

# Tidal influence on a fringing mangrove intertidal fish community as observed by *in situ* video recording: implications for studies of tidally migrating nekton

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**ABSTRACT:** The vegetated intertidal zone has long been acknowledged as an important habitat for fish, but our understanding of the dynamics of intertidal migrations by these fish is limited. Using *in situ* video recordings, we examined fish movements into and out of the waterward margin of a fringing mangrove forest during spring tides at 27 haphazardly chosen sites throughout the Rookery Bay National Estuarine Research Reserve, Florida. Our results indicate that fish respond to tide stage in a species-specific manner. Based on the changes in relative abundance throughout the tide cycle, we identified 4 general intertidal migration patterns: (1) tide-level proportionate, with greatest abundance during high tide; (2) flood- and ebb-tide concentrated, with lowest abundance during high tide; (3) peak abundance at ebb and low tide; and (4) depth-limited but tidally independent. Given that the distribution of the fish within the intertidal zone was heterogeneous, we suggest that the placement of sampling gear within the intertidal zone and the timing of samples within the tide cycle can greatly influence the species composition of fish inventories.

**KEY WORDS:** Fish · Tidal migration · Intertidal · Mangrove · Video · Sampling

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## INTRODUCTION

Threats to coastal wetlands are well documented (Ellison & Farnsworth 1996, Kennish 2001, Islam & Wahab 2005). As human populations and activities have encroached on these vegetated intertidal habitats, their total area has diminished (Parks & Bonifaz 1994, Thu & Populus 2007) with remaining fragments often left degraded (e.g. Eby et al. 2005). Effective management of these systems, including protective regulations and restoration efforts, require that we identify the essentially important habitat elements within them, and gain an understanding of the interaction between these elements and the associated fauna.

Given the ecological and commercial importance of nekton, they have been the focus of a considerable amount of research in this regard (Rountree & Able 2007). The vegetated intertidal zone is a potentially essential habitat for fish and crustaceans as significant

correlations have been identified between the areal extent of salt marshes, mangroves, and commercial catches from adjacent waters (Turner 1977, Barbier & Strand 1998, Manson et al. 2005). Nekton enter the intertidal zone when it is tidally inundated and generally depart prior to its complete drainage, returning to the subtidal zone (Sheaves 2005, but see Barletta et al. 2000). Species that make this tidal migration benefit through the exploitation of intertidal food sources (Hampel & Cattrijsse 2004, Hollingsworth & Connolly 2006, Rilov & Schiel 2006, Brenner & Krumme 2007) and reduced susceptibility to depth-restricted predators (Halpin 2000, Linehan et al. 2001, Ellis & Bell 2004). This is an active process for many species (e.g. Burrows 2001), rather than the result of passive dispersal via tidal currents (Commito et al. 1995). Therefore, the timing, duration, and destination of their migrations may reflect species-specific strategies to maximize the benefits of periodic incursions into the intertidal zone.

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Table 1. Survey of fish sample timing in the mangrove intertidal zone. Gear type designations are as described in Rozas &amp; Minello (1997)

Gear type/gear	Tide stages sampled	Area/volume defined	Source
<b>Enclosure samplers</b>			
Bottomless lift net	High tide	Yes	Hindell & Jenkins (2005)
Bottomless lift net	High tide	Yes	Smith & Hindell (2005)
Encircling net	High tide	Yes	Huxham et al. (2004)
Drop net	High tide	Yes	Ellis (2003)
Stake net	High tide	Yes	Rönnbäck et al. (1999)
Encircling net (rotenone)	Not reported, 'negligible tidal influence'	Yes	Ley et al. (1999)
Drop net (rotenone)	Not reported	Yes	Lorenz et al. (1997)
Stake net	High tide	Yes	Vance et al. (1996)
Encircling net	High tide	Yes	Mullin (1995)
Drop tube	Not reported	Yes	Sheridan (1992)
Encircling block net	High tide	Yes	Morton (1990)
Encircling net (rotenone)	Not reported	Yes	Blaber & Milton (1990)
Encircling net (rotenone)	High tide	Yes	Thayer et al. (1987)
<b>Passive samplers</b>			
Fyke net	Flood to ebb tide	No	Smith & Hindell (2005)
Fyke net	Flood to low tide	No	Hindell & Jenkins (2004)
Block net	High tide	Unknown	Halliday & Young (1996)
Trap net	High to low tide	No	Laegdsgaard & Johnson (1995)
Campechade	All tide stages	No	Louis et al. (1995)
Trap net	High to low tide	Yes	Robertson & Duke (1990)
<b>Traps or entanglement gear</b>			
Gill net	Flood to ebb tide	No	Smith & Hindell (2005)
Gill net	Flood to ebb tide	No	Hindell & Jenkins (2004)
Traps	Not reported	No	Boulon (1992)
<b>Visual census</b>			
Visual census	Not reported	Yes	Nagelkerken et al. (2000)
Visual census	Not reported, 'negligible tidal influence'	Yes	Ley et al. (1999)
Visual census	Not reported	No	Rooker & Dennis (1991)
Visual census	Not reported	No	Boulon (1992)
<b>Towed nets</b>			
Seine net	High tide	Yes	Hindell & Jenkins (2004)
Seine net	Ebb	No	Laegdsgaard & Johnson (1995)

Our knowledge of the habitat use and dynamics of intertidal migrations has been limited by the logistic difficulties inherent to sampling mobile fauna in structurally complex aquatic habitats (see review by Rozas & Minello 1997). Such sampling is often labor-intensive, may require habitat alteration (e.g. removal of vegetation) for the placement of sampling gear, and commonly relies on the ebbing tide to concentrate targeted species for collection. These challenges limit both spatial and temporal sampling replication, and largely prohibit *in situ* sequential sampling designs that are ideally suited for the study of the within-tide movements of intertidal migrants (Gibson 2003).

