that the number of fish entering the estuary varied significantly throughout the tidal cycle and that this depended on tidal direction (Table 1). For incoming fish, movements peaked about 3 h after the predicted low tide and slightly earlier during ebb tides (Fig. 2a). The numbers of incoming fish also varied significantly between tidal direction (Table 1), with greater numbers of incoming fish during flood tides (mean = 1155 ± 276 S.E.) than during ebb tides (mean = 862 ± 364; Fig. 2a). The number of outgoing fish on ebb tides varied significantly throughout the tidal cycle, but there was no difference in fish outgoing movements on flood tides (Fig. 2b). Numbers of outgoing fish also varied between tidal direction (Table 1); however, this effect was not as strong

**Table 1** Results from the two GAMMs testing whether fish movement varied throughout the tidal cycle

Incoming fish				
	Estimate	Std error	<i>t</i>	<i>P</i>
Intercept	2.133	0.280	7.61	<0.0001
<i>TideD</i>	1.070	0.397	2.69	0.007
	edf	<i>F</i>	<i>P</i>	
<i>s(TideT):ebb</i>	5.21	45.04	<0.0001	
<i>s(TideT):flood</i>	4.73	38.31	<0.0001	
	Intercept $\sigma$	Residual $\sigma$		
<i>Day</i>	0.852	0.841		
Deviance explained = 31.3 %				
Outgoing fish				
	Estimate	Std error	<i>t</i>	<i>P</i>
Intercept	1.995	0.189	10.57	<0.0001
<i>TideD</i>	0.641	0.268	2.39	0.017
	edf	<i>F</i>	<i>P</i>	
<i>s(TideT):ebb</i>	4.71	27.38	<0.0001	
<i>s(TideT):flood</i>	1.00	0.72	0.395	
	Intercept $\sigma$	Residual $\sigma$		
<i>Day</i>	0.561	0.919		
Deviance explained = 13.1 %				

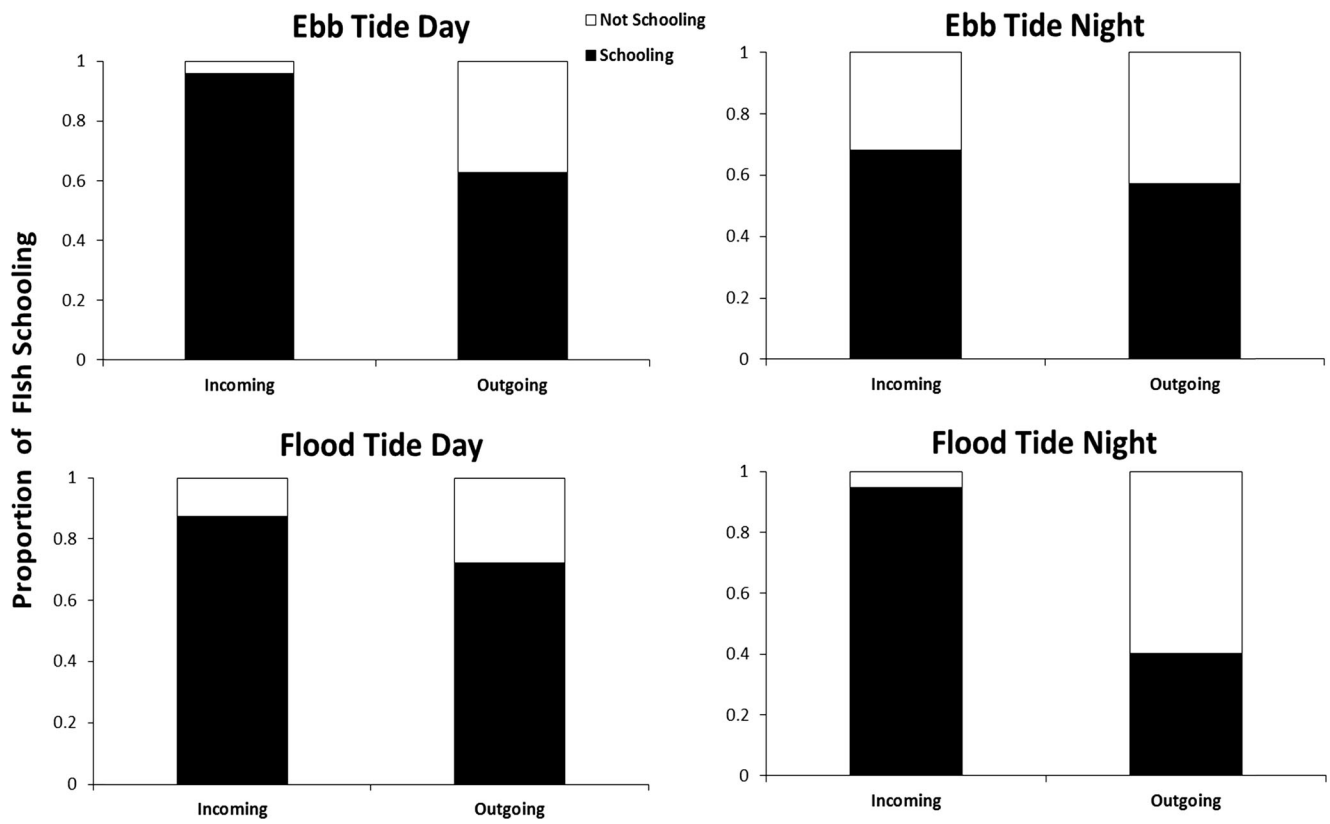
Variables are tidal direction (*TideD*; ebb and flood); smoothers (*s*) for hours since tide turned (*TideT*), with unique smoothers for ebb and flood tides; and the *Day* random effect. All variables were significant, except for the *TideT* smoother for outgoing fish on the flood tide. This had an effective degrees of freedom (*edf*) = 1, which indicates a linear relationship