In studies of nekton associated with mangrove habitats, the sampling period, when reported, has often been restricted to a single stage of the tide cycle (usually high tide), or if sampling was conducted over multiple tide stages, results have been reported as a cumulative total of individuals captured without mention of within-tide dynamics (Table 1). Quantitative sampling

in the mangrove intertidal zone (sensu Rozas & Minello 1997) using enclosure gear has been, to our knowledge, restricted to high tide (Table 1). Passive sampling gear (e.g. fyke nets and block nets, Table 1) that collects fish from generally undefined areas of the intertidal zone as they are drained is positioned at high tide or late flood tide. In each of these instances, the usually implicit, and untested, assumption upon which the sampling designs were based was that most fish swim into the mangrove habitat with the flood tide and depart the intertidal zone as it is drained during the ebb. This assumption is revealed when these studies are interpreted in such a manner that suggests that the nekton community present in the mangrove intertidal zone at high tide is indicative of that present at all other periods of the tide cycle during which the forest floor is inundated.

In the present study, using *in situ* video recordings of the mangrove fish community, we addressed the following hypotheses:

H<sub>0</sub>1: The relative abundance of each fish species in the fringing mangrove intertidal zone is constant throughout the tidal cycle.

H<sub>0</sub>2: The fish species composition of the fringing mangrove intertidal zone is constant throughout the tidal cycle.

## MATERIALS AND METHODS

**Site description.** This study was conducted in the Rookery Bay National Estuarine Research Reserve (NERR) (26° 1.6' N, 81° 43.8' W; Fig. 1), a shallow estuarine system in southwest Florida. The area experiences mixed semidiurnal tides with an average range of ~1 m. Mean annual water temperature in Rookery Bay is 25°C with a range of 13 to 34°C. The intertidal zone is mostly mangrove-forested (i.e. *Rhizophora mangle*, *Laguncularia racemosa*, and *Avicennia germinans*). *R. mangle* prop roots with affixed oysters (*Crassostrea* sp.) provided most of the structure at the waterward margin of the mangrove forest where video was recorded for the present study. The fringing mangrove forests of Rookery Bay are typically faced by a limited (~1 to 3 m) unvegetated (mud and shell hash substrate) lower intertidal margin, exposed on spring low tides.

**Sampling gear and recording method.** Video recordings of fish movements into and out of the waterward margin of the fringing mangrove forest were made during spring tides in January to March 2004 (the months when water clarity was most reliably high), at

27 haphazardly chosen sites throughout the Rookery Bay NERR (Fig. 1). Over the course of the study, a single recording, 24 h in duration, was made at each site, although the results presented here are limited to the diurnal observations (i.e. beginning during the morning low tide and continuing until sunset). At each site, a black and white video camera (1.27 cm sensor board, 795 × 596 pixels, Wattec WAT-902H) in a submersible housing (Fig. 2) was staked 10 cm off the bottom, 75 cm waterward of the mangrove rootline, providing a 1.5 m wide viewing area of the mangrove/open-water ecotone (Fig. 3). Each camera was equipped with an IR pass filter (Hoya IR72) that limited input from light wavelengths below 720 nm. Four LED infrared illuminators (880 nm, undetectable by most marine fish; Levine & MacNichol 1982), positioned by each camera, supplemented ambient infrared lighting, as the majority of infrared light from the sun is absorbed in the first few cm of the water surface. The combined effect of the filters and directed infrared illumination was to improve the image quality by reducing backscatter of visible light that typically reduces visibility in turbid waters (authors' unpubl. data). Given the turbidity of the water in Rookery Bay and the visual obstruction created by the mangrove prop roots, visibility was generally limited to no more than ~30 cm from the mangrove/open-water ecotone into the forest interior (i.e. ~1 m from the camera). The real-time (30 frames s<sup>-1</sup>) video was recorded in mpeg-2 format using digital video recorders (Darim B-DVR) housed in dry boxes. Concurrent with video recording,

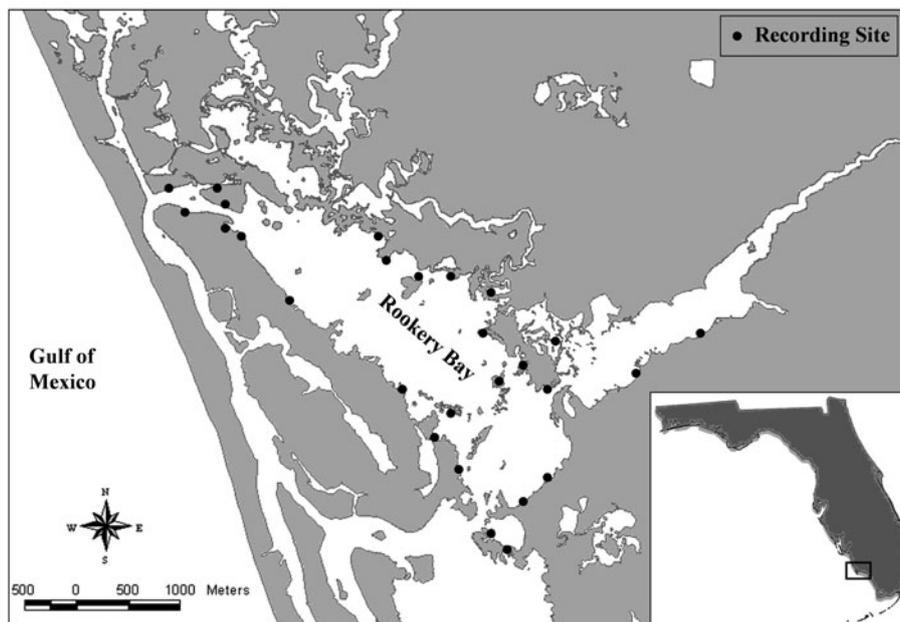


Fig. 1. Location of the recording sites in the Rookery Bay National Estuarine Research Reserve. The inset shows the reserve's location in southwest Florida