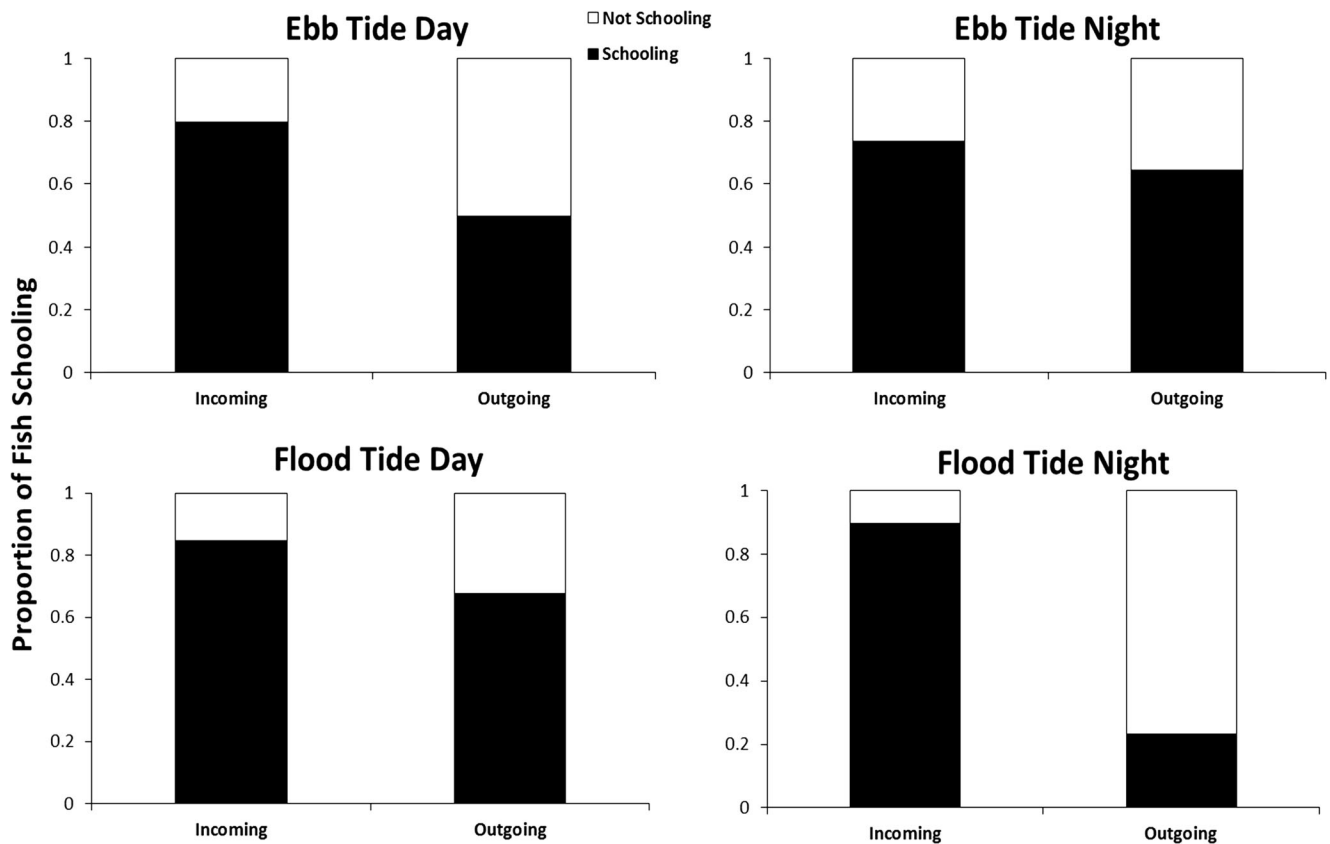
**Fig. 2** Plots of smoothers for the tide time variable (*TideT*) on ebb (black) and flood (red) tides, for both incoming (a) and outgoing (b) fish. Dashed lines are 95 % confidence bands. Note that the y-axis is truncated and not all data points are shown

as observed for incoming fish. More fish swam out of the estuary during ebb tides (mean = 396 ± 42 S.E.) than during flood tides (mean = 379 ± 71 S.E.; Fig. 2b). It is also clear from this analysis that there were generally more incoming than outgoing fish and that the most fish movement was incoming fish on flood tides.