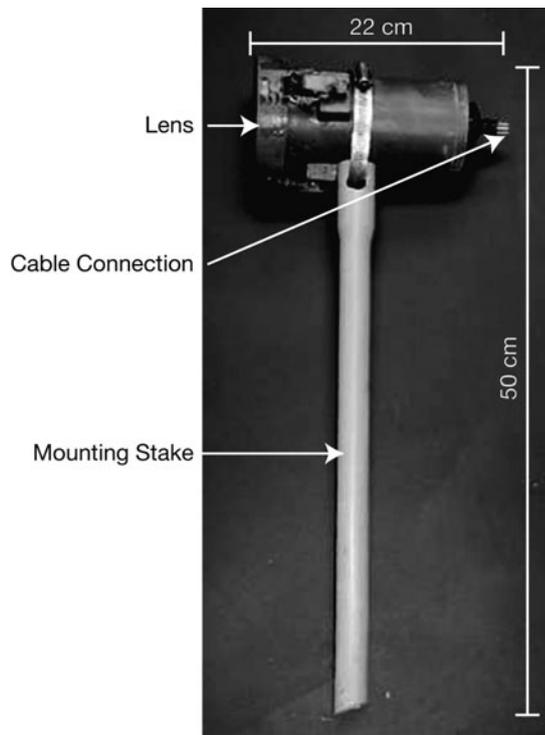


Fig. 2. Submersible camera on mounting stake inserted into the sediment so that the lens was elevated ~10 cm above the substrate. The camera was connected by wet-pluggable cable to a digital recorder and a power source

water depth was measured at 15 s intervals using Levellogger data loggers affixed to a prop root in the camera's field of view. Three sets of recording equipment permitted simultaneous recording at up to 3 sites on any given sampling date.

**Data analysis.** The video footage was manually reviewed in the laboratory on a PC using Adobe Premier Pro software as a viewer. The number of fish observed in the field of view per minute (FM) was quantified and each fish identified to the lowest taxonomic level possible (usually species). Since it was generally impossible to determine whether an individual fish left the field of view and then returned within a minute, no attempt was made to distinguish between these return visitors and newly arrived fish. However, most of the fish observed in our video recordings remained in the field of view for several minutes. Their movements consisted of brief, short distance (~5 cm) swimming, interrupted by pauses. Because of this, we are confident that the FM is an approximation of the relative abundance of individuals present at the exterior edge of the mangrove intertidal zone.

In order to avoid the daunting time requirements of viewing and scrutinizing the entirety of this video footage, the source video was subsampled. Bootstrap analysis (Bros & Cowell 1987) indicated that a review

of 10 min of video randomly selected out of every 30 min of source video provided an accurate estimate of the number of individuals present. Irregularly occurring (i.e. not systematically related to tide stage) instances of high turbidity occasionally prohibited accurate identification of fish observed in the video. A minute of video was rejected for use when the mangrove prop roots were indistinguishable for a portion of the minute greater than a total of 30 s. When this occurred, an alternative minute was selected for review.

The primary objective of the present study was to describe fish species composition and abundance in the fringing mangrove intertidal zone as a function of tide. However, tides within a region may vary daily in respect to their height, duration, and symmetry (i.e. flood vs. ebb duration). Therefore, the data for each site were organized into tide blocks created by dividing the flood tide (i.e. low tide to high) and ebb tide (i.e. high to low tide) each into 20 equal parts. Each complete tide cycle was 40 tide blocks in duration with tide blocks 20 and 21 representing high tide, and tide blocks 1 and 40 representing low tide. The data garnered from the subsampled video was classified according to this blocking scheme and used to produce a summary of the fish taxa and their mean frequency of occurrence in each tide block (Fig. 4).

Preliminary results revealed considerable spatial variability in the magnitude of fish abundance (FM) for each species. In order to minimize the effect of site-specific differences in total fish abundance on our ability to statistically detect tidal FM patterns, the data for the tide blocks at each site were expressed as a fraction of the site's maximum observed FM ( $\text{FracFM} = \text{FM} / \text{max FM}$ ). Thus, regardless of the absolute magnitude of fish at any site, values (FracFM) ranged from 0 to 1. Sites at which <10 individuals were observed for any species were omitted from the analysis for the rare spe-

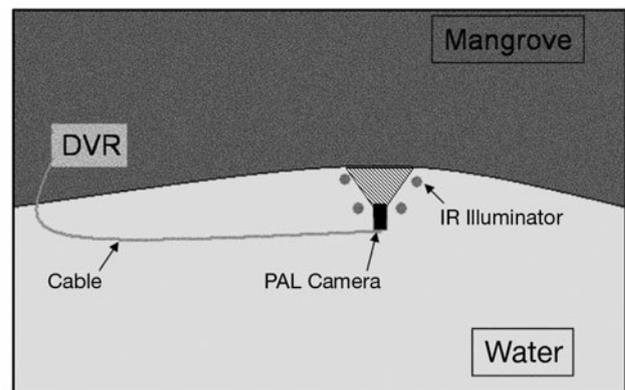


Fig. 3. Schematic view of equipment from above a sampling site. The hashed region represents the field of view of the submersible Phase Alternating Line (PAL) camera. DVR: digital video recorder; IR: infrared

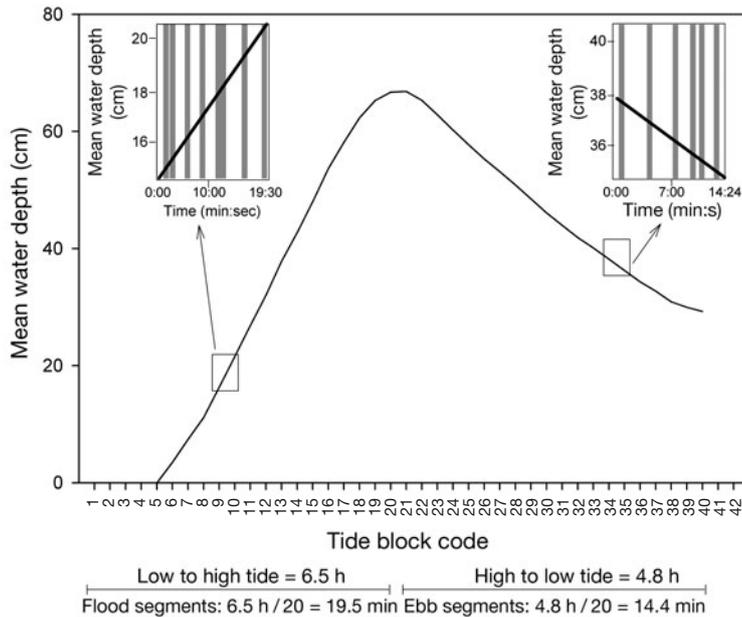


Fig. 4. Video subsampling methodology used to describe tidal abundance patterns of fish in the mangrove intertidal zone. Video recordings of the mangrove/open-water ecotone were reviewed in randomly selected (10 per 30 min of recording) 1 min video segments (shaded areas). The asymmetric tides were divided into 19 equal flood (i.e. tide blocks 1 to 19) and 19 equal ebb (i.e. tide blocks 22 to 40) blocks. Together, tide blocks 20 and 21 constituted high-tide samples. Mean fish abundance for each tide block was calculated using the reviewed video segments within each block. Insets illustrate the sampling scheme for block 9, a flood tide block, and block 34, an ebb tide block

cies. The remaining data were then analyzed for tidal patterns in 2 ways. First, the FracFM were analyzed by means of a 1-way repeated-measures ANOVA (on ranks if parametric assumptions not met), with tide class (flood tide: tide blocks 1 to 19; high tide: tide blocks 20 and 21; and ebb tide: tide blocks 22 to 40) as the factor of interest. Post hoc multiple comparison Tukey tests were performed to compare the flood, high, and ebb stages. In the absence of a tide pattern, we expected the mean FracFM values for each tide class to be statistically indistinguishable. The second means that we employed to identify a tidal influence on the fish abundance in the mangrove intertidal zone was regression analysis. We examined the relationship between FracFM (dependent variable) for each species and the water depth expressed as a fraction of each site's maximum depth at high tide ( $\text{FracDepth} = \text{water depth}/\text{maximum water depth}$ ). A statistically significant positive relationship was interpreted to indicate that relative increases in water depth coincide with relative increases in the FracFM.

Finally, for each study site, the species composition at high tide was compared to that observed at all other tide blocks (1 to 19, and 22 to 40) using the Bray-Curtis similarity measures applied to 4th root-transformed average FM values for each species, with 0.1 added

as a dummy value. The effect of tide block on similarity was examined using a 1-way repeated-measures ANOVA. The mean similarity of each tide block was compared with the Bray-Curtis value of 100 (i.e. the self similarity of within-site high-tide assemblages) using Dunnett's method of multiple comparison.

## RESULTS

A total of 204.17 h of video was recorded at the 27 field sites. Of that total, 4097 min were reviewed. The water depth at the mangrove root line during these recordings ranged from 0.0 to 79.8 cm ( $\bar{x} = 33.2$  cm,  $\text{SE} = 0.3$  cm). The tide was asymmetrical; the morning low tides completely drained the mangrove understory but the high low tide ( $\bar{x} = 22.8$  cm,  $\text{SE} = 0.8$  cm) that occurred in the late afternoons often left portions of the mangrove intertidal zone inundated.

The number of fish observed per minute (FM) of video ranged from 0 to 68 individuals (grand mean of all taxa combined,  $\bar{x} = 2.18$ ,  $\text{SE} = 0.07$ ). The highest mean FM per tide stage at the study sites occurred at water depths of 40 to 50 cm (Fig. 5). During the

flood tide, the mean FM generally increased over time, but the highest mean FM were found during the early stages of the ebbing tide (Fig. 6).

A total of 17 fish taxa were observed in the video recordings (Table 2). The 5 most common taxa (each >5% of the total FM), *Eucinostomus* spp., *Lagodon*

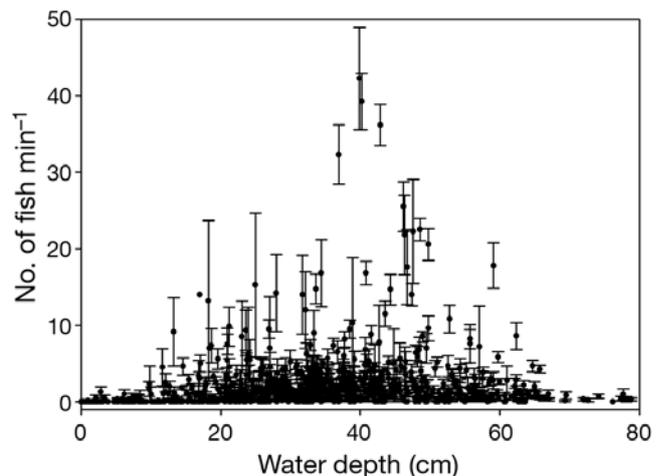


Fig. 5. Mean number of fish observed per minute during all tide blocks (1 to 40) at each of the 27 sampling sites versus the mean water depth at the mangrove prop-root line during each tide block. Error bars represent SE

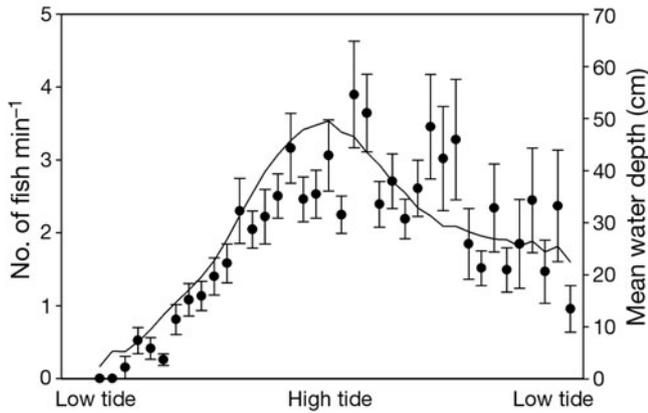


Fig. 6. Mean number of fish observed per minute in video recordings during each tide block in the mangroves (●). Line represents the mean water depth at the mangrove rootline during the recording periods. Error bars represent SE

*rhomboides*, *Orthopristis chrysopterus*, Hamulidae, and unidentified juveniles, collectively accounted for 89.5% of all instances that a fish was observed in the video. Five of the 17 taxa, *Eucinostomus* spp., *L. rhomboides*, *O. chrysopterus*, *Bathygobius soporator*, and *Lutjanus griseus*, were widely distributed (i.e. found at >50% of the 27 study sites).