Schooling behaviour was common; however, patterns in this behaviour still emerged. For fish in the 80–300-mm size class, those swimming into the estuary were more likely to form schools than those swimming out on ebb tides, with this trend stronger during the day ( $\chi^2 = 1489$ ,  $P < 0.001$ ) but also observed at night ( $\chi^2 = 23.8$ ,  $P < 0.001$ ; Fig. 3). Flood tides showed a similar pattern to ebb tides during the day with incoming fish more likely to school than outgoing fish ( $\chi^2 = 80.2$ ,  $P < 0.001$ ). At night, however, while incoming fish were again far more likely to form a school ( $\chi^2 = 146$ ,  $P < 0.001$ ), outgoing fish showed the reverse pattern and likely to transit as individuals ( $\chi^2 = 3201.7$ ,  $P < 0.001$ ) (Fig. 3). Larger fish (301+ mm) generally showed the same greater preference to school when swimming into the estuary; however, overall a lower proportion of fish formed schools. Significantly more of these larger fish schooled when coming into the estuary on ebb tides during the day ( $\chi^2 = 81.6$ ,  $P < 0.001$ ; Fig. 4) and at night ( $\chi^2 = 16.4$ ,  $P < 0.001$ ), as well as flood tides during the day ( $\chi^2 = 72.4$ ,  $P < 0.001$ ). Like the smaller fish, on flood tides during the night, incoming fish



**Fig. 3** Proportion of fish in the 80–300-mm TL size class which were members of a school during the day and at night during both ebb and flood tides



**Fig. 4** Proportion of fish in the 301+ mm TL size class which were members of a school during the day and at night during both ebb and flood tides

were far more likely to form schools, but outgoing fish were far more likely to pass through the mouth as individuals ( $\chi^2 = 619.2$ ,  $P < 0.001$ ; Fig. 4).

## Discussion

We consistently observed large numbers of fish moving between an estuary and the ocean over relatively short tidal periods; although this work was conducted in a single estuary, it demonstrates how small estuaries and the ocean may be highly connected via fish movements. Previous studies have highlighted the importance of connectivity during ontogenetic shifts in habitat use by fish over long time periods (Gillanders, Able, Brown, Eggleston, & Sheridan 2003) and seasonal changes in estuarine fish assemblages (Bretsch & Allen 2006; Hoeksema & Potter 2006). Our study builds on this by documenting a high level of connectivity over a much shorter time frame (hours).

Sizes of fish passing through the mouth were similar regardless of the direction of travel. This suggests we were not observing small juvenile fish passing into the estuary in search of nursery grounds and larger adults subsequently moving back out to coastal habitats (Sogard 1992; Gillanders & Kingsford 1996; Beck et al. 2001). The mouth of Narrabeen had been opened for several months prior to the commencement of this project, so the large numbers cannot be attributed to fish accessing new habitats or resources which had recently become available. It is possible this ingress is part of a seasonal pattern. Our observations over 4 months from late winter to spring may coincide with the movement of fish into the coastal lagoon, and they may depart in autumn-winter. Seasonal movements of mobile animals are common at various spatial scales as resources fluctuate among patches spatio-temporally throughout the broader landscape (Webster, Marra, Haig, Bensch, & Holmes 2002; Dingle & Drake 2007). Resources within estuaries are no exception, and sampling over longer time scales would help identify if the directions and abundance of fish movements are seasonal. Long-term datasets have also revealed the diversity of estuarine fish changes seasonally (Claridge, Potter, & Hardisty 1986); while it is difficult to identify fish species from DIDSON footage, differences between smaller and larger species would be apparent. Our results must be considered in the context of a single season. At shorter time scales, we standardized our sampling to coincide with the neap tide period. It is also possible that variations in fish movements between neap and spring cycles may occur and is certainly a direction new research could embark upon.

Regardless of whether there was ebb or flood tide, the peak in fish transit occurred during the middle of the tide and tidal flow. Larvae of many species of fish and invertebrates passively use flood tides to transport them from coastal habitats

into estuaries (Forward 2001; Gibson 2003; Trancart et al. 2012). Typically, these larvae have limited energy stores and it is believed this passive transport reduces energy requirements (Forward 2001). Tracking of limited numbers of adult fish has also shown tidal currents may be used for both short (<1 km) and long (70 km) distance movements (Arnold, Greer Walker, Emerson, & Holford 1994; Lacoste, Munro, Castonguay, Saucier, & Gagné 2001; Naesje et al. 2012), which has also been attributed to minimising energy use. While more fish travelled with the tide, we did observe fish swimming against the flow into the estuary on ebb tides. Emerging work has shown larvae and small juveniles can swim against an ebb tide into estuaries (Patrick & Strydom 2014). Our work shows that these patterns also extend to larger sized fish and appears to signify that while many fish may “ride the tide” (Gibson 2003; Naesje et al. 2012), substantial numbers of fish will also make movements against the tide. Significantly more fish swam out of the estuary into coastal habitats with the ebb tide compared to during flood tides, although the total numbers did not differ greatly. Like incoming fish, those leaving the estuary with the ebb tide showed a peak during the middle of the tidal cycle, again pointing to the relationship between peak tidal flow and peak movements of fish. However, there was no peak in movement in relation to the tide for outgoing fish on flood tides. While large numbers of fish entered the estuary almost always in large groups, there were far fewer leaving and those that did often swam as individuals. While tidal currents may act as a cue for the mass movements of fish, non-schooling individuals appear to be less influenced by tides.

As predicted, most fish observed passing through the mouth were in schools; this general pattern was consistent for both small (80–300 mm) and larger (301+ mm) fish. Schooling is a common anti-predatory response by fish (Pitcher & Parrish 1993) but is generally far more common during the day than at night (Ryer & Olla 1998; Becker & Suthers 2014). While passing through the mouth, fish are restricted in their ability to evade predators due to the shallow depths, narrow channel, and lack of structural habitat. Schooling may represent an important anti-predatory behaviour during a risky phase in their movement between estuarine and ocean habitats and would explain why it was not uncommon for passing fish to form schools even during the night. As noted above, we found that fish were more likely to form schools when coming into the estuary compared to when they were moving out into the coastal zone. This may be related to navigation and the mismatch of scales between an estuary and the open coast. Narrabeen Estuary is a relatively small, enclosed system, and navigating along open coastal habitat poses greater problems simply due to the significantly increased distances fish must travel. Group navigation is common in animals such as birds, which are often required to move over large spatial scales, and has been shown to increase

navigation success (Simons 2004). The “many wrongs” principal, first proposed by Simons (2004), describes how information may be pooled by members of a group to increase navigational accuracy and has been applied to numerous groups of animals (Codling et al. 2007; Bode, Franks, & Wood 2012). Therefore, moving as a group along the open coast towards an estuary provides benefits which are less important when moving from within the estuary towards the sea. Additionally, fish in the coastal zone often have a choice among several estuarine systems of which they may enter and therefore need to make decisions about the suitability of particular estuary prior to entry. A number of stimuli are believed to attract fish to the mouths of estuaries into which they may then recruit and include salinity, temperature, olfactory, and turbidity cues (Blaber & Blaber 1980; Montgomery, Tolimieri, & Haine 2001; James, Cowley, Whitfield, & Kaiser 2008). Based upon these cues from a particular estuary, a group of fish may make better decisions relating to whether or not to enter the system than an individual.

This study has provided a new perspective with new technology to reveal the tight coupling which can exist between estuaries and ocean habitats through the movements of large numbers of fish over tidal time scales. The abundance of transiting fish is influenced by tidal flow and probably direction, but further work is needed to understand the mechanisms driving tide’s influence. Insights into the schooling behaviour of these fish suggest that schooling may not only reduce predation but aid navigation into estuaries. These results are from a single estuary, and information needs to be collected across a broad geographical range, and for more fish species, for a greater understanding of the relationship between coastal fish and estuaries (Able 2005). Fish movements into estuaries are particularly likely to be influenced by the size of the system and width and depth of the mouth. For example, various studies have shown fish assemblages differ between smaller intermittently open and larger permanently open estuaries (Bennett 1989; Pollard 1994). Alternative patterns may have occurred in larger systems in which bigger fish and chondrichthyes regularly enter. While this study has provided novel insights into fish movements between estuaries and the ocean, there is considerable scope to build on these results across a range of estuaries that vary in size, mouth shape, and habitat characteristics. Anthropogenic impacts such as pollution and habitat alteration are an ever increasingly common stress facing coastal ecosystems, so the degree of development of estuaries would also be an important covariate. Carefully designed studies based upon the approach taken here could establish how anthropogenic impacts are affecting the recruitment of fish into estuaries and use similar measurements to ours as biological indicators. Data generated from these types of studies would be greatly beneficial in the management of estuaries across a broad scope of issues ranging from the impact of development, habitat restoration, and fisheries.

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