Not all taxa demonstrated the same tidal FM pattern, nor were depths of arrival in the mangrove intertidal zone consistent among species. Based on a statistical analysis of the FracFM patterns over the tidal cycle, we identified 4 general intertidal migration patterns: (1) tide-level proportionate, with peak abundance during

high tide; (2) flood- and ebb tide-concentrated, with lowest abundance during high tide; (3) ebb- and low tide-concentrated; and (4) depth-limited but tidally independent (Table 2). The only fish that clearly demonstrated a tide-level proportionate intertidal migration pattern was the most frequently observed fish, *Eucinostomus* spp. complex (Table 2, Fig. 7a). *Eucinostomus* spp. first entered the mangrove intertidal zone at 4 cm water depth and its mean FM per tide block closely paralleled the mean water depth throughout the tidal cycle (Fig. 7a). FracFM values varied by tide stage (repeated-measures ANOVA,  $F_{2,42} = 301.935$ ,  $p < 0.001$ ) and were highest during high tide (high > flood, high > ebb,  $p < 0.001$ ). FracFM at ebb tide was slightly greater than that during flood tide ( $p < 0.001$ ). The designation of *Eucinostomus* spp. as a tide-level proportionate taxon was further supported by a statistically significant positive relationship between FracFM and FracDepth values ( $r^2 = 0.232$ ,  $p < 0.05$ ).

The tidal migration pattern characterized by greater FM during the flood and ebb portions of the tide cycle was exhibited by several species (*Poecilia latipinna*, *Gambusia* sp., *Fundulus grandis*, and *Floridichthys carpio*) which were pooled together into the order Cyprinodontiformes due to low individual FM. These fish were more abundant during the flood and ebb tide stages compared to high tide (repeated-measures ANOVA,  $F_{2,6} = 9.681$ ,  $p = 0.013$ ) when they were absent (Table 2, Fig 7b). No individuals of these species were seen when the water depth was >40 cm. A statistically significant second order polynomial regression indicated that the maximum FM values of the

Table 2. Fish taxa observed in the 27 intertidal study sites using video recordings of diurnal tidal inundation. Residency designations from Ley et al. (1999); residents (R) 'complete their entire life cycle in the estuary', transients (T) 'spawn offshore; their young use the estuary as a nursery'. Tide pattern is an indication of fish prevalence in the video recordings: tide-level proportionate/peak abundance at high tide (TP), peak abundance at flood and ebb with low abundance at high tide (FE), peak abundance at ebb and low tide (EL), and depth-limited but tidally independent (N). Some fish occurred too infrequently to make a determination (-)

Taxon	Residency	Abundance (% of total)	No. of sites	Depth (cm) first observed	Tide pattern
<i>Anchoa</i> sp.	R	122 (1.4)	2	22	-
<i>Archosargus probatocephalus</i>	T	61 (<1)	9	18	N
<i>Bathygobius soporator</i>	R	149 (1.7)	17	10	EL
<i>Centropomus undecimalis</i>	T	1 (<1)	1	35	-
<i>Chaetodipterus faber</i>	T	4 (<1)	2	42	-
<i>Eucinostomus</i> spp.	R	4121 (46.2)	27	4	TP
<i>Floridichthys carpio</i>	R	39 (<1)	5	21	FE
<i>Fundulus grandis</i>	R	61 (<1)	7	6	FE
<i>Gambusia</i> sp.	R	14 (<1)	3	4	-
Gobiidae	R	2 (<1)	1	29	-
Haemulidae (juveniles)	T	819 (9.2)	6	36	N
<i>Lagodon rhomboides</i>	T	1654 (18.5)	17	6	EL
Unidentified early juveniles	-	859 (9.6)	9	4	N
<i>Lutjanus griseus</i>	T	282 (3.2)	25	16	N
<i>Lutjanus synagris</i>	T	12 (<1)	3	43	-
<i>Poecilia latipinna</i>	R	184 (2.1)	8	8	FE
<i>Orthopristis chrysopterus</i>	T	535 (6.0)	26	4	N

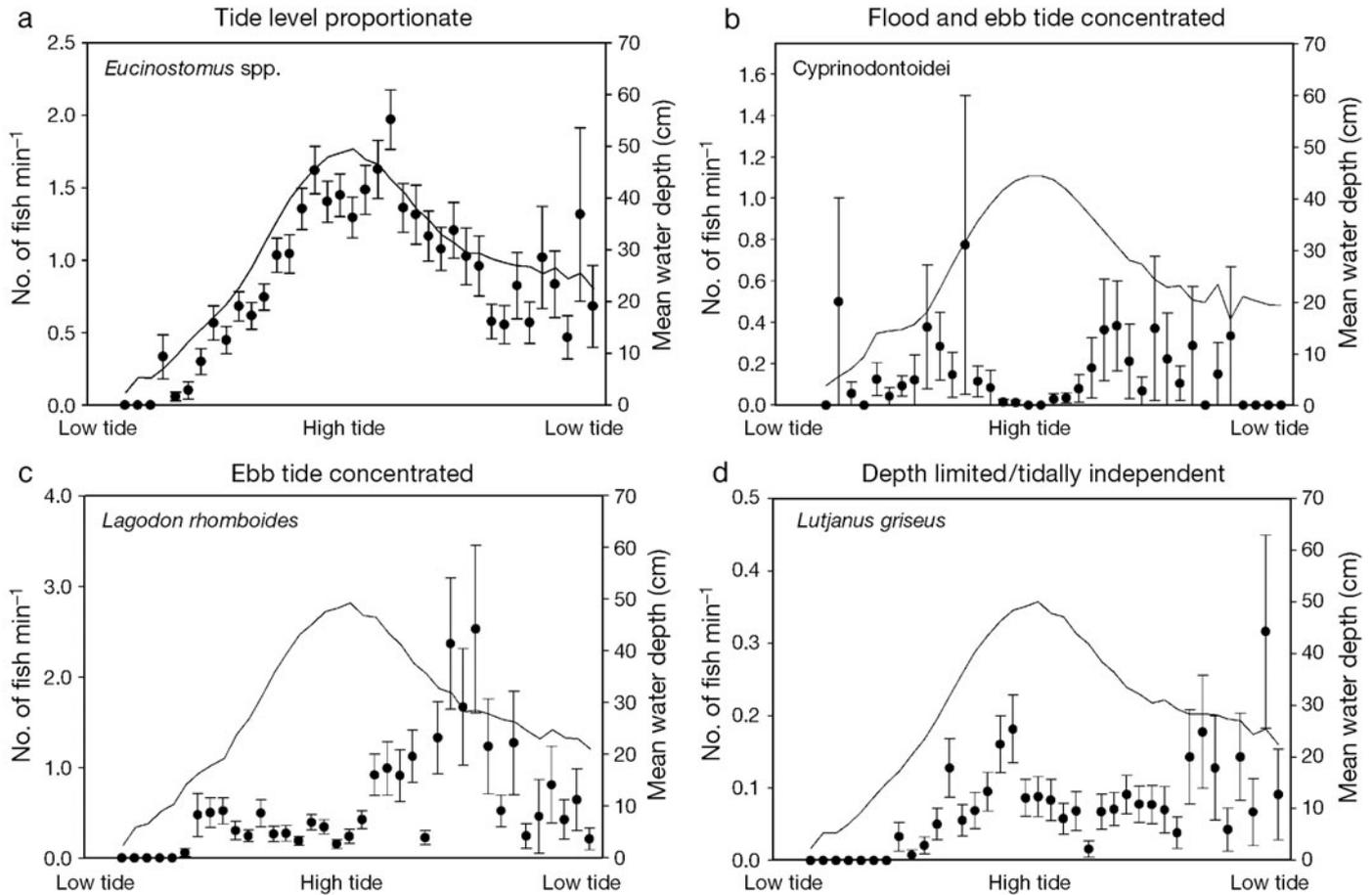


Fig. 7. Mean number of fish observed per minute in video recordings during each tide block in the mangroves (●). Line represents the mean water depth at the mangrove rootline during the recording periods at sites where the taxa were present. Each graph is an illustration of 1 example of the 4 tidal migration patterns identified in this study: (a) tide-level proportionate/peak abundance at high tide; (b) peak abundance at flood and ebb with low abundance at high tide; (c) peak abundance at ebb and low tide; and (d) depth-limited but tidally independent. Error bars represent SE

fish order generally occurred when the water depths were approximately one-half of the high tide depths ( $r^2 = 0.193$ ,  $p < 0.05$ ).

Two species, *Lagodon rhomboides* and *Bathygobius saporator*, were most frequently observed during the ebb or high low-tide stages (Fig. 7c). One-way repeated-measures ANOVA revealed that tide classes were statistically distinguishable for each species (*L. rhomboides*,  $F_{2,8} = 8.089$ ,  $p = 0.012$ ; *B. saporator* [repeated-measures ANOVA on ranks],  $p < 0.05$ ), with the greatest mean FracFM values occurring during ebb tide (ebb > flood; ebb > high, but high vs. flood was not significant). There was a weak, but significant, positive relationship between the FracFM of *L. rhomboides* and FracDepth ( $r^2 = 0.03$ ,  $p < 0.05$ ). This relationship was not significant for *B. saporator*. *L. rhomboides* and *B. saporator* were seen at almost all points of the tide cycle but peak FM occurred for *L. rhomboides* at ~40 cm whereas maximum FM values for *B. saporator* occurred at depths < 40 cm.

Several taxa (*Archosargus probatocephalus*, *Lutjanus griseus*, *L. synagris*, Haemulidae, and *Orthopristis chrysopterus*) did not exhibit a clearly discernible FM pattern over the tide cycle (i.e. all ANOVA results were not significant) (Fig. 7d). *A. probatocephalus*, *L. griseus*, and Haemulidae FracFM were weakly positively related to FracDepth ( $r^2 = 0.02$ ,  $p < 0.05$ ;  $r^2 = 0.05$ ,  $p < 0.05$ ; and  $r^2 = 0.04$ ,  $p < 0.05$ , respectively). *O. chrysopterus* did not demonstrate a significant relationship with water depth.

The species richness of the fish assemblage varied within the tide cycle. The total species richness at all sites increased with depth during the flood tide, but the maximum (13 species) was recorded during the ebbing tide (Fig. 8). Bray-Curtis similarity measures between the fish assemblage present during the various tide blocks indicate that, within site, species assemblages were, on average, less similar to the high-tide samples as low tide approached (repeated-measures ANOVA,  $F_{36,623} = 13.662$ ,  $p < 0.001$ ) (Fig. 9).

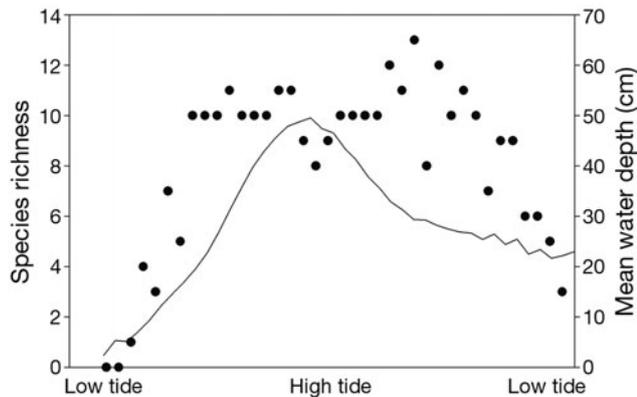


Fig. 8. Total number of species observed during all tide blocks (1 to 40) in the mangrove intertidal zone (●). Line represents the mean water depth at the mangrove rootline during the recording periods

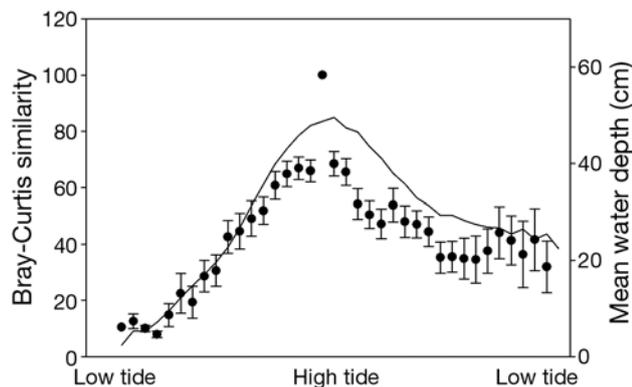


Fig. 9. Mean Bray-Curtis similarity between the high-tide fish assemblages observed at each site and the assemblages observed at each site during all other tide blocks in the mangrove intertidal zone (●). Line represents the mean water depth at the mangrove rootline during the recording periods. Error bars represent SE

## DISCUSSION

These diurnal video recordings represent the first continuous observations of the intertidal migration of fishes into a mangrove understory throughout a complete tidal cycle. It is clear from the results that the abundance of fishes in the fringing mangroves of Rookery Bay, as in other systems (Hibino et al. 2006), varies over the tidal cycle in a species-specific manner. As a consequence, the species composition of the fish assemblage varies considerably over the tidal cycle as well.

Video recordings revealed that fish in Rookery Bay did not make their initial entry into the intertidal zone in a uniform single 'ribbon', advancing with the shallow edge of incoming tide, as has been suggested

in other systems (Kneib & Wagner 1994, Peterson & Turner 1994, Krumme 2004, but see Morrison et al. 2002). Instead, fish species were first observed in the intertidal zone across a range of depths throughout the tide cycle. We did not experimentally test the effect of depth as an exogenous stimulus for intertidal migration (Burrows 2001), but several aspects of the data suggest that depth, or a feature correlated with depth, has an influence on the abundance of several species, as has been demonstrated in other intertidal habitats with vegetation (Thomas & Connolly 2001). Our results generally support the observations of Bretsch & Allen (2006) who found that estuarine resident species entered the intertidal zone at shallower depths during the flood tide than did larger transient species, and that both categories of fish depart the flooded intertidal at roughly the same depth at which they entered.

The tidal distribution patterns of some (e.g. *Eucinostomus* spp., *Poecilia latipinna*, *Fundulus grandis*, and *Floridichthys carpio*), but not all, taxa in the Rookery Bay mangroves were consistent with those predicted if the fish maintained position in species-specific ranges of preferred water depth (Gibson 2003). This may reflect a shift of some, but not all, individuals into the refuge of the flooded mangrove interior during the late flood and high tide after an unknown depth threshold has been surpassed, followed by a return to the edge of the mangrove intertidal zone prior to complete tidal drainage (Rangeley & Kramer 1998, Hibino et al. 2006). There is a precedent to suggest that *Eucinostomus* spp. respond to depth in this way. Ellis & Bell (2004) found that *Eucinostomus* spp., in Tampa Bay, Florida shifted their microhabitat preference from exposed, open water to shaded areas when the water depth exceeded 55 cm. This shift was possibly a response to variable predation pressure which was related to water depth in a quadratic rather than strictly linear relationship, with losses of tethered fish greatest at intermediate depths (60 cm). This is not to suggest that a specific depth is universally recognized by a species as an impetus to shift microhabitats; if depth avoidance is a characteristic of a species, the actual magnitude of the critical depth would most likely be conditionally based on a suite of additional criteria (Burrows 2001, Bretsch & Allen 2006, Rountree & Able 2007).

Several other species exhibited peak FMs at points in the tide cycle other than high tide. Three species (*Floridichthys carpio*, *Fundulus* sp., and *Poecilia latipinna*) were observed in the video entering the intertidal zone early during the flood tide. These species were completely absent from the video at high tide, and likely followed the water line into the root-filled mangrove understory as the water depth increased during the flood tide. These same species reappeared

at the mangrove/open-water ecotone as they left the mangrove understory during the ebbing tide. This pattern of tidal migration is well-known for fish from the order Cyprinodontiformes in mangrove systems and salt marshes (Butner & Brattstrom 1960, Kneib & Wagner 1994, Hampel et al. 2003) and has been speculated to be a means of maximizing the duration of foraging in the intertidal zone while minimizing exposure to predators (Hampel & Cattrijsse 2004).

*Lagodon rhomboides* and *Bathygobius soporator* were present at most points of the tide cycle, but were most common during the ebb tide and the high low-tide stages, respectively. Unlike the tide level-proportionate and ebb- and flood tide-concentrated patterns, the FM pattern of these species is asymmetric around high tide. This migration pattern may reflect increased fish activity that has been elicited in other species during ebbing and low tide elsewhere (Gibson & Hesthagen 1981, Krumme 2004). Alternatively, these species may have entered at positions in the intertidal zone that were unfortunately undersampled due to the limited field of view and placement of video cameras. Like plaice and sole in the sandy surf zone of Belgium, these fish may be concentrated as they are forced to retreat from the more shallow portions of the intertidal zone by the retreating tide (Beyst et al. 2002). For a more complete interpretation of this and other FM patterns, however, further research is required to elucidate the influence of tide stage on predation pressure and food availability in mangrove systems.

Other species were not observed to demonstrate any association with a particular interval of the tide cycle. Although the entry and exit of these species to and from the fringing mangrove intertidal zone may have been limited by a minimum water depth, they did not demonstrate any discernible trend in FM over the course of the tide cycle. Hampel et al. (2003), who made collections of intertidally migrating fish from an intertidal salt marsh creek, also found that the majority of species were present over all points of the tide cycle when the system was inundated by water.

### Implications for sampling design

The present study, like previous descriptions of mangrove and salt marsh intertidal fish communities, characterizes nekton distribution as heterogeneous (Kneib 1984, Vance et al. 1996, Rönnbäck et al. 1999, 2002, Meager et al. 2003, Hindell & Jenkins 2005), although the heterogeneity described in our work is temporal (i.e. by tide stage). If this heterogeneity is a function both of species-specific tide stage/depth associations and variable penetration into the vegetated intertidal zone, inventories of the intertidal fish community of

fringing mangrove systems can be expected to vary greatly depending on the tide stage sampled as well as the position of the sampling gear within the intertidal zone.

### Gear placement

The sampling artifacts attributable to gear placement can be fortuitously illustrated with a comparison of a fish community at the mangrove/open-water ecotone sampled using video recordings as contrasted with descriptions from previous studies using gear that sampled dissimilar portions of the fringing mangrove intertidal zone in Rookery Bay. For purposes of comparison we refer to 2 studies conducted previously in Rookery Bay: drop-tube samples collected in the interior of the mangrove intertidal zone directly adjacent to the waterward root line (Sheridan 1992), and block-net samples that enclosed the flooded mangrove intertidal zone from its subtidal margin to its landward edge (Ellis 2003). The drop tube (1.7 m diameter) used by Sheridan (1992) was dropped (presumably at spring high tide) so that it surrounded a portion of the flooded intertidal from which the fish were collected. The block nets used by Ellis (2003) (also triggered at high tide), on the other hand, extended from 0.5 m waterward of the mangrove open-water ecotone and 8.5 m into the mangrove forest, in most cases entirely enclosing the mangrove intertidal zone. Only data from the drop-tube and block-net studies collected in late winter and early spring, when our video recordings were made, were used in the comparisons.

All species captured in the drop tube were also observed in the video recordings, but 9 (out of a total of 17) taxa were unique to the video recordings. The majority of the species 'missed' by the drop tube (e.g. *Archosargus probatocephalus*, *Chaetodipterus faber*, *Lutjanus synagris*) are thought to inhabit the edges of structured habitats (Peterson & Turner 1994). In contrast, *C. faber*, a rare species in Rookery Bay (Ellis 2003), was the only positively identified taxon present in the video recordings that was absent in the block-net samples. When the video observations were restricted to the high-tide phase (blocks 20 and 21) of the tidal cycle, coinciding with the sample collection times of Ellis & Bell (2004), interior species (e.g. *Floridichthys carpio*, *Fundulus* sp., and *Poecilia latipinna*) (Kneib & Wagner 1994, Peterson & Turner 1994) were missed, as they typically abandoned the open water adjacent to the mangroves as the water depth increased. The drop-tube samples included these shallow water inhabitants. This suggests that if sampling gear was positioned at the exterior edge of the mangroves and sampling was conducted at high tide, the resulting

haul would have been biased against the inclusion of interior species. Block-net samples, which included all portions of the flooded mangrove intertidal zone, still 'missed' only *C. faber* when compared to the video samples, and contained 25 species that were missing from drop-tube samples. So, block-net samples, collected at high tide, included the interior species omitted in the high-tide video and the exterior species not captured by the drop tube. Given the temporal heterogeneity of the fish distribution in mangrove systems (Hindell & Jenkins 2005), it appears that samples that include anything less than the complete intertidal habitat are likely to under-represent species richness.

Incomplete and inaccurate descriptions of the intertidal fish community can result in a mischaracterization of the 'value' of natural systems as this valuation is often determined on the basis of 'biodiversity' (Burton et al. 1992, but see Schwartz et al. 2000), fisheries economic value (Ron & Padilla 1999, Gunawardena & Rowan 2005), or ecological function (Barbier & Strand 1998, Sheridan & Hays 2003, Nagelkerken & van der Velde 2004). For example, samples collected near high tide, using gear placed at the exterior edge of the mangroves, would omit the interior species that represented 17.1% of the fish collected in the drop-tube samples during the winter and early spring, underestimating diversity at the site (Sheridan 1992). In addition, the ecological importance of the site as an energy source for subtidal organisms would be overlooked; the intertidal migratory behavior of small nekton has been credited as a significant vector of energy transfer from the intertidal to the subtidal environments (Kneib & Wagner 1994). Clearly, an understanding of the tidal movements of fish species is necessary to understand the impact of gear placement on our perception of nekton communities in intertidal systems.

#### Sample timing during the tidal cycle

Most samples of fish from mangrove intertidal systems have been collected during the putative high tide. The results of our study indicate that the fish community of the fringing mangrove/open-water ecotone at high tide was not the cumulative total of all species that visit the intertidal zone during a tide cycle. In fact, unlike in other intertidal systems (Kneib & Wagner 1994), species richness was greatest during the ebb tide period, not high tide. Instead, some species abandoned the edge of the forest prior to high tide, whereas others increased in abundance during the ebb tide. The implications of this temporal heterogeneity are apparent for sampling designs that sample some, but not all intertidal habitats. However,

more subtle consequences may be associated with inexact sampling times during the tide cycle, even using gear that samples the entire intertidal zone. In an effort to maximize sample sizes in faunal surveys, it is not uncommon for multiple samples to be collected per day, each within a specified interval of time relative to a given tide stage. For example, Thayer et al. (1987) noted that block-net samples taken from the mangroves of Florida Bay were collected at high tide  $\pm 2$  h. Our results indicate that, in a given site of the fringing mangrove intertidal zone, samples become increasingly dissimilar from high-tide samples with greater divergence in inundation depth relative to high tide. Fish assemblages observed in the video approximately 16 to 45 min after the high tide were nearly 35% dissimilar to high-tide species assemblages from the same location. Such variability can be problematic when fish community composition is used as an indicator of system 'health' (Deegan et al. 1997, Whitfield & Elliott 2002), because the 'noise' introduced as an artifact of imprecise sample timing may obscure the 'signal' of environmental degradation and require increased sampling efforts (Meager et al. 2003). Variability of this sort, in addition to natural variability (Varnell et al. 1995, Hindell & Jenkins 2004, Huxham et al. 2004, Miller & Skilleter 2006) decreases the power of statistical tests to detect impacts in disturbed systems. As a result, impacts may not be detected until they are very severe.

#### CONCLUSIONS

The fish of the fringing mangrove intertidal zone in Rookery Bay responded to tidal influences in a species-specific fashion. As a result, the community composition was not constant throughout the tidal cycle. Our results suggest that unless particular care is used in the design and implementation of sampling efforts, poor and highly variable descriptions of the intertidal ichthyofauna will result, and our ability to use assemblages to statistically differentiate sites (e.g. pristine vs. damaged) will be compromised. Based upon the findings reported here, we suggest the following:

(1) In order to be complete, studies of nekton use of the mangrove intertidal zone should include samples over the full course of the tidal cycle. Although this is logistically challenging, the effort would likely provide a more accurate accounting of the intertidal ichthyofauna than studies restricted to a single tide interval. If it is necessary to restrict sampling to a portion of the tide cycle, interpretation of the data should be limited to the context of the tide stage sampled.

(2) When sampling is restricted by necessity to a portion of the tide cycle, temporal deviation from the

targeted tide stage should be minimized. The number of sites to be sampled per tide cycle may be reduced in order to accomplish this, but the return in increased statistical power that accompanies reduced sample variability may justify the sacrifice. Sufficient foreknowledge of the sampling site hydrography (Rozas 1995) is necessary when planning a sampling design.

(3) Enclosure gear that encompasses the full extent of accessible portions of the intertidal zone may permit more accurate representations of the intertidal fish community when less than the entire tide cycle can be sampled. Such inclusive sampling limits the susceptibility of the sampling design to artifacts associated with sample timing. However, even areally expansive enclosure gear is not immune to the concerns of tidal influence. For example, enclosure gear that includes the entire intertidal zone and is 'triggered' at high tide may inadequately numerate the species that become most abundant during the ebbing tide.

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